

# Annual spawning migrations in modelling brown trout population dynamics inside an arborescent river network

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## Abstract

In the present paper, the annual spawning migration of adults is introduced into a model, describing the *Salmo trutta* population dynamics in a hierarchically organized river network (four levels and 15 interconnected patches) model based on previous work. The model describes simultaneously demographic and migration processes taking place at different time scales: migrations of individuals between patches at a fast time scale (e.g. the week or the month), the annual spawning migration of adults and the demography at the slow time scale of the year. The *S. trutta* population is sub-divided into three age-classes (young of the year, juveniles, and adults). We used a Leslie-type model, coupled with a migration matrix associated with the annual spawning process, and a second migration matrix associated with fast movements of individuals between patches throughout the year. All demographic and migratory parameters are constant, leading to a linear model governing 45 state variables (15 patches  $\times$  three age-classes). By taking advantage of the two time scales and using aggregation techniques for the case of discrete time models, the complete model was approximated by a reduced one, with only three global variables (one per age-class) evolving at the slow time scale. Demographic indices were calculated for the population, and a sensibility analysis was performed to detect which parameters influence the most model predictions. We also quantified how modifications of the river network structure, by channels (change in connections between patches) or dams (patch deletion), influence the global population dynamics. We checked that the strategy of annual spawning migrations is actually beneficial for the population (the asymptotic population growth rate is increased), and that dams may have a more detrimental effect on the whole population dynamics than channelling. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Spawning migrations; Population dynamics; Leslie matrix; Aggregation techniques; Arborescent river network; *Salmo trutta*

## 1. Introduction

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In earlier contributions (Charles et al., 1998a,b), we showed that the use of variables

aggregation methods seemed a good compromise in modelling ecological system dynamics. Indeed, in such complex systems, numerous processes run at different time scales, involving either several species with different developmental stages, a single species implied in several actions (as breeding or feeding), or even both. Auger (1989) initiated such studies, coupling various processes at different time scales, in the framework of continuous time models. Aggregation methods were further developed and applied for linear as well as density-dependent models in the field of Ecology (Auger and Benoît, 1993; Auger and Roussarie, 1994; Auger and Poggiale, 1996, 1998; Michalsky et al., 1997; Auger and Pontier, 1998; Bernstein et al., 1999). The aim of aggregation methods is to construct the aggregated model that summarises the dynamics of the complex one simplifying thus their analytical study. Aggregation methods are based on the main idea that the aggregated model must reflect at one and the same time the slow and the fast dynamics of the general system.

In recent years, such methods were also implemented with discrete time models (Sánchez et al., 1995; Bravo de la Parra et al., 1995, 1997; Bravo de la Parra and Sánchez, 1998; Sanz and Bravo de la Parra, 1998, 1999). Indeed, discrete time models are widely used in population dynamics, as they are particularly well adapted to study the life cycle of most of populations (Caswell, 1989). For example, the Leslie matrix model (Caswell, 1989; Logofet, 1993) describes an age-structured population, and provides growth dynamics of the population density at successive generations.

The purpose of this study is to include the annual spawning migrations in the dynamics of a brown trout population (*Salmo trutta*), previously modelled with aggregation techniques in the case of discrete time models (Charles et al., 1998a,b). The population is sub-divided into three age-classes and located in an arborescent structure of four levels and 15 patches (called the reference river network). Based on the Leslie matrix model, some studies have dealt with such complex models designed as multi-regional Leslie models (Lebreton and Gonzales-Davila, 1993; Lebreton, 1996). However, unlike these works, here we considered that (1) the population can develop in each patch;

(2) all individuals can migrate from one patch to another according to some rules; (3) both processes (demography and migration) take place at two different time scales (Charles et al., 1998a,b). Reproduction taking place once a year, demography considered at the scale of the year represents the slow dynamics. Individual movements correspond to the fast process, at the scale of a week for example.

The causes of decline or extinction in fish populations are generally multifaceted, but often fall into three categories: overfishing, introduction of new species and stocking with hatchery fish, or habitat degradation due to the impact of human activities on rivers (Wootton, 1990; Hicks et al., 1991; Hindar et al., 1991; Nehlsen et al., 1991). Modelling is then a convenient tool to describe and understand fish population dynamics. Some recent models have been developed to describe these phenomena, especially with salmonids (Elliott, 1985; Davaine and Beall, 1992, 1997; Ratner et al., 1997; Sabaton et al., 1997; Jarry et al., 1998; Shuter et al., 1998; Gouraud et al., 1999), but always at a small spatial scale involving a single stream (one patch) and without considering a time scale faster for migration than for demography. Nevertheless, fishes, and *S. trutta* is a good example, generally migrate to achieve their life cycle: especially for reproduction once a year (Ovidio et al., 1998), or frequently for habitat or food searching. Even if homing behaviour is described for brown trout population, few studies have been performed to quantify either the proportion of returning adults into their natal stream, or the in-stream mortality during this spawning migration (Jarry et al., 1998; Ovidio et al., 1998). Other authors described individual movements of a brown trout population at fast time scales in food searching (Gowan et al., 1994). All of this emphasises the necessity to study population dynamics at the scale of the river network (Propst and Stefferud, 1997), by taking into account demography and spawning year migration coupled with fast individual migrations.

In our study, demographic and migration processes are supposed to be density-independent and all parameters are constant. The general model we propose evolves at the time scale of a year (corre-

sponding to demography), and couples a ( $45 \times 45$ ) Leslie-type matrix with two migration matrices. The first one operates numerous times during the year to describe fast movements of individuals between patches, the other one is associated with the annual upstream migration of adults for spawning. By applying the variables aggregation method, this general model is reduced into an aggregated system with only three global variables (one per age-class). The demographic parameters of the aggregated model are constant and expressed in terms of the corresponding parameters of the general system, weighted by the equilibrium proportions of individuals in the different patches. These equilibrium proportions are the result of the fast migration process.

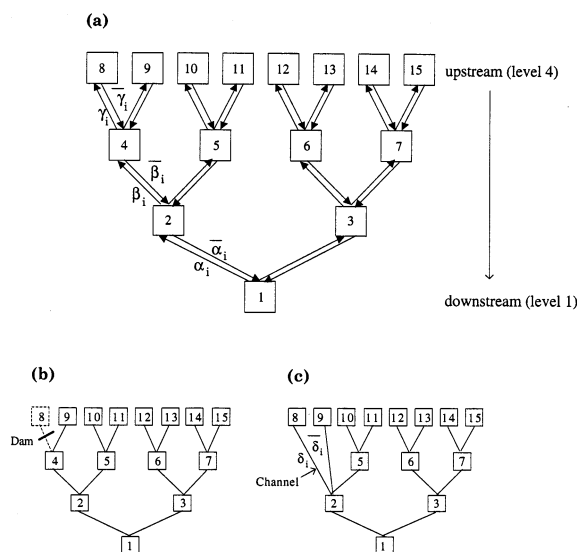


Fig. 1. (a) Schematic graph of the arborescent structure representing the reference river network, with four levels and 15 patches. Parameters  $\alpha_i$ ,  $\beta_i$ ,  $\gamma_i$  and  $\bar{\alpha}_i$ ,  $\bar{\beta}_i$ ,  $\bar{\gamma}_i$  are, respectively, the direct and the reverse migrations rates for each age-class through the river network. (b) Changes in connections by dams between levels 3 and 4. Some patches (here patch 8 only) are disconnected from the main network. (c) Changes in connections by channels between levels 2 and 4. The demographic process becomes impossible in some patches (here in patch 4), and new migration rates appear ( $\delta_i$  and  $\bar{\delta}_i$  in the present case;  $\varepsilon_i$  and  $\bar{\varepsilon}_i$  when channels directly connect levels 1 and 3).

From the aggregated model, classical demographic indices (as asymptotic population growth rate, stable age distribution, etc.) were derived, and the model sensibility to different parameters was evaluated. In particular, we first looked at the effect of the upstream annual spawning migration on the trout population dynamics, and then we tested different scenarios in spawning behaviour, to point out the best strategy as a trade-off between proportions of adult migrants and the in-stream mortality during migration. Finally, we try to quantify how modifications of the river network structure, by channels (change in connections between patches) or dams (patch deletion), influence the global population dynamics (Heggenes, 1988). In fact, channelling is not supposed to change the connectivity between patches, but to reduce both the quality and the amount of fish habitat. In our model, the impact of channels was considered as extreme as possible, i.e. all habitats, including spawning grounds, were suppressed in the impounded patches. The impact of dams was also considered as extreme, all patches upstream from the dams being deleted from the river network.

## 2. Biological framework

Biological data are those used in previous studies (Charles et al., 1998a,b). For more clarity of the new results, we will partly recall the biological framework.

