Some models in population dynamics

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Main notations

t	time
a	age
c	condition
$N^{(a)}$	active population
π	weight function
$\varphi(a,c)$	population distribution
$s(c)$	mortality rate
$\psi(N^{(a)})$	loss of condition rate
$n(c)$	birth distribution
$\theta(c)$	transmitted ~~robustness~~ condition
$m(a,c,N^{(a)},t)$	fecundity rate
$A(c, N^{(a)})$	maturation age
S	survival rates

1. The general model

1.1 The state space

The state of an individual (at a given time) is the pair formed by its age a and its condition c. Condition will decrease with age (see below), and cannot decrease below a minimal value (that we take to be 0). Condition at birth cannot exceed a maximal value c_{max}. The mortality rate will be set in order that no individual can reach a maximal age a_{max}. Therefore, the state space will be the product $[0, a_{max}) \times [0, c_{max}]$.

Comment: if one wants to choose a mortality rate that allows (few) individuals to reach arbitrarily high ages (for instance, $s =$ constant), one should probably replace condition c by an equivalent notion of biological age, starting from birth at some positive value depending on the biological age of the mother (via a θ function of the kind we are considering) and increasing at least as fast as chronological age (via a function ψ)

Normalization of units: the unit of "condition" is taken in order that the loss of condition at zero density is 1 ($\psi(0) = 1$), hence $c_{max} = a_{max}$.

The unit of time is taken in order to have:

- $a_{max} = 1$ in the unseasonal case
- period 1 for m in the seasonal case

1.2 The phase space

Because in best conditions ~~robu~~ condition is lost at speed 1, the state of an individual really lies in the triangle

$$0 \leq a+c \leq 1 \qquad (a, c \geq 0)$$

The phase space X^+ for the dynamics is the space of positive finite measures on this triangle. For most practical purposes, one could just consider just those measures that have a density $\varphi(a,c)$ with respect to Lebesgue measure $da\,dc$.
There are two reasons to consider the larger space X^+

- If the θ function describing the ~~densi~~ transmission of ~~robustness~~ condition has a plateau near c_{max}, the population cannot just be described by a density, but rather as the sum of two components: the part of population born with less than maximal ~~density~~ condition is described by a density, but the (positive) part of the population born with maximal ~~density~~ condition is rather described by a density on a curve in state space (the diagonal if $\psi \equiv 1$)

- It may help to consider Dirac measures, i.e groups of ~~po~~ individuals with same age and condition.

For notational reasons, I will write anyway a point in the phase space as $\varphi(a,c)\,da\,dc$. One should keep in mind that this should be interpreted as a measure.

The dynamics in the phase space are governed by three factors

- the mortality rate;
- the loss of condition by individuals;
- the birth of new offsprings.

This will produce (in the unseasonal case) a semi-group of applications

$$T^t : X^+ \longrightarrow X^+, t \geq 0; \quad T^{t_1+t_2} = T^{t_1} \circ T^{t_2}, \quad T^0 = id.$$

One should beware that the dynamics are irreversible: T^t is not invertible, and T^t cannot be defined for $t<0$; time cannot run backwards.

The dynamics will have the following important properties: there exists a compact subset K of phase space X^+ such that

(i) $T^t(K) \subset K$, for all $t \geq 0$

(ii) for any initial condition x_0 in X^+, there exists $t_0 \geq 0$ such that $T^{t_0}(x_0) \in K$.

[There are many possible choices for K].

Then, one defines the global attractor for the dynamics

$$\Lambda = \bigcap_{t \geq 0} T^t(K)$$

This does not depend on the choice of K, and satisfies

$$T^t \Lambda = \Lambda \quad , \quad \text{for all } t \geq 0.$$

The trajectories in Λ are the stationary regimes (evolution having run an infinite amount of time).

The aim is to understand Λ and the dynamics on it.

[In the seasonal case, one should add the time-circle in the picture; then we get similar statements]

1.3 Mortality rate

It is assumed that the mortality rate s only depends on the condition c (continuously).

In order to kill all individuals before their condition c reaches 0, we will assume that the integral

$$\int s(c)\, dc$$

diverges at 0; for instance $s(c) = s_0 \, c^{-1}$ is a reasonable choice.

It is also probably reasonable to assume that s decreases with c.

1.4 Active population

A weight function π on the state space is given, taking values between 0 and 1.

It is mathematically easier to take it to be continuous (so that it can be integrated against measures in the phase space), but reasonable $0-1$ functions should also be ok.

The active population is then

$$(1) \qquad N^{(a)} = \iint \varphi(a,c)\,\pi(a,c)\,da\,dc$$

1.5 Loss of condition

At any given time, the robustness of individuals will decrease according to

$$\frac{dc}{dt} = -\psi(N^{(a)})$$

where the loss of condition rate ψ is a continuous increasing function of $N^{(a)}$, with $\psi(0) = 1$.

1.6 Transmission of condition

The condition at birth of an offspring depends only on the condition of the mother at that moment: if this last condition is c, the condition of the offspring is $\theta(c)$.

The function θ is assumed to be increasing with c, $\theta(c_{max}) = c_{max}$, and also

$$\frac{d\theta}{dc} < 1 \qquad \text{for all } c.$$

Let us explain why to impose this last condition: assume that at zero density (for instance) an individual has two daughters at time $t_1 < t_2$; let c_1 be the condition at the mother at time t_1, c_2 the condition at time t_2. We have

$$c_2 = c_1 - (t_2 - t_1) \qquad (\psi(0) = 1)$$

The two daughters are born with conditions $\theta(c_1)$, $\theta(c_2)$ respectively.

