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

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#### Abstract

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


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

## 1. Introduction

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

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

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

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

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

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

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

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

For diadromous species, developing a model combining climatic requirements and population dynamics with explicit dispersal processes is a real challenge and will be a major step forward for guiding management policies. If successful, it could help to determine in which catchment and for which species restoration and restocking actions will be relevant. Moreover, the development of this kind of model for diadromous fish does not appear to be limited by the knowledge of their ecology and their population dynamics which are now well documented (at least for the continental phase) for several species such as Atlantic salmon Salmo salar (Peterson et al., 1977; Bagliniere and Maisse, 1985; Fleming, 1996; Friedland, 1998; Hutchings and Jones, 1998; Forseth et al., 2001; Jonsson
and Jonsson, 2009; Buoro et al., 2010), European eel Anguilla anguilla (Gatto and Rossi, 1979; Vollestad and Jonsson, 1988; De Leo and Gatto, 1995; Dekker, 2000; Lambert, 2005; Lambert and Rochard, 2007; Bevacqua et al., 2011), European sturgeon Acipenser sturio (Rochard and Lambert, 2011) or allis shad Alosa alosa (Lambert et al., 2001; Acolas et al., 2006; Lassalle et al., 2008b; Mota and Antunes, 2011; Rougier et al., 2012).

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

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

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

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

## 2. Materials and methods

### 2.1. Model description

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

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

### 2.1.1. Purpose

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

### 2.1.2. State variables and scales

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

Entities and spatial scales: Three types of entities compose the GR3D model: one for fish agents and two for environment elements. GR3D is spatially explicit with a continental
compartment and a sea compartment. The continental compartment is split up in "River Basins". Each "River Basin" (RB) is characterized by a name, a position (latitude and longitude at the mouth), a catchment area $\left(\mathrm{km}^{2}\right)$ and seasonal mean water temperatures at the mouth (Table 1).

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

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

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

### 2.1.3. Process overview and scheduling

GR3D is developed to cover the entire life cycle of any diadromous fish species trying to be the more generic as possible and taking into account the differences between anadromous and catadromous species. Hence, we structured the model in six submodels consistent with the life cycle events and processes of any diadromous species (reproduction, growth, survival, downstream migration, maturation, and upstream migration including dispersal). As the present test case deals with an anadromous species (see section 2.2.), we only presented the computational order of life cycle events and
processes in a conceptual diagram for an anadromous species with allis shad as an illustrative case (Fig. 1).

### 2.1.4. Design concepts

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

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

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

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

### 2.1.5. Initialization

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

### 2.1.6. Input

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

### 2.1.7. Submodels

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

### 2.1.7.1. Reproduction:

Reproduction occurs yearly during the reproduction season (defined as a population parameter, Table 2) in each river basin when spawners are present. We assumed that numbers of recruits $R_{j}$ produced by $S_{j}$ spawners in a spawning basin $j$ follows a Beverton \& Holt stock-recruitment relationship of parameters $\alpha_{j}$ and $\beta_{j}$ (BH S-R) (Beverton and Holt, 1957). However we modified the traditional BH S-R:

- We included an Allee effect (Eq. (1)) to take into account difficulties to settle a population with limited numbers of fish in new habitats. Depensation strength is modeled as a function of river basin watershed area through two species specific parameters: $\eta$ a parameter linking the basin watershed area $W A_{j}$ to its carrying capacity (the higher $\eta$ is, the higher the stock level to reach $95 \%$ of the asymptotic recruitment) and $\theta$ which controls the Allee effect strength (a high $\theta$ corresponds to a strong depensation, i.e. the stock level to produce half of the asymptotic recruitment is close to the stock level producing $95 \%$ of the asymptotic recruitment).

$$
\begin{equation*}
R_{j}=\frac{\alpha_{j} S_{j} \frac{1}{1+\mathrm{e}^{\left(-\ln (19) \frac{S_{j}-\eta / \cdot \cdot W A_{j}}{\eta \cdot W A_{j}-\eta / \theta \cdot W A_{j}}\right)}}}{\beta_{j}+S_{j} \frac{1}{1+\mathrm{e}^{\left(-\ln (19) \frac{S_{j}-\eta / / \cdot W A_{j}}{\eta \cdot W A_{j}-\eta / \theta \cdot W A_{j}}\right)}}} \tag{1}
\end{equation*}
$$

- By comparison to the traditional BH S-R, we considered that the non-density dependent mortality from egg to recruit (duration $\Delta t_{\text {rec }}$, Table 2) is a function of temperature, consequently parameters $\alpha_{j}$ and $\beta_{j}$ depend on temperature (Eq. (2) and Eq. (3)). Egg survival is optimal ( surv $_{\text {optRep }}$, Table 2) at $T_{\text {opt }}$ and there is no recruitment when temperature is out of the range $T_{\min }-T_{\max }$ (Eq. (4), Table 2). The density dependent mortality of the BH S-R is assumed to be dependent on the basin surface (through a population parameter $\lambda$, Table 2) to take into account resource limitations in small basins (Eq. (5)).

