

POPULATION DYNAMICS MODELLING IN AN HIERARCHICAL ARBORESCENT RIVER NETWORK: AN ATTEMPT WITH *Salmo trutta*

S. Charles^{1*}, R. Bravo de la Parra², JP. Mallet³,
H. Persat³ and P. Auger¹

¹ Laboratoire de Biométrie, Génétique et Biologie des Populations, UMR CNRS 5558, Université Claude Bernard Lyon 1, 43 bd du 11 novembre 1918, 69622 Villeurbanne Cedex, France.

² Departamento de Matematicas, Universidad de Alcala de Henares, 28871 Alcala de Henares, Madrid, Spain.

³ Laboratoire d'Ecologie des Eaux Douces et des Grands Fleuves, ESA CNRS 5023, Université Claude Bernard Lyon 1, 43 bd du 11 novembre 1918, 69622 Villeurbanne Cedex, France.

* Corresponding Author. E-mail: bajard@biomserv.univ-lyon1.fr

ABSTRACT

The balance between births and deaths in an age-structured population is strongly influenced by the spatial distribution of sub-populations. Our aim was to describe the demographic process of a fish population in an hierarchical dendritic river network, by taking into account the possible movements of individuals. We tried also to quantify the effect of river network changes (damming or channelling) on the global fish population dynamics. The *Salmo trutta* life pattern was taken as an example for.

We proposed a model which includes the demographic and the migration processes, considering migration fast compared to demography. The population was divided into three age-classes and subdivided into fifteen spatial patches, thus having 45 state variables. Both processes were described by means of constant transfer coefficients, so we were dealing with a linear system of difference equations. The discrete case of the variable aggregation method allowed the study of the system through the dominant elements of a much simpler linear system with only three global variables: the total number of individuals in each age-class.

From biological hypothesis on demographic and migratory parameters, we showed that the global population dynamics of fishes is well characterized in the reference river network, and that dams could have stronger effects on the global dynamics than channelling.

KEYWORDS: arborescent river network; Leslie matrix; aggregation methods; discrete time models; *Salmo trutta*.

1. INTRODUCTION

Ecological modelling often deals with very complex systems involving a large number of coupled variables, *i.e.*, a large number of degrees of freedom. To describe the population dynamics of an ecological system, we should consider a set of interacting subpopulations of different ages, because an ecosystem is made up of

different levels of organization: individuals, populations, communities (O'Neill *et al.*, 1986; Levin, 1989; May, 1989). Moreover, the geographical distribution of individuals must be taken into account, because migrations of individuals between different patches can influence the global demographic process.

A first approach to model this complexity is to ignore the internal structure of the population, which is thus considered as a whole and described by a single variable. But the effect of the internal population structure can rarely be neglected and this approach should be avoided. Another way is to build up complete models describing the real system in detail. Unfortunately, these models cannot be analytically processed and are difficult to handle; moreover, numerical simulations are needed, the robustness of which is still in question. Aggregation methods constitute an alternative way, allowing to approximate general complex systems into reduced ones, and justify, on a mathematical point of view, the aggregation process (Gardner *et al.*, 1982; Iwasa *et al.*, 1987, 1989; Gard, 1988). Such methods can be applied when at least two different time scales are involved, as in hierarchically organized systems (Auger, 1989).

Aggregation methods were first developed in the case of continuous time systems (Auger & Benoît, 1993; Auger & Roussarie, 1994; Auger & Poggiale, 1995; Auger & Poggiale, 1996 a, b; Poggiale & Auger, 1996; Michalski *et al.*, 1997). Recently, some authors applied these methods to discrete time models (Bravo de la Parra *et al.*, 1995, 1997; Sanchez *et al.*, 1995), which are widely used in population dynamics modelling. For example, the Leslie model is particularly well adapted to describe an age-structured population at discrete times (Caswell, 1989). Moreover, when the reproduction takes place each year, time discrete models provide the population density at successive generations.

