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1 **The GR3D model, a tool to explore the Global Repositioning Dynamics of**
2 **Diadromous fish Distribution**

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14

15 ABSTRACT

16 Within the context of ongoing environmental changes, the life history of diadromous fish
17 represents a real potential for exploring and colonizing new environments due to high
18 potential dispersal abilities. The use of dynamic approaches to assess how these species
19 will respond to climate change is a challenging issue and mechanistic models able to
20 incorporate biological and evolutionary processes are a promising tool. To this end we
21 developed an individual-based model, called GR3D (Global Repositioning Dynamics for
22 Diadromous fish Distribution), combining climatic requirements and population dynamics
23 with an explicit dispersal process to evaluate potential evolution of their distribution area
24 in the context of climatic change. This paper describes thoroughly the model structure and
25 presents an exploratory test case where the repositioning of a virtual allis shad (*Alosa alosa*
26 L.) population between two river catchments under a scenario of temperature increase was
27 assessed. The global sensitivity analysis showed that landscape structure and parameters
28 related to sea lifespan and to survival at sea were crucial to determine the success of
29 colonization. These results were consistent with the ecology of this species. The integration
30 of climatic factors directly into the processes and the explicit dispersal process make
31 GR3D an original and relevant tool to assess the repositioning dynamics and persistence of
32 diadromous fish facing climate change.

33

34 *Keywords: Climate change, Diadromous fish, Dispersal, Distribution, Individual-based*
35 *model, Population dynamics*

36

37

38 **1. Introduction**

39 Organisms have two ways to survive to the current major biodiversity threats such as
40 habitat loss and fragmentation, land use changes and more recently climate change. They
41 may adapt to new conditions on site through phenotypic plasticity or evolution, but this
42 might not be possible within the modification ranges or the timescales imposed by climate
43 change (Gienapp et al., 2008; Visser, 2008). Alternatively, species may shift their range,
44 searching for new suitable habitats. Regarding this last option, many studies have now
45 highlighted changes in distribution and community structure in various species (Thomas
46 and Lennon, 1999; Walther et al., 2002; Parmesan and Yohe, 2003; MacKenzie et al.,
47 2007; Nicolas et al., 2011). The success of these relocations or repositioning are contingent
48 upon the dispersal ability of the studied species and the availability of new suitable habitats
49 (Gaston and Blackburn, 2002; Thomas et al., 2004).

50 Many studies using statistical approaches and species distribution models (Guisan
51 and Zimmermann, 2000) have analysed the geographical distribution of species or
52 community with respect to their present environment and used the results to predict
53 expected distribution areas under climate change scenarios. This type of analysis has been
54 carried out for many taxa such as plants (Midgley et al., 2002; Thuiller, 2003;
55 Zimmermann et al., 2009), reptiles and amphibians (Segurado and Araújo, 2004; Araújo et
56 al., 2006), birds (Huntley et al., 2006), mammals (Thuiller et al., 2006), insects (Heikkinen
57 et al., 2007; Barrows et al., 2008), fish (Buisson, 2009) or diadromous fish (Lassalle,
58 2008). However, such projections do not consider populations' abilities to adapt to
59 changing environmental conditions (Pulliam, 2000; Guisan and Thuiller, 2005; Jackson et
60 al., 2009).

61 Despite a call by the scientific community in the last decade for developing a new
62 generation of models (Guisan and Thuiller, 2005; Keith et al., 2008; Thuiller et al., 2008;

63 Franklin, 2010) combining climatic suitability, population dynamics and dispersal
64 (Huntley et al., 2010), few studies have developed mechanistic or semi-mechanistic models
65 to deal with population dynamics and dispersal limitations of species under climate change
66 scenarios (but see Brooker *et al.*, (2007), Keith *et al.*, (2008), Engler and Guisan (2009),
67 Midgley *et al.*, (2010), Hein *et al.* (2011), Fennell *et al.*, (2012)). Mechanistic models aim
68 to incorporate the processes by which a species disperses through an environment (Merow
69 et al., 2011) and, unlike correlative models, allows one to compare potential and realized
70 distributions (Franklin, 2010; Gallien et al., 2010; Merow et al., 2011). Such models would
71 be a key point for guiding management and conservation of species in a period of rapid
72 environmental changes (Kinnison and Hairston, 2007) especially in fragmented and
73 heterogeneous environments. However, the development of these sorts of models is
74 generally limited by the lack of knowledge about population dynamics and on processes
75 involved in dispersal of the studied species.

76 The dispersal process is often a critical issue in modelling species movements
77 (Travis et al., 2012). Dispersal is generally defined as (non-returning) movements of
78 individuals away from where they are born, from where they have once reproduced to
79 another breeding site, or between social groups with potentially impacts on gene flow
80 (Clobert et al., 2001; Ronce, 2007; Clobert et al., 2009). It is described as a three-stage
81 process with departure (= emigration), transience (= transfer), and settlement as elementary
82 components (Clobert et al., 2009; Travis et al., 2012). Travis *et al.*, (2012) recently
83 proposed an eco-evolutionary framework for modelling dispersal. However, it is not
84 straightforward to transpose these definitions of dispersal and to define dispersers for
85 diadromous fish according to the diversity and complexity of their life cycles.

86 Diadromous fishes rely on freshwater, estuarine and marine ecosystems to complete
87 their life cycles (McDowall, 2009; Quinn et al., 2009). Anadromous species achieve most

88 of their growth at sea and migrate to freshwater to reproduce either in their natal river
89 (natal homing behavior) or in other rivers (straying) while catadromous species spend most
90 of their life in freshwaters and migrate to sea in order to reproduce (McDowall, 1988).
91 Diadromous life history strategies have evolved in phylogenetically diverse fish groups
92 (McDowall, 1997). This original life history characteristic has enabled them to adjust their
93 distribution to cope with environmental changes (McDowall, 1997; McDowall, 2009) and
94 could allow them to do the same in future changing environments (Lassalle et al., 2009).
95 Since diadromous species have a real potential to explore and colonize new environments
96 with a part of their life cycle at sea, a diadromous strategy is an adaptive asset compared to
97 a holobiotic life history strategy in a context of global change. In this paper, we will only
98 focus on anadromous species, for which we assume that dispersers are strayed spawners
99 (i.e. strayers) not making natal homing behavior (i.e. not returning to their natal stream for
100 spawning). However, processes involved in the determination of strayers as well as the
101 behavior of the strayers remain unknown for diadromous species. As dispersal is closely
102 linked to individual behavior, individual-based-models (IBMs) appear to be a promising
103 approach to address the question of dispersal and repositioning dynamics of diadromous
104 fishes. IBMs also offers a flexible and easy way to simulate different behaviors.

105 Despite their complexity often seen to hamper interpretation of their results, the use
106 of IBMs in ecological modelling has increased exponentially (Grimm, 1999) from the
107 seminal works of Huston *et al.* (1988). Moreover, recent progresses have been made to
108 allow complex IBMs to be better communicated and described (Grimm et al., 2006;
109 Grimm et al., 2010). Many IBMs have already involved fish populations (Van Winkle et
110 al., 1993; Van Winkle et al., 1998; Grimm, 1999; Charles et al., 2008) and more especially
111 diadromous fish such as chinook salmon, *Oncorhynchus tshawytscha* (Jager et al., 1997),
112 European eel, *Anguilla anguilla* (Lambert and Rochard, 2007) or more recently Sockeye

113 Salmon, *Onchorhynchus nerka* (Reed et al., 2011), brown trout, *Salmo trutta* (Frank and
114 Baret, 2013) and Atlantic salmon, *Salmo salar* (Piou and Prévost, 2012, 2013).
115 Furthermore, IBMs are powerful tools to represent biological and habitat mechanisms,
116 individual behavior and variability (Grimm, 1999). They also allow analysing potential
117 climate change effects on natural systems (Reed et al., 2011; Piou and Prévost, 2013) as
118 environmental effects can be directly incorporated in processes. Although complexity is an
119 essential feature of IBMs and can result in unforeseen emergent properties, they may
120 appear over-parameterized if compared to much more parsimonious statistical models.
121 Furthermore, a number of population dynamics parameters are often imprecise and poorly
122 estimated. Hence, it is important to carry out sensitivity analyses (Saltelli, 2004) of this
123 kind of model. Global sensitivity analysis methods are now well known to advance the
124 comprehension and exploration of system modelled (Faivre et al., 2013). In such an
125 analysis, parameters are varied simultaneously allowing identification of interactions by
126 statistical analysis of the simulation results. These methods have already been used in
127 industry (Kleijnen, 1998), ecology (Cariboni et al., 2007) or fishery science (Drouineau et
128 al., 2006; Drouineau et al., 2008; Lehuta et al., 2010).

