

THE NUMERICAL TOY MODEL

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This is a seasonal mode, fecundity being 1-periodic in time.

We call A_0 the maturation age, A_1 the maximal age and take the survival rate at age a to be

$$S(a) = 1 - \frac{a}{A_1}$$

The mature population $N(t)$ is

$$N(t) = \int_{A_0}^{A_1} S(a)n(t-a) da$$

where the number $n(t)\Delta t$ of births between t and $t + \Delta t$ is given by

$$n(t) = \int_{A_0}^{A_1} S(a)n(t-a)m(N(t), t) da$$

The fecundity rate $m(N, t)$ will be assumed to have the following form

$$m(N, t) = \bar{m}_\gamma(N)\tilde{m}_\rho(t)m_0$$

where

$$\bar{m}_\gamma(N) = \begin{cases} 1 & \text{for } N \leq 1 \\ N^{-\gamma} & \text{for } N \geq 1 \end{cases} \quad (\gamma > 0)$$

and

$$\tilde{m}_\rho(t) = \begin{cases} 0 & \text{for } 0 < t < \rho \bmod 1 \\ 1 & \text{for } \rho \leq t \leq 1 \bmod 1 \end{cases}$$

There are thus five parameters $A_0, A_1, \gamma, \rho, m_0$ in the model.

The exponent γ expresses how strongly fecundity depends on density above the threshold $N_{cr} = 1$.

The parameter m_0 is fecundity in the summer at zero density.

The parameter ρ is the seasonality parameter. When $\rho = 0$ we have the unseasonal model.

Because of the special form of the fecundity rate, we have just one equation

$$\begin{aligned} n(t) &= m(N(t), t)N(t) \\ \Rightarrow N(t) &= \int_{A_0}^{A_1} m_0 S(a)N(t-a)\bar{m}_\gamma(N(t-a))\tilde{m}_\rho(t-a) da \end{aligned}$$

The population has been scaled so that the cutoff level is $N_{cr} = 1$.

⁰The original manuscript was converted into 'tex' by Carlos Matheus. Up to some minor modifications, this article is faithful to the original text.

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It makes also sense to scale differently the population, replacing the parameter m_0 by a parameter N_{cr} : one now takes

$$m(\widehat{N}, t) = \widehat{m}_\gamma(\widehat{N})\widetilde{m}_\rho(t) \quad (\text{no } m_0!)$$

with now

$$\widehat{m}_\gamma(\widehat{N}) = \begin{cases} N_{cr}^{-\gamma} & \text{for } \widehat{N} \leq N_{cr} \\ \widehat{N}^{-\gamma} & \text{for } \widehat{N} > N_{cr} \end{cases}$$

The equation for \widehat{N} becomes

$$\widehat{N}(t) = \int_{A_0}^{A_1} S(a)\widehat{N}(t-a)\widehat{m}_\gamma(\widehat{N}(t-a))\widetilde{m}_\rho(t-a)da$$

The relation between N and \widehat{N} is

$$m_0 = N_{cr}^{-\gamma}, \quad N = N_{cr}^{-1}\widehat{N}, \quad \widehat{N} = m_0^{-1/\gamma}N$$

The second scaling (\widehat{N}) is more useful when discussing equilibria.

2. EQUILIBRIUM IN THE UNSEASONAL MODEL

In order to have a non trivial equilibrium when $\rho = 0$, we must have

$$\int_{A_0}^{A_1} S(a) da = \frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2 > N_{cr}^{+\gamma} = m_0^{-1},$$

a condition that we will always assume: with $A_1 \sim 2$, $A_0 \sim 0.1$, this amounts to $m_0 \gtrsim 1.1$.

Then, the equilibrium is given by

$$\widehat{N}_0 = \left[\frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2\right]^{1/\gamma} > N_{cr}$$

It does not depend on N_{cr} . We can actually make the following observation:

If, for a given cutoff level N_{cr}^0 , we have a solution $\widehat{N}(t)$, $t \in \mathbb{R}$, with

$$\widehat{N}(t) \geq N_{cr}^0 \quad \text{for all } t$$

then $\widehat{N}(t)$ will also be a solution for all cutoff levels $N_{cr} < N_{cr}^0$.

In particular, the cut-off level does not enter in the discussion of the stability of the equilibrium.

For solutions $\widehat{N}(t)$ above cut-off level, we have just

$$\widehat{N}(t) = \int_{A_0}^{A_1} S(a)\widehat{N}^{1-\gamma}(t-a) da$$

Writing $\widehat{N}(t) = \widehat{N}_0 + \widehat{\Delta N}(t)$ and keeping only first-order terms gives

$$\widehat{\Delta N}(t) = \left(\int_{A_0}^{A_1} S(a)\widehat{N}_0^{-\gamma}\widehat{\Delta N}(t-a) da\right)(1-\gamma)$$

or

$$\widehat{\Delta N}(t) = \frac{(1-\gamma)}{\frac{A_1}{2}(1-A_0/A_1)^2} \int_{A_0}^{A_1} S(a)\widehat{\Delta N}(t-a) da$$

The eigenvalues λ ($\widehat{\Delta N}(t) = \overline{\Delta N}e^{+\lambda t}$) are given by

$$F(\lambda) = \int_{A_0}^{A_1} S(a)e^{-a\lambda} da = \frac{A_1(1-A_0/A_1)^2}{2(1-\gamma)}$$

Observe that, if $\operatorname{Re} \lambda \geq 0$ ($\Rightarrow |e^{-a\lambda}| \leq 1$) we have

$$\left| \int_{A_0}^{A_1} S(a)e^{-a\lambda} da \right| \leq \int_{A_0}^{A_1} S(a) da = \frac{A_1}{2}(1 - A_0/A_1)^2$$

and therefore the equilibrium is stable as long as

$$\left| \frac{1}{1-\gamma} \right| > 1 \iff 0 < \gamma < 2$$

One can compute F :

$$F(\lambda) = \left(\frac{1}{\lambda} \left(1 - \frac{A_0}{A_1} \right) - \frac{1}{\lambda^2 A_1} \right) e^{-A_0 \lambda} + \frac{1}{\lambda^2 A_1} e^{-A_1 \lambda}$$

When $\lambda = -iu$, this gives

$$\begin{aligned} F(-iu) &= \left(iu^{-1} \left(1 - \frac{A_0}{A_1} \right) + \frac{1}{u^2 A_1} \right) (\cos A_0 u + i \sin A_0 u) \\ &\quad - \frac{1}{u^2 A_1} (\cos A_1 u + i \sin A_1 u) \end{aligned}$$

The number of unstable directions, i.e. the number of solutions of $F(\lambda) = \frac{A_1(1-A_0/A_1)^2}{2(1-\gamma)}$ in the half plane $\operatorname{Re} \lambda > 0$, is equal to the number of times that $F(-iu)$ turns around $\frac{A_1(1-A_0/A_1)^2}{2(1-\gamma)}$ (< 0) as u goes from $-\infty$ to $+\infty$ (we have $F(-iu) \rightarrow 0$ as $|u| \rightarrow +\infty$).