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

$$
\begin{equation*}
b_{j}=-\frac{1}{\Delta t_{\text {rec }}} \ln \left[\operatorname{surv}_{\text {optRep }} \frac{\left(T_{j}-T_{\text {minRep }}\right)\left(T_{j}-T_{\text {maxRep }}\right)}{\left(T_{j}-T_{\text {minRep }}\right)\left(T_{j}-T_{\text {maxRep }}\right)-\left(T_{j}-T_{\text {optRep }}\right)^{2}}\right], \tag{4}
\end{equation*}
$$

and

$$
\begin{equation*}
c_{j}=\frac{\lambda}{\operatorname{Surf}_{j}} . \tag{5}
\end{equation*}
$$

We introduce stochasticity in this process by drawing the value of the effective recruitment $R_{E f f, j}$ in a lognormal distribution of standard deviation $\sigma_{r e p}$ around the stock-recruitment relationship (Table 2).

After the reproduction, the population parameter $S p_{s p}$ (Table 2) defined the survival probability of the spawners to take into account the iteroparity of the studied species.

### 2.1.7.2. Downstream migration.

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

### 2.1.7.3. Growth.

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

$$
\begin{equation*}
\Delta L=\log N\left(\mu_{\Delta L}, \sigma_{\Delta L}\right), \tag{6}
\end{equation*}
$$

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

$$
\begin{equation*}
\mu_{\Delta L}=\log \left(\left(L_{\infty}-T L_{t}\right) \times\left(1-\exp ^{-\kappa \Delta t}\right)\right)-\frac{\sigma_{\Delta L}^{2}}{2} \tag{7}
\end{equation*}
$$

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

$$
\begin{equation*}
\kappa=\kappa_{\text {optGrow }} \frac{\left(T-T_{\text {minGrow }}\right)\left(T-T_{\text {maxGrow }}\right)}{\left(T-T_{\text {minGrow }}\right)\left(T-T_{\text {maxGrow }}\right)-\left(T-T_{\text {optGrow }}\right)^{2}} . \tag{8}
\end{equation*}
$$

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

### 2.1.7.4. Survival.

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

For individuals at sea, the seasonal survival probability, $S p_{\text {sea }}$, is calculated using the annual mortality coefficient at sea, $Z_{\text {sea }}$, defined as a population parameter (Table 2) and a survival equation

$$
\begin{equation*}
S p_{\text {sea }}=\exp ^{-Z_{\text {sea }} \times \Delta_{\text {seasos }}}, \tag{9}
\end{equation*}
$$

where $\Delta t_{\text {season }}$ is the duration of a season (i.e. 0.25 year $^{-1}$ ). We assumed that $Z_{\text {sea }}$ incorporates all sources of individual mortality at sea.

For individuals in river, the seasonal survival probability, $S p_{r i v}$, is calculated using two annual mortality coefficients $M_{\text {riv }}$ (natural mortality coefficient) and $H_{r i v}$ (human-induced mortality coefficient) defined as population parameters (Table 2) and a survival equation

$$
\begin{equation*}
S p_{r i v}=\exp ^{-\left(M_{r i v}+H_{r i v}\right) \times \Delta_{\text {scoson }}} . \tag{10}
\end{equation*}
$$

The natural mortality coefficient $M_{r i v}$ is assumed to be dependent on the river temperature $T_{j}$ and was computed as follows
where $T_{\text {minSurvRiv }}, T_{\text {opLSurvRiv }}, T_{\text {maxSurRRiv }}$ and surv optRiv were population parameters (Table 2). We assumed that the other mortality coefficient $H_{\text {riv }}$ incorporates the other sources of mortality in river (fishery, pollution, dams...).