129 For diadromous species, developing a model combining climatic requirements and
130 population dynamics with explicit dispersal processes is a real challenge and will be a
131 major step forward for guiding management policies. If successful, it could help to
132 determine in which catchment and for which species restoration and restocking actions will
133 be relevant. Moreover, the development of this kind of model for diadromous fish does not
134 appear to be limited by the knowledge of their ecology and their population dynamics
135 which are now well documented (at least for the continental phase) for several species such
136 as Atlantic salmon *Salmo salar* (Peterson et al., 1977; Bagliniere and Maisse, 1985;
137 Fleming, 1996; Friedland, 1998; Hutchings and Jones, 1998; Forseth et al., 2001; Jonsson

138 and Jonsson, 2009; Buoro et al., 2010), European eel *Anguilla anguilla* (Gatto and Rossi,
139 1979; Vollestad and Jonsson, 1988; De Leo and Gatto, 1995; Dekker, 2000; Lambert,
140 2005; Lambert and Rochard, 2007; Bevacqua et al., 2011), European sturgeon *Acipenser*
141 *sturio* (Rochard and Lambert, 2011) or allis shad *Alosa alosa* (Lambert et al., 2001; Acolas
142 et al., 2006; Lassalle et al., 2008b; Mota and Antunes, 2011; Rougier et al., 2012).

143 In this context, we developed an exploratory simulation model (GR3D: Global
144 Repositioning Dynamics for Diadromous fish Distribution) integrating the whole
145 population dynamics of diadromous fish (reproduction, growth, survival, maturation,
146 downstream and upstream migrations). The GR3D model is individual-based, stochastic
147 and spatially explicit. To test climate change effect on population dynamics, we introduced
148 temperature variations and their effects on demographic traits, such as growth,
149 reproduction and survival. We introduced individual variability through growth, survival,
150 reproduction and migration.

151 Models of high complexity require a substantial exploration phase to avoid
152 misinterpretation of simulation results (Grimm and Railsback, 2005). The more complex a
153 model is, the more its calibration, and the extrapolation and analysis of its results are
154 difficult (Levins, 1966; Caswell and John, 1992). From this consideration, testing a
155 complex model with simple exploratory cases is a reasonable and rational approach (Faivre
156 et al., 2013).

157 Here, we present the GR3D model and show how this generic model may be
158 relevant to study the repositioning dynamics and persistence of diadromous fish in a
159 context of climate change. To illustrate the potential of the model, we applied GR3D in a
160 virtual exploratory study where we assess the repositioning of a virtual anadromous allis
161 shad population between two river catchments under a scenario of temperature increase.

162 We run the associated sensitivity analysis in order to identify parameters influencing model
163 outputs.

164

165 **2. Materials and methods**

166 *2.1. Model description*

167 The GR3D model has been developed in Java using the "SimAquaLife" framework
168 (Dumoulin, 2007) which is an individual-based, process-oriented toolkit for aquatic life
169 simulation.

170 The description of the GR3D model follows the ODD protocol (Overview, Design
171 concepts, Details) for describing individual- and agent-based models (Grimm and
172 Railsback, 2005; Grimm et al., 2006; Grimm et al., 2010).

173 *2.1.1. Purpose*

174 The general purpose of GR3D is to evaluate diadromous fish local persistence
175 (defined as the probability for a species to maintain a population in a specific river
176 catchment) (Jager et al., 2013), global persistence (defined as the probability for a species
177 to maintain a population in at least one catchment) and concomitant potential evolution of
178 their distribution area, in the context of climatic change at a European scale combining
179 population dynamics, repositioning behaviors through dispersal processes and climatic
180 requirements.

181

182 *2.1.2. State variables and scales*

183 *Temporal scales:* GR3D simulates a seasonal time step with distinct processes and
184 scheduling in each of these steps.

185 *Entities and spatial scales:* Three types of entities compose the GR3D model: one for
186 fish agents and two for environment elements. GR3D is spatially explicit with a continental

187 compartment and a sea compartment. The continental compartment is split up in "River
188 Basins". Each "River Basin" (RB) is characterized by a name, a position (latitude and
189 longitude at the mouth), a catchment area (km²) and seasonal mean water temperatures at
190 the mouth (Table 1).

191 According to the studied species, the sea compartment is either split into "Sea
192 Basins" (SB) associated with one of the river basins, or composed of a unique "sea basin"
193 connected to all the river basins. Each SB is characterized by a name and seasonal mean
194 water temperatures (Table 1).

195 Temperatures in compartments are updated at each time step according to a virtual
196 scenario of water temperature increase or according to a real projection of climate change.
197 Actually, GR3D is designed to work either with virtual environments or real environments
198 such as the Atlantic coast.

199 *State variables of diadromous fish individuals:* Each diadromous fish is described
200 by an ID, a gender, a maturation stage (mature or immature), an age, a body length, a
201 location (a river basin or a sea basin), a birth place and a number of reproductions.

202

203 *2.1.3. Process overview and scheduling*

204 GR3D is developed to cover the entire life cycle of any diadromous fish species
205 trying to be the more generic as possible and taking into account the differences between
206 anadromous and catadromous species. Hence, we structured the model in six submodels
207 consistent with the life cycle events and processes of any diadromous species
208 (reproduction, growth, survival, downstream migration, maturation, and upstream
209 migration including dispersal). As the present test case deals with an anadromous species
210 (see section 2.2.), we only presented the computational order of life cycle events and

211 processes in a conceptual diagram for an anadromous species with allis shad as an
212 illustrative case (Fig. 1).

213

214 *2.1.4. Design concepts*

215 *Basic principles:* GR3D is a population dynamic model that explicitly includes
216 environmental effects in processes and that incorporates an original dispersal process.
217 During the upstream migration of anadromous fish, we distinguished two kinds of
218 individuals: individuals having a homing behavior (i.e. returning to their natal river to
219 spawn) or having a straying behavior (i.e. not returning to their natal stream). In the
220 absence of information on marine dispersion behavior, we assumed that the choice of a
221 river basin by an individual is the result of three components: 1) a propensity to adopt a
222 homing behavior (characteristic of the species), 2) the accessibility of the river basin, and
223 3) its attractiveness.

224 *Interactions:* Indirect interactions are included in the reproduction process (see
225 Section 2.1.7.1) through a demographic Allee effect (Allee, 1931; Stephens et al., 1999)
226 and through a density-dependant survival of eggs and larvae.

227 *Stochasticity:* Demographic stochasticity was incorporated for growth, survival,
228 reproduction and dispersal.

229 *Observation:* Graphical outputs from "SimAquaLife" interface directly show
230 population-level variables (declared as observable in GR3D) as well as spatial distribution
231 of the individuals. As example, the number of spawners (distinguishing those exhibiting
232 natal homing behavior from those exhibiting straying) and juveniles at each reproduction
233 for each river basin can be recorded as well as the year of the first non-null reproduction
234 and the last year without reproduction.

235

236 *2.1.5. Initialization*

237 The environment, the start and the number of year of simulations, the abundance, the age
238 and the initial distribution of the individuals are initialised according the application case.
239 Population parameters are initialised according to the studied species (see section 2.2.).

240

241 *2.1.6. Input*

242 In the current version of GR3D, environmental conditions changed over time via
243 temperature, which changed over space and season. The model is designed to integrate any
244 kind of seasonal temperature temporal series. In a same way, to define the environment, an
245 input file containing river basins characteristics (cf. § 2.1.2) can be used.

246

247 *2.1.7. Submodels*

248 GR3D contains 42 parameters, which are listed in [Table 2](#) according to the submodel they
249 are involved in. According to the studied species, their values are obtained either from
250 observations (literature) or are reasonable guessed (i.e. we have only an idea of what would
251 be a realistic value of the parameter) or are calibrated. GR3D is based on six submodels
252 representing fundamental biological processes.

253

254 *2.1.7.1. Reproduction:*

255 Reproduction occurs yearly during the reproduction season (defined as a population
256 parameter, [Table 2](#)) in each river basin when spawners are present. We assumed that
257 numbers of recruits R_j produced by S_j spawners in a spawning basin j follows a Beverton &
258 Holt stock-recruitment relationship of parameters α_j and β_j (BH S-R) ([Beverton and
259 Holt, 1957](#)). However we modified the traditional BH S-R:

260 • We included an Allee effect (Eq. (1)) to take into account difficulties to settle a
 261 population with limited numbers of fish in new habitats. Depensation strength is
 262 modeled as a function of river basin watershed area through two species specific
 263 parameters: η a parameter linking the basin watershed area WA_j to its carrying
 264 capacity (the higher η is, the higher the stock level to reach 95% of the asymptotic
 265 recruitment) and θ which controls the Allee effect strength (a high θ corresponds to a
 266 strong depensation, i.e. the stock level to produce half of the asymptotic recruitment is
 267 close to the stock level producing 95% of the asymptotic recruitment).

$$R_j = \frac{\alpha_j S_j \frac{1}{1 + e^{\left(\frac{-\ln(19) S_j - \eta / \theta \cdot WA_j}{\eta \cdot WA_j - \eta / \theta \cdot WA_j} \right)}}}{\beta_j + S_j \frac{1}{1 + e^{\left(\frac{-\ln(19) S_j - \eta / \theta \cdot WA_j}{\eta \cdot WA_j - \eta / \theta \cdot WA_j} \right)}}} \quad (1)$$

