

A CONTINUOUS SIZE-STRUCTURED RED CORAL GROWTH MODEL

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The aim of this paper is to derive and analyse the mathematical properties of a new continuous size-structured model for red coral (*Corallium rubrum*, L.) growth. Since historical Leslie models⁴ are often used to deal with some ecological problems, a new approach is here proposed and give some promising results. The main advantage of using continuous model is that we hope to describe precisely the mass mortality events, observed in Mediterranean sea, and its consequences on red coral dynamics. Simulations studies allow us to qualitatively discuss some questions about red coral populations dynamics. The development of this method should be useful for the study of the conservation of red coral populations.

Keywords: Population dynamics; size-structured continuous model; asymptotic analysis; conservation biology.

1. Introduction

The analysis of the consequences of environmental changes on the dynamics of natural populations takes advantage of modelling studies. For example the development of specific models may allow to evaluate the extinction risks of populations under various hypotheses (see examples in⁸). Such approaches may be particularly useful for the study of long lived marine invertebrates for which populations dynamics may take place at large time scales. Moreover the actual climate change

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and the increasing human impact raises important questions about the resilience and the conservation of the associated ecosystems, as in the case of coral reefs⁷ or of Mediterranean hard-substrate communities¹⁴. Some models have already been developed for some species in order to describe the growth and structure of individual colonies of tropical corals¹². These models were based on growth rate, nutrient transport and the hydrodynamics of the flow with different structure (more or less compact) for the coral. Other works dealt with some branching model using parameters and variables related to some special modular coral species¹⁶, on the calcification phenomenon¹⁰ or with the analysis of tropical coral populations dynamics^{9, 2}.

Such models are rare concerning Mediterranean sessile invertebrates such as the gorgonian red coral (*Corallim rubrum*, *L.*). This emblematic and patrimonial species is heavily exploited and has been affected by mass mortality events in the summers 1999 and 2003 along the coasts of Provence⁶. These events are probably linked with climate change¹⁵ and their potential repetitions might hinder the conservation of populations of this long-lived species with potentially low dispersal abilities¹⁹.

The main consequence of this mass mortality was the variable necrosis of some branches of the colony and their breaking. Moreover the exploitation of red coral for jewellery leads to the destruction or breaking of the largest colonies. The remaining population has thus an inferior size which may have a negative impact on population growth or persistence.

A continuous model of red coral growth is proposed in this paper taking into account possible mass mortality events and their consequences. The mathematical tools used for this model are differential systems for the whole red coral population (*i.e.* the number of coral branches) $n(t, l)$ depending on time t and on the size of branches l . Continuous model is here considered since historically Leslie-Lewis matrix transition of population growth have been frequently used^{17, 1} in ecology. This should enable us to describe more precisely the mass mortality and the impact on the red coral population dynamics.

We start by modelling the probability of break-up of one coral branch by estimating the connection between the size of a branch and its diameter. This would allow to take mass mortalities into account simply by rendering the branches weaker (with a smaller diameter). This leads us to a precise but rather complicated model which is simplified by assuming a low probability of break-up.

We then analyze the model that we obtained both mathematically and numerically.

2. The derivation of the model

2.1. Modelling one coral branch

Let us first consider only one coral branch. It begins with a very short length corresponding to one individual at time s .

Its length will then increase until the first break-up and its diameter regularly

increase too ring by ring (more or less one by year ¹¹). The size of this ring typically depends on the external conditions (an increase in temperature or low food) meaning that at a particular point of the branch length the diameter will also typically increase ^{11 18}.

Denote by $L(t, s)$ the length of the branch and $\delta(t, l, s)$ the diameter at distance $l \leq L(t)$ from the beginning. We will assume a linear growth of the branch (which seems reasonable) such that ³

$$L(t, s) = \sigma(t - s), \quad \text{for } t \geq s. \quad (2.1)$$

There is no need to be so specific for the growth rate of the diameter since as we said before, it may depend on external conditions. Consequently we take

$$\delta(t, l, s) = \delta_0 + \int_{s+l/\sigma}^t I(r) dr. \quad (2.2)$$

The integral is taken from $s + l/\sigma$ which is the time r such that $L(r) = l$. The function of time I represents the external conditions and in the simplest case would be taken constant with

$$\delta(t, l, s) = \delta_0 + I(t - s - l/\sigma). \quad (2.3)$$

Our main assumption concerns the probability of break-up of the branch at the point at a distance l . This break-up could be due to exploitation, necrosis caused by bacteria or a temperature increase as we said before. Focus on necrosis phenomenon, we assume that the flow of water around the branch is a shear flow and hence that the velocity of the water at a point l of the branch is proportional to l . If the flow has a small Reynolds number, it is reasonable to take a drag force at this point proportional to the velocity times the diameter.

Of course it would be illusory to try to compute exactly the distribution of mechanical strain along the coral branch. First of all its mechanical properties are mainly unknown and then our assumptions on the shape of the branch and the forces acting on it are such that the result would probably still be far from exact.