### 2.1.7.5. Maturation.

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

### 2.1.7.6. Upstream migration.

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

1. The emigration phase: in this phase, individuals have a probability to adopt a homing ( $\left.p_{\text {hom }}\right)$ or a straying behavior $\left(1-p_{\text {hom }}\right)$ which is assumed to be a characteristic of the species. $p_{\text {hom }}$ is defined as a population parameter (Table 2).
2. The movement phase: Individuals that do not become strayers simply migrate in their natal river (homing behavior). For strayers, the probability to migrate in each river basin is assumed to be a function of its accessibility and its attractiveness. We assumed that accessibility depends on the dispersal distance $D_{j \text {-birthPlacei }}$ between basin $j$ and the birth place of an individual $i$, and on the total length $T L_{i}$ of the individual $i$. The basin attractiveness is assumed to be a function of its watershed area $W A_{j}$ as a proxy of the river flow. Then, the "weight" of each basin relative to an individual $i$ is computed using a logit function

$$
\begin{aligned}
\operatorname{logit}\left(w_{i}^{j}\right) & =\alpha_{\text {const }}+\alpha_{\text {dist }}\left(\frac{D_{j \text {-birthPlace }}-\overline{D_{j \text {-birthPlace }}}}{\sigma_{j-\text { birthPlace }}}\right), \\
& +\alpha_{T L}\left(\frac{T L_{i}-\overline{T L}}{\sigma_{T L}}\right)+\alpha_{W A}\left(\frac{W A_{j}-\overline{W A}}{\sigma_{W A}}\right),
\end{aligned}
$$

where $\alpha_{\text {const }}, \alpha_{\text {dist }}, \alpha_{T L}$ and $\alpha_{W A}$ are four population parameters (Table 2). In order to have comparable parameters, we used standard cores values of each factor influencing the
function and we defined $\overline{D_{j-\text { birthPlace }}}, \sigma_{j \text {-birthPlace }}, \overline{T L}, \sigma_{T L}, \overline{W A}$ and $\sigma_{W A}$ as population parameters (Table 2).

We assumed that individuals may also not find any basin so we introduce a virtual "death basin" with a fixed weight $w^{\text {deathBasin }}$. Then $w_{i}^{j}$ are standardized so that their sum equals 1 , providing probabilities to choose each river basin (including death basin). The choice is then modelled by a simple multinomial process.
3. The settlement phase: Individuals enter in the selected destination, survive if conditions are suitable and reproduce if they find mating requirements.

### 2.2. The test case

### 2.2.1. Description of the studies species

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

### 2.2.2. Environment, time and initialization

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

Each simulation starts in summer and lasts 200 years (i.e. 800 time steps). During the first fifty years of simulation, a virtual population of allis shad was created in RB1 by introducing there 500000 juveniles at the first time step. From the year 50 to the year 150 , we introduced in the two basins a linear water temperature increase of $3^{\circ} \mathrm{C}$ in 100 years (i.e. water temperature increase by $0.0075^{\circ} \mathrm{C}$ at each time step) and RB 2 becomes suitable for allis shad reproduction. At the end of the temperature increase, only RB2 is suitable for allis shad for the last 50 years of simulations. Temperatures in RB1 and RB2 were initialized with the same values except for the spring temperature as we used it to control the suitability of each river during the simulation. In order to work with realistic values, we used daily estimates of Gironde estuarine water temperature $\left({ }^{\circ} \mathrm{C}\right)$ provided by EDF (Electricité De France) between 1991 and 2009 to initialize the winter, summer and autumn temperatures in RB1 and RB2 as the Gironde basin is located at the center of the allis shad distribution area (Baglinière, 2000; Lassalle, 2008). Spring temperature of RB1 was set to $3^{\circ} \mathrm{C}$ below $T_{\text {maxsurriv }}$ and set to $T_{\text {minRep }}$ in RB2. The watershed area of RB1 was set to $40000 \mathrm{~km}^{2}$. The environmental parameters $W A \_R B 2$ and intDist were included in the global sensitivity analysis to assess the influence of the environment configuration on model outputs (see section 2.2.4.).

The seasonal mean water temperatures of SB1 and SB2 were calculated as the mean between $12^{\circ} \mathrm{C}$ and the seasonal mean water temperatures of RB 1 and RB 2 , respectively.

