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Adult-mediated connectivity affects inferences on population dynamics and stock assessment of nursery-dependent fish populations

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Abstract :

We explore how alternative hypotheses on the degree of mixing among local subpopulations affect statistical inferences on the dynamics and stock assessment of a harvested flatfish population, namely, the common sole population in the Eastern Channel (ICES area VIIId). The current paradigm considers a single, well-mixed, spatially homogeneous population with juveniles from all coastal nursery grounds along the French and UK coasts that contribute to a single adult population and one pool of eggs. Based on the available data and ecological knowledge, we developed a spatial Bayesian integrated life-cycle model that consists of three subpopulations (one near the UK coast and two near the French coast, denoted UK, West FR and East FR, respectively) supported by their respective local nurseries, with the connectivity among the three components limited to low exchanges during larval drift. Considering the population dynamics among three subpopulations (instead of a single homogeneous one) drastically changes our inferences on the productivity of nursery sectors and their relative contribution to total recruitment. Estimates of the East FR subpopulation's contribution to total recruitment increase (29% in the single population model; 48% in the three subpopulation model), balanced by a decrease in the UK subpopulation's contribution (53%; 34%). Whereas an assessment based on the hypothesis of a single spatially homogeneous population in the EC indicates exploitation far above MSY (current $F/FMSY = 1.8$), an assessment that considers a metapopulation with three loosely connected subpopulations revealed a different status, with the UK and East FR subpopulations being exploited above MSY (current $F/FMSY = 1.9$ and 2 , respectively) and the West FR subpopulation approaching full exploitation (current $F/FMSY = 1.05$). This approach contributes to the quantitative assessment of spatial fishery and coastal habitat management plans.

Keywords : Solea solea, Spatial life-cycle model, Coastal nurseries, Connectivity, Stock assessment, Hierarchical bayesian model

43 1. Introduction

44 Integrated life-cycle modeling approaches that account for the spatial structure of populations
45 are needed to improve our understanding of the impacts of multiple pressures on populations
46 (Carson et al., 2011; Stelzenmuller et al., 2011; Wolfshaar et al., 2011; Petitgas et al. 2013).
47 The concepts of metapopulation were introduced long ago in the optimal harvesting theory for
48 fisheries (Tuck and Possingham, 1994 and references therein; Hilborn and Walters, 1992).
49 Spatially explicit models can help decision making in spatial management plans either to
50 adapt fisheries management to local productivities (Carruthers et al., 2011; Ying et al., 2011;
51 Guan et al., 2013) or to design networks for marine protected areas (Botsford et al., 2009;
52 Gaines et al., 2010; Grüss et al., 2011).

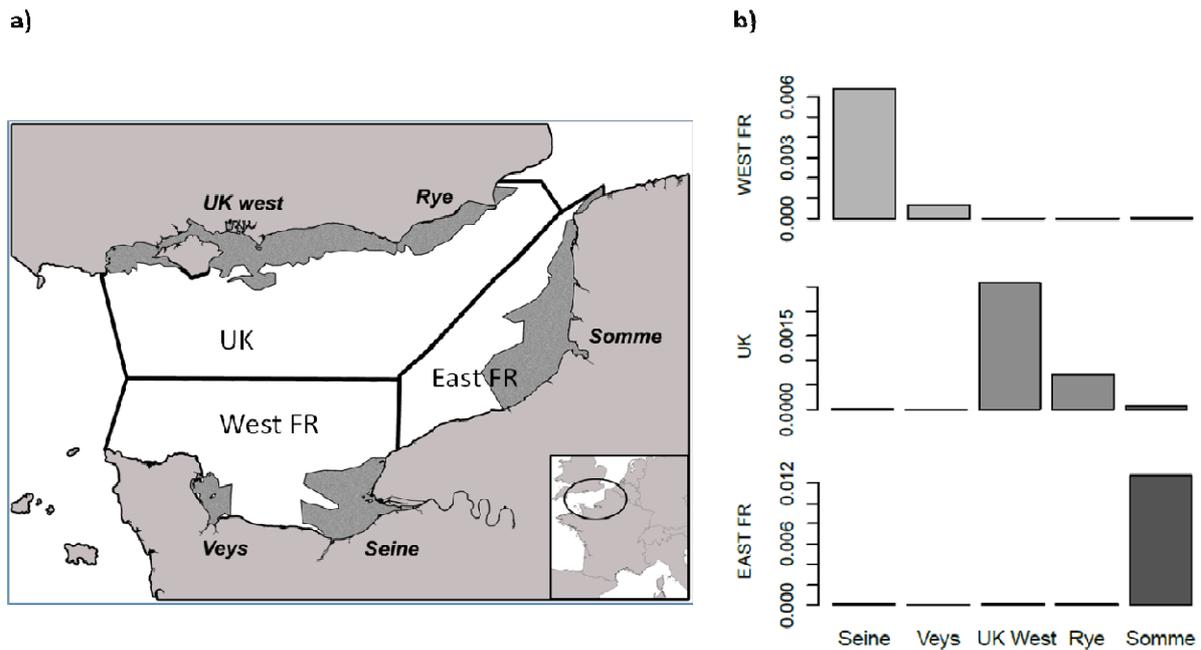
53 However, the current paradigm in population dynamics for the assessment of the most
54 exploited marine stocks continues to ignore metapopulation structure. One often assumes a
55 fish stock as a single, well-mixed and spatially homogeneous population that produces a
56 single larval pool that undergoes extensive dispersal and massive export covering the
57 population's entire distribution area. When it is addressed at all, the question of connectivity
58 and population structure is mostly focused on early life stages (Petitgas et al., 2013; Frisk et
59 al., 2014), with a large body of studies designed to evaluate the influence of physical and
60 biological processes on the survival and dispersion of eggs and larvae (Miller, 2007; Savina et
61 al., 2010; Hinrichsen et al., 2011; Peck and Hufnagl, 2012) that govern the variability of
62 recruitment in space and time (Chambers and Trippel, 1997; Gallego et al., 2012). The
63 importance of larval retention in marine populations has also been emphasized (Cowen et al.,
64 2000; Warner and Cowen, 2002), because populations that display strong retention may be
65 locally more vulnerable to local recruitment overfishing or depletion caused by catastrophic
66 events (Strathmann et al., 2002). However, although adult-mediated connectivity is suspected
67 to play a major role in population functioning, much less attention has been paid to its role
68 (Frisk et al., 2014). The movements of adults may determine the structure and dynamics of
69 metapopulations (Stelzenmuller et al., 2011; Cianelli et al., 2013), especially when larval and
70 juvenile retention occurs (Grosberg and Levitan, 1992), thus indicating the need for
71 population models that account for spatial structure and connectivity at all stages (Petitgas et
72 al., 2013; Frisk et al., 2014).

73 New challenges arise when building and parameterizing population models that account for
74 the spatial structure along the life cycle: (i) Long spatial data series of catches, abundance

75 indices and fishing effort are rarely available; (ii) Coupling oceanographic circulation models
76 and larval individual-based models provides a way to explore larval dispersal, but larval
77 stages are rarely accessible to observation and the validation of those models remains an open
78 question (Miller 2007); and (iii) Movements in the adult stage are difficult to quantify. Mark-
79 recapture data (Drouineau et al., 2010; Carruthers et al., 2011), natural markers and genetic
80 studies (Hellberg et al., 2002) are costly and sometimes fail to reveal the metapopulation
81 structure (Ward et al., 1994; Smedbol et al., 2002; Rolland et al., 2007).

82 It thus remains a methodological challenge to embed spatial life-cycle models within a
83 statistical approach to derive inferences on key parameters (Planque et al., 2011). The
84 Hierarchical Bayesian modeling (HBM) framework has proven successful for embedding
85 complex demographic processes with various sources of noisy and incomplete data on various
86 spatial and temporal scales (Clark, 2005; Buckland et al., 2007; Parent and Rivot, 2013); thus
87 it can help address some of these challenges. HBM has been successfully applied to build fish
88 population dynamic models that assimilate various sources of field surveys (Rivot et al., 2004;
89 Massiot-Granier et al., 2014), integrate mark-recapture data to capture the spatial structure of
90 populations (Cunningham et al., 2007; Taylor et al., 2011), and incorporate complex
91 interactions with environmental drivers of recruitment (Ruiz et al., 2009; Rochette et al.,
92 2013).

93 In this paper, using the common sole (*Solea solea*) population in the Eastern Channel (EC;
94 ICES area VIIId; Fig. 1a) as a case study, we investigate how considering alternative
95 hypotheses about adult-mediated connectivity can affect statistical inferences on population
96 dynamics and stock assessment. The common sole is a coastal and estuarine nursery-
97 dependent flatfish species (Le Pape et al., 2003a; Gibson, 2004). Its population in the EC is
98 exploited, with annual landings of approximately 4,000t. The sole's life cycle in the EC is
99 well described (Rochette et al., 2013 and references therein): adults reproduce in early spring;
100 pelagic eggs and larvae drift and survivors will eventually settle and metamorphose into
101 benthic juveniles in late spring in a restricted nursery in which they grow for 2 years (Riou et
102 al., 2001; Rochette et al., 2010). Afterwards, the fish move to wider and deeper adult areas,
103 where their migrations remain limited (Burt and Millner, 2008).



104

105 Figure 1. (a) Eastern Channel area with the spatial limits of the three subpopulations
 106 associated with the coastal nursery sectors, based on larval retention as suggested by results of
 107 the larval drift model. 1: West Fr (Veys, Seine); 2: UK (UK West, Rye); 3: East Fr (Somme).
 108 (b) Probability of successful settlement in one of the three nursery grounds (in column) given
 109 the origin of the eggs (three subpopulations as rows).

110

111 Rochette et al. (2013) have proposed an integrated life-cycle model for the EC's sole
 112 population that combines approaches that are usually considered independently: (i) Outputs of
 113 an individual-based model for larval drift that provided yearly estimates of the dispersion and
 114 mortality of eggs and larvae from spawning grounds to settlement in several coastal nurseries;
 115 (ii) A habitat suitability model based on juvenile trawl surveys combined with habitat maps to
 116 estimate the surface of each nursery sector and juvenile densities; and (iii) A statistical catch-
 117 at-age model for estimation of numbers-at-age and the fishing mortality of subadults and
 118 adults. A strong assumption in Rochette et al. (2013) considers that various nurseries
 119 contribute to the recruitment of a single homogeneous population in the EC. This hypothesis
 120 is consistent with the stock-assessment model (ICES, 2013). However, results from the larval
 121 drift model (Rochette et al., 2012) suggest consistent larval retention areas with strong
 122 relationships between spawning areas and nursery sectors. Additionally, ancillary data and
 123 expertise suggest only very low displacement of juveniles on nurseries (Coggan and Dando,
 124 1988; Anon., 1989; Riou et al., 2001; Le Pape and Cognez, 2016) and only moderate
 125 movements of adults (Kotthaus, 1963; Anon., 1965; Burt and Millner, 2008) that would result

126 in a low adult-mediated connectivity (Frisk et al., 2014). Thus, there is a strong presumption
127 that very low connectivity exists among the three isolated subpopulations associated with
128 different nurseries sectors, thus fostering an exploration of the impact of considering various
129 spatial structures on (meta)population dynamics.

130 In this paper, we elaborate on the HBM framework proposed by Rochette et al. (2013) to
131 explore how considering three (quasi)isolated subpopulations instead of a single
132 homogeneous one (as considered by ICES (2013) and Rochette et al. (2013)) can affect
133 statistical inferences on population dynamics. In particular, we assess how considering three
134 subpopulations of adults (instead of a single homogeneous one) can change our evaluation of
135 the productivity of each nursery area and its contributions to recruitment. We point out how
136 consideration of three adult subpopulations ultimately affects not only the estimation of
137 management reference points but also the assessment of the stock status with respect to the
138 fishery's spatial dynamics.

139 **2. Materials and methods**

140 We first describe the model considering three (quasi)isolated subpopulations of sole in the EC
141 (Fig. 2a), together with the available data and other model inputs based on results from
142 previous models (Table 1). The second model that assumes a single, homogeneous adult
143 population is derived as a simplification of the first model (Fig. 2b). Third, we provide details
144 of the simulation method used to derive management reference points.

145 The life-cycle model is written in a state-space form (hierarchical) that integrates stochasticity
146 in both the process equations for the population dynamics (process errors) and the observation
147 equations (observation errors). All of the model equations, priors and values on fixed
148 parameters are fully detailed in Appendix A. Posterior distributions were approximated via
149 Monte Carlo Markov Chain methods using JAGS software (see Sup. Mat. S1 for details about
150 the MCMC simulations and the convergence diagnostics).

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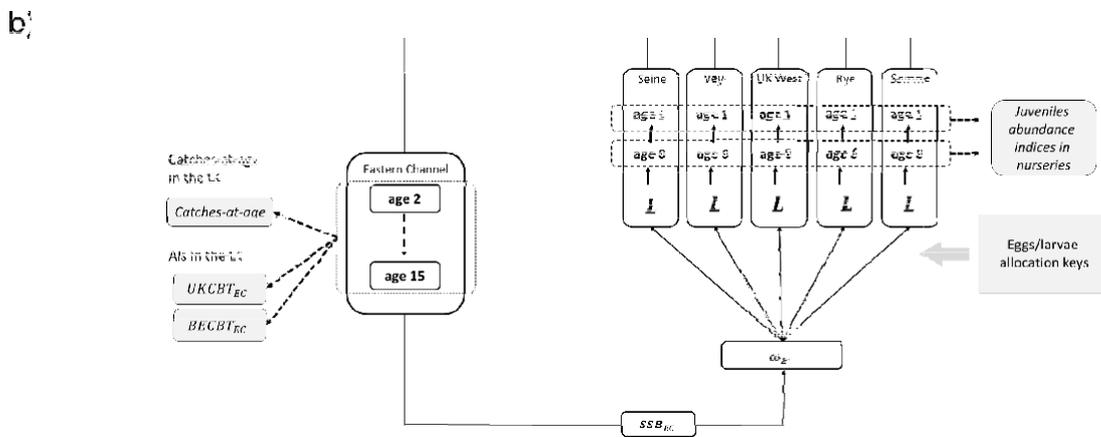
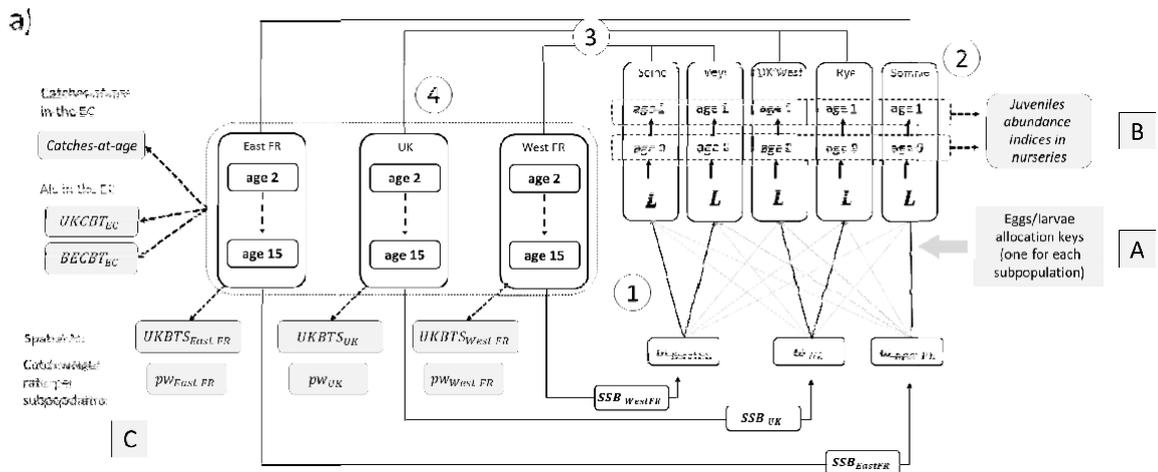
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154

155 Table 1. Synthesis of data and results of previous models used as inputs for the integrated life-
 156 cycle model.

		Nature of the information used	Source	Time series
EGGS & LARVAE	Survival and allocation from spawning areas to the five nursery sectors	Outputs of biophysical IBM model	Upgraded run of Rochette et al. (2012); Savina et al., in press.	1982-2007
	Abundance indices available for each nursery sector			
JUVENILES	West UK	Outputs of a habitat suitability model	Rochette et al. (2010)	1982-1999
	Rye	//	Rochette et al. (2010)	1982-2006
	Somme	//	Rochette et al. (2010)	1982-1983; 1987-2011
	Seine	//	Rochette et al. (2010) + GIP Seine Aval	1995-2002; 2006; 2008-2011
	Veys	//	Rochette et al. (2010)	2006;2010-2011
ADULTS	Available on the scale of the Eastern Channel			
	Catches at age	Data	ICES	1982-2011
	UK commercial CPUE (UKCBT)	Data	ICES	1986-2011
	Belgium commercial CPUE (BECBT)	Data	ICES	1982-2011
	Available for the three subpopulations			
	Spatial repartition of catches (total weights, no age structure) among the three areas (East FR, UK, West FR)	Data	ICES (2003-2011) Y. Vermard, Pers. comm. (1982-2002)	1982-2011
	Spatial Scientific Abundance Index (UKBTS)	Data	Y. Vermard, Pers. comm.	1990-2004; 2006-2011



158

159 Figure 2. Hierarchical Bayesian Models for the life cycle. (a) Model with three isolated
 160 subpopulations in which only very limited mixing occurs through egg and larval drift; (b)
 161 Model considering a single population. Lettering and numbering refer to corresponding points
 162 in the *Materials & Methods* section. White boxes: non-observed state variables; Shaded boxes:
 163 data or external model outputs considered as data. Dashed arrows indicate observation
 164 equations to link latent state variables to observations.

165

166 2.1. Model considering three quasi-isolated populations

167 2.1.1. Spatial structure

168 The EC population is supported by five nursery areas (Rochette et al., 2010) along the French
 169 (Veys, Seine and Somme nurseries) and UK coasts (UK West and Rye nurseries) (Fig. 1a).
 170 Rochette et al. (2012) demonstrate the low dispersion of eggs and larvae during the pelagic
 171 stages of the common sole (Fig. 1b). Indications of the reduced movements of juveniles and

172 adults suggest that connectivity is almost null for juveniles and only very limited for adults.
173 Considering this limited connectivity along the life cycle and the presence of natural barriers
174 (e.g., rocky shores in the central southern coast and deep gravel grounds in the central part of
175 the EC; Rochette et al., 2010), three subpopulations associated with three spawning areas
176 (denoted $r=1,2,3$) and attached nursery sectors were identified (Fig. 1a): the Western French
177 subpopulation (West FR; Seine and Veys nursery sectors), the UK subpopulation (UK West
178 and Rye nursery sectors) and the Eastern French subpopulation (East FR; Somme nursery
179 sector).

180 2.1.2. Population dynamics

181 The population dynamics were modeled for 30 years from 1982 to 2011. The model is stage-
182 structured from eggs to settled larvae and then age-structured from juveniles to adults (Fig.
183 2a).

184 *Eggs and larvae (see 1 in Fig. 2a)*

185 Egg hatching is parameterized following the characteristics of the spawning season and the
186 spatial distribution of eggs (Rochette et al., 2012), and the annual quantity of eggs spawned in
187 each of the three subpopulations directly depends on the spawning biomass. Eggs and larvae
188 are transported from spawning areas and settle in the five identified nursery sectors according
189 to a drift/survival matrix estimated from a biophysical model (Rochette et al. (2012). Outputs
190 from the larval-drift model (Rochette et al., 2012; Fig. 1b) indicate very low connectivity
191 between the three spawning areas and distant nursery sectors over the time series, each
192 spawning area almost exclusively feeding the closest coastal and estuarine nursery grounds.
193 Only very limited mixing of individuals between the three subpopulations then occurs through
194 larval drift (Fig. 2a). The UK—and in lesser proportions the East FR—subpopulations were
195 also subject to larval inputs from the North Sea's (NS) sole population (Savina et al., in press),
196 which were integrated into the model as a constant term (not shown in Fig. 2).

197 *Juvenile from age 0 to age 2 (see 2 in Fig. 2a)*

198 Because of competition for space and food resources (Iles and Beverton, 2000; Le Pape and
199 Bonhommeau, 2015), settled larvae experience density-dependent post-settlement mortality
200 over nursery sectors between settlement (late spring) and the end of summer (growth period).

201 Following previous modeling work in Rochette et al. (2013) and Archambault et al. (2014),
202 the resulting expected number of age-0 juveniles is modeled through a compensatory density-
203 dependent Beverton-Holt (BH) relationship parameterized with local parameters α_i , the
204 maximum survival rate (i.e., the survival rate without density dependence) and K_i , the
205 carrying capacity per unit of surface (i.e., the maximum number of age-0 juveniles that can
206 survive per unit of surface), which is then scaled to the total surface of each nursery, S_i
207 (fixed). Unexplained random variations are captured by independent lognormal random noise.

208 Because only limited information is available to estimate site-specific parameters,
209 exchangeable hierarchical structures (Gelman et al., 2004) were used to model the between-
210 nursery variability of parameters α_i and K_i , enabling “borrowing strength” between nursery
211 sectors (Rivot and Prévost, 2002; McAllister et al., 2004). Available juvenile abundance
212 indices on nursery sectors may contain enough information to estimate the carrying capacity
213 parameters K_i . However, because very few observations are available at low levels of settling
214 larvae, the maximum survival rates α_i could be difficult to estimate. Informative priors were
215 set on the α_i (see Appendix A) based on a meta-analysis of flatfish stock-recruitment
216 relationships (Archambault et al. 2014).

217 Late age-0 juveniles (in September, after the summer growth period) experience a fixed
218 natural mortality during 4 months until they reach age 1 in January. Age-1 juveniles spend
219 one year in nursery grounds with both natural (fixed) and fishing (estimated) mortalities.

220 *From nurseries to sub-adults (see 3 in Fig. 2a)*

221 Young fish are assumed to leave their nurseries at age 2, in January. No quantitative data were
222 directly available on the connectivity from nursery sectors to deeper areas where older fish
223 live (ages 2-15). Therefore, age-2 fish leaving nurseries are supposed to contribute directly to
224 the subpopulation adjacent to the nursery (Fig. 1a).

225 *Sub-adults and adults (see 4 in Fig. 2a)*

226 Fish from ages 2-15 are structured in three different subpopulations, with cohort dynamics
227 accounting for both natural (age-specific, fixed) and fishing (age-/ year-/ subpopulation-
228 specific, estimated) mortalities. All of the remaining fish are then assumed to die at age 15.
229 Because the cumulative natural mortality up to age 12 is near 1, including an age+ group in

230 the model would not change the results. Fishing mortality is a function of fishing effort
231 (estimated) and age-specific gear selectivity (estimated).

232 Fish between the age of 3 and 15 participate in reproduction. The number of eggs for each
233 year and each subpopulation is calculated from the spawning stock biomass.

234 **2.1.3. Integration of results of previous models, data sources and observation models**

235 *Eggs and larvae survival and allocation key (see A in Fig. 2a)*

236 Egg and larval survival and allocation from spawning areas to the five nursery sectors over 26
237 years between 1982 and 2007 were available as outputs from an upgraded run of Rochette et
238 al.'s (2012) biophysical model (Savina et al., in press). That model ultimately provided the
239 $3 \times 5 \times 26$ probability key that eggs from each of the 3 subpopulations would reach one of
240 the 5 different nursery sectors, accounting for inter-annual variability over the 26 years of
241 simulation. No outputs of larval drift model were available for the last 4 years (2008-2011;
242 Table 1). Because no particular time trend appears in the time series, the 3×5 probability key
243 for years 2008-2011 was set equal to the average over the entire series.

244 *Abundance indices of juveniles in each nursery sector (see B in Fig. 2a)*

245 The abundance indices (AI) of juveniles and the total surface of each nursery sector are
246 outputs from the habitat suitability model developed by Rochette et al. (2010) and used in
247 Rochette et al. (2013). Juvenile (ages 0 and 1) AIs over the five nursery sectors were obtained
248 from an upgrade of Rochette et al.'s (2010) habitat-suitability model, using updated scientific
249 trawl survey data. They were considered as lognormal random observations of juvenile
250 abundance accounting for gear/ age-specific catchability.