Instead let us make a very rough assumption, namely that the strain at one point l is proportional to the sum of forces applied on the part of the branch above l

$$\int_l^{L(t,s)} \delta(t, l', s) l' dl'.$$

This makes the strain vanish at the end of the branch ($l = L$) and it is maximal at the bottom $l = 0$ so it is not all together unreasonable. This should be multiplied by the corresponding physical constants but as this computation is only heuristic, we will not mention them.

The resistance of the branch at l is proportional to d^2 and we simply assume that the probability of break-up is proportional to the ratio between the strain and

the resistance

$$p(t, l, s) = \alpha \frac{1}{(\delta(t, l, s))^2} \int_l^{L(t, s)} \delta(t, l', s) l' dl'. \quad (2.4)$$

After a branch broke at a position l , it will start to grow again, both in length and in diameter. The new part of the branch will however have an initial diameter of δ_0 and (2.2) is therefore no longer true along all the branch.

Therefore consider a branch which broke k times: At time s_1 and position l_1 , then at time $s_2 > s_1$ and position l_2 and so on until time s_k and position l_k . The times are of course increasing $s_1 < s_2 < \dots < s_k$ but in fact we may also assume that the positions are increasing.

Indeed consider the case of a branch with a first break-up at s_1 and l_1 and a second at $s_2 > s_1$ and $l_2 < l_1$. Its length and diameter after s_2 is exactly the same as a branch with only one break-up at time s_2 and position l_2 .

Now taking $l_1 < l_2 < \dots < l_k$ with have for $t > s_k$

$$L(t, s, s_1, l_1, \dots, s_k, l_k) = l_k + \sigma(t - s_k), \quad (2.5)$$

and

$$\delta_k(t, l, s, s_1, l_1, \dots, s_k, l_k) = \delta_0 + \int_{s_i + (l - l_i)/\sigma}^t I(r) dr, \quad \text{for } l_i \leq l < l_{i+1}, \quad (2.6)$$

with the convention $l_0 = 0$ and $l_{k+1} = L(t)$.

Finally and according to the remark, we define δ_k when l_1, \dots, l_k is not increasing as follows. We extract $l_{\Sigma(1)}, \dots, l_{\Sigma(k')}$ such that this sequence is the longest increasing sequence that may be extracted from $l_1 \dots l_k$. Then we pose

$$\delta_k(t, l, s, s_1, l_1, \dots, s_k, l_k) = \delta_{k'}(t, l, s, s_{\Sigma(1)}, l_{\Sigma(1)}, \dots, s_{\Sigma(k')}, l_{\Sigma(k')}). \quad (2.7)$$

2.2. A first model with many branches

The first difficulty is to describe statistically a very large number of branches. Let us remark that these branches can describe more than only one colony. Here, the total number of branches considered in a parcel is modelled. Then let us denote by $n_k(t, l, s, s_1, l_1, \dots, s_k, l_k)$ the density of colonies with total length l at time t , being new at time $s < t$ and having had k break-up at times $s_1 < \dots < s_k$ and at corresponding positions l_1, \dots, l_k .

Let us now write down the equations satisfied by the n_k , starting by the one for $n_0(t, l, s)$

$$\partial_t n_0 + \sigma \partial_l n_0 = -(d + S_0(t, l)) n_0(t, s, l), \quad (2.8)$$

where d is the death rate of a colony (assumed to be constant and independent of the length or age of the colony to be simple) and $S_0(t, l)$ is the break-up probability of a branch of size l with no previous break-up namely

$$S_0(t, l) = \alpha \int_0^l p(t, l', t - l/\tau) dl', \quad (2.9)$$

with p given by (2.4) and δ by (2.2). In this case the age of the colony is simply of course l/τ . Note that if I does not depend on time, then S is also independent of time.

The equation for n_k with $k \geq 1$ is of course more complicated

$$\begin{aligned} \partial_t n_k + \sigma \partial_l n_k = & -dn_k - \alpha n_k \int_0^l \frac{\int_{l'}^l \delta_k(t, l'', \dots) l'' dl'' dl'}{(\delta_k(t, l', s, s_1, \dots, l_k))^2} \\ & + \alpha \int_l^\infty n_{k-1}(t, l', s, s_1, \dots, l_{k-1}) \frac{\int_{l_k}^{l'} \delta_{k-1}(t, l'', s, s_1, \dots, l_{k-1}) l'' dl''}{(\delta_{k-1}(t, l_k, s, s_1, \dots, l_{k-1}))^2} dl' \end{aligned} \quad (2.10)$$

The term $-dn_k$ is the mortality, the next term counts how many branches of n_k breaks (and therefore go to another population). The third term in the right hand side takes into account the branches of n_{k-1} (having had $k-1$ break-up) which splits once more after their last break-up position. The δ_k are given by formulas (2.6) and (2.7).

These equations have to be supplemented by conditions on the border $l=0$, which are for $k \geq 1$

$$n_k(t, 0, \dots) = 0, \quad (2.11)$$

as no new part of the colony may already have had a break-up. For n_0 the condition is

$$\begin{aligned} n_0(t, 0, s) = \delta(t-s) \sum_{k=0}^{\infty} \int_{0 < s' < s_1 < \dots < s_k < t} \int_{0 < l_1 < \dots < l_k < l} & B n_k(t, l, s', s_1, l_1, \dots, s_k, l_k) \\ & dl_1 \dots dl_k dl ds' ds_1 \dots ds_k. \end{aligned} \quad (2.12)$$

This represents all the new branches appearing in a parcel, with a birth rate B which could depend on all the parameters of the colonies. Notice that the Dirac mass $\delta(t-s)$ simply ensures that a new branch born at time t is indeed registered as such.