### 2.1. The river network

The reference river network can be schematised as on Fig. 1a, levels 4 and 1 corresponding to the top and bottom ends of the network. Individuals can develop in each patch and migrate between patches, according to rules indicated on the graph. At level  $n$ , all patches are equivalent and the river network considered here is symmetric and dichotomic (other configurations would be possible). Migration rates depend on the age-class and the arborescence level.

Table 1  
Individual fecundity of each age-class of the *S. trutta* population, at the different levels in the reference river network<sup>a</sup>

Level	YOY fecundity	Juvenile fecundity	Adult fecundity
1	0	0	$f/a^3$
2	0	0	$f/a^2$
3	0	0	$f/a$
4	0	0	$f$

<sup>a</sup>  $a$  describes the fecundity gradient:  $a = 2$  according to expert advice.  $f$  is the YOY number per female per year:  $f = 265$  according to Baglinière and Maisse (1991).

Table 2  
Individual survival rate of each age-class of the *S. trutta* population, at the different levels of the reference river network<sup>a</sup>

Level	YOY survival rate	Juvenile survival rate	Adult survival rate
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	$s_1$	$s_2/a^2$	$s_3/a^3$

<sup>a</sup>  $s_1$ ,  $s_2$  and  $s_3$  are optimal survival rates for each age-class:  $s_1 = 0.07$ ;  $s_2 = s_3 = 0.4$  (Baglinière and Maisse, 1991). The parameter  $a$  is the same as in Table 1:  $a = 2$ .

2.2. Modified river networks according to connections

Two kinds of changes in connections inside the river network were considered. Dams (Fig. 1b for example) reduce to zero, direct and reverse migration rates between some patches, while other migration rates are left unchanged. As the upstream effects of a dam (in the disconnected patches) cannot be quantified (upper patches can change

into lakes and/or demographic parameters can largely be modified), we only focused on what happens downstream in the river network. We considered dams either between levels 3 and 4, or between levels 2 and 3. Indeed, between levels 1 and 2, only one dam can be inserted in a realistic way, and we could not quantify the effect of an increase in the number of dams.

Channelling (Fig. 1c for example) between levels  $n$  and  $(n + 2)$  consists in forbidding the demographic process in the patch of the intermediate level  $(n + 1)$ . New migration rates are thus introduced between levels  $n$  and  $(n + 2)$  (see Appendix A). We considered that channels could be inserted either between levels 2 and 4 (with new migration rates  $\delta_i$  and  $\bar{\delta}_i$ ), or between levels 1 and 3 (with new migration rates  $\varepsilon_i$  and  $\bar{\varepsilon}_i$ ).

We studied effects on the overall fish population dynamics of a gradual increase in the number of dams (up to eight between levels 3 and 4, or four between 2 and 3), or channels (up to four between levels 2 and 4, or two between levels 1 and 3).

2.3. Biological data

The brown trout population (*S. trutta*) is subdivided into three age-classes: Young Of the Year or YOY (0 + ), juveniles (1 + ) and adults (> 1 + ). Only adults can reproduce and the mean age of adult death is not known a priori. Survival rates from age  $i$  to age  $i + 1$  and fecundity (number of YOY per female per year) depend on the arborescence level, and the gradient of survival rates depends on the age-class (Tables 1–3).

The fecundity, denoted by  $f$  afterwards, is estimated with a unit sex ratio (1:1) as the product of

Table 3  
Individual proportions of each age-class of the *S. trutta* population, at the different levels of the reference river network (Baglinière and Maisse, 1991)

Level	Proportion of YOY	Proportion of juveniles	Proportion of adults
1	4	45	43.7
2	12	35	40
3	33	18	16
4	51	2	0.3

the egg number per female per year by the egg-to-YOY survival rate. It is estimated in the most favourable environmental conditions (level 4) in which parameters determining the egg-to-YOY survival rate (substrate composition, level of O<sub>2</sub> supply, predation risk, Rubin and Glimsäter, 1996) are optimal. The decrease in fecundity with the arborescent level is thus the consequence of the degradation of the hatching and first stage developmental conditions from level 4 to 1. This gradient is then roughly approached by a parameter  $a$  (Table 1).

YOY survival rate is optimal at level 4 (upstream), while that of adults is the best at level 1 (downstream). For juveniles, we considered that they survive better at level 3 (Table 2). The parameter  $a$  represents the effect of the river network structure on demographic parameters. By way of simplicity, we did not distinguish a various effect on survival rate and fecundity ( $a=2$  in both cases). Moreover, the lack of relevant biological data did not allow estimation of such a difference.

The numerical values chosen for all demographic parameters are those estimated by Baglinière and Maisse (1991) in the Scorff watershed (Brittany). They correspond to means, but S.D.s were not available and their precision could not be quantified (Tables 1 and 2).

Concerning the migration process, spatial mixing being supposed to go faster than demography, individuals of the different age-classes spread over among patches, according to proportions varying with the arborescence levels. These proportions are given in Table 3.

### 3. Modelling process

#### 3.1. The complete model with annual spawning migrations

For convenience, the basic methodological framework developed in Charles et al. (1998a,b) is partially summarized.

We denote:

- $n_j^i(t)$  the number of individuals aged  $i$  on patch  $j$  at time  $t$ , with  $i=1,2,3$  and  $j=1\dots 15$ ;

- $\tilde{\mathbf{n}}_t = (\tilde{\mathbf{n}}_t^1, \tilde{\mathbf{n}}_t^2, \tilde{\mathbf{n}}_t^3)^T$  a vector of dimension 45 corresponding to the total population at time  $t$ , where  $\tilde{\mathbf{n}}_t^i = ((n_1^i(t), \dots, n_{15}^i(t))^T$  describes the internal structure of the age-class  $i$  at time  $t$  (super-script ‘ $T$ ’ denotes transposition).

Migration rates of the age-class  $i$ , as defined in Section 2.1, form a column stochastic matrix of dimension 15,  $\mathbf{P}_i$ , and the  $45 \times 45$  matrix  $\mathbf{P} = \text{diag}\{\mathbf{P}_1, \mathbf{P}_2, \mathbf{P}_3\}$  represents the complete migration process. The construction and the expression of matrix  $\mathbf{P}_i$  are detailed in Appendix A.1. Let  $\tau$  be the fast time interval corresponding to migrations. As all migration rates remain constant, the migration model is linear and can be written as follows:

$$\tilde{\mathbf{n}}_{\tau+1} = \mathbf{P}\tilde{\mathbf{n}}_{\tau} \quad (1)$$

The demography is considered density-independent and, therefore, it is defined by means of two kinds of constant transition coefficients (their numerical values are given in Table 1), as in the standard Leslie model:

- $f_j^3$ : fertility of adults (age-class 3) on patch  $j$  (only adults are able to reproduce, juveniles being still immature);
- $s_j^i$ : survival rates of age-class  $i$  in patch  $j$ ,  $i=1, 2, 3$  ( $s_j^3$  is not equal to zero as the exact age of death is not known).

If we define the matrices  $\mathbf{F}_3 = \text{diag}\{f_1^3 \dots f_{15}^3\}$  and  $\mathbf{S}_i = \text{diag}\{s_1^i \dots s_{15}^i\}$ , we finally get the following generalised Leslie matrix to describe the complete demographic process at the slow time scale:

$$\mathbf{L} = \begin{pmatrix} 0 & 0 & \mathbf{F}_3 \\ \mathbf{S}_1 & 0 & 0 \\ 0 & \mathbf{S}_2 & \mathbf{S}_3 \end{pmatrix} \quad (2)$$

The expression of the diagonal matrix  $\mathbf{F}_3$  is based on the hypothesis that adults in patch  $j$  reproduce only in patch  $j$ . Hence, at the slow time scale of demography, the model is linear and is simply:

$$\tilde{\mathbf{n}}_{t+1} = \mathbf{L}\tilde{\mathbf{n}}_t \quad (3)$$

In our new model, the specific migration of adults just before breeding is taken into account by first decomposing the matrix  $\mathbf{L}$  as follows:

$$\mathbf{L} = \begin{pmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{S}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{S}_2 & \mathbf{S}_3 \end{pmatrix} + \begin{pmatrix} \mathbf{0} & \mathbf{0} & \mathbf{F}_3 \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix} = \mathbf{S} + \mathbf{F} \quad (4)$$

Then, as the annual spawning migration only affects fecundity, by calling  $\mathbf{P}'$  the corresponding matrix and assuming that individuals enter their natal tributaries before breeding, we get:

$$\mathbf{L}' = \mathbf{S} + \mathbf{F}\mathbf{P}' \quad (5)$$

As detailed in Appendix A.2,  $\mathbf{P}' = \text{diag}\{\mathbf{I}, \mathbf{I}, \mathbf{P}'_3\}$  where  $\mathbf{P}'_3$  is a function of  $\omega$ , the proportion of individuals going to level 4 in order to breed, and of  $\beta$ , the in-stream mortality rate induced by migration from one level to the upper one. The proportion of migrating fishes unrolls according to a top-down gradient of factor  $\tilde{a}$  ( $\tilde{a} \neq a$ ). The in-stream mortality rate is set to zero for individuals going downstream.