251 *Catches-at-age (see C in Fig. 2a)*

252 Annual catches-at-age were available from stock assessment reports only at the scale of the
253 EC; however, they were not available separately for the three subpopulations. Catches-at-age
254 predicted by the model for each subpopulation were then first aggregated at the scale of the
255 EC and considered observed with lognormal errors.

256 Ancillary data for the catch weight ratio per subpopulation (total weight; no age structure)
257 also exist, thus showing that higher proportions of catches are regularly realized in the East
258 FR area (subpopulation associated with the Somme nursery sector). An additional likelihood
259 term for the catch weight ratio per subpopulation was added to assimilate this information in
260 the model.

261 *Abundance indices of adults (see C in Fig. 2a)*

262 Different AIs for adults were available at various spatial scales (EC and subpopulations). Two
263 time series of AIs were available at the scale of the EC: the UK (UKCBT) and the Belgium
264 (BEBCT) commercial fleet catch-per-unit effort. The scientific UK Bottom Trawl Survey
265 (UKBTS) provided AIs at the adult stage for each of the three subpopulations. One
266 observation equation is written for each time series of AIs, each contributing to the whole
267 likelihood function. All of the AIs were considered as lognormal random observations of
268 abundance at age, but with catchability parameters specific to the fleet (UKBCT, BEBCT,
269 UKBTS) age and year.

270 **2.1.4. Choice of priors and values of fixed parameters**

271 Some parameters were fixed from the literature (Appendix A, Table A.1). All of the estimated
272 parameters except for the selectivity curve parameters and the slopes of the BH relationships
273 over nursery areas (α_i) were given weakly informative *a priori* distributions in the sense of
274 Gelman (2004), i.e., they let the data speak while excluding unrealistic values (Appendix A).

275 **2.2. Simplifying the model to a single, homogeneous adult population**

276 The model considering three isolated subpopulations can easily be simplified into a single
277 population model that corresponds to the structure of Rochette et al. (2013) and to the stock-
278 assessment working group (ICES, 2013). This single population model assumes that the five
279 nursery sectors contribute to one single population covering the whole EC (Fig. 2b). The
280 distribution of eggs over the spawning area is assumed to follow the distribution observed in
281 1991 (Rochette et al., 2012). All other processes (e.g., juvenile dynamics) are unchanged
282 except for the fishing mortality of adults that is now considered homogeneous at the EC scale.
283 The same sources of data are used, but no catch weight ratios per subpopulation are

284 considered and only the adult AIs available at the EC scale (i.e., UKCBT and BECBT) are
285 used (Fig. 2b).

286 2.3. Evaluating the fit to each data sources

287 We conducted posterior predictive checking to evaluate the fit of the model to each data
288 source assimilated in the model. For each data source, observed data (denoted y^{obs}) were
289 compared to the distribution of replicated data sets (y^{pred}) simulated from their posterior
290 predictive distribution (Gelman et al., 2004). To check that the model was able to replicate
291 data similar to the observations, we compare synthetic statistics calculated from the observed
292 data ($T(y^{obs})$) with statistics calculated from replicated data ($T(y^{rep})$). We calculated
293 Bayesian *p-values* (Gelman et al., 2004), defined as the probability that the statistics
294 calculated from the replicated data $T(y^{rep})$ are more extreme than the statistics calculated
295 from the observed data $T(y^{obs})$:

$$296 \quad (1) \quad p\text{-values} = \Pr (T(y^{rep}) \geq T(y^{obs}))$$

297 We chose the standard discrepancy statistic calculated for the observed and simulated data as
298 follows:

$$299 \quad (2) \quad T(y^{obs}) = \sum (y^{obs} - E(y))^2 \text{ and } T(y^{pred}) = \sum (y^{pred} - E(y))^2$$

300 where y^{obs} is an observation, y^{pred} is a simulated value in the posterior predictive
301 distribution of the state variable y and $E(y)$ is the expected mean of y in the model (the fit of
302 the model). y^{obs} , y^{pred} and $E(y)$ were log-transformed for all variables observed with
303 lognormal random noise. Depending upon the data source, the sums in eq. (2) are calculated
304 either across the entire time series of available data (for age-0 and age-1 AIs in nursery
305 sectors and for the catch weight ratio per subpopulation) or across both time and age classes
306 (for adults AIs and aggregated catches-at-ages). *p-values* close to 0 or 1 reveal the potential
307 failure of the model (Gelman et al. 2004).

308 In addition, we assessed the contribution of the various data sources in the model, considering
309 three loosely connected populations by examining how the final inferences change when
310 cumulating the data sources. Three runs of the model were conducted, successively adding the
311 various spatial data series (i.e., spatial UKBTS AIs and catch weight ratio per subpopulation;
312 Table 2). In run (a), only spatial UKBTS AIs are introduced in the likelihood. Run (b)
313 considers a likelihood function for the catch weight ratio per subpopulation, but does not

314 integrate spatial UKBTS AIs. Finally, run (c) corresponds to the final model that assimilates
 315 both the spatial UKBTS AIs and the catch weight ratio per subpopulation.

316

317 Table 2. Configuration of the three model runs to explore the respective contributions of data
 318 sources to the fit of the model with three subpopulations.

Run	Spatial Abundance Index (UKBTS)	Proportion of total catches among subpopulations (total catches in weight, no age structure)
a	Yes	No
b	No	Yes
c	Yes	Yes

319

320 2.4. Stock-assessment and management reference points

321 The spawning stock biomass (SSB), recruitment (R), fishing mortality (F), and Maximum
 322 Sustainable Yield (MSY , the associated fishing mortality (F_{MSY}) and spawning stock biomass
 323 (SSB_{MSY}) were estimated on different scales (for each subpopulation and on the scale of the
 324 EC).

325 The evaluation of MSY , F_{MSY} , and SSB_{MSY} is not analytically straightforward, because the
 326 production of each subpopulation results from a combination of stochastic BH relationships
 327 fitted on each nursery sector (two in West Fr: Veys and Seine; two in the UK: UK West and
 328 Rye; and one in East FR: Somme; Fig. 1a). The empirical equilibrium curves were obtained
 329 using Monte Carlo simulations to integrate both process and parameter uncertainty (see the
 330 methods in Appendix B). In the model considering three subpopulations, reference
 331 equilibrium points for each subpopulation r , denoted $B_{MSY,r}$, $F_{MSY,r}$ and $C_{MSY,r}$, were
 332 estimated conditionally by fixing the fishing pressure for the two other subpopulations equal
 333 to the estimates averaged over the last five years of the data series (2007-2011).

334 3. Results

335 3.1. Model evaluation

336 For both of the model configurations, the convergence diagnostics indicate convergence of
337 the MCMC chains after 10^6 iterations for all variables (see Sup. Mat. S1 for more details
338 about the MCMC simulations and the convergence diagnostics). To reduce the autocorrelation
339 in the sample used for final inferences, one out of 100 iterations was kept (thinning = 100).
340 Final inferences were derived from a sample of $3 \times 10,000$ iterations that resulted from
341 merging the three chains.

342 Because the two models integrate different sources of data (e.g., the spatial AIs of adults and
343 catch weight ratios that are not included in the model considering a single, homogeneous
344 adult population), the usual goodness of fit criteria cannot be used directly to compare the two
345 model structures. The component of deviance associated with the data shared by the two
346 model structures (i.e., the juvenile AIs in the five nursery sectors and the non-spatial AIs for
347 ages 2-15) was revealed as slightly lower for the model with one single population than for
348 the model with three isolated subpopulations (not shown). However, the difference is very
349 low, indicating that the likelihood of the two models is quite comparable when considering
350 the data shared by the two model structures.

351 Although this is not formally considered in the likelihood function, we also compared egg
352 distribution among the three spawning areas (i.e., the function of the *SSB* associated with
353 each subpopulation) to the spatial distribution of eggs given by the single available
354 observation originating from the 1991 eggs survey (Rochette et al., 2012). Results indicate
355 that the spatial distribution of eggs derived from the fit of the model with three isolated
356 subpopulations (West FR, 29%; UK, 33%; East FR, 38%) was highly consistent with the egg
357 distribution observed in 1991 (25%, 34% and 41%), thus providing evidence that the spatial
358 repartition of the *SSB* inferred from the model considering three subpopulation is consistent
359 with some external data sources.

360 Overall, a posterior predictive check conducted for the two model configurations (one
361 homogeneous population and three isolated subpopulations) did not reveal any strong and
362 general inconsistencies between the fitted model and the data. Almost all of the *p-values* are
363 between 0.05 and 0.95 for all model compartments (Table 3). The additional figures included
364 in Sup. Mat. S2 (Fig. S2.1- S2.9) show a good consistency between the posterior predictive

365 distributions and the data, providing additional evidence of a lack of conflict between the
 366 different sources of observations assimilated in the model. Interestingly, the *p-values*
 367 associated with the data sources that are common to the two model configurations (juveniles
 368 AIs, aggregated catches-at-ages and commercial CPUEs) were quite similar between the two
 369 model configurations (Table 3).

370 Table 3. *p-values* of posterior predictive checking calculated for each source of observation
 371 and for the two model configurations: the model considering a single, homogeneous adult
 372 population and the model considering three subpopulations. *p-values* are the probability that
 373 the discrepancy static calculated for predicted values is greater than the one calculated with
 374 observed values (see text for details).

		One single population		Three subpopulations	
		Age-0	Age-1	Age-0	Age-1
JUVENILES	AI in each nursery sector				
	Solent (West UK)	0.72	0.74	0.92	0.51
	Rye	0.29	0.84	0.33	0.80
	Somme	0.12	0.26	0.23	0.11
	Seine	0.65	0.70	0.71	0.83
	Veys	0.61	0.55	0.72	0.64
Aggregated data (Eastern Channel)					
Catches-at-age		0.54		0.56	
UK commercial CPUE (UKCBT)		0.82		0.88	
Belgium commercial CPUE (BECBT)		0.72		0.78	
Spatial data					
ADULTS	Proportion of total catches (weight) among the three areas (East FR, UK, West FR)				
	West FR	-		0.54	
	UK	-		0.57	
	East FR	-		0.47	
	Spatial Scientific AI Index (UKBTS)				
	West FR	-		0.85	
	UK	-		0.91	
	East FR	-		0.27	

375
 376 There was however evidence of poor fit between the posterior predictive distribution from the
 377 model and the observed data for the abundance indices of age-0 juveniles in the Solent
 378 nursery sector in the case of a model considering three subpopulations (*p-value* = 0.92) (Fig.

379 S2.1). Additionally, *p-values* for commercial AIs (UKCBT and BECBT) and for the spatial
380 AIs of adults (UKBTS) for the UK subpopulation are relatively high, indicating that the
381 dispersion of the predictive distribution around the model fit is higher than the dispersion of
382 observations (see also Fig. S2.1 and S2.8).

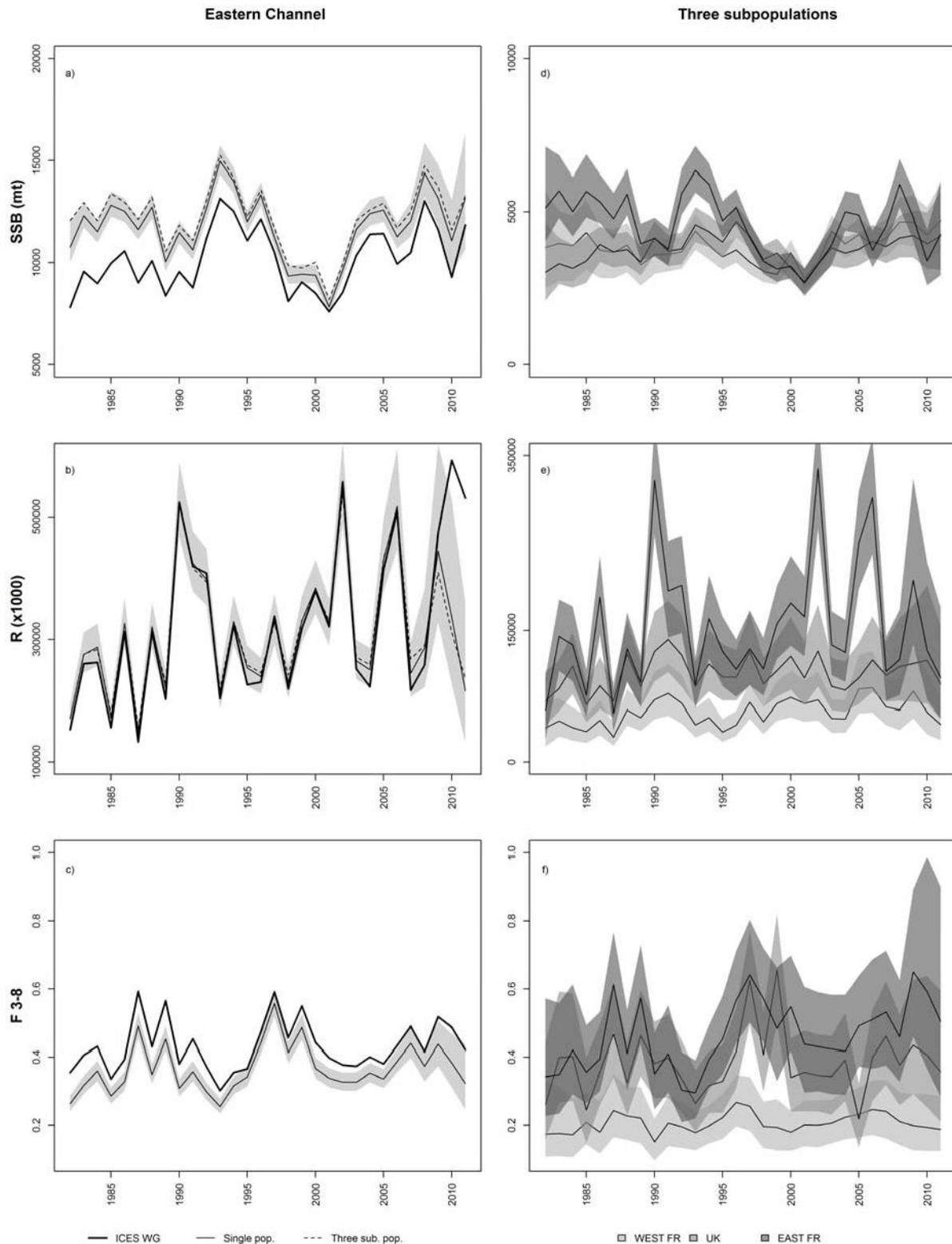
383 **3.2. Posterior estimates of parameters**

384 Marginal posterior distributions of all of the parameters obtained under both model
385 configurations reveal that the parameters are generally estimated with low uncertainty (Sup.
386 Mat. S3, Figs. S3.2 and S3.5 and Tabs. S3.1 and S3.2). Overall, the differences between the
387 prior and the posterior reveal that the distributions are mostly driven by the data (Sup. Mat. S3,
388 Figs. S3.2 and S3.5).

389 Interestingly, considering the more complex spatial structure of the population (three
390 subpopulations of adults versus a single, homogeneous population) does not increase the
391 posterior uncertainty about parameters. In contrast, uncertainty about posterior estimates of
392 biomass, recruitment, and fishing mortality is higher in the model that considers three
393 subpopulations (Fig. 3).

394 Nevertheless, one exception to this rule relates to the parameters for the density-dependent
395 recruitment process in each nursery sector; those parameters are estimated with much more
396 uncertainty than are the other parameters for both model configurations (Sup. Mat. S3, Fig.
397 S3.1 and S3.4). Uncertainty is particularly high for the maximum survival rate α for the
398 Somme and Rye nursery sectors. The posterior distribution of α for the Bay of Veys is not
399 different from the posterior predictive distribution because juvenile abundance indices are
400 only available for three years for this nursery sector.

401 For both model configurations, the selectivity parameters are estimated with very low
402 uncertainty that leads to a knife-edge selectivity curve, with selectivity near 0 for age-1 fish,
403 near 0.5 for age-2 fish and 1 for older fish.



404

405 Figure 3. Left column (a, b, c). Comparison of estimates of SSB , R and F_{3-8} at the Eastern
 406 Channel scale obtained by the ICES WG (bold line) both by the model considering one
 407 homogeneous adult population (solid line) and by the model considering three components of
 408 the adult population (dotted line). Right column (d, e, f). Estimates of SSB , R and F_{3-8} for the
 409 three subpopulations. Plain lines: posterior medians. Shaded areas: 95% Bayesian credible
 410 intervals.

411 As expected, the process error variance of the larvae to age-0 transition is greater than for the
412 age-0 to age-1 transition (Sup. Mat. S3, Tabs. S3.1 and S3.2). This residual variability does
413 not reveal any particular departure from the hypotheses of constant variance across the five
414 nursery grounds and of the time independence of residuals (not shown).

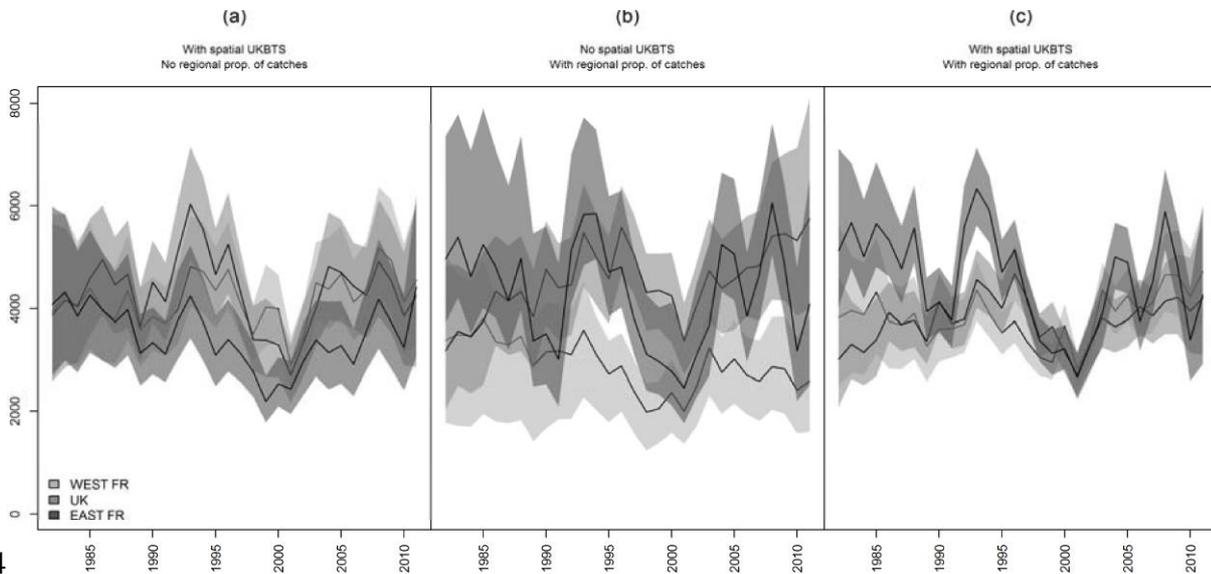
415 In both model configurations, the variance of observation error in catches is very low. In the
416 model considering a single, homogeneous population, the observation error on juveniles and
417 adults' abundance indices are of the same order of magnitude. In contrast, the variance of
418 observation error among juveniles is much higher in the model that considers three
419 subpopulations.

420 Additional results (Sup. Mat. S3, Tabs. S3.3 and S3.4) reveal that some parameters are
421 correlated and thus partially confounded. Results are similar for the two model configurations.
422 In particular, parameters (α, K) for each nursery sector are negatively correlated. Catchabilities
423 associated with age-0 and age-1 abundance indices (q_0 and q_1) are positively correlated;
424 moreover, they are positively correlated with the variance of observation errors on juveniles
425 (σ_{juv}^2). Similarly, catchabilities associated with adults' abundance indices (q_{UKCBT} , q_{BECBT}
426 and q_{UKBTS}) are positively correlated, and they are positively correlated with the variance of
427 observation error (σ_{Ad}^2).

428 **3.3. Contribution of the different data sources to posterior estimates**

429 We assessed the contribution of each dataset to the final estimations of the model with three
430 subpopulations. Three runs of the model were conducted, successively assimilating the
431 different sources of spatial data series (i.e., spatial UKBTS AIs and proportion of catches
432 among areas; Table 2). The spatial AIs and the spatial distribution of aggregated catches make
433 different contributions to the final estimates. In the run with spatial AIs only, although the
434 uncertainty about local SSB is relatively high, the total SSB at the scale of the EC is precisely
435 estimated (not shown) and the repartition is relatively balanced among the three
436 subpopulations (Fig. 4a), which is consistent with the information provided by the spatial
437 UKBTS AIs. When including spatial catches only (no spatial AIs), differences in SSB among
438 subpopulations are higher (Fig. 4b), with higher estimates of SSB in the UK and East FR
439 areas than in the West FR area, which is consistent with the higher proportion of catches
440 observed in the East FR area (see Fig. S2.6 in Sup. Mat. S2). Finally, when assimilating all
441 available data, uncertainty in SSB estimates is drastically reduced and the variability across

442 subpopulations is shrunken (Fig. 4c) according to the information provided by the spatial AIs,
443 and unbalanced catch ratios translate into unbalanced fishing mortality among subpopulations.



444

445 Figure 4. Time series of posterior estimates of *SSB* for the three subpopulations obtained with
446 the three data configurations of the Table 2. Solid lines: posterior medians. Shaded areas: 95%
447 Bayesian credibility intervals.

448

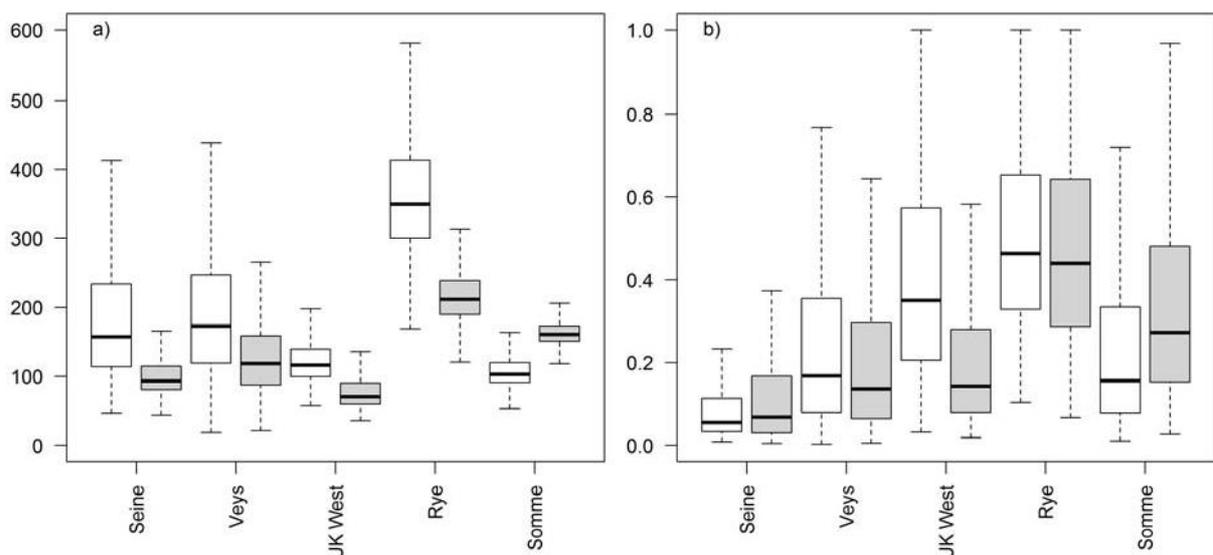
449 3.4. The effect of considering three isolated subpopulations on stock productivity

450 The effect of considering three isolated populations (instead of one homogeneous population)
451 depends upon the spatial scale considered. The single-population model and the model
452 considering three subpopulations provide similar estimates of *SSB*, recruitment and fishing
453 mortality considered on the EC scale (Fig. 3a,b,c). These estimates were also consistent with
454 ICES estimates, although overall they displayed a slightly higher *SSB* balanced by a lower *F*.
455 However, the consideration of three subpopulations provides a spatial perspective on
456 population dynamics. It also impacts inferences on stock productivity and therefore the
457 assessment of stock status with respect to reference points.

