

A density dependent model describing *Salmo trutta* population dynamics in an arborescent river network. Effects of dams and channelling

*Un modèle densité-dépendant décrivant la dynamique d'une population de *Salmo trutta* dans un réseau de rivière arborescent.*

Effets des barrages et des canaux

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Abstract – Our aim is to model the *Salmo trutta* population dynamics (three age-classes) in an arborescent river network (four levels, 15 patches), by considering both migrations (fast time scale) and demography (slow time scale). We study how the environmental management can influence the global population dynamics. We present a general model coupling both a linear discrete model for constant migrations and a non-linear density-dependent Leslie model for the demography, with (15×3) difference equations (15 patches, three age-classes). The variable aggregation method applied to discrete time models allows us to aggregate the previous model into a new one with only three equations. We assume fecundity and survival gradients with respect to the river network levels. The *Salmo trutta* whole population tends towards an equilibrium state depending on the environmental structure, and we show that dams have a stronger influence than channelling on this equilibrium. (© Académie des sciences / Elsevier, Paris.)

arborescent river network / Leslie matrix / aggregation methods / *Salmo trutta*

Résumé – La croissance d'une population de truites (trois classes d'âge) dans un réseau de rivière arborescent (quatre niveaux, 15 sites) est modélisée en considérant simultanément les migrations (échelle de temps rapide) et la démographie (échelle de temps lente). Nous étudions comment la gestion de l'environnement peut influencer la dynamique globale de la population. Nous présentons un modèle général discret, avec (15×3) équations récurrentes (15 sites, trois classes d'âge), couplant une matrice de migration à coefficients constants et une matrice de Leslie densité-dépendante pour la démographie. La méthode d'agrégation des variables permet d'agréger le modèle précédent en un nouveau modèle ne contenant plus que trois équations. Nous supposons qu'il existe des gradients de fécondité et de survie, fonction des différents niveaux du réseau de rivières.

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La population totale de truites tend vers un équilibre dépendant de la structure de l'environnement, et nous montrons que les barrages ont une influence plus négative que les canaux sur cet équilibre. (© Académie des sciences / Elsevier, Paris.)

réseau de rivière arborescent / matrice de Leslie / méthode d'agrégation / *Salmo trutta*

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La modélisation en écologie concerne souvent des systèmes biologiques impliquant un grand nombre de variables. Pour décrire la dynamique de ces populations, il faut généralement considérer un ensemble de sous-populations qui interagissent, chaque sous-population correspondant par exemple à un âge, un stade, un phénotype ou encore une stratégie comportementale. De plus, la distribution spatiale des individus doit être prise en compte, car leurs migrations entre différents sites peuvent influencer le processus démographique global.

L'approche la plus simple pour modéliser une telle dynamique est d'ignorer la structure interne de la population, considérée alors comme un tout et décrite par une seule variable globale. Cependant, le plus souvent on ne peut négliger cet effet et il convient alors de construire un modèle complet décrivant le système réel dans son intégralité. De tels modèles impliquent toutefois un nombre important de variables, ce qui les rend difficile à appréhender du point de vue analytique. Les méthodes d'agrégation des variables, basées sur la théorie des perturbations, sont une bonne alternative à ces problèmes. Lorsqu'au moins deux échelles de temps différentes sont mises en jeu dans le phénomène biologique, le système général complexe peut être approché par un système réduit comportant un petit nombre de variables. Ce système agrégé peut alors s'étudier analytiquement.

Les méthodes d'agrégation des variables ont initialement été développées dans le cas des systèmes dynamiques en temps continu. Plus récemment, certains auteurs les ont appliquées aux modèles récurrents, largement utilisés pour la modélisation de la dynamique des populations en écologie. Par exemple, les modèles de Leslie sont particulièrement adaptés pour décrire des populations structurées en âge dont la dynamique évolue de génération en génération.

Le but de notre travail a été de modéliser la dynamique d'une population type de truites, *Salmo trutta*, dans un réseau de rivière hiérarchisé (structure arborescente à quatre niveaux et 15 sites), en tenant compte à la fois des migrations des individus et de la croissance de la population. Nous avons considéré une population structurée en trois classes d'âge (les

jeunes, les juvéniles et les adultes), dont la dynamique a été décrite par une matrice de Leslie. Deux échelles de temps sont impliquées : une rapide (de l'ordre de la semaine) correspondant aux migrations, l'autre plus lente (l'année) pour la démographie,

Nous proposons un modèle général couplant un modèle récurrent linéaire pour les migrations (les taux de migrations étant constants), et un modèle de type Leslie densité-dépendant c'est-à-dire non linéaire pour la démographie (la survie des alevins dépend de la densité d'alevins dans le réseau). Ainsi, le modèle complet consiste en un système d'équations aux différences avec 15×3 variables d'état correspondant aux 15 sites et aux trois classes d'âge. Une fois appliquée la méthode d'agrégation des variables, le modèle général précédent est réduit en un système agrégé ne contenant plus que trois variables d'état (une pour chaque classe d'âge). Les paramètres démographiques du modèle agrégé sont fonction des paramètres correspondant dans le système général, pondérés par les proportions à l'équilibre (issues de la dynamique rapide de migration) des individus des trois classes d'âge dans les différents sites.