The imaginary part of $F(-iu)$ is

$$\operatorname{Im} F(-iu) = u^{-1} \left(1 - \frac{A_0}{A_1} \right) \cos A_0 u + u^{-2} A_1^{-1} (\sin A_0 u - \sin A_1 u)$$

We have $F(0) = \frac{A_1}{2} \left(1 - \frac{A_0}{A_1} \right)^2$

I suspect (and this could be checked numerically if needed, but there is no urgency) that for every integer $k \geq 0$, there is exactly one value u_k near $(\frac{\pi}{2} + k\pi)A_0^{-1}$ for which

$$\operatorname{Im} F(-iu_k) = 0,$$

and that the u_k give all positive roots of $\operatorname{Im} F(-iu) = 0$; the negative roots are then the $-u_k$, $k \geq 0$.

This is certainly true if k is large enough: if we look for the roots of

$$f(u) = \frac{A_1 u \operatorname{Im} F(-iu)}{A_1 - A_0} = \cos A_0 u + \frac{1}{u(A_1 - A_0)} (\sin A_0 u - \sin A_1 u)$$

which lie between $k\pi A_0^{-1}$ and $(k+1)\pi A_0^{-1}$, we have

$$\left| \frac{1}{u(A_1 - A_0)} (\sin A_0 u - \sin A_1 u) \right| \leq \frac{2A_0}{k\pi(A_1 - A_0)}$$

hence $|\cos A_0 u| \leq \frac{2A_0}{k\pi(A_1 - A_0)}$.

On the other hand

$$\begin{aligned} (uf(u))' &= -A_0 u \sin A_0 u + \cos A_0 u \\ &\quad + \frac{1}{A_1 - A_0} (A_0 \cos A_0 u - A_1 \cos A_1 u) \end{aligned}$$

where

$$\left| \cos A_0 u + \frac{1}{(A_1 - A_0)} (A_0 \cos A_0 u - A_1 \cos A_1 u) \right| \leq \frac{2A_1}{A_1 - A_0}$$

and, if $f(u) = 0$

$$|\sin A_0 u| \geq \sqrt{1 - \frac{4A_0^2}{k^2\pi^2(A_1 - A_0)^2}}$$

therefore $uf(u)$ will be *monotone* in the interval where $|\cos A_0 u| \leq \frac{2A_0}{k\pi(A_1 - A_0)}$ as soon as

$$\left(\frac{\pi}{2} + k\pi\right) \sqrt{1 - \frac{4A_0^2}{k^2\pi^2(A_1 - A_0)^2}} > \frac{2A_1}{A_1 - A_0}.$$

Taking $k \geq 1$, we are ok as long as

$$\frac{3\pi}{2} \sqrt{1 - \frac{4A_0^2}{\pi^2(A_1 - A_0)^2}} > \frac{2A_1}{A_1 - A_0}$$

or

$$4A_1^2 + 9A_0^2 \leq \frac{9\pi^2}{4}(A_1 - A_0)^2$$

which is perfectly safe for reasonable values of A_0, A_1 .

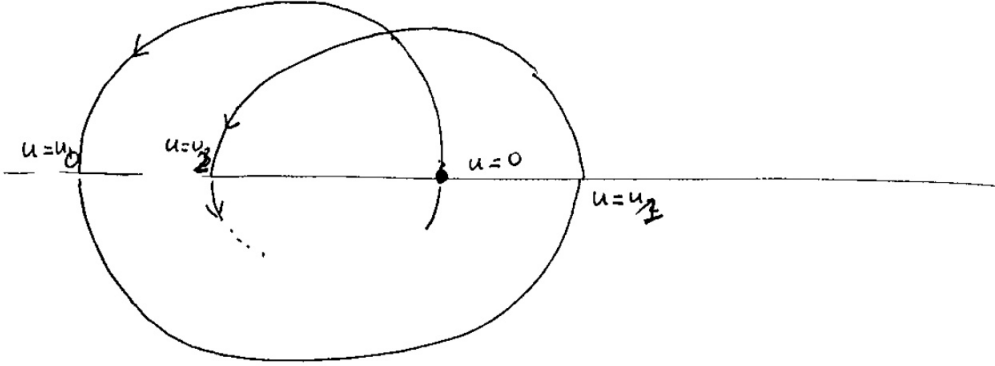
The case $k = 0$ must be investigated directly, but still looks ok for $A_0 = 0.1, A_1 = 2$.

Assuming the above to be true, we note that $\operatorname{Re} F(-iu)$ is equal to

$$\operatorname{Re} F(-iu) = -u^{-1} \left(1 - \frac{A_0}{A_1}\right) \sin A_0 u + \frac{1}{u^2 A_1} (\cos A_0 u - \cos A_1 u)$$

and it is not difficult to check that $\operatorname{Re} F(-iu_k)$ has the sign of $-\sin A_0 u_k$, i.e. is negative for even k and positive for odd k .

Thus, $F(-iu)$ behaves like this



The number of turns mentioned above is twice (because of $u < 0$) the number of integers k with

$$F(-iu_{2k}) < \frac{A_1(1 - A_0/A_1)^2}{2(1 - \gamma)}$$

(the sequence $F(-iu_{2k})$ increases to 0). Therefore, the equilibrium is stable if and only if

$$\gamma < 1 + \frac{A_1(1 - A_0/A_1)^2}{2|F(-iu_0)|}$$

(Exercise: compute $F(-iu_0)$ [for some values of A_0] and the corresponding values of γ).