2.3. A simplified model

The set of equations (2.8),(2.10) is quite complicated and in addition there is an infinite number of them. This would make studying or numerically compute solutions to this system quite challenging.

Instead we propose to derive a simplified model by assuming that the initial diameter δ_0 is much smaller than the average diameter some time later.

Consider the case of constant environmental conditions and let us precise the range of values of the parameters for which this is correct. Take one branch with no break-up yet (or the part of the branch which did not split yet), with length L at time t ; It was created at time $t-L/\sigma$ and so

$$\delta(t, l) = \delta_0 + \frac{I}{\sigma}(L-l).$$

The probability of break-up at l is then

$$p = \frac{\alpha}{(\delta_0 + I(L-l)/\sigma)^2} \int_l^L (\delta_0 + \frac{I}{\sigma}(L-l')) l' dl'.$$

Assume that

$$\delta_0 \ll \frac{IL}{\sigma}, \quad (2.13)$$

and consider only those l such that $L-l \gg (\sigma\delta_0)/I$, we obtain that

$$p \sim \frac{\alpha\sigma}{I(L-l)^2} \int_l^L (L-l') l' dl' = \frac{\alpha\sigma}{3I^2} (l + L/2). \quad (2.14)$$

The total probability of break-up of the branch (or the last part of it) is

$$P \sim \frac{3\alpha\sigma}{8I} L^2,$$

and so the typical length of the branch before break-up is

$$L \sim \sqrt{\frac{I}{\alpha\sigma}}.$$

Inserting this into (2.13), one finally finds the condition

$$\delta_0^2 < \frac{I^3}{\alpha\sigma^3}. \quad (2.15)$$

Now, notice that the probability of break-up given by (2.14) is increasing in l , until l is close enough to L ($L-l$ of the order of $\sigma\delta_0/I$). So a branch will typically rather break-up at the end.

Moreover consider a branch which already had a previous break-up and which has a second one. The typical time lapse between the two is of the same order than the time it took for the first break-up to occur. Hence the typical diameter of the first (or oldest) part of the branch is twice the one of the youngest part, making it even more likely that break-up will occur on the youngest part.

Therefore in the sequel we also assume that break-up always occur on the youngest part of the branch. This enables us to replace δ_k in the equation (2.10) on n_k by $\bar{\delta}(t, l, L)$ given by

$$\bar{\delta}(t, l, L) = \delta_0 + \int_{t-(L-l)/\sigma}^t I(s) ds. \quad (2.16)$$

Define the total population $n(t, l, s)$ by

$$n(t, l, s) = \sum_{k=0}^{\infty} \int_{l_1, \dots, l_k=0}^l \int_{s_1, \dots, s_k=s}^t n_k(t, l, s, s_1, \dots, l_k) ds_1 \dots ds_k dl_1 \dots dl_k.$$

This function now satisfies the relatively simple equation

$$\begin{aligned} \partial_t n(t, l, s) + \sigma \partial_l n &= -dn - \alpha n \int_0^l \frac{\int_{l'}^l \bar{\delta}(t, l'', l) l'' dl'' dl'}{(\bar{\delta}(t, l', l))^2} \\ &+ \alpha \int_l^{\infty} n(t, l', s) \frac{\int_l^{l'} \bar{\delta}(t, l'', l') l'' dl''}{(\bar{\delta}(t, l, l'))^2} dl'. \end{aligned} \quad (2.17)$$

If the birth rate B depends only on the size of the colony, the boundary condition becomes

$$n(t, 0, s) = \delta(t - s) \int_0^t \int_0^\infty B(l)n(t, l, s') dl ds'. \quad (2.18)$$

In the case where the environmental conditions are constant, (2.17) is even fully explicit and one does not need to take the difference between new part and old part of the colony (the age of the colony) into account, defining

$$\bar{n}(t, l) = \int_0^t n(t, l, s) ds,$$

we have that

$$\begin{aligned} \partial_t \bar{n}(t, l) + \sigma \partial_l \bar{n} &= -d\bar{n} - \alpha \bar{n} \int_0^l \frac{\int_{l'}^l (\delta_0 + I(l - l'')/\sigma) l'' dl''}{(\delta_0 + I(l - l')/\sigma)^2} \\ &+ \alpha \int_l^\infty \bar{n}(t, l') \frac{\int_l^{l'} (\delta_0 + I(l' - l'')/\sigma) l'' dl''}{(\delta_0 + I(l' - l)/\sigma)^2} dl'. \end{aligned} \quad (2.19)$$