Now assume that at a later time t_3, both daughters have offsprings.

The condition of the older daughter at this time is

$$\theta(c_1) - (t_3 - t_1)$$

while the condition of the younger is

$$\theta(c_2) - (t_3 - t_2)$$

It is reasonable to assume that the transmitted condition effect attenuates with generations, meaning that the condition of the offspring of the older mother should be smaller that the condition of the offspring of the younger mather. This means

$$\theta(c_2) - (t_3 - t_2) > \theta(c_1) - (t_3 - t_1)$$

or

$$\theta(c_1) - \theta(c_2) < t_2 - t_1 = c_1 - c_2$$

which explains the restriction on θ

1.7 The fecundity rate

A population of size $\varphi(a,c)\,\Delta a\,\Delta c$ of mothers, with age $\in [a, a+\Delta a]$ and condition $\in [c, c+\Delta c]$ at time t, will give birth between time t and $t+\Delta t$ to a number of female offsprings equal to $\varphi(a,c)\, m(a,c,N^{(a)},t)\,\Delta a\,\Delta c\,\Delta t$.
The condition of these offsprings at birth is according to 1.6 a number in $[\theta(c), \theta(c+\Delta c) = \theta(c) + \theta'(c)\Delta c]$.

As to the fecundity rate $m(a,c,N^{(a)},t)$, we will assume a number of properties described below.
We will consider both the unseasonal case, in which m does not depend explicitly on time, and the seasonal case; in this case, the function m is the product of a function (still denoted by m) depending on $a, c, N^{(a)}$ and a function $\tilde{m}$ depending only on time. This last function takes values between 0 and 1 and is periodic of period 1 in time, taking typically high values near 1 during half a period (the summer) and low value near 0 during the other half (the winter).

The function $m(a,c,N^{(a)})$ is assumed to be increasing with c, decreasing with $N^{(a)}$. Moreover it is 0 unless a is above the maturation age $A(c, N^{(a)})$ which is decreasing with c, increasing with $N^{(a)}$, and always larger than some strictly positive constant (In other terms $A(c_{max}, 0) > 0$)

[1.4' A remorse for the active population.

It is better to allow the weight function $\pi(a,c)$ used in defining the active population $N^{(a)}$ to depend also, in a decreasing way on the active population itself.
Equation (1)

$$N^{(a)} = \iint \varphi(a,c)\,\pi(a,c,N^{(a)})\,da\,dc$$

is now truly an equation (not a definition) which is however easily seen to have a unique solution: the left hand side is increasing with $N^{(a)}$ while the right hand side is decreasing with $N^{(a)}$.]

2 The equations

2.1 We have already written the first one

$$(1) \qquad N^{(a)}(t) = \iint \varphi(a,c,t)\, \pi(a,c,N^{(a)})\, da\, dc$$

which determines uniquely the active population at time t in terms of the point of the phase space $\varphi(a,c,t)\, da\, dc$ describing the population distribution at time t.

2.2 The second equation describes the evolution of the population born before time t, given by the mortality and loss of Condition laws:

$$(2) \qquad \frac{\partial\varphi}{\partial t} + \frac{\partial\varphi}{\partial a} - \psi(N^{(a)}(t))\frac{\partial\varphi}{\partial c} = -s(c)\,\varphi .$$

Technical comment: Strictly speaking, we can only write the left hand side when the population distribution has a density (so that φ exists) and is differentia-ble (so that we can take partial derivatives).

On a high-brow level, nevertheless, the left hand side always makes sense at the distributional sense.

Concretely, we can take any test function χ which is a smooth function on state space vanishing for $a=0$ (otherwise ~~one~~ the birth process should come in).

Write $<\chi,\varphi>$ for the integral of χ against a point φ in the phase space X^+. Then we will rewrite equation (2) as

$$\frac{d}{dt}<\chi,\varphi> = <\frac{\partial\chi}{\partial a} - \psi(N^{(a)})\frac{\partial\chi}{\partial c} - s(c)\,\chi\,,\varphi>$$

(Beware that the signs are not quite the same! this is due to an integration by parts). As χ is smooth, taking its partial derivative is no problem and we can integrate against the measure φ in phase space. The equation above should hold for any test function χ.

Equation (2) is, in a sense, not really a partial defferential equation, and one should think of it in the following way.

The product of the state space by the positive time axis is a 3-dimensional space foliated by a 2-parameter family of curves; each curve describes the time evolution ~~of~~ of age and conditions of individuals:

$$\frac{da}{dt} = 1\,, \qquad \frac{dc}{dt} = -\psi(N^{(a)}(t))\,,$$

the two parameters specifying the curve being the time of birth t_0 and the ~~...~~ condition at birth c_0.