269
 270 • By comparison to the traditional BH S-R, we considered that the non-density
 271 dependent mortality from egg to recruit (duration Δt_{rec} , Table 2) is a function of
 272 temperature, consequently parameters α_j and β_j depend on temperature (Eq. (2) and
 273 Eq. (3)). Egg survival is optimal ($surv_{optRep}$, Table 2) at T_{opt} and there is no recruitment
 274 when temperature is out of the range $T_{min} - T_{max}$ (Eq. (4), Table 2). The density
 275 dependent mortality of the BH S-R is assumed to be dependent on the basin surface
 276 (through a population parameter λ , Table 2) to take into account resource limitations
 277 in small basins (Eq. (5)).

$$\alpha_j = \frac{b_j e^{-b_j \Delta t_{rec}}}{c_j (1 - e^{-b_j \Delta t_{rec}})}, \quad (2)$$

$$\beta_j = \frac{b_j}{ac_j (1 - e^{-b_j \Delta t_{rec}})}, \quad (3)$$

280 The parameter a is linked to the fecundity of the species (Table 2),

$$281 \quad b_j = -\frac{1}{\Delta t_{rec}} \ln \left[\text{surv}_{optRep} \frac{(T_j - T_{minRep})(T_j - T_{maxRep})}{(T_j - T_{minRep})(T_j - T_{maxRep}) - (T_j - T_{optRep})^2} \right], \quad (4)$$

282 and

$$283 \quad c_j = \frac{\lambda}{\text{Surf}_j}. \quad (5)$$

284

285 We introduce stochasticity in this process by drawing the value of the effective recruitment
 286 $R_{Eff,j}$ in a lognormal distribution of standard deviation σ_{rep} around the stock-recruitment
 287 relationship (Table 2).

288 After the reproduction, the population parameter Sp_{sp} (Table 2) defined the survival
 289 probability of the spawners to take into account the iteroparity of the studied species.

290

291 2.1.7.2. Downstream migration.

292 This process occurs at different life stage and season according to the studied species. The
 293 age and the season at which this migration occurs are defined as population parameters
 294 (Table 2). In this process, individuals migrate from their river location to a determined sea
 295 compartment according to the studied species.

296

297 2.1.7.3. Growth.

298 The population parameter L_{ini} determines the initial length of individuals at age Δt_{rec} (i.e.
 299 after reproduction). We then use a von Bertalanffy growth function (von Bertalanffy, 1938)
 300 derived from Fabens (1965) for modelling of the growth process. Each season, each
 301 individual length is updated according to its previous length. In order to introduce
 302 individual variability and to avoid negative growth, we use a lognormal distribution to
 303 determine the growth increment

$$304 \quad \Delta L = \text{LogN}(\mu_{\Delta L}, \sigma_{\Delta L}), \quad (6)$$

305 with $\mu_{\Delta L}$ the mean and $\sigma_{\Delta L}$ the standard deviation of the variable's natural logarithm
 306 (Table 2). So, $\mu_{\Delta L}$ is expressed

$$307 \quad \mu_{\Delta L} = \log\left((L_{\infty} - TL_t) \times (1 - \exp^{-\kappa \Delta t})\right) - \frac{\sigma_{\Delta L}^2}{2}, \quad (7)$$

308 where TL_t is the total length of a fish at time unit t , L_{∞} is a population parameter
 309 corresponding to the asymptotic length of fish (Table 2) and κ is the growth coefficient.
 310 Since temperature is known to affect growth rate (Brown et al., 2004), Rosso's function
 311 (Rosso et al., 1995) is used to correlate the growth coefficient to temperature and introduce
 312 seasonal variability (Mallet et al., 1999; Dion and Hughes, 2004; Kielbassa et al., 2010;
 313 Bal et al., 2011). According to this function, the growth coefficient κ and temperature are
 314 linked by a bell-shaped relationship. In fact, κ is equal to 0 if the temperature is lower or
 315 equal to the minimal growth temperature $T_{minGrow}$; it increases with temperature up to an
 316 optimum $\kappa_{optGrow}$ at the optimal growth temperature $T_{optGrow}$. If temperature continues to
 317 increase, the growth coefficient κ rapidly decreases down to 0 at the maximal growth
 318 temperature $T_{maxGrow}$. The relationship is expressed

$$319 \quad \kappa = \kappa_{optGrow} \frac{(T - T_{minGrow})(T - T_{maxGrow})}{(T - T_{minGrow})(T - T_{maxGrow}) - (T - T_{optGrow})^2}. \quad (8)$$

320
 321
 322 Parameters $T_{minGrow}$, $T_{optGrow}$, $T_{maxGrow}$ and $\kappa_{optGrow}$ are population parameters (Table 2).

323

324 2.1.7.4. Survival.

325 At each time step, the survival of each individual is assessed depending on its location and
 326 stage.

327 For individuals at sea, the seasonal survival probability, Sp_{sea} , is calculated using the
 328 annual mortality coefficient at sea, Z_{sea} , defined as a population parameter (Table 2) and a
 329 survival equation

$$330 \quad Sp_{sea} = \exp^{-Z_{sea} \times \Delta t_{season}}, \quad (9)$$

331 where Δt_{season} is the duration of a season (i.e. 0.25 year⁻¹). We assumed that Z_{sea}
 332 incorporates all sources of individual mortality at sea.

333 For individuals in river, the seasonal survival probability, Sp_{riv} , is calculated using two
 334 annual mortality coefficients M_{riv} (natural mortality coefficient) and H_{riv} (human-induced
 335 mortality coefficient) defined as population parameters (Table 2) and a survival equation

$$336 \quad Sp_{riv} = \exp^{-(M_{riv} + H_{riv}) \times \Delta t_{season}}. \quad (10)$$

337 The natural mortality coefficient M_{riv} is assumed to be dependent on the river temperature
 338 T_j and was computed as follows

$$339 \quad M_{riv} = \frac{-\ln \left(\frac{surv_{optRiv} (T_j - T_{minSurvRiv})(T_j - T_{maxSurvRiv})}{(T_j - T_{minSurvRiv})(T_j - T_{maxSurvRiv}) - (T_j - T_{optSurvRiv})^2} \right)}{\Delta t_{season}}, \quad (11)$$

340 where $T_{minSurvRiv}$, $T_{optSurvRiv}$, $T_{maxSurvRiv}$ and $surv_{optRiv}$ were population parameters (Table 2).

341 We assumed that the other mortality coefficient H_{riv} incorporates the other sources of
 342 mortality in river (fishery, pollution, dams...).

343

344 2.1.7.5. Maturation.

345 In the current version of GR3D, individual maturation is not explicit and did not involve
 346 energy allocation processes. An individual becomes mature as soon as its length reached
 347 the length at first maturity L_{mat} (defined as a population parameter, Table 2) and its
 348 maturation stage changed from *immature* to *mature*.

349

350 2.1.7.6. *Upstream migration.*

351 This submodel is essential in the model since we assumed that dispersal is linked to this
 352 migration. This process occurs at different life stages and seasons depending on the studied
 353 species. The age and the season at which the downstream migration occurs are defined as
 354 population parameters (Table 2). It has been designed as a three-stage process with
 355 emigration, movement and settlement phases.

356 1. *The emigration phase:* in this phase, individuals have a probability to adopt a homing (
 357 p_{hom}) or a straying behavior ($1 - p_{hom}$) which is assumed to be a characteristic of the
 358 species. p_{hom} is defined as a population parameter (Table 2).

359

360 2. *The movement phase:* Individuals that do not become strayers simply migrate in their
 361 natal river (homing behavior). For strayers, the probability to migrate in each river basin is
 362 assumed to be a function of its accessibility and its attractiveness. We assumed that
 363 accessibility depends on the dispersal distance $D_{j-birthPlace_i}$ between basin j and the birth
 364 place of an individual i , and on the total length TL_i of the individual i . The basin
 365 attractiveness is assumed to be a function of its watershed area WA_j as a proxy of the river
 366 flow. Then, the “weight” of each basin relative to an individual i is computed using a logit
 367 function

$$\begin{aligned}
 \text{logit}(w_i^j) = & \alpha_{const} + \alpha_{dist} \left(\frac{D_{j-birthPlace_i} - \overline{D_{j-birthPlace}}}{\sigma_{j-birthPlace}} \right) \\
 & + \alpha_{TL} \left(\frac{TL_i - \overline{TL}}{\sigma_{TL}} \right) + \alpha_{WA} \left(\frac{WA_j - \overline{WA}}{\sigma_{WA}} \right), \tag{12}
 \end{aligned}$$

369 where α_{const} , α_{dist} , α_{TL} and α_{WA} are four population parameters (Table 2). In order to have
 370 comparable parameters, we used standard cores values of each factor influencing the

371 function and we defined $\overline{D_{j\text{-birthPlace}}}$, $\sigma_{j\text{-birthPlace}}$, \overline{TL} , σ_{TL} , \overline{WA} and σ_{WA} as population
372 parameters (Table 2).