In a first step, we applied the variable aggregation method for discrete time models to the case of a brown trout population (*Salmo trutta*), living in a river system with tributaries. This ecosystem was considered as an arborescent river network of interconnected patches at different stream orders (Cummins, 1979), the upper levels corresponding to the smallest tributaries and the lower ones to the main river. A medium sized river is generally well described by four levels of arborescence (Baglinière & Maisse, 1991) and the biggest ones by a maximum of twelve levels (e.g., Arizona or Mississippi). In our case, *i.e.*, a symmetric medium sized river network, the complete network was made up of four levels and 15 patches (reference river network, *cf.* Figure 1). Individuals could reproduce on these patches and migrate between them, the migration time scale (day) being much faster than the demographic one (year). Both dynamical systems, the one corresponding to the migratory movements and the other to the demographic process, were considered as linear, because migration rates and demographic parameters were supposed to be constant. Consequently, the general system and the associated aggregated system were linear, and the population dynamics was governed by the strictly dominant eigenvalue of the primitive aggregated matrix.

In a second step, some changes, as dams (*i.e.*, between patch connection breaking) or channelling (*i.e.*, patch deletion), were made on the reference river network, and we tried to evaluate their effects on the global fish population dynamics.

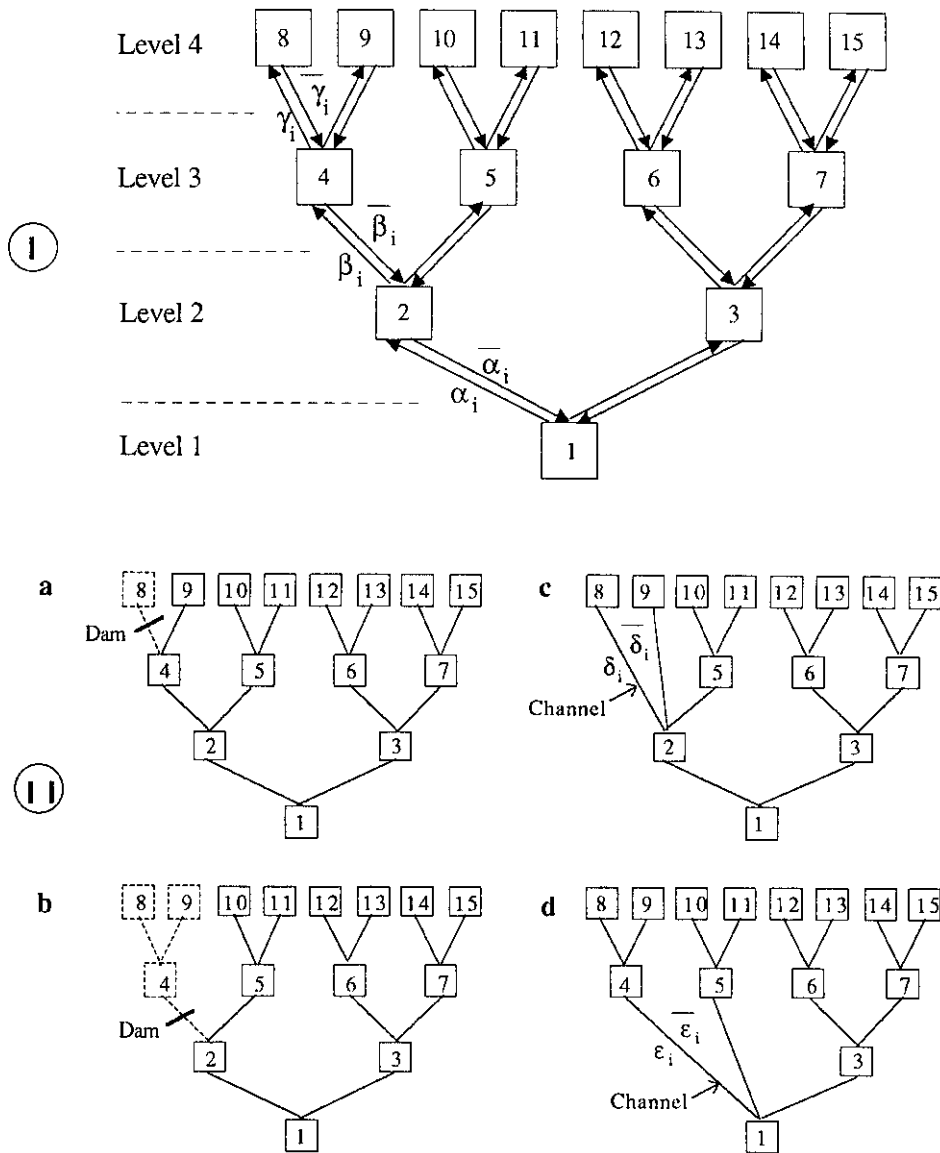


Figure 1. (I) Schematic representation of the dendritic river network with four levels and 15 patches (reference river network). Parameters $\alpha_i(\beta_i, \gamma_i)$ and $\bar{\alpha}_i(\bar{\beta}_i, \bar{\gamma}_i)$ are respectively the direct and the reverse migration rates between levels for individuals of the age-class i . (II) Schematic representation of the different changes of the reference river network; (a) and (b): dams between third-fourth and second-third levels; (c) and (d): third and second level patch deletion by channelling. The new migration rates in the changed river networks (c) and (d) are: $\frac{\delta_i}{\bar{\delta}_i} = \frac{\beta_i \gamma_i}{\bar{\beta}_i \bar{\gamma}_i}$ and $\frac{\epsilon_i}{\bar{\epsilon}_i} = \frac{\alpha_i \beta_i}{\bar{\alpha}_i \bar{\beta}_i}$.

2. BIOLOGICAL DATA

The Reference River Network

The reference river network can be schematized as on Figure 1(I): levels 4 and 1 correspond to the top and down ends of the network. The demographic process takes place in each patch, and the individuals can migrate between different patches. Migrations develop according to rules indicated on Figure 1(I), with migration rates varying according to the arborescence level. Direct migrations between patches of a same level are not allowed.

Simple hypotheses were made concerning the river network: at the same level n , all patches are equivalent (*i.e.*, the demographic parameters are the same) and migration rates are identical. Moreover, each patch of the level n is connected to only two patches of the level $(n+1)$, the river network is then symmetric. Finally, migration rates depend on the age-class, *i.e.*, the parameters $\alpha_i, \bar{\alpha}_i, \beta_i, \bar{\beta}_i, \gamma_i, \bar{\gamma}_i$ are the migration rates of the age-class i .

