ON POPULATION RESILIENCE TO EXTERNAL PERTURBATIONS

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On population resilience to external perturbations

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Abstract

This paper is devoted to the mathematical analysis of a spatially-explicit harvesting model in periodic or bounded environments. Mathematically, this model corresponds to a parabolic equation with a space-dependent mono-stable nonlinearity and a negative external forcing term. This equation is set either in the whole space $\mathbb{R}^N$, with periodic coefficients, or in a bounded domain. Analysing the stationary states, we defined two main types of solutions; the "significant" solutions, which always stay above a certain small parameter, and the "remnant" solutions, which are always below this parameter. Using sub- and super-solution methods and the characterisation of the first eigenvalue and first eigenfunction of some linear elliptic operators, we obtained existence and nonexistence results as well as some results on the number of stationary solutions. We also characterised the asymptotic behaviour of the evolution equation in function of the forcing term amplitude. In particular, we defined some thresholds on the forcing term below which the population density converges to a significant state, while it converges to a remnant state whenever the forcing term is set above the highest threshold. Besides, these bounds were shown to be useful for studying the influence of the environmental fragmentation on the long time behaviour of the population

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density, in terms of the forcing term amplitude. We present such results which were obtained numerically in the framework of stochastic environments.

1 Introduction

Overexploitation has led to the extinction of many species [4]. Traditionally, models of ordinary differential equations or difference equations have been used to estimate the maximum sustainable yields from populations and to permit a quantitative analysis of harvesting policies and management strategies [14]. Occulting age or stage structures as well as delay mechanisms, which will not be treated by the present paper, the ODEs models are generally of the following type:

$$\frac{dU}{dt} = F(t, U) - Y(t, U), \tag{1.1}$$

where U is the population biomass at time t, $F(t, U)$ is the growth function and $Y(t, U)$ corresponds to the harvest function. In these models, the most commonly used growth function is logistic, with $F(t, U) = U(\mu - \nu U)$ ([5], [19], [29]), where $\mu > 0$ is the intrinsic growth rate of the population and $\nu > 0$ models its susceptibility to crowding.

Different harvesting strategies $Y(t, U)$ have been considered in the literature, and are used in practical resource managing. A very common one is the *constant-yield harvesting* strategy, where a constant number of individuals are removed per unit of time: $Y(t, U) = \delta$, with δ a positive constant. This harvesting function naturally appears when a quota is set on the harvesters ([25], [26], [32]). Another frequently used harvesting strategy is the *proportional harvesting* strategy (also called *constant effort harvesting*), where a constant proportion of the population is removed. It leads to an harvesting function of the type $Y(t, U) = \delta U$.

From the point of view of spatially dependent reaction-diffusion models, much less seems to be achieved in this spirit, even if some recent related works have raised some aspects of the question ([18], [20], [23]). The aim of this paper is to perform an analysis of some harvesting models in the spirit of standard works which used ODEs, but within the framework of reaction-diffusion equations; it permits among others things, to consider the effect of environmental heterogeneity for such questions.

In that respect, before entering into the precise statements of the problem here considered, we need to recall some generalities on reaction diffusion models. One of the famous reaction-diffusion model is the one of Fisher [13] and Kolmogorov, Petrovsky and Piskunov [17], which has been widely used to model spatial propagation or spreading of biological species in homogeneous environments (see the books [19], [22] and [34] for review). The corresponding equation is

$$u_t = D\nabla^2 u + u(\mu - \nu u), \tag{1.2}$$

where $u = u(t, x)$ is the population density at time t and space position x, D is the diffusion coefficient, and μ and ν still correspond to the *constant* intrinsic growth rate and susceptibility to crowing coefficients. More recently, this model has been extended to heterogeneous environments by Shigesada et al. [31]. The corresponding model (called *SKT-model* in the sequel) is of the following type,

$$u_t = D\nabla^2 u + u(\mu(x) - \nu(x)u). \tag{1.3}$$

The coefficients $\mu(x)$ and $\nu(x)$ now depend on the space variable x, which can therefore include some effects of environmental heterogeneity. This model has revealed that the heterogeneous character of the environment plays an essential role on species persistence, in the sense that for different spatial configurations of the environment, a population can extinct or survive, depending on the arrangements of the habitat ([7], [11], [30]).

As mentioned above, the combination of an harvesting model with a Fisher-KPP model of population dynamics, leading to an equation of the form $u_t = D\nabla^2 u + u(\mu - \nu u) - Y(t, x, u)$ has been considered in some recent papers, with a spatially dependent proportional harvesting term $Y(x, u) = q(x)u$ in [20] [23], and a spatially dependent and time-constant harvesting term $Y(x) = h(x)$ in [18]. In these papers, the models were considered in bounded domains with Dirichlet (lethal) boundary conditions.

We study here a model of population dynamics of the SKT-type, with a spatially dependent harvesting term $Y(x, u)$. We then obtain a reaction-diffusion model of the following type:

$$u_t = D\nabla^2 u + u(\mu(x) - \nu(x)u) - Y(x, u). \tag{1.4}$$

We mainly focus on a "quasi-constant-yield" case, where the harvesting term only depends on u for very low population densities (guaranteeing the non-negativity of u), while it is of constant yield type for large enough values of

u. We consider two types of domains and of boundary conditions. In the first case, the domain is bounded with Neumann (reflective) boundary conditions; this framework is often the more realistic one for modelling species which cannot cross the domain boundary. In the second case, we consider the model (1.4) in the whole space $\mathbb{R}^N$ with periodic coefficients. This last situation, though being technically more complex, is useful for instance for studying spreading phenomena ([6], [8]), and for studying the effects of environmental fragmentation, independently of the boundary effects. Lastly, note that the effects of variability in time of the harvesting function will be postponed in a forthcoming publication [12]. We describe now the skeleton of our paper.

In § 2, we set a firm mathematical basis for this model. We prove existence and nonexistence results for the equilibrium equations as well as some results on the number of possible stationary states. We also establish the asymptotic behaviour of the solutions in large times. In § 3, we illustrate the practical usefulness of the results of § 2, by studying the effects of the amplitude of the harvesting term on the population density in terms of environmental fragmentation. Lastly, in § 4, we give some new results for the proportional harvesting case $Y(x, u) = q(x)u$.

2 Mathematical analysis of a quasi-constant-yield spatially-explicit harvesting model

2.1 Formulation of the model

The model we are interested in this paper, is essentially an externally perturbed SKT-model:

$$u_t = D\nabla^2 u + u(\mu(x) - \nu(x)u) - \delta h(x)\rho_\varepsilon(u), \ (t, x) \in \mathbb{R}_+ \times \Omega. \tag{2.5}$$

The function $u = u(t, x)$ denotes the population density at time t and space position x. The coefficient D, assumed to be positive, denotes the diffusion coefficient. The questions concerning other assumptions on the diffusion part of (2.5) and related consequences of our analysis, will be discussed in the conclusion. The functions $\mu(x)$ and $\nu(x)$ respectively stand for the spatially dependent intrinsic growth rate of the population, and for its susceptibility to crowding. Two different types of domains Ω are considered: either $\Omega = \mathbb{R}^N$

or Ω is a smooth bounded and connected domain of $\mathbb{R}^N$ ($N \geq 1$). We qualify the first case as the *periodic case*, and the second one as the *bounded case*. In the periodic case, we assume that the functions $\mu(x)$, $\nu(x)$ and $h(x)$ depend on the space variables in a periodic fashion. For that, let $L = (L_1, \ldots, L_N) \in (0, +\infty)^N$. We recall the following definition:

Definition 2.1 A function g is said to be *L-periodic* if $g(x + k) = g(x)$ for all $x = (x_1, \cdots, x_N) \in \mathbb{R}^N$ and $k \in L_1\mathbb{Z} \times \cdots \times L_N\mathbb{Z}$.

Thus we assume, in the periodic case, that μ, ν and h are L-periodic. In the bounded case we assume that Neumann boundary conditions hold: $\dfrac{\partial u}{\partial n} = 0$ on $\partial\Omega$, where n is the outward unit normal to $\partial\Omega$. The period cell C is defined by

$$C := (0, L_1) \times \cdots \times (0, L_N),$$

in the periodic case, and in the bounded case, we set

$$C := \Omega,$$

for the sake of simplicity of some forthcoming statements.

We assume furthermore that the functions μ and ν satisfy

$$\mu,\ \nu\ \in\ L^\infty(\Omega) \text{ and } \exists\ \underline{\nu}\,, \overline{\nu}\ \in\ \mathbb{R} \text{ s.t. } 0 < \underline{\nu} < \nu(x) < \overline{\nu},\ \forall\ x\ \in\ \Omega. \quad (2.6)$$

For μ and ν fixed, regions with higher values of $\mu(x)$ and lower values of $\nu(x)$ will be qualified as *more favourable*, while, on the other hand, regions with lower $\mu(x)$ and higher $\nu(x)$ values will be considered as *less favourable* or equivalently as *more hostile*.