Then, equation (2) just expresses how the density φ evolves along this curve γ

$$\frac{d}{dt}\varphi(\gamma(t)) = -s(c)\,\varphi(\gamma(t))$$

and we can solve this differential equation:

$$\varphi(\gamma(t)) = \varphi(0, c_0, t_0)\,\exp\left[-\int_{t_0}^{t} s(c(u))\,du\right]$$

(the condition c on curve γ being function of time)

2.3 The last two equations describe the birth process. We first write them in the simpler case where the population has a continuous density, and the function θ satisfies

$$\theta'(c) > 0 \quad \text{for all } c \in [0, c_{max}].$$

In this case, there is at time t a continuous function $n(c, t)$ such that $n(c,t)\,\Delta t\,\Delta c$ is the number of female offsprings born between time t and $t+\Delta t$ with ~~...~~ condition between c and $c+\Delta c$. On one side we have

$$(3) \quad n(c,t) = \varphi(0, c, t)$$

On the other (see 1.7)

$$(4) \quad n(\theta(c), t)\,\theta'(c) = \int m(a, c, N^{(a)}(t), t)\,\varphi(a, c, t)\,da$$

In the general case, one should reinterpret $n(c,t)\,dc$ as a positive measure, depending on time, on the condition interval $[0, c_{max}]$.
Taking any test function χ_0 on $[0, c_{max}]$ (continuous), multiplying (4) by $\chi_0(\theta(c))$ and integrating gives

$$\int n(c,t)\,\chi_0(c)\,dc = \iint m(a, c, N^{(a)}(t), t)\,\varphi(a,c,t)\,\chi_0(\theta(c))\,da\,dc$$

which now makes always sense and should hold for any test function χ_0.

On the other hand, in the general case, equation (3) should be joined to equation (2) (it is the initial condition for equation (2)). Instead of considering as in 2.2 only test functions

χ vanishing for $a=0$, we consider general test functions (still smooth!). The two equations (2) and (3) are equivalent to the single equation

(2)+(3) $$\frac{d}{dt}\langle \chi,\varphi\rangle = \langle \frac{\partial\chi}{\partial a} - \psi(N^{(a)})\frac{\partial\chi}{\partial c} - s(c)\,\chi,\varphi\rangle + \int n(c,t)\,\chi(0,c)\,dc$$

for any test function χ.

Putting (2),(3),(4) together gives

(2)+(3)+(4) = (5) $$\frac{d}{dt}\langle \chi,\varphi\rangle = \langle \tilde{\chi},\varphi\rangle,$$

where

$$\tilde{\chi}(a,c) = \frac{\partial\chi}{\partial a}(a,c) - \psi(N^{(a)}(t))\frac{\partial\chi}{\partial c}(a,c) - s(c)\,\chi(a,c) + m(a,c,N^{(a)}(t),t)\;\chi(0,\theta(c)).$$

(Observe that besides the basic data ψ, s, m, θ, the distribution φ enters in $\tilde{\chi}$ only through the active population $N^{(a)}$).

2.4 We thus have written the equations in the general setting. We want actually to consider several special situations.

- as has been mentioned before, the unseasonal case, where m does not depend explicitly on time.
- the constant loss of condition case, where we assume that $\psi \equiv 1$, i.e there is no effect of the active population on the way robustness evolves.
- the "mature = active" case: we will here assume that the weight function π is proportional to the fecundity rate m.
- ~~the toy-model case unconditional case: we assume that the function θ is constant equal to $c_{max}=a_{max}$ Then there is no need to consider condition c, which is relate~~
- the "maximal condition at birth" case: where θ is constant, equal to c_{max}.

We can (and will) also that several of these special conditions are met together.

If for instance we combine constant loss of condition with maximal condition at birth, the variable $c = a_{max} - a$ becomes useless.

If moreover, we ask for the "mature = active" condition, we get a much simpler model (studied later) that we call the "toy model".

2.5 Existence, uniqueness and boundedness of solutions.

The statement for existence and uniqueness of solutions is as follows.

Given an initial time t_0, and an initial position x_0 in phase space X^+, there exists a unique curve $(x(t))_{t \geq t_0}$ in phase space with the following properties

i) $x(t_0) = x_0$

ii) for any smooth test function χ on state space, the function $t \longmapsto \langle \chi, x(t) \rangle$ is continuously differentiable on $[t_0, +\infty)$, and (5) is satisfied for all $t \geqslant t_0$.

[A glimpse of the proof will be given later].

To get boundedness of all solutions, we need some natural hypotheses.

1) the mortality rate is bounded from below: $s(c_{max}) > 0$

2) the fecundity rate goes to 0 as the active population $N^{(a)}$ goes to $+\infty$.

3) All mature individuals are active: more precisely, ~~the~~ the function $m(a, c, N^{(a)})$ is bounded from above by a constant times the weight function $\pi(a, c, N^{(a)})$.

Assuming this, we claim that there exists N^+ such that

i) if at time t_0, the ~~active~~ total population is below N^+, it will remain so for all ~~posit~~ times $t \geqslant t_0$

ii) Given any initial condition x_0 at time t_0, there exists t_1 such that the ~~active~~ total population at times $t \geqslant t_1$ is less than N^+.

Proof: We choose N_0^+ ~~such~~ so large that

$$m(a,c,N^{(a)},t) \leq \frac{1}{2}\, s(c_{max})$$

for all a,c,t and all $N^{(a)} \geq N_0^+$. On the ~~h~~other hand, there exists $k>0$ such that

$$m(a,c,N^{(a)},t) \leq k\, s(c_{max})\, \pi(a,c,N^{(a)})$$

for all a,c,t and all $N^{(a)} (\geq 0)$. Let $N^+ = 2N_0^+ k$. Assume that at time t_0, the total population $N(t_0)$ is $\geq N^+$.