3. Mathematical study

We are led to study the following type of model, where $K(l, l')$ is the probability of a branch of size l' to break in a branch of size $l < l'$ and $S(l)$ the break-up rate

$$\begin{aligned} \partial_t n + \partial_l n &= -(d + S(l))n(t, l) + \int_l^{+\infty} K(l, l')S(l')n(t, l')dl' \\ n(t, 0) &= \int_0^{+\infty} b(l)n(t, l)dl \\ n(0, l) &= N_0(l) \end{aligned} \quad (3.1)$$

where $b(l)$ is the recruitment rate for a colony of size l and $d > 0$ a constant environmental death rate. Since $K(l, l')$ is a probability density, we have:

$$\int_0^{+\infty} K(l, l')dl = 1,$$

and since the probability of a branch of size l' to give a longer branch l is null:

$$\int_0^{l'} K(l, l')dl = 1.$$

We need some technical bounds on the various coefficients, namely we assume

$$\begin{aligned} b, K, S &\text{ are } C^1 \text{ functions} \\ \forall \delta, \exists C, \text{ s.t. } b(l) &\leq C e^{\delta l}, \liminf_{l \rightarrow \infty} b(l) > 0, \\ \exists C, k \text{ s.t. } S(l) &\leq C(1 + l)^k, \quad K(l, l') \leq C(1 + l')^k. \end{aligned} \quad (3.2)$$

These assumptions are quite reasonable as they are satisfied by about every coefficients we would like to consider.

Note that if the environmental conditions depend on time, both S and K should depend also on the time variable. As we mainly study the permanent regime of (3.1), we keep things simple and forgot for the moment about the extra dependency.

3.1. Permanent regime

To study the system (3.1), we first look for special solutions corresponding to populations with a constant shape and a constant rate of increase (or decrease) in time. They are of the form

$$n(t, l) = e^{\gamma t} n_\gamma(l).$$

The function $n_\gamma(l)$ satisfies the corresponding stationary equation:

$$\partial_l n_\gamma = -(d + S(l) + \gamma) n_\gamma + \int_{l' > l} K(l, l') S(l') n_\gamma(l') dl', \quad (3.3)$$

together with the normalized condition

$$n_\gamma(0) = 1 = \int_0^\infty b(l) n_\gamma(l) dl \text{ normalized condition.} \quad (3.4)$$

The normalized condition should determine the value of the parameter γ (Malthus parameter). In fact one has

Proposition 3.1. *Assume (3.2). There exists a unique γ_0 and a unique $n_{\gamma_0} \geq 0$ such that $(1 + b(l)) n_{\gamma_0} \in L^1(\mathbb{R}^+)$, for any l' , $S(l) K(l', l) n_{\gamma_0}(l) \in L^1(\mathbb{R}^+)$ and n_{γ_0} is a solution to (3.3) and satisfies (3.4).*

The mathematical analysis of this problem is very similar to the one developed in ¹³ for linear models of populations structured by age. Here the size plays the role of the so-called maturation velocity. There are of course some minor differences (our kernel K is not symmetric in l and l' for example) but not enough to justify doing again and thoroughly the analysis. We therefore only sketch the several steps and refer the reader to ¹³ for details.

Classical methods ⁵ give a condition for the existence of bounded solution $0 \leq n_\gamma$ to (3.3) (with sufficient decay at infinity in order to define $\int_{l' > l} K(l, l') S(l') n_\gamma(l') dl'$, which we will precise later). Namely we require $\gamma > -\sigma_0$ where σ_0 is such that for all l

$$d + S(l) \left(1 - \int_{l' < l} K(l', l) dl' \right) \geq \sigma_0 > 0$$

In our case as $\int_0^l K(l', l) dl' = 1$, which is the conservation of the number of colonies, integrating (3.3) of the whole \mathbb{R}_+ , we find

$$(d + \gamma) \int_0^\infty n_\gamma(l) dl = 1.$$

Hence $\sigma_0 = d$, and we have an estimate on the L^1 norm of n_γ . Now define

$$B(\gamma) = \int_0^\infty b(l) n_\gamma(l) dl.$$

There exists a unique γ such $B(\gamma) = 1$ and thus (3.4) is satisfied.

Notice first that B is decreasing in terms of γ . In fact n_γ itself is decreasing in γ ; Indeed if $\gamma_1 > \gamma_2$, then denoting $u = n_{\gamma_1} - n_{\gamma_2}$

$$\partial_l u = -(d + S(l) + \gamma_1)u + \int_{l' > l} K(l, l') S(l') u(l') dl' + (\gamma_1 - \gamma_2) n_{\gamma_2},$$

and as $(\gamma_1 - \gamma_2) n_{\gamma_2}$ is non positive and $u(0) = 0$, by the maximum principle one has $u \leq 0$.

