Population persistence without a compact attractor

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Overview

Dynamical systems, semiflows

Dynamics of populations (human, animal, plant)

Population persistence (survival of the population)

Global compact attractors

The existence of a global compact attractor facilitates persistence, but is not absolutely necessary.

**Dynamical Systems and Population Persistence**
Graduate Studies in Mathematics
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Semiflows and their state spaces

The temporal development of a natural or artificial system can conveniently be modeled by a semiflow.

Semiflow: a state space, $X$, a time-set, $J$, and a map, $\Phi$.

The state space $X$ comprehends all possible states of the system:

- the amounts or densities of the system parts.
- If structure, their structural distribution.

Epidemiological systems:

- the amounts or densities of susceptible and infective and possibly exposed and removed individuals.
- For spatial spread, spatial distributions
- Age-structure: age-distributions
Time set and semiflow map

Time can be considered as a continuum or in discrete units;

time-set \( J: \quad \mathbb{R}_+ = [0, \infty) \) or \( \mathbb{Z}_+ = \mathbb{N} \cup \{0\} = \{0, 1, \ldots\}. \)

Depending on the model, the time unit can be a year, month, or day.

**Semiflow (map)** \( \Phi: J \times X \to X. \)

If \( x \in X \) is the initial state of the system (at time 0), then \( \Phi(t, x) \) is the state at time \( t \).

\[
\Phi(0, x) = x, \quad x \in X.
\]

Semiflow property:

\[
\Phi(t + r, x) = \Phi(t, \Phi(r, x)), \quad r, t \in J, \quad x \in X.
\]
An endemic model with two stages of infection

Infectious disease divides the population into a **susceptible** part and an **infected** part,

\[ N(t) = S(t) + I(t). \]

The stage of infection has two substages,

\[ I(t) = I_1(t) + I_2(t). \]

\[ S' = \beta S + \beta (q_1 I_1 + q_2 I_2) - \mu S - (\kappa_1 I_1 + \kappa_2 I_2) S, \]

\[ I_1' = (\kappa_1 I_1 + \kappa_2 I_2) S - (\mu + \alpha_1 + \gamma) I_1, \]

\[ I_2' = \gamma I_1 - (\mu + \alpha_2) I_2. \]

\( \beta \) and \( \mu \) are the natural per capita **birth** and **death** rates, \( \beta > \mu. \)

The infection can **reduce fertility**: \( q_j \in [0,1] \) is the reduction factor.
Exponential growth in absence of the disease

state space: \( X = \mathbb{R}_+^3 \). time set \( J = \mathbb{R}_+ \)

solution semiflow:

\[
\Phi(t, x_0) = x(t), \quad x(t) = (S(t), I_1(t), I_2(t)), \quad x(0) = x_0.
\]

If \( I_1(0) = 0 = I_2(0) \), then

\[
S(t) = e^{(\beta - \mu)t} S(0), \quad \beta > \mu.
\]

\[
N' = (\beta - \mu)N - (\beta[1 - q_1] + \alpha_1)I_1 - (\beta[1 - q_2] + \alpha_2)I_2.
\]

Set \( q_\diamond = \min\{q_1, q_2\} \), \( \alpha_\diamond = \max\{\alpha_1, \alpha_2\}. \)

Since \( I_1 + I_2 \leq N \),

\[
N' \geq (q_\diamond \beta - \mu - \alpha_\diamond)N.
\]

If \( q_\diamond \beta - \mu - \alpha_\diamond > 0 \), \( N \) grows exponentially even in presence of the disease.
Endemic models in exponentially growing populations

May, Anderson (1985)  
Busenberg, Haderler (1990)  
Haderler, Ngoma (1990)  
Mena-Lorca, Hethcote (1992)  
Gao, Mena-Lorca, Hethcote (1996)  
Iannelli, Martcheva (2000)  
Busenberg, van den Driessche (1990)  
Busenberg, Cooke, Thieme (1991)  
Hethcote (2000)  
Inaba, Nishiura (2008)  

Mostly frequency-dependent rather than density-dependent incidence.
To see that the model displays non-trivial dynamics, we look at the endemic equilibrium.