The mortality rate is at least $s(c_{max})$. The number of newborn is given

$$\iint m(a,c,N^{(a)},t)\, \varphi(a,c)\, da\, dc$$

hence it is $\leq \frac{1}{2} s(c_{max}) N(t_0)$ if $N^{(a)} \geq N_0^+$, and $\leq k\, s(c_{max}) N^{(a)}(t_0)$ in all cases. We have thus

$$\frac{dN}{dt} \leq s(c_{max})(-N + k N^{(a)}) \quad \text{in all cases}$$
$$\leq -\frac{1}{2} s(c_{max}) N \quad \text{if } N^{(a)} \geq N_0^+.$$

But ~~if~~ as $N(t_0) \geq N^+ = 2N_0^+ k$, if $N^{(a)} < N_0^+$ we must have

$$-N + kN^{(a)} \leq -\frac{1}{2} N$$

and therefore we have proven that

$$\frac{dN}{dt}(t_0) \leq -\frac{1}{2} s(c_{max})\, N(t_0)$$

as long as $N(t_0)$ remains $\geq N^+$. This clearly imply the required properties. (N cannot cross upwards the threeshold N^+).

From the eventual boundednes of N, the eventual boundednes of the birthcount

$$\int n(c)\, dc$$

immediately follows (the fecundity rate being bounded).

3. Equilibria in the unseasonal case.

3.1 We are considering the unseasonal case (m indefendent of t).

A point $\varphi_0(a,c)\,da\,dc$ in phase space is an equilibrium if the solution starting from it at time 0 is constant.
The zero population is such a point. We are looking for other equilibria.

We will show that there is exactly one such equilibrium, provided that the fecundity rate at zero population is high enough.
~~For simplicity, we~~
The equilibrium must satisfy the equation

$$(5)\quad 0 = \iint \Big[\frac{\partial \chi}{\partial a} - \psi(N_0^{(a)})\frac{\partial \chi}{\partial c} - s\chi + m(a,c,N_0^{(a)})\,\chi(0,\theta(c))\Big]\varphi_0(a,c)\,da\,dc$$

together with

$$(1)\qquad N_0^{(a)} = \iint \varphi_0(a,c)\,\pi(a,c,N_0^{(a)})\,da\,dc$$

At first we forget (1), and treat (5) with $N_0^{(a)}$ as a free parameter. Equation (5) must be satisfied for any test function χ.

~~With fixed $N_0^{(a)}$, we let $\hat{c} = c + a\psi(N_0^{(a)})$, the state space will be now~~

$$\cancel{\{(a,\hat{c}),\ 0 \le a \le a_{max},\ 0 \le \hat{c} \le a_{max} = c_{max}\}}$$

~~the "life trajectories" being $\hat{c} = c^{te}$. In the $a,\hat{c}$ coordinates, we have~~
Working with (2),(3) instead for the sake of simplicity, we have

$$(6)\qquad \varphi_0(a,c) = n_0(c + a\psi(N_0^{(a)}))\ S(a,c)$$

where the survival rate $S(a,c)$ is given by

$$S(a,c) = \exp\Big(-\int_0^a s(c + u\psi(N_0^{(a)}))\,du\Big)$$

Then (4) gives an equation for n_0:

$$(7)\qquad n_0(\theta(c))\,\theta'(c) = \int m(a,c,N_0^{(a)})\,n_0(c + a\psi(N_0^{(a)}))\,S(a,c)\,da$$

The proof of the existence and uniqueness of non trivial equilibrium runs now more or less as follows

1) We rewrite (7) in integrated form as in page 7:

$$\int n_0(c)\,\chi_0(c)\,dc = \iint m(a,c,N_0^{(a)})\,S(a,c)\,n_0(c+a\psi(N_0^{(a)}))\,\chi_0(\theta(c))\,da\,dc$$

for any continuous test function on $[\theta(0), c_{max}]$.

After a change of variables the right hand side becomes

$$\int_{\theta(0)}^{c_{max}} n_0(c)\,T\chi_0(c)\,dc$$

where the operator T, depending on $N_0^{(a)}$, is defined by

$$T\chi_0(c) = \int_0^c m\left(\frac{c-a}{\psi(N_0^{(a)})}, a, N_0^{(a)}\right) S\left(\frac{c-a}{\psi(N_0^{(a)})}, a\right) \frac{1}{\psi(N_0^{(a)})}\,\chi_0(\theta(a))\,da$$

2) Due to the hypotheses on θ, m, ψ, the operator $T = T_{N_0^{(a)}}$ has the following properties

+ there exists N_{cr} such that for $0 \leq N_0^{(a)} < N_{cr}$, there exists a unique probability measure $\mu_{N_0^{(a)}}$ on $[\theta(0), c_{max}]$ such that

$$\int T\chi_0\,d\mu_{N_0^{(a)}} = \lambda(N_0^{(a)}) \int \chi_0\,d\mu_{N_0^{(a)}}$$

for some $\lambda(N_0^{(a)}) > 0$. One has $\lim_{N_0^{(a)} \to N_{cr}} \lambda(N_0^{(a)}) = 0$, and λ is decreasing strictly with $N_0^{(a)}$!

Therefore if we assume $\lambda(0) > 1$ (this will hold if the ~~density is lar~~ fecundity is large enough), there will exist a unique value of $N_0^{(a)}$ with $\lambda(N_0^{(a)}) = 1$.

3) The last step is just to scale the probability $\mu_{N_0^{(a)}}$ in order to satisfy (1).
In the equation

$$N_0^{(a)} = \iint \pi(a,c,N_0^{(a)})\,n_0(c+a\psi(N_0^{(a)}))\,S(a,c)\,da\,dc$$

we just take $n_0(c)\,dc$ to be the right multiple of $\mu_{N_0^{(a)}}$.