3. GENERAL PROPERTIES OF THE DYNAMICS

3.1. The unseasonal case. A reasonable (but not unique) choice for the phase space is the space of continuous functions $\widehat{N}(t)$, taking some positive values, defined on $[-A_1, 0]$ and satisfying

$$\widehat{N}(0) = \int_{A_0}^{A_1} S(a)\widehat{N}(-a)\widehat{m}_\gamma(\widehat{N}(-a)) da$$

Call this space Y . It is also reasonable to consider the space \widetilde{Y} of positive continuous functions defined on $(-\infty, 0]$ which satisfy

$$\widehat{N}(t) = \int_{A_0}^{A_1} S(a)\widehat{N}(t-a)\widehat{m}_\gamma(\widehat{N}(t-a)) da, \quad \text{for all } t \leq 0.$$

In both cases, the relations define a closed subspace of the space of continuous functions.

In the unseasonal case, the dynamics define a semi-group of transformations $(T^t)_{t \geq 0}$ from Y to itself

$$T^{t_1} \circ T^{t_2} = T^{t_1+t_2}, \quad t_1, t_2 \geq 0.$$

Because $A_0 > 0$, we can actually compute T^t for small t : for $0 \leq s \leq A_0$, $0 \geq t \geq -A_1$

$$T^s \widehat{N}(t) \begin{cases} = \widehat{N}(t+s) & \text{if } -A_1 \leq t \leq -s \\ = \int_{A_0}^{A_1} S(a)\widehat{N}(t+s-a)\widehat{m}_\gamma(\widehat{N}(t+s-a)) da & \text{if } -s \leq t \leq 0 \end{cases}$$

The dynamics on Y are not invertible: one cannot define T^t for $t < 0$.

On the other hand, one can define also $\widetilde{T}^t : \widetilde{Y} \rightarrow \widetilde{Y}$ for $t \geq 0$ by the same formula; these dynamics are invertible: for $s \leq 0$

$$\widetilde{T}^s \widehat{N}(t) = \widehat{N}(t+s), \quad \forall t \leq 0$$

Finally one has a “forget” map: $\widetilde{Y} \xrightarrow{\pi} Y$ (restricting N to $[-1, 0]$), which gives a commutative diagram

$$\begin{array}{ccc} \widetilde{Y} & \xrightarrow{\widetilde{T}^s} & \widetilde{Y} \\ \downarrow \pi & & \downarrow \pi \\ Y & \xrightarrow{T^s} & Y \end{array}$$

The map π is *not* surjective: actually most elements of Y cannot have an infinite past.

Boundedness of solutions. If $\gamma \geq 1$, we have $\widehat{N}\widehat{m}_\gamma(\widehat{N}) \leq N_{cr}^{1-\gamma}$ for all \widehat{N} , hence

$$\widehat{N}(t) \leq \frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2 N_{cr}^{1-\gamma} = \widehat{N}_{\max}$$

We will not be interested in the case $\gamma < 1$. (The bound is different in this case)

Differentiability of solutions. We can rewrite the equation as

$$\widehat{N}(t) = \int_{t-A_1}^{t-A_0} S(t-u)\widehat{N}(u)\widehat{m}_\gamma(\widehat{N}(u)) du$$

which gives

$$\frac{d\widehat{N}}{dt}(t) = \left(1 - \frac{A_0}{A_1}\right)\widehat{N}(t-A_0)\widehat{m}_\gamma(\widehat{N}(t-A_0)) - \frac{1}{A_1} \int_{t-A_1}^{t-A_0} \widehat{N}(u)\widehat{m}_\gamma(\widehat{N}(u)) du$$

which gives, for $\gamma \geq 1$

$$\left| \frac{d\widehat{N}}{dt}(t) \right| \leq \left(1 - \frac{A_0}{A_1}\right) N_{cr}^{1-\gamma}$$

The formula also shows that solutions become smoother and smoother as time runs.

In particular, every function in \widetilde{Y} is actually *infinitely differentiable*, and we could compute bounds for all derivatives.

I will now give an idea of a more involved result: that active population will always, after some transition period, stay *above* a determined level independent of the initial conditions.

Consider for simplicity a solution $N(t)$, $t \leq 0$, with infinite past, i.e. an element of \widetilde{Y} . I will prove that if $N(0)$ is small enough, then $N(t) \rightarrow 0$ as $t \rightarrow -\infty$ exponentially fast.

To prove this needs several steps. It is easier for this result to consider the first scaling, with cutoff at 1 ($N = \widehat{N}/N_{cr}$).

① The estimates on the last page read

$$N(t) \leq N_{\max} = m_0 \frac{A_1}{2} (1 - A_0/A_1)^2$$

$$\left| \frac{dN}{dt}(t) \right| \leq m_0 (1 - A_0/A_1)$$

They easily imply that there exists N_1 such that

$$N(t_0) \leq N_1 \Rightarrow N(t) \leq 1 \quad \text{for all } t \in [t_0 - A_1, t_0 - A_0]$$

Also, if $N(t_0) \leq N_1$, we will then have

$$N(t_0) = m_0 \int_{A_0}^{A_1} N(t_0 - a)S(a) da,$$

where $m_0 \int_{A_0}^{A_1} S(a) da = m_0 \frac{A_1}{2} (1 - A_0/A_1)^2 = \theta > 1$, therefore there exists $t_1 \in [t_0 - A_1, t_0 - A_0]$ with $N(t_1) \leq \theta^{-1}N(t_0)$

② Therefore, if $N(0) \leq N_1$, there exists a decreasing sequence

$$t_0 = 0 > t_1 > t_2 > \dots$$

with

$$A_1 \geq t_i - t_{i+1} \geq A_0$$

and

$$N(t_i) \leq \theta^{-i}N_1$$

③ Assume that $N(t) \leq N_1$; then

$$N(t) = m_0 \int_{A_0}^{A_1} N(t-a)S(a) da$$

Let \bar{N} the maximum value of $N(t-a)$, $A_0 \leq a \leq A_1$. It is clear that the integral must be bigger or equal to the value it takes if we have

$$N(t-A_1) = \bar{N}, \quad N(t-A_1+s) = \bar{N} - m_0(1-A_0/A_1)s$$

for $0 \leq s \leq \bar{N}m_0^{-1}(1-A_0/A_1)^{-1}$, $N(t-A_1+s) = 0$ if $\bar{N}m_0^{-1}(1-A_0/A_1)^{-1} \leq s \leq A_1 - A_0$. (Recall that $|\frac{dN}{dt}| \leq m_0(1-A_0/A_1)$). In this case, the integral is equal to

