

The numerical toy model.

1. This is a seasonal model, 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

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

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

$$\tilde{m}_p(t) = \begin{cases} 0 & \text{for } 0 \leq t \leq p \pmod{1} \\ 1 & \text{for } p \leq t \leq 1 \pmod{1} \end{cases}$$

There are thus five parameters A_0, A_1, γ, p, 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 p is the seasonality parameter. When $p=0$ we have the unseasonal model.

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

$$\dot{N}(t) = m(N(t), t) N(t)$$

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

$\Big|_{t-a}^t$

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

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

$$m(\hat{N}, t) = \hat{m}_\gamma(\hat{N}) \tilde{m}_p(t) \quad (\text{no } m_0!)$$

with now

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

The equation for \hat{N} becomes

$$\hat{N}(t) = \int_{A_0}^1 S(a) \hat{N}(t-a) \hat{m}_\gamma(\hat{N}(t-a)) \tilde{m}_p(t-a) da$$

The relation between N and \hat{N} is

$$m_0 = N_{cr}^{-\delta}, \quad N = N_{cr}^{-1} \hat{N}, \quad \hat{N} = m_0^{-1/\delta} N$$

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

2. Equilibrium in the unseasonal case.

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

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

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

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

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

If, for a given cut off level N_{cr}^0 , we have a solution $\hat{N}(t)$, $t \in \mathbb{R}$, with $\hat{N}(t) \geq N_{cr}^0$ for all t

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

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

(3)

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

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

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

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

$$\text{or} \quad \Delta \hat{N}(t) = \frac{(1-\gamma)}{A_{1/2} (1 - A_0/A_1)^2} \int_{A_0}^{A_1} s(a) \Delta \hat{N}(t-a) da$$

The eigenvalues λ ($\Delta \hat{N}(t) = \Delta \bar{N} e^{+\lambda t}$) 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 $\text{Re } \lambda \geq 0$ ($\Rightarrow |e^{-a\lambda}| \leq 1$) 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

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

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 $\text{Re } \lambda > 0$, 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

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

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

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 $(\pi/2 + k\pi) A_0^{-1}$ for which

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

and that the u_k give all positive roots of $\text{Im } F(-iu) = 0$; 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

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

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

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

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

On the other hand

$$(u f(u))' = \cancel{A_0 \cos A_0 u} - A_0 u \sin A_0 u + \cos A_0 u + \frac{1}{A_1 - A_0} (A_0 \cos A_0 u - A_1 \cos A_1 u)$$

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 $u f(u)$ 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 .

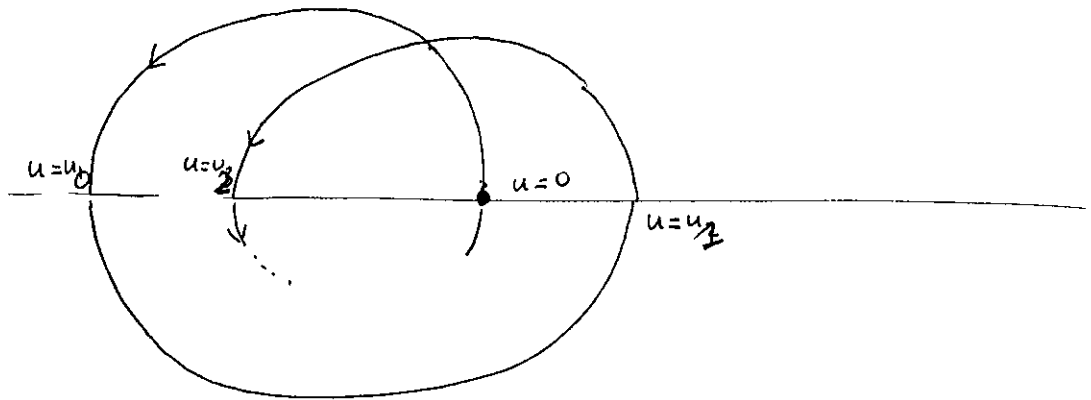
The case $k=0$ must be investigated directly, but still looks ok for $A_0=0.1, A_1=2$.