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

### 2.2.3. Model parameterisation

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

For the off-line calibration, we used a previous work (Rougier et al., 2012) about the population dynamics of allis shad in the Gironde basin for the parameterization of the reproduction process (i.e. parameter $\eta, \theta, \operatorname{surv}_{\text {optRep }}$ and $\lambda$ of the BH S-R relationship, Table 2) and used their estimates of $\alpha_{\text {Gironde }}, \beta_{\text {Gironde }}$ and $\eta$. We assumed that the recruitment was a number of juveniles in estuary and set $\Delta t_{\text {rec }}$ to 0.33 year (4 months) as it corresponds to the average duration of the juvenile downstream migration towards the sea (Lochet et al., 2008).

We assumed dispersal of allis shad was only dependant of the distance between the suitable habitats. Hence, $\alpha_{T L}$ and $\alpha_{W A}$ were set to 0 . We set $\sigma_{j \text {-birhPlace }}$ to 978 km (using the EuroDiad 2.0 database of European river basins from Lassalle (2008)). We set $\overline{D_{j-\text { birthPlace }}}$ to 300 km as we assumed that this value was close to the maximal distance of dispersal for allis shad. Then we assumed a weight of 0.95 and 0.05 for a basin located at a
distance of 10 km and 300 km respectively. In consequence, $\alpha_{\text {const }}$ and $\alpha_{\text {dist }}$ were set to -2.9 and 19.7 respectively (Table 2).

### 2.2.4. Sensitivity analysis

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

We defined two variables using the $f s$ output variable. $f_{s} P$ indicated the presence/absence of fish in RB2 (i.e. $f_{s}=0$ for absence and $f_{s}>0$ for presence). Considering only positive values of $f s$, we defined $f s S$ as a variable describing a kind of stability of the RB2 population (i.e. relatively unstable for $f s=1$ because it means that there is high variation in the recruitment values in the ten last year of simulation, and stable for $f s=2$ because it means that recruitment values are stable in the ten last years of simulation). Hence, we used these two variables to analyze the influence of parameters on both the presence/absence of fish in RB2 and on the stability of the population in RB2. mlr was a metric indicating the abundance of fish in RB2. As the null values described absence of fish in RB2, we only used positive values of $m l r$ to analyze the influence of parameters on abundance in RB2.

In order to screen non-influential and influential parameters on GR3D model outputs, we conducted a global sensitivity analyses by varying both the model and the environmental parameters. We identified 20 uncertain population dynamics parameters of
the GR3D model to incorporate in the sensitivity analysis and we added 2 environmental parameters in the analysis $\left(W A \_R B 2\right.$ the watershed area of RB2 and intDist the distance between RB1 and RB2; Table 3). Considering a maximal range of variation of $20 \%$ often used in sensitivity analysis (Drouineau et al., 2006; Lehuta et al., 2010), we set a low and a high value for each population parameter based on our own expertise and knowledge of allis shad population dynamics (Table 3). Concerning environmental parameters, we considered three modalities for $W A_{-} R B 2$ and four for intDist (Table 3). As a complete design would have taken too much time since it would involve more than 12 million simulations without replicates $\left(2^{20} \times 3 \times 4\right)$, we first used an experimental design to identify the most influential parameters on model outputs. Regarding the number of factors and modalities, the most appropriate experimental design are D-optimal designs (Drouineau et al., 2006; Faivre et al., 2013). In this type of design, the estimations of the effects are partially correlated (i.e. that contrary to factorial design, confusion between effects estimates may exist, but an algorithm is used to find the set of experiments), maximizing the determinant of the information matrix ( $X X^{\prime}$, with X , the matrix of the different combinations of modalities for each experiment) of the design, equivalent to maximizing the efficiency of the estimation (Droesbeke et al., 1997; Drouineau et al., 2006). We use the AlgDesign R package (Wheeler, 2011) to generate our D-Optimal design and, finally, the resulting experimental design consisted of 1300 simulations that we replicated 10 times. Only main effects were estimated with this design using a logistic regression model for $f_{s} P$ and $f s S$ and analysis of variance (ANOVA) for $m l r$. For each model output response $y$, first order indices $(S I)$ of a parameter $x_{i}$ measuring the importance of the deviance (or variance for $m l r$ output) of the $y$ mean conditionally on factor $x_{i}$, were considered as a sensitivity index (Saltelli, 2004; Saltelli et al., 2008; Faivre et al., 2013) and were calculated as follows

$$
\begin{equation*}
S I\left(x_{i}\right)=\frac{\operatorname{Dev}\left[E\left(y \mid x_{i}\right)\right]}{\operatorname{Dev}(y)} . \tag{18}
\end{equation*}
$$

