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# First step of a modeling approach to evaluate spatial heterogeneity in a fish (Cottus gobio) population dynamics

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We use a spatially explicit modeling strategy in order to describe the dynamics of a bull-head population living in a river network in the South of France. We propose a multipatch Leslie model, which integrates the spatial heterogeneity of demographic rates and takes into account dispersion processes. The model is based on very first data coming from a field study. First, we test different hypothesis on survival (age variability, spatial heterogeneity, and density-dependence) and on dispersion (density-dependent recruitment of young fish) in terms of fit between modeled and field population features (population growth rate, local density, and spatial distribution). There, we show how such a model constitutes a tool to precisely examine the biology of bullhead. Indeed, the modeling approach leads us to operate a feedback from outputs of the model to biological assumptions. Second, we analyze the weight of dispersion in the population dynamics, which appears to affect seriously the spatial distribution of fish. Finally, we discuss our results in the framework of impact assessment of potential climate changes for the bullhead population.

## 1. Introduction

Potential global climate change should disrupt most of the ecosystems because it could alter their physical and chemical conditions and consequently the species living in these habitats (Wilson and Peter, 1990; Webb and Bartlein, 1992; Gates, 1993; Vitousek, 1994). The biodiversity is then in question regarding possible future climate changes. In this framework, a big challenge for ecology is the assessment of such impacts on populations and communities, which are elsewhere strongly influenced by human activities. Regional climate

changes should deeply affect aquatic ecosystems, especially river systems due to their weak capacity to absorb variations of the atmospheric temperature (Poff et al., 2002; Sweeney et al., 1992). Moreover, spatial fragmentation and spatial heterogeneity condition the population response to perturbations (Hanski, 1999). For instance, changes in spatial pattern (induced by damming, channeling, pollution, ...) highly influence the dynamics of fish populations in river networks (Morita and Yamamoto, 2002; Charles et al., 2000; Chaumot et al., 2003b). For cold water species, warming may shift populations in the upstream levels of river networks

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and then it may increase spatial fragmentation (Rahel et al., 1996).

We studied a bullhead population (*Cottus gobio*) living in a river system in the South of France (the Bez River, Drôme). Bullhead is known for its sensitivity to temperature (Elliott and Elliott, 1995; Pont, 2003). We aim at assessing the potential effect of spatial fragmentation on the population dynamics of this fresh water fish. For this, we have to disclose the spatial running of this population. Indeed, the habitat suitable for bullhead is here a network of non-contiguous areas: so, we have to deal either with a simple set of non-interacting isolated local populations, either with a metapopulation *sensu stricto* (Levin, 1970; Hanski and Simberloff, 1997) – a population of local populations with migratory links and where local dynamics are influenced by migratory flows only at a long time scale (allowing recolonization after local extinction) – or with a single spatially distributed population, where dispersal among populations is so frequent that local dynamics could not be understood at a short time scale without considering migratory flows. Potential impacts of increasing spatial fragmentation would of course be highly shaped by the kind of spatial dynamics occurring inside the fish population. We required three complementary strategies to answer this issue: first, a medium term study of the population (estimation of physical conditions and biological features regarding spatial heterogeneity) completed by experimental protocols (analyzing the effect of temperature on the bullhead physiology); second, a genetic approach to estimate the reproductive fragmentation (using micro-satellite polymorphism) (Kaufmann and Charles, 2003); and third, a modeling approach calling upon matrix population models (Caswell, 2001).

This paper presents the results of the modeling phase, based on the first data coming from the field population study (Abdoli, 2005; Abdoli et al., 2005). The model built here in the case of bullhead is one application of previous theoretical contributions to the modeling of fish populations in river networks (Charles et al., 2000; Chaumot et al., 2003a). We adopted matrix population models (i.e. Leslie models) allowing taking into account age structure, spatial distribution and spatial heterogeneity in the demographic and migratory dynamics (Caswell, 2001; Lebreton, 1996). Our modeling approach consists in integrating local features (i.e. vital rates estimated by field study) with a given dispersal pattern to extrapolate the global population dynamics at the scale of the whole river network. This modeling process gives rise to two main contributions. First, it constitutes a tool for checking the validity of biological data supplied by the field study. Considering the lack of field knowledge of adult survival and migratory processes (first data relative to census performed during only 1 year), we test different hypothesis on survival (age variability, spatial heterogeneity, and density-dependence). The fit between modeled and field population features (population growth rate, density, and spatial distribution) leads us to correct estimates of adult survival and to infer that spatial heterogeneity in survival should highly condition the spatial structure of the bullhead population. Second, sensitivity analysis of the model allows determining the weight of dispersion on the global population dynamics. Such information on the fish population running is of broad interest for discussing

the potential impact of population fragmentation potentially induced by climate changes.