À partir d'hypothèses biologiques simples sur les valeurs numériques des paramètres démographiques et de migration, des simulations ont été réalisées. Nous avons d'abord montré, sur la base d'un précédent modèle dans lequel les modèles migratoire et démographique sont tous les deux linéaires (paramètres constants), que le modèle agrégé est une bonne approximation du modèle complet de départ, c'est-à-dire que son comportement asymptotique est le même. Nous avons ensuite étudié la dynamique globale de la population de truites dans le réseau de rivière arborescent complet (réseau de référence) à l'aide du modèle agrégé non linéaire densité-dépendant; la dynamique de la population est dans ce cas caractérisée par un état d'équilibre. Nous avons alors étudié l'impact, sur cet état d'équilibre, de certains aménagements du réseau tels que des barrages (suppression de connexions entre les sites) ou des canaux (suppression d'un ou plusieurs sites intermédiaires). Enfin, nous avons montré que les barrages pouvaient avoir un effet global plus important que les canaux sur l'état d'équilibre de la population de truites.

1. Introduction

Ecological modelling often deals with systems involving a large number of coupled variables. To describe the population dynamics of such a system, one should consider a set of interacting subpopulations of different ages. More-

over, the geographical distribution of individuals must be taken into account, migrations of individuals between different patches influencing the global demographic process.

A first approach to modelling this complexity is to ignore the internal structure of the population, which is

thus considered as a whole and described by a single variable. In that case, intra-population processes are usually ignored and equations govern macro-variables. However, the effect of the internal population structure can rarely be neglected and it is thus necessary to build up complete models describing the real system in detail with micro-variables. Such models usually concern populations living in fragmented habitats, with, for example, connections between different patches [1, 2]. Unfortunately, these models often involve too many variables to be analytically processed and are difficult to handle; moreover, numerical simulations are needed, the robustness of which being still in question (but see [2] for some analytical results with particular Leslie-type models). Aggregation methods constitute an interesting alternative way, as they allow an approximation of general complex systems, governing many time scales, by reduced ones. They can be applied when at least two different time scales are involved, e.g. one for migrations, another one for demography. In such methods, macro-variables are defined as linear combinations of micro-variables.

Aggregation methods were first developed in the case of continuous time systems [3–5]. Recently, some authors applied these methods to discrete time models [6–9], which are widely used in population dynamic modelling in ecology. For example, the Leslie model is particularly well adapted to describing an age-structured population at discrete time intervals [10].

The aim of our work was to mathematically describe the *Salmo trutta* population dynamics in a hierarchically organized river network, an arborescent structure of four levels and 15 patches. Fish populations dynamic modelling is of a major interest in evaluating the impact of human activities on rivers. Some recent attempts have been made in this way, especially with salmonids [11, 12], but always on a small spatial scale involving a single stream (one patch). Nevertheless, fishes, and *Salmo trutta* is a good example [13], generally migrate to achieve their life cycle (for reproduction, food searching, etc.) at a fast time scale compared to the demographic process. This emphasizes the necessity to study population dynamics at the river network level [14], by taking into account both demography and migrations at two different times scales. Moreover, our model allows an assessment of the effect of density-dependent factors on the global fish population dynamics, often associated with intra-specific competition for food or space, and of great importance in the regulation of the number of individuals [15]. Even if the action of density dependence on demographic parameters (mainly survival and migration rates) is not well known, the method we propose may suggest various ways of investigation, by testing different density-dependent models (Beverton-Holt, Ricker, etc.).

We propose a general model, which couples both a linear discrete model for migrations (with constant migration rates) and a non-linear Leslie-type model for demography (with a density-dependant young survival rate). Thus, the

complete model consists of a difference equation system with (15×3) state variables corresponding to the 15 patches and the three age-classes. Once the variable aggregation method is applied, the previous general model is reduced to an aggregated system with only three state variables (one per age-class). The demographic parameters of the aggregated system are expressed in terms of the corresponding parameters of the general system, weighted by the equilibrium proportions of individuals in the different patches, which arise from the fast migration process.

Assuming both fecundity and survival gradients with respect to the levels in the river network, numerical simulations were performed. First, we briefly revisited the strictly linear model presented by Charles et al. [16], in which all parameters were constant, to show the concordance between the general and the aggregated models.

Our main interest being to model the density-dependence phenomenon, we then focused on the non-linear aggregated model and we characterized the global trout population dynamics in the reference river network by an equilibrium state. The impact of the environmental management on this equilibrium was studied, and we showed that dams (i.e. breaking connections between patches) lead to a more important decrease in the equilibrium state than channelling (i.e. intermediate patch deletion).

2. Materials and methods

2.1. The reference river network and the changes

The reference river network can be schematized as in *figure 1* (I), levels 4 and 1 corresponding to the top and down ends of the network. Individuals can develop in each patch and migrate between patches, according to rules indicated in *figure 1* (I). At a same level n , all patches are equivalent and the river network is symmetric. Migration rates depend on the age-class and the arborescence level.

Two kinds of changes were considered. Dams (*figure 1, IIa, b*) consist in reducing to zero direct and reverse migration rates between two patches, while other migration rates are left unchanged. Channelling (*figure 1, IIc, d*) between levels n and $(n + 2)$ consists in suppressing a patch at the intermediate level $(n + 1)$. Individuals can thus migrate directly between levels n and $(n + 2)$, with new migration rates re-calculated by assessing 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 (see Appendix).

We studied the effects on the overall fish population growth of a gradual increase in the number of dams (from 1 to 8 between levels 3 and 4, from 1 to 4 between levels 2 and 3) or channels (from 1 to 4 between levels 2 and 4, from 1 to 2 between levels 1 and 3).