The Changed River Networks

Two kinds of changes of the reference river network were considered: dams or channels. The construction of a dam between two patches consists, in terms of migration, in reducing to zero the direct and reverse migration rates between these two patches, while other migration rates are left unchanged (Figure 1(IIa and IIb)); the upper dam patches are consequently deleted from the network.

The construction of a channel between a patch of the level n and a patch of the level $(n+2)$ consists in forbidding the demographic process to take place at the level $(n+1)$; individuals can migrate directly between levels n and $(n+2)$ with new migration rates (Figure 1(II c and d)) that can be calculated by supposing that the ratio of the total number of individuals at level n over the total number of individuals at level $(n+2)$ is the same for the reference and the changed river network.

The Demographic Model

An hypothetical brown trout population (*Salmo trutta*) was considered in this study. The population was subdivided into three age-classes: Young Of the Year or YOY (in their first year of life, 0+), juveniles (two summer old, 1+) and adults (>1+). Only adults can reproduce and the mean age of adult death is not known *a priori*. Survival rates (probability that an individual in age-class i will survive from year to year) and fecundity (number of YOY per female produced each year) are assumed to depend on the arborescence level, and the gradient of survival rates depends on the age-class (Table 1).

One additional hypothesis was also needed to determine the proportions of individuals of the different age-classes in all patches: the proportions are the same in all patches at the same level (Table 1).

Table 1. Fecundity, survival rates and proportions of individuals of each age-class at the different levels of the reference river network for an hypothetical trout population.

	Level	YOY	Juveniles	Adults
Fecundities	1	0	0	f/a^3
	2	0	0	f/a^2
	3	0	0	f/a
	4	0	0	f
Survival rates	1	s_1/a^3	s_2/a	s_3
	2	s_1/a^2	s_2	s_3/a
	3	s_1/a	s_2/a	s_3/a^2
	4	s_1	s_2/a^2	s_3/a^3
Proportions (%)	1	4	45	43.7
	2	12	35	40
	3	33	18	16
	4	51	2	0.3

a : gradient of fecundity and survival rates; f : number of YOY per female produced each year; s_1 , s_2 and s_3 : optimal survival rates of each age-class. Parameters a , f , s_1 , s_2 and s_3 were estimated from Baglinière and Maise data (1991): $a = 2$; $f = 265$; $s_1 = 0.07$; $s_2 = s_3 = 0.4$.

3. MATHEMATICAL MODELLING

The General Model

Two different time scales are involved in the evolution of the global population, a fast one corresponding to the migration process and a slow one to the demography.

The migration process, *i.e.*, the fast dynamics, is represented by the following stochastic matrix:

$$\mathbf{P} = \text{diag}\{\mathbf{P}_1, \mathbf{P}_2, \mathbf{P}_3\}$$

where each matrix \mathbf{P}_i can be written as shown in the matrix on the following page.