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

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

and it is not difficult to check that $\text{Re } F(-iu_k)$ 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 $F(-iA_0)$ [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 $\hat{N}(t)$, taking positive values, defined on $[-A_1, 0]$ and satisfying

$$\hat{N}(0) = \int_{A_0}^{A_1} s(a) \hat{N}(-a) \hat{m}_Y(\hat{N}(-a)) da.$$

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

$$\hat{N}(t) = \int_{A_0}^{A_1} s(a) \hat{N}(t-a) \hat{m}_Y(\hat{N}(t-a)) da, \text{ for all } t \leq 0.$$

In both cases, the relations define a ~~linear~~ ^{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 $0 \leq s \leq A_0$, $0 \geq t \geq -A_1$

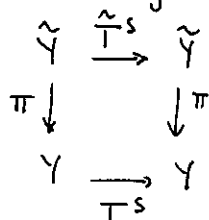
$$T^s \hat{N}(t) \begin{cases} = \hat{N}(t+s) & \text{if } -A_1 \leq t \leq -s \\ = \int_{A_0}^{A_1} s(a) \hat{N}(t+s-a) \hat{m}_Y(\hat{N}(t+s-a)) da & \text{if } -s \leq t \leq 0. \end{cases}$$

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

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

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

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



The map π is not surjective : actually most elements of \mathcal{Y} cannot have an infinite past.

Boundedness of solutions

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

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

If $\gamma < 1$, we still have the same inequality if $\hat{N}(t-a) \leq N_{cr}$ for $A_0 \leq a \leq A_1$. Otherwise we have

$$\hat{N}(t) \leq \frac{A_1}{2} \left(1 - \frac{A_0}{A_1}\right)^2 \left[\max_{A_0 \leq \alpha \leq A_1} \hat{N}(t-\alpha) \right]^{1-\gamma}$$

But we have assumed

$$\frac{A_1(1 - \frac{A_0}{A_1})^2}{2}$$

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

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

which gives

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

which gives, for $\gamma \geq 1$

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

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

In particular, every function in $\tilde{\mathcal{Y}}$ 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 $\tilde{\mathcal{Y}}$. 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. ~~The first is to consider an adjoint operator.~~ ($N = \hat{N}/N_{cr}$)

① The estimates on last page read

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

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

They easily imply that there exists N_1 such that

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

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 $m_0 \int_{A_0}^{A_1} S(a) da = m_0 \frac{A_1}{2} (1 - \frac{A_0}{A_1})^2 = \theta > 1,$

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

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

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

for $0 \leq \delta \leq \bar{N} m_0^{-1} (1 - A_0/A_1)^{-1}$, $N(t-A_1+\delta) = 0$

if $\bar{N} m_0^{-1} (1 - A_0/A_1)^{-1} \leq \delta \leq A_1 - A_0$. (Recall that

$| \frac{dN}{dt} | \leq m_0 (1 - A_0/A_1)$). In this case, the integral is equal to

$$m_0 \int_{A_1 - \bar{N} m_0^{-1} (1 - A_0/A_1)^{-1}}^{A_1} (1 - \frac{a}{A_1}) (\bar{N} - m_0 (1 - A_0/A_1) (A_1 - a)) da$$

$$= m_0 \int_0^{\bar{N} m_0^{-1} (1 - A_0/A_1)^{-1}} \frac{\delta}{A_1} (\bar{N} - m_0 (1 - A_0/A_1) \delta) d\delta$$

$$= m_0^{-1} A_1^{-1} (1 - A_0/A_1)^{-2} \int_0^{\bar{N}} u (\bar{N} - u) du$$

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

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

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

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

$$\text{Max}_{t-2A_1 \leq s \leq t-2A_0} N(s) \leq C (\text{Max}_{t-A_1 \leq s \leq t-A_0} N(s))^{1/3} \leq C^{4/3} N(t)^{1/9}$$

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

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

showing the desired result.

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

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

~~4 The seasonal case: τ -periodic solutions.~~

~~Again, it is easier to revert to the second scaling \tilde{N} .~~

~~We start with the following simple observation. Let~~

~~$$\tilde{N}_{0,0}(t) = \int_{A_0}^{A_1} S(a) \tilde{m}_p(t-a) da$$~~

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

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

and

$$\begin{cases} \hat{N}^s(u) = \hat{N}(u+s) & \text{if } -A_1 \leq u \leq -s \\ \hat{N}^s(u) = \int_{A_0}^{A_1} S(a) \hat{N}(u+s-a) \hat{m}_Y(\hat{N}(u+s-a)) \hat{m}_P(t+u+s-a) da \end{cases}$$

Again, 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

$$(\hat{N}_0^0, 0) \text{ in } Y \times \{0\}, \text{ if we know } T^k(\hat{N}_0^0, 0) = (\hat{N}_0^k, 0)$$

for all positive integers we know completely the trajectory because \hat{N}_0^k determines the solution between time $t_k - A_1$ and t_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 $\tilde{T} : Y \times \{t_0\} \rightarrow Y \times \{t_0\}$; this map is conjugated to the preceding one)

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

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

As before, solutions are bounded (same proof)

~~and~~ Because we have taken a discontinuous \hat{m}_P ,

solutions will be Lipschitz but not C^1 ; indeed

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

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

(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 non trivial equilibrium (= constant non zero mature population) as soon as

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

i.e. fecundity at small density is high enough. [When on

the opposite one has $A_{1/2} \left(1 - \frac{A_0}{A_1}\right)^2 < m_0^{-1}$, 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).