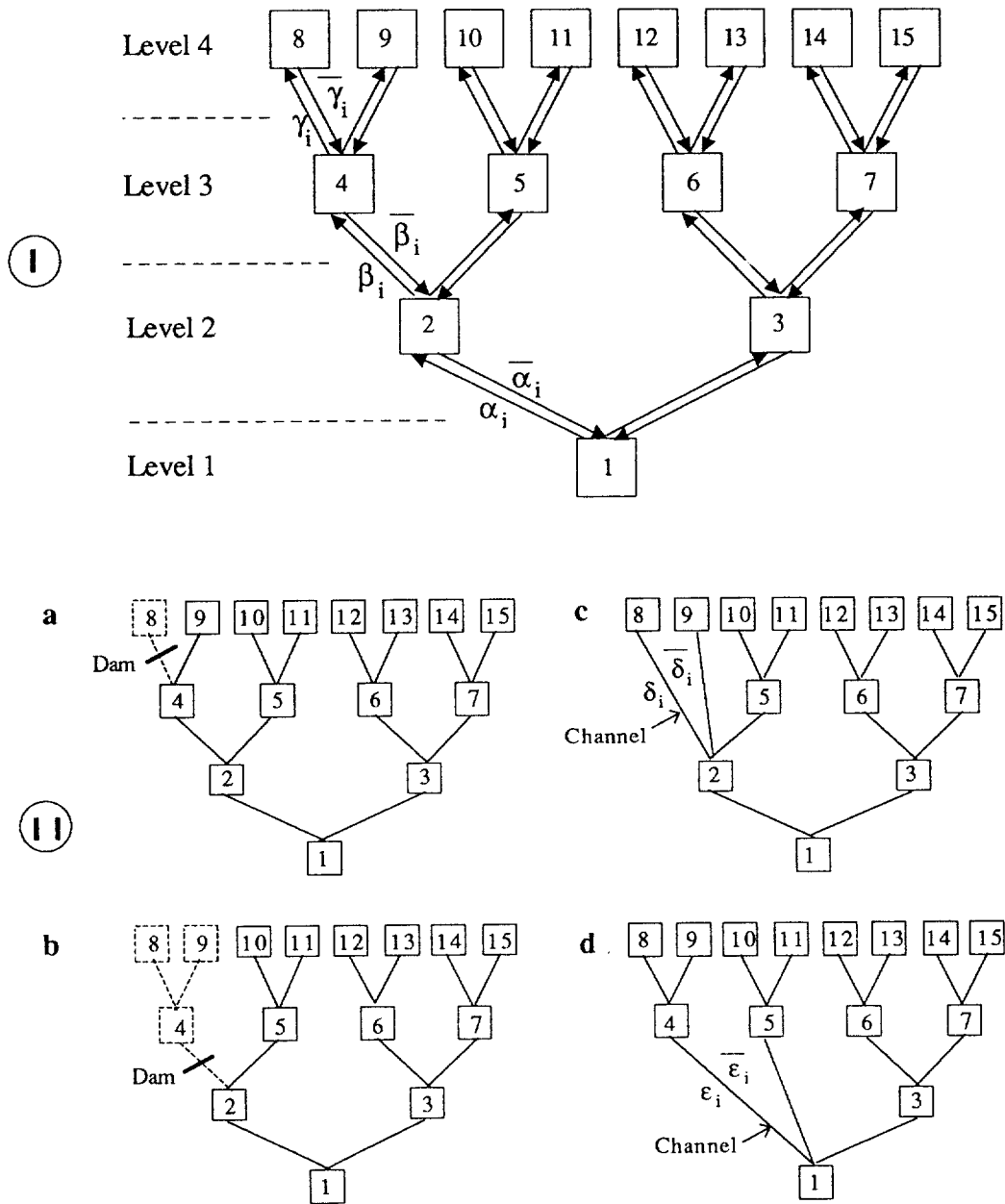


Figure 1.I. Schematic graph of the arborescent river network with four levels and 15 patches (reference river network). Parameters $(\alpha_i, \beta_i, \gamma_i)$ and $(\bar{\alpha}_i, \bar{\beta}_i, \bar{\gamma}_i)$ are the direct and the reverse migration rates between different levels for individuals aged i , respectively.

1.II. Schematic graph of the different changes in 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 $\frac{\epsilon_i}{\bar{\epsilon}_i} = \frac{\alpha_i \beta_i}{\bar{\alpha}_i \bar{\beta}_i}$, respectively.

2.2. The demographic model for *Salmo trutta*

The brown trout population (*Salmo trutta*) is subdivided into three age-classes: young of the year or YOY (in their first year of life, 0+), juveniles (two summers 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 individuals survive from age i to age $i + 1$) and fecundity (number of YOY per females produced each year) depend on the arborescence level, and

Table 1. Fecundity, survival rates and proportions of individuals in each age-class at the different levels of the reference river network for a 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	$s_1(Y^1)/a^3$	s_2/a	s_3
	2	$s_1(Y^1)/a^2$	s_2	s_3/a
	3	$s_1(Y^1)/a$	s_2/a	s_3/a^2
	4	$s_1(Y^1)$	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 females produced each year; s_2 and s_3 : optimal survival rates of juveniles and adults; $s_1(Y^1) = p/(1 + qY^1)$, where Y^1 is the total number of YOY in the river network.

Parameters a , f , s_2 and s_3 were obtained from Baglinière and Maisse [19]: $a = 2$; $f = 265$; $s_2 = s_3 = 0.4$. Parameters p and q were estimated from Le Cren data [22]: $p = 1.77$; $q = 0.23$ (in the linear case, $s_1 = 0.07$).

the gradient of survival rates depends on the age-class (table 1). For example, the adult survival rate is supposed to be optimal at level 1, while juveniles have an optimal survival rate in smaller tributaries at level 2.

The fecundity is estimated, with a unit sex ratio, as the product of the number of eggs produced per female each year by the egg-to-fry survival rate. It is estimated in the most favourable environmental conditions (i.e. level 4) in which the parameters determining the egg-to-fry survival rate (substrate composition, level of O_2 supply, predation risk [17]) are considered as optimal. Thus, the decrease in fecundity with the arborescent level is the consequence of the degradation of the developmental conditions from levels 4 to 1. This gradient is then approximately approached by the parameter $a = 2$ according to expert advice (Persat, pers. comm.).