373 We assumed that individuals may also not find any basin so we introduce a virtual “death
374 basin” with a fixed weight $w^{\text{deathBasin}}$. Then w_i^j are standardized so that their sum equals 1,
375 providing probabilities to choose each river basin (including death basin). The choice is
376 then modelled by a simple multinomial process.

377 *3. The settlement phase:* Individuals enter in the selected destination, survive if conditions
378 are suitable and reproduce if they find mating requirements.

379

380 2.2. The test case

381 2.2.1. Description of the studied species

382 Allis shad (*Alosa alosa* L.) is an anadromous clupeid spawning in the higher middle
383 watercourse of rivers. Fish migrate to sea during their first year, where they grow and
384 return to freshwater to spawn at between 3 and 6 years (Bagliniere and Elie, 2000;
385 Baglinière et al., 2003). Currently, populations of allis shad exist along the northeastern
386 Atlantic coasts in some large rivers of France (Loire, Gironde-Garonne-Dordogne, and
387 Adour) and Portugal (Minho and Lima) (Lassalle et al., 2008b) and despite some
388 protective measures, this species appears to have been in serious decline for a number of
389 years (Limburg and Waldman, 2009; Rougier et al., 2012). Biology and ecology of allis
390 shad have therefore received a great deal of attention in the last 30 years (Mennesson-
391 Boisneau and Boisneau, 1990; Prouzet et al., 1994; Bagliniere and Elie, 2000; Acolas et
392 al., 2004; Acolas et al., 2006) and several studies also dealt with its population dynamics
393 (Martin Vandembulcke, 1999; Lambert et al., 2001; Rougier et al., 2012).

394

395 2.2.2. *Environment, time and initialization*

396 An environment with two rivers basins (RB1 and RB2) and two sea basins (SB1 and SB2)
397 highly associated to the river basins (i.e. RB1 with SB1 and RB2 with SB2) was used for
398 the test case. Our experiment mimics a situation where temperature increase opened the
399 opportunity for a stable allis shad population in RB1 to expand into a new suitable river
400 RB2. Two environmental parameters were defined to determine the initial configuration of
401 the environment: *WA_RB2* corresponding to the watershed area of the uninhabited river
402 basin RB2 and *intDist* describing the distance between RB1 and RB2.

403 Each simulation starts in summer and lasts 200 years (i.e. 800 time steps). During
404 the first fifty years of simulation, a virtual population of allis shad was created in RB1 by
405 introducing there 500000 juveniles at the first time step. From the year 50 to the year 150,
406 we introduced in the two basins a linear water temperature increase of 3°C in 100 years
407 (i.e. water temperature increase by 0.0075°C at each time step) and RB2 becomes suitable
408 for allis shad reproduction. At the end of the temperature increase, only RB2 is suitable for
409 allis shad for the last 50 years of simulations. Temperatures in RB1 and RB2 were
410 initialized with the same values except for the spring temperature as we used it to control
411 the suitability of each river during the simulation. In order to work with realistic values, we
412 used daily estimates of Gironde estuarine water temperature (°C) provided by EDF
413 (Electricité De France) between 1991 and 2009 to initialize the winter, summer and
414 autumn temperatures in RB1 and RB2 as the Gironde basin is located at the center of the
415 allis shad distribution area (Baglinière, 2000; Lassalle, 2008). Spring temperature of RB1
416 was set to 3°C below $T_{maxSurvRiv}$ and set to T_{minRep} in RB2. The watershed area of RB1 was
417 set to 40000 km². The environmental parameters *WA_RB2* and *intDist* were included in the
418 global sensitivity analysis to assess the influence of the environment configuration on
419 model outputs (see section 2.2.4.).

420 The seasonal mean water temperatures of SB1 and SB2 were calculated as the
421 mean between 12°C and the seasonal mean water temperatures of RB1 and RB2,
422 respectively.

423 Initial length of each individual is set at 2 centimetres. The individual state
424 variables were initialized as follows for each new individual: gender was assigned
425 according to a sex ratio of 1:1; stage was set to “immature”, the number of reproduction
426 was set to 0; and the birth place was set according to their birth location.

427

428 2.2.3. Model parameterisation

429 For this test case with allis shad, 20 population dynamics parameters were obtained from
430 literature, 18 were parameterized as reasonable guesses (based upon expertise), and 4 were
431 estimated using off-line calibration (Table 2).

432 For the off-line calibration, we used a previous work (Rougier et al., 2012) about
433 the population dynamics of allis shad in the Gironde basin for the parameterization of the
434 reproduction process (i.e. parameter η , θ , $surv_{optRep}$ and λ of the BH S-R relationship,
435 Table 2) and used their estimates of $\alpha_{Gironde}$, $\beta_{Gironde}$ and η . We assumed that the
436 recruitment was a number of juveniles in estuary and set Δt_{rec} to 0.33 year (4 months) as it
437 corresponds to the average duration of the juvenile downstream migration towards the sea
438 (Lochet et al., 2008).

439 We assumed dispersal of allis shad was only dependant of the distance between the
440 suitable habitats. Hence, α_{TL} and α_{WA} were set to 0. We set $\sigma_{j-birthPlace}$ to 978 km (using
441 the EuroDiad 2.0 database of European river basins from Lassalle (2008)). We set
442 $\overline{D_{j-birthPlace}}$ to 300 km as we assumed that this value was close to the maximal distance of
443 dispersal for allis shad . Then we assumed a weight of 0.95 and 0.05 for a basin located at a

444 distance of 10 km and 300 km respectively. In consequence, α_{const} and α_{dist} were set to
445 -2.9 and 19.7 respectively (Table 2).

446

447 2.2.4. Sensitivity analysis

448 For these simulations, we mainly focused on the success of the colonization of RB2.
449 Hence, we recorded the following 2 output variables: (i) fs was a qualitative variable
450 describing the final state of RB2 using the value of the coefficient of variation (CV) of the
451 recruitment in RB2 during the last ten years of simulations, i.e. that it took either the value
452 0 if the CV was null, or the value 1 if the CV was higher than a threshold arbitrarily set to
453 5%, or the value 2 if the CV was positive and lower than the threshold; (ii) mlr was the
454 mean of the recruitment in RB2 during the last ten years of simulations.

455 We defined two variables using the fs output variable. fsP indicated the
456 presence/absence of fish in RB2 (i.e. $fs = 0$ for absence and $fs > 0$ for presence).
457 Considering only positive values of fs , we defined fsS as a variable describing a kind of
458 stability of the RB2 population (i.e. relatively unstable for $fs = 1$ because it means that
459 there is high variation in the recruitment values in the ten last year of simulation, and stable
460 for $fs = 2$ because it means that recruitment values are stable in the ten last years of
461 simulation). Hence, we used these two variables to analyze the influence of parameters on
462 both the presence/absence of fish in RB2 and on the stability of the population in RB2. mlr
463 was a metric indicating the abundance of fish in RB2. As the null values described absence
464 of fish in RB2, we only used positive values of mlr to analyze the influence of parameters
465 on abundance in RB2.

466 In order to screen non-influential and influential parameters on GR3D model
467 outputs, we conducted a global sensitivity analyses by varying both the model and the
468 environmental parameters. We identified 20 uncertain population dynamics parameters of

469 the GR3D model to incorporate in the sensitivity analysis and we added 2 environmental
470 parameters in the analysis (*WA_RB2* the watershed area of RB2 and *intDist* the distance
471 between RB1 and RB2; [Table 3](#)). Considering a maximal range of variation of 20% often
472 used in sensitivity analysis ([Drouineau et al., 2006](#); [Lehuta et al., 2010](#)), we set a low and a
473 high value for each population parameter based on our own expertise and knowledge of
474 allis shad population dynamics ([Table 3](#)). Concerning environmental parameters, we
475 considered three modalities for *WA_RB2* and four for *intDist* ([Table 3](#)). As a complete
476 design would have taken too much time since it would involve more than 12 million
477 simulations without replicates ($2^{20} \times 3 \times 4$), we first used an experimental design to
478 identify the most influential parameters on model outputs. Regarding the number of factors
479 and modalities, the most appropriate experimental design are D-optimal designs
480 ([Drouineau et al., 2006](#); [Faivre et al., 2013](#)). In this type of design, the estimations of the
481 effects are partially correlated (i.e. that contrary to factorial design, confusion between
482 effects estimates may exist, but an algorithm is used to find the set of experiments),
483 maximizing the determinant of the information matrix (XX' with X, the matrix of the
484 different combinations of modalities for each experiment) of the design, equivalent to
485 maximizing the efficiency of the estimation ([Droesbeke et al., 1997](#); [Drouineau et al.,](#)
486 [2006](#)). We use the AlgDesign R package ([Wheeler, 2011](#)) to generate our D-Optimal
487 design and, finally, the resulting experimental design consisted of 1300 simulations that we
488 replicated 10 times. Only main effects were estimated with this design using a logistic
489 regression model for *fsP* and *fsS* and analysis of variance (ANOVA) for *mlr*. For each
490 model output response y , first order indices (*SI*) of a parameter x_i measuring the importance
491 of the deviance (or variance for *mlr* output) of the y mean conditionally on factor x_i , were
492 considered as a sensitivity index ([Saltelli, 2004](#); [Saltelli et al., 2008](#); [Faivre et al., 2013](#))
493 and were calculated as follows