## 2. The biological features of the bullhead population in the Bez River

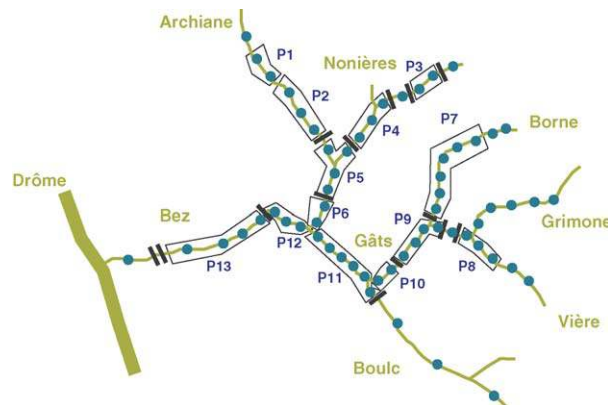
We only detail here the biological points, which underlie the building of the mathematical model. We do not expose precisely how data have been obtained from the field and we refer to specific publications concerning this aspect (Abdoli, 2005; Abdoli et al., 2005).

### 2.1. The Bez River network

The Bez River network in the South of France (Drôme) is an arborescent network composed by 40 km of river. The field study was performed with 60 spots, regularly spaced along the river. We distinguished 13 stretches of river, which present homogeneous conditions of habitat and which are delimited by confluence, dams, or waterfalls (Fig. 1). Table 1 reports dimensions and particularly the surface of these different river stretches. Such stretches of river are commonly called “patches” in a spatial modeling point of view.

### 2.2. The life cycle of bullhead in the Bez River

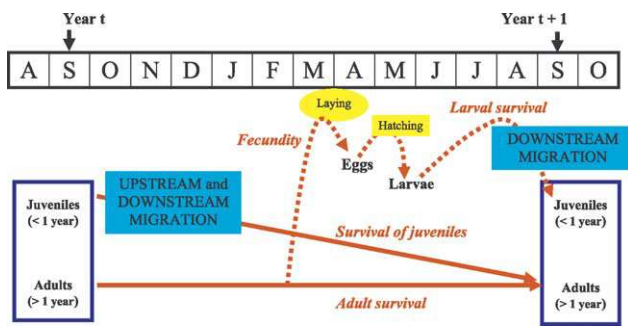
Bullheads (*C. gobio*) are found in clean, fast-flowing shallow rivers. Bullhead is a small fish (length found in the river network are between 37 and 146 mm) with a high territorial behavior. The population in the Bez River network is resident and totally closed. Fig. 2 reports the life cycle graph. Bullheads lay their eggs in late March–April, and the male guard the eggs until they hatch 1 month later. Larvae become juveniles in fall. Juveniles establish their territory during the first winter of their life. We distinguished five classes of adults. The first reproduction occurs when adults are 2-year-old but it can also be delayed 1 year later. Adults do not move between the dif-



**Fig. 1 – The Bez River network in Drôme (France) with the 13 stretches of river we used as patches in our model. Different rivers which make up the network are named. Grey points correspond to the 60 spots followed during experiments. Short black lines correspond to obstacles of various kind between patches (waterfall, diversion threshold, confluence, ... see Table 2).**

**Table1–Various dimensions of the 13 patches in the river network Bez (Drôme): length (m), width (m), depth (m), and surface (per 100 m<sup>2</sup>)**

	Length (m)	Width (m)	Depth (m)	Surface (per 100 m <sup>2</sup> )
Patch 1	1689	7.43	0.16	125.57
Patch 2	1736	5.93	0.27	102.91
Patch 3	790	2.58	0.09	20.42
Patch 4	2325	3.69	0.13	85.75
Patch 5	3215	5.87	0.19	188.59
Patch 6	1835	6.35	0.14	116.52
Patch 7	4325	3.51	0.10	151.91
Patch 8	2425	2.81	0.09	68.07
Patch 9	3683	4.75	0.11	175.05
Patch 10	1422	4.69	0.12	66.73
Patch 11	3775	6.42	0.13	242.46
Patch 12	2220	10.13	0.19	224.96
Patch 13	4130	12.37	0.22	510.88