\[ 0 = (\beta - \mu)S^* + \beta (q_1 I_1^* + q_2 I_2^*) - (\kappa_1 I_1^* + \kappa_2 I_2^*)S^*, \]
\[ 0 = (\kappa_1 I_1^* + \kappa_2 I_2^*)S^* - (\mu + \alpha_1 + \gamma)I_1^*, \]
\[ 0 = \gamma I_1^* - (\mu + \alpha_2)I_2^*. \]

There exists a (unique) endemic equilibrium if and only if

\[ 1 > \frac{\beta q_1}{\mu + \alpha_1 + \gamma} + \frac{\beta q_2}{\mu + \alpha_2} \frac{\gamma}{\mu + \alpha_1 + \gamma} =: R. \]

\( R \) can be interpreted as the reproduction ratio of infected hosts.
The endemic equilibrium is unstable if \( q_1 \) and \( q_2 \) are sufficiently small and

\[
0 < \kappa_1 (\alpha_2 - \alpha_1) + (\kappa_2 - \kappa_1) \gamma.
\]  

(1)

(1) holds if the first stage is an incubation stage.

Computational evidence shows that the endemic equilibrium can also be unstable if \( q_1 = 1 = q_2 \) and \( \kappa_1 = 0 \)

(Gao, Mena-Lorca, Hethcote, 1996).

No simple dynamics. Equilibrium analysis does not tell us much about global dynamics.
Persistence

Does the dynamical system persist (remains safely away from extinction) as a whole or at least in parts (which parts?).

Mathematically formulated by using a persistence functional

\[ \rho : X \to \mathbb{R}_+. \]

For \( x \in X \), \( \rho(x) \) is the abundance of the part of the system that is of particular interest.

If emphasis is on whether the disease becomes endemic or can be eradicated, \( \rho(S, I) = I \) is the number or density of infective (or infected) individuals.

If emphasis is on whether the disease threatens to drive the host population into extinction, \( \rho(S, I) = S + I = N \) is the total number of hosts.
The semiflow $\Phi$ is **uniformly $\rho$-persistent** if there exists some $\epsilon > 0$ s.t.

$$\liminf_{t \to \infty} \rho(\Phi(t, x)) \geq \epsilon \quad \text{whenever } x \in X, \rho(x) > 0.$$  \hspace{1cm} (2)

$\Phi$ is **uniformly weakly $\rho$-persistent** if (2) holds with $\limsup$ replacing $\liminf$.

**Overall assumptions**

- $X$ is a metric space.
- $\rho$ is continuous
- $\rho \circ \Phi$ is continuous.
Persistence with a compact attracting set

Theorem

Let $X$ be a metric space. Assume there exists a compact set $A$ s.t.

1. $\Phi(t, x) \to A$ as $t \to \infty$ for every $x \in X$ with $\rho(x) > 0$
2. there are no $y \in A$, $s, t \in J$:
   \[ \rho(y) > 0, \quad \rho(\Phi(s, y)) = 0, \quad \text{and} \quad \rho(\Phi(t + s, y)) > 0. \]

Then $\Phi$ is uniformly persistent if it is uniformly weakly persistent.

$\Phi(t, x) \to A$: for every open set $U \supseteq A$ there exists some $r \in J$

s.t. $\Phi(t, x) \in U$ for all $t \in J, t \geq r$.

Endemic model, special case

\[ I(t) = I_1(t) + I_2(t). \]

\[ S' = \beta S + \beta (q_1 I_1 + q_2 I_2) - \mu S - (\kappa_1 I_1 + \kappa_2 I_2) S, \]

\[ I'_1 = (\kappa_1 I_1 + \kappa_2 I_2) S - (\mu + \alpha_1 + \gamma) I_1, \]

\[ I'_2 = \gamma I_1 - (\mu + \alpha_2) I_2. \]

Assume \( q_1 = q_2, \quad \kappa_1 = \kappa_2, \quad \alpha_1 = \alpha_2. \)

\[ S' = \beta S + \beta q I - \mu S - \kappa SI, \quad I' = \kappa SI - (\mu + \alpha) I. \]

If \( q = 0, \) Lotka-Volterra predator-prey model

\[ S' = (\beta - \mu) S - \kappa_2 SI, \quad I' = \kappa_2 SI - (\mu + \alpha_2) I. \]

unif. weakly but not uniformly persistent, no compact attracting set \( A. \)
Pedagogic transition to a simpler model

\[ S' = \beta S + \beta q I - \mu S - \kappa SI, \]
\[ I' = \kappa SI - (\mu + \alpha)I. \]