494
$$SI(x_i) = \frac{Dev[E(y|x_i)]}{Dev(y)}. \quad (18)$$

495 Focusing on the ten highest SI of the 3 model outputs, we selected the most influential
496 parameters. For computation time reasons, we were not able to select more than 13
497 parameters. Then with the most influential selected parameters, we used a complete
498 sampling with 10 replicates in order to estimate main effects and first order interactions
499 effects on the sensitivity of model outputs. We used the same models as those used with
500 the experimental design to estimate SI and global sensitivity indices (*TSI*). *TSI*, that
501 measured the mean of the y deviance (or variance for *mlr* output) on the uncertain
502 parameters different from x_i (Saltelli, 2004; Saltelli et al., 2008; Faivre et al., 2013), were
503 calculated for each parameter as follows

504
$$TSI(x_i) = \frac{E[Dev(y|x_j, j \neq i)]}{Dev(y)}. \quad (19)$$

505 *TSI* corresponds also to a measure of the sum of the main effect of a parameter x_i and the
506 effects of interactions of this parameter with all the other uncertain parameters (Saltelli,
507 2004; Saltelli et al., 2008; Faivre et al., 2013). Both indices *SI* and *TSI* are between 0 and 1
508 but *TSI* is higher than *SI* as it includes interaction effects. Estimating the impact of first
509 order interaction was necessary to assess the combined effect of uncertainties on two
510 parameters, which may be different from the sum of the main effects of the two
511 parameters. We expressed SI and TSI in percentage and we assumed the more distant from
512 0 they were, the more impact they have on model results.

513 Statistical analyses of model outputs were carried out using R (R Core Team,
514 2013). To run all our simulations of the sensitivity analysis, we used OpenMOLE which is
515 a workflow engine specifically tailored for the distributed exploration of simulation models
516 (Reuillon et al., 2013).

517

518 3. Results

519 We present in Fig 2 an illustrative example of model output where we followed the
520 dynamics over time in RB1 and RB2 of the recruitment for a same set of parameters by
521 just varying the value of the distance between RB1 and RB2.

522 3.1. Selection of the most influential parameters

523 Among the 13000 simulations with the D-Optimal design, we observed failure of
524 colonization of RB2 in 48% of simulations (i.e. $fs = 0$). Thirteen percent of simulations led
525 to an unstable population (i.e. $fs = 1$) and 39% led to stable situations in RB2 (i.e. $fs = 2$).
526 The logistic regression applied to fsP and fsS explained 78% and 70% of the null deviance
527 respectively and the analysis of variance of mlr explained 60% of the null variance (Table
528 4). Focusing on the ten highest SI of the three model outputs, we identified 13 different
529 parameters meaning that model outputs are relatively sensitive to the same parameter (Fig.
530 3). It was especially true for fsP and fsS which were very sensitive to the distance between
531 RB1 and RB2 that explained around 50% of the deviance for these two variables (Fig. 3).
532 These two variables were also sensitive to parameters of the growth ($\kappa_{optGrow}$), maturation
533 (L_{mat}), and survival processes (Z_{sea}) which are highly linked to the duration of the
534 individual life at sea (Fig. 3). So, the success of colonization and the stability of the
535 population were, not surprisingly, negatively linked to $intDist$, but also to parameters that
536 increased the duration of the life at sea. mlr was mainly sensitive to the watershed area of
537 RB2 (Fig. 3) with a positive correlation between mlr and WA_{RB2} as this parameter is
538 involved in the reproduction process to determine the production capacity of RB2. mlr was
539 also sensitive to the other parameters of the reproduction process ($Surv_{optRep}$, λ and T_{optRep})
540 and to the environmental parameter $intDist$. To select the most influential parameters, we
541 kept 12 of the 13 parameters identified in the ten highest SI of the three model outputs.
542 Actually, as the outputs were not very sensitive to $T_{maxSurvRiv}$ which was a parameter used to

543 control the suitability of RB1 in our test case, we did not select this parameter and rather
544 selected the parameter $w^{deathBasin}$ involved in dispersal. Among the 13 selected parameters,
545 four concerned the reproduction process, two concerned the growth, survival and upstream
546 migration (i.e. dispersal) processes, one concerned the maturation process and the last two
547 were environmental parameters (Table 3). Consequently, in the second step of the
548 sensitivity analysis, the complete sampling consisted in 24576 simulations that we
549 replicated 10 times.

550 3.2. Analysis of interaction effects

551 Among the 245760 simulations, we observed 49% of unsuccessful colonization, 11% of
552 simulations led to an unstable population in RB2 and 40% led to a stable situation.
553 Although we considered fewer parameters than with the D-Optimal design, the explained
554 deviance and variance of the outputs analysis increased in this second step of the
555 sensitivity analysis because we took first order interactions effects into account. We
556 explained 90% and 85% of the deviance for fsP and fsS respectively and 79% of the
557 variance for mlr (Table 4). The output variables were globally sensitive to the same
558 parameters than those observed with the D-Optimal design (Fig. 4). This sensitivity
559 analysis confirmed that the model outputs fsP and fsS were particularly sensitive to the
560 environmental parameter $intDist$ and to parameters increasing the duration of the life at sea
561 ($\kappa_{optGrow}$, L_{mat} , and Z_{sea}) and that mlr was sensitive to the two environmental parameters and
562 to parameters of the reproduction process. Additionally, we observed a great importance of
563 the interaction effects for two parameters: the homing probability p_{hom} and the parameter
564 θ of the reproduction process which is linked to the strength of the Allee effect (Fig. 4).
565 This was especially true for the fsS output where the main effect of the homing probability
566 and the parameter θ were very low (0.02% and 0.03% respectively) while the interaction
567 effects of these factors with other parameters explained 6.3% and 4.9% of the null

568 deviance respectively (Fig. 4). Interaction effects of the homing probability were
569 particularly high with the distance between RB1 and RB2 and the optimal growth
570 coefficient $\kappa_{optGrow}$. For the parameter θ , interaction effects were high with the length at
571 first maturity, the optimal growth coefficient and the annual mortality coefficient at sea.
572 We also observed a high interaction between the weight of the death basin and the distance
573 between RB1 and RB2 to explain the stability of the population in RB2.

574 To summarize, the success and the stability of the colonization of RB2 are very
575 sensitive to the landscape structure represented through the distance between RB1 and RB2
576 and to parameters related to the duration of the life at sea and the survival condition in this
577 compartment. Interaction effects mainly highlighted that the role of the homing and the
578 Allee effect should be considered with attention. Concerning the abundance of the
579 recruitment in RB2, it is sensitive to parameters of the reproduction process and to the
580 watershed area of RB2.

581

582 **4. Discussion**

583 We developed, implemented and tested an individual-based model combining population
584 dynamics, dispersal and temperature requirements. GR3D has been designed to assess the
585 persistence of diadromous fish and the evolution of their distribution area in a context of
586 global warming. To our knowledge, this is the first attempt to incorporate dispersal
587 abilities of diadromous fish within a dynamic approach at the scale of their distribution
588 range. This article focuses on the individual-based model description and its exploration
589 with a basic virtual test case. We deliberately chose to run our simulations in a simple,
590 virtual environment in order to clearly disentangle the effect of the environment and the
591 effect of uncertainties in population dynamics on model outputs using a global sensitivity
592 analysis. We demonstrated the sensitivity of the outputs to some key population dynamics

593 parameters and to environmental parameters which were consistent with our knowledge of
594 this species. We considered our results are satisfactory enough to address more precisely,
595 in further studies, the issue of allis shad persistence in a context of global change at the real
596 scale of its distribution range. GR3D has been designed as a flexible and generic model
597 and can represent an integrative tool to study persistence of diadromous fish whose
598 population dynamics is well documented. After discussing the innovations and the
599 structure of the model, we come back to the understandings brought by our test case and its
600 associated sensitivity analysis.