When  $\beta = 0$ , individual number must remain invariant; there are no spawning migrations, but the spatial mixing is still active, which implies (see Appendix A.2):

$$\omega \left( 1 + \frac{1}{\tilde{a}} + \frac{1}{\tilde{a}^2} + \frac{1}{\tilde{a}^3} \right) = 1 \quad (6)$$

At the slow time scale, the model finally reads:

$$\tilde{\mathbf{n}}_{t+1} = \mathbf{L}'\tilde{\mathbf{n}}_t \text{ with } \mathbf{L}' = \begin{pmatrix} \mathbf{0} & \mathbf{0} & \mathbf{F}_3\mathbf{P}'_3 \\ \mathbf{S}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{S}_2 & \mathbf{S}_3 \end{pmatrix} \quad (7)$$

At last, by considering the demographic time interval as the projection interval to describe the coupled demographic and migration processes, the general model combines models (1) and (7). It consists of the following system of linear difference equations (Sánchez et al., 1995; see also Charles et al., 1998a,b for an application):

$$\tilde{\mathbf{n}}_{t+1} = \mathbf{L}'\mathbf{P}^k\tilde{\mathbf{n}}_t \quad (8)$$

where  $k$  is a large integer signifying that the migration process acts a large number of times during one single time unit of the demographic one.

### 3.2. The aggregated model with annual spawning migrations

Let  $N_t^i$  be global variables defined as total numbers of individuals in each age-class. They are invariant for the fast dynamics, and read as follows:

$$N_t^i = \sum_{j=1}^{15} n_j^i(t) \quad (9)$$

If we denote  $\mathbf{1}$  the row vector of dimension 15 with all entries equal to 1, we have  $N_t^i = \mathbf{1}\tilde{\mathbf{n}}_t^i$  and  $\tilde{\mathbf{N}}_t = \mathbf{U}\tilde{\mathbf{n}}_t$  where  $\mathbf{U} = \text{diag}\{\mathbf{1}, \mathbf{1}, \mathbf{1}\}$  of dimension  $(3 \times 45)$  is the aggregation matrix.

The vector  $\tilde{\mathbf{N}}_t = (N_t^1, N_t^2, N_t^3)^T$  represents the total population vector of dimension 3, whose components are the total number of individuals in each age-class.

The fast dynamics is internal for each age-class and, for every fixed value of the global variables, asymptotically leads to equilibrium, i.e. to certain constant proportions of each age-class in each patch. We denote  $v_j^{*i}$  the fast equilibrium frequencies for the age-class  $i$  in patch  $j$ ; their numerical values correspond to the individual proportions of each age-class in each patch, which are given in Table 3. As detailed in Appendix A.1, the fast equilibrium frequencies can be expressed in terms of migration ratios.

We define the  $(45 \times 3)$  matrix  $\bar{\mathbf{P}}_c = \text{diag}\{\mathbf{v}^{*1}, \mathbf{v}^{*2}, \mathbf{v}^{*3}\}$  with  $\mathbf{v}^{*i} = (v_1^{*i}, \dots, v_{15}^{*i})^T$ . For every  $i = 1, 2, 3$ , the stochastic matrix  $\mathbf{P}_i$  is primitive ( $\mathbf{P}_i^6 > 0$ ) and then the vector  $\mathbf{v}^{*i}$  of equilibrium frequencies is nothing but its eigenvector associated to the eigenvalue 1 and normalized so that  $\sum_{j=1}^{15} v_j^{*i} = 1$ . Hence,  $\lim_{k \rightarrow \infty} \mathbf{P}^k = \mathbf{P}^\infty = \bar{\mathbf{P}}_c \mathbf{U}$  (Bravo de la Parra and Sánchez, 1998).

The general model (Eq. (8)) can be approximated by the following aggregated model, which governs the global variables at the slow time scale of demography (Sánchez et al., 1995):

$$\tilde{\mathbf{N}}_{t+1} = \bar{\mathbf{L}}'\tilde{\mathbf{N}}_t \text{ with } \bar{\mathbf{L}}' = \mathbf{U}\mathbf{L}'\bar{\mathbf{P}}_c \quad (10)$$

All biological processes involved in this model being density-independent, the matrix  $\bar{\mathbf{L}}'$  is a Leslie-type matrix with constant transition coefficients, leading to the linear model (Eq. (10)):

$$\bar{\mathbf{L}}' = \begin{pmatrix} 0 & 0 & \bar{F}_3(a, f, v_j^{*3}, \tilde{a}, \omega, \beta) \\ \bar{S}_1 & 0 & 0 \\ 0 & \bar{S}_2 & \bar{S}_3 \end{pmatrix} \quad (11)$$

The entries of the matrix  $\bar{\mathbf{L}}'$  of the aggregated model are functions of the fast equilibrium frequencies (i.e. of the migration ratios), as well as of the demographic and spawning parameters:

$$\bar{S}_i = \sum_{j=1}^{15} \mathbf{1S}_i \mathbf{v}^{*i}$$

and  $\bar{F}_3$  is a combination of  $a, f, v_j^{*3}, \tilde{a}, \omega, \beta$ .

We have then collapsed the original complete system (Eq. (8)) into an aggregated system (Eq. (10)) with only three state variables, one per age-class.

### 3.3. Analysis of the aggregated model

The aggregated model (Eq. (10)) is a good approximation of the complete model (Eq. (8)) as soon as  $k$  is great enough, as demonstrated by Bravo de la Parra et al. (1995) and Sánchez et al. (1995). In Charles et al. (1998a), we illustrated with simulations the fact that the dominant eigenvalues of both models are similar for a  $k$  value greater than 12 (a patch change at least once a month). Thus, the population dynamics of *S. trutta* can entirely be characterised from model (Eq. (10)), with respect to the asymptotic growth rate and the asymptotic age-structure.

The matrix  $\bar{\mathbf{L}}'$  is a primitive matrix of constant coefficients, thus Perron-Frobenius Theorem applies (Caswell, 1989) and the dominant eigenvalue  $\bar{\lambda}'_1$  of  $\bar{\mathbf{L}}'$ , with the corresponding right eigenvector  $\mathbf{w}'_1$ , completely determines the asymptotic properties of the population growth.

The asymptotic growth rate  $\bar{\lambda}'_1$  and the stable population structure  $\mathbf{w}'_1$  describe the long-term dynamics of the population. The growth rate  $\bar{\lambda}'_1$  is also related to the *intrinsic rate of increase*  $r = \ln(\bar{\lambda}'_1)$ .

Some other demographic indices can be calculated from the demographic matrix  $\bar{\mathbf{L}}'$  (Caswell, 1989):

- The left eigenvector  $\mathbf{v}'_1$ , associated with the dominant eigenvalue  $\bar{\lambda}'_1$ , gives the age-specific

reproductive values, i.e. the contribution of each age-class to the future reproduction;  $\mathbf{v}'_1$  comprises for each age-class the amount of future reproduction, the probability of surviving to realise it, and the time required for the offspring to be produced.

- The *net reproductive rate* corresponding to the expected number of offspring by which a newborn individual will be replaced by the end of its life, i.e. to the renewal rate of each age-class, is given in our case by:

$$R_0 = \sum_{i=1}^{\infty} \bar{F}_i \prod_{j=1}^{i-1} \bar{S}_j = \bar{F}_3 \bar{S}_1 \bar{S}_2 (1 + \bar{S}_3 + \bar{S}_3^2 + \bar{S}_3^3 + \dots) = \frac{\bar{F}_3 \bar{S}_1 \bar{S}_2}{1 - \bar{S}_3} \quad (12)$$

- The *generation time*, that is the mean age of the parents of the offspring produced by the population at the stable age distribution, can be calculated as follows:

$$T = \sum_{i=1}^{\infty} i \bar{\lambda}'_1^{(-i)} \bar{F}_i \prod_{j=1}^{i-1} \bar{S}_j = 3 \bar{\lambda}'_1^{(-3)} \frac{\bar{F}_3 \bar{S}_1 \bar{S}_2}{1 - \bar{S}_3} \quad (13)$$

Another important part of the study of the aggregated model is the *sensitivity analysis*, which consists in investigating how results might depend on changes in the matrix coefficients. Such changes represent variations in the life cycle, and may be of great interest in measuring how important vital rates are to population dynamics, or in evaluating the effects of errors in estimation. Such an analysis makes possible for example to define sampling procedures, in order to enhance the accuracy of the parameter estimation. According to Caswell (1989), the sensitivity of  $\bar{\lambda}'_1$  with respect to a coefficient  $a_{ij}$  is defined as:

$$\sigma_{ij} = \frac{\partial \bar{\lambda}'_1}{\partial a_{ij}} = \frac{v'_{1i} w'_{1j}}{\langle \mathbf{w}'_1, \mathbf{v}'_1 \rangle} \quad (14)$$

where  $\mathbf{v}'_1$  and  $\mathbf{w}'_1$  are, respectively, the left and right eigenvectors associated with  $\bar{\lambda}'_1$ ,  $v'_{1i}$  and  $w'_{1i}$  corresponding to their coordinates.