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

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

which is a linear equation. Now, a "Perron-Frobenius-like" theorem tells us the following: there exists a unique (up to scaling) T -periodic positive function \tilde{N} , and a unique positive real number $\tilde{\lambda} = \lambda(p)$ such that

$$\tilde{N}(t) = \tilde{\lambda} \int_{A_0}^{A_1} S(a) \tilde{N}(t-a) \hat{m}_p(t-a) da.$$

The discussion now runs as follows

- * if $m_0 A < 1$, all solutions will collapse exponentially fast to zero: no non trivial equilibrium (or anything else)
- * if $m_0 A \geq 1$, 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

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

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 map 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 $K(\epsilon_0, N_{\max}, L)$ ~~den~~ with a convenient choice of parameters ϵ_0, N_{\max}, L , and defined as follows.

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

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

Then $K(\epsilon_0, N_{\max}, L)$ is the set of

continuous 1-periodic functions (i.e. elements of E)

which moreover satisfy

$$(i) \text{ for all } t \quad \varepsilon_0 \tilde{N}(t) \leq N(t) \leq N_{\max}$$

$$(ii) \text{ for all } t, t' \quad |N(t) - N(t')| \leq L |t - t'|.$$

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

$$N(t-a) \bar{m}_\gamma(N(t-a)) \leq 1$$

and therefore

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

Therefore, it is reasonable to take

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

Next comes the choice of L . One has

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

hence

$$\frac{dS(N)}{dt}(t) = \left(1 - \frac{A_0}{A_1}\right) m_0 N(t-A_0) \bar{m}_\gamma(N(t-A_0)) \tilde{m}_p(t-A_0) - \frac{m_0}{A_1} \int_{t-A_0}^{t-A_0+p} N(u) \bar{m}_\gamma(N(u)) \tilde{m}_p(u) du$$

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

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

We will take

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

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

First, ~~assume that N is a positive continuous~~

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 $p \leq t \leq 1$, we have not only (i) but

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

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

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

so any ε_0 will do in this case.

b) there exists $t_0 \in [p, 1]$ 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 around containing t_0 , contained in $[p, 1]$, of length

$$\ell = \text{Min} \left(\frac{1}{2L}, A_1 - A_0 - 1, 1 - p \right)$$

such that

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

For such t we will have

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

Now, when we write

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

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 than $A_1 - A_0 - 1$); on $J+k$ we will have

$$\tilde{m}_p(u) = 1$$

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

Therefore

$$\begin{aligned} S(N)(t) &\geq m_0 \left[\int_{J+k} S(t-u) du \right] \text{Min} \left(\frac{1}{2}, N_{\max}^{1-\gamma} \right) \\ &\geq m_0 \frac{\ell^2}{2A_1} \text{Min} \left(\frac{1}{2}, N_{\max}^{1-\gamma} \right) \stackrel{\text{def.}}{=} \epsilon_0 \geq \epsilon_0 \tilde{N}(t) \end{aligned}$$

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

Remark: When $m_0 A > 1$, 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 $m_0 A = 1$).
Actually we even cannot have

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

(same argument).

4.2 The linearized equation at an equilibrium

Let

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

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

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

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

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

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

$$\bar{\Delta N}(t) = m_0 \int_{\lambda_0}^{\lambda_1} S(a) \bar{\Delta N}(t-a) e^{-\lambda a} \tilde{m}_p(t-a) \chi(t-a) da.$$

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, for $k \in \mathbb{Z}$:

$$U_\lambda (e^{2\pi i k t} \bar{\Delta N}(t)) = e^{2\pi i k t} U_{\lambda + 2\pi i k} (\bar{\Delta N}(t))$$

thus U_λ and $U_{\lambda + 2\pi i k}$ 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: ~~for~~ if we perturb slightly the values of m_0, ρ, γ , we will 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 $\Lambda = \Lambda(p)$ of 4.1, page (11), is decreasing with p . Therefore the threshold level Λ^{-1} for fecundity m_0 is increasing with p .
- b) Let $0 \leq p < 1$, $m_0 \Lambda(p) > 1$. 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 $p' \geq p$, we have $\tilde{m}_{p'} \leq \tilde{m}_p$ and the assertion follows from general considerations on "Perron-Frobenius like" operators.