For *Salmo trutta*, survival rates are generally dependent on growth conditions and the balance between energy gain and the avoidance of predation risk induces a change in habitat preference growth [18]. For instance, large individuals select deep slow flowing pools (more and more abundant from levels 4 to 1), whereas YOY prefer shallow fast flowing riffle (increasing from levels 1 to 4).

The numerical estimations of these demographic parameters as they were given in [19] (see table 1) correspond to means, but standard deviations were not available and their precision could not have been quantified.

Furthermore, the survival rate 'observed' for the YOY individuals is supposed to be density dependent as mentioned by several authors [20, 21]. According to data from [22], and using a Beverton-Holt type model [23], the following relationship between survival rate and density can be proposed to describe the observed data:

$$s_1(Y^1) = p/(1 + qY^1)$$

where Y^1 represents the total number of YOY in the river network. Parameters p and q were estimated from experimental data by a linear regression of $1/s_1$ against Y^1 according to the least square criterion. Their numerical values are given in table 1.

In our work, the YOY survival rate is supposed to depend on the total number of YOY in the river network. This assumption is biologically justified as during one time step of demography: all individuals and especially YOY migrate between patches. Hence, all YOY individuals can a priori influence the YOY survival rate (spatial mixing).

Table 1 also presents the individual proportions of the different age-classes in all patches, which are the same at a same level but differ from one level to another. As explained in section 3.1., these values will be used to estimate migration ratios along the river network.

2.3. The mathematical model

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

Let $n_j^i(t)$ be the number of individuals aged i on patch j at time t ($i = 1, 2, 3$ and $j = 1, \dots, 15$), $N_t^i = (n_t^1(t), \dots, n_t^i(t))^T$ and $N_t = (N_t^1, N_t^2, N_t^3)^T$ (T denotes transposition).

According to Bravo de la Parra et al. [7], the following complete model (15×3 state variables) can describe the global population dynamics:

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

where $\mathbf{L}(Y^1)$ is the density-dependent Leslie matrix associated with the demographic process and \mathbf{P} the stochastic migration matrix; the integer k must be great enough to

account for migratory movements of individuals between t and $t + 1$ being faster than the reproduction phenomenon.

The matrix $L(Y^1)$ is written as a block matrix:

$$L(Y^1) = \begin{pmatrix} \mathbf{0} & \mathbf{0} & \mathbf{F} \\ \mathbf{S}_1(Y^1) & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{S}_2 & \mathbf{S}_3 \end{pmatrix}$$

where $\mathbf{F} = \text{diag}\{f_1^3, \dots, f_{15}^3\}$, with the hypothesis that adults (age-class 3) of patch j reproduce only in patch j , and $\mathbf{S}_i = \text{diag}\{s_1^i, \dots, s_{15}^i\}$, $i = 1, 2, 3$. Parameters f_j^i and s_j^i are those defined in table 1 for age-class i on patch j .

The matrix \mathbf{P} is a block diagonal matrix, $\text{diag}\{\mathbf{P}_1, \mathbf{P}_2, \mathbf{P}_3\}$, where \mathbf{P}_i describes movements of the age-class i between patches. As migrations are fast, individual proportions in each patch tend rapidly towards equilibrium frequencies, denoted by \bar{v}_j^i . Numerical values of \bar{v}_j^i correspond to equilibrium proportions per level as given in table 1. From a biological point of view, the existence of the fast equilibrium is a realistic assumption as observed experimental data confirm that individual proportions remain stable for each age-class in each patch [19].

We call \mathbf{P}_c the matrix $\text{diag}\{\bar{v}_1^{-1}, \bar{v}_2^{-3}, \bar{v}_3^{-3}\}$, with $\bar{v}^{-1} = (\bar{v}_1^1, \dots, \bar{v}_{15}^1)^T$.

Let now $Y_t^i = \sum_{j=1}^{15} n_j^i(t)$ be the total number of individuals

aged i at time t and $Y_t = (Y_t^1, Y_t^2, Y_t^3)^T$. Then $Y_t = \mathbf{U}N_t$ with $\mathbf{U} = \text{diag}\{\mathbf{1}, \mathbf{1}, \mathbf{1}\}$, the (3×45) aggregation matrix, and $\mathbf{1} = (1, \dots, 1)$ a vector of dimension 15.

Following a similar method to that developed by Sanchez et al. [9], we obtain the following aggregated model (three equations):

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

The matrix $\bar{\mathbf{L}}(Y^1)$ is a Leslie-type matrix:

$$\bar{\mathbf{L}}(Y^1) = \begin{pmatrix} \mathbf{0} & \mathbf{0} & \bar{\mathbf{F}} \\ \bar{\mathbf{S}}_1(Y^1) & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \bar{\mathbf{S}}_2 & \bar{\mathbf{S}}_3 \end{pmatrix}$$

where $\bar{\mathbf{F}} = \mathbf{1}\mathbf{F}\bar{\mathbf{v}}^{-3}$, $\bar{\mathbf{S}}_2 = \mathbf{1}\mathbf{S}_2\bar{\mathbf{v}}^{-2}$ and $\bar{\mathbf{S}}_3 = \mathbf{1}\mathbf{S}_3\bar{\mathbf{v}}^{-3}$; the expression of the YOY survival rate is:

$$\bar{\mathbf{S}}_1(Y^1) = \mathbf{1}\mathbf{S}_1(Y^1)\bar{\mathbf{v}}^{-1} = \frac{p}{1 + qY^1}K \quad \text{where } K \text{ depends}$$

only on a and \bar{v}_j^{-1} , $j = 1, \dots, 15$.