458 3.4.1. Reevaluation of the productivity of nurseries

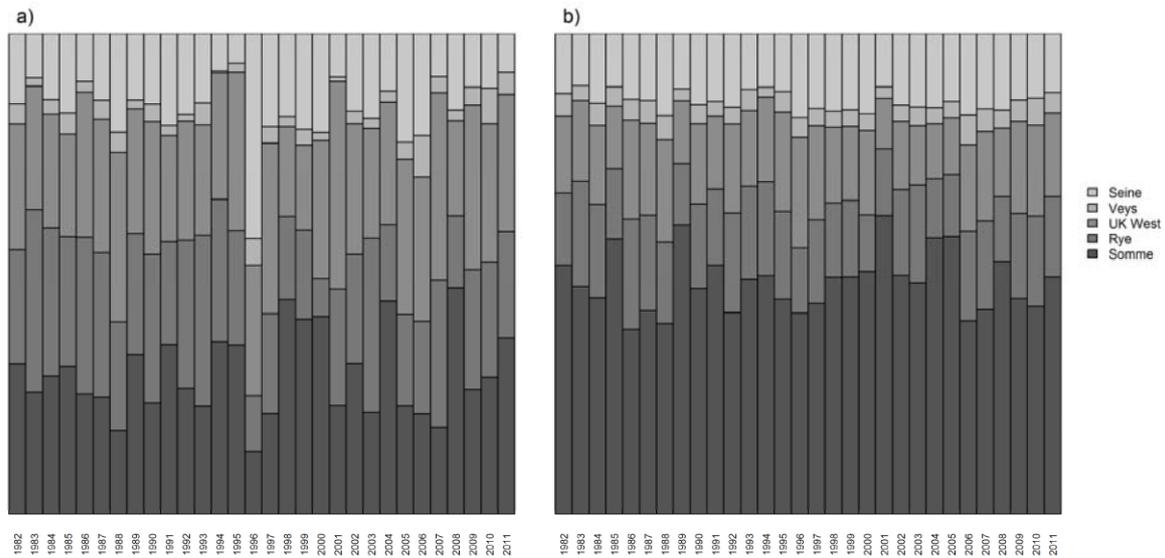
459 The hypothesis on the spatial structure of the population strongly affects estimates of the
460 carrying capacity per unit of surface (Fig. 5a), with *K* for the Somme nursery sector being
461 largely reevaluated when considering a model structure with three isolated subpopulations,
462 balanced by a decrease in estimates of *K* for all other nursery sectors. Estimates of parameters

463 α for the UK West and Veys decrease when considering a model with three subpopulations,
 464 whereas the estimate increases for the Somme (Fig. 5b). Additional figures S3.3 and S3.6 in
 465 Sup. Mat. S3 provide a plot of the resulting Beverton-Holt curve in each nursery sector that
 466 illustrates the change in the local recruitment dynamics between the two model configurations.
 467 As a result, the contributions of each nursery sector to recruitment in the EC are also strongly
 468 affected. In the single-population model, the Seine, Veys, UK West, Rye and Somme sectors
 469 contributed an average of 16, 3, 28, 24 and 29%, respectively, but with high variability among
 470 years (Fig. 6a). When considering three isolated subpopulations (Fig. 6b), these contributions
 471 were estimated at 14, 4, 17, 17 and 48% and were much less variable in time. At the
 472 subpopulation level, this translates into a strong increase in the contribution from East FR
 473 subpopulation (Somme: from 29% to 48%) balanced by decreases in contributions from West
 474 FR (Seine + Veys: from 19% to 18%) and UK subpopulations (UK West + Rye: from 52% to
 475 34%).



476
 477 Figure 5. Marginal posterior distributions of the nursery-specific Beverton-Holt parameters K
 478 (a) and α (b) obtained with the model considering one homogeneous adult population (white)
 479 and with the model considering three isolated subpopulations (gray). K is in thousands of fish
 480 per km². α is a maximum survival rate.

481
 482 Overall, those results are consistent with the high proportion of catches recorded in the East
 483 FR area (the area associated with the Somme nursery sector), logically leading to a high SSB
 484 in this area in the model that considers three subpopulations (Fig. 3d); in turn, this leads to
 485 higher recruitment in the Somme nursery sector.



486

487 Figure 6. Contributions of the five nursery sectors to the total 0+ recruitment obtained from
 488 the model considering a) one single adult population and b) three isolated subpopulations. The
 489 contribution is calculated from the posterior median estimates of the recruitment (age-0
 490 abundance).

491 **3.4.2. Management reference points and stock assessment**

492 Whereas the results obtained on the scale of the entire EC indicate that the sole population is
 493 overexploited, the results obtained when considering a three-subpopulation structure revealed
 494 highly contrasting levels of exploitation among subpopulations.

495 When considering a single population, the average SSB and F_{3-8} over the past four years
 496 were approximately 12,950t and 0.38, respectively (Fig. 3a,b,c). SSB_{MSY} , C_{MSY} and F_{MSY} are
 497 estimated at 28,090t, 5,470t and 0.21, respectively (Table 4; Fig. 7a), thus indicating that the
 498 sole population is currently overexploited, with an average ratio of F/F_{MSY} near 1.8 and that of
 499 SSB/SSB_{MSY} near 0.5 during the last four years.

500 The model with three isolated populations provides a spatial perspective on the population
 501 dynamics and the impact of fishing pressure. Estimates of SSB among the various
 502 subpopulations (Fig. 3d) are essentially equivalent, with an average SSB of 4,570t for the
 503 West FR subpopulation, 4,130t for the UK subpopulation, and 4,590t for the East FR
 504 subpopulation. By contrast, average F are highly contrasted among populations, with average
 505 F over the past 4 years estimated at 0.20, 0.39 and 0.55 for the West FR, UK and East FR
 506 subpopulations, respectively.

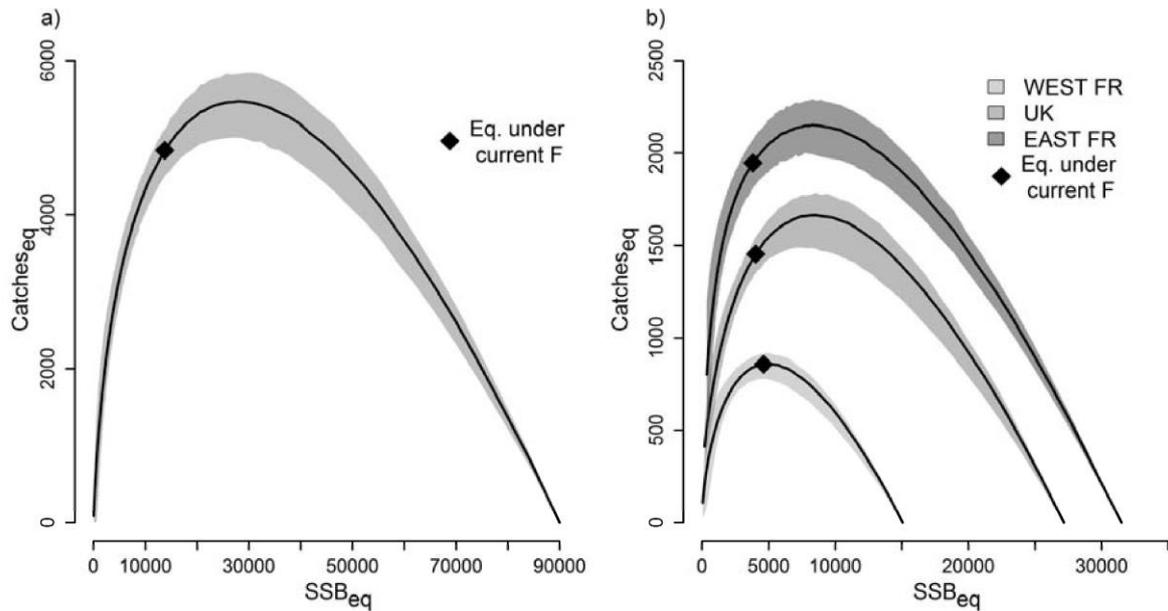
507

508 Table 4. Summary of point estimates of the management reference points SSB_{MSY} , C_{MSY} and
 509 F_{MSY} obtained in the models considering (i) a single population and (ii) three isolated
 510 subpopulations.

Reference points	One single population	Three subpopulations	
SSB_{MSY}	28,090	West FR	4,880
		UK	8,540
		East FR	8,300
C_{MSY}	5,470	West FR	870
		UK	1,670
		East FR	2,150
F_{MSY}	0.21	West FR	0.19
		UK	0.21
		East FR	0.28

511

512 The reference points SSB_{MSY} , C_{MSY} , F_{MSY} (Table 4; Fig. 7b) associated with each
 513 subpopulation were estimated at 4,880t, 870 t and 0.19 for West FR, 8,540t, 1,670t and 0.21
 514 for UK and 8,300t, 2,150t and 0.28 for East FR, respectively. When considering the current
 515 state of exploitation (average over four years), it appears that the West FR subpopulation is at
 516 full exploitation level, with F/F_{MSY} at 1.05 and SSB/SSB_{MSY} at 0.94, whereas the UK and East
 517 FR subpopulations are overexploited (Fig. 7b), with F/F_{MSY} dramatically greater than 1 (1.9
 518 and 2.0, respectively) and SSB/SSB_{MSY} dramatically lower than 1 (0.48 and 0.54, respectively).



519

520 Figure 7. Relation between the SSB and catches at equilibrium obtained through the
 521 simulation approach in the model considering (a) a single population and (b) three isolated
 522 subpopulations. Shaded area: 50% credibility interval obtained from the Monte Carlo
 523 simulation integrating both process and parameters uncertainty. Black diamond: *Eq. under*
 524 *current F* represents the position on the equilibrium curve obtained with the current fishing
 525 mortalities (average over the 4 most recent years).

526

527 4. Discussion

528 4.1. An integrated modeling framework for a better understanding of 529 metapopulation dynamics

530 Our results make a significant contribution to the understanding of the sole population
 531 dynamics in the EC. The model used to assess the stock of the sole population in the EC
 532 considers a simple, homogeneous population with no spatial structure (ICES, 2013). Using
 533 the HBM framework, Rochette et al. (2013) make an important contribution by establishing
 534 the fundamental basis for a population model that embeds egg and larval drift and survival
 535 derived from an oceanic circulation model within a stage-structured life cycle, accounting for
 536 the spatial nature of the recruitment process in distinct coastal nursery sectors. The model
 537 presented here elaborates on Rochette et al. (2013) and provides additional insights into
 538 population dynamics by exploring a metapopulation structure with very low connectivity
 539 among three subpopulations. The capacity of Bayesian models to incorporate prior

540 information also presented the possibility of an efficient use of the available information
541 through the informative prior distribution for the maximum survival rate between settled
542 larvae and 0+ juveniles derived from a meta-analysis on flatfish (Archambault et al., 2014).

543 The consideration of three loosely connected subpopulations increased the model's state-
544 space dimension of the model. But because the two models integrate different sources of data
545 (e.g., spatial AIs of adults and catches that are not included in the model considering one
546 single homogeneous adult population), the usual goodness-of-fit criteria such as the deviance
547 information criterion (Spiegelhalter et al., 2014) are not adapted to compare the tradeoff
548 between the two model structures' complexity and quality of fit. A posterior predictive check
549 conducted for both model configurations did not reveal any strong, general inconsistencies
550 between the fitted model and the different sources of data for both model configurations.

551 Interestingly, when considering the data sources that are common to the two model
552 configurations (*i.e.*, juveniles AIs, catch-at-ages and commercial CPUEs aggregated at the
553 scale of the EC), both model configurations showed similar quality of fit. Additional results
554 (not shown) indicate that the likelihood components restricted to the data shared by the two
555 model structures are comparable between the two models.

556 However, although we were unable to demonstrate that the model considering three isolated
557 subpopulations provides a better fit to the data, a body of ecological knowledge and clues
558 continues to strongly argue for *a priori* consideration of such a metapopulation structure, and
559 posterior inferences provide a portfolio of ecologically meaningful results.

560 First, strong prior knowledge exists in favor of the limited movements of juveniles (Coggan
561 and Dando, 1988; Anon., 1989; Le Pape and Cognez, 2016) and adults (Kotthaus, 1963;
562 Anon., 1965; Burt and Millner, 2008), and barriers linked to sediment structure limit
563 exchanges between regions (Rochette et al., 2010; 2012). This knowledge was used *a priori*
564 to define the spatial contours of three subpopulations of the common sole in the EC.

565 Second, taking into account the moderate connectivity between the successive life stages, we
566 were able to produce a diagnosis of the population that, while consistent with ICES estimates
567 at the scale of the EC, provided contrasting, meaningful results on a local scale. This approach
568 allowed us to reconstruct local biomasses' evolution during the past three decades that were
569 revealed as consistent with the time series of spatial abundance indices and catches. The
570 consideration of three subpopulations also led to a substantial reevaluation of the productivity
571 of the various nursery sectors that are quantitatively consistent with the juveniles AIs, catches

572 and local biomasses estimated for their associated subcomponents. It also drastically reduced
573 the between-years variability of the relative contribution of each nursery sector to total 0+
574 recruitment, which is consistent with both the concentration hypothesis (Rijnsdorp et al., 1992;
575 Iles and Beverton, 2000; Rooper et al., 2004) and the low recruitment variability described for
576 common sole (Le Pape et al., 2003b; Archambault et al., 2014).

577 Finally, results indicate that the spatial distribution of eggs derived from the fit of the model
578 with three subpopulations with low connectivity matches the observed egg repartition derived
579 from the 1991 eggs survey (Rochette et al., 2012). Because the comparison between the
580 spatial distribution of eggs observed (1991) and simulated *a posteriori* by the model is not
581 included in the likelihood function, this result can be considered as an element that validates
582 the spatial structure of the adult population.

583 **4.2. Weaknesses and directions for future research**

584 Our modeling approach has some weaknesses. Below, we discuss some of those weaknesses
585 along with some critical needs for knowledge and data about the spatial ecological process
586 that the modeling approach has helped identify. Finally, we highlight a few research avenues
587 that would improve both the knowledge and the models.

588 **4.2.1. Simulations to explore the tradeoff between model complexity and data** 589 **availability**

590 Several studies have shown that in the case of complex spatial population dynamics, the
591 explicit consideration of spatial structures in stock-assessment models that are better aligned
592 with ecological reality (instead of simpler models) provide better estimates, when sufficiently
593 informative data are available (Hulson et al., 2013; Hintzen et al., 2015). However, our case
594 study is a data-poor situation because only a few data provide information about the spatial
595 structure of the population. In particular, no time series of spatial catch-at-age data are
596 available. Thus, it is difficult to formally conclude that fitting a spatial structure to the
597 available data results in reliable estimates of abundance and population dynamics. To
598 reinforce the analysis, one interesting perspective for future work would consist of conducting
599 simulations that would cross a few hypotheses about how the dynamics of the true population
600 work with various model and data configurations for the statistical stock-assessment model.
601 This would enable us not only to show which type of assessment might provide reliable

602 estimates given our data limitations but also to illustrate how gathering more informative data
603 about the spatial processes (for instance spatial catch-at-age or mark-recapture data) would
604 improve the quality of our inferences.

605 **4.2.2. Sensitivity to priors**

606 Uncertainty about estimates and sensitivity to the prior choice varied according to model
607 compartment. As analyzed (with respect to a previous version of the model) by Rochette et al.
608 (2013), numbers-at-age and all other variables associated with the demographic of ages 1-15,
609 such as *SSB*, recruitment and fishing mortality, are estimated with low uncertainty. Indeed,
610 the demographics of ages 1-15 consist of a catch-at-age model for 14 age classes tracked over
611 30 years; both catch and abundance indices are available for almost all years and ages.

612 By contrast, parameters for the density-dependent recruitment process in nursery sectors are
613 estimated with much more uncertainty and are partly confounded. Those parameters are
614 generally difficult to estimate from the data alone (Conn et al., 2010) and we therefore
615 developed a method based on a previous meta-analysis on flatfish (Archambault et al., 2014)
616 to build an informative prior distribution about the maximum survival rates of settled larvae
617 on nursery ground (α). Relying on a previous analysis by Rochette et al. (2013), our results
618 are likely to be sensitive to the choice of priors on those parameters, and using weakly
619 informative priors on the α_i 's would certainly lead to poor inferences about stock productivity.
620 Because the models developed in this manuscript have many similarities and the data are the
621 same, and to keep the main message centered on the impact of changing the spatial structure
622 of the model, we did not report any additional sensitivity analysis.

623 **4.2.3. Improving the model for the recruitment process**

624 Based on previous modeling work by Rochette et al. (2013), strong hypotheses were made on
625 the recruitment process: (i) Within each nursery sector, variability of the recruitment process
626 was modeled as independent lognormal random noise, with no time series autocorrelation; (ii)
627 The variance of lognormal process noise was considered homogeneous among nurseries; and
628 (iii) Between-years random variations were considered as independent among nursery sectors.
629 Consistent with results found by Rochette et al. (2013), a careful examination of the residual
630 variability did not reveal any particular departure from the hypotheses of constant variance
631 across the five nursery grounds and the time independence of residuals. This is consistent

632 with previous analysis on the low synchronicity in inter-annual variability of juvenile
633 abundance between the nursery sectors (Riou et al., 2001). Because there are many gaps in the
634 time series of juvenile-abundance indices on nursery sectors (47% missing data; see Tab. 1),
635 data are lacking to estimate parameters for the covariance in the recruitment process among
636 nursery sectors. Including covariance in the recruitment process among nursery sectors would
637 likely impact the population dynamics and stock assessment (Ranta et al., 1997; Liebhold et
638 al., 2004). Therefore, an investigation of how the inclusion of covariance in the time series of
639 recruitment process noise among nursery sectors would change estimates and population
640 dynamics for the sole population in the EC would be an interesting focus for future research.

641 **4.2.4. The need for better knowledge of adult-mediated connectivity**

642 Data on sub-adult and adult migration were lacking, and we were unable to estimate the
643 degree of mixing among the three subpopulations. Our approach thus considered two extreme
644 scenarios of adult-mediated connectivity: full connectivity and full spatial segregation
645 between subpopulations associated with nursery sectors. Whereas a body of ecological
646 knowledge advocates for a loose connectivity among the three subpopulations, improved data
647 collection on movements and connectivity is a top priority. Natural markers, which include
648 genetic markers, xenobiotics, stable isotopes, otolith microchemistry and parasites and their
649 possible combination (Selkoe et al., 2008; Fodrie and Herzka, 2013), are a first source of data.
650 The analysis of genetic-neutral markers could help infer population structure (Smedbol et al.,
651 2002), although the open nature of the marine environment may prevent a significant signal
652 from emerging (Waples, 1998; Exadactylos et al., 2003; Rolland et al., 2007). Recent
653 approaches using genetic-adaptive markers (Diopere et al., 2013) and combined multi-marker
654 approaches (Cuveliers et al., 2012) provide fruitful perspectives to quantify connectivity
655 among marine subpopulations with a finer spatial resolution. Analyses of the differences in
656 otolith elemental composition have been used to identify the estuarine origin of individuals
657 (Cuveliers et al., 2010). Mark-recapture is also widely used to quantify migration (Hilborn,
658 1990; Rijnsdorp and Pastoors, 1995; Polacheck et al., 2010). Recent work focusing on older
659 juvenile, sub-adult and adult flatfish emphasizes the interest of these approaches (Sackett et
660 al., 2008; Fairchild et al., 2009; Furey et al., 2013). Future methodological work should
661 include the development of integrated models that enables the consideration of multiple
662 sources of data into space-structured population models (Darnaude and Hunter, 2008; Korman
663 et al., 2012; Goethel et al., 2014).

664 **4.3. Implications for spatial management**

665 The sole population in the EC, like most exploited marine fish stocks, is currently assessed as
666 a single population. However, our results suggest that the consideration of metapopulation
667 dynamics strongly impacts inferences on stock productivity and conclusions about both stock
668 assessment and (ultimately) fisheries advice.

669 The consideration of three subpopulations induced a substantial reevaluation of the
670 productivity of the various nursery sectors; estimates of the contribution of the East FR
671 subpopulation to the total recruitment doubled, balanced by a decrease in contributions from
672 the West FR and UK subpopulations. Whereas results obtained on the scale of the entire EC
673 indicate that the sole population is exploited far above MSY, assessments obtained when
674 considering a three-subpopulation structure revealed highly contrasting levels of exploitation
675 among subpopulations, with over-exploitation of some of the metapopulation components.
676 Indeed, estimates of local management reference points associated with each subpopulation
677 revealed that the West FR subpopulation is approaching full exploitation, whereas the UK and
678 East FR subpopulations are overexploited. The practical consequences of our conclusions
679 may even increase when considering the local fisheries, which are characterized by fleets with
680 limited movement, without large-scale tracking of fish (Tidd et al., 2015).

681 Beyond our case study, this work emphasizes the role of space in population functioning for
682 species whose different life-history stages are segregated among specific habitats. Larval
683 retention in marine populations is suspected to occur more than originally thought (Cowen et
684 al., 2000; Warner and Cowen, 2002). Juvenile segregation in restricted nursery areas is also a
685 common feature of fish populations (Vasconcelos et al., 2014). As noted by Frisk et al. (2014),
686 our case study stresses the need to more thoroughly assess the importance of adult-mediated
687 connectivity. Spatial integrated life-cycle models such as the one developed in this work
688 provides a contribution to the quantitative assessment of spatial fishery and coastal habitat
689 management plans. First, as previously shown by several authors, ignoring metapopulation
690 structure in stock assessment models could result in local over/under exploitation (Tuck and
691 Possingham, 1994; Ying et al., 2011; Yau et al., 2014) and improving data collection and
692 statistical methods to estimate the parameters of spatial life-cycle models is a top priority for
693 the optimal allocation of fishing pressure. Second, accounting for metapopulation dynamics is
694 critical for an optimal assessment of essential habitat preservation and/or restoration that

695 could be at least as efficient as assessing fishing pressure for restoring populations of nursery-
696 dependent species (Levin and Stunz, 2005; van de Wolfshaar et al., 2011).

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704 **References**

- 705 Anon. 1965. Report of the working group on sole. ICES Coop.Res. Rep. 5: 1-126.
- 706 Anon. 1989. Report of ad hoc study group on juvenile sole tagging. ICES CM 1989/G: 21,
707 34pp.
- 708 Archambault, B., Le Pape, O., Bousquet, N., and Rivot, E. 2014. Density-dependence can be
709 revealed by modelling the variance in the stock–recruitment process: an application to flatfish.
710 ICES J. Mar. Sci. 71(8): 2127–2140.
- 711 Botsford, L.W., Brumbaugh, D.R., Grimes, C., Kellner, J.B., Largier, J., O’Farrell, M.R.,
712 Ralston, S., Soulanille, E., and Wespestad, V. 2009. Connectivity, sustainability, and yield:
713 bridging the gap between conventional fisheries management and marine protected areas. Rev.
714 Fish Biol. Fish. 19: 69–95.
- 715 Buckland, S.T., Newman, K.B., Fernández, C., Thomas, L., and Harwood, J. 2007.
716 Embedding population dynamics models in inference. Stat. Sci. 22(1): 44–58.
- 717 Burt, G. J., and Millner, R. S. 2008. Movements of sole in the southern North Sea and eastern
718 English Channel from tagging studies (1955–2004). Sci. Ser. Tech. Rep. 44.
- 719 Brooks, S. P., and Gelman, A. 1998. General methods for monitoring convergence of iterative
720 simulations. J. Comp. Graph. Stat. 7(4): 434–455.
- 721 Carruthers, T.R., McAllister, M.K., and Taylor, N.G. 2011. Spatial surplus production
722 modeling of Atlantic tunas and billfish. Ecol. Appl. 21: 2734–2755.
- 723 Carson, H.S., Cook, G.S., López-Duarte, P.C., and Levin, L.A. 2011. Evaluating the
724 importance of demographic connectivity in a marine metapopulation. Ecology 92: 1972–1984.
- 725 Chambers, R.C., and Trippel, E.A. 1997. Early life history and recruitment in fish populations.
726 Chapman and Hall, New York.
- 727 Cianelli, L., Fisher, J., Skern-Mauritzen, M., Hunsicker, M., Hidalgo, M., Frank, K., and
728 Bailey, K. 2013. Theory, consequences and evidence of eroding population spatial structure in
729 harvested marine fishes: a review. Mar. Ecol. Prog. Ser. 480: 227–243.
- 730 Clark, J.S. 2005. Why environmental scientists are becoming Bayesians? Ecol. Lett. 8: 2–14.
- 731 Coggan, R.A., and Dando, P.R. 1988. Movements of juvenile Dover sole, *Solea solea* (L.), in
732 the Tamar Estuary, South-western England. J. Fish Biol. 33: 177–184.