We now describe and explain our choice for the last term in (2.5): $\delta h(x)\rho_\varepsilon(u)$. It corresponds to a *quasi-constant-yield harvesting* term. Indeed, the function ρ_ε defines a "regularised Heaviside function": it is a $C^1(\mathbb{R})$ nondecreasing function such that

$$\rho_\varepsilon(s) = 0 \text{ for all } s \leq 0 \text{ and } \rho_\varepsilon(s) = 1 \text{ for all } s \geq \varepsilon,$$

where ε is a non-negative parameter. Such a function lead to consider two different types of yield: constant yield in time when $u \geq \varepsilon$, and yield depending almost proportionally on the population density u when $u < \varepsilon$. In the sequel, the parameter ε will be taken to be very small. As we prove in the next sections, there are many situations where the solutions of the model always remain larger than ε. For these reasons, we qualify our model as quasi-constant-yield harvesting SKT-model, the "dominant" regime being the constant-yield one. Note that the function ρ_ε guarantees the non-negativity of the solutions of (2.5), and from a biological viewpoint, ε can correspond to a threshold bellow which harvesting is progressively abandoned. Considering constant-yield harvesting functions without this threshold value would be unrealistic since it would lead to harvest on zero-populations.

Finally, we specify that $\delta \geq 0$ and that h is a function in $L^\infty(\Omega)$ such that

$$\text{there exists } \alpha > 0 \text{ with } \alpha < h(x) < 1 \text{ for all } x \in \Omega. \tag{2.7}$$

We will call h the *harvesting scalar field*, and δ will designate by this way the amplitude of this field.

Before starting our analysis of this model, we consider the no-harvesting case, i.e. when $\delta = 0$, for recalling the main results obtained in this case and in order to introduce some elements of analysis and comparison with the quasi-constant-yield harvesting SKT model.

2.2 The no-harvesting case

When $\delta = 0$ in equation (2.5), our model reduces to the SKT model of population dynamics in heterogeneous environments described by equation (1.3). The behaviour of the solutions of this model has been extensively studied in [7] and [8]. In this section, we recall some results that will be useful in the analysis of the general case of (2.5).

These results are formulated in terms of first (smallest) eigenvalue λ_1 of the following Schrödinger operator $\mathcal{L}_\mu$ defined by

$$\mathcal{L}_\mu \phi := -D\nabla^2 - \mu(x)I,$$

with either periodic boundary conditions (on the period cell C) in the periodic case or Neumann boundary conditions in the the bounded case. This operator is the linearized one of the full model around the trivial solution. Recall that λ_1 is defined as the unique real number such that there exists a function $\phi > 0$, the first eigenfunction, which satisfies

$$\begin{cases} -D\nabla^2\phi - \mu(x)\phi = \lambda_1\phi \text{ in } C, \\ \phi > 0 \text{ in } C, \ \|\phi\|_\infty = 1, \end{cases} \tag{2.8}$$

with either periodic or Neumann boundary conditions, depending on Ω. The function ϕ is uniquely defined by (2.8) ([6]), and belongs to $W^{2,\tau}(C)$ for all $1 \le \tau < \infty$ (see [1] and [2] for further details). We set

$$\underline{\phi} := \min_{x \in C} \phi(x).$$

We recall that a stationary state p of equation (1.3) satisfy the equation,

$$-D\nabla^2 p = p(\mu(x) - \nu(x)p). \tag{2.9}$$

The following result on the stationary states of (2.9) is proved in [7].

Theorem 2.2 *(i) If $\lambda_1 < 0$, the equation* (2.9) *admits a unique nonnegative, nontrivial and bounded solution, p_0.*

(ii) If $\lambda_1 \ge 0$, the only nonnegative and bounded solution of (2.9) *is* 0.

Moreover, in the periodic case the solution p_0 is L-periodic. Throughout this paper, p_0 always denotes to the stationary solution given by Theorem 2.2, Part (i).

In order to emphasise that this solution can be "far" from 0 (cf. Definition 2.5, and the commentary following (2.12) for a precise statement), we give a lower bound for p_0, which will be essential in particular for the study of the asymptotic behaviour (cf. Theorem 2.11).

Proposition 2.3 *Assume that $\lambda_1 < 0$, then $p_0 \ge \dfrac{-\lambda_1 \underline{\phi}}{\overline{\nu}}$ in Ω.*

Note: For the sake of readability, the proofs of the results of § 2 are postponed to § 2.5.

The asymptotic behaviour of the solutions of (1.3) is also detailed in [7]. In this particular case $\delta = 0$, they show that $\lambda_1 < 0$ is a necessary and sufficient condition for species persistence, whatever the initial population u^0 is:

Theorem 2.4 *Let u^0 be an arbitrary bounded and continuous function in Ω such that $u^0 \ge 0$, $u^0 \not\equiv 0$. Let $u(t, x)$ be the solution of (1.3), with initial data $u(0, x) = u^0(x)$.*

(i) If $\lambda_1 < 0$, then $u(t, x) \to p_0(x)$ in $W^{2,\tau}_{loc}(\Omega)$, for all $1 \le \tau < \infty$, as $t \to +\infty$ (uniformly in the bounded case).

(ii) If $\lambda_1 \ge 0$, then $u(t, x) \to 0$ uniformly in Ω as $t \to +\infty$.

The situation (i) corresponds to persistence, while in the case (ii) the population tends to extinction. In the sequel, unless otherwise specified, we therefore always assume that $\lambda_1 < 0$, so that the population survives, at least when there is no harvesting. We are now in position to start our main analysis of steady states and related asymptotic behaviour of solutions of (2.5).

2.3 Stationary states analysis

As it is classically demonstrated in finite dimensional dynamical system theory and many problems in the infinite dimensional setting (see e.g. [33]), and in particular for semi-linear parabolic equations, the asymptotic behaviour of the solutions of (2.5) is governed by the steady states and their relative stability properties. In that respect, we study in this section the positive stationary solutions of (2.5), namely the solutions of

$$-D\nabla^2 p_\delta = p_\delta(\mu(x) - \nu(x)p_\delta) - \delta h(x)\rho_\varepsilon(u), \ x \ \in \ \Omega. \tag{2.10}$$

No boundary conditions are imposed in the periodic case, while we again assume Neumann boundary conditions in the bounded case. When needed, we may note (2.10,δ) instead of (2.10).

Note that, provided $p_\delta \geq \varepsilon$ in Ω, p_δ is equivalently a solution of the simpler equation

$$-D\nabla^2 p_\delta = p_\delta(\mu(x) - \nu(x)p_\delta) - \delta h(x), \ x \ \in \ \Omega. \tag{2.11}$$

This last equation has been analysed in the case of Dirichlet boundary conditions in [23], in the particular case of constant coefficients μ and ν.

In the following analysis, two main types of solutions of (2.10) will be found. Hence we introduce the following definition.

Definition 2.5 Set $\varepsilon_0 := \dfrac{\varepsilon}{\underline{\phi}} \geq \varepsilon$. We say that a nonnegative function σ is *remnant* whenever $\max\limits_C \sigma < \varepsilon_0$, whereas it is *significant* if it is a bounded function satisfying $\min\limits_C \sigma \geq \varepsilon_0$.

Since ε_0 is assumed to be small in our model, the remnant solutions of (2.10) correspond to very low population densities. On the other hand, significant solutions are everywhere above ε_0. In particular, a constant yield is guaranteed in that case. Stationary solutions which are not remnant neither significant may exist, as outlined in the next theorems. However, as we will see while studying the long-time behaviour of the solutions of the model (2.5), they are of less importance in our study (cf. Theorem 2.11 and § 3).

Note: The threshold ε_0 is different from ε in general. We had to define remnant and significant functions using ε_0 for technical reasons (see the proof of Theorem 2.10, part (ii), equation (2.28)). Since ε is assumed to be very small, it has no implication on the biological interpretation of our results. Moreover, most of our results still work when ε_0 is replaced by ε.

In the sequel, we always assume that that

$$\varepsilon_0 < \frac{-\lambda_1 \underline{\phi}}{4\overline{\nu}}, \tag{2.12}$$

so that, in particular, from Proposition 2.3, the solution p_0 of (2.9) is significant.

We begin by proving that there exists a threshold δ^* such that, if the amplitude δ is below δ^*, the equation (2.10) admits significant solutions, while it does not in the other case.

Theorem 2.6 *Assume that $\lambda_1 < 0$, then there exists $\delta^* \geq 0$ such that*

(i) if $\delta \leq \delta^*$ there exists a positive significant solution $p_\delta \leq p_0$ of (2.10) *and* (2.11).