601

602 *4.1. Innovations and model structure*

603 The GR3D model incorporates an explicit dynamic model of diadromous fish dispersal
604 process at large scale. This is particularly relevant in a context of climate change since
605 [Brooker et al. \(2007\)](#) has demonstrated that dispersal ability of individuals interacts with
606 the rate of climate change to determine range shifting dynamics. To model dispersal in
607 GR3D, we took both landscape structure and individual dispersal abilities into account. We
608 defined a generic accessibility model for available habitats (i.e. river basins) that depends
609 on the dispersal distance and the size of the individuals (as it represents a proxy of their
610 swimming capacities). Dispersal distance has already been recognized as an important
611 factor in dispersal processes and is often represented through dispersal kernels in dispersal
612 modelling approaches ([Chesson and Lee, 2005](#); [Slone, 2011](#); [Bocedi et al., 2012](#)).
613 Moreover the individual size has been recognized as closely linked to dispersal potential of
614 individuals with potential impacts on species' range shifts through phenotype dependent
615 dispersal processes ([McCauley and Mabry, 2011](#)). Furthermore, incorporating the size of
616 individuals in a context of climate change is relevant as shifts in body size and its
617 consequences in dispersal (and also in a lot of other life history parameters) have been

618 identified as the third major response to climate change (Gardner et al., 2011). In our
619 dispersal process, we also modelled the attractiveness of the available habitats as a function
620 of their watershed area as we assumed it was a proxy of the river flow. River flow has
621 already been showed as being the vector of attractive factors for diadromous species such
622 as larval pheromone by the sea lamprey (*Petromyzon marinus*) (Vrieze and Sorensen,
623 2001) or natural stream odor by salmon (Barinaga, 1999). The function we used for
624 dispersal modelling can then be parameterized and calibrated according to the studied
625 species and the knowledge of its population dynamics. This process has been designed in
626 order to integrate easily other effects that could potentially influence dispersal of a species.

627 Moreover, although our test case dealt with an anadromous species, the GR3D
628 model could also be adapted to catadromous species assuming for these species that
629 dispersers are strayed juveniles that do not use the same growing area (river catchment or
630 estuary) than their parents and have to choose consequently another river basin for their
631 freshwater life. However, the high heterogeneity of diadromous fish species life histories
632 (McDowall, 1988; McDowall, 1997) imply that further specific and local adjustments
633 might be required for different species. For instance, in its current version, GR3D is not
634 able to deal with the diversity and complexity of Atlantic salmon life cycle. A large
635 amount of literature is available for this species describing its population dynamics in
636 many catchments (Mangel, 1994; Rivot et al., 2004; Reed et al., 2011). Recently, Piou and
637 Prevost (2012) developed and parameterized IBASAM, a complex individual-based model
638 to simulate population dynamics of Atlantic salmon in the Scorff River (Brittany, France).
639 Despite the high complexity of this model, it does not incorporate all phenotypes of
640 Atlantic salmon life histories and further developments would also be needed according to
641 the Atlantic salmon population studies. The IBASAM model, described as a tool for the
642 investigation of potential climate change effects on Atlantic salmon population structure,

643 did not consider individual dispersal and so potential modification of distribution range in
644 response to environmental change. Consequently, the GR3D and IBASAM models might
645 be complementary dynamic approaches in order to study Atlantic salmon response to
646 climate change.

647 As GR3D is a complex model integrating numerous parameters, our study dealt
648 also with the question of the degree of complexity that should be incorporated in modeling
649 approach as the more the complexity is high in a model, the more the model is able to
650 reproduce the observed reality but the more it is difficult to calibrate, to extrapolate and to
651 analyze the model results (Levins, 1966; Caswell and John, 1992). Some authors consider
652 that simple models are the best way to lead to generality in ecology (Holling, 1966) while
653 other authors argue that this point of view may be an obstacle to the progress of ecological
654 research and demonstrate that in some cases at least, complex models are desirable,
655 general, and can be linked with simple models (Lassalle, 2008; Evans et al., 2013). In the
656 GR3D model, several simplifications were made in the structure of the model. First, in its
657 current version, GR3D does not deal with genetic and evolution issues although future
658 works have already been envisaged in this aim. Second, we did not represent explicit
659 movements of individuals within compartments (e.g. with a random walk process
660 (O'Sullivan and Perry, 2009)) and we assumed homogeneous conditions within a
661 compartment. Third, despite the expected impact of climate change on precipitation and
662 therefore river discharge, we did not incorporate the effect of discharge on population
663 dynamics processes as we were not able to link the effect of this parameter on life history
664 traits, largely because models linking precipitation to river flow are complex and focus
665 mostly at local scales (Milly et al., 2005; Qi et al., 2009; Beyene et al., 2010). Finally,
666 GR3D is a generic mono-species model and thus does not take into account potential
667 interactions between or among species. There are thus opportunities for further

668 improvements of the model. However, these improvements would undoubtedly lead to a
669 significant increase in model complexity and consequently of the computation time. In our
670 opinion, our mechanistic representation is realistic enough to address the issue of
671 diadromous fish dispersal and their persistence under climate change at a large scale.
672 Consequently, GR3D appears as a great step forward in management of diadromous fish
673 species. It could be used as an integrative tool to assess potential impact of climate change
674 on endangered diadromous fish species. For instance, we might be able to identify for an
675 endangered population if demographic rescue from neighboring populations will be likely
676 or if restocking program would be relevant and necessary (Seddon et al., 2009; Loss et al.,
677 2011). The GR3D model is able to generate predictions of change in the distribution of
678 species but also predictions of population abundances under defined climate change
679 scenario.

680

681 *4.2. Model parameterization and sensitivity*

682 GR3D was parameterized to reproduce dispersal and population dynamics of a virtual allis
683 shad population between two river catchments in a context of temperature increase. After
684 50 years of simulations to initialise an abundant and stable population in RB1, temperature
685 started to increase and RB2 became gradually suitable while suitability of RB1 gradually
686 decreases. This scenario was a way to mimic a situation where a population threatened by
687 temperature warming had an opportunity to colonize a new suitable habitat. Consequently
688 for analyzing model results, we mainly focused on the colonization of previously
689 uninhabited river basin RB2. With a more complex environment, it would have been
690 difficult to clearly disentangle the effect of the environment and the effect of uncertainties
691 in population dynamics on model outcomes. We chose therefore this simple test case.

692 GR3D is a complex model incorporating a high number of parameters.
693 Consequently, several analyses were necessary to further understand the relative role of
694 different parameters in the model outputs. Such analyses are essential for complex models
695 to avoid misinterpretation of simulation results (Grimm and Railsback, 2005). From this
696 consideration, the fast computation time of the GR3D model is a real advantage. Actually,
697 in our simple test case, the model dealt with millions of individuals but each simulation of
698 200 years took less than one second with a mean duration of simulations around 0.3
699 second. We tested the model with more complex virtual environment (e.g. with 25 river
700 basins) and the duration of simulation was always below one minute.

701 In the test case, we assumed that dispersal depended only on the dispersal distance.
702 We did not incorporate an effect of the individual length as we considered only one
703 population and as the length of allis shad spawners (i.e. potential dispersers for this
704 species) has always been observed as relatively homogeneous within a population
705 (Bagliniere and Elie, 2000). We also ignored the effect of the watershed area in the
706 dispersal function, as only one river was available for dispersers.

707 Analyzing the success of the colonization of RB2 and the stability of the population
708 in RB2, our sensitivity analyses showed the importance of dispersal distance and of
709 parameters related to the duration of the life at sea ($\kappa_{optGrow}$, L_{mat}) and the survival condition
710 in this compartment (Z_{sea}). These results were consistent with our expectation and
711 reproduced the expected dynamics of the model. We populated the environment initially in
712 order to have an abundant and stable population in RB1. Consequently, a high number of
713 dispersers were able to colonize the uninhabited river and were only limited by the distance
714 they have to cross. The duration of the life at sea is highly linked to the resilience of
715 diadromous species (i.e. the more the individuals stay at sea, the more the mortality of
716 individuals is high and the resilience of the studied species is low) and so unsurprisingly

717 influences dispersal and stability of population as well as the survival conditions at sea.
718 The analysis of interactions effects showed the importance of the homing (p_{hom}) and of the
719 Allee effect (parameter θ). As the probability of homing determines the number of
720 dispersers, it was also not surprising to obtain a high interaction effect with the dispersal
721 distance. In a same way, we introduced an Allee effect in the reproduction dynamics in
722 order to take into account potential difficulties to establish a population in an uninhabited
723 river basin such as mate limitation and reproductive facilitation problems or a decrease of
724 juvenile mortality with decreasing stock size (Berec et al., 2007). It explains consequently
725 the high effect of the interactions of this parameter. Concerning the abundance of the RB2
726 population, the most influential parameters were, as expected, parameters linked to the
727 success of the reproduction. Actually, parameters $surv_{optRep}$, λ and T_{optRep} defined the
728 survival of individuals between egg and recruit stages and the watershed area of RB2 were
729 directly linked to its production capacity.

730 Furthermore, model outcomes were not very sensitive to thermal parameters. This
731 result might be explained by a high thermal tolerance of the allis shad species and by the
732 use of the Gironde basin temperature to initialize temperature of RB1 and RB2 (except the
733 spring temperature that we modified to control the suitability of the two rivers). The
734 Gironde system is located in the middle of the allis shad distribution range and, although
735 the Gironde allis shad population is endangered, this might not be because of an
736 environmental change (Rougier et al., 2012).