Because of the density dependence in the YOY survival rate, model (1) and, as a consequence, model (2) are non-linear. The mathematical analysis needs then particular techniques, as finding fixed points and the study of their stability.

2.4. Analysis of the aggregated model

The aggregated model (2) is a non-linear system of difference equations, for which a fixed point Y^* exists; Y^* is solution of:

$$Y^* = \bar{\mathbf{L}}(Y^{1*})Y^*$$

where $Y^* = (Y^{1*}, Y^{2*}, Y^{3*})$ with:

$$Y^{1*} = \frac{1}{q} \left[\frac{\bar{\mathbf{F}}\bar{\mathbf{S}}_2 p K}{1 - \bar{\mathbf{S}}_3} - 1 \right], \quad Y^{2*} = \frac{1 - \bar{\mathbf{S}}_3}{\bar{\mathbf{F}}\bar{\mathbf{S}}_2}, \quad Y^{3*} = \frac{1}{\bar{\mathbf{F}}} Y^{1*} \quad (3)$$

The asymptotic stability of the equilibrium state Y^* cannot be studied in the usual way with non-linear discrete time models (based on the trace and the determinant of the Jacobian matrix), but has to be studied by a Jury's test [24]. The total population at the equilibrium can thus be

$$\text{calculated by } Y^{T*} = \sum_{i=1}^3 Y^{i*}.$$

The reference river network is then characterized by a reference value Y_{ref}^{T*} , and the river network with one or more dams or channels by a value Y^{T*} ; the effect of changes, that is of the river management, on the global population dynamics is quantified by comparison between Y_{ref}^{T*} and Y^{T*} .

3. Results and discussion

3.1. Concordance between complete and aggregated models: the linear case revisited

In order to argue that the aggregated model is a good approximation of the complete one (mathematically demonstrated in Bravo de la Parra et al. [6]), we used the linear model developed by Charles et al. [16], in which both migration rates and demographic parameters were constant. The complete model is written as $N_{t+1} = \mathbf{L}\mathbf{P}^k N_t$, while the aggregated one is $Y_{t+1} = \bar{\mathbf{L}}Y_t$. Parameter values are those of table 1, except for the YOY survival rate s_1 , which is constant and equal to 0.07 (estimated from Baglinière and Maisse [19]).

We compared the dominant eigenvalue of the $\bar{\mathbf{L}}$ matrix corresponding to the aggregated model ($\bar{\lambda}_{ref} = 1.04$ [16]), to that of the $\mathbf{L}\mathbf{P}^k$ matrix corresponding to the complete model, for increasing k -values. Such an analysis needs to choose particular values for migration rates, i.e. for the matrix \mathbf{P} . As detailed in Charles et al. [16], only migration ratios can be related to fast equilibrium frequencies (i.e. individual proportions on the different patches), but an infinity of solutions exists for each migration rate (see Appendix). Nevertheless, the choice is limited to reasonable values, as migration rates must verify two constraints: a) each migration rate must strictly remain between 0 and 1 (from a biological point of view, null – any migrations or unit – whole exchange of individuals for each pair of patches – migrations rates are unrealistic); b) ratios of direct and inverse migration rates must be equal to fixed numerical values calculated from

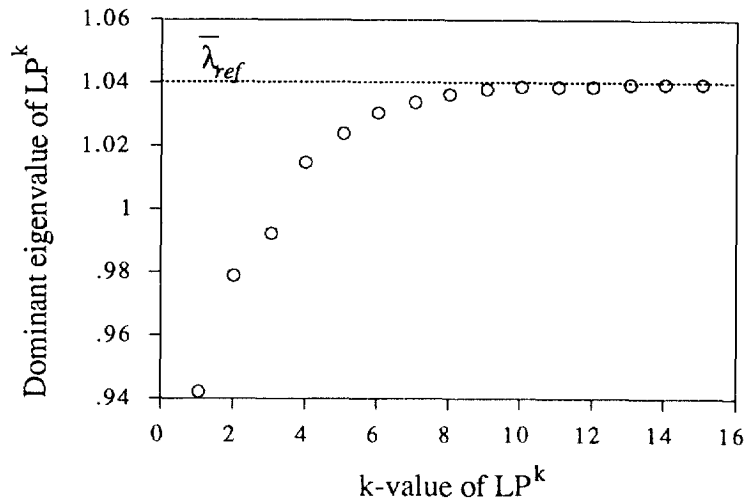


Figure 2. Dominant eigenvalue of the matrix LP^k for increasing k -values. The reference value, $\bar{\lambda}_{ref} = 1.04$, corresponding to the linear aggregated model [16] is also indicated.