Proof of b) (only a rough sketch).

The main point is to establish that any non trivial equilibrium should be stable.

Then we are able to show uniqueness by letting the seasonality p decrease to 0, following the corresponding equilibrium, and using uniqueness of the unseasonal case. (When p decreases

to zero, the threshold $\Lambda(p)$ will decrease and therefore we stay above it if we started above [we do not change m_0]. For $p=0$, we get back the threshold of the unseasonal case

$$\Lambda^{-1} = A_{1/2} (1 - A_0/A_1)^2$$

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

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 $\operatorname{Re} \lambda \geq 0$, $a \geq 0$)

$$|U_\lambda(\Delta \bar{N}(t))| \leq m_0 \int_{A_0}^{A_1} S(a) \tilde{m}_p(t-a) |X(t-a)| |\Delta \bar{N}(t-a)| da.$$

We define

$$\tilde{U}_0(\Delta \bar{N})(t)^\ddagger = m_0 \int_{A_0}^{A_1} S(a) \tilde{m}_p(t-a) |X(t-a)| \Delta \bar{N}(t-a) da$$

which is a linear operator of "Perron Frobenius type". It has, up to scaling, a unique positive eigenvector $\Delta \bar{N}_0$. 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

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

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

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

When we replace in the definition of \tilde{U}_0 the function $|X|$ by the larger function $\bar{m}_\gamma \circ N_0$, 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.

Remark: 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 page 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 $z \in \mathbb{C}$

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

therefore

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

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 $\text{Det}(1 - zU)$

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

$$U^m(\varphi)(x) = \iiint_{\mathbb{R}/\mathbb{Z}} u(x,x_1) u(x_1,x_2) \dots u(x_{m-1},x_m) \overbrace{\varphi(x_m)}^{(\varphi(x_m))} dx_1 \dots dx_m$$

with kernel

$$u^{(m)}(x,y) = \iint_{\mathbb{R}/\mathbb{Z}} u(x,x_1) u(x_1,x_2) \dots u(x_{m-1},y) dx_1 \dots dx_{m-1}$$

Which gives

$$\text{Tr}(U^m) = \iiint_{\mathbb{R}/\mathbb{Z}} u(x_0,x_1) u(x_1,x_2) \dots u(x_{m-1},x_0) dx_0 dx_1 \dots dx_{m-1}$$

Let us come back to our situation. We have

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

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, $0 \leq t, u \leq 1$).

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

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

(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

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

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

In particular

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

If $A_1 = 2$, we have actually $S(-n) \neq 0$ only for $n = -1$, which gives (as $S(+1) = 1/2$ then)

~~$$\text{Tr}(U_\lambda) = m_0 \int_{\mathbb{R}/\mathbb{Z}} \tilde{m}_p(t) \chi(t) dt$$~~

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

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

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

The kernel for U_λ^m is given by

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

We have

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

with
$$Z(t_0, \dots, t_{m-1}) = \sum_{-\infty}^{+\infty} \underbrace{\sum_{-\infty}^{+\infty} \dots \sum_0^{m-1}}_m e^{-\lambda(t_i - t_{i+1} - n_i)} S(t_i - t_{i+1} - n_i)$$

(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

$$-m A_1 \leq n = \sum n_i \leq -m A_0$$

Therefore Z_1 is a polynomial of in θ^{-1} :

$$Z_1(t_0, \dots, t_{m-1}) = \sum_{\substack{m A_0 \leq n \leq m A_1 \\ n_0 + \dots + n_{m-1} = n \\ A_0 \leq t_i - t_{i+1} + n_i \leq A_1}} \theta^{-n} \left(\sum_{\substack{n_0 + \dots + n_{m-1} = n \\ A_0 \leq t_i - t_{i+1} + n_i \leq A_1}} \left(\prod_0^{m-1} S(t_i - t_{i+1} + n_i) \right) \right)$$

(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 $m A_0 \leq n \leq m A_1$

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

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

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

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

I would expect (this needs justification !!) that

- a) the power series (in $\zeta = \theta^{-1}$) $\sum Z_n \zeta^n$ converges for $|\zeta|$ small enough. ~~It is~~
- b) The holomorphic function $\exp(-\sum Z_n \zeta^n)$ extends analytically to an entire function, defined on all of \mathbb{C} .
- 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.