Rewrite in term of \( N = S + I \) and \( I \),

\[ N' = \beta(N - I) - \mu N + (\beta q - \alpha)I, \]
\[ I' = \kappa(N - I)I - (\mu + \alpha)I. \]

Rewrite in terms of \( N \) and \( y = I/N \),

\[ N' = N \left( \beta(1 - y) - \mu + (q\beta - \alpha)y \right), \]
\[ y' = y \left( (\kappa N - \alpha - \beta)(1 - y) - q\beta y \right). \]

The set \( \{y = 1\} \) is invariant iff \( q = 0 \); on this set

\[ N' = -N(\mu + \alpha). \]
Uniform weak host persistence

\[ N' = N \left( \beta (1 - y) - \mu + (q \beta - \alpha) y \right), \]
\[ y' = y \left( (\kappa N - \alpha - \beta)(1 - y) - q \beta y \right). \]

Lemma

If \( q > 0 \), there exists some \( \epsilon > 0 \) such that

\[ \limsup_{t \to \infty} N(t) \geq \epsilon \]

for all solutions with \( N(0) > 0 \) and \( y(0) \leq 1 \).

If \( q = 0 \), this only holds for solutions with \( N(0) > 0, y(0) < 1 \).
Compact attracting set relaxed

from now one \( J = \mathbb{R} \).

**Theorem**

Assume there exists a closed set \( A \) in \( X \) s.t.

- \( \Phi(t, x) \to A \) as \( t \to \infty \) for every \( x \in X \) with \( \rho(x) > 0 \)
- there are no \( y \in A, s, t \in J \):
  \[
  \rho(y) > 0, \quad \rho(\Phi(s, y)) = 0, \quad \text{and} \quad \rho(\Phi(t + s, y)) > 0.
  \]
- if \( 0 < \epsilon_1 < \epsilon_2 < \infty \), then \( A \cap \{ \epsilon_1 \leq \rho \leq \epsilon_2 \} \) is compact.

Then \( \Phi \) is uniformly persistent if it is uniformly weakly persistent.

Host persistence if \( q > 0 \):

\[
\rho(N, y) = N, \quad X = A = \{(N, y); \ N \geq 0, \ 0 \leq y \leq 1\}.
\]

\[
A \cap \{ \epsilon_1 \leq \rho \leq \epsilon_2 \} = \{(N, y); \ \epsilon_1 \leq N \leq \epsilon_2, \ 0 \leq y \leq 1\}.
\]
Uniform host persistence

Theorem

If $q > 0$, there exists some $\epsilon > 0$ such that

$$\liminf_{t \to \infty} N(t) \geq \epsilon$$

for all solutions with $N(0) > 0$ and $y(0) \leq 1$. 
Uniform weak disease persistence

Infected proportion $y(t)$

\[ N' = N \left( \beta (1 - y) - \mu + (q \beta - \alpha) y \right), \]
\[ y' = y \left( (\kappa N - \alpha - \beta)(1 - y) - q \beta y \right). \]

**Lemma**

Let $q \geq 0$. There exists some $\epsilon > 0$ s.t.

\[ \limsup_{t \to \infty} y(t) \geq \epsilon \]

for all solutions with $N(0) > 0$, $0 < y(0) \leq 1$.

\[ \rho(N, y) = y. \quad \rho \text{ does not control } N. \]
Karl Friedrich Hieronymus Freiherr von Münchhausen
(* 11. Mai 1720 in Bodenwerder; 22. Februar 1797 ibidem)

German nobleman
soldier in Russian services

escapes from a swamp lifting himself and his horse up
by pulling at his own hair

drawing by Theodor Hosemann
Define \( \sigma(t, x) = \rho(\Phi(t, x)) \).

Assume there exists a closed set \( B \subseteq X \) such that, for each \( x \in X \cap \{\rho > 0\} \), there is \( \tau \in \mathbb{R}_+ \) s.t. \( \Phi([\tau, \infty) \times \{x\}) \subseteq B \).