(ii) if $\delta > \delta^*$, there is no positive significant solution of (2.10).

(iii) If $\lambda_1 \geq 0$, there is no positive bounded solution of (2.10)*, whatever δ is.*

(iv) If $\lambda_1 < 0$ and $\delta > \delta^*$, or if $\lambda_1 \geq 0$, there is no positive bounded solution of (2.11).

Under stronger hypotheses, we are able to prove that (2.10) admits *at most* two significant solutions. In order to state this result, we need some definitions. Let G be the space defined in the periodic case by

$$G := H^1_{per} = \left\{\varphi \in H^1_{loc}(\mathbb{R}^N) \text{ such that } \varphi \text{ is L-periodic}\right\}, \tag{2.13}$$

and by

$$G := H^1(C), \tag{2.14}$$

in the bounded case. Let us define the standard Rayleigh quotient, for all $\phi \in G$, $\phi \not\equiv 0$, and for all $\sigma \in L^\infty(C)$,

$$\mathcal{R}_\sigma(\phi) := \frac{\displaystyle\int_C |\nabla\phi|^2 - \sigma(x)\phi^2}{\displaystyle\int_C \phi^2}. \tag{2.15}$$

Then, the second smallest eigenvalue λ_2 of the operator $\mathcal{L}_\mu$ can be computed thanks to the following variational formula:

$$\lambda_2 = \min_{E_k \subset G, \dim(E_k)=2} \max_{\phi \in E_k,\ \phi \not\equiv 0} \mathcal{R}_\mu(\phi). \tag{2.16}$$

We are now in position to state the following theorem:

Theorem 2.7 *Assume that $\lambda_1 < 0 \leq \lambda_2$, then, in the bounded case, the equation* (2.10) *admits at most two significant solutions. In the periodic case,* (2.10) *admits at most two L'-periodic significant solutions for all $L' \in (0, +\infty)^N$. Moreover, under these hypotheses, if two solutions $p_{1,\delta}$ and $p_{2,\delta}$ exist, they are ordered in the sense that, for instance, $p_{1,\delta} < p_{2,\delta}$ in Ω.*

Note: Similar methods also allow us to assess a result on the number of solutions of equation (2.11). Indeed, if $\lambda_1 < 0 \leq \lambda_2$, then, in the bounded case, we obtain that (2.11) admits at most two non-negative bounded (and periodic in the periodic case) solutions. If these solutions exist, they are ordered.

In the periodic case, Theorem 2.7 also gives some information on the periodicity of the significant solutions of (2.10), which are actually found to have the same periodicity as the coefficients of the equation (2.10):

Corollary 2.8 *Assume that $\lambda_1 < 0 \leq \lambda_2$. Then, in the periodic case, the significant periodic solutions of* (2.10) *are L-periodic.*

The fact that $\lambda_1 < 0$ is directly related to the instability of the trivial solution in the SKT model. The additional condition $\lambda_2 \geq 0$ in this theorem is linked to the existence of a stable manifold or centre manifold of the steady state 0 of the SKT model, in some appropriate functional spaces (see [33]). Therefore the assumptions of Theorem 2.7, and the Krein Rutmann theory, allow us to conclude that under these assumptions, the unstable manifold of 0 is of dimension equal to *one* or equivalently the stable manifold is of codimension one. Such results on multiplicity of solutions of elliptic nonlinear equations with a source term have been investigated in the past, and are known nowadays as Ambrosetti-problem type. These results also involve manifolds of codimension 1 (but in the functional space of forcing), and first and second eigenvalues (but for the opposite of the Laplacian only) (see [21] for a survey of these results).

At all events, our Theorem 2.7 relies on the assumption that $\lambda_2 \geq 0$, thus in order to get a better idea of when λ_2 may become positive, and how its sign depends on μ, we compute a lower bound for λ_2 in the periodic or bounded case.

Proposition 2.9 *(i) In the periodic case,*

$$\lambda_2(C) \geq D\left(\frac{\pi}{L_d}\right)^2 - \max_C \mu,$$

where L_d denotes the length of the longest diagonal of C.

(ii) In the bounded case, if C is a convex domain with diameter d,

$$\lambda_2(C) \geq D\left(\frac{\pi}{d}\right)^2 - \max_C \mu.$$

If C is not assumed to be convex, we have

$$\lambda_2(C) \geq D\left(\frac{\pi}{d'}\right)^2 - \max_C \mu,$$

where d' is the diameter of the smallest ball containing C.

For instance, when $C = [0,1] \times [0,1]$, we have $d = \sqrt{2}$; thus, for $D = 1$ and $\max_C \mu = 4$, we get $\lambda_2 > 0.9$. However, this lower bound is far from being optimal. Indeed, in all our computations of § 3, and under the same hypothesis on C and D, we always had $\lambda_2 > 0$, while $\max_C \mu = 10$. More precise lower bounds for λ_2 can be found in [10]; however, these bounds are also more sensitive to the geometry of the domain, and thus less general, and are therefore not detailed here.

We now introduce an important result for studying the effect of the environmental heterogeneity on the harvesting from a quantitative point of view.

One of the main drawbacks of Theorem 2.6 is that it gives no computable bounds of δ^*; and obtaining information on the value of δ^* is precious for more inclined ecological questions such that the study of the relationships between δ^* and the environmental heterogeneities, which are, we recall it, included in the coefficients $\mu(x)$ and $\nu(x)$. In the next theorem we are able to produce some estimates that allows us to answer in part to this important practical question (cf. also § 3 for an illustration of this theorem).

For that, let us define

$$\delta_1 := \frac{\lambda_1^2 \underline{\phi}}{\overline{\nu}(1+\underline{\phi})^2} \text{ and } \delta_2 := \frac{\lambda_1^2}{4\alpha\underline{\nu}}. \tag{2.17}$$

Note that δ_1 and δ_2 do not depend on δ and ε.

Theorem 2.10 *(i) If $\lambda_1 < 0$ and $\delta \leq \delta_1$, then there exists a positive significant solution p_δ of* (2.10) *such that $p_\delta \geq -\dfrac{\lambda_1 \phi}{\overline{\nu}(1+\underline{\phi})}$. In the periodic case, there exists a L-periodic solution.*

(ii) If $\lambda_1 < 0$ and $\delta > \delta_2$, the only possible positive bounded solutions of (2.10) *are remnant.*

(iii) If $\lambda_1 < 0$ and $\delta > \delta_2$, there is no positive bounded solution of (2.11).

The lower bound of Part (i), for p_δ, does not depend on ε. Thus, there is a clear distinction between the remnant and significant solutions. Note that, of course, $\delta_1 \leq \delta_2$.

Related to λ_1 and $\underline{\phi}$, the formulae (2.17) allow numerical evaluations. An important quantity to compute is the size of the gap $\delta_2 - \delta_1$, and its fluctuations in terms of environmental configurations. This question is addressed in § 3 through a numerical study, exploiting the formulae given by (2.17) and some recent results on stochastic modelling of heterogeneous landscapes [28].

2.4 Asymptotic behaviour

In this section, we prove that the quantity δ^* in fact corresponds to a maximum sustainable yield, in the sense that when δ is smaller than δ^*, the population density $u(t,x)$ converges to a significant stationary state of (2.5) as $t \to \infty$, whereas when δ is larger than δ^*, the population density converges to a stationary state which is not significant. In fact, when δ is larger than the quantity δ_2 defined by (2.17) we even prove that the population converges to a remnant stationary state of (2.5).

We consider here that the harvesting starts on a stabilised population governed by the standard SKT-model with $\delta = 0$. From Theorem 2.4, this means that we study the behaviour of the solutions $u(t, x)$ of our model (2.5), starting with the initial datum $u(0, x) = p_0(x)$. Since we have assumed that $\lambda_1 < 0$, it follows from Theorem 2.2, Proposition 2.3 and (2.12) that p_0 is well defined and significant.

Let us describe, with the following theorem, the large time behaviour of the population density.

Theorem 2.11 *Let $u(t, x)$ be the solution of* (2.5) *with initial datum $u(0, x) = p_0(x)$. Then u is non-increasing in t and,*

(i) if $\delta \le \delta^*$, $u(t, x) \to p_\delta(x)$ uniformly in Ω as $t \to +\infty$, where p_δ is the maximal significant solution of (2.10). *Moreover p_δ is L-periodic in the periodic case;*

(ii) if $\delta > \delta^*$, then the function $u(t, \cdot)$ converges uniformly in Ω to a solution of (2.10) *which is not significant;*

(iii) if $\delta > \delta_2$, the function $u(t, \cdot)$ converges uniformly in Ω to a remnant solution of (2.10).