$$\begin{aligned} & m_0 \int_{A_1 - \bar{N}m_0^{-1}(1-A_0/A_1)^{-1}}^{A_1} \left(1 - \frac{a}{A_1}\right) (\bar{N} - m_0(1-A_0/A_1)(A_1-a)) da \\ = & m_0 \int_0^{\bar{N}m_0^{-1}(1-A_0/A_1)^{-1}} \frac{s}{A_1} (\bar{N} - m_0(1-A_0/A_1)s) ds \\ = & m_0^{-1} A_1^{-1} (1-A_0/A_1)^{-2} \int_0^{\bar{N}} u(\bar{N}-u) du \\ = & \frac{1}{6} \bar{N}^3 m_0^{-1} A_1^{-1} (1-A_0/A_1)^{-2} \end{aligned}$$

We have therefore

$$N(t) \geq \frac{1}{6} \bar{N}^3 m_0^{-1} A_1^{-1} (1-A_0/A_1)^{-2}$$

or

$$\max_{t-A_1 \leq s \leq t-A_0} N(s) \leq [6m_0 A_1 (1-A_0/A_1)^2]^{1/3} (N(t))^{1/3} = C(N(t))^{1/3}.$$

(4) If $N(t) \leq (N_1/C)^3$ and $N(t) \leq N_1$, we can apply this twice, because we get $\max_{t-A_1 \leq s \leq t-A_0} N(s) \leq N_1$. We obtain

$$\max_{t-2A_1 \leq s \leq t-2A_0} N(s) \leq C \left(\max_{t-A_1 \leq s \leq t-A_0} N(s) \right)^{1/3} \leq C^{4/3} N(t)^{1/9}$$

(5) Let finally $t \ll 0$. For reasonable values of A_0, A_1 , the interval $[t+2A_0, t+2A_1]$ has length $> A_1$ (if $A_1 > 2A_0$) and thus, must contain one of the points t_i of (2).

One has $t_i \geq -iA_1 \Rightarrow t \geq -(i+2)A_1 \Rightarrow i \geq \frac{|t|}{A_1} - 2$. Therefore,

$$N(t_i) \leq N_1 \theta^2 \theta^{-|t|/A_1}$$

and we deduce from (4) that

$$\underline{N(t) \leq C^{4/3} N_1^{1/9} \theta^{2/9} \theta^{-|t|/9A_1}}$$

showing the desired result.

Remark 3.1. with more work, one can compute the exact exponential rate; $N(t)$, for $t \rightarrow -\infty$ is of order $e^{\lambda t}$ where

$$m_0 \int_{A_0}^{A_1} e^{-\lambda a} S(a) da = 1, \quad \lambda > 0.$$

3.2. The seasonal case. A standard procedure is to view the time-periodic evolution equation as an *autonomous* equation, taking time into the phase space.

Thus, our phase space now should¹ be $Y \times \mathbb{R}/\mathbb{Z}$, where Y is the same space than² in page (6). The semi-group is now as follows (for $0 \leq s \leq A_0$)

$$T^s(\widehat{N}, t) = (\widehat{N}^s, t + s), \quad \text{where } t + s \text{ is taken mod } \mathbb{Z}$$

and

$$\begin{cases} \widehat{N}^s(u) = \widehat{N}(u + s) & \text{if } -A_1 \leq u \leq -s \\ \widehat{N}^s(u) = \int_{A_0}^{A_1} S(a) \widehat{N}(u + s - a) \widehat{m}_\gamma(\widehat{N}(u + s - a)) \widetilde{m}_\rho(t + u + s - a) da \end{cases}$$

To understand the long-term behaviour of solutions, it is enough actually to see how trajectories come back to $Y \times \{0\}$.

[This is a general method; in our case, even more is true do the special nature of the evolution equation: given an initial condition $(\widehat{N}^0, 0)$ in $Y \times \{0\}$, if we know $T^k(\widehat{N}^0, 0) = (\widehat{N}^k, 0)$ for *all positive integers* we know *completely* the trajectory because \widehat{N}^k determines the solution between time $k - A_1$ and k , and it is reasonable to assume $A_1 \geq 1$]

Therefore, our basic dynamical object is the map $T = T^1 : Y \times \{0\} \rightarrow Y \times \{0\}$. (There is nothing special with time 0. We could as well consider any $t_0 \in \mathbb{R}/\mathbb{Z}$ and consider $T : Y \times \{t_0\} \rightarrow Y \times \{t_0\}$; this map is conjugated to the preceding one)

As in the unseasonal case, we can also consider the space \widetilde{Y} and the *invertible* map

$$T : \widetilde{Y} \rightarrow \widetilde{Y}$$

As before, solutions are *bounded* (same proof)

Because we have taken a *discontinuous* \widetilde{m}_ρ , solutions will be Lipschitz but *not* C^1 ; indeed

$$\frac{d\widehat{N}}{dt}(t) = \left(1 - \frac{A_0}{A_1}\right) \widehat{N}(t - A_0) \widehat{m}_\gamma(\widehat{N}(t - A_0)) \widetilde{m}_\rho(t - A_0) - \frac{1}{A_1} \int_{t - A_1}^{t - A_0} \widehat{N}(u) \widehat{m}_\gamma(\widehat{N}(u)) \widetilde{m}_\rho(u) du$$

with discontinuities when $t \equiv A_0$ or $A_0 + \rho \pmod{\mathbb{Z}}$.

(So solutions are C^1 piecewise, with two ‘‘angles’’ in each year).

The more difficult result, that solutions stay *above* a certain level provided fecundity at small density is high enough, is discussed below, together with equilibria.

4. EQUILIBRIUM IN THE SEASONAL CASE

4.1. Recall that in the unseasonal case, one gets a nontrivial equilibrium (= constant non zero mature population) as soon as

$$\frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2 > N_{cr}^\gamma = m_0^{-1},$$

i.e. fecundity at small density is high enough. [When on the opposite one has $\frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2 < m_0^{-1}$, all solutions collapse to zero exponentially fast.]

In the seasonal case, an equilibrium should be interpreted as a *fixed point* of the map T (distinct from the trivial fixed point 0).