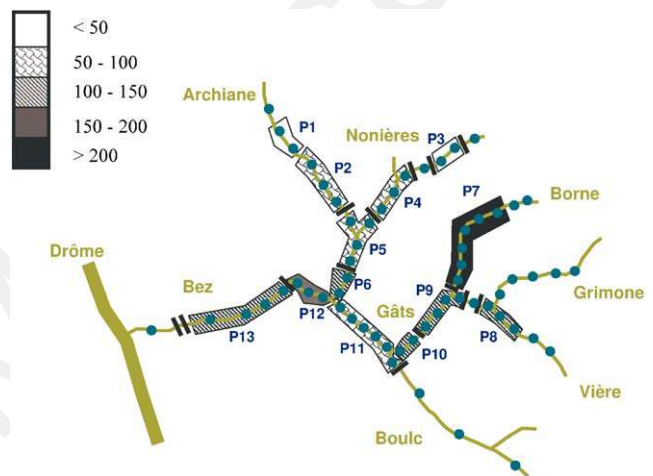


**Fig. 2 – Life cycle graph of *Cottus gobio*, running from September in year t to September in year t + 1.**

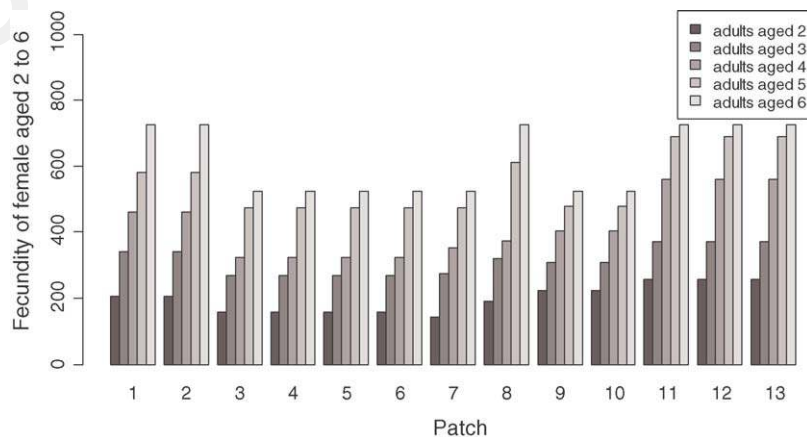
ferent stretches of river. Nevertheless, larvae can be passively dispersed downstream after hatching. We also assumed that juveniles actively “explore” neighboring areas before choosing a territory (see Section 2.3).

### 2.3. Biological data

The population is broken into the 13 stretches of river according to densities given in Fig. 3. Fecundity rates were well examined. They depend both on the age-class and on the localization in the network (Fig. 4). Moreover, 100% of adults



**Fig. 3 – Observed spatial distribution of individuals in patches, expressed in density (individual per 100 m<sup>2</sup>) with a gradient from patches with less than 50 individuals per 100 m<sup>2</sup> (colored in white) to patches with more than 200 individuals per 100 m<sup>2</sup> (colored in black).**



**Fig. 4 – Observed mean fecundity of each adult-age-class in each patch of the river network (5 age-classes, 13 patches).**

**Table 2–Up to downstream and down to upstream coefficients of franchissability related to the active dispersion of juveniles**

Patches	Kind of connection	Up to downstream crossing	Down to upstream crossing
P1–P2	Waterfall	0.75	0.25
P2–P5	Diversion threshold	0.5	0.25
P3–P4	Waterfall	0.5	0
P4–P5	Waterfall	0.5	0.25
P5–P6	Diversion threshold	0.25	0
P6–P11	Confluence	1	1
P6–P12	Confluence	1	1
P12–P13	Simple threshold	0.25	0
P7–P9	Diversion threshold	0.25	0
P8–P9	Waterfall	0.5	0.5
P9–P10	Log threshold	0.5	0.25
P10–P11	Confluence	1	1
P11–P12	Thermal threshold	1	1

These coefficients depend on the type of connection existing between patches.

aged three and more can reproduce, while the proportion of adults aged two which reproduce depends on the patch: 18% in patches 1 and 2, 89% in patches 3–6, 93% in patch 7, and 100% in patches 8–13. Differences in growth rates (depending on the temperature) mainly explain the spatial heterogeneity observed in the age at first reproduction. In fact, the northern area of the network (patches 1–6 on Fig. 1) is fresher than the southern and downstream stretches of river. The fertilization rate was estimated at 0.93 (Fox, 1978), the larval survival (during the first summer) at 0.075, and the annual survival of juveniles at 0.12. Annual survival rates of adults were less precisely estimated and 0.16 was the first value we tested for all adults (Mann, 1971).

We formulated several assumptions for dispersal pattern, because the field estimates of migratory rates are more difficult. Due to the vulnerability of young stages and to the benthic ecology of bullhead, we only consider in our simplistic migratory model that movement can occur from one patch to the directly connected ones (up and downstream). A proportion  $\alpha$  of larvae passively migrate in the adjacent downstream stretch of river following the flow (e.g. from patch 1 to patch 2, or from patch 6 to patch 12). During the active movements of juveniles, a given patch of river loses a proportion  $\beta$  of individuals through each of its connections to other patches (up and downstream): for instance, juveniles present in the patch 5 can migrate to patches 4, 2, or 6. Moreover, the connections between patches present different kinds (dam, waterfall, ...). Thus we apply coefficients of franchissability (Table 2) to the dispersal rate  $\beta$  considering the kind of connection, the sense (up or down) of migration, the speed of flow, and the height of dams. Regarding the weak knowledge on these migratory rates, we firstly set  $\alpha$  and  $\beta$  at 5%, but we secondly made these rates vary in order to examine the impact of dispersion on the population dynamics (Section 4).

### 3. The multipatch Leslie model

#### 3.1. Mathematical building of the first model

We consider the population in September: individuals are juveniles or adults (five age-classes of adults). Let  $n_{(i,j)}(t)$  be the

number of individuals of age-class  $i$  on patch  $j$  ( $i$  varies from 1 to 6 and  $j$  from 1 to 13). Then we gather these state variables in the vector  $\mathbf{n}(t)$  in order to describe the total population in September of year  $t$ . This vector is a set of population vectors  $\mathbf{n}_i(t)$  describing the internal structure of each age-class as follows:

$$\mathbf{n}(t) = [\mathbf{n}_1(t) \dots \mathbf{n}_6(t)]^T \quad (1)$$

where

$$\mathbf{n}_i(t) = [n_{(i,1)}(t) \dots n_{(i,j)}(t) \dots n_{(i,13)}(t)]^T \quad (2)$$

NB: superscript T denotes transposition.