Note: If, in addition, we assume that $\lambda_2 \ge 0$, then Theorem 2.7 says that, whenever $\delta \le \delta^*$, the equation (2.5) admits at most two significant stationary states (which are periodic stationary states in the periodic case). In that case, the stationary state p_δ selected at large times is the higher one. If we do not assume that $\lambda_2 \ge 0$, this stationary state can still be defined as "the maximal one" that can be constructed by a sub- and super- solution method (cf. [3]).

From the above theorem, we observe that, when $\delta \le \delta^*$, the solution $u(t, x)$ of (2.5), with initial data p_0, remains significant for all times $t \ge 0$. This guarantees a constant yield in time, and justifies the name of the model.

Even if it is ecologically relevant, we can argue that such a result seems limited on a mathematical standpoint since we describe the asymptotic behaviour only for a particular initial datum. In fact, similar results can be obtained for a wider class of initial data. Indeed, with similar methods, the convergence of $u(t, x)$ to a significant solution of (2.10) can be obtained whenever $\delta \le \delta^*$ for all bounded and continuous initial data $u(0, x)$ which are larger than the smallest significant solution of (2.10). In particular, when

$u(0,x)$ is larger than the maximal significant solution of (2.10), $u(t,x)$ converges to this maximal significant solution as $t \to +\infty$. A more detailed analysis of the basin of attraction related to the maximal significant solution will be further investigated in the forthcoming paper [12].

Returning to the question pointed out at the end of the preceding section, on the size of the gap $\delta_2 - \delta_1$, we can now assert that this question is in fact related to the practical determination of the maximum sustainable yield. As we will see in § 3, the thickness of the interval (δ_1, δ_2) can be very narrow in certain situations. In those cases, the numerical computation of δ_1 and δ_2 therefore gives a sharp localisation of the maximum sustainable quota $\delta^* \in [\delta_1, \delta_2]$, that can be of non negligible ecological interest.

2.5 Proofs of the results of § 2

Proof of Proposition 2.3: Let ϕ be defined by (2.8), with the appropriate boundary conditions. Set $\kappa_0 := \dfrac{-\lambda_1}{\overline{\nu}}$. Then the function $\kappa_0\phi$ satisfies

$$\begin{aligned} -D\nabla^2(\kappa_0\phi) - \mu(x)\kappa_0\phi + \nu(x)(\kappa_0\phi)^2 &= \lambda_1\kappa_0\phi + \nu(x)(\kappa_0\phi)^2, \\ &= \kappa_0\phi(\lambda_1 + \nu(x)\kappa_0\phi) \le 0. \end{aligned}$$

Thus $\kappa_0\phi$ is a subsolution of the equation (2.9) satisfied by p_0. Since for $M \in \mathbb{R}$ large enough, M is a supersolution of (2.9), it follows from the uniqueness of the positive bounded solution p_0 of (2.9) that $p_0 \ge \kappa_0\phi \ge \dfrac{-\lambda_1\phi}{\overline{\nu}}$. □

Before proving Theorem 2.6, we begin with the following lemma.

Lemma 2.12 *For all $\delta > 0$, if p_δ is a nonnegative bounded solution of* (2.10)*, then $p_\delta \le p_0$.*

Proof of Lemma 2.12: Assume that there exists $x_0 \in \Omega$ such that $p_\delta(x_0) > p_0(x_0)$. The function p_δ satisfies

$$-D\nabla^2 p_\delta - p_\delta(\mu(x) - \nu(x)p_\delta) = -\delta h(x)\rho_\varepsilon(p_\delta) \le 0,$$

thus p_δ is a subsolution of the equation (2.9) satisfied by p_0. Since for $M \in \mathbb{R}$ large enough, M is a supersolution of (2.9) we can apply a classic iterative method to infer the existence of a solution p_0' of (2.9) (with Neumann boundary conditions in the bounded case since both p_δ and M satisfy Neumann boundary conditions) such that $p_\delta \leq p_0' \leq M$. In particular $p_0'(x_0) > p_0(x_0)$, which is in contradiction with the uniqueness of the positive bounded solution of (2.9). □

Proof of Theorem 2.6: Let us define

$$\delta^* := \sup\{\delta \geq 0, (2.10) \text{ admits a significant solution}\}.$$

For $\delta = 0$, we know from Proposition 2.3 that p_0 is a significant solution of (2.10). Moreover, for δ large enough, the nonexistence of significant solutions of (2.10) is a direct consequence of the maximum principle (it is also a consequence of the proof of Theorem 2.10, Part (ii)). Thus δ^* is well defined and bounded.

Assume that $\delta^* > 0$, and let us prove that equation (2.10,δ^*) admits a significant solution. By definition of δ^*, there exists a sequence $(p_{\delta_k})_{k\in\mathbb{N}}$ of solutions of (2.10,δ_k) with $0 < \delta_k \leq \delta^*$ and $\delta_k \to \delta^*$ as $k \to +\infty$. Moreover, from Lemma 2.12, $\varepsilon_0 \leq p_{\delta_k} \leq p_0$ for all $k \geq 0$. Thus, from standard elliptic estimates and Sobolev injections, the sequence $(p_{\delta_k})_{k\in\mathbb{N}}$ converges (up to the extraction of some subsequence) in $W^{2,\tau}_{loc}$, for all $1 \leq \tau < \infty$, to a significant solution p_{δ^*} of (2.10,δ^*).

Now, let $0 \leq \delta < \delta^*$. Then

$$-D\nabla^2 p_{\delta^*} - p_{\delta^*}(\mu(x) - \nu(x)p_{\delta^*}) + \delta h(x) = (\delta - \delta^*)h(x) < 0,$$

thus p_{δ^*} is a subsolution of (2.10,δ). Since p_0 is a supersolution of (2.10,δ), a classical iterative method gives the existence of a significant solution p_δ of (2.10,δ) (with Neumann boundary conditions in the bounded case since both p_δ and M satisfy Neumann boundary conditions). This concludes the proof of Theorem 2.6. □

Proof of Theorem 2.7: As a preliminary, we prove that if two solution exist, then they cannot intersect. Let $p_{1,\delta}$ and $p_{2,\delta}$ be two significant solutions of (2.10). In the bounded case, we assume that $p_{1,\delta}$ and $p_{2,\delta}$ satisfy Neumann boundary conditions. In the periodic case, we assume that there exists $\mathrm{L}' \in (0, +\infty)^N$ such that $p_{1,\delta}$ and $p_{2,\delta}$ are L'-periodic, we then denote the period cell by C'. Let us set $q_\delta := p_{2,\delta} - p_{1,\delta}$. Then q_δ verifies

$$-D\nabla^2 q_\delta - [\mu(x) - \nu(x)(p_{1,\delta} + p_{2,\delta})]q_\delta = 0, \tag{2.18}$$

thus, setting $\rho(x) := \mu(x) - \nu(x)(p_{1,\delta} + p_{2,\delta})$, we obtain

$$-D\nabla^2 q_\delta - \rho(x) q_\delta = 0, \tag{2.19}$$

with the same boundary conditions that were satisfied by $p_{1,\delta}$ and $p_{2,\delta}$.

Let $\widehat{\lambda_1}$ and $\widehat{\lambda_2}$ be respectively the first and second eigenvalues of the operator $\mathcal{L}_\rho := -D\nabla^2 - \rho I$. Let $\mathcal{R}_\sigma(\phi)$, be defined by equation (2.15). Since $\rho(x) < \mu(x) - 2\underline{\nu}\varepsilon_0$ for all $x \in \Omega$, we get

$$\mathcal{R}_\rho(\phi) \geq \mathcal{R}_\mu(\phi) + 2\underline{\nu}\varepsilon_0,$$

for all $\phi \in G'$, where $G' := H^1(\Omega)$ in the bounded case and

$$G' := H^1_{per} = \left\{\varphi \ \in \ H^1_{loc}(\mathbb{R}^N) \text{ such that } \varphi \text{ is L}'\text{-periodic}\right\},$$

in the periodic case. Thus, by the classical min-max formula (2.16), it follows that

$$\widehat{\lambda_2} \geq \lambda_2 + 2\underline{\nu}\varepsilon_0 > 0. \tag{2.20}$$

Furthermore, from (2.19), 0 is an eigenvalue of the operator $\mathcal{L}_\rho$. Thus, (2.20) implies that $\widehat{\lambda_1} = 0$. As a consequence, q_δ is a principal eigenfunction of the operator $\mathcal{L}_\rho$. The principal eigenfunction characterisation thus implies that q_δ has a constant sign. Finally, we get that $p_{1,\delta}$ and $p_{2,\delta}$ do not intersect each other.