737 The results of this test case are a good way to illustrate the dynamics included in the
738 GR3D model. This step was necessary before applying GR3D to a more complex case
739 study to avoid misinterpretation on the model results. Simulation results of the GR3D
740 model might also be compared with results of a species distribution model applied to the
741 same species by Lassalle (2008). We could quantify the divergence in prediction of future

742 potential distribution between static and dynamic approaches as has already be done for
743 two virtual plant species by [Engler and Guisan \(2009\)](#), who showed significant differences
744 between the two kind of approach. Recently, [Estes *et al.* \(2013\)](#) also compared mechanistic
745 and empirical model projections for the suitability of a crop species and concluded that
746 both approaches might be complementary. [Lassalle *et al.* \(2008a\)](#) described the 1900
747 observed distribution of European diadromous fish species. Using this 1900 distribution in
748 GR3D as an input defining the initial distribution of individuals, and then, simulate
749 population dynamics from 1900 to today might be a way to validate the GR3D model. We
750 could thus compare projected distributions of GR3D simulation results with the current
751 distribution of European diadromous fish species to analyze whether species have
752 responded in the way that the GR3D model suggests ([Kerr and Dobrowski, 2013](#)).

753

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761

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List of tables :

Table1. List of agents intervening in the GR3D individual-based model, with their state variables and corresponding status or measure unit.

Agent	State Variable	Description	Status/unit of measure
Sea basin	name	Name ID	SB and a number
	seasonal temperature	Water temperature	Numeric (°C)
River basin	name	Name ID	RB and a number
	longitude	Longitude at the mouth	Numeric (°)
	latitude	Latitude at the mouth	Numeric(°)
	watershed area	Watershed area of the river basin	Numeric (km ²)
	seasonal temperature	Water temperature	Numeric (°C)
Diadromous fish	ID	Fish identification	Numeric (-)
	gender	Sex	M, F
	stage	Stage	Mature, immature
	age	Age	Numeric (-)
	body-length	Body length	Numeric (cm)
	location	Current location	Name of the compartment
	birth place	Birth place	Name of the birth compartment
	number of reproduction	Number of reproduction	Numeric (-)

Table 2. GR3D parameters description and selected nominal values for the test case with allis shad.

Parameter name	Description	Value	Reference or remarks
Reproduction			
repSeason	Season of the reproduction	Spring	(Mennesson-Boisneau et al., 2000b)
Δt_{rec}	Assumed age of juvenile produced by the reproduction (Year)	0.33	As we assumed that recruitment were juveniles in estuary, we used the study from Lochet et al. (2008)
η	Parameter to relate $S_{95,j}$ and the surface of a spawning place (Ind/km ²)	2.4	Offline calibration using the study from Rougier et al. (2012)
θ	Ratio between $S_{95,j}$ and $S_{50,j}$ in each spawning place	1.9	Offline calibration using the study from Rougier et al. (2012)
a	Parameter of the S-R relationship linked to the fecundity of the studied species (Eggs/individual)	135000	(Cassou-Leins et al., 2000; LANUV, 2010)
$surv_{optRep}$	Optimal survival rate of an individual from eggs to the age Δt_{rec}	$1.7 \cdot 10^{-3}$	Offline calibration using the study from Rougier et al. (2012)
$T_{minRep}, T_{optRep}, T_{maxRep}$	Water temperature (°C) regulating survival of an individual from eggs to the age Δt_{rec}	14, 20, 26	(Cassou-Leins et al., 2000; Kottelat and Freyhof, 2007)
λ	Parameter to relate c_j and the surface of a spawning place	$4.1 \cdot 10^{-4}$	Offline calibration using the study from Rougier et al. (2012)
σ_{rep}	Standard deviation of log-normal distribution of the recruitment	0.2	Reasonable guessed
Sp_{sp}	Survival probability of spawners after reproduction (i.e. iteroparous rate)	0.1	(Mennesson-Boisneau et al., 2000b)
Downstream migration			
downMigAge	Age of individual when it runs toward the sea (Year)	0.33	(Lochet et al., 2008); In the test case, this migration concerns also spawners which survive after reproduction but, as mature individuals, they migrate automatically at sea the season following the reproduction
downMigSeason	Season of the run of individuals toward the sea	summer	In the test case, both juveniles and spawners which survive after reproduction migrate in summer (Cassou-Leins et al., 2000)
Growth			
L_{mi}	Initial length of juvenile in estuary (cm)	2	As we considered juveniles in estuary, we used the study from Lochet et al. (2008)
$\sigma_{\Delta L}$	Standard deviation of log-normal distribution of the	0.2	Reasonable guessed

L_{∞}	growth increment Asymptotic length of the individual (cm)	60	(Mennesson-Boisneau et al., 2000a)
$T_{minGrow}$, $T_{optGrow}$, $T_{maxGrow}$	Water temperature (°C) regulating the growth	3, 17, 26	Reasonable guessed
$K_{optGrow}$	Optimal growth coefficient (cm/season)	0.3	(Bagliniere and Elie, 2000; Aprahamian et al., 2002)
Survival			
Z_{sea}	Annual mortality coefficient at sea (Year ⁻¹)	0.4	Reasonable guessed based upon Rougier et al. (2012)
H_{riv}	Annual mortality (different from natural) coefficient in river (Year ⁻¹)	0	Reasonable guessed to 0 to limit the complexity of the test case
$T_{minSurvRiv}$, $T_{optSurvRiv}$, $T_{maxSurvRiv}$	Water temperature (°C) regulating survival of individual in river	10, 20, 23	In the test case, it concerns only spawners during the reproduction run and this phase has been shown highly dependent of water temperature (Cassou-Leins et al., 2000; Kottelat and Freyhof, 2007) Natural mortality was assumed to be negligible at optimal conditions during the reproduction run as it concerns a short period of 3 months (Cassou-Leins et al., 2000)
$surv_{optRiv}$	Optimal natural survival rate of individuals in river (Year ⁻¹)	1	
Maturation			
L_{mat}	Length at first maturity (cm)	40	(Cassou-Leins et al., 2000; Lassalle et al., 2008b)
Upstream migration			
upMigAge	Age of individual when it runs toward the river (Year)	-	In the test case, this migration concerns only mature individuals and is not age-specific consequently
upMigSeason	Season of the return of spawners in river for spawning	spring	All mature individuals at sea migrate in river at this season
P_{hom}	Probability to do natal homing behavior	0.75	(Tomas et al., 2005)
α_{const} , α_{dist} , α_{TL} , α_{WA}	Parameters of the logit function used to determine the weight of each accessible basin for dispersers	-2.9, 19.7, 0, 0	Reasonable guessed assuming a weight of 0.95 and 0.05 for a basin located at a distance of 10km and 300km respectively and assuming no effect of individual size and surface of basins on dispersal
$\overline{D}_{j-birthPlace}$, $\overline{\sigma}_{j-birthPlace}$, \overline{TL} , $\overline{\sigma}_{TL}$, \overline{WA} , $\overline{\sigma}_{WA}$	Mean and standard deviation used for standard core values in the logit function	300, 978,-,-,-,-	Reasonable guessed assuming that 300 km was close to the maximal distance of allis shad dispersal and from EuroDiad 2.0 database (Lassalle, 2008). Parameters linked to fish length and surface basin were not relevant in the test case.
$W^{deathBasin}$	Weight of the death basin used to introduced a mortality of dispersers	0.4	Reasonable guessed

Table 3. Uncertain population dynamics parameters of the GR3D model and environmental parameters tested in the sensitivity analysis of the test case.

Parameter name	Tested values	Selected for complete sampling (Yes or No)
Reproduction SM1		
η	[2.2; 2.6]	N
θ	[1.8; 2]	Y
$surv_{optRep}$	[$1 \cdot 10^{-3}$; $2 \cdot 10^{-3}$]	Y
T_{minRep}	[13.3; 14.6]	N
T_{optRep}	[19.3; 20.6]	Y
T_{maxRep}	[25.3; 26.6]	N
λ	[$3 \cdot 10^{-4}$; $5 \cdot 10^{-4}$]	Y
σ_{rep}	[0.1; 0.3]	N
Growth SM2		
$\sigma_{\Delta L}$	[0.1; 0.3]	N
$T_{minGrow}$	[2.3; 3.6]	N
$T_{optGrow}$	[16.3; 17.6]	Y
$T_{maxGrow}$	[25.3; 26.6]	N
$\kappa_{optGrow}$	[0.2; 0.4]	Y
Survival SM3		
Z_{sea}	[0.3; 0.5]	Y
$T_{minSurvRiv}$	[9.3; 10.6]	N
$T_{optSurvRiv}$	[19.3; 20.6]	Y
$T_{maxSurvRiv}$	[22.3; 23.6]	N
Maturation SM5		
L_{mat}	[36; 44]	Y
Anadromous migration SM6		
P_{hom}	[0.6; 0.9]	Y
$W^{deathBasin}$	[0.2; 0.6]	N
Environmental parameters		
WA_{RB2}	[20000; 40000; 80000]	Y
$intDist$	[100; 300; 600; 900]	Y

Table 4. Percentage of explained deviance (for *fsP* and *fsS*) and explained variance (for *mlr*) by the model applied to outputs variables according to the experimental.