Let  $s_{(i,j)}$  represent the annual survival rate of age-class  $i$  on patch  $j$ ,  $f_{(i,j)}$  be the fecundity of adult females of age-class  $i$  ( $i$  from 2 to 6) on patch  $j$  (Fig. 4), and  $r_{(i,j)}$  be the proportion of adult females which effectively breed (see Section 2.3). Moreover, we consider  $s_{\text{larv}}$  the survival of larvae from spring to September, and  $e$  the fertilization rate.

First, we translate the life cycle graph in equations ignoring dispersion. Juveniles in year  $t$  become adult in year  $t+1$  with the survival rate  $s_{(1,j)}$ :

$$n_{(2,j)}(t+1) = s_{(1,j)}n_{(1,j)}(t) \quad (3)$$

So we can link  $\mathbf{n}_1(t)$  and  $\mathbf{n}_2(t+1)$  with the following matrix equation:

$$\mathbf{n}_2(t+1) = \mathbf{S}_1\mathbf{n}_1(t) \quad (4)$$

with

$$\mathbf{S}_1 = \text{diag}\{s_{(1,1)}, \dots, s_{(1,j)}, \dots, s_{(1,13)}\} \quad (5)$$

We could model the survival between the adult age-classes in a same way:

$$\mathbf{n}_{i+1}(t+1) = \mathbf{S}_i\mathbf{n}_i(t) \quad \text{for } i \text{ from 2 to 4} \quad (6)$$

**Table 3 – Adult survival rates as proposed by De Silva (1985). These values were used to parametrize both the linear model with heterogeneity, and the density-dependant model**

Age-class	Adults aged 2	Adults aged 3	Adults aged 4	Adults aged 5 and 6
Survival rate	0.553	0.619	0.423	0.16

with

$$\mathbf{S}_i = \text{diag}\{s_{(i,1)}, \dots, s_{(i,j)}, \dots, s_{(i,13)}\} \quad (7)$$

For the last age-class:

$$\mathbf{n}_6(t+1) = \mathbf{S}_5 \mathbf{n}_5(t) + \mathbf{S}_6 \mathbf{n}_6(t) \quad (8)$$

In patch  $j$ , a proportion  $r_{(i,j)}$  of adult females (age-class  $i$ ) produces eggs with fecundity rates  $f_{(i,j)}$ . Moreover, we consider that adult survival on patch  $j$  during half a year (between September and March) is given by  $(s_{(i,j)})^{1/2}$ . So, if we assume that the sex ratio is 0.5 for the adult class, the number of eggs laid in March in patch  $j$  would be:

$$0.5f_{(i,j)}r_{(i,j)}(s_{(i,j)})^{1/2}\mathbf{n}_{(i,j)}(t) \quad (9)$$

The number of new bullhead juveniles on patch  $j$  in year  $t+1$  would be calculated considering fertilization and survival rates, and taking into account the five adult age-classes which breed:

$$n_{(1,j)}(t+1) = \sum_{i=2}^6 0.5s_{\text{larv}}f_{(i,j)}r_{(i,j)}(s_{(i,j)})^{1/2}\mathbf{n}_{(i,j)}(t) \quad (10)$$

$$\mathbf{L} = \begin{bmatrix} 0 & s_{\text{larv}}\mathbf{D}_{\text{larv}}\mathbf{F}_2(\mathbf{S}_2)^{1/2} & s_{\text{larv}}\mathbf{D}_{\text{larv}}\mathbf{F}_3(\mathbf{S}_3)^{1/2} & s_{\text{larv}}\mathbf{D}_{\text{larv}}\mathbf{F}_4(\mathbf{S}_4)^{1/2} & s_{\text{larv}}\mathbf{D}_{\text{larv}}\mathbf{F}_5(\mathbf{S}_5)^{1/2} & s_{\text{larv}}\mathbf{D}_{\text{larv}}\mathbf{F}_6(\mathbf{S}_6)^{1/2} \\ \mathbf{S}_1\mathbf{D}_{\text{juv}} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{S}_2 & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{S}_3 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{S}_4 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{S}_5 & \mathbf{S}_6 \end{bmatrix} \quad (18)$$

so

$$\mathbf{n}_1(t+1) = \sum_{i=2}^6 s_{\text{larv}}\mathbf{F}_i(\mathbf{S}_i)^{1/2}\mathbf{n}_i(t) \quad (11)$$

with

$$\mathbf{F}_i = 0.5e \times \text{diag}\{r_{(i,1)}f_{(i,1)}, \dots, r_{(i,j)}f_{(i,j)}, \dots, r_{(i,13)}f_{(i,13)}\} \quad (12)$$

and

$$(\mathbf{S}_i)^{1/2} = \text{diag}\{(s_{(i,1)})^{1/2}, \dots, (s_{(i,j)})^{1/2}, \dots, (s_{(i,13)})^{1/2}\} \quad (13)$$

In addition, we have to deal with migration events during the life cycle. Then, we define two square matrices of dispersion  $\mathbf{D}_{\text{larv}}$  and  $\mathbf{D}_{\text{juv}}$ , which integrate the topology of the network, the migration rates  $\alpha$  and  $\beta$ , and the coefficients of franchissability (see Appendices A and B). Each matrix is conservative. In the case of juveniles, the entry at row  $r$  and column  $c$  of  $\mathbf{D}_{\text{juv}}$  is the proportion of juvenile bullhead on

patch  $c$  going to patch  $r$  during the active dispersion. The structure of the juvenile age-class just after the dispersion is given by:

$$\mathbf{D}_{\text{juv}}\mathbf{n}_1(t) \quad (14)$$

Then, the Eq. (4), which stands for survival of these juveniles, has to be replaced by:

$$\mathbf{n}_2(t+1) = \mathbf{S}_1\mathbf{D}_{\text{juv}}\mathbf{n}_1(t) \quad (15)$$