By applying Eq. (14) to the aggregated matrix  $\bar{\mathbf{L}}'$ , we obtain:

$$\sigma_{\bar{F}_3} = \frac{v'_{11}w'_{13}}{\langle \mathbf{w}'_1, \mathbf{v}'_1 \rangle}, \quad \sigma_{\bar{S}_1} = \frac{v'_{12}w'_{11}}{\langle \mathbf{w}'_1, \mathbf{v}'_1 \rangle}, \quad \sigma_{\bar{S}_2} = \frac{v'_{13}w'_{12}}{\langle \mathbf{w}'_1, \mathbf{v}'_1 \rangle} \text{ and } \sigma_{\bar{S}_3} = \frac{v'_{13}w'_{13}}{\langle \mathbf{w}'_1, \mathbf{v}'_1 \rangle}$$

It is noteworthy that the sensitivity of  $\bar{\lambda}'_1$  to changes in aggregated global parameters ( $\bar{F}_3$ ,  $\bar{S}_1$ ,  $\bar{S}_2$ ,  $\bar{S}_3$ ) is proportional to the sensitivity of  $\bar{\lambda}'_1$  to changes in optimal parameters ( $f$ ,  $s_1$ ,  $s_2$ ,  $s_3$ ). In fact, global and optimal parameters are proportional, and for example:

$$\begin{aligned} \bar{S}_1 &= \frac{s_1}{a^3} v_1^* + \frac{s_1}{a^2} (v_2^* + v_3^*) \\ &+ \frac{s_1}{a} (v_4^* + v_5^* + v_6^* + v_7^*) \\ &+ s_1 (v_8^* + v_9^* + v_{10}^* + v_{11}^* + v_{12}^* + v_{13}^* + v_{14}^* \\ &+ v_{15}^*) = s_1 \times C \end{aligned}$$

$$\begin{aligned} \text{where } C &= \frac{v_1^*}{a^3} + \frac{1}{a^2} (v_2^* + v_3^*) \\ &+ \frac{1}{a} (v_4^* + v_5^* + v_6^* + v_7^*) \\ &+ (v_8^* + v_9^* + v_{10}^* + v_{11}^* + v_{12}^* + v_{13}^* \\ &+ v_{14}^* + v_{15}^*) \end{aligned}$$

Hence, we obtain:

$$\sigma_{\bar{S}_1} = \frac{\partial \bar{\lambda}'_1}{\partial \bar{S}_1} = \frac{\partial \bar{\lambda}'_1}{\partial (s_1 \times C)} = \frac{1}{C} \frac{\partial \bar{\lambda}'_1}{\partial s_1} = \frac{s_1}{\bar{S}_1} \sigma_{s_1} \quad (15-1)$$

In the same way

$$\sigma_{\bar{S}_2} = \frac{s_2}{\bar{S}_2} \sigma_{s_2}, \quad \sigma_{\bar{S}_3} = \frac{s_3}{\bar{S}_3} \sigma_{s_3} \text{ and } \sigma_{\bar{F}_3} = \frac{f}{\bar{F}_3} \sigma_f \quad (15-2)$$

The study of the sensitivity of  $\bar{\lambda}'_1$  to spawning migration parameters  $\tilde{a}, \omega, \beta$  has also been performed by calculating partial derivatives of  $\bar{\lambda}'_1$  with respect to each parameter, according to values selected within a biologically realistic range of variation.

### 3.4. Analysis of changes in connections

When connections are modified between patches in the reference river network, all demographic indices of the global population are affected.

In the case of dams, we suppose in fact that some patches are disconnected from the main river network, with null migration rates towards these patches, but without modifying other migration rates. Hence, individuals of each age-class are distributed with new fast equilibrium frequencies, and global demographic parameters change.

In the case of channelling, the demographic process is considered as impossible in channelled patches and new migration rates are introduced. Proportions of each age-class in each patch are then modified, leading to new global demographic indices.

Appendix B gives some guidelines to build up matrices  $\mathbf{P}$  (fast migration matrix) and  $\mathbf{P}'$  (annual spawning migration matrix) in the case of dams or channelling.

In this work, we studied the effects of changes in connections on the global population dynamics, when annual migrations of adults just before reproduction are taken into account. We used the same method as detailed in Charles et al. (1998a,b), but on the basis of model (Eq. (10)).

In both cases of dams or channelling, changes in connections modify the aggregated matrix  $\bar{\mathbf{L}}'$  of model (Eq. (12)), and new demographic indices can be estimated. We paid particular attention on the new population growth rates denoted by  $\bar{\lambda}'_{1,C}$ , that we compared with  $\bar{\lambda}'_{1,\text{Ref}}$  corresponding to the reference river network.

## 4. Application to the brown trout *S. trutta*

### 4.1. Modelling global population dynamics

All simulations were performed with Mathematica 3.0.1™ software. The numerical values we used for demographic parameters (matrix  $\mathbf{L}$ ) and individual proportions of each age-class at each level (matrix  $\mathbf{P}_c$ ) are those given in Tables 1–3.

#### 4.1.1. Choice of parameters $\tilde{a}$ , $\omega$ and $\beta$ (matrix $\mathbf{P}'$ )

There is a good evidence that in many salmonid populations, individuals can home accurately to their natal stream in order to spawn (Wootton, 1990) and for some migratory anadromous popu-



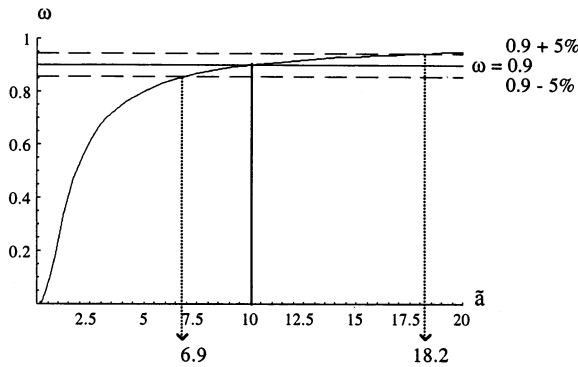


Fig. 2. Relationship between  $\omega$ , the proportion of returning individuals to their natal tributaries during spawning, and  $\tilde{a}$ , the factor characterizing the gradient in returning individual proportions. The more realistic values of  $\omega$  and  $\tilde{a}$  are, respectively, 0.9 and 10.

Table 4

Demographic indices<sup>a</sup> characterizing the global population dynamics in the reference river network

Aggregated matrix	$\bar{L}'$
	$= \begin{pmatrix} 0 & 0 & 185.171 \\ 0.0497 & 0 & 0 \\ 0 & 0.268 & 0.27095 \end{pmatrix}$
Asymptotic population growth rate	$\bar{\lambda}'_1 = 1.447$
Stable age distribution	$w'_1 = (95.96 \ 3.29 \ 0.75)$
Reproductive values	$v'_1 = (1.0 \ 29.1 \ 157.4)$
Net reproductive rate	$R_0 = 3.4$
Generation time	$T = 3.34$ years
Sensitivities	$\sigma_{\bar{F}_3} = 0.0017 \ \sigma_{\bar{S}_1} = 6.403$ $\sigma_{\bar{S}_2} = 1.120 \ \sigma_{\bar{S}_3} = 0.258$

<sup>a</sup> Calculated according to Caswell (1989) from the aggregated model (Eq. (10)).

lations, fewer than 5% of the returning fish get lost (Quinn, 1984). The homing behaviour in brown trout was widely accepted but it was poorly documented for spawning (a reference is given in Stuart, 1957). More studies dealt with the accurate return of displaced brown trout to their initial home range after artificial displacement (Halvorsen and Stabell, 1990; Armstrong and Herbert, 1997). Consequently, we fixed the proportion of returning individuals to their natal tributaries  $\omega$  at 0.9. The mortality rate during spawning migration from one level to the upper

( $\beta$ ) was fixed at 0.1 on the basis of the 0.1–0.2 range used by Ratner et al. (1997) for the in-stream mortality of returning spawners of chinook salmon (*Oncorhynchus tshawytscha*).

Hence, from Eq. (6), we get  $\tilde{a} = 10$ . This value, imposed by the conservation relationship (Eq. (6)), signifies that 0.09% ( $\omega/\tilde{a}^3$ ) of mature individuals will return breeding to level 1 (see Appendix A.2), which corresponds to the observation that most of adults will breed in the upper level of the river network (level 4). The parameter  $\tilde{a}$  might be considered as a measure of the intensity of homing behaviour.