¹This is not quite true, but this mistake doesn’t affect the conclusions: see the subsection ‘‘Visualizing the attractor(s): the $N(t), N(t+1), N(t+2)$ representation’’ of Jean-Christophe Yoccoz’s subsequent notes *Informal commentaries on the numerical investigation of the ‘‘toy model’’* [H. Birkeland – J.-C.Y. – Orsay – Sept. 98] (available at the webpage dedicated to his mathematical archives, for instance).

²I.e., the beginning of Subsection 3.1.

To see under which circumstances one gets such an equilibrium, let us consider the evolution equation (in the first scaling) at *low density*:

$$N(t) = m_0 \int_{A_0}^{A_1} S(a)N(t-a)\tilde{m}_\rho(t-a) da,$$

which is a *linear* equation. Now, a ‘‘Perron–Frobenius-like’’ theorem tells us the following: there exists a *unique* (up to scaling) 1-*periodic positive* function \tilde{N} , and a unique *positive* real number $\Lambda = \Lambda(\rho)$ such that

$$\tilde{N}(t) = \Lambda \int_{A_0}^{A_1} S(a)\tilde{N}(t-a)\tilde{m}_\rho(t-a) da.$$

The discussion now runs as follows

- if $m_0\Lambda < 1$, all solutions will collapse exponentially fast to zero: no non trivial equilibrium (or anything else)
- if $m_0\Lambda \geq 1$, it is not unreasonable to expect a non trivial equilibrium (for the non linear equation of course).

I will try to prove below that such a non trivial equilibrium exists.

The question of the *uniqueness* of such a non trivial equilibrium seems far from obvious.

To prove the existence of a non trivial equilibrium, one considers the map S defined by

$$S(N)(t) = m_0 \int_{A_0}^{A_1} S(a)N(t-a)\bar{m}_\gamma(N(t-a))\tilde{m}_\rho(t-a) da$$

where N is a *positive 1-periodic* continuous function and $S(N)$ has the same properties. We want to find a *fixed point* of S .

We would like to apply the so-called ‘‘Leray–Schauder–Tichonoff theorem’’ which says the following:

If, in a topological vector space E , we have a *convex compact* subset K and a *continuous* map S sending K to K , then S has *at least* one fixed point in K .

The problem here is to take the right E and K .

There is no problem with E : E is just the space of *continuous 1-periodic function*, which is a Banach space with the usual *sup-norm*.

For K , I want to take a subset of the form $K(\varepsilon_0, N_{\max}, L)$ with a convenient choice of parameters $\varepsilon_0, N_{\max}, L$, and defined as follows.

We scale the function \tilde{N} at the end³ of page (11) in order to have (for instance)

$$\max_{0 \leq t \leq 1} \tilde{N}(t) = 1.$$

Then $K(\varepsilon, N_{\max}, L)$ is the set of *continuous 1-periodic functions* (i.e. elements of E) which moreover satisfy

- (i) for all t $\varepsilon_0\tilde{N}(t) \leq N(t) \leq N_{\max}$
- (ii) for all t, t' $|N(t) - N(t')| \leq L|t - t'|$.

This is easily seen to be a *compact convex* subset of E

What remains to be done is to show that we can select $\varepsilon_0, N_{\max}, L$ such that S sends K into K .

We assume as before $\gamma \geq 1$. Then, whatever N , we have

$$N(t-a)m_\gamma(N(t-a)) \leq 1$$

³I.e., 21 lines above

and therefore

$$S(N)(t) \leq m_0 \int_{A_0}^{A_1} S(a) \tilde{m}_\rho(t-a) da \leq m_0 \frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2$$

Therefore, it is reasonable to take

$$N_{\max} = m_0 \frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2$$

Next comes the choice of L . One has

$$S(N)(t) = m_0 \int_{t-A_1}^{t-A_0} S(t-u) N(u) \bar{m}_\gamma(N(u)) \tilde{m}_\rho(u) du$$

hence

$$\begin{aligned} \frac{dS(N)}{dt}(t) &= \left(1 - \frac{A_0}{A_1}\right) m_0 N(t-A_0) \bar{m}_\gamma(N(t-A_0)) \tilde{m}_\rho(t-A_0) \\ &\quad - \frac{m_0}{A_1} \int_{t-A_1}^{t-A_0} N(u) \bar{m}_\gamma(N(u)) \tilde{m}_\rho(u) du \end{aligned}$$

(with discontinuities when $t = A_0$ or $A_0 + \rho \bmod \mathbb{Z}$) giving again

$$\left| \frac{dS(N)}{dt}(t) \right| \leq \left(1 - \frac{A_0}{A_1}\right) m_0$$

We will take

$$L = \frac{\left(1 - \frac{A_0}{A_1}\right) m_0}{\varepsilon_0}$$

So far so good. There remains to choose conveniently ε_0 .

We will prove that any ε_0 *small enough* will do.

Let N an element of $K(\varepsilon_0, N_{\max}, L)$. We distinguish two cases

a) for $\rho \leq t \leq 1$, we have not only (i) but

$$\varepsilon_0 \tilde{N}(t) \leq N(t) \leq 1.$$

Then, $\bar{m}_\gamma(N(t)) = 1$ whenever $\tilde{m}_\rho(t) \neq 0$. Therefore

$$\begin{aligned} S(N)(t) &= m_0 \int_{A_0}^{A_1} S(a) N(t-a) \tilde{m}_\rho(t-a) da \\ &\geq m_0 \varepsilon_0 \int_{A_0}^{A_1} S(a) \tilde{N}(t-a) \tilde{m}_\rho(t-a) da = m_0 \varepsilon_0 \Lambda \tilde{N}(t) \\ &\geq \varepsilon_0 \tilde{N}(t) \end{aligned}$$

so any ε_0 will do in this case.

b) there exists $t_0 \in [\rho, 1]$ with $N(t_0) \geq 1$.