That is the same deal with the larval dispersion, and the Eq. (11) becomes:

$$\mathbf{n}_1(t+1) = \sum_{i=2}^6 s_{\text{larv}}\mathbf{D}_{\text{larv}}\mathbf{F}_i(\mathbf{S}_i)^{1/2}\mathbf{n}_i(t) \quad (16)$$

Using matrix, Eqs. (1), (6), (8), (11), and (16) allow building a transition matrix between the population vectors from year to year:

$$\mathbf{n}(t+1) = \mathbf{L}\mathbf{n}(t) \quad (17)$$

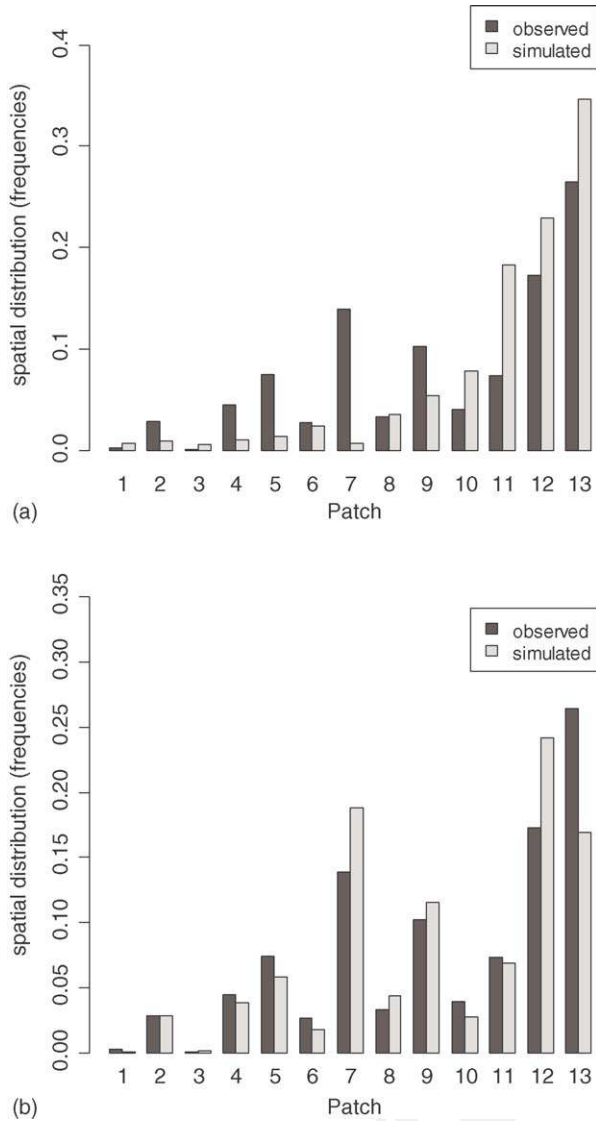
where

$\mathbf{0}$  being a submatrix of  $\mathbf{0}$  with 13 rows and 13 columns.

$\mathbf{L}$  is a multiregional Leslie matrix. It presents a first dominant eigenvalue  $\lambda$  corresponding to the asymptotic population growth rate (Caswell, 2001). The right eigenvector associated to this first eigenvalue gives the asymptotic structure of the population. So it yields either the asymptotic spatial distribution of each age-class or the stable age-structure of the population. The study of the population behavior requires both analytical methods (asymptotic results of linear algebra; Caswell, 2001) and numerical simulations as well.

### 3.2. First results

We used the biological parameters introduced in Section 2.3. The population always tends to extinction with an asymptotic population growth rate less than 1 ( $\lambda = 0.86$ ). Thus, we went back to the biological data and the estimate of the adult survival rate seems us to be critical (only one value for all age-classes and very few precision comparing to fecundity data, for instance). So we examined the literature, which supplies adult



**Fig. 5 – Simulated (after 20 generations) and observed spatial distributions of fish in the river network. Simulations coming from the linear multiregional Leslie model (Eq. (17)) with numerical values proposed by De Silva (1985) for the adult survival rates (Table 3). (a) without spatial heterogeneity of survival rates; (b) with spatial heterogeneity on survival rates (see Appendix C).**

survival values bigger than our first estimate and above all age-dependent values. We introduced the survival rates reported by De Silva (1985) (Table 3). Simulations show then a population growth and the algebraic analysis gives an asymptotic population growth rate bigger than 1 ( $\lambda = 1.27$ ).

Nevertheless, the spatial distribution does not fit with the field observations (Fig. 5a), leading us to test two other hypotheses.