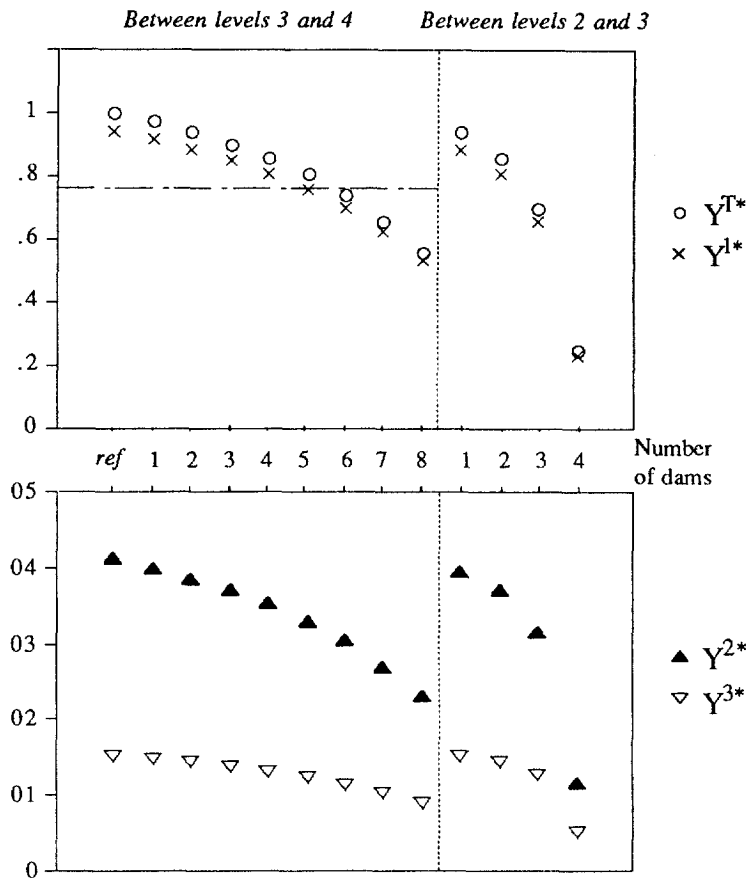


Figure 3. Effect of a gradual increase in dam number in the reference river network, either between levels 3 and 4 (left part) or between levels 2 and 3 (right part), either on the total equilibrium state of the population (Y^{T*}), or on YOY (Y^1), juvenile (Y^2) and adult (Y^3) populations.

$$Y^{T*} = \sum_{i=1}^3 Y^{i*} \text{ is an index of the global population density within the river network.}$$

individual proportions given in *table 1*. As a consequence, migration rates are never close to extreme values (0 or 1), which ensures a fast convergence to the migratory equilibrium.

As shown in *figure 2*, there is a good adequacy between the two models as soon as k is equal to 12. In fact, the approximation seems good for $k = 9$ or 10, but the dominant eigenvalue of LP^k is exactly that of \bar{L} from $k = 12$. The reproduction taking place once a year, which means that individuals must migrate at least 12 times during this interval, that is at least once a month. Such migratory movements of trout have actually been observed for feeding or territory research [25], cited in Baglinière and Maisse [19].

3.2. Characterization of the reference river network in the non-linear case

From the aggregated model (equation 2) and numerical values given in *table 1*, the reference river network can be characterized by a steady state $Y^* = (Y^{1*}, Y^{2*}, Y^{3*})$ and a global equilibrium state for the population Y_{ref}^{T*} , nor-

malized to 1 as a measure of clearness. Hence after normalization, we obtain $Y^* = (0.945, 0.041, 0.015)$. The quantity Y_{ref}^{T*} can be considered as an index of the global density in the river network.

3.3. Effects of dams

Figure 3 shows how a gradual increase in the number of dams between levels 3 and 4 (left part of *figure 3*) or between levels 2 and 3 (right part of *figure 3*) affects the total population at the equilibrium: Y^{T*} gradually decreases as the number of dams increases. As expected, the equilibrium population of YOY, juveniles or adults also decreases, even if adults seem less affected than the other age-classes (Y^{3*} varies from 0.015 to 0.005).

Moreover, as underlined by comparison between the left and right parts of *figure 3*, an insertion of dams between levels 2 and 3 is more drastic than an insertion between levels 3 and 4. The global population varies from 1 to 0.562 in the first case, and from 1 to 0.246 in the second.

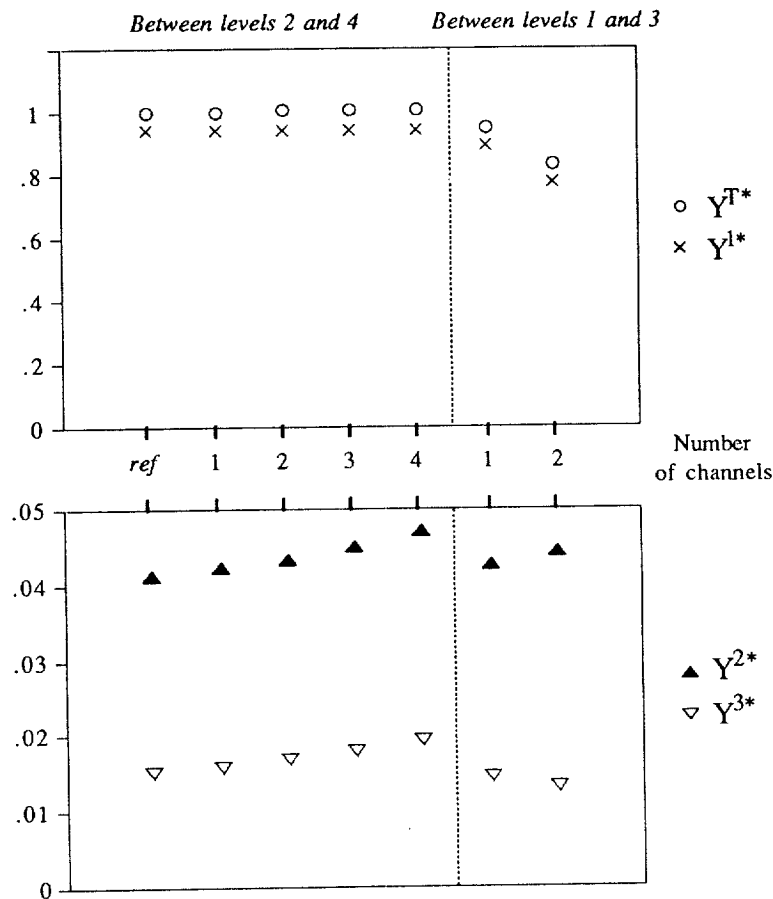


Figure 4. Effect of a gradual increase in channel number in the reference river network, either between levels 2 and 4 (left part) or between levels 1 and 3 (right part), either on the total equilibrium state of the population (Y^{T*}), or on YOY (Y^{1*}), juvenile (Y^{2*}) and adult (Y^{3*}) populations.