Let us now prove that equation (2.10) admits at most two significant solutions. Arguing by contradiction, we assume that there exist three significant (L$'$-periodic in the periodic case, for some $\text{L}' \in (0, +\infty)^N$) solutions $p_{1,\delta}$, $p_{2,\delta}$, and $p_{3,\delta}$ of (2.10). From the above result, we may assume, without loss of generality, that $p_{3,\delta} > p_{2,\delta} > p_{1,\delta} > \varepsilon_0$. Set $q_{2,1} := p_{2,\delta} - p_{1,\delta}$ and $q_{3,2} := p_{3,\delta} - p_{2,\delta}$, then these functions satisfy the equations

$$-D\nabla^2 q_{2,1} - \rho_{2,1}(x) q_{2,1} = 0, \tag{2.21}$$

and

$$-D\nabla^2 q_{3,2} - \rho_{3,2}(x) q_{3,2} = 0, \tag{2.22}$$

with $\rho_{2,1} := \mu(x) - \nu(x)(p_{1,\delta} + p_{2,\delta})$ and $\rho_{3,2} := \mu(x) - \nu(x)(p_{2,\delta} + p_{3,\delta})$. Moreover, $q_{2,1} > 0$ and $q_{3,2} > 0$. Thus 0 is the first eigenvalue of the operators $\mathcal{L}_{\rho_{2,1}} := -D\nabla^2 - \rho_{2,1} I$ and $\mathcal{L}_{\rho_{3,2}} := -D\nabla^2 - \rho_{3,2} I$ with either Neumann or L$'$-periodic boundary conditions.

From the strong maximum principle (together with Hopf's Lemma in the bounded case, and using the L$'$-periodicity of $q_{3,2}$ in the periodic case), we obtain the existence of $\theta > 0$ such that $q_{3,2} > \theta$. Since the operator $\mathcal{L}_{\rho_{3,2}}$ is self-adjoint, we have the following formula for its first eigenvalue $\widehat{\lambda_1}^{3,2}$,

$$\widehat{\lambda_1}^{3,2} = \min_{\phi \in G'} \mathcal{R}_{\rho_{3,2}}(\phi),$$

thus

$$\begin{aligned}\widehat{\lambda_1}^{3,2} = \min_{\phi \in G'} \left\{ \mathcal{R}_{\rho_{2,1}}(\phi) + \frac{\int_C \nu(p_{3,\delta} - p_{1,\delta})\phi^2}{\int_C \phi^2} \right\} &\geq \min_{\phi \in G'} \left\{ \mathcal{R}_{\rho_{2,1}}(\phi) \right\} + \underline{\nu}\theta, \\ &\geq \widehat{\lambda_1}^{2,1} + \underline{\nu}\theta,\end{aligned}$$

where $\widehat{\lambda_1}^{2,1}$ is the first eigenvalue of the operator $\mathcal{L}_{\rho_{2,1}}$. Since the first eigenvalues of the operators $\mathcal{L}_{\rho_{2,1}}$ and $\mathcal{L}_{\rho_{3,2}}$ are both 0, we deduce that $0 \geq 0 + \underline{\nu}\theta > 0$, hence a contradiction. Theorem 2.7 is proved. □

Proof of Corollary 2.8: Let p_δ be a significant L$'$-periodic solution of (2.10), and let $k \in \prod_{i=1}^N L_i\mathbb{Z}$. From the L-periodicity of the equation (2.10), $p_\delta(\cdot + k)$ is also a solution of (2.10). By periodicity of p_δ, the functions p_δ and $p_\delta(\cdot + k)$ intersect each other. Thus, from Theorem 2.7, since p_δ and $p_\delta(\cdot + k)$ are both L$'$-periodic, $p_\delta \equiv p_\delta(\cdot + k)$. Therefore, p_δ is a L-periodic function. □

Proof of Proposition 2.9: In the bounded case, when C is a convex domain with diameter d, it was proved in [24] that the second Neumann eigenvalue of Laplace operator ∇^2 was smaller than $\left(\frac{\pi}{d}\right)^2$. Thus, the second eigenvalue of $\mathcal{L}_0 = D\nabla^2$ on C is smaller than $D\left(\frac{\pi}{d}\right)^2$. Using formula (2.16), we obtain that the second eigenvalue of $\mathcal{L}_\mu$ in the bounded case satisfies $\lambda_2 \geq D\left(\frac{\pi}{d}\right)^2 - \max_C \mu$. Since $H^1_{per}(C)$ is a subset of $H^1(C)$, it also follows from (2.16) that the second eigenvalue in the periodic case is larger than in the bounded case. Thus, in both cases $\lambda_2 \geq D\left(\frac{\pi}{d}\right)^2 - \max_C \mu$. In the periodic case d is the length of the longest diagonal of the period cell C. This proves the point (i) and the first part of (ii).

In the bounded case, when C is no more assumed to be convex, there exists a ball $B_{d'}$, of diameter d', such that $C \subset B_{d'}$. The formula (2.16) then implies that the second eigenvalue of the operator $\mathcal{L}_\mu$ on the set $B_{d'}$ is smaller than on the set C. This concludes the proof of Proposition 2.9. $\square$

Proof of Theorem 2.10, Part (i): Let λ_1 and ϕ be defined by (2.8), and let κ be a nonnegative real number such that $\kappa > \varepsilon_0$. Then we have

$$\begin{aligned} -D\nabla^2(\kappa\phi) - \kappa\phi(\mu(x) - \kappa\phi\nu(x)) + \delta h(x)\rho_\varepsilon(\kappa\phi) &\leq \lambda_1\kappa\phi + \kappa^2\phi^2\nu(x) + \delta \\ &\leq \kappa\phi(\lambda_1 + \kappa\phi\nu(x)) + \delta \\ &\leq \max_{\tau\in I}\{\tau(\lambda_1 + \tau\overline{\nu})\} + \delta, \end{aligned} \tag{2.23}$$

where $I = \{\kappa\phi(x),\ x \in C\}$. Setting $g(\tau) := \tau(\lambda_1 + \tau\overline{\nu})$, since $\|\phi\|_\infty = 1$, and since g is a convex function, it follows from (2.23) that

$$-D\nabla^2(\kappa\phi) - \kappa\phi(\mu(x) - \kappa\phi\nu(x)) + \delta h(x)\rho_\varepsilon(\kappa\phi) \leq \max\{g(\kappa), g(\kappa\underline{\phi})\} + \delta. \tag{2.24}$$

Let us take κ_0 be such that $g(\kappa_0) = g(\kappa_0\underline{\phi})$, namely $\kappa_0 = -\dfrac{\lambda_1}{\overline{\nu}(1+\underline{\phi})}$ (note that $\kappa_0\phi > \varepsilon$). We get

$$-D\nabla^2(\kappa_0\phi) - \kappa_0\phi(\mu(x) - \kappa_0\phi\nu(x)) + \delta h(x) \leq -\frac{\lambda_1^2\underline{\phi}}{\underline{\nu}(1+\underline{\phi})^2} + \delta \leq 0, \tag{2.25}$$

from the hypothesis on δ of Theorem 2.10, Part (i). Therefore, $\kappa_0\phi$ is a subsolution of (2.10) with either L-periodic or Neumann boundary conditions. Moreover, if M is a large enough constant, M is a supersolution of (2.10) with L-periodic or Neumann boundary conditions. Thus, it follows from a classical iterative method that there exists a solution $\underline{p_\delta}$ of (2.10), with the required boundary conditions, and which satisfies $\kappa_0\phi \leq \underline{p_\delta} \leq M$ in Ω. Moreover, in the periodic case, since $\kappa_0\phi$ and M are L-periodic and since the equation (2.10) is also L-periodic, it follows that p_δ is L-periodic. Theorem 2.10, Part (i) is proved. $\square$

Proof of Theorem 2.10, Parts (ii), (iii) and (iv): Assume that $\lambda_1 < 0$, $\delta > \delta_2$ and that there exists a positive bounded solution p_δ of (2.10) which is not remnant, i.e.

$$\text{there exists } x_0 \text{ with } p_\delta(x_0) \geq \varepsilon_0. \tag{2.26}$$

Since ϕ is bounded from below away from 0 and p_δ is bounded, we can define

$$\gamma^* = \inf \{\gamma > 0,\ \gamma\phi > p_\delta \text{ in } \Omega\} \geq 0. \tag{2.27}$$

As $\|\phi\|_\infty$=1, it follows from (2.26) that $\gamma^* \geq \varepsilon_0$. Thus,

$$\gamma^*\phi \geq \varepsilon_0 \underline{\phi} = \varepsilon. \tag{2.28}$$

Therefore we have the following inequality,

$$-D\nabla^2(\gamma^*\phi) - \gamma^*\phi(\mu(x) - \gamma^*\phi\nu(x)) + \delta h(x)\rho_\varepsilon(\gamma^*\phi) \geq \gamma^*\phi(\lambda_1 + \gamma^*\phi\nu(x)) + \delta\alpha,$$

on Ω, and, since if $\lambda_1 < 0$ and $\delta > \delta_2$,

$$-D\nabla^2(\gamma^*\phi) - \gamma^*\phi(\mu(x) - \gamma^*\phi\nu(x)) + \delta h(x)\rho_\varepsilon(\gamma^*\phi) \geq -\frac{\lambda_1^2}{4\underline{\nu}} + \delta\alpha > 0, \tag{2.29}$$

on Ω. Therefore, $\gamma^*\phi$ is a supersolution of (2.10). Set $z := \gamma^*\phi - p_\delta$. Then $z \geq 0$, and there exists a sequence $(x_n)_{n\in\mathbb{N}}$ in Ω such that $z(x_n) \to 0$ as $n \to +\infty$.