### 3.3. Improvements of the model

With regard to results of Fig. 5a, we formulate two hypotheses allowing explaining the spatial repartition of bullheads in

the network. Hence, when we examine the case of patch 1, we see that the density is very low (Fig. 3), although fecundity rates (Fig. 4) are very high in this stretch of the river. So, regarding the spatial fecundity profile and the spatial distribution of bullheads, we assumed that heterogeneity in survival processes should occur, which could explain the previous bad fit. Our first idea was then to artificially integrate spatial heterogeneity in the adult survival rates (see Appendix C), since we did not have sufficient field knowledge of this parameter. Indeed, data from De Silva (1985) only allow us to consider age variability of survival but not spatial heterogeneity. With such a coefficient of spatial heterogeneity in the model, we obtain an asymptotic population growth rate  $\lambda$  equal to 1.06, and we are able to improve the fit between the model predictions and the field observations (Fig. 5b).

The second hypothesis to explain the observed distribution between stretches of river is to consider a spatial heterogeneity of the recruitment of young fish. Density-dependent regulations during the first life-stage (stock recruitment models) are well described for freshwater fish (Elliott, 1985). Such regulations are explained by competitive mechanisms (competition for the habitat). We thus integrated two Beverton-Holt functions to describe the density-dependence of juvenile survival and migratory rate (see Appendix D). These ones are compensation functions following the equation:

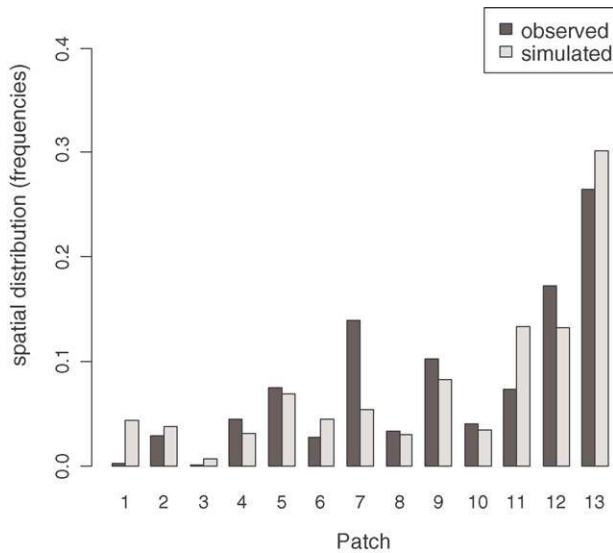
$$f(x) = \frac{\alpha x}{1 + bx} \quad (19)$$

where  $x$  stands for density,  $a$  and  $b$  are constant.

Such a function is well adapted to freshwater fish because it deals with the concept of habitat carrying capacity. In our case, survival and migratory rates of juveniles are functions of their local densities. The density-dependent model was examined using simulations, since its analytical treatment leads to difficulties due to the dimension 78 of the system. Nevertheless, caring about the robustness of these numerical results, we solved this analysis in the case of a reduced population model by considering only one age-class for adults (Bajard and Cacaly, 2004). Analysis and simulations yield coherent results in that case. For the complete system (five adult age-classes), the outputs of the density-dependent model give equilibrium densities, corresponding to a population size coherent with field densities. On the other hand, spatial distributions of the predicted equilibrium do not fit with the field observations (Fig. 6). To conclude with, the observed spatial repartition of bullhead appears not to be understandable without heterogeneity on survival. Our future works currently focus on combined effects of heterogeneity on survival, coupled with density-dependence.

## 4. The effect of dispersion

We examined the sensitivity of the population dynamics to the changes in the parameters of dispersion ( $\alpha$  and  $\beta$ ). We used the linear model with spatial heterogeneity on the adult survival (see Fig. 5b for the “reference” case). We made  $\alpha$  and  $\beta$  vary from 0.01 to 0.1. For the passive larval dispersion, changes in  $\alpha$  influence the spatial distribution of bullheads (Fig. 7a). The intensity of this downstream migration is negatively corre-



**Fig. 6 – Simulated (after 20 generations) and observed spatial distributions of fish in the river network, simulations coming from the density-dependent multiregional Leslie model (see Section 3.3).**

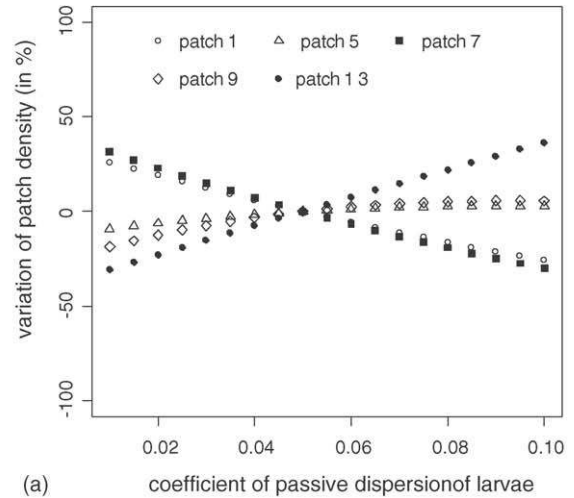
lated with the densities of the upstream levels (e.g. patches 1 and 7), contrary to the benefit observed in the downstream location (patch 13) as  $\alpha$  increases. The effect is less significant for medium patches (patches 5 and 9). We calculated the effect of a shift from 0.01 to 0.1 for  $\alpha$  on patch densities in order to have a whole description of the behavior of the population in the river network (Fig. 7b). Upstream stretches of river (patches 1–4, 7, and 8) are negatively affected by an increase in larval dispersion, contrary to the more downstream location (patch 13). “Intermediate” patches in the network (patches 5, 9, 11, and 12) are less disturbed. And interestingly, the “confluence” areas (patches 6 and 10) take advantage from such an increase of  $\alpha$ . This dynamic pattern would lead us to describe the spatial structure of the population as two sub-networks (patches 1-2-3-4-5-6 on one side, and patches 7-8-9-10 on the other side) connected downstream to a third one (patches 11-12-13), with three “collecting” areas downstream of each one (patches in bold characters).