Assume there is \( \tilde{\varepsilon} > 0 \) s.t. for each \( \varepsilon \in (0, \tilde{\varepsilon}) \), there are \( D \subseteq X, \delta > 0 \):

\begin{itemize}
  \item \( B \cap D \cap \{\rho = \varepsilon\} \) is compact.
  \item If \( t \in \mathbb{R}_+ \) and \( x \in B \) and \( \rho(x) = \varepsilon = \sigma(t, x) \) and \( \sup_{0 < s < t} \sigma(s, x) \leq \varepsilon \), then

\end{itemize}

\[
\begin{cases}
  \inf_{0 < s < t} \sigma(s, x) > 0, & \text{if } x \in D, \\
  \inf_{0 < s < t} \sigma(s, x) \geq \delta, & \text{if } x \notin D.
\end{cases}
\]

Then, \( \Phi \) is uniformly \( \rho \)-persistent if it is uniformly weakly \( \rho \)-persistent.
More about disease persistence

\[ N' = N \left( \beta (1 - y) - \mu + (q \beta - \alpha) y \right), \]
\[ y' = y \left( (\kappa N - \alpha - \beta) (1 - y) - q \beta y \right). \]

\[ X = \{(N, y); \; N > 0, \; 0 \leq y \leq 1\}. \]

Use host persistence: \[ \liminf_{t \to \infty} N(t) > \epsilon_0. \]

\[ B = \{(N, y); \; N \geq \epsilon_0, \; 0 \leq y \leq 1\}. \]

\[ D = \{(N, y); \; 0 < N \leq c, \; 0 \leq y \leq 1\}. \]

where \( c > 0 \) is chosen large enough.
Uniform disease persistence

**Theorem**

Let $q > 0$. Then the disease is uniformly persistent: there exists some $\epsilon > 0$ s.t.

$$\liminf_{t \to \infty} y(t) > \epsilon$$

for all solutions with $N(0) > 0$, $0 < y(0) \leq 1$.

This holds both if the host is bounded and the host is exponentially increasing.
Lemma

Let $q\beta < \mu + \alpha$. Then there exists some $c > 0$ such that

$$\liminf_{t \to \infty} N(t) \leq c$$

for all solutions with $0 < y(0) \leq 1$.

$$N' = N\left(\beta(1 - y) - \mu + (q\beta - \alpha)y\right),$$

$$y' = y\left((\kappa N - \alpha - \beta)(1 - y) - q\beta y\right).$$

This result is sharp: if $q\beta > \mu + \alpha$ and $N(0) > 0$, then $N(t) \to \infty$ as $t \to \infty$. 
Theorem

Let $q\beta < \mu + \alpha$. Then there exists some $c > 0$ such that

$$\limsup_{t \to \infty} N(t) \leq c$$

for all solutions with $0 < y(0) \leq 1$.

$$X = \{(N, y); N > 0, 0 < y \leq 1\}, \quad \rho(N) = \frac{1}{N}.$$ 

The solution semiflow is uniformly weakly $\rho$-persistent on $X$.

Use uniform disease persistence: $\liminf_{t \to \infty} y(t) > \epsilon_0$.

Point-attracting set $A = \{(N, y); N > 0, \epsilon_0 \leq y \leq 1\}$.

If $0 < \epsilon_1 < \epsilon_2 < 1$, then $A \cap \{\epsilon_1 \leq \rho \leq \epsilon_2\} = \left[\frac{1}{\epsilon_2}, \frac{1}{\epsilon_1}\right] \times [\epsilon_0, 1]$. 
Dividing cells in a chemostat

Cell biomass at time $t$ (age-structured)

$$C(t) = \int_{0}^{\infty} c(t, a) da.$$  

Biomass of the resource, $R(t)$,

$$R'(t) = D(R^\circ - R(t)) - f(R(t)) \int_{0}^{\infty} \kappa(a) c(t, a) da,$$

$$(\partial_t + \partial_a) c(t, a) = \left(\kappa(a) f(R(t)) - D - \beta(a)\right) c(t, a),$$

$$c(t, 0) = \int_{0}^{\infty} \beta(a) c(t, a) da,$$

with initial data $R(0) = \tilde{R}$, $c(0, a) = \tilde{c}(a)$. 