$Y^{T*} = \sum_{i=1}^3 Y^{i*}$ is an index of the global population density inside the river network.

These results can be explained by our hypotheses on dams. In fact, if a dam is inserted between patches 4 and 8, for example, we consider then a changed river network in which patch 8 does not exist yet. Hence, a patch in which the YOY survival rate and above all the adult fecundity are high is deleted. In the same way, the effect of dams between two patches of levels 2 and 3 (for example between patches 2 and 4) will be much more drastic since, in this case, patches 4, 8 and 9 will be deleted from the river network.

Figure 3 shows that the trout population seems rather resistant to dam insertion, since it is necessary to break more than half the connections between patches of levels 3 and 4 to delete a quarter of the total population. Moreover, with dams between all patches of levels 3 and 4, almost 50 % of the adult density at the equilibrium are preserved. And in the same way, almost 75 % of the total equilibrium density remain in the river with two dams between levels 2 and 3, i.e. with only nine patches among 15.

3.4. Effects of channelling

Figure 4 highlights the effect of channelling on the global population at the equilibrium. As shown in the left part of figure 4, the insertion of channels between levels 2 and 4 has almost no effect on the global equilibrium population: the YOY population is stable, while the juvenile and adult populations tend to increase.

On the other hand, the insertion of channels between levels 1 and 3 leads to a decrease in the equilibrium global population; YOY and adult populations also decrease, while the juvenile population increases. Nevertheless, this slight increase is not sufficient to compensate negative effects of channelling on age-classes 1 and 3.

All these results are due to our hypotheses on new migration ratios issued from direct connections between levels 2 and 4 or 1 and 3.

The comparison between the left and right parts of figure 4 shows that an insertion of channels between levels 1 and 3 has more effect than an insertion between levels 2 and 4 on the global population. It varies very little in the first case (from 1 to 1.01), but much more in the second case (from 1 to 0.831).

Finally, the comparison between figures 3 and 4 shows that dams have a stronger effect on the global trout population dynamics than channelling. For example, the total variation of Y^{T*} in the case of dams is equal to $1 - 0.562 = 0.438$, but to $1 - 0.831 = 0.169$ in the case of channelling. Hence, with a maximum number of channels, only 16.9 % of the total equilibrium state is deleted.

4. Conclusion

The aggregated model, simultaneously coupling migratory and demographic processes, allowed us to describe the global dynamics of a trout-like population in an arbo-

rescent river network, by using mathematical tools of non-linear discrete time models, and by taking into account a density-dependent survival rate of YOY.

Our method, based on simple biological hypotheses, seems sufficiently relevant for it to be implemented for environmental management. It allows us to estimate both qualitatively and quantitatively the effects of environmental changes on the global fish population dynamics. Such an approach might, for example, be applied either in decision making to improve waterbody management, or from an ecological point of view to preserve certain fish species, rare or endangered. Nevertheless, the parameter numerical values, on which all our simulation results are based, should be improved, particularly if relevant experimental data were available. Parameters would then be better identified and conclusions more reliable. However, the time and money required to obtain such data mean that they cannot be taken into account in impact studies.

The biological hypotheses involved in this work seem very simple compared to the complexity of the real ecological system, but a more sophisticated model is not necessarily needed, especially for an administrator, who has to deal with both waterbody management and its cost. However, aggregation methods have been widely developed over the last 2 years [26–28] and many mathematical tools are now available to build biologically more realistic models. We can now include density-dependent migrations, time varying parameters for both demography and migrations, and environmental variability (aggregation methods combined with stochastic processes).

Hence, the density-dependent effect of other demographic parameters such as juvenile survival rate [20, 29, 30] or adult fecundity could be considered. Moreover, data from Le Cren [22], on which our density-dependence hypothesis for the YOY survival rate is based, were taken from a closed system, that is the response to an excessive density is in fact an increase in mortality. But, in natural ecosystems, the real response is a migration of the weakest individuals (especially YOY) towards less favourable habitats [20]. In this case, migrations become density dependent and the coefficients of the matrix \mathbf{P} are not yet constant. The demographic model could also be improved, particularly if a time dependence of adult fecundity or survival rates is included [31]. In this case, the complete model, and then the aggregated one, are non-autonomous. Finally, both demographic and migration parameters have a weak precision, first because of the lack of data, and second because of random environmental changes. Hence, aggregation techniques in the case of stochastic models could be applied and would improve the predictive ability of the model (e.g. with the estimation of the probability of extinction).

The generality of our method makes it possible to implement it in many ecological problems. The recruitment and stock management might be controlled by quantifying the fishing effect, which affects demographic

and migration parameters, and consequently the global population dynamics. Other fish or animal species (such as birds or mammals) might also be studied, and the effects of some environmental changes on their growth dynamics predicted. Moreover, this type of model allows us to quantify the effects of local changes in the patch network. Each patch might be divided into three smallest patches, the middle one corresponding to the river channel, the two others to the riverbanks. In fact, a different distribution of young between the riverbank and the chan-

nel is commonly observed in fish; for example, in the European grayling [32]. Finally, even if a dendritic river network has been studied in this work, our method could be extended to other kinds of systems, such as a concentric patch network, to model population dynamics in a lake, or rectangular systems to describe, for example, the spatial heterogeneity in a coppice. In the same way, more than two time scales could be involved in the model to integrate many hierarchically organized levels (individual–population–community).