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

$$
\begin{equation*}
\operatorname{TSI}\left(x_{i}\right)=\frac{E\left[\operatorname{Dev}\left(y \mid x_{j}, j \neq i\right)\right]}{\operatorname{Dev}(y)} . \tag{19}
\end{equation*}
$$

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

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

## 3. Results

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

### 3.1. Selection of the most influential parameters

Among the 13000 simulations with the D-Optimal design, we observed failure of colonization of RB2 in $48 \%$ of simulations (i.e. $f s=0$ ). Thirteen percent of simulations led to an unstable population (i.e. $f s=1$ ) and $39 \%$ led to stable situations in RB2 (i.e. $f s=2$ ). The logistic regression applied to $f_{s} P$ and $f s S$ explained $78 \%$ and $70 \%$ of the null deviance respectively and the analysis of variance of $m l r$ explained $60 \%$ of the null variance (Table 4). Focusing on the ten highest $S I$ of the three model outputs, we identified 13 different parameters meaning that model outputs are relatively sensitive to the same parameter (Fig. 3). It was especially true for $f_{s} P$ and $f_{s} S$ which were very sensitive to the distance between RB1 and RB2 that explained around $50 \%$ of the deviance for these two variables (Fig. 3). These two variables were also sensitive to parameters of the growth ( $\kappa_{\text {optGrow }}$ ), maturation ( $L_{\text {mat }}$ ), and survival processes $\left(Z_{\text {sea }}\right)$ which are highly linked to the duration of the individual life at sea (Fig. 3). So, the success of colonization and the stability of the population were, not surprisingly, negatively linked to intDist, but also to parameters that increased the duration of the life at sea. $m l r$ was mainly sensitive to the watershed area of RB2 (Fig. 3) with a positive correlation between $m l r$ and $W A \_R B 2$ as this parameter is involved in the reproduction process to determine the production capacity of RB2. mlr was also sensitive to the other parameters of the reproduction process (Surv optRep, $\lambda$ and $T_{\text {optRep }}$ ) and to the environmental parameter intDist. To select the most influential parameters, we kept 12 of the 13 parameters identified in the ten highest $S I$ of the three model outputs. Actually, as the outputs were not very sensitive to $T_{\text {maxSurviiv }}$ which was a parameter used to
control the suitability of RB1 in our test case, we did not select this parameter and rather selected the parameter $w^{\text {deathBasin }}$ involved in dispersal. Among the 13 selected parameters, four concerned the reproduction process, two concerned the growth, survival and upstream migration (i.e. dispersal) processes, one concerned the maturation process and the last two were environmental parameters (Table 3). Consequently, in the second step of the sensitivity analysis, the complete sampling consisted in 24576 simulations that we replicated 10 times.

### 3.2. Analysis of interaction effects

Among the 245760 simulations, we observed $49 \%$ of unsuccessful colonization, $11 \%$ of simulations led to an unstable population in RB2 and $40 \%$ led to a stable situation. Although we considered fewer parameters than with the D-Optimal design, the explained deviance and variance of the outputs analysis increased in this second step of the sensitivity analysis because we took first order interactions effects into account. We explained $90 \%$ and $85 \%$ of the deviance for $f_{s} P$ and $f_{s} S$ respectively and $79 \%$ of the variance for $m l r$ (Table 4). The output variables were globally sensitive to the same parameters than those observed with the D-Optimal design (Fig. 4). This sensitivity analysis confirmed that the model outputs $f_{s} P$ and $f_{s} S$ were particularly sensitive to the environmental parameter intDist and to parameters increasing the duration of the life at sea ( $\kappa_{\text {oplGrow }}, L_{m a t}$, and $Z_{\text {sea }}$ ) and that $m l r$ was sensitive to the two environmental parameters and to parameters of the reproduction process. Additionally, we observed a great importance of the interaction effects for two parameters: the homing probability $p_{\text {hom }}$ and the parameter $\theta$ of the reproduction process which is linked to the strengh of the Allee effect (Fig. 4). This was especially true for the $f s S$ output where the main effect of the homing probability and the parameter $\theta$ were very low ( $0.02 \%$ and $0.03 \%$ respectively) while the interaction effects of these factors with other parameters explained $6.3 \%$ and $4.9 \%$ of the null
deviance respectively (Fig. 4). Interaction effects of the homing probability were particularly high with the distance between RB1 and RB2 and the optimal growth coefficient $\kappa_{\text {optGrow }}$. For the parameter $\theta$, interaction effects were high with the length at first maturity, the optimal growth coefficient and the annual mortality coefficient at sea. We also observed a high interaction between the weight of the death basin and the distance between RB1 and RB2 to explain the stability of the population in RB2.