The possible range of values for  $\tilde{a}$  corresponding to an  $\omega$  value around 0.9 is very large (Fig. 2). For example, when  $\omega$  varies between 0.855 (0.9 – 5%) and 0.945 (0.9 + 5%), then  $\tilde{a}$  varies from 6.9 (10 – 31%) to 18.2 (10 + 82%). Hence, a total variation of 9.5% on  $\omega$  involves a total variation of 163.7% on  $\tilde{a}$ .

#### 4.1.2. Global demographic indices

The aggregated matrix corresponding to the global aggregated model (Eq. (10)) reads as follows:

$$\bar{L}' = \begin{pmatrix} 0 & 0 & 185.171 \\ 0.0497 & 0 & 0 \\ 0 & 0.268 & 0.27095 \end{pmatrix}$$

All classical demographic indices calculated from  $\bar{L}'$  are summarized in Table 4, in particular, the asymptotic population growth rate is  $\bar{\lambda}'_1 = 1.447$ . All these results corroborate what is observed in real systems. For example, a generation time equal to 3.34 years broadly corresponds to the mean age of the most fertile trout, which reproduce for the first time in their third year of life (Baglinière, pers. commun.). It must also be highlighted that the annual spawning migration appears really beneficial for the global population dynamics of *S. trutta*. Indeed, in a previous model (Charles et al., 1998b) without this phenomenon, the asymptotic population growth rate was set around 1.04. In the present case, this value is increased to 1.447, what allows to quantify, in terms of global population growth, the benefit for

individuals to return breeding into their natal tributaries.

#### 4.1.3. Sensitivity analysis

Table 4 also provides results of sensitivity analysis on global parameters. With respect to the optimal demographic parameters (Eqs. (15-1) and (15-2)), we obtain:

$$\sigma_{\bar{F}_3} = 0.0024 \Rightarrow \sigma_f = 0.0017$$

$$\sigma_{\bar{s}_1} = 9.018 \Rightarrow \sigma_{s_1} = 6.403$$

$$\sigma_{\bar{s}_2} = 1.672 \Rightarrow \sigma_{s_2} = 1.120$$

$$\sigma_{\bar{s}_3} = 0.381 \Rightarrow \sigma_{s_3} = 0.258$$

The sensitivity of  $\bar{\lambda}'_1$  to  $s_1$  is very strong comparatively to other parameters, which indicates how important the estimation is of this parameter. Hence, a decrease of 5% in  $s_1$  leads to a decrease of 1.6% in  $\bar{\lambda}'_1$ , while a decrease of 5% in  $s_3$  leads to a decrease of only 0.35% in  $\bar{\lambda}'_1$ .

This strong sensitivity of  $\bar{\lambda}'_1$  to  $s_1$  and the relatively high value obtained for  $\bar{\lambda}'_1$  (1.447) suggest a

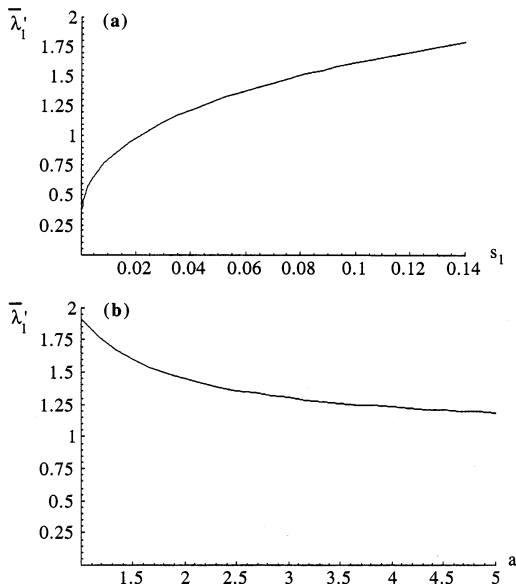


Fig. 3. Asymptotic population growth rate ( $\bar{\lambda}'_1$ ) in the whole river network, with respect to (a) the YOY survival rate  $s_1$ , and (b) the factor  $a$  characterizing fecundity and survival gradients.

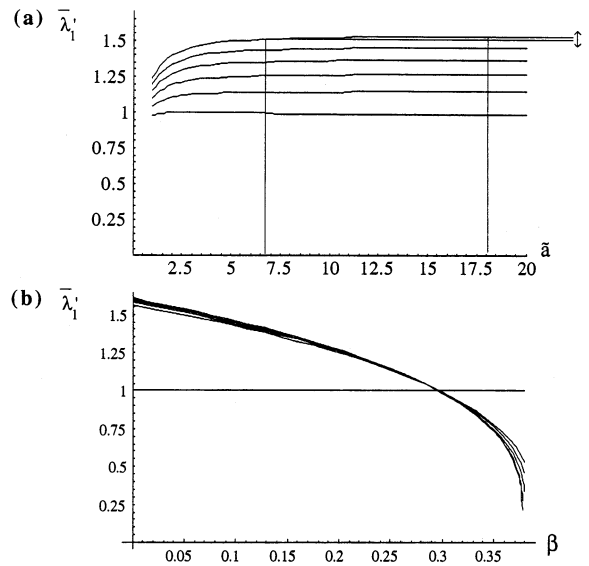


Fig. 4. (a) Sensitivity of the asymptotic population growth rate ( $\bar{\lambda}'_1$ ) in the whole river network, with respect to the factor  $\bar{a}$  characterizing the gradient in proportions of adults returning to their natal tributaries in order to breed, for  $\beta$  varying between 0.05 (upper curve) and 0.30 (lower curve). (b) Sensitivity of the asymptotic population growth rate ( $\bar{\lambda}'_1$ ) in the whole river network, with respect to the in-stream mortality  $\beta$  of returning adults during spawning, for  $\bar{a}$  varying between 6.9 (upper curve) and 18.2 (lower curve).

probable over-estimation of  $s_1$ . Fig. 3a shows how  $\bar{\lambda}'_1$  varies versus  $s_1$ , between 0.01 and 0.14 (twice the observed value 0.07). For example, with  $s_1 = 0.035$  ( $0.07/2$ ), we get  $\bar{\lambda}'_1 = 1.171$  a value closer to 1, but over the whole range of its realistic values (0.01–0.14), the overall variation in  $\bar{\lambda}'_1$  is approximately 55%.

Another important parameter is the factor  $a$  of the fecundity and survival gradients, which has arbitrarily been fixed to 2 according to expert opinion (Persat, pers. commun.). As shown in Fig. 3b for example, a decrease of 5% in  $a$  leads to an increase of 1.6% in  $\bar{\lambda}'_1$ , and if  $a$  varies in the whole range of realistic values (1–3), the total variation in  $\bar{\lambda}'_1$  is about 31.8%.

Fig. 4 shows that  $\bar{\lambda}'_1$  is influenced by spawning migration parameters  $\bar{a}$  and  $\beta$ . On a general point of view,  $\bar{\lambda}'_1$  seems less sensitive to these parameters than to the demographic ones (especially  $s_1$ ). The above mentioned variation of 163.7% on  $\bar{a}$  leads to a variation of 1.4% on  $\bar{\lambda}'_1$ , if the in-stream

mortality equals 0.1 (Fig. 4a). Nevertheless, the effect of  $\tilde{a}$  on  $\bar{\lambda}'_1$  decreases when  $\beta$  increases. For  $\beta = 0.1$ , any optimal value for  $\bar{\lambda}'_1$  can be observed, but, when  $\beta = 0.3$ , the relationship between  $\bar{\lambda}'_1$  and  $\tilde{a}$  exhibits an optimum for a particular of  $\tilde{a}$  (lower curve on Fig. 4a).

We also remark that the sensitivity of  $\bar{\lambda}'_1$  to  $\beta$  (Fig. 4b) is almost the same whatever  $\tilde{a}$  in the range 6.9–18.2, which corresponds to the range  $[\omega - 5\%; \omega + 5\%]$ . Hence, with  $\beta = 0.095$  ( $0.1 - 5\%$ ),  $\bar{\lambda}'_1 = 1.455$ , and when  $\beta = 0.105$  ( $0.1 + 5\%$ ),

then  $\bar{\lambda}'_1 = 1.439$ , i.e. a variation of 9.5% on  $\beta$  involves a variation of 1.1% on  $\bar{\lambda}'_1$ . In the same way, the previous variation of 163.7% on  $\tilde{a}$  corresponds to a variation of 1.4% on  $\bar{\lambda}'_1$ .

Consequently, once the proportions of returning individuals ( $\omega$ ) are determined, the gradient factor  $\tilde{a}$  is fixed (Eq. (6)), and the choice of the in-stream mortality  $\beta$  slightly influences the final population growth rate ( $\bar{\lambda}'_1$ ).