733 Conn, P.B., Williams, E.H., and Shertzer, K.W. 2010. When can we reliably estimate the
734 productivity of fish stocks? *Can. J. Fish. Aquat. Sci.* 67:511–523.

735 Cowen, R.K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B., and Olson, D.B. 2000. Connectivity
736 of Marine Populations: Open or Closed? *Science* 287: 857–859.

737 Cunningham, C., Reid, D., McAllister, M., Kirkwood, G., and Darby, C. 2007. A Bayesian
738 state-space model for mixed-stock migrations, with application to Northeast Atlantic
739 mackerel *Scomber scombrus*. *Afr. J. Mar. Sci.* 29(3): 347-367.

740 Cuveliers, E.L., Geffen, A.J., Guelinckx, J., Raeymaekers, J.A.M., Skadal, J., Volckaert,
741 F.A.M., and Maes, G.E. 2010. Microchemical variation in juvenile *Solea solea* otoliths as a
742 powerful tool for studying connectivity in the North Sea. *Mar. Ecol. Prog. Ser.* 401: 211–220.

743 Cuveliers, E., Larmuseau, M., Hellemans, B., Verherstraeten, S., Volckaert, F., and Maes, G.
744 2012. Multi-marker estimate of genetic connectivity of sole (*Solea solea*) in the North-East
745 Atlantic Ocean. *Mar. Biol.* 159: 1239–1253.

746 Darnaude, A., and Hunter, E. 2008. Coupled use of data storage tags and otolith
747 microchemistry to assess population dispersal and intra-specific diversity in migratory
748 behaviour in North Sea plaice (*Pleuronectes platessa* L.). *Comp. Biochem. Phys. A* 150: S205.

749 Diopere, E., Hellemans, B., Volckaert, F.A.M., and Maes, G.E. 2013. Identification and
750 validation of single nucleotide polymorphisms in growth- and maturation-related candidate
751 genes in sole (*Solea solea* L.). *Mar. Genom.* 9: 33–38.

752 Drouineau, H., Mahévas, S., Bertignac, M., and Duplisea, D. 2010. A length-structured
753 spatially explicit model for estimating hake growth and migration rates. *ICES J. Mar. Sci.*
754 67(8) 1697–1709.

755 Exadactylos., A., Geffen, A.J., Panagiotaki, P., and Thorpe, J.P. 2003. Population structure of
756 Dover sole *Solea solea*: RAPD and allozyme data indicate divergence in European stocks.
757 *Mar. Ecol. Prog. Ser.* 246: 253–264.

758 Fairchild, E.A., Rennels, N., and Howell, H. 2009. Using telemetry to monitor movements
759 and habitat use of cultured and wild juvenile winter flounder in a shallow estuary. In *Tagging
760 and Tracking of Marine Animals with Electronic Devices*, Springer Netherlands. pp. 5–22.

761 Fodrie, F., and Herzka, S. 2013. A comparison of otolith geochemistry and stable isotope
762 markers to track fish movement: describing estuarine ingress by larval and post-larval halibut.
763 *Estuar. Coast.* 39: 906–917.

764 Frisk, M.G., Jordaan, A., and Miller, T.J. 2014. Moving beyond the current paradigm in
765 marine population connectivity: are adults the missing link? *Fish Fish.* 15(2): 242-254.

766 Furey, N., Dance, M., and Rooker, J. 2013. Fine-scale movements and habitat use of juvenile
767 southern flounder *Paralichthys lethostigma* in an estuarine seascape. *J. Fish Biol.* 82: 1469–
768 1483.

769 Gaines, S.D., White, C., Carr, M.H., and Palumbi, S.R. 2010. Designing marine reserve
770 networks for both conservation and fisheries management. *P. Natl. Acad. Sci.* 107: 18286–
771 18293.

772 Gallego, A., North, E.W., and Houde, E.D. 2012. Understanding and quantifying mortality in
773 pelagic, early life stages of marine organisms - Old challenges and new perspectives. *J.*
774 *Marine Syst.* 93: 1–3.

775 Gelman, A. 2009. Bayes, Jeffreys, prior distributions and the philosophy of statistics. *Stat. Sci.*
776 24(2):176–178.

777 Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 2004. *Bayesian Data Analysis.*
778 Chapman & Hall/CRC. 717 pp.

779 Gibson, R.N. 2004. *Flatfishes: Biology and Exploitation.* Wiley. 419 pp.

780 Goethel, D.R., Legault, C.M., and Cadrin, S.X. 2014. Demonstration of a spatially explicit,
781 tag-integrated stock assessment model with application to three interconnected stocks of
782 yellowtail flounder off of New England. *ICES J. Mar. Sci.* 72(1): 164–177.

783 Grosberg, R.K., and Levitan, D.R. 1992. For adults only? Supply-side ecology and the history
784 of larval biology. *Trends Ecol. Evol.* 7: 130–133.

785 Grüss, A., Kaplan, D., Guenette, S., Roberts, C., and Botsford, L. 2011. Consequences of
786 adults and juvenile movement for marine protected areas. *Biol. Conserv.* 144: 692–702.

787 Guan, W., Cao, J., Chen, Y., and Cieri, M. 2013. Impacts of population and fishery spatial
788 structures on fishery stock assessment. *Can. J. Fish. Aquat. Sci.* 70: 1178–1189.

789 Hellberg, M.E., Burton, R.S., Neigel, J.E., and Palumbi, S.R. 2002. Genetic assessment of
790 connectivity among marine populations. *B. Mar. Sci.* 70: 273–290.

791 Hilborn, R. 1990. Determination of Fish Movement Patterns from Tag Recoveries using
792 Maximum Likelihood Estimators. *Can. J. Fish. Aquat. Sci.* 47: 635–643.

793 Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics
794 and uncertainty. *Rev. Fish Biol. Fisher.* 2: 177–178.

795 Hinrichsen, H.-H., Dickey-Collas, M., Huret, M., Peck, M.A., and Vikebø, F.B. 2011.
796 Evaluating the suitability of coupled biophysical models for fishery management. *ICES J.*
797 *Mar. Sci.* 68: 1478–1487.

798 Hintzen, N.T., Roel, B., Benden, D., Clarke, M., Egan, A., Nash, R.D.M., Rohlf, N. and
799 Hatfield, E. M. C. 2015. Managing a complex population structure: exploring the importance
800 of information from fisheries-independent sources. *ICES J. Mar. Sci.* 72(2) : 528–542.

801 Hulson, P.J. F., Quinn, T.J., Hanselman, D.H. and Ianelli, J.N. 2013. Spatial modeling of
802 Bering Sea walleye pollock with integrated age-structured assessment models in a changing
803 environment. *Can. J. Fish. Aquat. Sci.* 70(9), 1402–1416.

804 ICES 2010. Report of the Working Group on the Assessment of Demersal Stocks in the North
805 Sea and Skagerrak (WGNSSK), 5–11 May 2010. ICES CM 2010/ACOM:13. Copenhagen,
806 ICES Headquarters, 1058 pp.

807 ICES. 2013. Report of the Working Group on the Assessment of Demersal Stocks in the
808 North Sea and Skagerrak (WGNSSK), 24–30 April 2013, ICES Headquarters, Copenhagen.
809 ICES Document CM 2013/ACOM:13. 1435 pp.

810 Iles, T.C., and Beverton, R.J.H. 2000. The concentration hypothesis: the statistical evidence.
811 *ICES J. Mar. Sci.* 57: 216–227.

812 Korman, J., Martell, S.J.D., Walters, C.J., Makinster, A.S., Coggins, L.G., Yard, M.D., and
813 Persons, W.R. 2012. Estimating recruitment dynamics and movement of rainbow trout
814 (*Oncorhynchus mykiss*) in the Colorado River in Grand Canyon using an integrated
815 assessment model. *Can. J. Fish. Aquat. Sci.* 69(11): 1827–1849.

816 Kotthaus, A. 1963. Tagging experiments with the North Sea sole (*Solea solea*) in 1959 and
817 1960. In Special Publication number 4 of the International Commission for the Northwest
818 Atlantic Fisheries, pp. 123–129. Headquarters of the Commission, Dartmouth, Nova Scotia,
819 Canada.

820 Le Pape, O., Chauvet, F., Mahévas, S., Lazure, P., Guérault, D., and Désaunay, Y. 2003a.
821 Quantitative description of habitat suitability for the juvenile common sole (*Solea solea*, L.) in
822 the Bay of Biscay (France) and the contribution of different habitats to the adult population. *J.*
823 *Sea Res.* 50: 139–149.

824 Le Pape, O., Chauvet, F., Désaunay, Y., Guérault, G. 2003b. Relationship between
825 interannual variations of the river plume and the extent of nursery grounds for the common
826 sole (*Solea solea*, L.) in Vilaine Bay. Effects on recruitment variability. *J. Sea Res.* 50: 177-
827 185.

828 Le Pape, O., and Bonhommeau, S. 2015. The food limitation hypothesis for juvenile marine
829 fish. *Fish Fish.* 16(3): 373–398.

830 Le Pape, O. and Cognez, N. 2016. The range of juvenile movements of estuarine and coastal
831 nursery dependent flatfishes: estimation from a meta-analytical approach. *J. Sea Res.* 107(1):
832 43-55

833 Levin, P.S., and Stunz, G.W. 2005. Habitat triage for exploited fishes: Can we identify
834 essential ‘Essential Fish Habitat?’ *Estuar. Coast. Shelf S.* 64: 70–78.

835 Liebhold, A., Koenig, W. D., and Bjørnstad, O.N. 2004. Spatial synchrony in population
836 dynamics. *Annu. Rev. Ecol. Evol. S.* 35(1) 467–490.

837 Massiot-Granier, F., Prévost, E., Chaput, G., Potter, T., Smith, G., White, J., Mantyniemi, S.,
838 Rivot, E. 2014. Embedding stock assessment within an integrated hierarchical Bayesian life
839 cycle modelling framework: an application to Atlantic salmon in the Northeast Atlantic. *ICES*
840 *J. Mar. Sci.* 71(7): 1653–1670.

841 McAllister, M., Hill, S., Agnew, D., Kirkwood, G., and Beddington, J. 2004. A Bayesian
842 hierarchical formulation of the De Lury stock assessment model for abundance estimation of
843 Falkland Islands' squid (*Loligo gahi*). *Can. J. Fish. Aquat. Sci.* 61:1048–1059.

844 Miller, T.J. 2007. Contribution of individual-based coupled physical-biological models to
845 understanding recruitment in marine fish populations. *Mar. Ecol. Prog. Ser.* 347: 127–138.

846 Parent, E., and Rivot, E. 2013. Introduction to Hierarchical Bayesian Modeling for Ecological
847 Data. *Applied Environmental Statistics*. Chapman & Hall/CRC. 427 pp.

848 Peck, M., and Hufnagl, M. 2012. Can IBMs tell us why most larvae die in the sea? Model
849 sensitivities and scenarios reveal research needs. *J. Marine Syst.* 93: 77–93.

850 Petitgas, P., Rijnsdorp, A., Dickey-Collas, M., Engelhard, G., Peck, M., Pinnegar, J.,
851 Drinkwater, K., Huret, M., and Nash, R.D.M. 2013. Impacts of climate change on the
852 complex life cycles of fish. *Fish Oceanogr.* 22: 121–139.

853 Planque, B., Loots, C., Petitgas, P., Lindstrom, U., and Vaz, S. 2011. Understanding what
854 controls the spatial distribution of fish populations using a multi-model approach. *Fish.*
855 *Oceanogr.* 20: 1–17.

856 Polacheck, T., Paige Eveson, J., and Laslett, G.M. 2010. Classifying tagging experiments for
857 commercial fisheries into three fundamental types based on design, data requirements and
858 estimable population parameters. *Fish and Fish.* 11(2): 133–148.

859 Punt, A.E., Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian
860 approach. *Rev. Fish Biol. Fisher.* 7: 35–63.

861 Ranta, E., Kaitala, V., Lindström, J., and Helle, E. 1997. The Moran effect and synchrony in
862 population dynamics. *Oikos*, 78(1): 136–142.

863 Rijnsdorp, A.D., and Pastoors, M.A. 1995. Modelling the spatial dynamics and fisheries of
864 North Sea plaice (*Pleuronectes platessa* L.) based on tagging data. *ICES J. Mar. Sci.* 52: 963–
865 980.

866 Rijnsdorp, A.D., Van Beek, F.A., Flatman, S., Millner, R.M., Riley, J.D., Giret, M., and De
867 Clerck, R. 1992. Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic. *Neth.*
868 *J. Sea Res.* 29: 173–192.

869 Riou, P., Le Pape, O., and Rogers, S.I. 2001. Relative contributions of different sole and
870 plaice nurseries to the adult population in the Eastern Channel : application of a combined
871 method using generalized linear models and a geographic information system. *Aquat. Living*
872 *Resour.* 14: 125–135.

873 Rivot, E., Prévost, E., Parent, E., and Baglinière, J.L. 2004. A Bayesian state-space modelling
874 framework for fitting a salmon stage-structured population dynamic model to multiple time
875 series of field data. *Ecol. Model.* 179: 463–485.

876 Rivot, E., Prévost, E. 2002. Hierarchical bayesian analysis of capture-mark-recapture data.
877 *Can. J. Fish. Aquat. Sci.* 59: 1768–1784

878 Rochette, S., Huret, M., Rivot, E., and Le Pape, O. 2012. Coupling hydrodynamic and
879 individual-based models to simulate long-term larval supply to coastal nursery areas. *Fish.*
880 *Oceanogr.* 21: 229–242.

881 Rochette, S., Le Pape, O., Vigneau, J., and Rivot, E. 2013. A hierarchical Bayesian model for
882 embedding larval drift and habitat models in integrated life cycles for exploited fish. *Ecol.*
883 *Appl.* 23: 1659–1676.

884 Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., and Le Pape, O. 2010. Effect of
885 nursery habitat degradation on flatfish population: Application to *Solea solea* in the Eastern
886 Channel (Western Europe). *J. Sea Res.* 64: 34–44.

887 Rolland, J.-L., Bonhomme, F., Lagardere, F., Hassan, M., and Guinand, B. 2007. Population
888 structure of the common sole (*Solea solea*) in the Northeastern Atlantic and the Mediterranean
889 Sea: revisiting the divide with EPIC markers. *Mar. Biol.* 151: 327–341.

890 Rooper, C.N., Gunderson, D.R., and Armstrong, D.A. 2004. Application of the concentration
891 hypothesis to English sole in nursery estuaries and potential contribution to coastal fisheries.
892 *Estuaries* 27: 102–111.

893 Ruiz, J., González-Quirós, R., Prieto, L., and Navarro, G. 2009. A Bayesian model for
894 anchovy (*Engraulis encrasicolus*): the combined forcing of man and environment. *Fish.*
895 *Oceanogr.* 18: 62–76.

896 Sackett, D.K., Able, K.W., and Grothues, T.M. 2008. Habitat dynamics of summer flounder
897 *Paralichthys dentatus* within a shallow USA estuary, based on multiple approaches using
898 acoustic telemetry. *Mar. Ecol. Prog. Ser.* 364: 199–212.

899 Savina, M., Lacroix, G., and Ruddick, K. 2010. Modelling the transport of common sole
900 larvae in the southern North Sea: Influence of hydrodynamics and larval vertical movements.
901 *J. Marine Syst.* 81: 86–98.

902 Savina, M., Lunghi, M., Archambault, B., Baulier, L., Huret, M., and Le Pape, O. *in press*.
903 Sole larval supply to coastal nurseries: Interannual variability and connectivity at
904 interregional and interpopulation scales. *J. Sea. Res.*
905 <http://doi.org/10.1016/j.seares.2015.11.010>.

906 Selkoe, K., Henzler, C., and Gaines, S. 2008. Seascape genetics and the spatial ecology of
907 marine populations. *Fish and Fish.* 9: 363–377.

908 Smedbol, R.K., McPherson, A., Hansen, M.M., and Kenchington, E. 2002. Myths and
909 moderation in marine ‘metapopulations’? *Fish Fish.* 3: 20–35.

910 Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and van der Linde, A. 2014. The deviance
911 information criterion: 12 years on. *J. Roy. Statist. Soc. Ser. B.* 76(3): 485–493.

912 Stelzenmuller, V., Schulze, T.F.H.O., and Berkenhagen, J. 2011. Integrating modelling tools
913 to support risk-based decision-making in marine spatial management. *Mar. Ecol. Prog. Ser.*
914 441: 197–212.

915 Strathmann, R.R., Hughes, T.P., Kuris, A.M., Lindeman, K.C., Morgan, S.G., Pandolfi, J.M.,
916 and Warner, R.R. 2002. Evolution of local recruitment and its consequences for marine
917 populations. *B. Mar. Sci.* 70: 377–396.

918 Taylor, N.G., McAllister, M.K., Lawson, G.L., Carruthers, T., and Block, B.A. 2011. Atlantic
919 bluefin tuna: A novel multistock spatial model for assessing population biomass. *PLoS One*
920 6(12): e27693.

921 Tidd, A.N., Vermard, Y., Marchal, P., Pinnegar, J, Blanchard, J.L., Milner-Gulland E.J. 2015.
922 Fishing for space: Fine-scale multi-sector maritime activities influence fisher location choice.
923 *PLoS One* 10(1): e0116335.

924 Tuck, G., and Possingham, H. 1994. Optimal harvesting strategies for a metapopulation. *B.*
925 *Math. Biol.* 56(1): 107–127.

926 Vasconcelos, R., Eggleston, D.B., Le Pape, O., Tulp, I. 2014. Patterns and processes of
927 habitat-specific demographic variability in exploited marine species. *ICES J. Mar. Sci.* 71:
928 638-647.

929 Waples, R.S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in
930 high gene flow species. *J. Hered.* 89: 438–450.

931 Ward, R.D., Woodwark, M., and Skibinski, D.O.F. 1994. A comparison of genetic diversity
932 levels in marine, freshwater, and anadromous fishes. *J. Fish Biol.* 44: 213–232.

933 Warner, R.R., and Cowen, R.K. 2002. Local retention of production in marine populations:
934 Evidence, mechanisms, and consequences. *B. Mar. Sci.* 70: 245–249.

935 Wolfshaar, K. E. van de, HilleRisLambers, R., and Grdmark, A. 2011. Effect of habitat
936 productivity and exploitation on populations with complex life cycles. *Mar. Ecol. Prog. Ser.*
937 438: 175–184.

938 Yau, A.J., Lenihan, H.S., and Kendall, B.E. 2014. Fishery management priorities vary with
939 self-recruitment in sedentary marine populations. *Ecol. Appl.* 24(6): 1490–1504.

940 Ying, Y., Chen, Y., Lin, L., Gao, T., and Quinn, T. 2011. Risks of ignoring fish population
941 spatial structure in fisheries management. *Can. J. Fish. Aquat. Sci.* 68: 2101–2120.

942 **Appendix A**

943 **Equations for the Hierarchical Bayesian Life-cycle Model**

944 The equation below stand for the model considering three loosely connected subpopulations.
945 The model is written in a state-space form that integrates stochasticity in both the process
946 equations of the population dynamics (process errors) and the observation equations
947 (observation errors). Following this logic, the appendix below first provides the equation for
948 the population dynamics and then provides the equation for the observation process.

949 Subscript y denotes the years in the time series, i denotes the nursery sector ($i=1,\dots,5$, with
950 1=Seine, 2=Veys, 3= UK West, 4=Rye, 5=Somme), and r denotes the component of the
951 metapopulation ($r=1,2,3$ with 1=West FR, associated with nursery grounds Seine and Veys;
952 2=UK, associated with nursery grounds UK West and Rye; 3=East FR, associated with
953 nursery ground Somme).

954 Prior distribution or fixed values for parameters are defined in Table A1. The surface of each
955 nursery sector (in km^2) is given in Table A.2.

956 **Process equations**

957 **Eggs and larval drift**

958 The number of settling larvae (i.e., post-larvae) in nursery sector i at year y , $L_{y,i}$, is defined as
959 follows:

$$960 \quad (A.1) \quad L_{y,i} = \sum_{r=1}^3 \omega_{y,r} \cdot D_{y,r,i}$$

961 where $\omega_{y,r}$ is the egg pool for the subpopulation r at year y and $D_{y,r,i}$ is the probability of
962 success for an egg from the egg pool r to reach the nursery sector i at year y (fixed). The egg
963 pool for each year and each subpopulation is calculated from the spawning stock biomass (all
964 fish between age 3 and 15 take part in reproduction; ICES (2010)):

$$965 \quad (A.2) \quad \omega_{y,r} = \sum_{a \geq 3} N_{a,y,r} \cdot pfa \cdot fec_{a,y}$$

966 where pfa is the proportion of females for age class a (known, considered constant over the
967 time series and homogeneous across areas), and $fec_{a,y}$ is the number of eggs per female of
968 age a , calculated from the weight at age $w_{a,y}$ as (ICES, 2010; Rochette et al., 2012):

$$969 \quad (A.3) \quad fec_{a,y} = e^{5.6 + 1.17 * \log(w_{a,y})}$$

970 **Post-larvae to juvenile on nursery grounds, from settlement to summer's end**

971 The expected number of age-0 fish at year y in nursery i , $E(N_{0,y,i})$, is defined from a density
972 dependent lognormally distributed around an expected mean defined from a Beverton-Holt
973 equation parameterized with α_i , the nursery-specific maximum survival rate (estimated); K_i ,

974 the nursery-specific carrying capacity per unit of surface (1000 fish· km⁻², estimated); and S_i,
 975 the surface of nursery sector i (km², fixed; Tab. A.2):

$$976 \quad (A.4) \quad E(N_{0,y,i}) = \frac{\alpha_i \cdot L_{y,i}}{1 + \frac{\alpha_i}{K_i \cdot S_i} \cdot L_{y,i}}$$

977 Unexplained random variations are captured by independent lognormal random noise with the
 978 same variance σ_{BH}^2 for all nurseries (estimated):

$$979 \quad (A.5) \quad N_{0,y,i} = E(N_{0,y,i}) \cdot e^{s_{L,y,i} - 0.5 \cdot \sigma_{BH}^2}$$

980 **Natural mortality of age 0 from summer's end to December**

981 The number of age-1 fish in nursery i, $N_{1,y+1,i}$, is defined as

$$982 \quad (A.6) \quad N_{1,y+1,i} = N_{0,y,i} \cdot e^{-1/3 \cdot M_0} \cdot e^{s_{0,y,i} - 0.5 \cdot \sigma_0^2}$$

983 where $N_{0,y,i}$ is the number of age-0 fish in the nursery i, M_0 is the annual natural mortality
 984 rate at age 0 (fixed) and $s_{0,y,i}$ is normal environmental noise with variance σ_0^2 (estimated).