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Cell division models with age-structure


Webb (2002)

Shanthidevi, Matsumoto, Oharu (2008)

Not biomass, but number of cells
Cell-division: the linear problem

\[
(\partial_t + \partial_a)c(t, a) = -\beta(a)c(t, a),
\]

\[
c(t, 0) = \int_0^\infty \beta(a)c(t, a)da,
\]

\[
c(0, a) = g(a).
\]

We introduce a cell’s probability of not dividing before age \(a\),

\[
\mathcal{F}(a) = \exp\left(-\int_0^a \beta(s)ds\right).
\]

By differentiation we see that

\[
\beta(a) = -\frac{\mathcal{F}'(a)}{\mathcal{F}(a)}.
\]
A $C_0$-semigroup

For $t, a \geq 0$ and $g \in L^1(\mathbb{R}_+)$, with $b(t) = c(t, 0)$,

$$c(t, a) = \begin{cases} 
  b(t - a)F(a), & t > a, \\
  g(a - t)\frac{F(a)}{F(a-t)}, & t < a,
\end{cases}$$

$$= [S(t)g](a)$$

where $b$ is the unique solution of

$$b(t) = \int_0^t b(t - a)\beta(a)da + \int_t^{\infty} \frac{g(a - t)}{F(a-t)}\beta(a)da.$$ 

$\{S(t); t \geq 0\}$ family of bounded linear operators on $L^1(\mathbb{R}_+)$, semigroup

$$S(t)S(r) = S(t + r), \quad t, r \geq 0, \quad S(0) = I.$$ 

$S(t)g$ continuous in $t \geq 0$, $\|S(t)\| = 1$.

Trouble, part 1: $S(t)$ compact for no $t$. 
Mild solutions

Let \( u(t) = c(t, \cdot) \) and \( \tilde{u} = \tilde{c}(\cdot) \).

Introduce the bounded linear operator \( B \),

\[
[Bu](a) = \kappa(a)u(a).
\]

Abstract integral equation

\[
R(t) = \tilde{R}e^{-Dt} + \int_0^t e^{-D(t-s)}(DR^\diamond - f(R(s)))\|Bu(s)\|)ds,
\]

\[
u(t) = e^{-Dt}S(t)\tilde{u} + \int_0^t e^{-D(t-s)}S(t-s)f(R(s))Bu(s)ds.
\]

Use Banach’s fixed point thm for existence and uniqueness of solutions.

Webb, 1985

double trouble for qualitative behavior:

\( S(t) \) not compact for any \( t > 0 \), \( B \) not compact
The power of an abstract L space

In $X = L^1(\mathbb{R}_+)$, the norm has the property

$$\|x + y\| = \|x\| + \|y\| \text{ for } x, y \in L^1_+(\mathbb{R}_+);$$

so for non-negative solutions,

$$\|u(t)\| = \|S(t)\tilde{u}\|e^{-Dt} + \int_0^t e^{-D(t-r)}f(R(r))\|S(t-r)Bu(r)\|\,dr$$

$$= \|\tilde{u}\|e^{-Dt} + \int_0^t e^{-D(t-r)}f(R(r))\|Bu(r)\|\,dr.$$

So $\|u(t)\|$ is differentiable and

$$\frac{d}{dt}\|u(t)\| = -D\|u(t)\| + f(R(t))\|Bu(t)\|.$$

Recall

$$R' = D(R^\diamond - R) - f(R)\|Bu\|.$$
Conservation of mass

Let $M(t) = R(t) + \|u(t)\|$ be the total biomass,

\[
\begin{aligned}
M' &= D(R^\diamond - M), \\
R(t) &= M(t) - \|u(t)\|,
\end{aligned}
\]

\[
u(t) = e^{-Dt} S(t) \tilde{u} + \int_0^t S(t - r) e^{-D(t-r)} f(R(r)) B u(r) dr.
\]

We integrate the first equation,

\[
M(t) = \tilde{M} e^{-Dt} + R^\diamond (1 - e^{-Dt}),
\]

\[M(t) \to R^\diamond, \quad t \to \infty.\]
The basic production ratio

\( \mathcal{P}_0 \) basic biomass production number,

\[
\mathcal{P}_0 = \int_{\mathbb{R}^+} \exp \left( \int_0^a \kappa(s) f(R^\circ) ds - Da \right) \beta(a) da.
\]

expected amount of biomass produced by a unit of biomass during one cell cycle at resource equilibrium level \( R = R^\circ \).