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

## 4. Discussion

We developed, implemented and tested an individual-based model combining population dynamics, dispersal and temperature requirements. GR3D has been designed to assess the persistence of diadromous fish and the evolution of their distribution area in a context of global warming. To our knowledge, this is the first attempt to incorporate dispersal abilities of diadromous fish within a dynamic approach at the scale of their distribution range. This article focuses on the individual-based model description and its exploration with a basic virtual test case. We deliberately chose to run our simulations in a simple, virtual environment in order to clearly disentangle the effect of the environment and the effect of uncertainties in population dynamics on model outputs using a global sensitivity analysis. We demonstrated the sensitivity of the outputs to some key population dynamics
parameters and to environmental parameters which were consistent with our knowledge of this species. We considered our results are satisfactory enough to address more precisely, in further studies, the issue of allis shad persistence in a context of global change at the real scale of its distribution range. GR3D has been designed as a flexible and generic model and can represent an integrative tool to study persistence of diadromous fish whose population dynamics is well documented. After discussing the innovations and the structure of the model, we come back to the understandings brought by our test case and its associated sensitivity analysis.

### 4.1. Innovations and model structure

The GR3D model incorporates an explicit dynamic model of diadromous fish dispersal process at large scale. This is particularly relevant in a context of climate change since Brooker et al. (2007) has demonstrated that dispersal ability of individuals interacts with the rate of climate change to determine range shifting dynamics. To model dispersal in GR3D, we took both landscape structure and individual dispersal abilities into account. We defined a generic accessibility model for available habitats (i.e. river basins) that depends on the dispersal distance and the size of the individuals (as it represents a proxy of their swimming capacities). Dispersal distance has already been recognized as an important factor in dispersal processes and is often represented through dispersal kernels in dispersal modelling approaches (Chesson and Lee, 2005; Slone, 2011; Bocedi et al., 2012). Moreover the individual size has been recognized as closely linked to dispersal potential of individuals with potential impacts on species' range shifts through phenotype dependent dispersal processes (McCauley and Mabry, 2011). Furthermore, incorporating the size of individuals in a context of climate change is relevant as shifts in body size and its consequences in dispersal (and also in a lot of other life history parameters) have been
identified as the third major response to climate change (Gardner et al., 2011). In our dispersal process, we also modelled the attractiveness of the available habitats as a function of their watershed area as we assumed it was a proxy of the river flow. River flow has already been showed as being the vector of attractive factors for diadromous species such as larval pheromone by the sea lamprey (Petromyzon marinus) (Vrieze and Sorensen, 2001) or natural stream odor by salmon (Barinaga, 1999). The function we used for dispersal modelling can then be parameterized and calibrated according to the studied species and the knowledge of its population dynamics. This process has been designed in order to integrate easily other effects that could potentially influence dispersal of a species.

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

As GR3D is a complex model integrating numerous parameters, our study dealt also with the question of the degree of complexity that should be incorporated in modeling approach as the more the complexity is high in a model, the more the model is able to reproduce the observed reality but the more it is difficult to calibrate, to extrapolate and to analyze the model results (Levins, 1966; Caswell and John, 1992). Some authors consider that simple models are the best way to lead to generality in ecology (Holling, 1966) while other authors argue that this point of view may be an obstacle to the progress of ecological research and demonstrate that in some cases at least, complex models are desirable, general, and can be linked with simple models (Lassalle, 2008; Evans et al., 2013). In the GR3D model, several simplifications were made in the structure of the model. First, in its current version, GR3D does not deal with genetic and evolution issues although future works have already been envisaged in this aim. Second, we did not represent explicit movements of individuals within compartments (e.g. with a random walk process (O'Sullivan and Perry, 2009)) and we assumed homogeneous conditions within a compartment. Third, despite the expected impact of climate change on precipitation and therefore river discharge, we did not incorporate the effect of discharge on population dynamics processes as we were not able to link the effect of this parameter on life history traits, largely because models linking precipitation to river flow are complex and focus mostly at local scales (Milly et al., 2005; Qi et al., 2009; Beyene et al., 2010). Finally, GR3D is a generic mono-species model and thus does not take into account potential interactions between or among species. There are thus opportunities for further
improvements of the model. However, these improvements would undoubtedly lead to a significant increase in model complexity and consequently of the computation time. In our opinion, our mechanistic representation is realistic enough to address the issue of diadromous fish dispersal and their persistence under climate change at a large scale. Consequently, GR3D appears as a great step forward in management of diadromous fish species. It could be used as an integrative tool to assess potential impact of climate change on endangered diadromous fish species. For instance, we might be able to identify for an endangered population if demographic rescue from neighboring populations will be likely or if restocking program would be relevant and necessary (Seddon et al., 2009; Loss et al., 2011). The GR3D model is able to generate predictions of change in the distribution of species but also predictions of population abundances under defined climate change scenario.