985 **Natural and fishing mortality at age 1 and emigration from nursery to adult population**

986 The number of age-2 fish in nursery i at the very beginning of year $y + 1$, $N_{2,y+1,i}$, is defined
 987 as

$$988 \quad (A.7) \quad N_{2,y+1,i} = N_{1,y,i} \cdot e^{-Z_{1,y,i}} \cdot e^{s_{1,y,i} - 0.5 \cdot \sigma_p^2}$$

989 where $Z_{1,y,i} = M_1 + F_{1,y,r}$ is the total mortality, M_1 is the annual natural mortality rate at age
 990 1 (fixed), $F_{1,y,r}$ is the fishing mortality in subpopulation r associated with nursery i
 991 (estimated), and $s_{1,y,i}$ is normal environmental noise with variance σ_p^2 .

992 Age-2 fish leave nurseries at the very beginning of the year and are supposed to contribute
 993 directly to the subpopulation r adjacent to the nursery. Fish from the Seine and Veys nurseries
 994 contribute to subpopulation $r=1$ =West FR; UK West and Rye nurseries contribute to
 995 subpopulation $r=2$ =UK; and the Somme nursery contributes to subpopulation $r=3$ =East FR.
 996 Starting from $N_{2,y+1,i}$ as defined in eq. (A.7), the number of age-2 fish in each subpopulation
 997 r , $N_{2,y+1,r}$ (note the subscript r and not i), is defined as follows:

$$998 \quad (A.8) \quad \begin{cases} N_{2,y+1,r=1} = \sum_{i=1}^{i=2} N_{2,y+1,i} \\ N_{2,y+1,r=2} = \sum_{i=3}^{i=4} N_{2,y+1,i} \\ N_{2,y+1,r=3} = N_{2,y+1,i=5} \end{cases}$$

999 **Natural and fishing mortality at the adult stage**

1000 The number of fish from age 2 to 15 then follows the classical dynamics:

$$1001 \quad (A.9) \quad N_{a+1,y+1,r} = N_{a,y,r} \cdot e^{-Z_{a,y,r}} \cdot e^{s_{a,y,r} - 0.5 \cdot \sigma_p^2}$$

1002 where $N_{a,y,r}$ is the number of fish of age a in component r at year y , $Z_{a,y,r}$ is the total
 1003 mortality rate and $s_{a,y,r}$ is a normal environmental noise with variance σ_p^2 . All remaining fish
 1004 are assumed to die at age 15.

1005 **Model for total mortality Z**

1006 $Z_{a,y,r}$ is defined as the sum of natural mortality M_a , considered constant across years and
 1007 subpopulations (Tab. A.1), and fishing mortality $F_{a,y,r}$. For any given age, year and
 1008 subpopulation r , the expected mean of the fishing mortality is defined as $E(F_{a,y,r}) = S_a \cdot E_{y,r}$
 1009 with S_a as an age-specific selectivity (logistic function considered homogeneous in time and
 1010 space, estimated, Tab. A.1) and $E_{y,r}$ as the fishing effort specific to each year and
 1011 subpopulation. The time variability of fishing effort $E_{y,r}$ was a priori modeled as a random
 1012 walk in the log-scale (Tab. A.1). Additional random variability of $F_{a,y,r}$ around the expected
 1013 mean $E(F_{a,y,r})$ was captured through a random gamma hierarchical structure with the
 1014 coefficient of variation CV_F (Tab A.1).

1015 **Observation equations**

1016 **Juvenile abundance indices**

1017 The abundance indices of age-0 and age-1 juveniles in nursery i are considered as lognormal
 1018 random observations of abundance $N_{0,y,i}$ and $N_{1,y,i}$, respectively:

$$1019 \quad (A.10) \quad I_{0,y,i} = q_0 \cdot N_{0,y,i} \cdot e^{s_{I_{0,y,i}} - 0.5 \cdot \sigma_{I_{juv}}^2}$$

$$1020 \quad (A.11) \quad I_{1,y,i} = q_1 \cdot N_{1,y,i} \cdot e^{s_{I_{1,y,i}} - 0.5 \cdot \sigma_{I_{juv}}^2}$$

1021 with q_0 and q_1 the age-specific catchability, $s_{I_{0,y,i}}$ and $s_{I_{1,y,i}}$ independent normal random
 1022 noise with the same observation error variance $\sigma_{I_{juv}}^2$ (estimated).

1023 **Adult abundance indices**

1024 In the model considering three subpopulations, three time series of abundance indices (AI) of
 1025 age-2 to age-15 fish are used: CPUEs from the UK and Belgium commercial fleet (UKBCT
 1026 and BEBCT, respectively), both of which are available on the scale of the entire Eastern
 1027 Channel, and UK bottom-trawl surveys available for each subpopulations ($r = 1,2,3$). One
 1028 observation equation is written for each AI, with each observation equation contributing to the
 1029 whole likelihood function. The same general form of observation equation is used for all AIs,
 1030 which are all considered as lognormal random observations of the abundance at age but with
 1031 parameters specific for the fleet (UKBCT, BEBCT, UKBTS) age, year (and eventually
 1032 subpopulation for UKBTS):

$$1033 \quad (A.12) \quad AI_{fleet}^{a,y,(r)} = q_{fleet} \cdot S_a \cdot N_{a,y,i,(r)} \cdot e^{s_{fleet,a,y,(r)} - 0.5 \cdot \sigma^2}$$

1034 where $AI_{fleet}^{a,y,(r)}$ is the observed AI of age a at year y on a different spatial scale (in
 1035 subpopulations r for the UKBTS survey; in the whole EC for other indices), q_{fleet} is the fleet-

1036 specific catchability, S_a is the age-specific selectivity (considered homogeneous among fleets),
 1037 and $s_{\text{fleet},a,y,(r)}$ is independent random noise with the same observation error variance σ_{Ad}^2
 1038 (estimated; homogeneous among fleets).

1039 Catches-at-age aggregated on the scale of the Eastern Channel

1040 Catches-at-age predicted by the model ($H_{a,y,r}$) were calculated for each subpopulation with
 1041 the standard Baranov equation:

$$1042 \quad (A.13) \quad H_{a,y,r} = N_{a,y,r} \cdot \left(\frac{F_{a,y,r}}{F_{a,y,r} + M_a} \right) \cdot (1 - e^{-(F_{a,y,r} + M_a)})$$

1043 Annual catches-at-age ($C_{a,y}$; observed) were available from stock assessment reports only on
 1044 the scale of the Eastern Channel; however, they were not available separately for the three
 1045 subpopulations. Catches-at-age predicted by the model were then first aggregated at the scale
 1046 of the Eastern Channel ($H_{a,y} = \sum_{r=1}^3 H_{a,y,r}$) and considered observed with lognormal errors:

$$1047 \quad (A.14) \quad C_{a,y} = H_{a,y} \cdot e^{s_{Ca,y} - 0.5 \cdot \sigma_c^2}$$

1048 where $s_{Ca,y}$ are independent normal random noise with observation error variance σ_c^2
 1049 (estimated).

1050 Spatial repartition of catches (weight) among subpopulations

1051 A likelihood function for the catch weight ratio per subpopulation ($pw_{t,r}$, $\sum_{r=1:3} pw_{t,r} = 1$)
 1052 was also incorporated into the model. The catch weight ratio was originally available using
 1053 the ICES statistical rectangle from 2003 to 2011; however, it was here aggregated at the scale
 1054 of the three areas associated with each subpopulation. Before 2003, the catch weight ratio per
 1055 subpopulation was derived from the catch ratio per country (weight; known for the entire time
 1056 series) combined with the average repartition of catches (weight) among the three areas
 1057 calculated for each country over the most recent time series 2003-2011. This procedure only
 1058 assumes a constant spatial repartition of national fleets among the three areas and is a
 1059 reasonable hypothesis because no major change in the national fleet strategies has been
 1060 observed between 1982 and 2011 (Y. Vermard, com. Pers.). The catch ratio predicted by the
 1061 model ($\pi_{y,r}$) was calculated from the catches-at-age predicted by the model ($C_{a,y,r}$) and the
 1062 weight-at-age ($w_{a,y}$; observed). A Dirichlet likelihood function was used to capture
 1063 observation errors between the observed and predicted catch ratio. The predicted catch weight
 1064 ratio was scaled to mimic the precision that would be obtained with a sample of 500 tones:

$$1065 \quad (A.15) \quad (pw_{t,r=1}, pw_{t,r=2}, pw_{t,r=3}) \sim \text{Dirichlet}(500 \times (\pi_{t,r=1}, \pi_{t,r=2}, \pi_{t,r=3}))$$

1066 Parameters and priors

1067 Prior distributions or fixed values of parameters are given in Tab. A1.

1068 Following Rochette et al. (2013), informative priors were set for parameters of the selectivity
 1069 S_a , based on ICES (2013). The priors on the carrying capacity of nursery sectors, K_i 's, were
 1070 weakly informative in the sense of Gelman (2009), i.e., it allows the data to speak while being
 1071 strong enough to exclude unrealistic values (the 90% percentile of the prior predictive

1072 distribution is more than 100 times greater than the highest estimated density in nurseries of
 1073 the Bay of Biscay; Le Pape et al., 2003a).

1074 Informative priors were set on the nursery-specific maximum survival rates α_i . Taking away
 1075 the EC sole dataset from the database used for the meta-analysis in Archambault et al. (2014),
 1076 the posterior predictive distribution of α was derived and considered to build an informative
 1077 prior for this study. The method developed in Archambault et al. (2014) provides a predictive
 1078 distribution for the slope at origin calculated from a Beverton-Holt relationship calculated
 1079 from egg-to-egg (denoted α_{meta}). By contrast, parameter α in our model (denoted α_{HBM})
 1080 stands for the survival rate from settled larvae to 0+ juveniles (in September). To transfer the
 1081 information from α_{meta} to α_{HBM} , average demographic parameters specific to the Eastern
 1082 Channel were used to complete the life cycle from the age-0 juveniles in September to eggs:

$$1083 \quad (A.16) \quad S_{\omega-L} \cdot \alpha_{HBM} \cdot e^{-M_0 \cdot 4/12} \cdot \overline{Fec} \cdot SPR_{F=0} = \alpha_{meta}$$

1084 with $S_{\omega-L}$ as the average eggs to post-larvae survival, \overline{Fec} as the average fecundity, $SPR_{F=0}$
 1085 the spawning biomass produced in the absence of fishing and $e^{-M_0 \cdot 4/12}$ as the natural
 1086 mortality from observation in September to recruitment at age 1 in January. Finally, because
 1087 the meta-analysis of Archambault et al. (2014) was derived using recruitment estimated by
 1088 ICES (recruitment at age 1 back-calculated from age 2), we also took into account the
 1089 differences between the mortality used by ICES ($M_{1ICES}=0.1$) and the one used in our model
 1090 ($M_{1HBM}=2.6$). The following final equation was then used to scale the posterior predictive of
 1091 α_{meta} to obtain the informative prior of α_{HBM} :

$$1092 \quad (A.17) \quad \alpha_{HBM} = \frac{\alpha_{meta}}{S_{\omega-L} \cdot e^{-M_0 \cdot 4/12} \cdot \overline{Fec} \cdot SPR_{F=0}} \cdot e^{M_{1HBM} - M_{1ICES}}$$

1093

1094 Table A.1. Prior distribution (or fixed values) for the parameters of the Hierarchical Bayesian
 1095 Life-cycle Model.

Parameters	Value / prior / structure	Description
M_a	Age 0: 1.5; Age 1: 2.6 ; Age 3-11: 0.1 ; Age 12: 0.2 ; Age 13: 0.3 ; Age 14: 0.4 ; Age 15: 0.5	Natural mortality at age a (y^{-1})
S_a	$a_{50} \sim \text{Gamma}(E = 3, CV = 0.1)$ $\delta \sim \text{Gamma}(E = 1, CV = 0.2)$	Age-specific gear selectivity. Logistic curve parameterized with (a_{50}, δ). a_{50} : the age at which $S_a = 0.5$; δ : the difference (in years) between $S_a = 0.25$ and $S_a = 0.75$. S_a is scaled to 1 for $a=15$.
σ_p^2	$\sigma_p^2 = 0.001$	Variance of process errors on the dynamics of adult stages (fixed to a very low value)
$E_{y,r}$	$\log(E_{y=1,r}) \sim \text{Norm}(E = 0, \sigma = \sqrt{10})$ $\log(E_{y,r}) \sim \text{Norm}(E = \log(E_{y-1,r}), \sigma_E)$ $\sigma_E \sim \text{Unif}(0.01, 0.5)$	Fishing effort Prior defined as a random walk in the log- scale
$F_{a,y,r}$	$F_{a,y,r} \sim \text{Gamma}(E = E_{y,r} \cdot S_a, CV_F)$ $CV_F \sim \text{Unif}(0,1)$	Fishing mortality Exchangeable hierarchical structure
α_i	$\log(\alpha_i) \sim \text{Norm}(E = \mu_{\log\alpha}, \sigma = \sigma_{\log\alpha}), [0]$ $\mu_{\log\alpha} \sim \text{Norm}(E = -3, \sigma = \sqrt{0.1})$ $\sigma_{\log\alpha} \sim \text{Unif}(0, 2.5)$	Nursery-specific maximum survival rates. Hierarchical structure with informative priors derived from Archambault et al. (2014)
K_i	$K_i \sim \text{Norm}(E = \mu_K, \sigma = \sigma_K) 1_{>0}$ $\mu_K \sim \text{Norm}(E = 100, \sigma = 100)$ $\sigma_K \sim \text{Unif}(10, 300)$	Nursery-specific carrying capacity per unit of surface (1000 fish·km ²). Hierarchical structure with weakly informative priors
σ_{BH}^2	$\log(\sigma_{BH}^2) \sim \text{Unif}(-10, 10)$	Variance of process errors on the post- larvae to juvenile BH relationship
σ_0^2	$\log(\sigma_0^2) \sim \text{Unif}(-10, 10)$	Variance of process errors from age-0 to age-1 fish
$\sigma_{I_{juv}}^2$	$\sigma_{I_{juv}}^2 \sim \text{Unif}(-10, 10)$	Variance of observation errors on surveys of juveniles on nurseries
$\sigma_{I_{Ad}}^2$	$\sigma_{I_{Ad}}^2 \sim \text{Unif}(-10, 10)$	Variance of observation errors on all abundance indices of adults (UKCBT, BECBT, UKBTS)
σ_c^2	$\sigma_c^2 \sim \text{Unif}(-10, 10)$	Variance of observation errors on catches
q_0	$\log(q_0) \sim \text{Unif}(-10, 10)$	Catchability of age-0
q_1	$\log(q_1) \sim \text{Unif}(-10, 10)$	Catchability of age-1
q^{fleet}	$\log(q^{fleet}) \sim \text{Unif}(-10, 10)$	Catchability related to abundance indices of adults (fleet: UKCBT, BECBT, UKBTS)

1096

1097

1098 Table A.2. Surface of nursery sector i (km^2). All surfaces are derived from the habitat
 1099 suitability model in Rochette et al. (2010).

Subpopulation	Nursery sector	Surface (km^2)
West Fr ($r = 1$)	Seine ($i = 1$)	967
	Veys ($i = 2$)	320
UK ($r = 2$)	UK West ($i = 3$)	1,650
	Rye ($i = 4$)	504
East FR ($r = 3$)	Somme ($i = 5$)	1,680

1100

1101

1102 **Appendix B**

1103 **Catches at equilibrium as a function of fishing mortality**

1104 Empirical equilibrium curves were obtained by Monte Carlo simulations. The population was
1105 simulated with constant F in time and space during 200 years to reach an equilibrium state.
1106 Results obtained by varying F in a wide range (from 0 to 2, with a step of 0.01) were used to
1107 empirically construct the equilibrium curve relating Catches and SSB at equilibrium, thus
1108 enabling the estimation of management reference points such as B_{MSY} , F_{MSY} and C_{MSY} . Drift
1109 and survival parameters for eggs and larvae were considered constant during the simulations
1110 and set to their average values (1982-2007). In the model considering three subpopulations,
1111 reference equilibrium points for each subpopulation r (denoted $B_{MSY,r}$, $F_{MSY,r}$ and $C_{MSY,r}$)
1112 were estimated conditionally by fixing the fishing pressure for the two other subpopulations
1113 equal to the estimates averaged over the last five years of the data series (2007-2011).

1114 Monte Carlo simulations were run to account for both process errors and parameters
1115 uncertainty. For a given value of F , the population dynamics was simulated over 200 years,
1116 including process error. The equilibrium (ergodic) state is considered after 100 years of
1117 simulation and the process error was integrated out by considering the distribution of the
1118 results between year 101 and 200. To integrate the parameter uncertainty, the procedure was
1119 repeated 1,500 times with 1,500 sets of parameters directly drawn in the joint posterior
1120 distribution of model parameters, ensuring that the statistical covariance structure between the
1121 parameters is fully accounted for (Punt and Hilborn, 1997; Parent and Rivot, 2013).

1122

1 **Supplementary Material S1**

2 **MCMC simulations and convergence diagnosis**

3 Bayesian posterior distributions were approximated via Monte Carlo Markov Chain (MCMC)
4 methods using the JAGS software (<http://mcmc-jags.sourceforge.net> ; release 3.4.0) through
5 the Rjags (www.Rproject.org) package. The same procedure detailed below was used for all
6 model configurations.

7 Following the seminal idea of Meyer and Millar (1999) who proposed a parameterization of
8 the biomass dynamic production model in terms of biomass relative to the carrying capacity
9 to improve the convergence speed of the MCMC sampler, equations for the cohort dynamics
10 (eqs. A.7 and A.9) in the JAGS code was written with numbers at age relative to the
11 recruitment of the cohort measured at age 1.

12 Three MCMC-independent chains with dispersed initialization points were used. For each
13 chain, the first 10,000 iterations were first discarded. The three chains were run during 10^6
14 iterations. Autocorrelation in the MCMC sampling process was rather high (> 0.5 at lag 50
15 for almost all variables). To reduce the autocorrelation in the sample used for inferences, one
16 out of 100 iterations was kept (thinning = 100). The autocorrelation in the resulting thinned
17 chained was less than 0.2 for all variables. Final inferences were derived from a sample of
18 $3 \times 10,000$ iterations resulting from merging the three chains.

19 Convergence of the MCMC chains was assessed using the Gelman-Rubin (Brooks and
20 Gelman, 1998) and the Heidelberg and Welch tests as implemented in the R Coda package
21 (gelman.diag() and heidel.diag() function, respectively). The Gelman-Rubin tests for the
22 mixing of multiple chains. It is based on the computation of the R-ratio that compares within
23 and between-chain variances. Values of the R-ratio substantially above 1 indicate lack of

24 convergence. The Heidelberg and Welch diagnostic is a “single chain diagnostic” that
25 calculates a statistics to test for the null hypothesis that the chain is from a stationary
26 distribution.

27 For both models, trace plot display good mixing for all variables (see examples in Fig. S1.1).

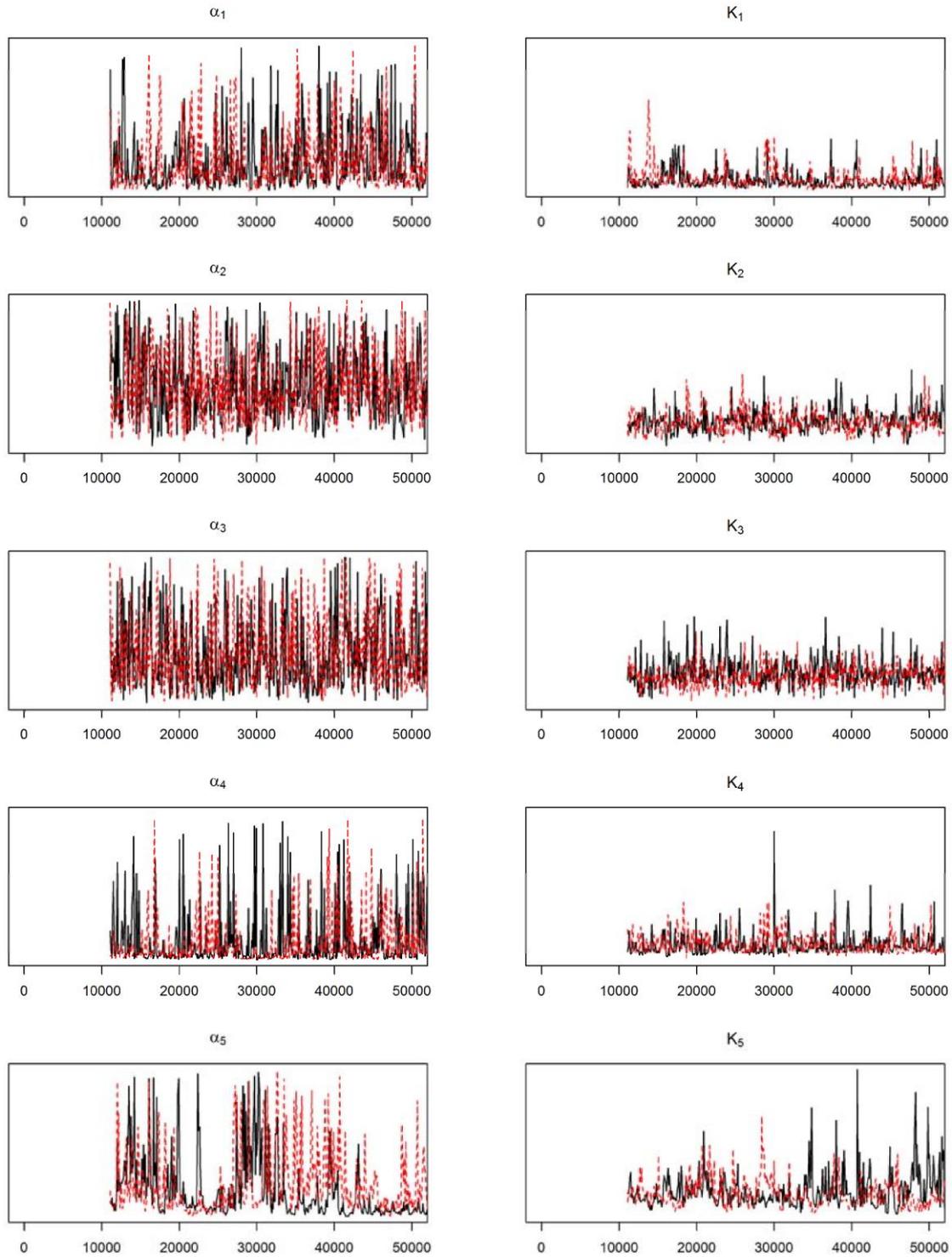
28 All variables pass the two convergence diagnostics. The R ratio of the Gelman Rubin test was

29 < 1.05 for all variables and p-values of the Heidelberg test were all < 0.05 . However, it is

30 worth noting that convergence was more difficult to achieve for the parameters of the

31 BevHolt density dependence recruitment process associated with nursery sector “Bay of Veys”

32 for which the juveniles abundance indices are only available for 3 years.