3.2 Stability of non trivial equilibrium: the linearized system.

Let $N_0^{(a)}$, φ_0, n_0 characterize the equilibrium that we have just found. Assuming for simplicity that θ has no plateau, and even $\theta'(c) > 0$, φ_0 and n_0 will really be functions (instead of measures).

The linearized system will be:

$$\begin{cases} (1') & \Delta N^{(a)}(t) = \iint \pi_0 \Delta\varphi(t) + \Delta N^{(a)} \iint \pi_0' \varphi_0 \qquad \left(\pi_0 = \pi(a,c,N_0^{(a)}),\ \pi_0' = \frac{\partial \pi}{\partial N}(a,c,N_0^{(a)}) < 0\right) \\ (2') & \frac{\partial}{\partial t}\Delta\varphi + \frac{\partial}{\partial a}\Delta\varphi - \psi_0 \frac{\partial}{\partial c}\Delta\varphi = -s\,\Delta\varphi + \psi_0' \frac{\partial \varphi_0}{\partial c}\Delta N^{(a)} \\ & \left(\text{with } \psi_0 = \psi(N_0^{(a)}),\ \psi_0' = \frac{d\psi}{dN}(N_0^{(a)})\right) \\ (3') & \Delta\varphi(0,c,t) = \Delta n(c,t) \\ (4') & \Delta n(\theta(c),t)\,\theta'(c) = \int m_0 \Delta\varphi\, da + \Delta N^{(a)} \int m_0' \varphi_0\, da \end{cases}$$

$$\left(\text{with } m_0 = m_0(a,c) = m(a,c,N_0^{(a)}),\ m_0' = \frac{\partial m}{\partial N}(a,c,N_0^{(a)})\right)$$

We will look for solutions of the form

$$\begin{cases} \Delta N^{(a)}(t) = e^{\lambda t}\,\overline{\Delta N}^{(a)} \\ \Delta\varphi(a,c,t) = e^{\lambda t}\,\overline{\Delta\varphi}(a,c) \\ \Delta n(c,t) = e^{\lambda t}\,\overline{\Delta n}(c) \end{cases}$$

where λ is a complex parameter. Then we get the new system

$$\begin{cases} (1'') & \overline{\Delta N}^{(a)} = \left(1 - \iint \pi_0' \varphi_0\right)^{-1} \iint \pi_0 \overline{\Delta\varphi} \\ (2'') & \left(\frac{\partial}{\partial a} - \psi_0 \frac{\partial}{\partial c}\right)\overline{\Delta\varphi} = -(s+\lambda)\,\overline{\Delta\varphi} + \overline{\Delta N}^{(a)} \psi_0' \frac{\partial \varphi_0}{\partial c} \\ (3'') & \overline{\Delta\varphi}(0,c) = \overline{\Delta n}(c) \\ (4'') & \overline{\Delta n}(\theta(c))\,\theta'(c) = \int m_0 \overline{\Delta\varphi}\, da + \Delta N^{(a)} \int m_0' \varphi_0\, da \end{cases}$$

We can here solve directly the first-degree system (2''), (3''):

writing
$$\overline{\Delta\varphi}(a,c) = S(a,c,\lambda)\,\overline{\overline{\Delta\varphi}}(a,c),$$

with
$$S(a,c,\lambda) = \exp(-a\lambda)\,S(a,c) = \exp\left(-\int_0^a (s(c+\psi_0 u)+\lambda)\,du\right)$$

we have

$$\left(\frac{\partial}{\partial a} - \psi_0 \frac{\partial}{\partial c}\right) \Delta\overline{\overline{\varphi}} = \psi_0' \frac{\partial \varphi_0}{\partial c} S^{-1} \Delta\overline{N}^{(a)}.$$

This gives

$$(8) \qquad \Delta\overline{\varphi}(a,c) = S(a,c,\lambda)\left[\Delta\overline{n}(c+a\psi_0) + Z_0(a,c,\lambda)\,\Delta\overline{N}^{(a)}\right]$$

with

$$(9) \qquad Z_0(a,c,\lambda) = \psi_0' \int_0^a \frac{\partial \varphi_0}{\partial c}(a-u, c+u\psi_0)\, S^{-1}(a-u, c+u\psi_0, \lambda)\, du.$$

Next, we solve (1″) for $\Delta\overline{N}^{(a)}$; setting

$$(10) \qquad Z_1(\lambda) = \iint \left[\frac{\partial \pi}{\partial N}(a,c,N_0^{(a)})\,\varphi_0(a,c) + \pi(a,c,N_0^{(a)})\, S(a,c,\lambda)\, Z_0(a,c,\lambda)\right] da\, dc$$

we have

$$(11) \qquad \Delta\overline{N}^{(a)} = (1 - Z_1(\lambda))^{-1} \iint \pi(a,c,N_0^{(a)})\, S(a,c,\lambda)\, \Delta\overline{n}(c+a\psi_0)\, da\, dc.$$

We are left with (4″), which gives

$$(12) \qquad \Delta\overline{n}(\theta(c))\,\theta'(c) = \int m(a,c,N_0^{(a)})\, S(a,c,\lambda)\, \Delta\overline{n}(c+a\psi_0)\, da + Z_2(c,\lambda)\, \Delta\overline{N}^{(a)},$$

where

$$(13) \qquad Z_2(c,\lambda) = \int m(a,c,N_0^{(a)})\, S(a,c,\lambda)\, Z_0(a,c,\lambda)\, da + \int \frac{\partial m}{\partial N}(a,c,N_0^{(a)})\, \varphi_0(a,c)\, da$$