In the bounded case, up to the extraction of some subsequence, $x_n \to \overline{x} \in \Omega$ as $n \to +\infty$. By continuity, $z(\overline{x}) = 0$. Moreover, subtracting (2.10) to (2.29), we get

$$-D\nabla^2 z - b(x)z > 0 \text{ in } \Omega, \tag{2.30}$$

for some bounded function b. Using the strong elliptic maximum principle and the Hopf Lemma, we obtain $z \equiv 0$, thus $\gamma^*\phi \equiv p_\delta$ is a positive solution of (2.10), which in contradiction with (2.29).

In the periodic case, we must also consider the situation where the sequence $(x_n)_{n\in\mathbb{N}}$ is not bounded. Let $(\overline{x}_n) \in \overline{C}$ be such that $x_n - \overline{x}_n \in \prod_{i=1}^N L_i\mathbb{Z}$. Up to the extraction of some subsequence, we can assume that there exists $\overline{x}_\infty \in \overline{C}$ such that $\overline{x}_n \to \overline{x}_\infty$ as $n \to +\infty$. Set $\phi_n(x) = \phi(x + x_n)$ and $p_{\delta,n}(x) = p_\delta(x + x_n)$. From standard elliptic estimates and Sobolev injections, it follows that (up to the extraction of some subsequence) $p_{\delta,n}$ converge in $W^{2,\tau}_{loc}$, for all $1 \leq \tau < \infty$, to a function $p_{\delta,\infty}$ satisfying

$$-\nabla^2(Dp_{\delta,\infty}) - p_{\delta,\infty}(\mu(x + \overline{x}_\infty) - p_{\delta,\infty}\nu(x + \overline{x}_\infty)) + \delta h(x + \overline{x}_\infty)\rho_\varepsilon(p_{\delta,\infty}) = 0,$$

in $\mathbb{R}^N$, while $\gamma^*\phi_n$ converges to $\gamma^*\phi_\infty := \gamma^*\phi(\cdot + \overline{x}_\infty)$, and

$$-\nabla^2(D\gamma^*\phi_\infty) - \gamma^*\phi_\infty(\mu(x + \overline{x}_\infty) - \gamma^*\phi_\infty\nu(x + \overline{x}_\infty)) + \delta h(x + \overline{x}_\infty)\rho_\varepsilon(\gamma^*\phi_\infty) > 0,$$

in $\mathbb{R}^N$. Let us set $z_\infty(x) := \gamma^*\phi_\infty(x) - p_{\delta,\infty}(x)$. Then $z_\infty(x) = \lim_{n\to+\infty} z(x+x_n)$, therefore $z_\infty \geq 0$ and $z_\infty(0) = 0$. Moreover, there exists a bounded function b_∞ such that

$$-D\nabla^2 z_\infty - b_\infty z_\infty > 0 \text{ in } \mathbb{R}^N. \tag{2.31}$$

It then follows from the strong maximum principle that $z_\infty \equiv 0$ and we again obtain a contradiction. Finally, we necessarily have $p_\delta \leq \varepsilon_0$, and the proof of Theorem 2.10, Part (ii) is complete. Parts (iii) and (iv) can be proved with similar arguments. □

Proof of Theorem 2.11, Part (i): Assume that $\delta \leq \delta^*$. Let p_δ be the unique maximal significant solution defined in the proof of Theorem 2.10, Part (i). Then, from Lemma 2.12,

$$p_\delta(x) \leq p_0(x) = u(0,x) \ \forall\ x \ \in \ \Omega, \tag{2.32}$$

which implies

$$p_\delta(x) \leq u(t,x) \text{ in } \mathbb{R}_+ \times \Omega, \tag{2.33}$$

since p_δ is a stationary solution of (2.5). Moreover, since p_0 is a supersolution of (2.10), u is nonincreasing in time t, and standard parabolic estimates imply that u converges in $W^{2,\tau}_{loc}(\Omega)$, for all $1 \leq \tau < \infty$, to a bounded stationary solution u_∞ of (2.5). Furthermore, from (2.33) we deduce that $p_\delta \leq u_\infty \leq p_0$. Since p_δ is the maximal positive solution of (2.10), it follows that $u_\infty \equiv p_\delta$. Moreover, in the periodic case, since p_0 and the equation (2.5) are L-periodic, $u(t,x)$ is also L-periodic in x. Therefore the convergence is uniform in Ω. Part (i) of Theorem 2.11 is proved. □

Proof of Theorem 2.11, Parts (ii) and (iii): Assume that $\delta > \delta^*$. Since 0 is a stationary solution of (2.5) and $u(0,x) = p_0 > 0$, we obtain that $u(t,x) > 0$ in $\mathbb{R}^+ \times \Omega$, and again, from standard parabolic estimates, we know that u converges in $W^{2,\tau}_{loc}(\Omega)$ (for all $1 \leq \tau < \infty$) to a bounded stationary solution $\underline{u_\infty} \geq 0$ of (2.5) as $t \to +\infty$. Moreover, in the periodic case, from the L-periodicity of the initial data and of the equation (2.5), we know that $u(t,\cdot)$ and $\underline{u_\infty}$ are L-periodic. Therefore the convergence is uniform in Ω. It follows from Theorem 2.6, Part (ii) that $\underline{u_\infty}$ cannot be a significant solution of (2.10). Moreover, if $\delta > \delta_2$, Theorem 2.10, Part (ii) ensures that $\underline{u_\infty}$ is a remnant solution of (2.10). □

3 Numerical investigation of the effects of the environmental fragmentation

We propose here to apply our results concerning the estimation of the maximal sustainable yield with respect to environmental fragmentation. We show that, firstly, the gap $\delta_2 - \delta_1$, obtained from (2.17) and Theorem 2.10, remains small whatever the degree of fragmentation is. This gap corresponds to the values of the harvesting quota δ for which we do not know whether the population density will converge to a significant or a remnant solution of the stationary equation (2.10), practically speaking. Secondly, we show that there is a monotone increasing relation between the maximal sustainable yield δ^* and the habitat aggregation.

In order to lessen the boundary effects, and to focus on fragmentation, we placed ourselves in the periodic case. For our numerical computations, we assumed that the environment was made of two components, favourable and unfavourable regions. It is expressed in the model (2.5) through the coefficient $\mu(x)$, which takes two values μ^+ or μ^-, depending on the space variable x. We also assumed that

$$\mu^+ > \mu^-, \ \nu(x) \equiv 1, \ h(x) \equiv 1 \text{ and } D = 1.$$

Using a stochastic model for landscape generation [28], we built 2000 samples of binary environments, on the 2-dimensional period cell $C = [0,1]^2$, with different degrees of fragmentation. In all these environments, the favourable region, where $\mu(x) = \mu^+$, occupies 20% of the period cell. The environmental fragmentation was defined as follows. We discretised the cell C into $n_C = 50 \times 50$ equal squares C_i. The lattice made of the cells C_i was equipped with a 4-neighbouring system $V(C_i)$ (see Fig. 1), with toric conditions. On each cell C_i, we assumed that the function μ either took the value μ^+ or μ^-, while the number $n_+ = \text{card}\{i, \mu \equiv \mu^+ \text{ on } C_i\}$ was fixed to $n_C \times \frac{20}{100} = 125$. For each landscape sample ω , we set $s(\omega) = \frac{1}{2} \sum_{C_i \subset C} \sum_{C_j \in V(C_i)} \mathbb{1}\{\mu(C_j) = \mu(C_i)\}$, the number of pairs of similar neighbours (C_i, C_j) such that μ takes the same value on C_i and C_j ($\mathbb{1}\{\cdot\}$ is the indicator function). The number $s(\omega)$ is directly linked to the environmental fragmentation: a landscape pattern is all the more aggregated as $s(\omega)$ is high, and all the more fragmented as $s(\omega)$ is small (Fig. 2). Thus, we shall refer to s as the "habitat aggregation index".