It is even possible to be more precise. Define $v = e^{(\gamma_1 - \gamma_2)l} n_{\gamma_1}$, then

$$\begin{aligned} \partial_l v &= -(d + S(l) + \gamma_1)v + \int_{l' > l} K(l, l') S(l') e^{(\gamma_1 - \gamma_2)(l - l')} v(l') dl' \\ &\leq -(d + S(l) + \gamma_1)v + \int_{l' > l} K(l, l') S(l') v(l') dl'. \end{aligned}$$

By the maximum principle on $n_{\gamma_2} - u$, we hence get for $\gamma_1 > \gamma_2$

$$n_{\gamma_1}(l) \leq e^{-(\gamma_1 - \gamma_2)l} n_{\gamma_2}(l).$$

As b is dominated by an exponential and $n_\gamma \in L^1$ for every γ , this implies that $B(\gamma)$ is finite for γ large enough. It also shows that

$$B(\gamma) \longrightarrow 0, \quad \text{as } \gamma \rightarrow \infty.$$

Note that this exponential decay is also enough to define

$$\int_l^\infty K(l, l') S(l') n_\gamma(l') dl'.$$

It only remains to prove that $B(\gamma) \rightarrow \infty$ as $\gamma \rightarrow -d$. Of course

$$\int_0^\infty n_\gamma(l) dl = \frac{1}{d + \gamma} \longrightarrow +\infty, \quad \text{as } \gamma \rightarrow -d.$$

On the other hand n_γ also satisfies

$$\begin{aligned} n_\gamma(l) &= e^{-D(l) - \gamma l} \left(1 + \int_0^l e^{D(l'') + \gamma l''} \int_{l' > l''} K(l'', l') S(l') n_\gamma(l') dl' dl'' \right) \\ &= e^{-D(l) - \gamma l} \left(1 + \int_0^\infty \left(\int_0^{\min(l, l')} e^{D(l'') + \gamma l''} K(l'', l') dl'' \right) S(l') n_\gamma(l') dl' \right). \end{aligned} \tag{3.5}$$

with $D(l)$ such that $\partial_l D(l) = d + S(l)$. Hence

$$n_\gamma(l) \geq e^{-D(l) - \gamma l} \left(1 + \int_0^l S(l') n_\gamma(l') dl' \right).$$

Now fix L large enough such that $b(l) \geq c > 0$ for all $l \geq L$. As $\gamma \rightarrow -d$ either $\int_0^L n_\gamma \rightarrow \infty$ or $\int_L^\infty n_\gamma \rightarrow \infty$.

In the second case as $B(\gamma) \geq c \int_L^\infty n_\gamma(l) dl$, we deduce immediately that $B(\gamma) \rightarrow \infty$.

In the first case we see that for any $l \geq L$

$$n_\gamma(l) \geq e^{-D(l)-\gamma l} \left(1 + S(0) \int_0^L n_\gamma(l') dl' \right),$$

and so $n_\gamma(l) \rightarrow +\infty$ for any $l \geq L$ as $\gamma \rightarrow -d$ which is enough to show that $B(\gamma) = \int_0^\infty b(l)n_\gamma(l) \rightarrow +\infty$ as b is bounded from below on $l \geq L$.

Concluding B is decreasing and maps $] -d, +\infty[$ onto $]0, +\infty[$. Therefore there is a unique γ_0 such that $B(\gamma_0) = 1$.

Note that formula (3.5) may be used to obtain n_γ through a fixed point argument, the operator

$$Tn = e^{-D(l)-\gamma l} \int_0^\infty \left(\int_0^{\min(l,l')} e^{D(l'')+\gamma l''} K(l'', l') dl'' \right) S(l') n_\gamma(l') dl',$$

satisfying

$$\int_0^\infty (d + \gamma + S(l)) Tn(l) dl \leq \int_0^\infty S(l) n(l) dl.$$

3.2. Existence of solution for the time-dependent system (3.1)

Obtaining solutions to (3.1) only requires enough decay in l on the initial data in order to define $\int K(l, l') S(l') n(l') dl'$ and the birth term. Therefore we assume that

$$\int_0^\infty \phi(l) n^0(l) dl < \infty, \quad (3.6)$$

with ϕ non decreasing, continuous and satisfying

$$\phi \geq 0, \quad \phi' \leq C \phi, \quad \frac{\phi(l)}{S(l)} \xrightarrow{l \rightarrow \infty} +\infty, \quad \frac{\phi(l)}{b(l)} \xrightarrow{l \rightarrow \infty} +\infty. \quad (3.7)$$

We then have

Proposition 3.2. *Existence : Assume (3.2), (3.6) and (3.7). There exists a unique $n \in L^\infty([0, T], L^1(\mathbb{R}_+))$ for any T with*

$$\int_0^\infty \phi(l) n(t, l) dl \in L^\infty([0, T]),$$

$n(t=0, l) = n^0(l)$ and n is a solution in the sense of distributions to (3.1).

This is an easy consequence (stability through approximation) of the two a priori estimates

$$\frac{d}{dt} \int_0^l n(t, l) dl = -d \int_0^\infty n(t, l) dl + \int_0^\infty b(l) n(t, l) dl,$$

together with

$$\begin{aligned} \frac{d}{dt} \int_0^l \phi(l)n(t,l) dl &= -d \int_0^\infty \phi(l)n(t,l) dl + \phi(0) \int_0^\infty b(l) n(t,l) dl \\ &\quad + \int_0^\infty \phi'(l) n(t,l) dl + \int_0^\infty n(t,l) S(l) \int_0^l (\phi(l') - \phi(l))K(l',l) dl' dl \\ &\leq -d \int_0^\infty \phi(l)n(t,l) dl + \int \phi'(l) n dl + \phi(0) \int_0^\infty b(l) n(t,l) dl. \end{aligned}$$

As ϕ is asymptotically larger than b , these two estimates provides a bound for any finite time for $\int n dl$ and $\int \phi n dl$. This is enough to handle every term in (3.1).