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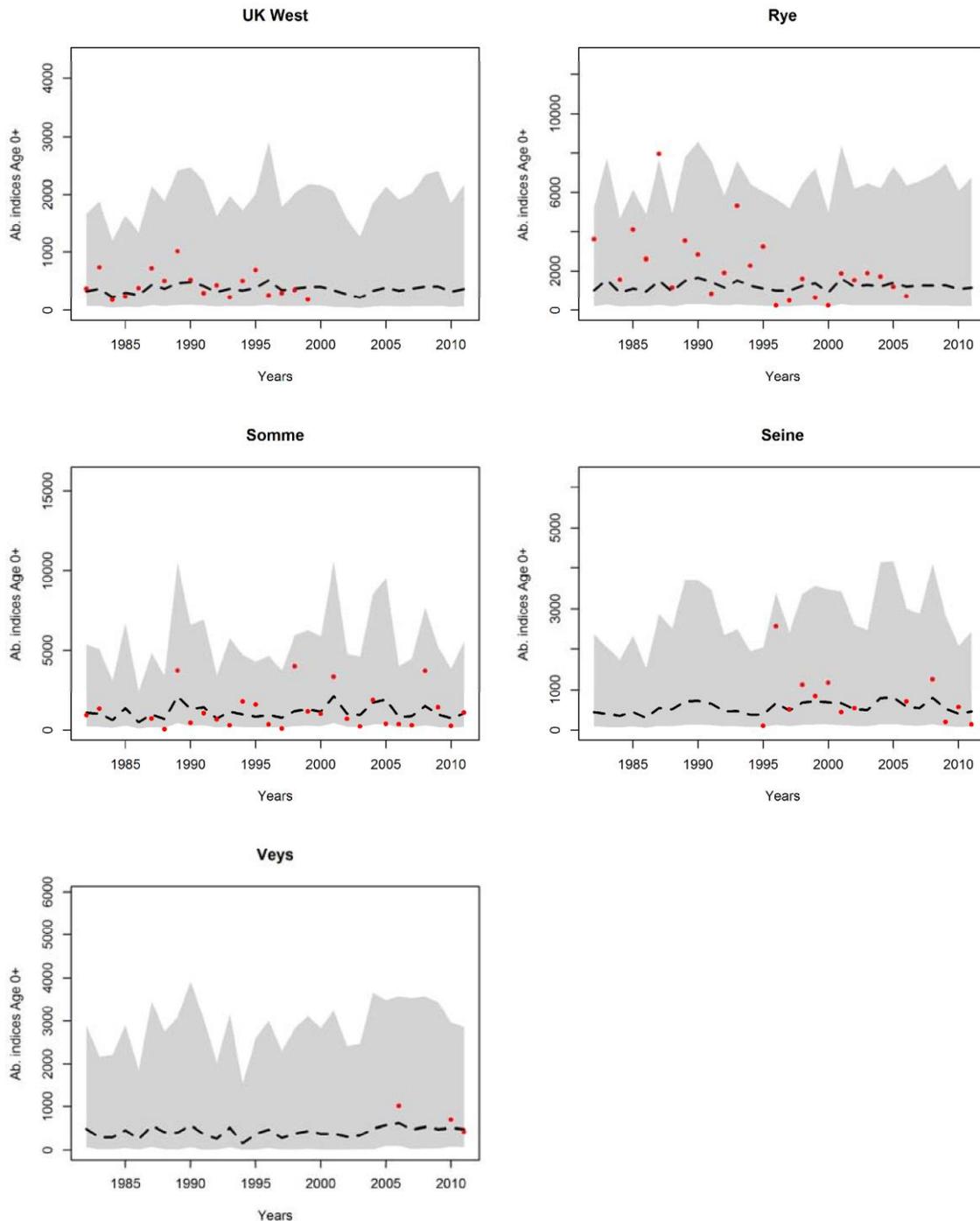
34 Fig. S1.1. Trace plots of Beverton-Holt parameters (α_i, K_i) in the 5 nursery sectors (for the
 35 model considering three sub-populations). To keep the figure as clear as possible, trace plots
 36 are drawn for two independent chains (out of three) and for the first 100 000 iterations (out of
 37 a total of 10^6). But final inferences have been drawn from longer MCMC chains of length 10^6 .

38

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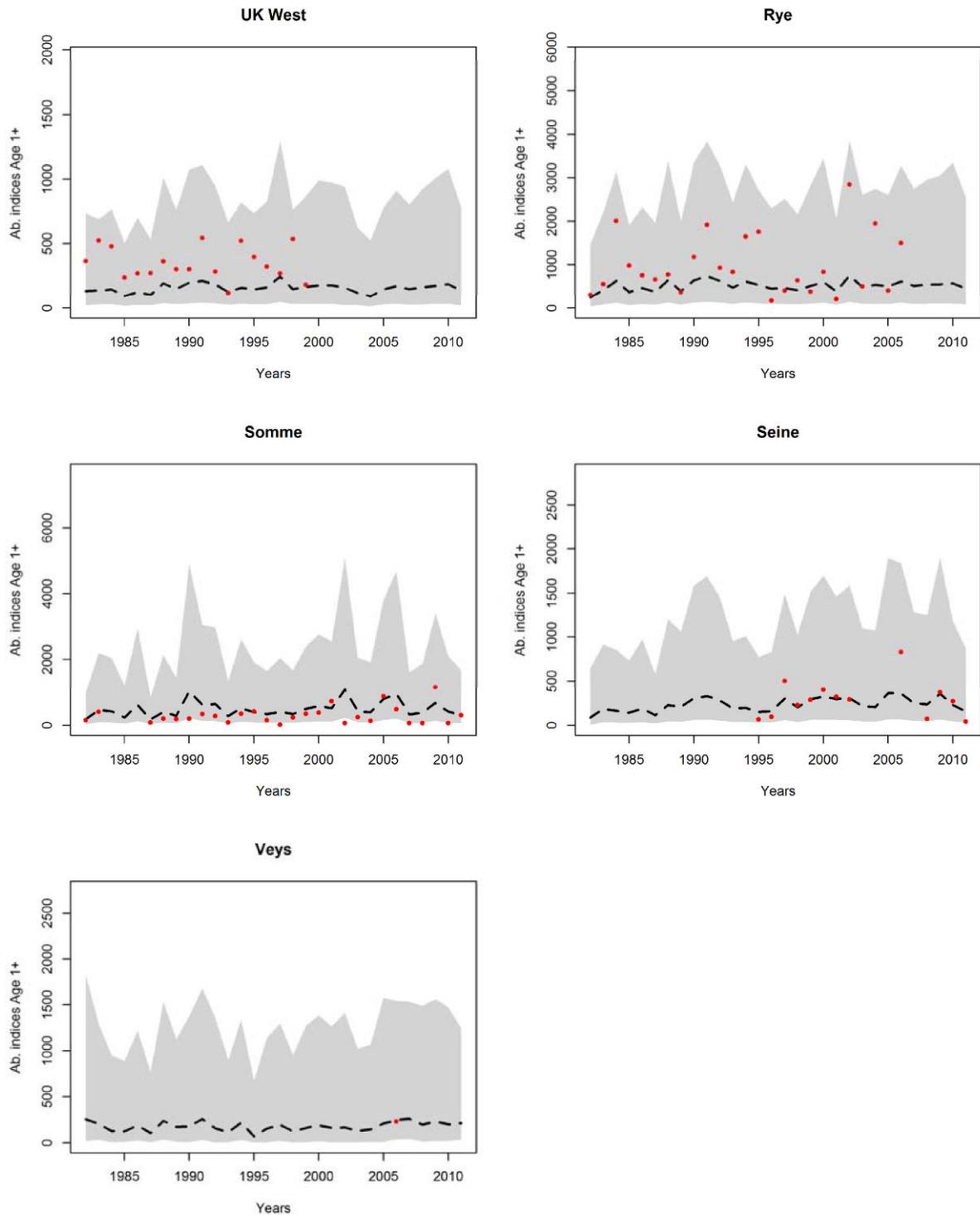
40 Supplementary Material S2

41 **Posterior predictive distribution for the different sources of observations in the model**
42 **considering three subpopulations.**



43

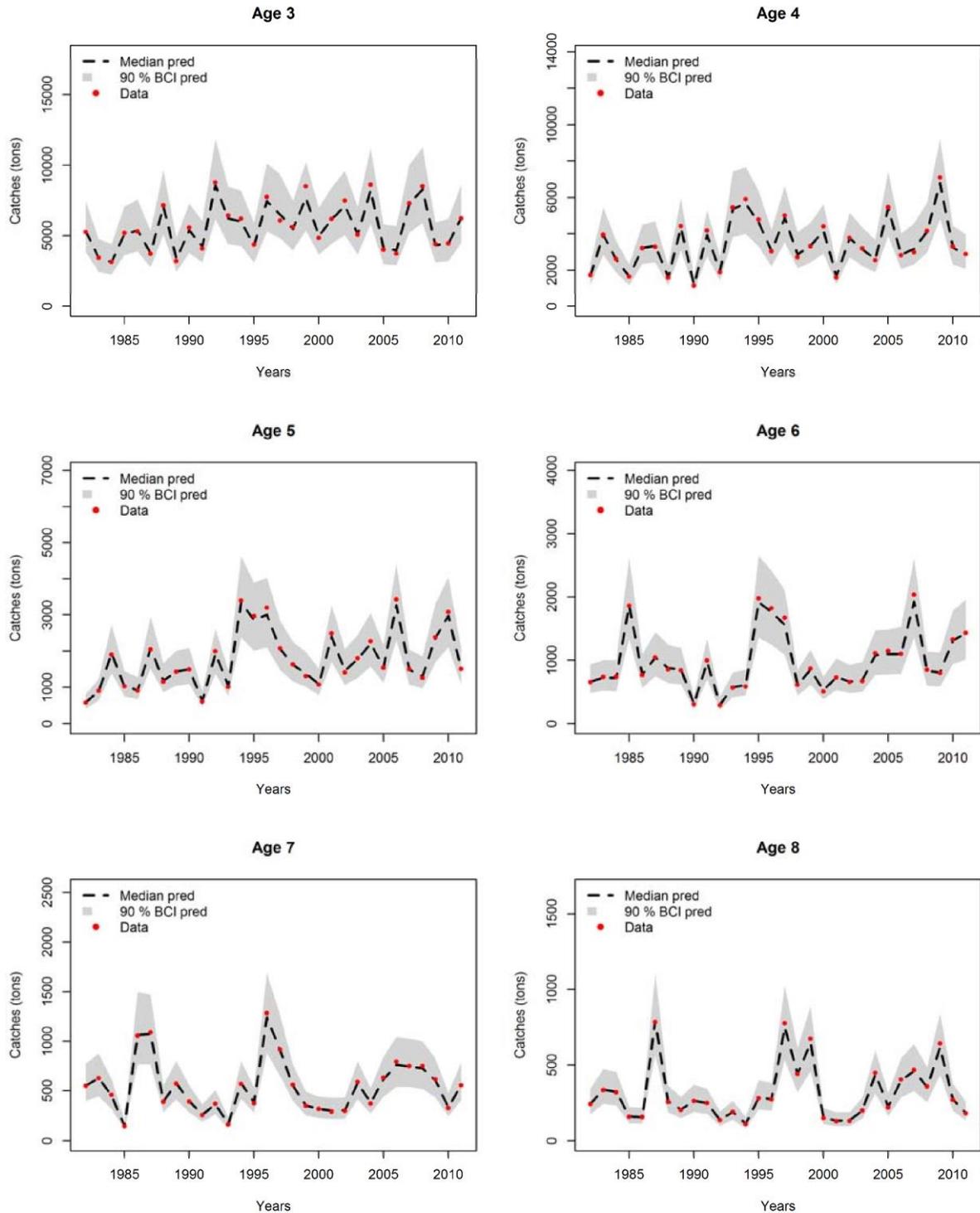
44 Fig. S2.1. Posterior predictive distribution and observations for Age-0 abundance indices in
45 the five nursery sectors. Dots : Observations; Dotted lines: medians of the posterior predictive
46 distribution; Shaded areas: 90% Bayesian credible intervals for the posterior predictive
47 distribution.



48

49 Fig. S2.2. Posterior predictive distribution and observations for Age-1 abundance indices in
 50 the five nursery sectors. Dots : Observations; Dotted lines: medians of the posterior predictive
 51 distribution; Shaded areas: 90% Bayesian credible intervals for the posterior predictive
 52 distribution.

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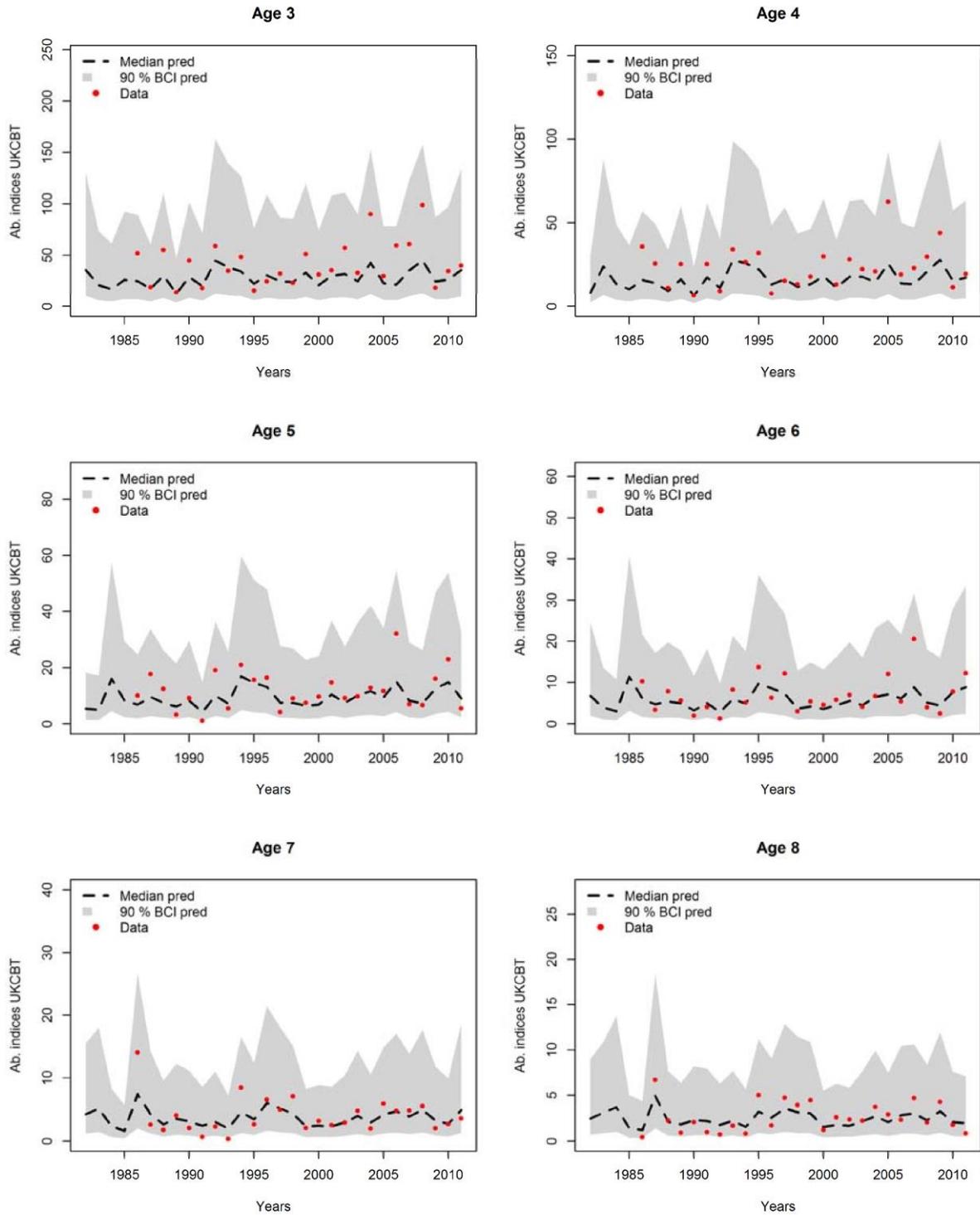


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55 Fig. S2.3. Posterior predictive distribution and observations for catches (tons) of age-3 to age-
 56 8 fish in the Eastern Channel. Dots : Observations; Dotted lines: medians of the posterior
 57 predictive distribution; Shaded areas: 90% Bayesian credible intervals for the posterior
 58 predictive distribution.

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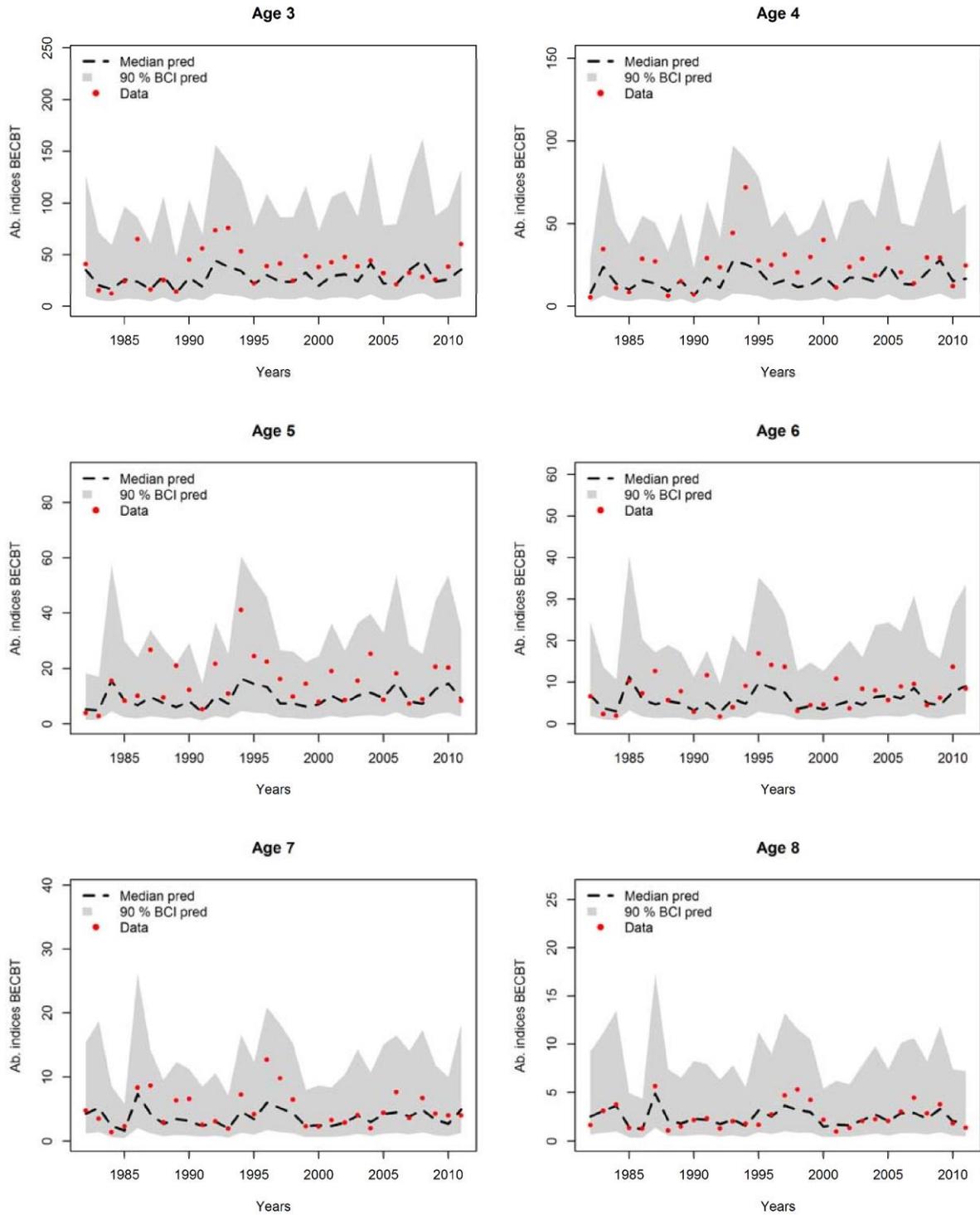


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62 Fig. S2.4. Posterior predictive distribution and observations for commercial abundance
 63 indices UKCBT (age-3 to age-8 fish) in the Eastern Channel. Dots : Observations; Dotted
 64 lines: medians of the posterior predictive distribution; Shaded areas: 90% Bayesian credible
 65 intervals for the posterior predictive distribution.

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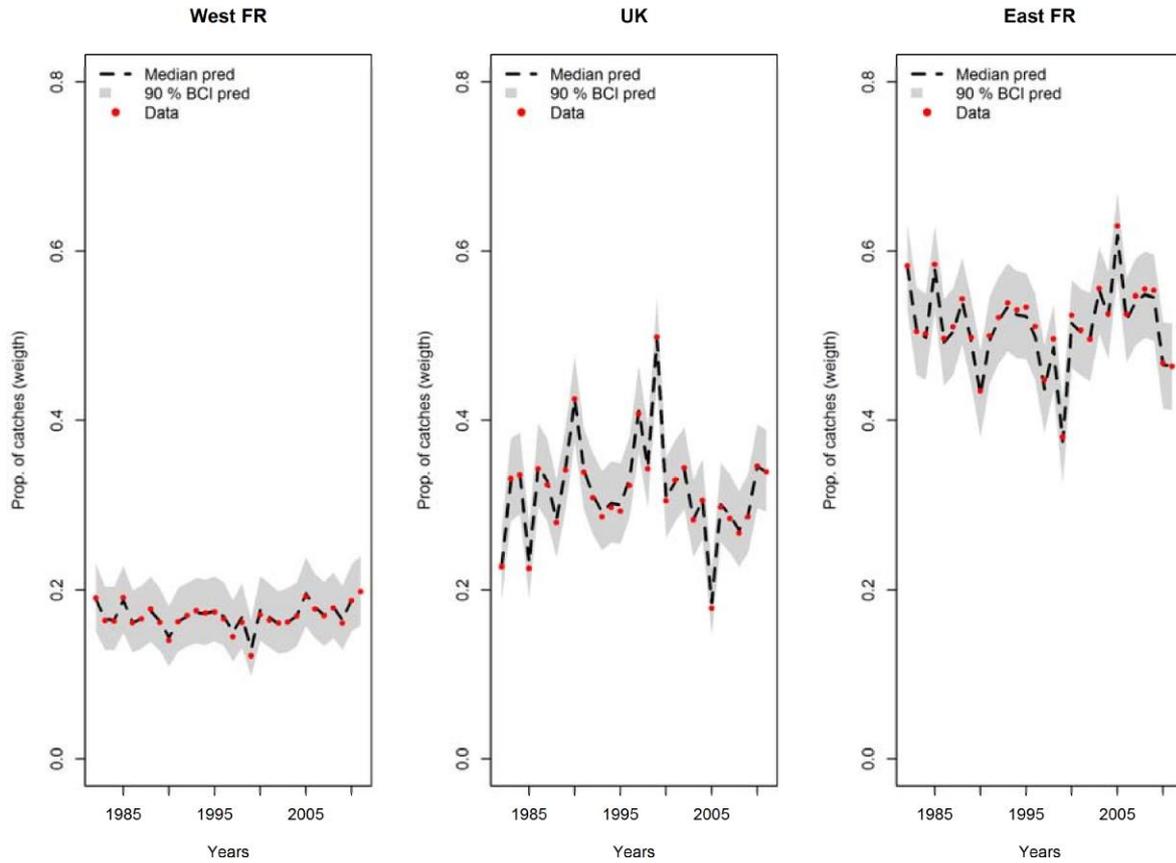


68

69 Fig. S2.5. Posterior predictive distribution and observations for commercial abundance
 70 indices BECBT (age-3 to age-8 fish) in the Eastern Channel. Dots : Observations; Dotted
 71 lines: medians of the posterior predictive distribution; Shaded areas: 90% Bayesian credible
 72 intervals for the posterior predictive distribution.

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76 Fig. S2.6. Posterior predictive distribution and observations for the proportion of catches
 77 (total weight) in the three areas considered in the Eastern Channel. Dots : Observations;
 78 Dotted lines: medians of the posterior predictive distribution; Shaded areas: 90% Bayesian
 79 credible intervals for the posterior predictive distribution.