On the other hand, the impact of  $\beta$  on the spatial distribution is very less important (Fig. 8). That may be explained by the fact that the active migration is assumed to occur both in the upstream and in the downstream senses. The flows are then symmetrical (except when the coefficients of franchissability differ with the sense of downstream franchissability), thus what is lost in one sense is won in the other one.

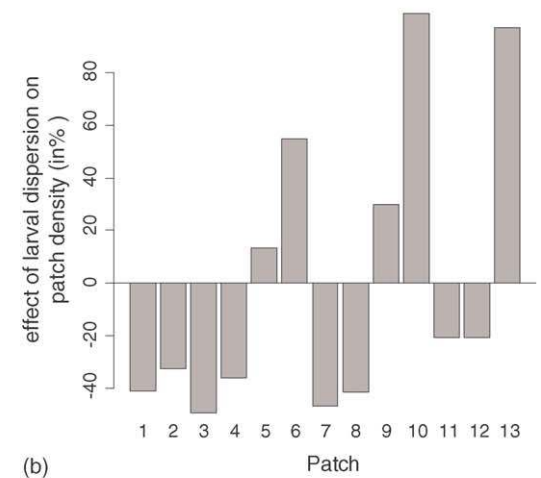
Finally, contrary to the deep disruptions affecting the spatial repartition of fish, only a weak impact is observed on the whole population dynamics (assessed with  $\lambda$ , the asymptotic population growth rate; Fig. 7c).

## 5. Discussion

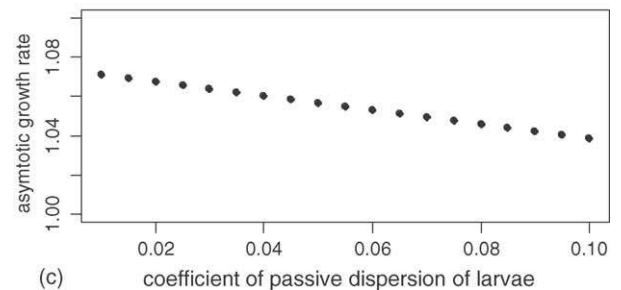
We showed how we can use our model as a tool for checking the validity of the experimental estimates of biological



(a)

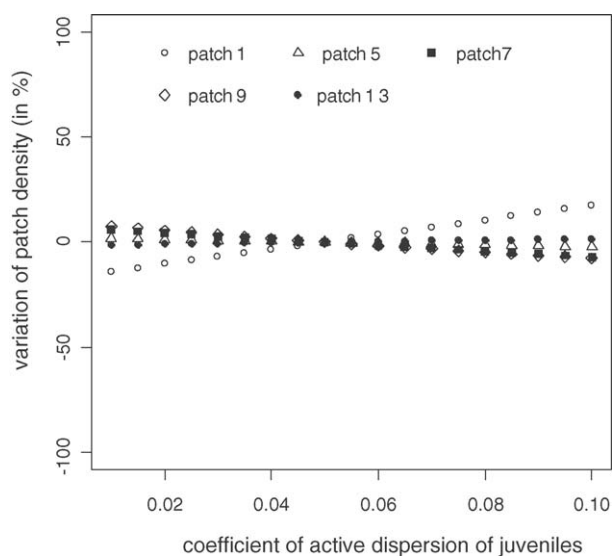


(b)



(c)

**Fig. 7 – Sensitivity of the simulated patch densities to a change in  $\alpha$  (proportion of larvae, which migrate to the downstream patch during one time step). Simulations are performed using the linear multiregional Leslie model with spatial heterogeneity on survival rates (20 generations). (a) Decrease or increase in patch density when  $\alpha$  varies from 0.01 to 0.1. We present relative differences (expressed in %) between the densities obtained for the tested value of  $\alpha$  (absciss axis) and for the reference case ( $\alpha = 0.05$ ). (b) Relative difference in patch density (expressed in %) when  $\alpha$  is equal to 0.01 or equal to 0.1 for the 13 patches. (c) Decrease in the asymptotic population growth rate when  $\alpha$  varies from 0.01 to 0.1.**



**Fig. 8 – Sensitivity of the simulated patch densities to a change in  $\beta$  (emigration rate of juveniles). Simulations come from the linear multiregional Leslie model with spatial heterogeneity on survival rates (20 generations). Decrease or increase in patch density when  $\beta$  varies from 0.01 to 0.1. We present relative differences (expressed in %) between the densities obtained for the tested value of  $\beta$  (absciss axis) and for the reference case ( $\beta = 0.05$ ).**

rates. For instance, the adult survival in the bullhead population seemed to have been underestimated in our first data. This feedback on input data of the model (data extracted from the field study) constitutes a broad contribution of the modeling approach. It underlines the complementarity of the different strategies we adopted in order to disclose the spatial dynamics of the bullhead population. That is the same philosophy when we tried to explain the spatial distribution of fish throughout the river network. We observed that neither the heterogeneity in fecundity rates nor the differences in the carrying capacity of each stretch of river (influencing the recruitment by density-dependence) allowed alone to explain the spatial distribution of bullhead. Only heterogeneity in survival made us able to get a good fit between the predictions of the model and the observed distribution. Thus, the modeling process leads us to formulate hypothesis about the population biology of bullhead (level and heterogeneity of survival rates), and we have to go back to field to test them.