### 4.2. Model parameterization and sensitivity

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

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

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

Analyzing the success of the colonization of RB2 and the stability of the population in RB2, our sensitivity analyses showed the importance of dispersal distance and of parameters related to the duration of the life at sea ( $\kappa_{\text {oplGrow }}, L_{\text {mat }}$ ) and the survival condition in this compartment $\left(Z_{\text {sea }}\right)$. These results were consistent with our expectation and reproduced the expected dynamics of the model. We populated the environment initially in order to have an abundant and stable population in RB1. Consequently, a high number of dispersers were able to colonize the uninhabited river and were only limited by the distance they have to cross. The duration of the life at sea is highly linked to the resilience of diadromous species (i.e. the more the individuals stay at sea, the more the mortality of individuals is high and the resilience of the studied species is low) and so unsurprisingly
influences dispersal and stability of population as well as the survival conditions at sea. The analysis of interactions effects showed the importance of the homing ( $p_{\text {hom }}$ ) and of the Allee effect (parameter $\theta$ ). As the probability of homing determines the number of dispersers, it was also not surprising to obtain a high interaction effect with the dispersal distance. In a same way, we introduced an Allee effect in the reproduction dynamics in order to take into account potential difficulties to establish a population in an uninhabited river basin such as mate limitation and reproductive facilitation problems or a decrease of juvenile mortality with decreasing stock size (Berec et al., 2007). It explains consequently the high effect of the interactions of this parameter. Concerning the abundance of the RB2 population, the most influential parameters were, as expected, parameters linked to the success of the reproduction. Actually, parameters survoptRep, $\lambda$ and $T_{\text {optRep }}$ defined the survival of individuals between egg and recruit stages and the watershed area of RB2 were directly linked to its production capacity.

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

The results of this test case are a good way to illustrate the dynamics included in the GR3D model. This step was necessary before applying GR3D to a more complex case study to avoid misinterpretation on the model results. Simulation results of the GR3D model might also be compared with results of a species distribution model applied to the same species by Lassalle (2008). We could quantify the divergence in prediction of future
potential distribution between static and dynamic approaches as has already be done for two virtual plant species by Engler and Guisan (2009), who showed significant differences between the two kind of approach. Recently, Estes et al. (2013) also compared mechanistic and empirical model projections for the suitability of a crop species and concluded that both approaches might be complementary. Lassalle et al. (2008a) described the 1900 observed distribution of European diadromous fish species. Using this 1900 distribution in GR3D as an input defining the initial distribution of individuals, and then, simulate population dynamics from 1900 to today might be a way to validate the GR3D model. We could thus compare projected distributions of GR3D simulation results with the current distribution of European diadromous fish species to analyze whether species have responded in the way that the GR3D model suggests (Kerr and Dobrowski, 2013).

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## $\underline{\text { List of tables : }}$