3.3. Convergence of the time-dependent solution toward the permanent regime

We follow again ¹³ to prove that $n(t,l)$ converges towards $\beta e^{\gamma_0 t} n_{\gamma_0}$. For simplicity we assume that $\gamma_0 = 0$ (this can be ensured by rescaling every solution in time by $e^{\gamma_0 t}$ thus changing d in the equation).

First define an auxiliary function $H(l)$ that solves the dual problem to (3.3):

Proposition 3.3. *Assume (3.2). There exists a positive $H \in C^1(\mathbb{R}_+)$ solution to*

$$\begin{aligned} \frac{\partial H}{\partial l} &= (d + S(l))H - S(l) \int_0^l K(l',l) H(l') dl' - b(l) \\ H(0) &= 1, \int_0^\infty H(l) n_{\gamma_0}(l) dl < \infty. \end{aligned} \quad (3.8)$$

Proof. There is of course a unique solution H to

$$\frac{\partial H}{\partial l} = (d + S(l))H - S(l) \int_0^l K(l',l) H(l') dl' - b(l),$$

with $H(0) = 1$. But a priori nothing garantees that H stays non negative for example.

For any γ , note that

$$\begin{aligned} H(L)n_\gamma(L) &= n_\gamma(0) - \gamma \int_0^L H(l)n_\gamma(l) dl - \int_0^L b(l) n_\gamma(l) dl \\ &\quad + \int_0^L H(l) \int_L^\infty K(l,l')S(l')n_\gamma(l') dl' dl. \end{aligned}$$

Taking $\gamma = \gamma_0 = 0$, one first gets the positivity of H by

$$H(L) n_{\gamma_0}(L) > 0.$$

On the other hand, for $\gamma > 0$, letting $L \rightarrow \infty$, one finds

$$\int_0^\infty H(l) n_\gamma(l) dl = \frac{1 - \int_0^\infty b(l)n_\gamma(l) dl}{\gamma}.$$

Now $\partial_\gamma n_\gamma$ is a solution to

$$\partial_l \partial_\gamma n_\gamma = -(d + S(l) + \gamma) \partial_\gamma n_\gamma + \int_{l' > l} K(l,l')S(l') \partial_\gamma n_\gamma(l') dl' - n_\gamma,$$

and hence for any $\gamma > -d$, $\int b(l)\partial_\gamma n_\gamma(l) dl$ is uniformly bounded. Consequently the limit of $\int H(l)n_\gamma(l) dl$ as $\gamma \rightarrow 0$ is finite and

$$\int H(l)n_{\gamma_0}(l) dl < \infty. \quad \square$$

Now we may state

Theorem 3.1. *Assume that $b(l)$ for almost all l . Assume that (3.2) holds and (3.6), (3.7) are satisfied for the initial data n^0 with $H(l)/\Phi(l) \rightarrow 0$ as $l \rightarrow \infty$. Assume finally that for a constant C , $n^0(l) \leq C n_{\gamma_0}(l)$. Let $n(t, l)$ the solution to (3.1) given by Proposition 3.2. Let $\beta > 0$ be such that*

$$\int_0^\infty H(l) n^0(l) dl = \beta \int_0^\infty H(l) n_{\gamma_0}(l) dl.$$

Then as $t \rightarrow \infty$, $n(t, l) - \beta n_{\gamma_0}(l)$ converges to 0 in $L^1_{loc}(\mathbb{R}_+)$.

Proof. Let us denote

$$u(t, l) = n(t, l) - \beta n_{\gamma_0}(l).$$

Then of course by linearity of the system, u is a solution to (3.1). Now multiplying by a regularization of $\text{sign}(u)$ and passing to the limit, we get

$$\begin{aligned} \partial_t |u| + \partial_l |u| &\leq -(d + S(l)) |u| + \int_l^\infty S(l') K(l, l') |u(t, l')| dl', \\ |u(t, 0)| &\leq \int_0^\infty b(l) |u| dl - \min \left(\int_0^\infty b(l) u_+ dl, \int_0^\infty b(l) u_- dl \right), \end{aligned}$$

with u_+ and u_- the positive and negative parts of u . Multiplying by $H(l)$ and integrating one gets

$$\begin{aligned} \frac{d}{dt} \int H(l) |u(t, l)| dl &\leq \int \left(\partial_l H - (d + S(l))H + S(l) \int_0^l H(l') K(l', l) dl' \right) |u(t, l)| dl \\ &\quad + H(0) |u(t, 0)|. \end{aligned}$$

As H satisfies (3.8), we get

$$\frac{d}{dt} \int H(l) |u(t, l)| dl \leq - \min \left(\int_0^\infty b(l) u_+ dl, \int_0^\infty b(l) u_- dl \right).$$

This shows that $\int H |u| dl$ has a limit and that as $t \rightarrow \infty$, either u_+ or u_- converges toward 0 pointwise (thanks to $b > 0$ a.e.).