The next step now would be to understand the biological process, which give rise to spatial heterogeneity in survival. One can assume that two kinds of mechanisms (biotic or abiotic factors) may be implied. First, Petty and Grossman (2004) demonstrated, for a similar species, *Cottus bairdi*, that adult movement, and probably survival, can be influenced by competitive interactions between individuals for suitable space. We will also be interested in competition with other species (e.g. trout) or predation (on eggs). Second, physical conditions certainly constitute one source of heterogeneity for the sur-

vival process. We will specially focus on the potential key-role of temperature for this cold water fish species (Elliott and Elliott, 1995; Pont, 2003), already studied regarding fecundity process (Abdoli, 2005; Abdoli et al., 2005). Water temperature recordings are already available for the different stretches of river. We will soon get the estimate of adult survival rates (based on census relative to successive years). Then we will perform the analysis of the correlation between temperature and survival (statistical analysis and experimental validation). One perspective for improving the model will be then to integrate the local temperatures as a second order variable, on which survival rates will depend.

In the first attempt of modeling we presented in this paper, few changes in the dispersion pattern influences the whole population dynamics. On the other hand, potential migratory disruptions can affect seriously the spatial distribution of bullhead in the river network. Nevertheless, these conclusions result from the simplistic migratory pattern, we integrated in the model. So, if we aim at more pertinent predictions, we need quantitative estimates of the migratory rates between the different stretches of the river network. For this purpose, we could use the results of the genetic approach (microsatellite polymorphism) or direct field measures (tagging experiments).

Hence, what can we conclude about the possible impact of future climate changes (warming)? Several results of our modeling approach can contribute to the answer. First, the intensity of dispersion in the bullhead population influences the spatial distribution of fish in the river network. The effect differs from one stretch of river to the other. Second, a modeling approach coupling heterogeneity and density-dependence on survival seems to be promising. For instance, heterogeneity on survival should highly be explained by differences of water temperature inside the river network. Third, the very first results of the genetic study (Kaufmann and Charles, 2003) would lead us to think that fishes living in the upstream levels are relatively isolated. Finally, a warming event, which could give rise to the fragmentation of the population in several upstream areas in the river network (Rahel et al., 1996), would highly affect the population dynamics. Indeed, the reduction of the living area could drop the total population size due to density-dependent mechanisms (during recruitment). In addition, the arborescent topology with central stretches of river (downstream) tends to compensate the spatial heterogeneity of upstream levels. That would no more be the same in the case of an upstream shift of the population induced by warming: such a fragmentation would exacerbate the impact of survival (and fecundity) heterogeneity and it would expose the population to an environmental instability in each of the disconnected area.

All these general and qualitative conclusions need to be completed by more precise and quantitative results about the population effects of warming. Some of these results should be supplied by the future developments of our model (introduction of the effect of temperature on survival rates). Nevertheless, as we have already stressed on, such an improvement would only be achieved by calling upon the complementarity between field and/or experimental studies, genetic analysis and spatial modeling.

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## Appendix A. Dispersion matrix for larvae

Here is the dispersion matrix for larvae, considering the topology of the river network (see Fig. 1):

$$D_{\text{larv}} = \begin{bmatrix} 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \alpha & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \alpha & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \alpha & 0 & \alpha & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \alpha & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\alpha & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & \alpha & 1-\alpha & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 1-\alpha & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 1-\alpha & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \alpha & 0 & 0 & 0 & 0 & \alpha & 1-\alpha & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \alpha & 1 \end{bmatrix}$$

with  $\alpha$ , the proportion of larvae, which passively migrate (following the flow) from one stretch of river to the adjacent downstream one.

## Appendix B. Dispersion matrix for juveniles

The matrix Down contains coefficients  $d_{i,j}$  ( $1 \leq i, j \leq 13$ ), coefficients of crossing from up- to downstream for juveniles (see Table 2).

$$\text{Down} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.75 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0.5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.25 & 0.5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.25 & 0 \end{bmatrix}$$

The matrix Up contains coefficients  $u_{i,j}$  ( $1 \leq i, j \leq 13$ ), coefficients of crossing from down- to upstream for juveniles (see

Table 2).

$$\text{Up} = \begin{bmatrix} 0 & 0.25 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.25 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.25 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

The dispersion matrix for juveniles ( $D_{\text{juv}}$ ) is then built regarding the topology of the river network (Fig. 1) and the coefficients of crossing as follows:

$$D_{\text{juv}} = I + \beta E$$

where  $I$  is the identity matrix (dimension 13),  $\beta$  the proportion of fish emigrating from a given stretch of river through each of its connections to the network (upstream and/or downstream directions), and  $E$  is the following matrix:



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