For every age-class, fast dynamics keeps invariant the total number of individuals and in the long-term distributes them among the different patches according to certain equilibrium frequencies.

Let \bar{v}_j^i be the equilibrium frequency of individuals aged i in patch j , and $\bar{\mathbf{P}}_c$ the matrix containing the \bar{v}_j^i for the three age-classes and the 15 patches:

$$\bar{\mathbf{P}}_c = \text{diag}\{\bar{v}^1, \bar{v}^2, \bar{v}^3\} \quad \text{with} \quad \bar{v}^i = (\bar{v}_1^i, \dots, \bar{v}_{15}^i)^T$$

where T denotes transposition.

This matrix $\bar{\mathbf{P}}_c$ will later be used to build the aggregated model.

$$\mathbf{P}_i = \begin{pmatrix}
 1-2\alpha_i & \bar{\alpha}_i & \bar{\alpha}_i & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 \alpha_i & A_i & 0 & \bar{\beta}_i & \bar{\beta}_i & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 \alpha_i & 0 & A_i & 0 & 0 & \bar{\beta}_i & \bar{\beta}_i & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & \beta_i & 0 & B_i & 0 & 0 & 0 & \bar{\gamma}_i & \bar{\gamma}_i & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & \beta_i & 0 & 0 & B_i & 0 & 0 & 0 & \bar{\gamma}_i & \bar{\gamma}_i & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & \beta_i & 0 & 0 & B_i & 0 & 0 & 0 & 0 & \bar{\gamma}_i & \bar{\gamma}_i & 0 & 0 & 0 \\
 0 & 0 & \beta_i & 0 & 0 & 0 & B_i & 0 & 0 & 0 & 0 & 0 & \bar{\gamma}_i & \bar{\gamma}_i & 0 \\
 0 & 0 & 0 & \gamma_i & 0 & 0 & 0 & C_i & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & \gamma_i & 0 & 0 & 0 & 0 & C_i & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & \gamma_i & 0 & 0 & 0 & 0 & C_i & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & \gamma_i & 0 & 0 & 0 & 0 & 0 & C_i & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & \gamma_i & 0 & 0 & 0 & 0 & 0 & C_i & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & \gamma_i & 0 & 0 & 0 & 0 & 0 & C_i & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma_i & 0 & 0 & 0 & 0 & 0 & C_i & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \gamma_i & 0 & 0 & 0 & 0 & 0 & C_i
 \end{pmatrix}$$

with $A_i = 1 - 2\beta_i - \bar{\alpha}_i$, $B_i = 1 - 2\gamma_i - \bar{\beta}_i$, $C_i = 1 - \bar{\gamma}_i$

For every $i = 1, 2, 3$, the stochastic matrix \mathbf{P}_i is primitive, $\mathbf{P}_i^6 > 0$, and so the vector \bar{v}^i of equilibrium frequencies if nothing but its eigenvector associated to eigenvalue 1 and normalized so that: $\sum_{j=1}^{15} \bar{v}_j^i = 1$. Straightforward, calculations yield:

$$\bar{v}_1^i = \frac{1}{D_i}$$

$$\bar{v}_2^i = \bar{v}_3^i = \frac{1}{D_i} \frac{\alpha_i}{\bar{\alpha}_i}$$

$$\bar{v}_4^i = \bar{v}_5^i = \bar{v}_6^i = \bar{v}_7^i = \frac{1}{D_i} \frac{\alpha_i \beta_i}{\bar{\alpha}_i \bar{\beta}_i}$$

$$\bar{v}_8^i = \bar{v}_9^i = \bar{v}_{10}^i = \bar{v}_{11}^i = \bar{v}_{12}^i = \bar{v}_{13}^i = \bar{v}_{14}^i = \bar{v}_{15}^i = \frac{1}{D_i} \frac{\alpha_i \beta_i \gamma_i}{\bar{\alpha}_i \bar{\beta}_i \bar{\gamma}_i}$$

where $D_i = 1 + 2 \frac{\alpha_i}{\bar{\alpha}_i} + 4 \frac{\alpha_i \beta_i}{\bar{\alpha}_i \bar{\beta}_i} + 8 \frac{\alpha_i \beta_i \gamma_i}{\bar{\alpha}_i \bar{\beta}_i \bar{\gamma}_i}$

For the reference river network, numerical values of \bar{v}_j^i are given in Table 1 allowing to estimate D_i , $\frac{\alpha_i}{\bar{\alpha}_i}$, $\frac{\beta_i}{\bar{\beta}_i}$ and $\frac{\gamma_i}{\bar{\gamma}_i}$ numerical values (Table 2).