#### 4.2. Effects of changes in the river network

When changes in connections are introduced, the new population growth rate becomes  $\bar{\lambda}'_{1,C}$  (see Appendix B, for modifications in migration matrices). In order to compare this value to the reference one ( $\bar{\lambda}'_{1,\text{ref}}$ ), we can calculate a relative variation in  $\bar{\lambda}'_1$  as follows:

$$\Delta \bar{\lambda}'_1 = \left( \frac{\bar{\lambda}'_{1,\text{ref}} - \bar{\lambda}'_{1,C}}{\bar{\lambda}'_{1,\text{ref}}} \right) \times 100 \quad (16)$$

Fig. 5a shows how an increasing number of dams affects the asymptotic population growth rate. When dams are inserted between levels 3 and 4, the maximum variation in  $\bar{\lambda}'_1$  is 22.4%, but when dams are inserted between levels 2 and 3, the global population can quickly go to extinction, and the maximum variation in  $\bar{\lambda}'_1$  can reach 47.2%. Thus in the worst case (four dams between levels 2 and 3), the global trout population exhibits a growth rate 47.2% lower than the maximum (0.765 instead of 1.447).

From Fig. 5b, channels seem almost not to affect the global population dynamics. With channels between levels 2 and 4, an unexpected slight increase in  $\bar{\lambda}'_1$  can even be observed, the maximum value of  $\bar{\lambda}'_1$  being 1.562 (7.9% more than the reference value 1.447). In the worst case (two channels between levels 1 and 3), the global trout population is affected very little, as the variation in  $\bar{\lambda}'_1$  is only 5.8% at the maximum.

Even if both kinds of changes in connections cannot be compared, as their effects inside the river network are different (patch deletion for dams, new migration rules for channels), it seems more detrimental for the population to insert dams than channels. For example, only one dam between levels 2 and 3 but two channels between

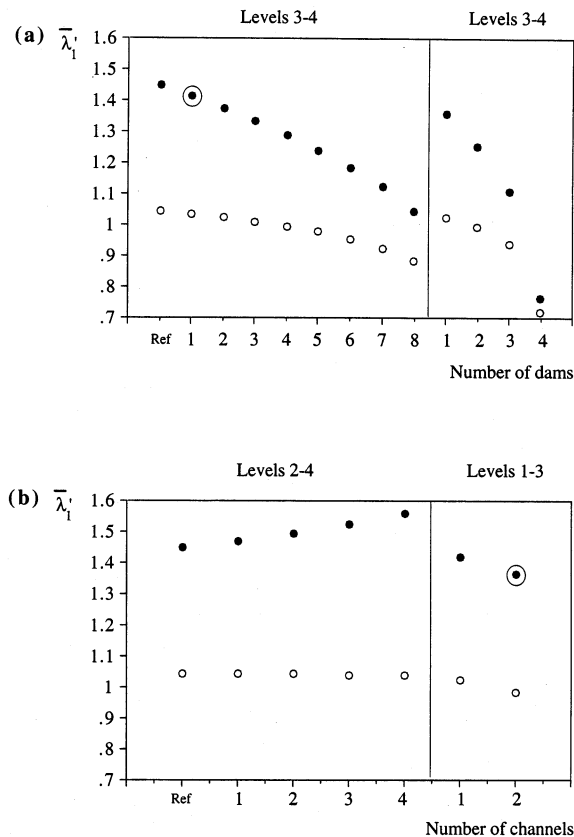


Fig. 5. (a) Effect on the asymptotic population growth rate ( $\bar{\lambda}'_1$ ) of an increasing number of dams, either between levels 3 and 4, or between levels 2 and 3. (b) Effect on the asymptotic population growth rate ( $\bar{\lambda}'_1$ ) of an increasing number of channels, either between levels 3 and 4, or between levels 2 and 3. Filled circles (●) correspond to simulations obtained with model (Eq. (10)); open circles (○) were obtained with a previous model without annual spawning migrations (Charles et al., 1998b). Surrounded points correspond to a same relative variation of 5.8% in the asymptotic population growth rate  $\bar{\lambda}'_1$ .

levels 1 and 3 (surrounded points on Fig. 5a,b) lead to the same variation in  $\bar{\lambda}'_1$  (5.8%).

All these results confirm the tendency we showed with our previous simple model (Charles et al., 1998b). For example, an increase in the number of dams leads both models to a decrease in  $\bar{\lambda}'_1$  (Fig. 5, comparison between black and white points). Moreover, the ‘advantageous’ effect of channels is reinforced, as the slight increase in  $\bar{\lambda}'_1$  becomes obvious with the model including the annual spawning migration.

## 5. Conclusion

The model presented here makes it possible to describe the brown trout population dynamics in a hierarchical river network, by coupling individual migration at a fast time scale, with annual spawning migrations and demography at the scale of the year. The overall population dynamics appeared obviously reinforced by including spawning migration, a commonly admitted but rarely demonstrated statement. The proportion of individuals returning into their natal tributaries strongly determines the whole population dynamics, while, for a given value of this parameter, the others (the migration mortality and the top-down migration gradient) affect very little the predictions of the model.

However, if the introduction of the spawning migration behaviour provided a fundamental increase of the population dynamics, the sensitivity analysis revealed that, in this model, the parameters of this behaviour influence more slightly the asymptotic population growth rate than the demographic parameters, especially the YOY survival rate.

Indeed, calculated values of population growth rate appeared rather large and biologically unrealistic. Numerous factors might explain these observations, but, according to the sensitivity analysis and the biological background of fish population dynamics, YOY survival rate must be the most important determinant. Indeed,  $s_1$  values are suspected to be highly variable and strongly dependent on environmental conditions. For example, under gravel, survival rate of eggs may vary from 20 to 80% for brown trout in the Scorff watershed (Baglinière, pers. commun.). In the same way, the

YOY survival is actually hard to estimate because it does not usually exceed 5% and deals with fishes too small to be correctly sampled.

Our modelling principle also makes possible to evaluate both qualitatively and quantitatively the relative effects of some changes in the connections of the river network. Such an approach might be a convenient tool to help in decision making, for example to improve water-body management, or to preserve some endangered species.

Further developments are considered on the basis of a previous study on the effect of density-dependence on the population dynamics (Charles et al., 1998a). Indeed, we are now intending to extend our model by taking into account either physical parameters (like temperature, discharge and other habitat parameters) with their effects on both migration and vital rates, or chemical water quality and its possible effects especially on survival rates. Such developments in modelling brown trout population dynamics might lead us to use some recent contributions in variables aggregation methods (Bravo de la Parra et al., 1999). For example, some tools are now available to deal with temporal variations of the environment (Sanz and Bravo de la Parra, 1998, 1999).

## Acknowledgements

We thank Jean-Luc Baglinière for very helpful comments on biological data and parameter estimation. This work was in part supported by a grant from the PIR Environnement, Vie et Sociétés 98N62/0069 of the National Centre for the Scientific Research (CNRS). One of the authors is partially supported by the ‘Proyecto PSPGC PB98-0702’.

## Appendix A. Matrices associated with migration processes

### A.1. Migration matrix associated with the fast migration process

Only the migration process is studied here. We denote  $\tau$  the fast time associated with migrations.

The complete system of 15 difference equations describing migrations for one age-class can be written as follows:

$$\begin{cases}
 n_1^i(\tau+1) = n_1^i(\tau) + \bar{\alpha}_i(n_2^i(\tau) + n_3^i(\tau)) - 2\alpha_i n_1^i(\tau) \\
 n_2^i(\tau+1) = n_2^i(\tau) + \alpha_i n_1^i(\tau) + \bar{\beta}_i(n_4^i(\tau) + n_5^i(\tau)) - (2\beta_i + \bar{\alpha}_i)n_2^i(\tau) \\
 n_3^i(\tau+1) = n_3^i(\tau) + \alpha_i n_1^i(\tau) + \bar{\beta}_i(n_6^i(\tau) + n_7^i(\tau)) - (2\beta_i + \bar{\alpha}_i)n_3^i(\tau) \\
 n_4^i(\tau+1) = n_4^i(\tau) + \beta_i n_2^i(\tau) + \bar{\gamma}_i(n_8^i(\tau) + n_9^i(\tau)) - (2\gamma_i + \bar{\beta}_i)n_4^i(\tau) \\
 n_5^i(\tau+1) = n_5^i(\tau) + \beta_i n_2^i(\tau) + \bar{\gamma}_i(n_{10}^i(\tau) + n_{11}^i(\tau)) - (2\gamma_i + \bar{\beta}_i)n_5^i(\tau) \\
 n_6^i(\tau+1) = n_6^i(\tau) + \beta_i n_3^i(\tau) + \bar{\gamma}_i(n_{12}^i(\tau) + n_{13}^i(\tau)) - (2\gamma_i + \bar{\beta}_i)n_6^i(\tau) \\
 n_7^i(\tau+1) = n_7^i(\tau) + \beta_i n_3^i(\tau) + \bar{\gamma}_i(n_{14}^i(\tau) + n_{15}^i(\tau)) - (2\gamma_i + \bar{\beta}_i)n_7^i(\tau) \\
 n_8^i(\tau+1) = n_8^i(\tau) + \gamma_i n_4^i(\tau) - \bar{\gamma}_i n_8^i(\tau) \\
 n_9^i(\tau+1) = n_9^i(\tau) + \gamma_i n_4^i(\tau) - \bar{\gamma}_i n_9^i(\tau) \\
 n_{10}^i(\tau+1) = n_{10}^i(\tau) + \gamma_i n_5^i(\tau) - \bar{\gamma}_i n_{10}^i(\tau) \\
 n_{11}^i(\tau+1) = n_{11}^i(\tau) + \gamma_i n_5^i(\tau) - \bar{\gamma}_i n_{11}^i(\tau) \\
 n_{12}^i(\tau+1) = n_{12}^i(\tau) + \gamma_i n_6^i(\tau) - \bar{\gamma}_i n_{12}^i(\tau) \\
 n_{13}^i(\tau+1) = n_{13}^i(\tau) + \gamma_i n_6^i(\tau) - \bar{\gamma}_i n_{13}^i(\tau) \\
 n_{14}^i(\tau+1) = n_{14}^i(\tau) + \gamma_i n_7^i(\tau) - \bar{\gamma}_i n_{14}^i(\tau) \\
 n_{15}^i(\tau+1) = n_{15}^i(\tau) + \gamma_i n_7^i(\tau) - \bar{\gamma}_i n_{15}^i(\tau)
 \end{cases} \quad (A1)$$

System (1) can be rewritten with the matrix  $\mathbf{P}_i$  as follows:

$$\hat{\mathbf{n}}_{\tau+1}^i = \mathbf{P}_i \hat{\mathbf{n}}_{\tau}^i \quad (A2)$$

where the stochastic matrix  $\mathbf{P}_i$  reads:

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

With  $A_i = 1 - 2\beta_i - \bar{\alpha}_i$ ;  $B_i = 1 - 2\gamma_i - \bar{\beta}_i$ ;  $C_i = 1 - \bar{\gamma}_i$ .

Thus, at equilibrium  $n_j^i(\tau+1) = n_j^i(\tau) = n_j^{*i}$ , we obtain with

$$v_j^{*i} = n_j^{*i} \left/ \sum_{j=1}^{15} n_j^{*i} \right.$$

$$\begin{cases}
 v_1^{*i} = \frac{1}{D_i} \\
 v_2^{*i} = v_3^{*i} = \frac{1}{D_i} \frac{\alpha_i}{\bar{\alpha}_i} \\
 v_4^{*i} = v_5^{*i} = v_6^{*i} = v_7^{*i} = \frac{1}{D_i} \frac{\alpha_i \beta_i}{\bar{\alpha}_i \bar{\beta}_i} \\
 v_8^{*i} = v_9^{*i} = v_{10}^{*i} = v_{11}^{*i} = v_{12}^{*i} = v_{13}^{*i} = v_{14}^{*i} = v_{15}^{*i} = \frac{1}{D_i} \frac{\alpha_i \beta_i \gamma_i}{\bar{\alpha}_i \bar{\beta}_i \bar{\gamma}_i}
 \end{cases} \quad (A4)$$

with

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

Hence,  $v_j^{*i}$  values being known from individual proportions given in Table 3, we can estimate numerical values for migrations ratios.

#### A.2. Migration matrices associated with spawning migrations

We call  $\omega$  the spawning migration rate of adults upstream just before reproduction, and  $\beta$  the extra ‘in-stream’ mortality during spawning from one level to the upper one (in the reverse sense,  $\beta$  is assumed equal to zero). As detailed in Section 3.1, the Leslie matrix associated with demography reads  $\mathbf{L} = \mathbf{S} + \mathbf{F}\mathbf{P}'$ , where  $\mathbf{P}'$  describes the migration process of adults breeding where they were born. Our main hypotheses are: (1) The *in-stream mortality* occurs before breeding; (2) After fast migrations, adults of patch  $i$  were a priori born in any patch of the river network according to a top-down gradient.

$\mathbf{P}'$  is a stochastic block diagonal matrix of dimension 45, written as  $\text{diag}\{\mathbf{I}, \mathbf{I}, \mathbf{P}_3\}$  with  $\mathbf{I}$  the identity matrix of dimension 15. Coefficients of matrix  $\mathbf{P}_3$  are the product of the returning adult

proportion, by the surviving adult proportion along the way followed to go to their natal tributaries. For example, the coefficient (8, 1) of  $\mathbf{P}'_3$  corresponds to individuals of patch 1 returning to patch 8. The proportion of returning adults being  $\omega/8$  and the proportion of surviving adults along the way followed reading  $1 - 3\beta$ , this coefficient writes  $(\omega/8)(1 - 3\beta)$ .

To ensure the stochasticity of matrix  $\mathbf{P}'_3$  (and then of  $\mathbf{P}'$ ) when  $\beta = 0$ , parameters  $\omega$  and  $\tilde{a}$  must verify:

$$\omega = \left(1 + \frac{1}{\tilde{a}} + \frac{1}{\tilde{a}^2} + \frac{1}{\tilde{a}^3}\right) = 1 \Leftrightarrow \omega = \frac{\tilde{a}^3}{1 + \tilde{a} + \tilde{a}^2 + \tilde{a}^3} \quad (\text{A5})$$

The complete expression of matrix  $\mathbf{P}'_3$  is too long to be directly given here, but  $\mathbf{P}'_3$  can be viewed as the product  $\mathbf{AB}$  of two matrices without any biological significance:

$\mathbf{A} = \text{diag}$

$$\left\{ \frac{\omega}{\tilde{a}^3}, \frac{\omega}{2\tilde{a}^2}, \frac{\omega}{2\tilde{a}^2}, \frac{\omega}{4\tilde{a}}, \frac{\omega}{4\tilde{a}}, \frac{\omega}{4\tilde{a}}, \frac{\omega}{4\tilde{a}}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8} \right\}$$

$$\mathbf{B} = \begin{pmatrix} 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1-\beta & 1 & 1-\beta & 1 & 1 & 1-\beta & 1-\beta & 1 & 1 & 1 & 1 & 1-\beta & 1-\beta & 1-\beta & 1-\beta & 1 \\ 1-\beta & 1-\beta & 1 & 1-\beta & 1-\beta & 1 & 1 & 1-\beta & 1-\beta & 1-\beta & 1-\beta & 1 & 1 & 1 & 1 & 1 \\ 1-2\beta & 1-\beta & 1-2\beta & 1 & \beta & 1-2\beta & 1-2\beta & 1 & 1 & \beta & \beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta \\ 1-2\beta & 1-\beta & 1-2\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta & 1-\beta & 1-\beta & 1 & 1 & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta \\ 1-2\beta & 1-2\beta & 1-\beta & 1-2\beta & 1-2\beta & 1 & 1-\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1 & 1 & 1-\beta & 1-\beta & 1 \\ 1-2\beta & 1-2\beta & 1-\beta & 1-2\beta & 1-2\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-\beta & 1-\beta & 1 & 1 & 1 \\ 1-3\beta & 1-2\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1 & 1-\beta & 1-2\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\ 1-3\beta & 1-2\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\ 1-3\beta & 1-2\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1 & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\ 1-3\beta & 1-2\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1-\beta & 1 & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\ 1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1 & 1-\beta & 1-2\beta & 1-2\beta & 1-2\beta \\ 1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta & 1-2\beta \\ 1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1 & 1-\beta & 1-\beta \\ 1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1-\beta & 1 & 1 \end{pmatrix}$$

## Appendix B. How dams or channels change migration matrices

### A.1. How channels change migration ratios in matrix $\mathbf{P}$

When a channel is introduced, either between

levels 2 and 4 or between levels 1 and 3, some migration ratios are changed (respectively called  $\delta_i/\bar{\delta}_i$  and  $\varepsilon_i/\bar{\varepsilon}_i$ ), allowing level  $i$  to be directly connected to level  $(i+2)$ . By way of example, here is how to calculate the migration ratio  $\delta_i/\bar{\delta}_i$  (Fig. 1c). The corresponding system of difference equations describing the migration process reads:

$$\begin{cases} \vdots \\ n_2^i(\tau+1) = n_2^i(\tau) + \alpha_i n_1^i(\tau) + \bar{\delta}_i(n_8^i(\tau) + n_9^i(\tau)) + \bar{\beta}_i n_5^i(\tau) - (2\delta_i + \beta_i + \bar{\alpha}_i)n_2^i(\tau) \\ \vdots \\ n_8^i(\tau+1) = n_8^i(\tau) + \delta_i n_2^i(\tau) - \bar{\delta}_i n_8^i(\tau) \\ n_9^i(\tau+1) = n_9^i(\tau) + \delta_i n_2^i(\tau) - \bar{\delta}_i n_9^i(\tau) \\ \vdots \end{cases} \quad (\text{B1})$$

$\vdots$  indicates that equations remain the same as in system (A1).