Design	Output variable		
	<i>fsP</i>	<i>fsS</i>	<i>mlr</i>
D-Optimal design	78%	70%	60%
Complete sampling			
Without interaction effects	81%	69%	54%
With interaction effects	90%	85%	79%

List of figures :

Fig. 1. Conceptual diagram of the life cycle of anadromous species (adapted for allis shad) represented in the GR3D individual-based model.

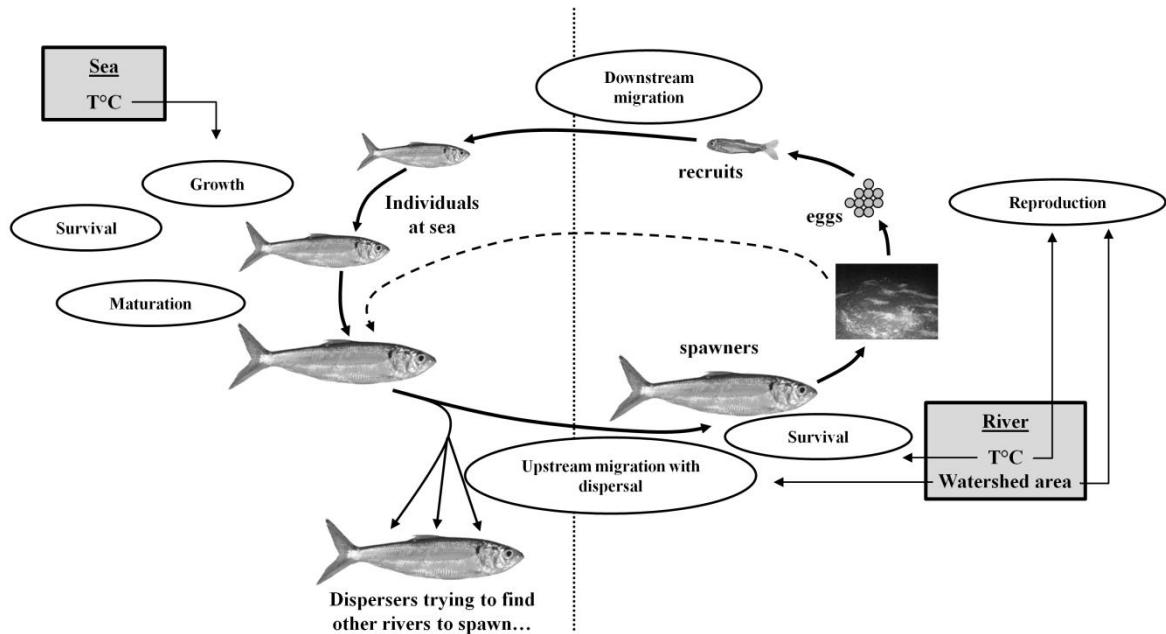


Fig. 2. Illustrative example of simulation results over 200 years showing the dynamics over time of the recruitment in RB1 and RB2 using the nominal values of the model parameters and with (A) a distance of 300 km between RB1 and RB2 and a success of the colonization of RB2 ($f_s = 2$), (B) a distance of 600 km between RB1 and RB2 and very low recruitments in RB2 at the end of simulation ($f_s = 1$), and (C) a distance of 900 km between RB1 and RB2 and no colonization of RB2 ($f_s = 0$).

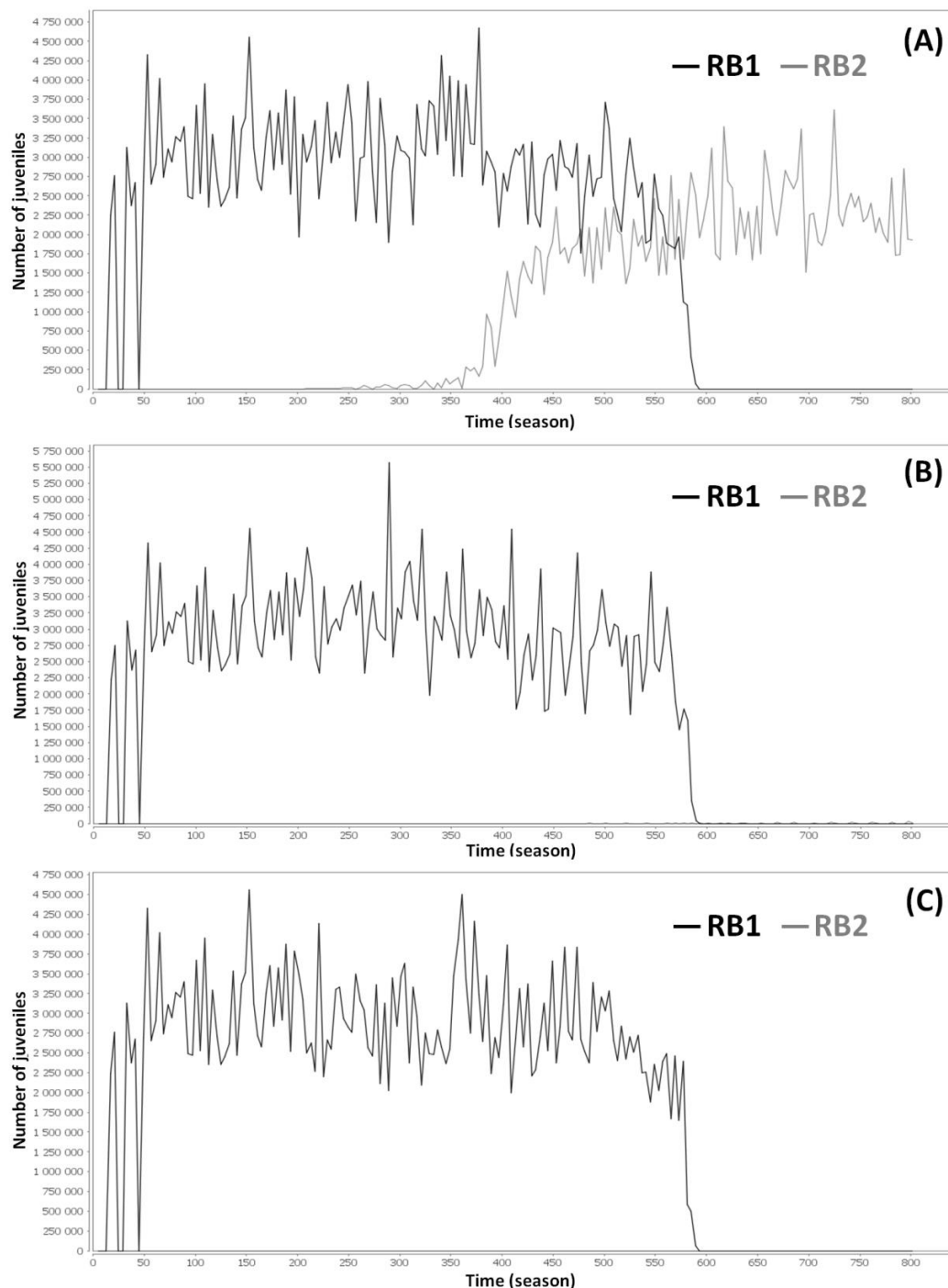


Fig. 3. Ten highest SI values (in %; the higher the percentage, the more sensitive the model is to the considered parameter) for the *fsP* (A), *fsS* (B) and *mlr* (C) output variables calculated from logistic regression for *fsP* and *fsS* and ANOVA for *mlr* with the D-Optimal experimental design (theta and lambda correspond to the parameters θ and λ of the reproduction process respectively).

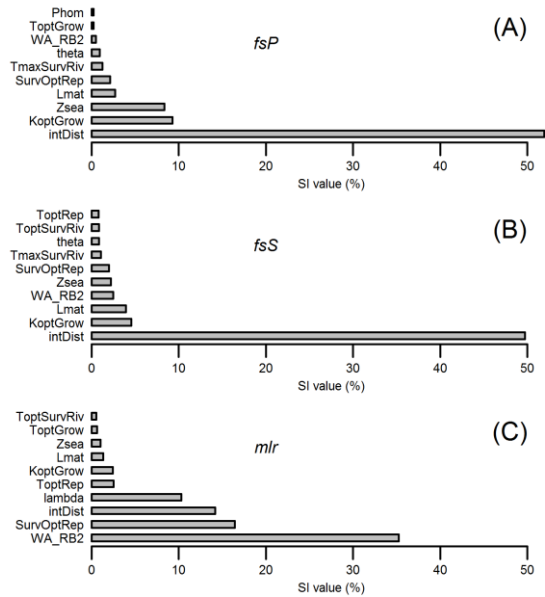


Fig. 4. TSI values (in %; the higher the percentage, the more sensitive the model is to the considered parameter) for the *fsP* (A), *fsS* (B) and *mlr* (C) output variables calculated from logistic regression on *fsP* and *fsS* and ANOVA on *mlr* with the complete sampling design (theta, lambda, weightDB correspond to the parameters θ , λ and $w^{deathBasin}$ respectively).