Table 2. Migration ratio estimates for YOY, Juveniles and Adults in the reference river network ($\alpha_i/\bar{\alpha}_i$, $\beta_i/\bar{\beta}_i$ and $\gamma_i/\bar{\gamma}_i$), and in the river network changed by dams ($\delta_i/\bar{\delta}_i$) or channels ($\varepsilon_i/\bar{\varepsilon}_i$). Underlined values are those discussed in the Results and Discussion section.

		YOY	Juveniles	Adults
Levels 1↔2	$\alpha_i/\bar{\alpha}_i$	<u>1.5</u>	0.39	0.46
Levels 2↔3	$\beta_i/\bar{\beta}_i$	1.38	0.26	0.20
Levels 3↔4	$\gamma_i/\bar{\gamma}_i$	0.77	0.06	<u>0.01</u>
Levels 2↔4	$\delta_i/\bar{\delta}_i$	1.06	0.01	0.002
Levels 1↔3	$\varepsilon_i/\bar{\varepsilon}_i$	2.06	0.1	0.09

The demography process is defined by means of a matrix:

$$\mathbf{L} = \begin{pmatrix} \mathbf{0} & \mathbf{0} & \mathbf{F} \\ \mathbf{S}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{S}_2 & \mathbf{S}_3 \end{pmatrix}$$

where $\mathbf{F} = \text{diag}\{f_1^3, \dots, f_{15}^3\}$ and $\mathbf{S}_i = \text{diag}\{s_1^i, \dots, s_{15}^i\}$. The parameter f_j^3 corresponds to the fertility of adults on patch j , while s_j^i represents the survival rate of age-class i on patch j (Table 1).

The expression of the matrix \mathbf{F} is based on the hypothesis that adults of patch i reproduce only in patch i .

Let $n_j^i(t)$ be the number of individuals aged i on patch j at time t , $i = 1, 2, 3$ and $j = 1, \dots, 15$. We use the vector N_t to describe the total population at time t . This vector is a set of population vectors N_t^i describing the internal structure of each subpopulation as follows:

$$N_t = (N_t^1, N_t^2, N_t^3)^T \quad \text{where} \quad N_t^i = (n_1^i(t), \dots, n_{15}^i(t))^T$$

We consider here as projection interval the one associated to the slow dynamics, that is to the matrix \mathbf{L} . According to Sanchez *et al.* (1995), the general model consists of the following system of linear difference equations:

$$N_{t+1} = \mathbf{L}\mathbf{P}^k N_t \quad (1)$$

where k is a big enough integer allowing migrations to reach the equilibrium state.

The Aggregated Model

The global variables, whose dynamics are going to be approximated by the aggregated system, are the total number of individuals in every subpopulations. They form the vector $Y_t = (Y_t^1, Y_t^2, Y_t^3)^T$ where:

$$Y_t' = \sum_{j=1}^{15} n_j'(t)$$

The vectors Y_t and N_t are related by $Y_t = \mathbf{U}N_t$, where $\mathbf{U} = \text{diag}\{\mathbf{1}, \mathbf{1}, \mathbf{1}\}$ is called the aggregation matrix, the vector $\mathbf{1}$ being the (1×15) vector $(1, \dots, 1)$.

According to these notations, we get the following aggregated system (Sanchez *et al.*, 1995):

$$Y_{t+1} = \bar{\mathbf{L}}Y_t \quad \text{where} \quad \bar{\mathbf{L}} = \mathbf{U}\mathbf{L}\bar{\mathbf{P}}_c \quad (2)$$

The matrix $\bar{\mathbf{L}}$ can be expressed as follows:

$$\bar{\mathbf{L}} = \begin{pmatrix} 0 & 0 & \bar{F} \\ \bar{S}_1 & 0 & 0 \\ 0 & \bar{S}_2 & \bar{S}_3 \end{pmatrix}$$

where $\bar{F} = \mathbf{1}\mathbf{F}\bar{\mathbf{v}}^3$, $\bar{S}_1 = \mathbf{1}\mathbf{S}_1\bar{\mathbf{v}}^1$, $\bar{S}_2 = \mathbf{1}\mathbf{S}_2\bar{\mathbf{v}}^2$ and $\bar{S}_3 = \mathbf{1}\mathbf{S}_3\bar{\mathbf{v}}^3$

Characterization of the Different River Networks

As demonstrated in Sanchez *et al.* (1995), the global system (1) and the aggregated one (2) exhibit a similar asymptotic behaviour, that is, the dominant eigenvalue and the associated eigenvector of both systems are practically equal when the migration dynamics is fast enough. The global fish population dynamics through the arborescent river network can then be studied by means of the aggregated model.