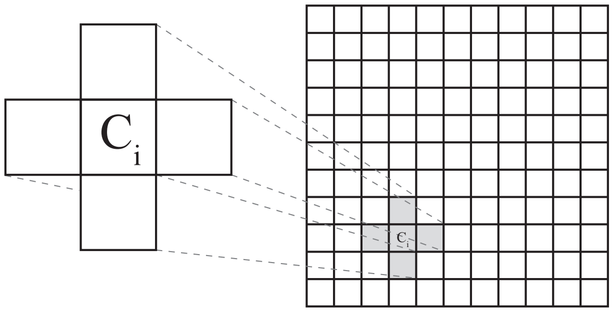
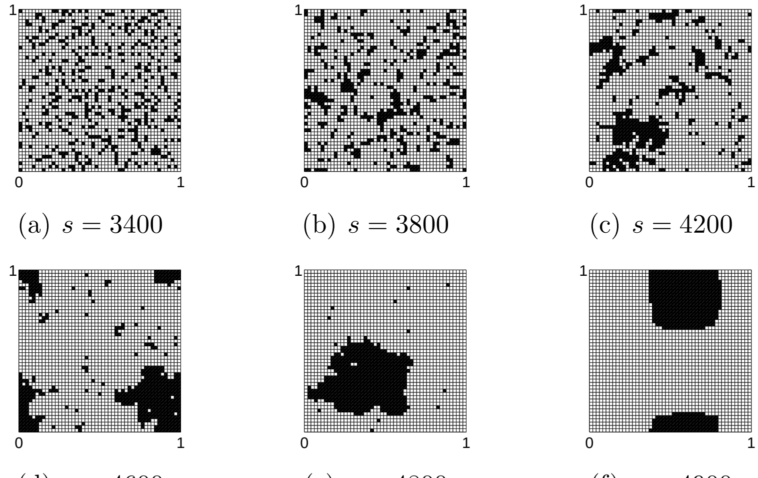


Figure 1: The 4-neighbourhood system: an element C_i of C and its four neighbours.



(a) $s = 3400$ (b) $s = 3800$ (c) $s = 4200$

(d) $s = 4600$ (e) $s = 4800$ (f) $s = 4900$

Figure 2: Some samples of the landscapes used for the computations of δ_1 and δ_2, with different values of the habitat aggregation index s. The black areas correspond to more favourable environment, where $\mu(x) = \mu^+$.

For our computations, we took $\mu^+ = 10$ and $\mu^- = 0$, and we computed the corresponding values of λ_1^i, δ_1^i and δ_2^i on each landscape sample ω^i of aggregation index s^i, for $i = 1 \dots 2000$. The eigenvalues λ_1^i were computed with a finite elements method. We fitted the data sets $\{(s^i, \delta_1^i)\}_{i=1\dots 2000}$ and $\{(s^i, \delta_2^i)\}_{i=1\dots 2000}$ using ninth degree polynomials (it is enough to assess if the relations between s and δ_1, δ_2 tend to be monotonic or not). The resulting fitted curves $\delta_{1,f}$ and $\delta_{2,f}$ are presented in Fig. 3. Under the assumption of normally distributed values of δ_1 and δ_2 for fixed s values, we computed a lower prediction bound ($\delta_{1,lo}$) for new observation of δ_1 and an upper prediction bound for δ_2 ($\delta_{2,up}$), with a level of certainty of 99%. Thus, given a configuration ω, with a fixed value of s, when δ is smaller than $\delta_{1,lo}$, we take a 0.5% chance of being above δ_1, while when δ is smaller than $\delta_{2,up}$, we take a 0.5% chance of being below δ_2. The small thickness of the intervals $(\delta_{1,lo}, \delta_{2,up})$ emphasises the quality of the relationship between the habitat aggregation index s and the maximum sustainable yield $\delta^* \in [\delta_1, \delta_2]$. This also indicates that the criteria of Theorems 2.10 and 2.11 are close to be optimal, at least in some situations.

Furthermore, as we can observe, the values of δ_1 and δ_2 tend to increase as s increases, and thus as the environment aggregates. Since $\delta^* \in [\delta_1, \delta_2]$, we deduce from the computations represented in Fig. 3 that δ^* tends to increase with environmental aggregation.

These tests were performed for particular values of μ^+ and μ^-. However, the thickness of the interval (δ_1, δ_2) can be determined for all values of μ^+, μ^- without further numerical computations, provided that $\mu^+ - \mu^- = 10$. Indeed, let us set $B := \mu^+ - \mu^-$, and for a fixed value of B, let $\mu_0(x)$ be a given L-periodic function in $L^\infty(\mathbb{R}^N)$ taking only the two values $\mu_0^+ = B$ and $\mu_0^- = 0$. Let $\lambda_{1,0}$ be the first eigenvalue of the operator $-\nabla^2 - \mu_0 I$ on C, with L-periodicity conditions, ϕ_0 the associated eigenfunction with minimal value $\underline{\phi_0}$ and

$$\delta_{1,0} := \frac{\lambda_{1,0}^2 \underline{\phi_0}}{(1 + \underline{\phi_0})^2} \text{ and } \delta_{2,0} := \frac{\lambda_{1,0}^2}{4}.$$

We have the following proposition.

Proposition 3.1 *Assume that $\mu(x) = \mu_0(x) + \mu^-$, with $\mu^- > \lambda_{1,0}$. Let δ_1 and δ_2 be defined by (2.17). Then we have* $\delta_2 - \delta_1 = \left(1 - \dfrac{\mu^-}{\lambda_{1,0}}\right)^2 (\delta_{2,0} - \delta_{1,0})$.

This result also indicates that the information on δ^* is all the more precise as

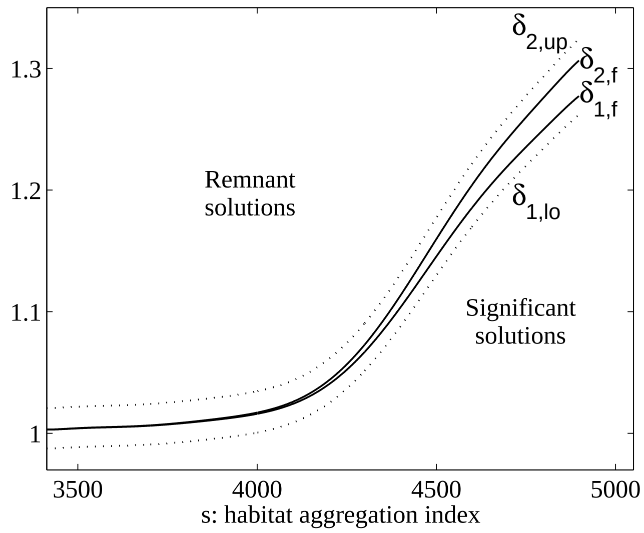


Figure 3: Solid lines: $\delta_{1,f}$ and $\delta_{2,f}$ correspond respectively to the data sets $\{(s^i, \delta_1^i)\}_{i=1...2000}$ and $\{(s^i, \delta_2^i)\}_{i=1...2000}$, fitted with ninth degree polynomials. Dashed lines: $\delta_{1,lo}$ is a lower prediction bound for new observations of δ_1 and $\delta_{2,up}$ an upper prediction bound for new observations of δ_2, with in both cases a level a certainty of 99%.

the growth rate function takes low values. However, the "relative thickness" of the interval (δ_1, δ_2), compared to δ_1, $\frac{\delta_2 - \delta_1}{\delta_1}$, does not depend on μ^-, as is can be easily noticed.

Proof of Proposition 3.1: The relation $\lambda_1[\mu(x)] = \lambda_{1,0} - \mu^-$ is a direct consequence of the uniqueness of the first eigenvalue λ_1. We assume that $\mu^- > \lambda_{1,0}$, so that $\lambda_1[\mu(x)] < 0$. From the uniqueness of the eigenfunction ϕ associated to λ_1, it also follows that ϕ does not depend on μ^-. Therefore, δ_1 and δ_2 satisfy $\delta_1 = \frac{(\lambda_{1,0} - \mu^-)^2 \underline{\phi_0}}{(1 + \underline{\phi_0})^2}$ and $\delta_2 = \frac{(\lambda_{1,0} - \mu^-)^2}{4}$. The result immediately follows. $\Box$

4 A few comments on the spatially-explicit proportional harvesting model

In this model, the population density u is governed by the following equation

$$u_t = D\nabla^2 u + u(\mu(x) - \nu(x)u) - q(x)u, \ x \ \in \ \Omega, \tag{4.34}$$

with L-periodicity of the functions $\mu(x)$, $\nu(x)$ and $q(x)$ in the periodic case, and with Neumann or Dirichlet boundary conditions in the bounded case. Thus, setting

$$\tau(x) := \mu(x) - q(x),$$

this model is equivalent to the SKT model (1.3). Hence, many properties of the solutions of this model are described in the existing literature. In particular the existence, nonexistence and uniqueness results of Theorems 2.2 and 2.4 apply. The condition $\lambda_1[\mu(x) - q(x)] < 0$ is therefore necessary and sufficient for species persistence. Furthermore, the theoretical results of [7], [11], [27] on the effects of habitat arrangement on species persistence are also true for this model.