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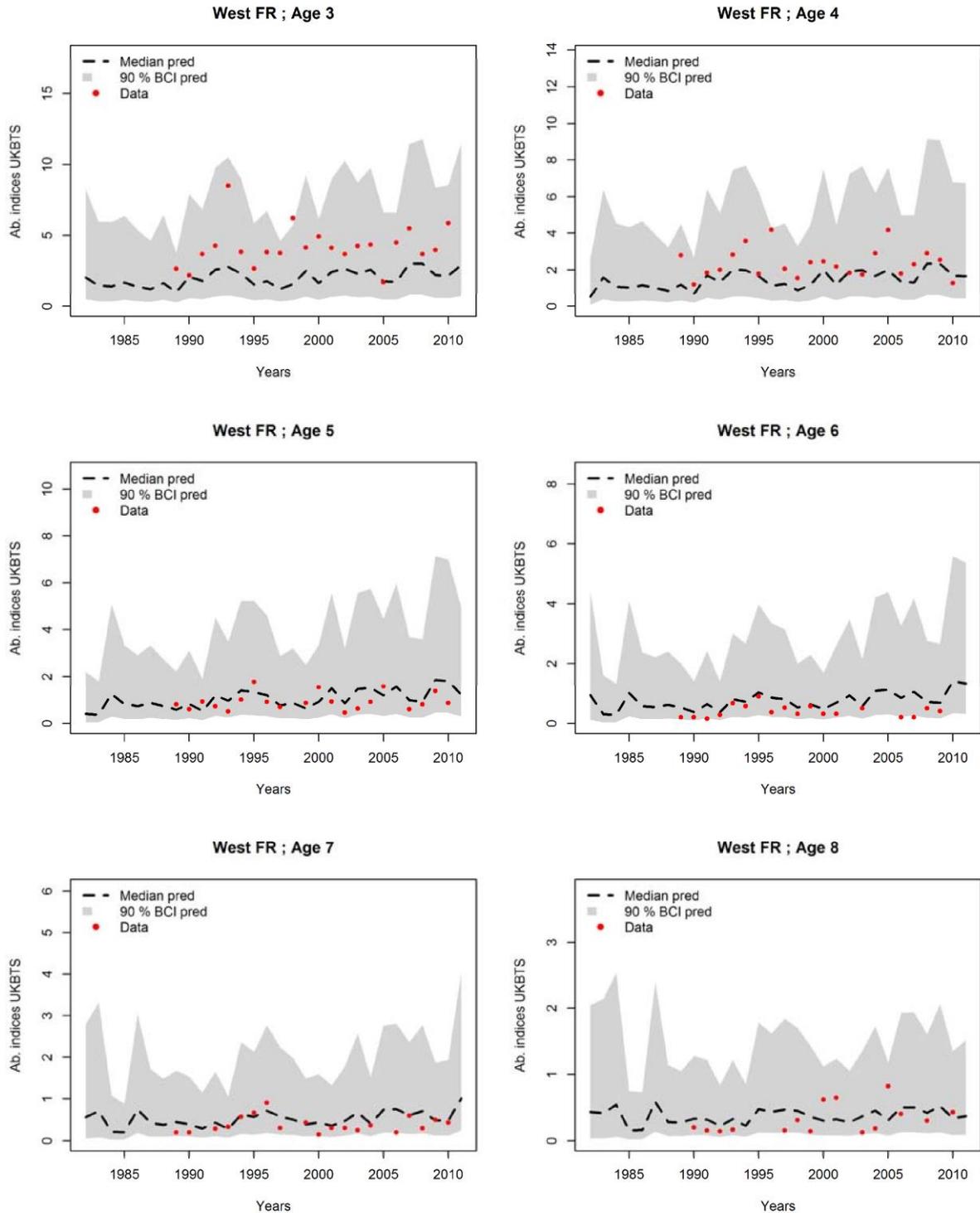
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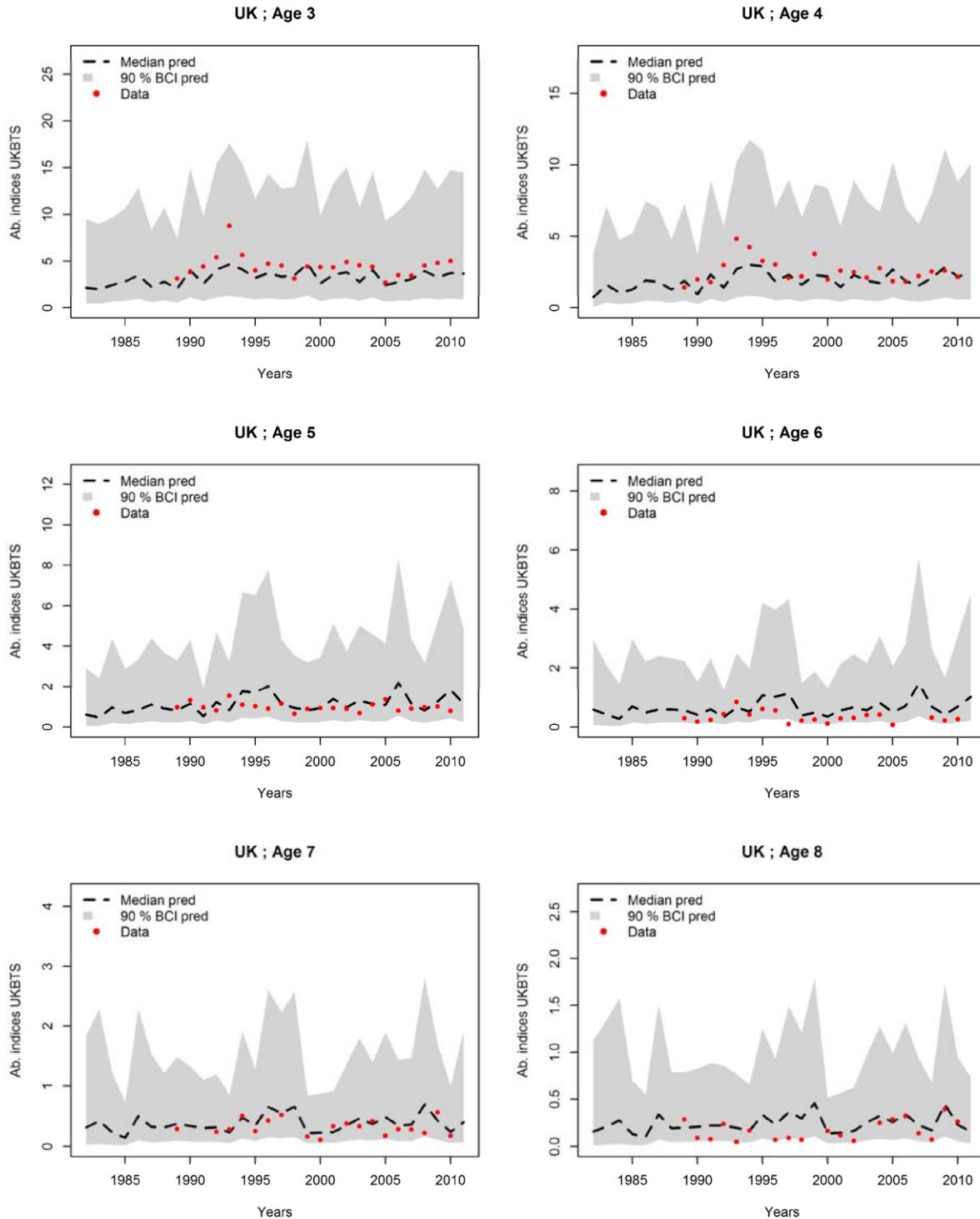


92

93 Fig. S2.7. Posterior predictive distribution and observations for the spatial scientific
 94 abundance indices in the West FR area (age-3 to age-8). Dots : Observations; Dotted lines:
 95 medians of the posterior predictive distribution; Shaded areas: 90% Bayesian credible
 96 intervals for the posterior predictive distribution.

97

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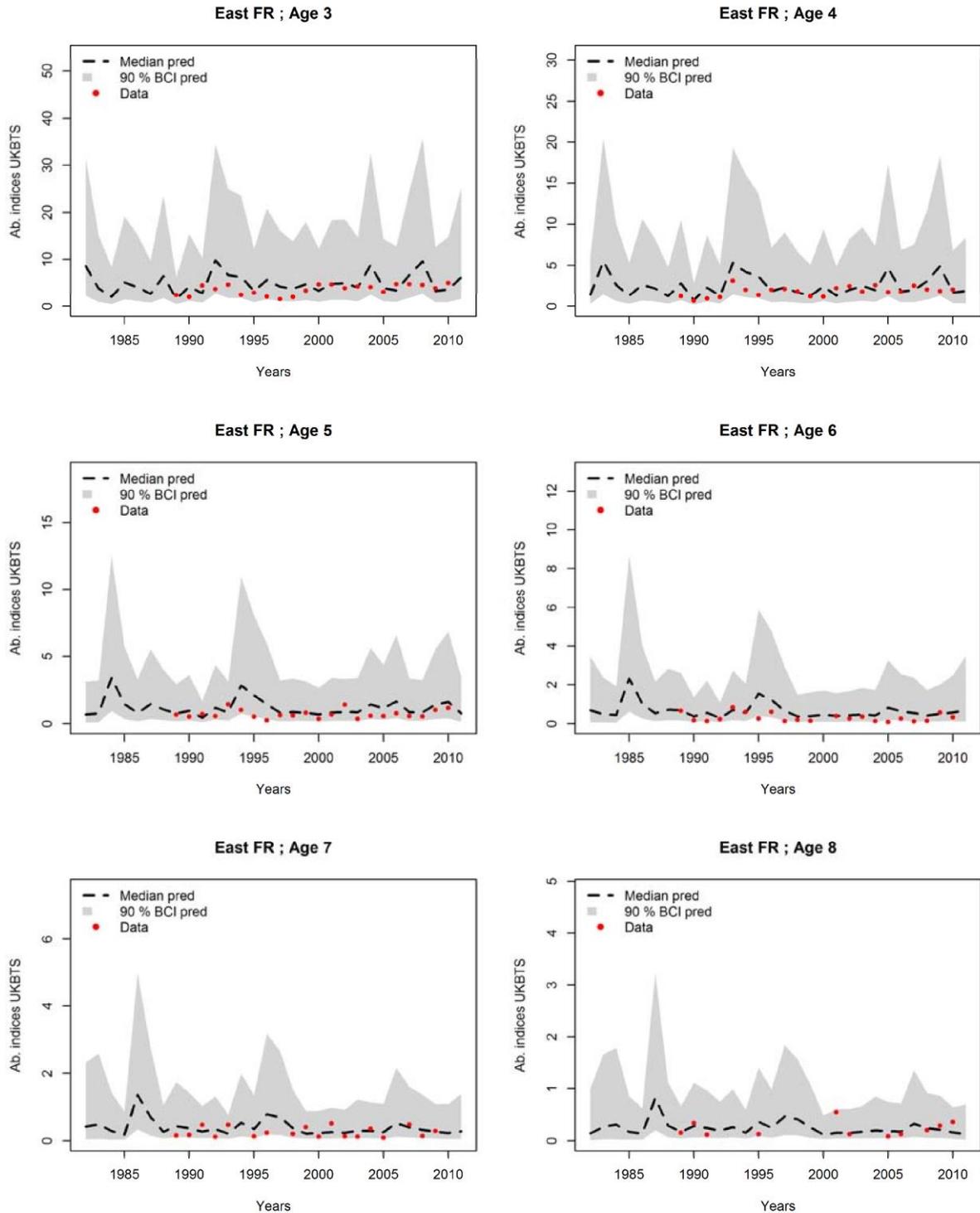


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100 Fig. S2.8. Posterior predictive distribution and observations for the spatial scientific
 101 abundance indices in the UK area (age-3 to age-8). Dots : Observations; Dotted lines:
 102 medians of the posterior predictive distribution; Shaded areas: 90% Bayesian credible
 103 intervals for the posterior predictive distribution.

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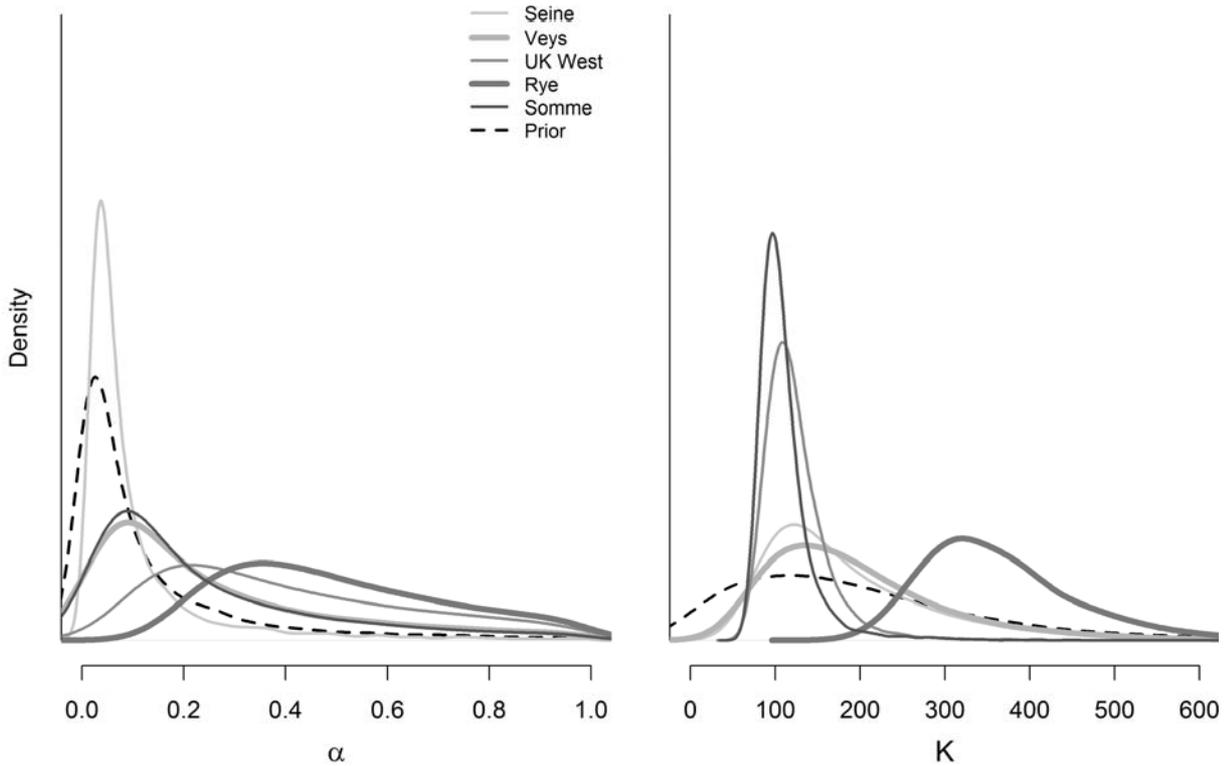
107 Fig. S2.9. Posterior predictive distribution and observations for the spatial scientific
 108 abundance indices in the East FR area (age-3 to age-8). Dots : Observations; Dotted lines:
 109 medians of the posterior predictive distribution; Shaded areas: 90% Bayesian credible
 110 intervals for the posterior predictive distribution.

111

112 **Supplementary Material S3**

113 **Posterior distributions of estimated parameters for the model considering one single**
114 **populations and the model considering three subpopulations.**

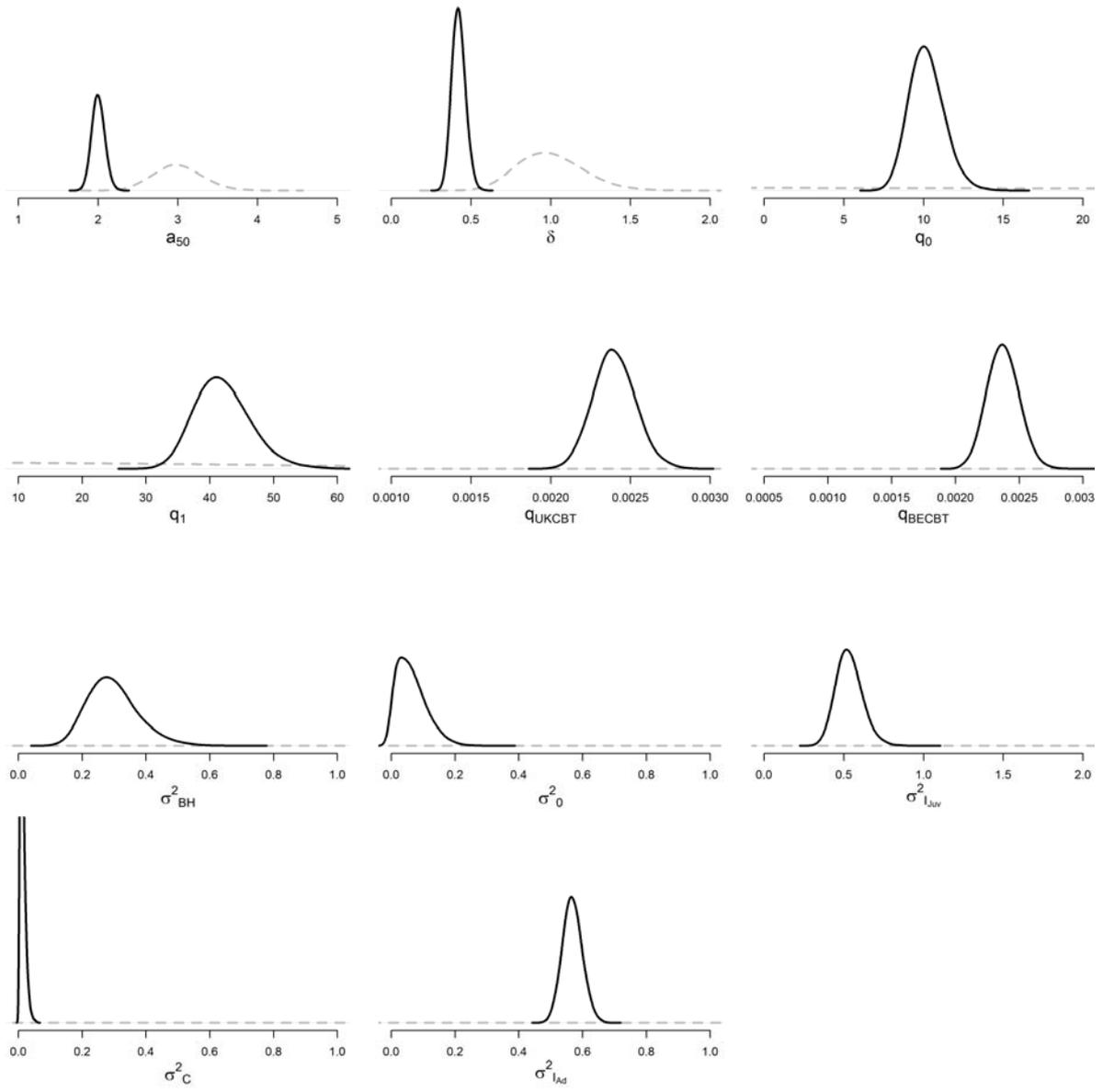
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117 Fig. S3.1. Prior and marginal posterior distributions of the parameters α_i 's and K_i 's (in log-
118 scale) for the five nursery sectors obtained with the model considering one single
119 homogeneous population. The prior distributions on the α_i 's is informative (See Appendix A).
120 The prior distribution on the K_i 's is weakly informative. An additional constraint ($\alpha < 1$) is
121 introduced in the model ($\alpha > 1$ would mean more 0+ juveniles than settled larvae).

122



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124 Fig. S3.2 Prior and marginal posterior distributions of all parameters obtained with the model
 125 considering one single homogeneous population. Dotted gray line: prior; Solid black line:
 126 posterior.

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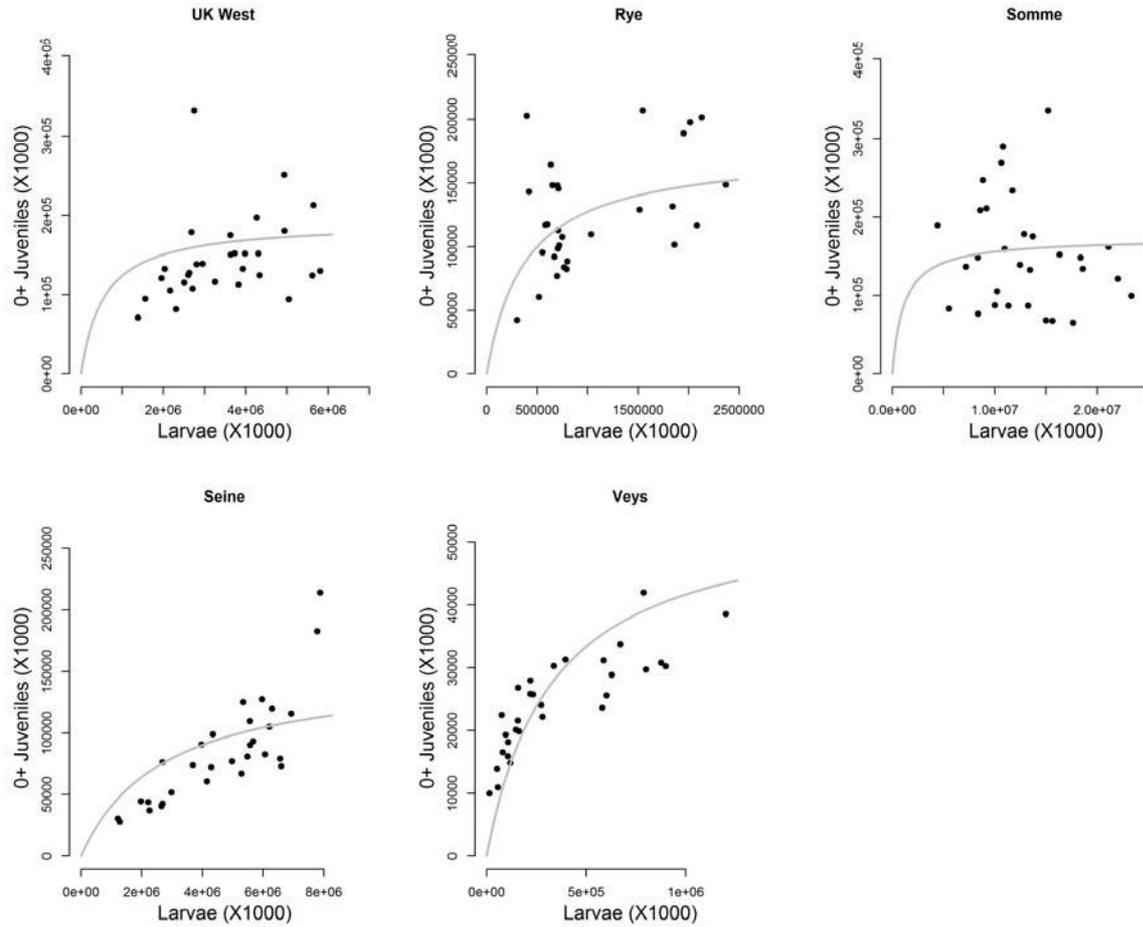
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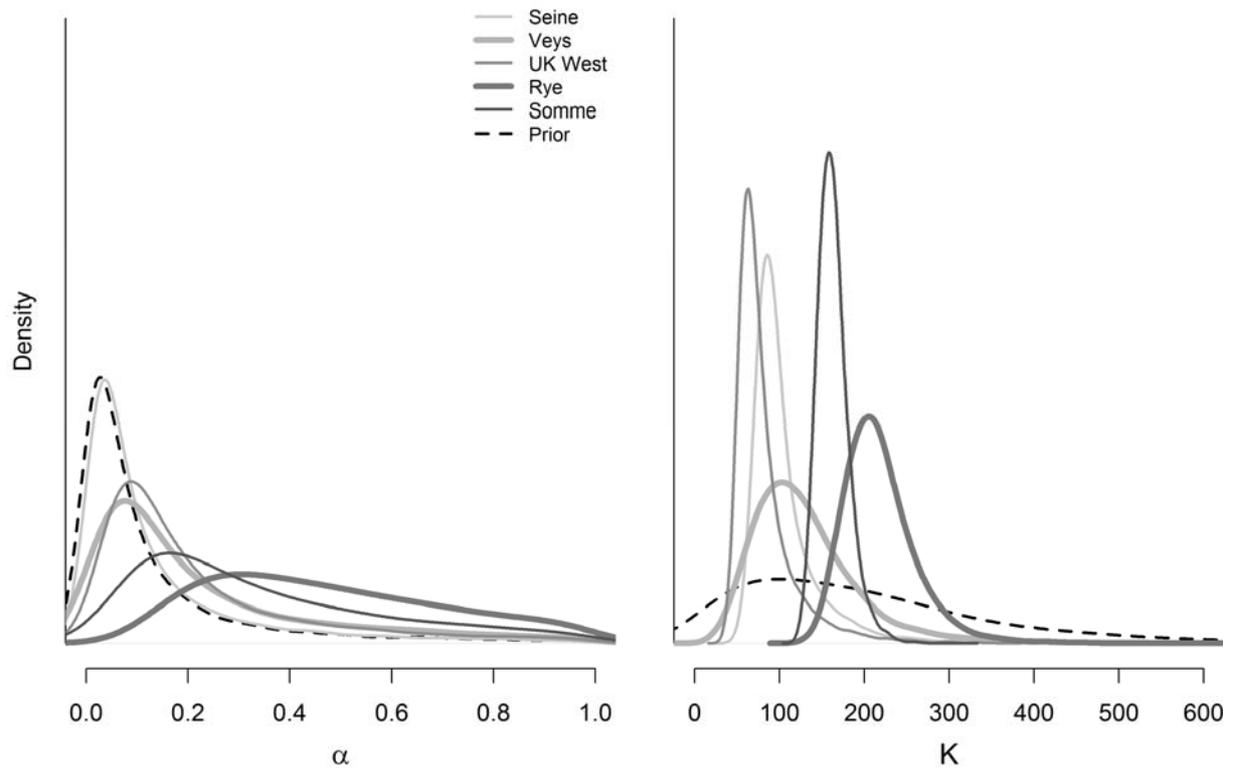
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136 Fig. S3.3. Fit of the Beverton-Holt recruitment curve in each nursery sectors obtained with the
 137 model considering one single homogeneous population. Plain line: Bev-Holt curve drawn
 138 with the posterior medians of the (α, K) parameters. Black points: posterior medians of the
 139 number of larvae (x-axis) and age-0 juveniles (y-axis).