$\bar{\mathbf{L}}$ is a primitive matrix of constant coefficients, $\bar{\mathbf{L}}^4 > 0$. So, Perron-Frobenius Theorem (Caswell, 1989) applies and the long-term dynamics of the global population is characterized by the unique positive eigenvalue of the matrix $\bar{\mathbf{L}}$ and its corresponding eigenvector. Let $\bar{\lambda}_{ref}$ be the dominant eigenvalue of the reference river network and $\bar{\lambda}_T$ that of the changed river network. The effect of each change is quantified by comparison of $\bar{\lambda}_{ref}$ and $\bar{\lambda}_T$.

In both cases (dams and channels), we studied the effects of a gradual increase in changes in the river network on the dominant eigenvalue of the aggregated matrix.

4. RESULTS AND DISCUSSION

The Reference River Network

Given numerical values of the demographic parameters and the equilibrium frequencies (Table 1), the migration rates were estimated and are given in Table 2. Hence, the direct migration rate of YOY from level 1 to level 2 (underlined value in Table 2) is one and a half times as big as the reverse one, which indicates that YOY are rather present at the top of the river network. In the same way, the direct migration rate of adults from level 3 to level 4 is hundred times as small as the reverse one, which indicates that adults are mainly present at the down side. These results coincide with our biological hypotheses.

The aggregated parameters were calculated and the aggregated matrix $\bar{\mathbf{L}}$ can be written:

$$\bar{\mathbf{L}} = \begin{pmatrix} 0 & 0 & 62.9 \\ 0.0497 & 0 & 0 \\ 0 & 0.268 & 0.271 \end{pmatrix}$$

Finally, the reference dominant eigenvalue was estimated: $\bar{\lambda}_{ref} = 1.04$. This means that the global size of the brown trout population slightly increases in the reference river network each year.

Effects of Dams

Figure 2 shows the effect on the dominant eigenvalue of the aggregated matrix, in case 1 when the number of dams increases from 1 to 8 between levels 3 and 4, and in case 2, when the number of dams increases from 1 to 4 between levels 2 and 3.

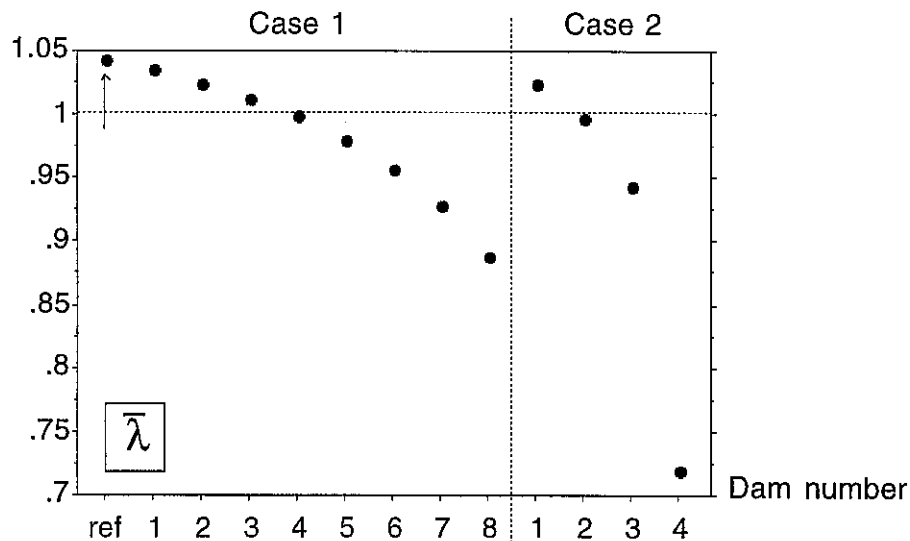


Figure 2. Effect, on the dominant eigenvalue of the aggregated matrix, of a gradual increase in the number of dams from 1 to 8 between levels 3 and 4 (case 1) and from 1 to 4 between levels 2 and 3 (case 2). The reference value $\bar{\lambda}_{ref}$ is indicated on the graph.