For instance, when the function $\mu(x)$ is constant, with $\mu(x) \equiv \mu_1 > 0$, and if the domain Ω is convex and symmetric with respect to each axis $\{x_1 = 0\}, ..., \{x_N = 0\}$, the following result is a straightforward consequence of the paper [7],

Theorem 4.1 *(i) In the periodic case,* $\lambda_1[\mu_1 - q_k^*(x)] \leq \lambda_1[\mu_1 - q(x)]$.

(ii) In the bounded Dirichlet case, $\lambda_1[\mu_1 - q_k^*(x)] \leq \lambda_1[\mu_1 - q(x)]$,

(iii) In the bounded Neumann case, if Ω is a rectangle, $\lambda_1[\mu_1 - q_k^\sharp(x)] \leq \lambda_1[\mu_1 - q(x)]$.

where q_k^* denotes the symmetric decreasing Steiner rearrangement of the function q with respect to the variable x_k, and $q_k^\sharp$ denotes the monotone rearrangement of q with respect to x_k (see [7] and [9] for the definition of these rearrangements). These rearrangements of a function q not only preserve its mean value, but also its distribution function. This means that if, for instance, q corresponds to a "patch" function taking the values q_1, q_2 and q_3 in some regions A_1, A_2 and A_3 respectively, with $A_1 + A_2 + A_3 = |C|$, then the areas of the regions where the rearranged function q^* of $q^\sharp$ takes the value q_1, q_2 and q_3 remain equal to A_1, A_2 and A_3 respectively.

Theorem 4.1, combined with Theorem 2.4 say that the spatially rearranged harvesting strategies are better for species survival. This result can be helpful from a resource management point of view. Indeed, the authorities can rearrange the position of the harvested areas in order to improve the chances of population persistence. The result of Theorem 4.1 shows that, in the framework of these models, the creation of a large reserve gives more chance of persistence than the creation of several small reserves, and is in accordance with the former results of [18] and [20] in the Dirichlet case. See Fig. 4 for some illustrations in the bounded case with Dirichlet and Neumann boundary conditions.

5 Discussion

We have proposed a model for studying populations in heterogeneous environments, submitted to an external negative forcing term, which corresponds to a quasi-constant-yield harvesting. The introduction of a "regularised Heaviside" term $\rho_\varepsilon(u)$, which multiplies the constant-yield harvesting term $\delta h(x)$, enabled us to guarantee the nonnegativity of the solutions of our model, and thus its actuality.

We carried out new mathematical results on the elliptic equation satisfied by the stationary states of the model, and on the associated parabolic equation. Both qualitative and quantitative results were obtained. On the qualitative standpoint, we described the behaviour of the solutions of the model in terms of the amplitude δ of the harvest function. Two main types of solutions were found: the remnant solutions, which are always below a fixed small threshold, and therefore close to 0, and the significant solutions, which are

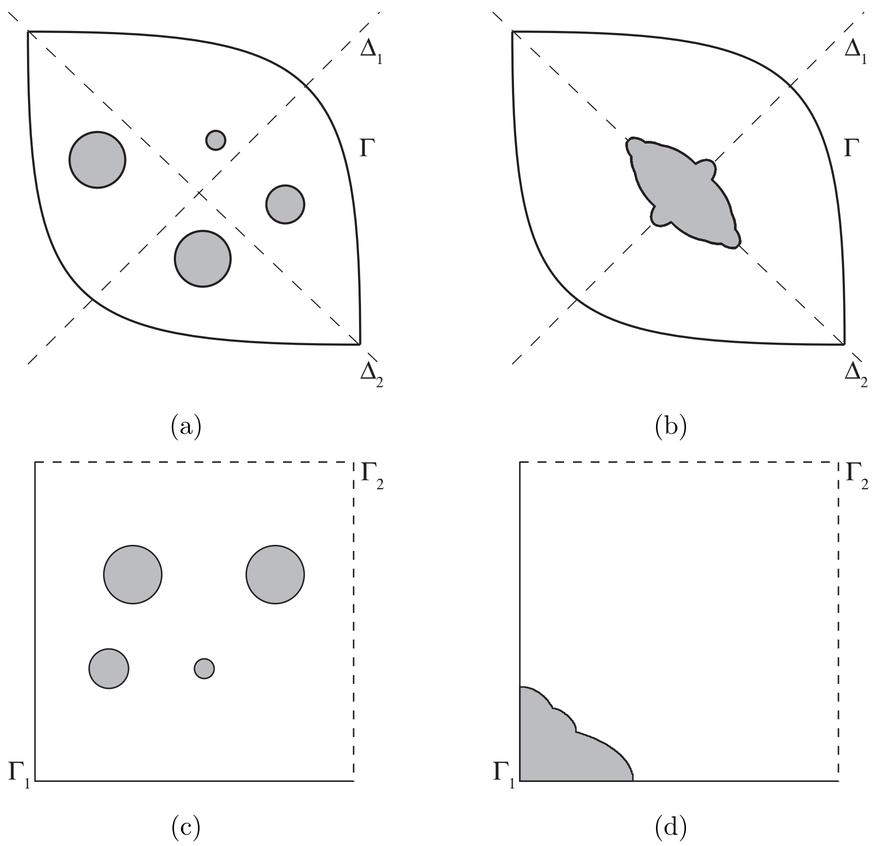


Figure 4: Examples of applications of Theorem 4.1, Parts (ii) and (iii) to reserves management. In the figures (a) and (b), the boundary Γ of Ω is lethal (Dirichlet boundary conditions). (a): The initial effort function $q(x)$ takes two values, $q^+ > 0$ in the white area and $q^- = 0$ in the shadowed regions, which correspond to reserves. (b): Position of the reserves after a symmetric decreasing Steiner rearrangement along the Δ_1 and Δ_2 axes, successively. The rearranged configuration (b) always give more chances of species persistence. In the figures (c) and (d), the boundary Γ is divided into two parts: $\Gamma = \Gamma_1 \cup \Gamma_2$. Γ_1 is represented with a solid line and can correspond to a coast, while Γ_2 is represented with a dashed line, and can correspond to a non-physical limit that the species cannot cross (Neumann boundary conditions). (c): The effort function $q(x)$ again takes two values, $q^+ > 0$ in the white area and $q^- = 0$ in the reserves. (d): Position of the reserves after monotone rearrangement along the horizontal and vertical axes, successively. The chances of persistence are better in the rearranged configuration (d).

always above this threshold, and guarantee a constant yield. We discussed the maximum possible number of significant solutions, which was found to be equal to 2, under an hypothesis of positivity of the second eigenvalue of the linearized around the steady state 0, of the (time independent part of the) SKT-model. We established quantitative formula for some thresholds δ_1 and δ_2 such that a population density initially driven by the SKT model converges to a significant solution if an harvesting quota $\delta \leq \delta_1$ is applied, whereas it decreases to a remnant solution if $\delta \geq \delta_2$. The quantitative aspects of our study essentially consisted in discussing the effect of environmental heterogeneity on the long time behaviour of the population density. Namely, computing the values of δ_1 and δ_2 on 2000 samples of stochastically obtained patchy environments, with different levels of fragmentation we found a monotone increasing relationship between these two coefficients and an environmental aggregation index s. This indicates that, for given areas of favourable and unfavourable regions, the harvesting quota that a species can sustain while guaranteeing and time-constant yield is higher when the favourable regions are aggregated.

The reader may note that, in our model, the species mobility is not affected by the environmental heterogeneity. These effects could be modelled by using a more general dispersion term, of the form $\nabla \cdot (A(x)\nabla u)$, instead of $D\nabla^2 u$, where $A(x)$ stands for the diffusion matrix (see [7], [30]). In fact, most of our results still work when the matrix A is of class $C^{1,\alpha}$ (with $\alpha > 0$) and uniformly elliptic; i.e. when there exists $\tau > 0$ such that $A(x) \geq \tau I_N$ for all $x \in \Omega$. Indeed, Theorems 2.2, 2.4, 2.7, 2.10, 2.11 remain true under this more general assumption. However, the effects of environmental heterogeneity may differ, depending on the way $A(x)$ and $\mu(x)$ are correlated (see [16]). The results of § 4 on the effects of the arrangements of the harvested regions in the proportional harvesting case may also not be valid with this dispersion term. However, in situations where $A(x)$ takes low values (slow motion) when $q(x)$ is low ("reserves", see § 4), as underlined in [27], a simultaneous rearrangement of the functions $A(x)$ and $q(x)$ leads to lower λ_1 values and therefore to higher chances of species survival.

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