We assume that, at equilibrium, ratios between the individual numbers at level 3 and 1 remain equal in the reference network and in the changed one with a channel.

From system (A1) at equilibrium, we get:

$$\begin{cases} (\text{eq. 1}) \Rightarrow \bar{\alpha}_i(n_2^{*i} + n_3^{*i}) = 2\alpha_i n_1^{*i} \\ (\text{eq. 2}) + (\text{eq. 3}) \Rightarrow 2\alpha_i n_1^{*i} + \bar{\beta}_i(n_8^{*i} + n_9^{*i} + n_6^{*i} + n_7^{*i}) = (2\beta_i + \bar{\alpha}_i)(n_2^{*i} + n_3^{*i}) \\ (\text{eq. 8}) + (\text{eq. 9}) \Rightarrow \bar{\gamma}_i(n_8^{*i} + n_9^{*i}) = 2\gamma_i n_4^{*i} \end{cases} \Rightarrow 2\bar{\alpha}_i n_2^{*i} + 4\bar{\beta}_i n_4^{*i}$$

$$\begin{aligned}
&= 2(2\beta_i + \bar{\alpha}_i)n_2^{*i} \text{ as } \begin{cases} n_2^{*i} = n_3^{*i} \\ n_4^{*i} = n_5^{*i} = n_6^{*i} = n_7^{*i} \end{cases} \\
&\Rightarrow \bar{\beta}_i \frac{\bar{\gamma}_i}{2\gamma_i} (n_8^{*i} + n_9^{*i}) = \beta_i n_2^{*i} \\
&\Rightarrow \frac{n_8^{*i}}{n_2^{*i}} = \frac{\beta_i \gamma_i}{\bar{\beta}_i \bar{\gamma}_i} \text{ as } n_8^{*i} = n_9^{*i} \quad (\text{B2-1})
\end{aligned}$$

From Eq. (B1) at equilibrium, we get:

$$\begin{aligned}
&(\text{eq. 2}) \Rightarrow \bar{\delta}_i (n_8^{*i} + n_9^{*i}) = 2\delta_i n_2^{*i} \\
&\Rightarrow \frac{n_8^{*i}}{n_2^{*i}} = \frac{\delta_i}{\bar{\delta}_i} \quad (\text{B2-2})
\end{aligned}$$

By identifying Eqs. (B2-1) and (B2-2), we finally obtain:

$$\frac{\delta_i}{\bar{\delta}_i} = \frac{\beta_i \bar{\gamma}}{\bar{\beta}_i \bar{\gamma}_i} \quad (\text{B3})$$

$$\mathbf{B} = \begin{pmatrix}
1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\
1-\beta & 1 & 1-\beta & 1 & 1 & 1-\beta & 1-\beta & 1 & 1 & 1 & 1-\beta & 1-\beta & 1-\beta & 1-\beta & 1-\beta \\
1-\beta & 1-\beta & 1 & 1-\beta & 1-\beta & 1 & 1 & 1-\beta & 1-\beta & 1-\beta & 1 & 1 & 1 & 1 & 1 \\
1-2\beta & 1-\beta & 1-2\beta & 1 & 1-\beta & 1-2\beta & 1-2\beta & 1 & 1-\beta & 1-\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta \\
1-2\beta & 1-\beta & 1-2\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta & 1-\beta & 1 & 1 & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta \\
1-2\beta & 1-2\beta & 1-\beta & 1-2\beta & 1-2\beta & 1 & 1-\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1 & 1 & 1-\beta & 1-\beta & 1-\beta \\
1-2\beta & 1-2\beta & 1-\beta & 1-2\beta & 1-2\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta & 1-2\beta & 1-\beta & 1-\beta & 1 & 1 & 1 \\
1-3\beta & 1-2\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1 & 1-2\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\
1-3\beta & 1-2\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1 & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\
1-3\beta & 1-2\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-\beta & 1 & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\
1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1 & 1-\beta & 1-2\beta & 1-2\beta & 1-2\beta \\
1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta & 1-2\beta \\
1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1 & 1-\beta & 1-\beta \\
1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1-\beta & 1 & 1
\end{pmatrix}$$

In the case of Fig. 1c, the new matrix  $\mathbf{P}$  then reads:

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

With  $D_i = 1 - (2\delta_i + \beta_i + \bar{\alpha}_i)$ .

(B4)

with  $D_i = 1 - (2\delta_i + \beta_i + \bar{\alpha}_i)$

### A.2. How dams change the spawning migration matrix

By introducing dams in the river network, some patches are not accessible to the fishes, which cannot breed where they were born. We assume that these individuals will reproduce in the patch just downstream to the dam.

For instance, if a dam is introduced between patches 4 and 8 (Fig. 1b), individuals, which should breed in patch 8, will reproduce in patch 4. Matrices  $\mathbf{A}$  and  $\mathbf{B}$  become of dimension  $(14 \times 14)$  and are modified as follows:

$$\begin{aligned}
\mathbf{A} = \text{diag} & \left\{ \frac{\omega}{\bar{a}^3}, \frac{\omega}{2\bar{a}^2}, \frac{\omega}{2\bar{a}^2}, \frac{\omega}{4\bar{a}} \right. \\
& \left. + \frac{\omega}{8}, \frac{\omega}{4\bar{a}}, \frac{\omega}{4\bar{a}}, \frac{\omega}{4\bar{a}}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8} \right\} \quad (\text{B5})
\end{aligned}$$

### A.3. How channels change the spawning migration matrix

By introducing channels in the river network between levels  $i$  and  $(i+2)$ , reproduction is not possible at level  $(i+1)$ . We then assume that individuals, born at level  $(i+1)$ , will migrate towards level  $(i+2)$ . As one patch of level  $(i+1)$  is connected to two patches of level  $(i+2)$ , we suppose that individuals will be evenly distributed.

For instance, with a channel between patch 2 and patches 8 and 9 (Fig. 1c), half the individuals which should breed in patch 4, will reproduce in patch 8, the other half in patch 9. Matrices **A** and **B** now read:

$$\mathbf{A} = \text{diag} \left\{ \frac{\omega}{\tilde{a}^3}, \frac{\omega}{2\tilde{a}^2}, \frac{\omega}{2\tilde{a}^2}, \frac{\omega}{4\tilde{a}}, \frac{\omega}{4\tilde{a}}, \frac{\omega}{4\tilde{a}}, \frac{\omega}{8}, \frac{\omega}{8} + \frac{\omega}{8\tilde{a}}, \frac{\omega}{8} \right. \\ \left. + \frac{\omega}{8\tilde{a}}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8}, \frac{\omega}{8} \right\} \quad (\text{B6})$$

$$\mathbf{B} = \begin{pmatrix} 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1-\beta & 1 & 1-\beta & 1 & 1-\beta & 1-\beta & 1 & 1 & 1 & 1 & 1-\beta & 1-\beta & 1-\beta & 1-\beta \\ 1-\beta & 1-\beta & 1 & 1-\beta & 1 & 1 & 1-\beta & 1-\beta & 1-\beta & 1-\beta & 1 & 1 & 1 & 1 \\ 1-2\beta & 1-\beta & 1-2\beta & 1 & 1-2\beta & 1-2\beta & 1-\beta & 1-\beta & 1 & 1 & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta \\ 1-2\beta & 1-2\beta & 1-\beta & 1-2\beta & 1 & 1-\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1 & 1 & 1-\beta & 1-\beta \\ 1-2\beta & 1-2\beta & 1-\beta & 1-2\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta & 1-2\beta & 1-2\beta & 1-\beta & 1-\beta & 1 & 1 \\ 1-3\beta & 1-2\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1 & 1-2\beta & 1-2\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\ 1-3\beta & 1-2\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1 & 1-2\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\ 1-3\beta & 1-\beta & 1-3\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1 & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\ 1-3\beta & 1-\beta & 1-3\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1-\beta & 1 & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta \\ 1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1 & 1-\beta & 1-2\beta & 1-2\beta \\ 1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-\beta & 1-2\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-\beta & 1 & 1-2\beta & 1-2\beta \\ 1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1 & 1-\beta \\ 1-3\beta & 1-3\beta & 1-2\beta & 1-3\beta & 1-2\beta & 1-\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-3\beta & 1-2\beta & 1-2\beta & 1-\beta & 1 \end{pmatrix}$$

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