In the general case, ~~with~~ allowing plateaux for θ, we should rather write an integrated version of (12): multiplying (12) by $\chi(\theta(c))$, χ a test function, and integrating, we get

$$(12') \qquad \int \chi(c)\,\Delta\overline{n}(c)\, dc = \iint m(a,c,N_0^{(a)})\, S(a,c,\lambda)\, \chi(\theta(c))\, \Delta\overline{n}(c+a\psi_0)\, da\, dc + \Delta\overline{N}^{(a)} \int Z_2(c,\lambda)\, \chi(\theta(c))\, dc$$

which should hold for any test function χ.

We want to know for which values of the complex parameter λ the system (11) + (12) (or (12′)) has a solution.

Let me explain informally how to do this in the general case. I omit many mathematical technalities that are needed to justify the process. Also, in special cases, things will be simpler, and even much simpler.

One first rewrite the right-hand sides of (11), (12'):

$$\iint \pi(a,c,N_0^{(a)})\, S(a,c,\lambda)\, \Delta\bar{n}\,(c+a\psi_0)\, da\, dc = \int Z_3(c,\lambda)\, \Delta\bar{n}(c)\, dc,$$

with

$$Z_3(c,\lambda) = \int \pi(a, c-a\psi_0, N_0^{(a)})\, S(a, c-a\psi_0, \lambda)\, da$$

Similarly

$$\iint m(a,c,N_0^{(a)})\, S(a,c,\lambda)\, \chi(\theta(c))\, \Delta\bar{n}(c+a\psi_0)\, da\, dc = \int T_\lambda^0 \chi(c)\, \Delta\bar{n}(c)\, dc,$$

with

$$T_\lambda^0 \chi(c) = \int m(a, c-a\psi_0, N_0^{(a)})\, S(a, c-a\psi_0, \lambda)\, \chi(\theta(c-a\psi_0))\, da$$

and thus the right hand side of (12') can be rewritten as

$$\int T_\lambda \chi(c)\, \Delta\bar{n}(c)\, dc$$

where

$$T_\lambda \chi(c) = T_\lambda^0 \chi(c) + (1 - Z_1(\lambda))^{-1} Z_3(c,\lambda) \int Z_2(u,\lambda)\, \chi(\theta(u))\, du$$

We have here a linear operator T_λ acting on test functions χ, which depends on the complex parameter λ.
On general principles of spectral theory, equation (12') has a solution if and only if 1 is an eigenvalue of T_λ.

It happens that, although the space of test functions is infinite-dimensional, the operator T_λ is of a kind (said "trace-class") such that the determinant

$$P(\lambda) = \det(1 - T_\lambda)$$

still makes sense. As T_λ depends holomorphically on λ, the same will be true for $P(\lambda)$ (it may have poles, however); what we want to now are the zeroes of P (as in the finite dimensional case, 1 will be an eigenvalue of T_λ if and only if $P(\lambda) = 0$)

The equilibrium will be stable if and only if P does not vanish in the half-plane $\mathrm{Re}\,\lambda \geq 0$.

In any case, there can be only <u>finitely many</u> zeroes of P in the half plane $\mathrm{Re}\,\lambda \geq 0$.
This is because P actually is near 1

when $Re(\lambda)$ is large, or when $|Im(\lambda)|$ is large and $Re(\lambda)$ stays bounded from below.

There are as many unstable directions at the equilibrium as there are zeroes of P in the half-plane $\{Re\lambda > 0\}$. Those zeroes of P that happen to be on the imaginary axis give rise to neutral directions. (In both cases, one should count zeroes with multiplicity).

4. The "constant loss of condition" case

4.1 We assume here that $\psi \equiv 1$ does not depend on the active population.
In this case, equation (2) in 2.2, page 6, can be solved directly using the initial condition provided by equation (3), page 7. One has

$$\varphi(a,c,t) = n(a+c, t-a)\, S(a,c),$$

with $$S(a,c) = \exp\left(-\int_c^{c+a} s(u)\,du\right)$$

Therefore, we are left with equations (1) and (4) which are rewritten as

(14) $$N^{(a)}(t) = \iint \pi(a,c,N^{(a)}(t))\, n(a+c,t-a)\, S(a,c)\,da\,dc\,,$$

(15) $$n(\theta(c),t)\,\theta'(c) = \int m(a,c,N^{(a)}(t),t)\, n(a+c,t-a)\, S(a,c)\,da\,.$$

As above, if one wants to allow plateaux for θ, one should take "$n(c)dc$" as a positive measure on $[\theta(0), c_{max}]$ (for each t). This means that, to make sense of equation (15) in this case, one should replace it by

(15') $$\int n(c)t\, \chi(c)\,dc = \iint m(a,c,N^{(a)}(t),t)\, n(a+c,t-a)\, S(a,c)\, \chi(\theta(c))\,da\,dc$$

which should hold for any test function χ on $[\theta(0), c_{max}]$.