We assume $A_1 - A_0 > 1$ (it seems reasonable)

Because of (ii), we can find an interval J containing t_0 , contained in $[\rho, 1]$, of length

$$\ell = \frac{\min\left(\frac{1}{2L}, A_1 - A_0 - 1, 1 - \rho\right)}{2}$$

such that

$$\frac{1}{2} \leq N(t) \leq N_{\max} \quad \text{for all } t \in J.$$

For such t we will have

$$\begin{aligned} N(t)\overline{m}_\gamma(N(t)) &\geq N_{\max}^{1-\gamma} \quad (\text{if } N(t) \geq 1) \\ &\geq 1/2 \quad (\text{if } 1/2 \leq N(t) \leq 1) \end{aligned}$$

Now, when we write

$$S(N)(t) = \int_{t-A_1}^{t-A_0} m_0 S(t-u) N(u) \overline{m}_\gamma(N(u)) \tilde{m}_\rho(u) du$$

we can find an integer $k \in \mathbb{Z}$ such that $J+k$ is contained in $[t-A_1, t-A_0]$ (because the length ℓ of J is smaller $A_1 - A_0 - 1$); on $J+k$ we will have

$$\tilde{m}_\rho(u) = 1$$

$$N(u)\overline{m}_\gamma(N(u)) \geq \min\left(\frac{1}{2}, N_{\max}^{1-\gamma}\right).$$

Therefore

$$\begin{aligned} S(N)(t) &\geq m_0 \left[\int_{J+k} S(t-u) du \right] \min\left(\frac{1}{2}, N_{\max}^{1-\gamma}\right) \\ &\geq m_0 \frac{\ell^2}{2A_1} \min\left(\frac{1}{2}, N_{\max}^{1-\gamma}\right) = \varepsilon_0 \geq \varepsilon_0 \tilde{N}(t) \end{aligned}$$

We have just defined ε_0 so that the proof is complete.

Remark 4.1. When $m_0\Lambda > 1$, a non trivial equilibrium $N(t)$ cannot satisfy

$$N(t) \leq 1 \quad \text{for all } t.$$

(Otherwise N would be proportional to \tilde{N} and we would have $m_0\Lambda = 1$).

Actually we even *cannot* have

$$N(t) \leq 1 \quad \text{for all } t \in [\rho, 1]$$

(same argument).

4.2. The linearized equation at an equilibrium. Let

$$N_0(t) = m_0 \int_{A_0}^{A_1} S(a) N_0(t-a) \overline{m}_\gamma(N_0(t-a)) \tilde{m}_\rho(t-a) da$$

be an equilibrium, i.e. a 1-periodic solution of the evolution equation.

Writing $N = N_0 + \Delta N$ and keeping only first order terms, we get the linearized equation

$$\Delta N(t) = m_0 \int_{A_0}^{A_1} S(a) \Delta N(t-a) \tilde{m}_\rho(t-a) \chi(t-a) da$$

where

$$\chi(t-a) = \begin{cases} 1 & \text{if } N_0(t-a) \leq 1 \\ (1-\gamma)N_0^{-\gamma}(t-a) & \text{if } N_0(t-a) > 1 \end{cases}$$

(This is discontinuous but should not be too troublesome.)

Looking for eigenvalues for the linearized equation, we write

$$\Delta N(t) = e^{\lambda t} \overline{\Delta N}(t), \quad \lambda \in \mathbb{C}$$

where now $\overline{\Delta N}$ is a 1-periodic function. This gives

$$\overline{\Delta N}(t) = m_0 \int_{A_0}^{A_1} S(a) \overline{\Delta N}(t-a) e^{-\lambda a} \tilde{m}_\rho(t-a) \chi(t-a) da.$$

Let us define the linear operator U_λ , acting on *continuous 1-periodic functions*, by the right-hand side of the last formula.

THEN

1) We have, $k \in \mathbb{Z}$:

$$U_\lambda(e^{2\pi ikt} \overline{\Delta N}(t)) = e^{2\pi ikt} U_{\lambda+2\pi ik}(\overline{\Delta N}(t))$$

thus U_λ and $U_{\lambda+2\pi ik}$ are conjugated.

2) Let $\theta \in \mathbb{C}^*$, and $\lambda \in \mathbb{C}$ such that $e^\lambda = \theta$

Then θ is an *eigenvalue* of the evolution map T of 3.2, at equilibrium N_0 , if and only if

$$\underline{\text{id} - U_\lambda \text{ is non invertible}}$$

(in fact has a non trivial kernel)

By the first point, this does *not* depend on the choice of λ , but only on θ .

- 3) If $\text{id} - U_\lambda$ is invertible for all λ with $\text{Re } \lambda \geq 0$, the equilibrium N_0 is *stable*
 4) If $\text{id} - U_0$ is invertible, the equilibrium N_0 is *non degenerate*. In this case we can use the *implicit function theorem*: if we perturb slightly the values of m_0, ρ, γ , we still get for this new values of the parameters a *unique equilibrium close to N_0* .

4.3. The case $0 < \gamma < 2$. We assume $0 < \gamma < 2$. I want to give some indication of the proof of the following results.

- a) the eigenvalue $\Lambda = \Lambda(\rho)$ of 4.1, page (11), is *decreasing* with ρ . Therefore the threshold level Λ^{-1} for fecundity m_0 is *increasing* with ρ
 b) Let $0 \leq \rho < 1$, $m_0 \Lambda(\rho) > 1$. Then there exists a *unique non trivial equilibrium* and it is *stable*.

Proof of a). this is easy (and does not use $0 < \gamma < 2$). For $\rho' \geq \rho$, we have $\tilde{m}_{\rho'} \leq \tilde{m}_\rho$ and the assertion follows from general considerations on ‘‘Perron–Frobenius like’’ operators. \square

Proof of b) (only a rough sketch). The main point is to establish that any non trivial should be *stable*.

Then we are able to show uniqueness by letting the seasonality ρ decrease to 0, following the corresponding equilibrium, and using uniqueness of the *unseasonal* case. (When ρ decreases to zero, the threshold $\Lambda^{-1}(\rho)$ will decrease and therefore we stay *above* it if we started above [we do not change m_0]. For $\rho = 0$, we get back the threshold of the unseasonal case $\Lambda^{-1} = \frac{A_1}{2}(1 - A_0/A_1)^2$)

Let us now show the *stability* of equilibrium N_0 (assuming $0 < \gamma < 2$ and $m_0 \Lambda(\rho) > 1$).

We want to show that, if $\text{Re } \lambda \geq 0$, the operator $\text{id} - U_\lambda$ is invertible. To do this we will show that U_λ is a *contraction*.