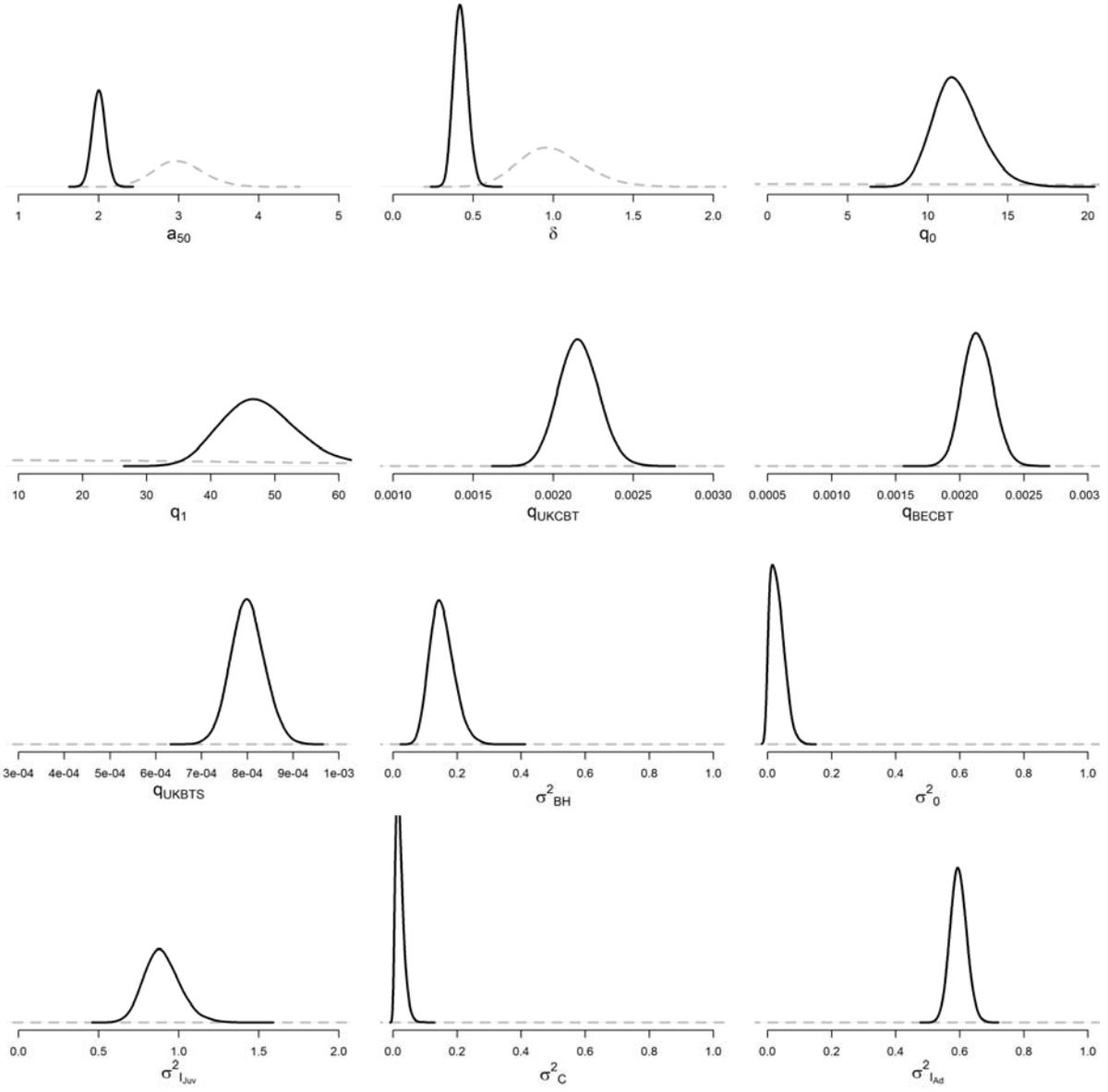
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141

142 Fig. S3.4. Prior and marginal posterior distributions of the parameters α_i 's and K_i 's (in log-
 143 scale) for the five nursery sectors obtained with the model considering three subpopulations.
 144 The prior distributions on the α_i 's is informative (See Appendix A). The prior distribution on
 145 the K_i 's is weakly informative. An additional constraint ($\alpha < 1$) is introduced in the model
 146 ($\alpha > 1$ would mean more 0+ juveniles than settled larvae).

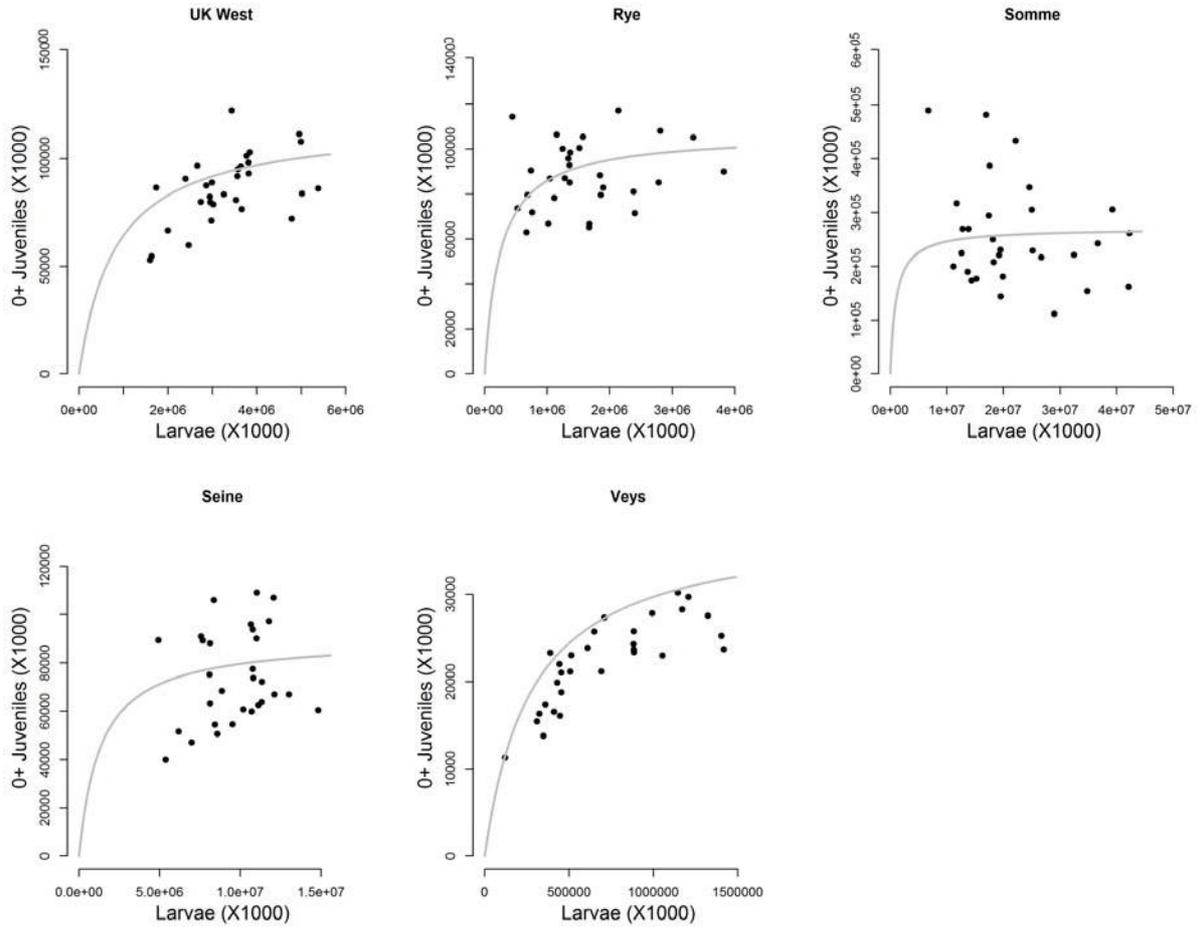
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148

149 Fig. S3.5. Prior and marginal posterior distributions of all parameters obtained with the model
 150 considering three subpopulations. Dotted gray line: prior; Solid black line: posterior.

151



152

153 Fig. S3.6. Fit of the Beverton-Holt recruitment curve in each nursery sectors obtained with the
 154 model considering three subpopulations. Plain line: Bev-Holt curve drawn with the posterior
 155 medians of the (α, K) parameters. Black points: posterior medians of the number of larvae (x-
 156 axis) and age-0 juveniles (y-axis).

157 Tab. S3.1. Mean, median, standard deviation (sd) and quantiles 10 and 90% for marginal
 158 posterior distributions of parameters in the model considering one single homogeneous
 159 population.

160

Parameters	Mean	Median	Sd	q10	q90
α_1	0.41	0.35	0.24	0.13	0.78
α_2	0.5	0.46	0.21	0.25	0.83
α_3	0.24	0.16	0.22	0.044	0.58
α_4	0.11	0.056	0.15	0.024	0.25
α_5	0.25	0.17	0.23	0.041	0.61
K_1	120	120	39	87	170
K_2	370	350	96	260	490
K_3	110	100	38	82	140
K_4	190	160	110	89	330
K_5	200	170	110	86	340
a_{50}	2	2	0.034	1.9	2
δ	0.44	0.44	0.019	0.41	0.46
σ_{BH}^2	0.3	0.29	0.078	0.2	0.4
σ_b^2	0.064	0.056	0.046	0.012	0.13
σ_C^2	0.013	0.012	0.0083	0.0048	0.025
$\sigma_{I_{juv}}^2$	0.53	0.53	0.082	0.44	0.64
$\sigma_{I_{Ad}}^2$	0.57	0.57	0.03	0.53	0.61
q_0	10	10	1.1	8.9	12
q_1	42	42	4.4	37	48
q_{BECBT}	0.0024	0.0024	0.00012	0.0022	0.0025
q_{UKCBT}	0.0024	0.0024	0.00013	0.0022	0.0026

161

162

163 Tab. S3.2. Mean, median, standard deviation (sd) and quantiles 10 and 90% for marginal
 164 posterior distributions of parameters in the model considering three subpopulations.

165

Parameters	Mean	Median	Sd	q10	q90
α_1	0.22	0.14	0.2	0.051	0.53
α_2	0.48	0.44	0.23	0.2	0.82
α_3	0.34	0.27	0.24	0.096	0.72
α_4	0.14	0.068	0.18	0.017	0.37
α_5	0.22	0.14	0.22	0.034	0.56
K_1	82	71	39	53	120
K_2	220	210	43	170	270
K_3	160	160	19	140	190
K_4	110	93	47	72	150
K_5	130	120	65	66	210
a_{50}	2	2	0.026	1.9	2
δ	0.4	0.4	0.014	0.38	0.42
σ_{BH}^2	0.15	0.15	0.037	0.11	0.2
σ_0^2	0.031	0.027	0.021	0.0054	0.06
σ_C^2	0.021	0.019	0.013	0.0073	0.038
$\sigma_{I_{juv}}^2$	0.9	0.89	0.11	0.77	1
σ^2	0.6	0.59	0.025	0.56	0.63
q0	12	12	1.5	10	14
q1	48	47	5.9	41	56
q _{BECBT}	0.0021	0.0021	0.00011	0.002	0.0023
q _{UKCBT}	0.0022	0.0022	0.00012	0.002	0.0023
q _{UKBTS}	0.0008	0.0008	0.000036	0.00076	0.00085

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168 Tab. S3.3. Correlation matrix (joint posterior distribution) for parameters in the model considering one single homogeneous population.

Param.	α_1	α_2	α_3	α_4	α_5	K_1	K_2	K_3	K_4	K_5	a_{50}	δ	q_0	q_1	q	q_{UKCBT}	σ_{BH}^2	σ_0^2	$\sigma_{\mu\nu}^2$	σ_c^2	σ_{Ad}^2
α_1		0.06	0	0.03	0.05	-0.46	-0.06	-0.04	-0.02	-0.04	0.01	0.01	-0.05	-0.02	-0.01	0.00	-0.02	0.00	-0.01	0.00	-0.02
α_2	0.06		0	0.03	0.05	-0.06	-0.49	-0.02	-0.07	-0.09	-0.01	-0.01	-0.05	-0.05	-0.01	-0.01	0.04	-0.01	0.02	0.01	0.00
α_3	0.05	0.05		0.03	0.05	-0.05	-0.02	-0.35	-0.01	-0.04	-0.01	-0.01	-0.03	-0.03	0.00	0.01	-0.01	0.00	0.00	0.01	0.01
α_4	0.03	0.03	0		0.04	-0.01	0.00	0.02	-0.43	-0.04	0.00	-0.01	-0.03	-0.01	0.00	-0.01	0.12	0.07	0.02	0.01	-0.01
α_5	0.05	0.05	0	0.04		-0.04	-0.08	-0.04	-0.05	-0.21	-0.01	-0.01	0.04	0.07	-0.02	-0.02	0.03	0.00	0.01	0.00	0.00
K_1	-0.46	-0.06	-	-0.01	-0.04		0.00	0.02	-0.04	0.00	0.02	0.02	0.05	0.06	0.01	-0.02	0.09	-0.04	0.04	0.00	0.01
K_2	-0.06	-0.49	-	0.00	-0.08	0.00		0.01	0.08	0.10	0.01	0.00	-0.11	-0.08	-0.01	-0.01	0.06	0.12	-0.07	0.02	-0.01
K_3	-0.04	-0.02	-	0.02	-0.04	0.02	0.01		-0.02	0.00	0.01	0.01	-0.06	-0.04	-0.01	-0.02	0.10	0.05	-0.01	0.01	0.02
K_4	-0.02	-0.07	-	-0.43	-0.05	-0.04	0.08	-0.02		0.04	0.01	0.01	0.02	0.01	-0.01	0.01	-0.12	-0.06	-0.02	0.00	-0.01
K_5	-0.04	-0.09	-	-0.04	-0.21	0.00	0.10	0.00	0.04		0.01	0.01	0.04	0.08	0.00	0.00	0.03	0.03	-0.02	-0.01	-0.01
a_{50}	0.01	-0.01	-	0.00	-0.01	0.02	0.01	0.01	0.01	0.01		0.71	0.00	-0.01	0.27	0.25	0.02	-0.01	0.00	0.04	0.02
δ	0.01	-0.01	-	-0.01	-0.01	0.02	0.00	0.01	0.01	0.01	0.71		0.01	-0.01	0.15	0.15	0.01	-0.02	-0.01	-0.07	0.01
q_0	-0.01	-0.05	-	-0.03	0.04	0.05	-0.11	-0.06	0.02	0.04	0.00	0.01		0.33	0.05	0.05	0.06	-0.21	0.39	-0.07	0.01
q_1	-0.02	-0.05	-	-0.01	0.07	0.06	-0.08	-0.04	0.01	0.08	-0.01	-0.01	0.33		0.04	0.05	0.04	-0.01	0.36	-0.05	-0.01
q_{BECBT}	-0.01	-0.01	0	0.00	-0.02	0.01	-0.01	-0.01	-0.01	0.00	0.27	0.15	0.05	0.04		0.46	0.01	0.01	-0.01	-0.08	0.32
q_{UKCBT}	0.00	-0.01	0	-0.01	-0.02	-0.02	-0.01	-0.02	0.01	0.00	0.25	0.15	0.05	0.05	0.46		0.01	0.00	-0.01	-0.06	0.29
σ^2	-0.02	0.04	-	0.12	0.03	0.09	0.06	0.10	-0.12	0.03	0.02	0.01	0.06	0.04	0.01	0.01		0.07	-0.19	-0.01	0.00
σ_{BH}^2	0.00	-0.01	0	0.07	0.00	-0.04	0.12	0.05	-0.06	0.03	-0.01	-0.02	-0.21	-0.01	0.01	0.00	0.07		-0.24	-0.01	0.00
σ_0^2	-0.01	0.02	0	0.02	0.01	0.04	-0.07	-0.01	-0.02	-0.02	0.00	-0.01	0.39	0.36	-0.01	-0.01	-0.19	-0.24		0.00	-0.02
$\sigma_{\mu\nu}^2$	0.00	0.01	0	0.01	0.00	0.00	0.02	0.01	0.00	-0.01	0.04	-0.07	-0.07	-0.05	-0.08	-0.06	-0.01	-0.01	0.00		-0.02
σ_c^2	-0.02	0.00	0	-0.01	0.00	0.01	-0.01	0.02	-0.01	-0.01	0.02	0.01	0.01	-0.01	0.32	0.29	0.00	0.00	-0.02	-0.02	

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171 Tab. S3.4. Correlation matrix (joint posterior distribution) for parameters of parameters in the model considering three subpopulations.

Param.	α_1	α_2	α_3	α_4	α_5	K_1	K_2	K_3	K_4	K_5	a_{50}	δ	q_0	q_1	q	q_{UKBTS}	q_{UKCBT}	σ_{BH}^2	σ_0^2	$\sigma_{I_{juv}}^2$	σ_c^2	$\sigma_{I_{Ad}}^2$
α_1		0.02	0	0.03	0.07	-0.45	-0.04	-0.04	0.01	-0.02	0.00	0.00	-0.01	-0.01	0.00	0.01	-0.01	0.00	0.00	-0.02	0.01	0.00
α_2	0.02		0	0.03	0.08	-0.02	-0.46	-0.08	0.00	-0.05	0.01	-0.01	-0.03	-0.02	-0.01	0.00	0.00	-0.05	0.02	0.01	0.01	-0.01
α_3	0.04	0.11		0.03	0.05	-0.03	-0.10	-0.38	0.02	-0.02	0.00	-0.01	-0.01	-0.01	0.00	0.02	-0.01	-0.07	-0.02	0.00	0.02	0.01
α_4	0.02	0.03	0		-0.02	-0.04	-0.01	0.01	-0.35	-0.05	-0.01	0.00	0.00	-0.01	0.00	0.01	0.02	0.02	0.01	0.01	-0.01	0.02
α_5	0.07	0.08	0	-0.02		-0.04	-0.07	-0.05	-0.03	-0.29	0.01	-0.01	0.01	0.03	0.02	0.01	0.01	0.04	0.01	-0.04	0.02	0.00
K_1	-0.45	-0.02	-	-0.04	-0.04		-0.06	0.04	0.04	0.05	0.01	0.00	0.00	0.02	0.00	-0.02	0.00	0.06	-0.01	0.01	0.01	0.01
K_2	-0.04	-0.46	-	-0.01	-0.07	-0.06		0.10	0.00	0.08	0.01	0.01	-0.08	-0.07	-0.02	-0.02	-0.02	0.08	0.06	-0.05	0.03	0.00
K_3	-0.04	-0.08	-	0.01	-0.05	0.04	0.10		-0.01	0.03	0.03	0.00	-0.02	0.00	-0.06	-0.05	-0.05	0.15	-0.02	0.04	0.03	-0.02
K_4	0.01	0.00	0	-0.35	-0.03	0.04	0.00	-0.01		-0.01	0.01	0.01	-0.03	-0.01	0.00	-0.02	-0.02	-0.05	-0.01	0.00	0.02	-0.01
K_5	-0.02	-0.05	-	-0.05	-0.29	0.05	0.08	0.03	-0.01		0.01	0.00	-0.01	0.02	-0.01	-0.01	-0.01	0.01	0.01	-0.01	0.01	0.01
a_{50}	0.00	0.01	0	-0.01	0.01	0.01	0.01	0.03	0.01	0.01		0.66	0.00	0.00	0.25	0.31	0.24	0.02	0.00	0.02	-0.02	0.02
δ	0.00	-0.01	-	0.00	-0.01	0.00	0.01	0.00	0.01	0.00	0.66		0.00	0.00	0.17	0.22	0.16	0.04	0.01	0.00	-0.15	0.00
q_0	-0.01	-0.03	-	0.00	0.01	0.00	-0.08	-0.02	-0.03	-0.01	0.00	0.00		0.27	0.01	0.05	0.04	0.04	-0.04	0.47	-0.07	0.00
q_1	-0.01	-0.02	-	-0.01	0.03	0.02	-0.07	0.00	-0.01	0.02	0.00	0.00	0.27		0.03	0.04	0.05	0.03	0.01	0.45	-0.07	0.01
q_{BECBT}	0.00	-0.01	0	0.00	0.02	0.00	-0.02	-0.06	0.00	-0.01	0.25	0.17	0.01	0.03		0.41	0.48	0.03	0.01	-0.02	-0.16	0.26
q_{UKBTS}	0.01	0.00	0	0.01	0.01	-0.02	-0.02	-0.05	-0.02	-0.01	0.31	0.22	0.05	0.04	0.41		0.41	0.05	0.02	-0.01	-0.20	0.32
q_{UKCBT}	-0.01	0.00	-	0.02	0.01	0.00	-0.02	-0.05	-0.02	-0.01	0.24	0.16	0.04	0.05	0.48	0.41		0.03	0.00	0.01	-0.14	0.24
σ^2	0.00	-0.05	-	0.02	0.04	0.06	0.08	0.15	-0.05	0.01	0.02	0.04	0.04	0.03	0.03	0.05	0.03		-0.19	-0.04	-0.18	0.02
σ_{BH}^2	0.00	0.02	-	0.01	0.01	-0.01	0.06	-0.02	-0.01	0.01	0.00	0.01	-0.04	0.01	0.01	0.02	0.00	-0.19		-0.03	-0.07	0.02
σ^0	-0.02	0.01	0	0.01	-0.04	0.01	-0.05	0.04	0.00	-0.01	0.02	0.00	0.47	0.45	-0.02	-0.01	0.01	-0.04	-0.03		-0.01	0.00
$\sigma_{I_{juv}}^2$	0.01	0.01	0	-0.01	0.02	0.01	0.03	0.03	0.02	0.01	-0.02	-0.15	-0.07	-0.07	-0.16	-0.20	-0.14	-0.18	-0.07	-0.01		-0.04
σ_c^2	0.00	-0.01	0	0.02	0.00	0.01	0.00	-0.02	-0.01	0.01	0.02	0.00	0.00	0.01	0.26	0.32	0.24	0.02	0.02	0.00	-0.04	