Moreover the same computation also shows that

$$\frac{d}{dt} \int H(l) u(t, l) dl = 0.$$

Notice also that the control on the decay of n and $H(l)n_\gamma$ is good enough to make all the previous steps rigorous.

By the choice of β , we deduce that

$$\int H(l) u(t, l) dl = 0.$$

Finally as $n^0 \leq n_{\gamma_0}$ then by the maximum principle $n(t, l) \leq Cn_{\gamma_0}$ and therefore $H(l)|u(t, l)|$ is uniformly integrable in time. The limit of $\int H(l)|u| dl$ is equal to $|\lim \int H(l)u dl|$. Therefore

$$\int_0^\infty H(l) |u(t, l)| dl \longrightarrow 0,$$

which also implies the convergence of u toward 0. □

4. Numerical simulations

4.1. The stationary solution

Theorem 3.1 says that the behaviour of the solution is governed by the stationary one. The behaviour of this last one in terms of the break-up rate $S(l)$ (which is typically modified by the environmental conditions), is however not so easy to investigate theoretically. So instead we performed some numerical simulations.

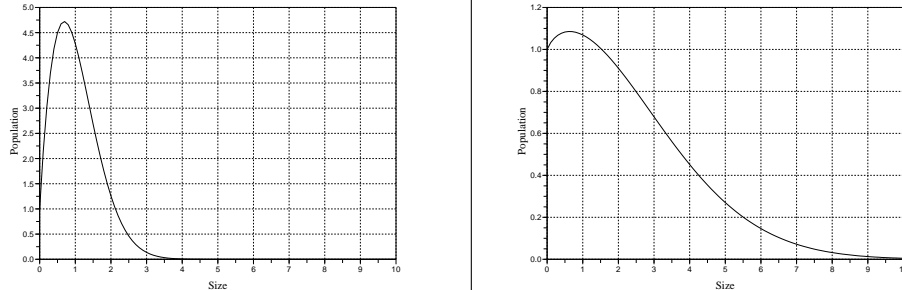


Fig. 1. Stationary solution of model 3.1. The break-up rate $S(l) = l$ and $S(l) = l/10$.

We proposed to study the different cases taking the break-up rate $S(l) = l$ and $S(l) = l/10$. The very classical Euler scheme is used in order to perform the simulations but since the integral term of equation (3.1) does not begin in zero we have to integrate this equation in reverse time. For the other parameters values, we take $K(l, l') = 1/l'$ and $d = 0.1$ which seems reasonable compare with the available data ⁶. Since a lot of numerical simulations were performed with different initial conditions and since the same result is obtained, we can assume that probably the stationary solution is globally asymptotically stable.

Fig 1 shows the evolution of the stationary solution of equation (3.1). One can see that the more the break-up rate is important (*i.e.* $S(l) = l$) the more the death

of the big size colony is important. The population is then mainly constituted of small size colonies (less than size 4 with $S(l) = l$ or size 10 with $S(l) = l/10$). This confirms the biological observation made in ⁶.

4.2. Evolution of the complete solution

Some simulations of the complete model are then proposed in order to evaluate qualitatively the demographic consequences of protection rules. To perform these simulations, the classical Euler discretization in time and in size is used.

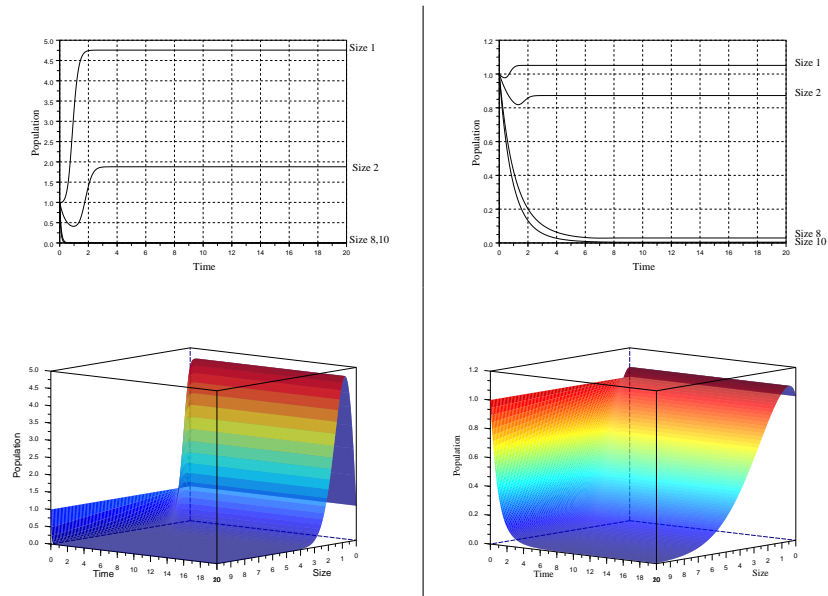


Fig. 2. Time evolution of all the size class. Break-up rate $S(l) = l$ and $S(l) = l/10$.