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APPENDIX

Calculation of various migrations ratios

In this Appendix, only the migration process will be studied, and we will denote τ the fast time associated with migrations. The complete system of 15 difference equations describing migrations for one age-class can be written as follows:

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

Thus, at this equilibrium $n_j^i(\tau+1) = n_j^i(\tau) = \bar{n}_j^i$, we obtain with $\bar{v}_j^i = \bar{n}_j^i / \sum_{j=1}^{15} \bar{n}_j^i$:

$$\left\{ \begin{array}{l} \bar{v}_1^i = 1/D_i \\ \bar{v}_2^i = \bar{v}_3^i = (1/D_i)(\alpha_i/\bar{\alpha}_i) \\ \bar{v}_4^i = \bar{v}_5^i = \bar{v}_6^i = \bar{v}_7^i = (1/D_i)(\alpha_i/\bar{\alpha}_i)(\beta_i/\bar{\beta}_i) \\ \bar{v}_8^i = \bar{v}_9^i = \bar{v}_{10}^i = \bar{v}_{11}^i = \bar{v}_{12}^i = \bar{v}_{13}^i = \bar{v}_{14}^i = \bar{v}_{15}^i = (1/D_i)(\alpha_i/\bar{\alpha}_i)(\beta_i/\bar{\beta}_i)(\gamma_i/\bar{\gamma}_i) \end{array} \right.$$

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, \bar{v}_j^i values known from individual proportions in *table I*, it is easy to obtain numerical values for migrations ratios.

When a channel is introduced, either between levels 2 and 4 or between levels 1 and 3, new migration ratios ($\delta_i/\bar{\delta}_i$ and $\varepsilon_i/\bar{\varepsilon}_i$) are introduced. By way of example, here is how to calculate the migration ratio $\varepsilon_i/\bar{\varepsilon}_i$. Suppose that a channel is introduced, directly relating patches 1, 4 and 5 (*figure 1, Ilc*); the new system of difference equations describing the migration process is:

$$\left\{ \begin{array}{l} n_1^i(\tau+1) = n_1^i(\tau) + \bar{\varepsilon}_i(n_4^i(\tau) + n_5^i(\tau)) - 2\varepsilon_i n_1^i(\tau) \\ n_3^i(\tau+1) = n_3^i(\tau) + \alpha_i n_1^i(\tau) + \bar{\beta}_i(n_6^i(\tau) + n_7^i(\tau)) - (2\beta_i + \bar{\alpha}_i)n_3^i(\tau) \\ n_4^i(\tau+1) = n_4^i(\tau) + \varepsilon_i n_1^i(\tau) + \bar{\gamma}_i(n_8^i(\tau) + n_9^i(\tau)) - (2\gamma_i + \bar{\beta}_i)n_4^i(\tau) \\ n_5^i(\tau+1) = n_5^i(\tau) + \varepsilon_i n_1^i(\tau) + \bar{\gamma}_i(n_{10}^i(\tau) + n_{11}^i(\tau)) - (2\gamma_i + \bar{\beta}_i)n_5^i(\tau) \\ \dots \dots \end{array} \right. \quad (2)$$

where "... " signifies that equations are not changed.

By assuming that, at equilibrium, the ratio between the number of individuals at levels 3 and 1 remain equal between the reference network and the one with a channel, we obtain the following.

– From system (1) at the equilibrium (equations 1–3)

$$\begin{cases}
 \bar{\alpha}_i(\bar{n}_2 + \bar{n}_3) = 2\alpha_i\bar{n}_1 \\
 \alpha_i\bar{n}_1 + \bar{\beta}_i(\bar{n}_4 + \bar{n}_5) = (2\beta_i + \bar{\alpha}_i)\bar{n}_2 \\
 \alpha_i\bar{n}_1 + \bar{\beta}_i(\bar{n}_6 + \bar{n}_7) = (2\beta_i + \bar{\alpha}_i)\bar{n}_3
 \end{cases}$$

$$\Rightarrow \begin{cases}
 \bar{\alpha}_i(\bar{n}_2 + \bar{n}_3) = 2\alpha_i\bar{n}_1 \\
 2\alpha_i\bar{n}_1 + \bar{\beta}_i(\bar{n}_4 + \bar{n}_5 + \bar{n}_6 + \bar{n}_7) = (2\beta_i + \bar{\alpha}_i)(\bar{n}_2 + \bar{n}_3)
 \end{cases}$$

$$\Rightarrow 2\alpha_i\bar{n}_1 + \bar{\beta}_i(\bar{n}_4 + \bar{n}_5 + \bar{n}_6 + \bar{n}_7) = (2\beta_i + \bar{\alpha}_i)2\frac{\alpha_i\bar{n}_1}{\alpha_i}$$

$$\Rightarrow \frac{\bar{n}_4 + \bar{n}_5 + \bar{n}_6 + \bar{n}_7}{\bar{n}_1} = 4\frac{\alpha_i\bar{\beta}_i}{\alpha_i\bar{\beta}_i}$$

$$\Rightarrow \frac{\bar{n}_4 + \bar{n}_5}{\bar{n}_1} = 2\frac{\alpha_i\bar{\beta}_i}{\alpha_i\bar{\beta}_i} \quad \text{as} \quad \bar{n}_4 = \bar{n}_5 = \bar{n}_6 = \bar{n}_7 \quad (3.1)$$

– From system (2) at the equilibrium (equation 1)

$$\begin{aligned}
 \bar{\varepsilon}_i(\bar{n}_4 + \bar{n}_5) &= 2\varepsilon_i\bar{n}_1 \\
 \Rightarrow \frac{\bar{n}_4 + \bar{n}_5}{\bar{n}_1} &= 2\frac{\varepsilon_i}{\varepsilon_i} \quad (3.2)
 \end{aligned}$$

By identifying expressions (3.1) and (3.2), we finally obtain:

$$\frac{\varepsilon_i}{\varepsilon_i} = \frac{\alpha_i\bar{\beta}_i}{\alpha_i\bar{\beta}_i}$$