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

| Agent | State Variable | Descritpion | Status/unit of measure |
| :--- | :--- | :--- | :--- |
| Sea basin | name | Name ID | SB and a number |
| River basin | seasonal temperature | Water temperature | Numeric $\left({ }^{\circ} \mathrm{C}\right)$ |
|  | name | Name ID | RB and a number |
|  | longitude | Longitude at the mouth | Numeric $\left({ }^{\circ}\right)$ |
|  | latitude | Latitude at the mouth | Numeric $\left({ }^{\circ}\right)$ |
| Diadromous fish | watershed area | Watershed area of the | Numeric $\left(\mathrm{km}^{2}\right)$ |
|  | seasonal temperature | Water temperature | Numeric $\left({ }^{\circ} \mathrm{C}\right)$ |
|  | ID | Fish identification | Numeric $(-)$ |
|  | gender | Sex | M, F |
|  | stage | Stage | Mature, immature |
|  | age | Age | Numeric (-) |
|  | body-length | Body length | Numeric $(\mathrm{cm})$ |
|  | location | Current location | Name of the compartment |
|  | birth place | Birth place | Name of the birth |
|  | 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) |
| $\Delta t_{\text {rec }}$ | 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) |
| $\eta$ | Parameter to relate $S_{95, j}$ and the surface of a spawning place (Ind/km²) | 2.4 | Offline calibration using the study from Rougier et al. (2012) |
| $\theta$ | 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; <br> LANUV, 2010) |
| surv ${ }_{\text {optRep }}$ | Optimal survival rate of an individual from eggs to the age $\Delta t_{\text {rec }}$ | $1.7 * 10^{-3}$ | Offline calibration using the study from Rougier et al. (2012) |
| $T_{\text {minRep }}, T_{\text {optRep }}, T_{\text {maxRep }}$ | Water temperature $\left({ }^{\circ} \mathrm{C}\right)$ regulating survival of an individual from eggs to the age $\Delta t_{\text {rec }}$ | 14, 20, 26 | (Cassou-Leins et al., 2000; <br> Kottelat and Freyhof, 2007) |
| $\lambda$ | Parameter to relate $c_{j}$ and the surface of a spawning place | $4.1 * 10^{-4}$ | Offline calibration using the study from Rougier et al. (2012) |
| $\sigma_{\text {rep }}$ | Standard deviation of lognormal distribution of the recruitment | 0.2 | Reasonable guessed |
| $S p_{s p}$ | 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); <br> 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 |  |  |  |
| $L_{i n i}$ | 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 lognormal distribution of the | 0.2 | 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 |  |  |
| $\eta$ | [2.2; 2.6] | N |
| $\theta$ | [1.8; 2] | Y |
| Surv ${ }_{\text {optRep }}$ | $\left[1 * 10^{-3} ; 2 * 10^{-3}\right]$ | Y |
| $T_{\text {minRep }}$ | [13.3; 14.6] | N |
| $T_{\text {optRep }}$ | [19.3; 20.6] | Y |
| $T_{\text {maxRep }}$ | [25.3; 26.6] | N |
| $\lambda$ | $\left[3 * 10^{-4} ; 5 * 10^{-4}\right]$ | Y |
| $\sigma_{\text {rep }}$ | [0.1; 0.3] | N |
| Growth SM2 |  |  |
| $\sigma_{\Delta L}$ | [0.1; 0.3] | N |
| $T_{\text {minGrow }}$ | [2.3; 3.6] | N |
| $T_{\text {optGrow }}$ | [16.3; 17.6] | Y |
| $T_{\text {maxGrow }}$ | [25.3; 26.6] | N |
| $\kappa_{\text {optGrow }}$ | [0.2; 0.4] | Y |
| Survival SM3 |  |  |
| $Z_{\text {sea }}$ | [0.3; 0.5] | Y |
| $T_{\text {minSurvRiv }}$ | [9.3; 10.6] | N |
| $T_{\text {optSurvRiv }}$ | [19.3; 20.6] | Y |
| $T_{\text {maxSurvRiv }}$ | [22.3; 23.6] | N |
| Maturation SM5 |  |  |
| $L_{\text {mat }}$ | [36; 44] | Y |
| Anadromous migration SM6 |  |  |
| $p_{\text {hom }}$ | [0.6; 0.9] | Y |
| $w^{\text {deathBasin }}$ | [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 $f_{s} P$ and $f_{s} S$ ) and explained variance (for $m l r$ )
by the model applied to outputs variables according to the experimental.

|  | Output variable |  |  |
| :--- | :--- | :--- | :--- |
| Design | $f s P$ | $f_{s} S$ | mlr |
| 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 $\left(f_{s}=2\right)$, (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 $(\mathrm{C})$ 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 $f_{s} P(\mathrm{~A}), . f s S$ (B) and $m l r$ (C) output variables calculated from logistic regression for $f_{s} P$ and $f s S$ and ANOVA for $m l r$ with the D-Optimal experimental design (theta and lambda correspond to the parameters $\theta$ and $\lambda$ 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 $f s P(\mathrm{~A}), . f s S$ (B) and $m l r$ (C) output variables calculated from logistic regression on $f_{s} P$ and $f_{s} S$ and ANOVA on $m l r$ with the complete sampling design (theta, lambda, weightDB correspond to the parameters $\theta, \lambda$ and $w^{\text {deathBasin }}$ respectively).