4.2 Equilibrium in the unseasonal case:

The equations for equilibrium are now (see (1), (6), (7), p.12)

(16) $$n_0(\theta(c))\,\theta'(c) = \int m(a,c,N_0^{(a)})\, n_0(a+c)\, S(a,c)\,da$$

(17) $$N_0^{(a)} = \iint \pi(a,c,N_0^{(a)})\, n_0(a+c)\, S(a,c)\,da\,dc$$

with the integrated version of (16) being

(16') $$\int n_0(c)\,\chi(c)\,dc = \iint m(a,c,N_0^{(a)})\, n_0(a+c)\, S(a,c)\, \chi(\theta(c))\,da\,dc.$$

4.3 Linearized system at equilibrium

We have now $\psi_0' = 0$ in equation (2') page 13,

which gives much simpler equations. Indeed, keeping notations of pages 13 - 15, we have then

$$Z_0(a,c,\lambda) \equiv 0,$$

$$Z_1(\lambda) = \iint \frac{\partial \pi}{\partial N}(a,c,N_0^{(a)})\, n_0(a+c)\, S(a,c)\, da\, dc$$

(independent of λ)

$$Z_2(c,\lambda) = \int \frac{\partial m}{\partial N}(a,c,N_0^{(a)})\, n_0(a+c)\, S(a,c)\, da$$

(independent of λ)

and therefore equations (11), (12) page 14 give

(18) $$\Delta\bar N^{(a)} = (1-Z_1)^{-1} \iint \pi(a,c,N_0^{(a)})\, \Delta\bar n(a+c)\, S(a,c)\, e^{-a\lambda}\, da$$

(19) $$\Delta\bar n(\theta(c))\, \theta'(c) = \int m(a,c,N_0^{(a)})\, \Delta\bar n(a+c)\, S(a,c)\, e^{-a\lambda}\, da + \Delta\bar N^{(a)} \cancel{\int} Z_2(c)$$

or in integrated form

(19') $$\int X(c)\, \Delta\bar n(c)\, dc = \int T_\lambda X(c)\, \Delta\bar n(c)\, dc$$ (see p. 15)

with

$$T_\lambda X(c) = \int m(a,c-a,N_0^{(a)})\, S(a,c-a)\, X(\theta(c-a))\, e^{-a\lambda}\, da + (1-Z_1)^{-1} Z_3(c,\lambda) \int Z_2(u)\, X(\theta(u))\, du,$$

$$Z_3(c,\lambda) = \int \pi(a,c-a,N_0^{(a)})\, S(a,c-a)\, e^{-a\lambda}\, da$$

5. The "mature = active" case

5.1 We here assume that the fecundity rate is of the form

$$m(a,c,N^{(a)},t) = \hat m(N^{(a)})\, \tilde m(t)\, \pi(a,c,N^{(a)})$$

(with 1-periodic $\tilde m$, $\tilde m \equiv 1$ in the unseasonal case, and $\hat m$ decreasing with $N^{(a)}$)

It is now natural to introduce the active population with condition c, namely

(20) $$N^{(a)}(c,t) = \int \varphi(a,c,t)\ \pi(a,c,N^{(a)}(t))\, da$$

(again one should rather think, at any given time t, of the distribution of ~~popula~~ active population $N^{(a)}(c,t)\,dc$ as a positive measure on $[0, c_{max}]$, not assuming it has a density).

Then we have

(21) $$n(\theta(c),t)\ \theta'(c) = \hat{m}(N^{(a)}(t))\ \tilde{m}(t)\ N^{(a)}(c,t)$$

or rather, in integrated form

(21′) $$\int n(c,t)\ \chi(c)\, dc = \hat{m}(N^{(a)}(t))\ \tilde{m}(t) \int N^{(a)}(c,t)\ \chi(\theta(c))\, dc.$$

On the other hand, ~~even~~ in the general case (not assuming "mature = active") we have:

(22) $$\varphi(a,c,t) = n\Big(c + \int_{t-a}^{t} \psi(N^{(a)}(s))\, ds,\ t-a\Big) \exp\Big[-\int_{t-a}^{t} s\Big(c + \int_{u}^{t} \psi(N^{(a)}(s))\, ds\Big)\, du\Big]$$

(see page 7)

and therefore, using (21′)

(23) $$\int N^{(a)}(c,t)\ \chi(c)\, dc = \iint \varphi(a,c,t)\ \pi(a,c,N^{(a)}(t))\ \chi(c)\, da\, dc$$

$$= \iint \hat{m}(N^{(a)}(t-a))\ \tilde{m}(t-a)\ N^{(a)}(c,t-a)\ \tilde{\chi}(a,c)\, da\, dc,$$

where here

(24) $$\tilde{\chi}(a,c) = \exp\Big[-\int_{t-a}^{t} s\Big(\theta(c) - \int_{t-a}^{u} \psi(N^{(a)}(s))\, ds\Big)\, du\Big]$$
$$\pi\Big(a,\ \theta(c) - \int_{t-a}^{t} \psi(N^{(a)}(s))\, ds,\ N^{(a)}(t)\Big)$$
$$\chi\Big(\theta(c) - \int_{t-a}^{t} \psi(N^{(a)}(s))\, ds\Big)$$

5.2 Equilibrium in the unseasonal case

Let $N_0^{(a)}(c)\,dc$ be the equilibrium distribution, with active population $N_0^{(a)}$. Set $\psi_0 = \psi(N_0^{(a)})$. We have

(25) $$\int N_0^{(a)}(c)\ \chi(c)\, dc = \hat{m}(N_0^{(a)}) \iint N_0^{(a)}(c)\ \underbrace{\tilde{\chi}(a,c)}_{T\chi(c)}\, da\, dc,$$

where now

$$(26)\quad T\chi(c) = \int \exp\left[-\int_0^a s(\theta(c)-u\psi_0)\,du\right] \pi(a, \theta(c)-a\psi_0, N_0^{(a)})\, \chi(\theta(c)-a\psi_0)\, da$$