Fig 2 shows the evolution of the initial model without no new hypotheses. This confirm the simulation of the stationary solution since we obtain the same limit values for both simulations for a given size. Then Fig 3 illustrates the possible protection of the colony. At time 5, we take a break-up rate $S(l)$ equal to zero in order to simulate population without mortality due to necrosis or exploitation. One can see that the behavior of the solution is also governed by the stationary one. In this particular case this stationary solution can be explicitly (and easily) computed. One can compute this solution and find that it is proportionnal to $exp(-dl)$ which can be also verified in Fig 3. More biologically speaking, Fig 3 shows the maintenance of the highest colonies after some times depending on the break-up rate. The more the break-up rate is important the more the recuperation of the large colonies is long. This qualitative result seems to confirm the possible conservation of the population

but it confirms also the very long time to obtain this preservation considering the biological values of the growth rate ⁶.

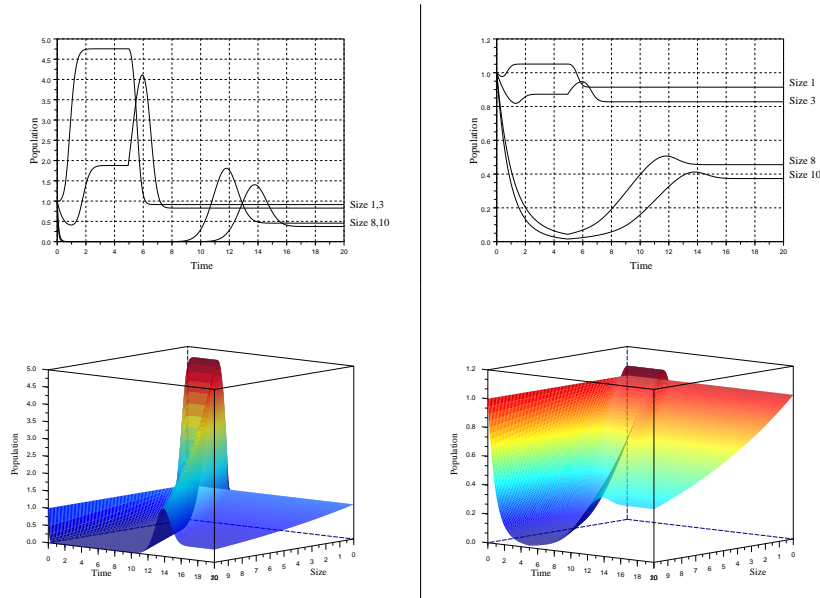


Fig. 3. Time evolution of different size class. Protection at time $T = 5$. Break-up rate $S(l) = l$ and $S(l) = l/10$

In Fig 4 we take $S(l) = 0$ for $t = 5$ to $t = 15$ and $S(l) = l$ (or $S(l) = l/10$) otherwise. This represents the protection of the colony during ten years. Once again, the behavior of the solution is governed by the stationary one. A discontinuity in the break-up rate $S(l)$ is enabled to destabilize the behavior of the solution. This means that the model is very robust to perturbations and it confirms in the probably global convergence of the system. More biologically speaking, this qualitative result could describe the exploitation phenomenon. Indeed during the period of protection the big size colonies reappear then a period of exploitation remove all this new big size colonies and only the small size remain alive. This result can also describe a mass mortality event due to the temperature increase after ten years without any changes and one can see that the big size colonies are all affected. So this enlightens the necessity of managing this species on long time scales.

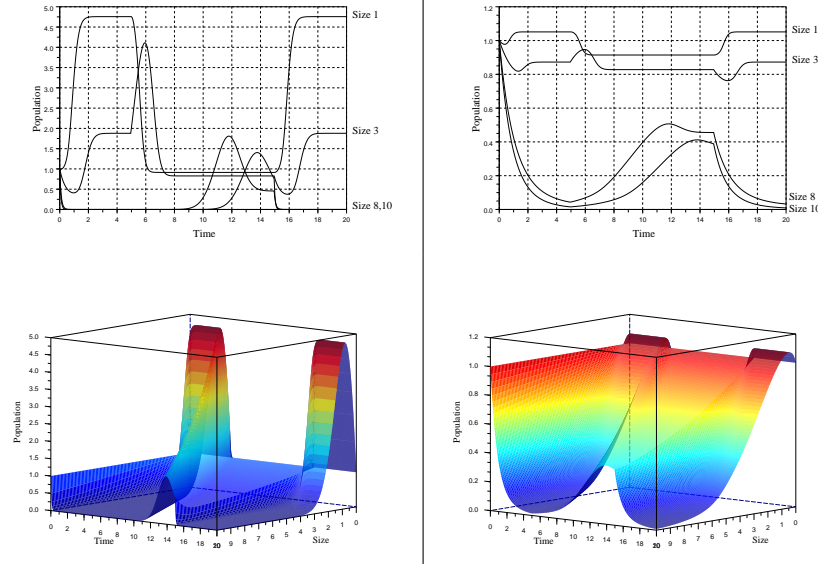


Fig. 4. Time evolution of different size class. Protection at time $T = 5$ and Mortality event at time $T = 15$. Break-up rate $S(l) = l$ and $S(l) = l/10$

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