We first observe that (as $|e^{-\lambda a}| \leq 1$ if $\text{Re } \lambda \geq 0$, $a \geq 0$)

$$|U_\lambda(\overline{\Delta N}(t))| \leq m_0 \int_{A_0}^{A_1} S(a) \tilde{m}_\rho(t-a) |\chi(t-a)| |\overline{\Delta N}(t-a)| da.$$

We define

$$\tilde{U}_0(\overline{\Delta N})(t) = m_0 \int_{A_0}^{A_1} S(a) \tilde{m}_\rho(t-a) |\chi(t-a)| \overline{\Delta N}(t-a) da$$

which is a linear operator of ‘‘Perron–Frobenius type’’. It has, up to scaling, a unique positive eigenvector $\overline{\Delta N}_0$. Let us call $0 < \tilde{\Lambda}$ the corresponding eigenvalue. If $\tilde{\Lambda} < 1$, then \tilde{U}_0 will be a contraction, and the inequality above will show that U_λ is also a contraction.

But recall that

$$|\chi(t-a)| = \begin{cases} 1 & \text{if } N_0(t-a) \leq 1 \\ |1 - \gamma|N_0^{-\gamma}(t-a)| & \text{if } N_0(t-a) > 1 \end{cases}$$

which, as $0 < \gamma < 2$, is smaller than

$$\overline{m}_\gamma(N_0(t-a)) = \begin{cases} 1 & \text{if } N_0(t-a) \leq 1 \\ N_0^{-\gamma}(t-a) & \text{if } N_0(t-a) > 1 \end{cases}$$

When we replace in the definition of \tilde{U}_0 the function $|\chi|$ by the *larger* function $\overline{m}_\gamma \circ N_0$, the eigenvalue (associated to the unique positive eigenvector) will *increase*. But after doing this, we *know* the eigenvector: it is the equilibrium N_0 , and the eigenvalue is *equal* to 1. Therefore the eigenvalue $\tilde{\Lambda}$ is < 1 , which allows to conclude. \square

Remark 4.2. There are a number of technical points to be taken care of in this sketch of proof. I don’t want to address them now.

4.4. ‘‘Computing’’ eigenvalues of equilibria. If N_0 is an equilibrium, the eigenvalues of the linearized equations associated to it are the *complex numbers* $\theta \in \mathbb{C}^*$ such that, with $e^\lambda = \theta$, the linear operator $\text{id} - U_\lambda$ of page⁴ 16 is non invertible.

Thus, formally, we want to solve

$$\det(\text{id} - U_\lambda) = 0,$$

seeing the left hand side as a function of $\theta = e^\lambda$ [because $U_{\lambda+2\pi i}$ is conjugated to U_λ , the function $\lambda \mapsto \det(\text{id} - U_\lambda)$ will be $2\pi i$ -periodic, and thus can be considered as a function of θ].

Because U_λ acts on the infinite dimensional Banach space of continuous 1-periodic functions, one has to be careful considering determinants.

Nevertheless, this can be done, the heuristics being the following

- a) Assume first that U is a linear operator, acting on a *finite-dimensional* vector space and having eigenvalues $\theta_1, \dots, \theta_d$ (counted with multiplicities).

We have, for small $z \in \mathbb{C}$

$$\begin{aligned} \det(1 - zU) &= \prod_1^d (1 - \theta_i z) \\ \Rightarrow \log \det(1 - zU) &= \sum_1^d \log(1 - \theta_i z) \\ &= - \sum_1^d \sum_{m \geq 1} \frac{\theta_i^m z^m}{m} \\ &= - \sum_{m \geq 1} \text{Trace}(U^m) \frac{z^m}{m} \end{aligned}$$

⁴I.e., page 12.

therefore

$$\det(1 - zU) = \exp\left(- \sum_{m \geq 1} \text{Trace}(U^m) \frac{z^m}{m}\right)$$

The idea is to use this formula as a *definition* of the determinant when now U acts on an infinite-dimensional vector space, provided we can define $\text{Tr}(U^m)$ and the series converge (for small z).

If everything is ok, we get for $\det(1 - zU)$ an *entire function* (holomorphic in the whole complex plane) whose zeros are the *inverses* of the eigenvalues of U .

- b) Assume that U acts (say) on the space of 1-periodic continuous function on the circle, and is defined by a *kernel* u

$$U(\varphi)(x) = \int_{\mathbb{R}/\mathbb{Z}} u(x, y)\varphi(y)dy$$

where u is a continuous function on $\mathbb{R}/\mathbb{Z} \times \mathbb{R}/\mathbb{Z}$. Then, U has a *trace* equal to

$$\text{Trace}(U) = \int_{\mathbb{R}/\mathbb{Z}} u(x, x) dx$$

(the “same” formula that in the finite dimensional case)

For iterates, one get

$$U^m(\varphi)(x) = \underbrace{\int \int \int}_m u(x, x_1)u(x_1, x_2) \dots u(x_{m-1}, x_m)\varphi(x_m) dx_1 \dots dx_m$$

with kernel

$$u^{(m)}(x, y) = \underbrace{\int \int}_{m-1} u(x, x_1)u(x_1, x_2) \dots u(x_{m-1}, y) dx_1 \dots dx_{m-1}$$

Which gives

$$\text{Tr}(U^m) = \underbrace{\int \int \int}_m u(x_0, x_1)u(x_1, x_2) \dots u(x_{m-1}, x_0) dx_0 dx_1 \dots dx_{m-1}$$

Let us come back to our situation. We have⁵

$$U_\lambda(\varphi)(t) = m_0 \int_{t-A_0}^{t-A_1} S(t-u)e^{-\lambda(t-u)} \tilde{m}_\rho(u) \chi(u) \varphi(u) du$$

To compute the trace, we first suppress the bounds in the integral: we extend the definition of S as

$$S(a) = \begin{cases} 0 & \text{if } a \leq A_0 \text{ or } a \geq A_1 \\ (1 - \frac{a}{A_1}) & \text{if } a \in [A_0, A_1] \end{cases}$$

Then, we can replace $\int_{t-A_0}^{t-A_1}$ by $\int_{-\infty}^{+\infty}$.

We next want to replace the integral $\int_{-\infty}^{+\infty}$ by an integral on a *single period* (we take, say, $0 \leq t, u \leq 1$).

⁵N.B.: it seems that Jean-Christophe forgot a minus sign here.