Generally, the gradual insertion of dams in the river network has a negative effect on $\bar{\lambda}$. When five or more dams are built between levels 3 and 4, $\bar{\lambda}$ becomes smaller than 1, *i.e.*, the global population tends to become extinct.

Moreover, insertion of dams between levels 2 and 3 has a more drastic effect on the global population dynamics of *Salmo trutta*. The construction of one dam between two patches of levels 2 and 3 (Figure 1(Ib)), is indeed equivalent to delete simultaneously three patches, which are precisely very favourable for the YOY survival and the adult reproduction (see Table 1). This may explain the effect observed on $\bar{\lambda}$ in case 2.

Effects of Channelling

Figure 3 shows the effect on the dominant eigenvalue of the aggregated matrix, in case 1 when the number of channels increases from 1 to 4 at level 3, and in case 2, when the number of channels increases from 1 to 2 at level 2.

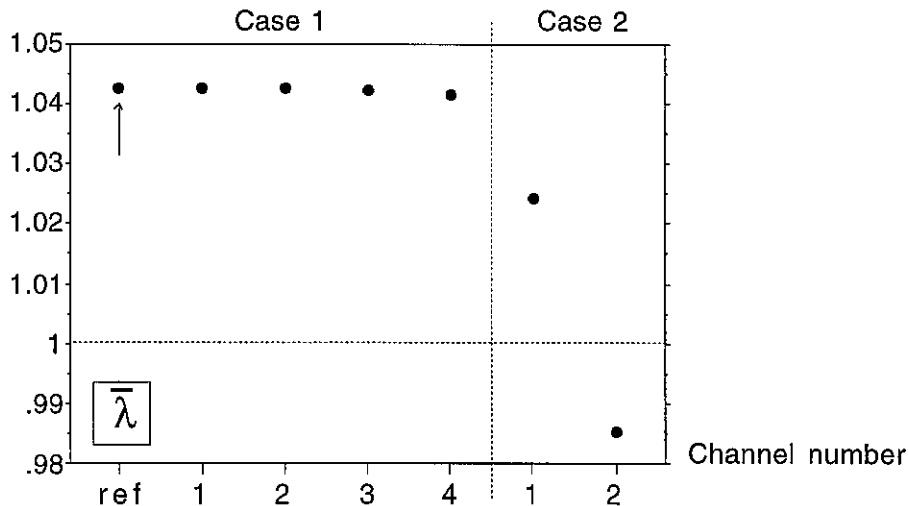


Figure 3. Effect, on the dominant eigenvalue of the aggregated matrix, of a gradual increase in the number of channelled patches (from 1 to 4 in the level 3, case 1, and from 1 to 2 in the level 2, case 2). The reference value $\bar{\lambda}_{ref}$ is indicated on the graph.

In case 1, the gradual increase in the number of channels has only a little effect on $\bar{\lambda}$ (which does not become visible on the graph because of the scale), while in case 2, $\bar{\lambda}$ is seriously affected. When two channels are constructed at level 2, $\bar{\lambda}$ becomes smaller than 1, *i.e.*, the global population tends but slowly ($\bar{\lambda} = 0.985$) to the extinction.

Nevertheless, by comparing figures 2 and 3, it appears that dams have a more drastic effect than channels on the global population dynamics in the arborescent river network considered here. Hence, in case of dams, $\bar{\lambda}$ decreases from 1.04 to 0.720, while in case of channels, $\bar{\lambda}$ decreases only from 1.04 to 0.985.

5. CONCLUSION

The aggregated model allowed us to describe the global dynamics of a trout like population in an arborescent river network. It also allowed the effects of various river network changes on these dynamics to be quantified. However, the complexity of the studied ecosystem is far from being completely described and the mathematical model could be improved. Hence, it would be interesting to take into account the density dependence effect of either demographic parameters or migration rates (Crisp, 1993; Newman, 1993). In that case, the general and the aggregated systems should be non-linear and the corresponding global dynamics become rather complicated. Moreover,

additional biological hypotheses might be introduced in the demographic model, for example time-dependent fecundity or survival rates (Debowski, 1991).

Our method is above all a general method and might be applied to other fish species (with a greater number of age-classes for example), or other types of population. However, our model remains to be validated by comparing simulation results with experimental data, that do not seem to be available yet.