5.3 Linearized system at equilibrium, with constant loss of condition

[I will do later, if necessary, the calculation with variable loss; it is much more complicated, as always, that in the constant loss case, but follows the same principles]

In the "constant loss of condition + "mature = active" unseasonal case, equations (23), (24) are written

$$(27)\quad \int N^{(a)}(c,t)\,\chi(c)\,dc = \iint \hat{m}(N^{(a)}(t-a))\, N^{(a)}(c,t-a)\,\tilde{\chi}(a,c)\,da\,dc,$$

$$\tilde{\chi}(a,c) = \chi(\theta(c)-a)\,\pi(a, \theta(c)-a, N^{(a)}(t)) \exp\left[-\int_0^a s(\theta(c)-u)\,du\right]$$

Equilibrium satisfies

$$(28)\quad \int N_0^{(a)}(c)\,\chi(c)\,dc = \hat{m}(N_0^{(a)}) \iint N_0^{(a)}(c)\,\tilde{\chi}(a,c)\,da\,dc$$

(with $N_0^{(a)}$ instead of $N^{(a)}(t)$ in the formula for $\tilde{\chi}$).

Writing $N^{(a)}(c,t) = N_0^{(a)}(c) + \Delta N^{(a)}(c,t)$, and keeping only first-order terms, we have

$$(29)\quad \int \Delta N^{(a)}(c,t)\,\chi(c)\,dc = (\mathrm{I}) + (\mathrm{II}) + (\mathrm{III}), \quad \text{with}$$

$$(30)\quad \begin{cases} (\mathrm{I}) = \hat{m}_0' \iint \Delta N^{(a)}(t-a)\, N_0^{(a)}(c)\, \hat{S}(a,c)\, \pi(a, \theta(c)-a, N_0^{(a)})\, \chi(\theta(c)-a)\,da\,dc \\ (\mathrm{II}) = \hat{m}_0 \iint \Delta N^{(a)}(c,t-a)\, \hat{S}(a,c)\, \pi(a, \theta(c)-a, N_0^{(a)})\, \chi(\theta(c)-a)\,da\,dc \\ (\mathrm{III}) = \hat{m}_0\, \Delta N^{(a)}(t) \iint N_0^{(a)}(c)\, \hat{S}(a,c)\, \frac{\partial \pi}{\partial N}(a, \theta(c)-a, N_0^{(a)})\, \chi(\theta(c)-a)\,da\,dc \end{cases}$$

and

$$\hat{m}_0 = \hat{m}(N_0^{(a)}), \qquad \hat{m}_0' = \frac{\partial}{\partial N}\hat{m}(N_0^{(a)})$$

$$\hat{S}(a,c) = \exp\left[-\int_0^a s(\theta(c)-u)\,du\right]$$

Writing as before $\Delta N^{(a)}(c,t) = \overline{\Delta N}^{(c)}(c)\, e^{\lambda t}$, $\Delta N^{(a)}(t) = \overline{\Delta N}^{(a)} e^{\lambda t}$, we get:

$$(29') \quad \int \overline{\Delta N}^{(a)}(c)\ \chi(c)\ dc = (I') + (II') + (III'),$$

$$(I') = \hat{m}_0'\ \overline{\Delta N}^{(a)} \iint N_0^{(a)}(c)\ \hat{S}(a,c)\ \pi(a, \theta(c)-a, N_0^{(a)})\ \chi(\theta(c)-a)\, e^{-\lambda a}\, da\, dc$$

$$(30') \quad (II') = \hat{m}_0 \iint \overline{\Delta N}^{(a)}(c)\ \hat{S}(a,c)\, \pi(a, \theta(c)-a, N_0^{(a)})\ \chi(\theta(c)-a)\, e^{-\lambda a}\, da\, dc$$

$$(III') = \hat{m}_0\ \overline{\Delta N}^{(a)} \iint N_0^{(a)}(c)\ \hat{S}(a,c)\ \frac{\partial \pi}{\partial N}(a, \theta(c)-a, N_0^{(a)})\ \chi(\theta(c)-a)\, da\, dc$$

I will stop here this calculation, and come back later to it if needed.

6. The toy-model.

6.1 We assume here that "mature = active", constant loss of condition and maximal ~~birth~~ ~~at~~ condition at birth.

In this case, condition is a useless variable.

We write (as in §5, but without c)

$$(31) \quad m(a, N^{(a)}, t) = \hat{m}(N^{(a)})\ \tilde{m}(t)\ \pi(a, N^{(a)})$$

and now have

$$(32) \quad N^{(a)}(t) = \int \varphi(a,t)\ \pi(a, N^{(a)}(t))\, da$$

with

$$(33) \quad \varphi(a,t) = n(t-a)\ S(a)$$

$$(34) \quad S(a) = \exp\left(-\int_0^a s(u)\, du\right)$$

and

$$(35) \quad n(t) = \tilde{m}(t)\ \hat{m}(N^{(a)}(t))\ N^{(a)}(t).$$

This allows by substitution to write the single equation

$$(36) \quad N^{(a)}(t) = \int S(a)\, \pi(a, N^{(a)}(t))\ \tilde{m}(t-a)\ \hat{m}(N^{(a)}(t-a))\, N^{(a)}(t-a)\, da$$