In the formula for U_λ , the functions $\tilde{m}_\rho, \chi, \varphi$ are periodic but S and $e^{-\lambda(t-u)}$ are not. We write

$$\begin{aligned} U_\lambda(\varphi)(t) &= m_0 \int_{-\infty}^{+\infty} S(t-u)e^{-\lambda(t-u)}\tilde{m}_\rho(u)\chi(u)\varphi(u) du \\ &= m_0 \sum_{-\infty}^{+\infty} \int_n^{n+1} S(t-u)e^{-\lambda(t-u)}\tilde{m}_\rho(u)\chi(u)\varphi(u) du \\ &= m_0 \sum_{-\infty}^{+\infty} \int_0^1 S(t-u-n)e^{-\lambda(t-u-n)}\tilde{m}_\rho(u)\chi(u)\varphi(u) du \\ &= m_0 \int_0^1 \left(\sum_{-\infty}^{+\infty} e^{-\lambda(t-u-n)}S(t-u-n) \right) \tilde{m}_\rho(u)\chi(u)\varphi(u) du \end{aligned}$$

(If $A_1 = 2$, there are at most two non zero terms in the series!)

We thus can see U_λ has an operator with *kernel*

$$k_\lambda(t, u) = m_0 \tilde{m}_\rho(u)\chi(u) \sum_{-\infty}^{+\infty} e^{-\lambda(t-u-n)}S(t-u-n)$$

(with $t, u \in [0, 1]$).

In particular

$$k_\lambda(t, t) = m_0 \tilde{m}_\rho(t)\chi(t) \sum_{-\infty}^{+\infty} e^{\lambda n}S(-n)$$

Taking $1 < A_1 \leq 2$, we will have $S(-n) = 0$ except for $n = -1$ in which case $S(1) = (1 - 1/A_1)$.

We obtain

$$\text{Tr}(U_\lambda) = m_0(1 - 1/A_1)\theta^{-1} \int_{\mathbb{R}/\mathbb{Z}} \tilde{m}_\rho(t)\chi(t) dt$$

The formulas for the traces of the U_λ^m are slightly more complicated.

The kernel for U_λ^m is given by

$$k_\lambda^{(m)}(t, u) = \underbrace{\int \int}_{m-1} k_\lambda(t, t_1) \dots k_\lambda(t_{m-1}, u) dt_1 \dots dt_{m-1}$$

We have

$$k_\lambda(t_0, t_1) \dots k_\lambda(t_{m-1}, t_0) = m_0^m \left(\prod_0^{m-1} \tilde{m}_\rho(t_i)\chi(t_i) \right) Z(t_0, \dots, t_{m-1})$$

with

$$Z(t_0, \dots, t_{m-1}) = \underbrace{\sum_{-\infty}^{+\infty} \sum_{-\infty}^{+\infty} \dots}_{m} \left[\prod_0^{m-1} e^{-\lambda(t_i - t_{i+1} - n_i)} S(t_i - t_{i+1} - n_i) \right]$$

(and we put $t_m = t_0$). We have

$$\prod_0^{m-1} e^{-\lambda(t_i - t_{i+1})} = e^{-\lambda(t_0 - t_m)} = 1$$

and we reorganize Z as follows

$$Z(t_0, \dots, t_{m-1}) = \sum_{n=-\infty}^{+\infty} \theta^n \left(\sum_{n_0 + \dots + n_{m-1} = n} \left(\prod_0^{m-1} S(t_i - t_{i+1} - n_i) \right) \right)$$

For the product in the left hand side to be non zero, we must have $A_0 \leq t_i - t_{i+1} - n_i \leq A_1$ for every i which gives

$$-mA_1 \leq n = \sum n_i \leq -mA_0.$$

Therefore Z is a *polynomial* in θ^{-1} :

$$Z(t_0, \dots, t_{m-1}) = \sum_{mA_0 \leq n \leq mA_1} \theta^{-n} \left(\sum_{\substack{n_0 + \dots + n_{m-1} = n \\ A_0 \leq t_i - t_{i+1} + n_i \leq A_1}} \left(\prod_0^{m-1} S(t_i - t_{i+1} + n_i) \right) \right)$$

(One should think of n as a number of *years*, m as a number of *generations*, and t_i as the instants of birth of the various *generations*)

We define, for $mA_0 \leq n \leq mA_1$

$$Z_{m,n}(t_0, \dots, t_{m-1}) = \sum_{\substack{n_0 + \dots + n_{m-1} = n \\ A_0 \leq t_i - t_{i+1} + n_i \leq A_1}} \left(\prod_0^{m-1} S(t_i - t_{i+1} + n_i) \right)$$

$$Z_{m,n} = \underbrace{\int \int \int}_m \prod_0^{m-1} (\tilde{m}_\rho(t_i) \chi(t_i)) Z_{m,n}(t_0, \dots, t_{m-1}) dt_0 \dots dt_{m-1}$$

and we will have

$$\text{Trace}(U_\lambda^m) = \sum_{mA_0 \leq n \leq mA_1} \theta^{-n} Z_{m,n}$$

Finally, we will obtain

$$\begin{aligned} \det(\text{id} - U_\lambda) &= \exp\left(-\sum_{m \geq 1} \frac{1}{m} \text{Tr}(U_\lambda^m)\right) \\ &= \exp\left(-\sum_{m \geq 1} \sum_{mA_0 \leq n \leq mA_1} \frac{1}{m} \theta^{-n} Z_{m,n}\right) \\ &= \exp\left(-\sum_{n \geq 1} \theta^{-n} Z_n\right) \end{aligned}$$

where

$$Z_n = \sum_{\frac{n}{A_1} \leq m \leq \frac{n}{A_0}} m^{-1} Z_{m,n}.$$

I would expect (this needs justification !!) that

- the power series (in $\zeta = \theta^{-1}$) $\sum Z_n \zeta^n$ converges for $|\zeta|$ small enough.
- The holomorphic function $\exp(-\sum Z_n \zeta^n)$ extends analytically to an entire function, defined on *all of* \mathbb{C} .
- The zeros of this entire function are the inverses of the eigenvalues we are looking for.

- d) In particular, the eigenvalue with largest modulus, which decides stability, corresponds to the zero with smallest modulus, hence to the singularity of $\sum Z_n \zeta^n$ (log 0 !!) with smallest modulus, given by the *radius of convergence* of the power series: if the radius of convergence is > 1 , we have a stable equilibrium; otherwise, an unstable one.