Finally, although a dendritic river network has been studied in this work, our method could be extended to the study of other types of systems, like concentric patch network (to model a population dynamics in a lake) or rectangular systems (in a more general case).

REFERENCES

- Auger, P. (1989). Dynamics and Thermodynamics in Hierarchically Organized Systems. Applications in Physics, Biology and Economics. Oxford, Pergamon Press.
- Auger, P. and E. Benoît (1993). A prey-predator model in a multipatch environment with different time scales. *Journal of Biological Systems* 1: 187-197.
- Auger, P. and J.C. Poggiale (1995). Emerging properties in population dynamics with different time scales. *Journal of Biological Systems* 3: 591-602.
- Auger, P. and J.C. Poggiale (1996a). Aggregation and Emergence in hierarchically organized systems: population dynamics. *Acta Biotheoretica* 44: 301-316.
- Auger, P. and J.C. Poggiale (1996b). Emergence of population growth models: fast migration and slow growth. *Journal of Theoretical Biology* 182: 99-108.
- Auger, P.M. and R. Roussarie (1994). Complex ecological models with simple dynamics: from individuals to populations. *Acta Biotheoretica* 42: 111-136.
- Baglinière, J.L. and G. Maisse (1991). Biologie de la truite commune (*Salmo trutta* L.) dans les rivières françaises. In: J.L. Baglinière and G. Maisse, eds., *La Truite, Biologie et Écologie*, pp 25- 45. INRA Editions.
- Bravo de la Parra, R., E. Sanchez and P. Auger (1995). Aggregation methods in discrete models. *Journal of biological Systems* 3: 603-612.
- Bravo de la Parra, R., E. Sanchez and P. Auger (1997). Time scales in density dependent discrete models. *Journal of biological Systems* 5: 111-129.
- Caswell, H. (1989). *Matrix Population Models*. Sunderland, Sinauer Associates Inc.
- Crisp, D.T. (1993). Population densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. *Journal of Applied Ecology* 30: 759-771.
- Cummins, K.W. (1979). The natural stream ecosystem. In: J.V. Ward and J.A. Stanford, eds., *The Ecology of Regulated Stream*, 398p. New York, Plenum Press.
- Debowski, P. (1991). Density and mortality of Brown trout (*Salmo trutta* morpha fario L.) in two tributaries of the Pasleka River. *Polskie Archiwum Hydrobiologii* 38: 265 - 281.
- Gard, T.C. (1988). Aggregation in stochastic ecosystem models. *Ecological Modelling* 4: 153-164.
- Gardner, R.H., W.G. Cale and R.V. O'Neill (1982). Robust analysis of aggregation error. *Ecology* 63: 1771-1779.
- Iwasa, Y., V. Andreasen and S.A. Levin (1987). Aggregation in model ecosystems. I. Perfect aggregation. *Ecological Modelling* 37: 287-302.
- Iwasa, Y., S.A. Levin and V. Andreasen (1989). Aggregation in model ecosystems II. Approximate aggregation. *IMA J. Math. Appl. Med. Biol.* 6: 1-23.
- Levin, S.A. (1989). Challenges in the development of a theory of community and ecosystem structure and function. In: J. Roughgarden, R.M. May and S.A. Levin, eds., *Perspectives in Ecological Theory*, pp. 242-255. Princeton, Princeton University Press.

- May, R.M. (1989). Levels of organization in ecology. In: *Ecological Concepts. The Contribution of Ecology to an Understanding of the Natural World*. BES Symposium, pp 339-363. Oxford, Blackwell Scientific Publications.
- Michalsky, J., J.C. Poggiale, R. Arditi and P. Auger (1997). Macroscopic dynamic effects of migrations in patchy predator-prey systems. *Journal of Theoretical Biology* 185: 459-474.
- Newman, R.M. (1993). A conceptual model for examining density dependence in the growth of stream trout. *Ecology of Freshwater Fish* 2: 121-131.
- O'Neill, R.V., D.L. De Angelis, J.B. Waide and T.F.H. Allen (1986). *A Hierarchical Concept of Ecosystems*. Princeton, Princeton University Press.
- Poggiale, J.C and P. Auger (1996). Fast oscillating migrations in a predator-prey model. *Mathematical Models and Methods in Applied Sciences* 6: 217-226.
- Sanchez, E., R. Bravo de la Parra and P. Auger (1995). Linear discrete models with different time scales. *Acta Biotheoretica* 43: 465-479.