\[ \exp \left( \int_0^a \kappa(s) f(R^\circ) ds \right) \]

amplification factor of a cell’s biomass from age 0 to age \( a \).

\[ e^{-Da} \]

probability of not being washed out before age \( a \).
Extinction via Laplace transform

**Theorem**

Let $P_0 < 1$ and

$$\text{ess- sup}_{s \geq 0} \int_s^\infty \exp \left( f(R^\diamond) \int_s^a \kappa(r) dr - D(a - s) \right) \frac{F(a)}{F(s)} da < \infty. \quad (3)$$

Then the cell population goes extinct: \[ \int_0^\infty \int_0^\infty c(t, a) dt da < \infty \text{ and } \int_0^\infty c(t, a) da \to 0 \text{ as } t \to \infty. \]

Condition (3) means that, at high cell-age, cell division is faster than biomass acquisition.
Uniform weak persistence via Laplace transform

**Theorem**

Let

\[
1 < P_0 = \int_{\mathbb{R}_+} \exp \left( \int_0^a \kappa(s) f(R^\diamond) ds - Da \right) m(da).
\]

Then the cell population persists uniformly weakly, i.e. there exists some \( \epsilon > 0 \) such that

\[
\limsup_{t \to \infty} \int_0^\infty c(t, a) da \geq \epsilon
\]

for every solution with \( \int_0^\infty c(0, a) da > 0 \).

Suppose \( \int_0^\infty c(t, a) da = \|u(t)\| \leq \epsilon \) for all \( t \geq 0 \).

Then \( \lambda \int_0^\infty e^{-\lambda t} \|u(t)\| dt \leq \epsilon \) for all \( \lambda > 0 \).
**Theorem**

Let $P_0 > 1$. Then the cell population persists uniformly

(i.e. there exists some $\epsilon > 0$ such that $\liminf_{t \to \infty} \int_0^\infty c(t, a) da \geq \epsilon$ for every solution with $\int_0^\infty c(0, a) da > 0$) if

(i) $\frac{\mathcal{F}(a + s)}{\mathcal{F}(s)} \to 0$ as $s \to \infty$ for every $a > 0$, OR

(ii) $\mathcal{D}$ is bounded.

$$\mathcal{F}(a|s) = \frac{\mathcal{F}(a + s)}{\mathcal{F}(s)}$$

conditional probability that a cell does not divide before age $a + s$ given it has not divided at age $s$.

$$\mathcal{D}(s) = \int_0^\infty \mathcal{F}(a|s) da$$

expected remaining time till division at age $s$. 
Abstract persistence theorem

Semiflow $\Phi$ is uniformly $\rho$-persistent if it is uniformly weakly $\rho$-persistent and there exist some $\epsilon_0 > 0$ and a sequence $(B_k)$ of subsets of $X$:

\begin{itemize}
  \item[♡] If $x \in X$, $\rho(x) > 0$, and $k \in \mathbb{N}$, then there exists some $t_k \geq 0$ such that $\Phi(t, x) \in B_k$ for all $t \geq t_k$.

(The burden of proof is on $\rho \circ \Phi$.)

\item[♣] If $(y_k)$ is a sequence in $X$ such that $\Phi(t, y_k) \in B_k$ for all $k \in \mathbb{N}$ and $t \geq 0$ and if $0 < \rho(y_k) = \rho(y_1) \leq \epsilon_0$ for all $k \in \mathbb{N}$, then

\begin{itemize}
  \item the continuity of $\rho(\Phi(t, y_k))$ in $t \geq 0$ holds uniformly in $k$ (possibly after choosing subsequences).
\end{itemize}
Abstract persistence theorem continued

- if $\tau \in (0, \infty)$ and
  
  $$\sigma(t) = \lim_{k \to \infty} \rho(\Phi(t, y_k))$$

  exists uniformly for $t \in [0, \tau]$ and if
  
  $$\sigma(t) \leq \sigma(0) = \sigma(\tau)$$

  for all $t \in [0, \tau]$,

  then $\sigma(t) > 0$ for all $t \in (0, \tau)$.

- if $\sigma(t) = \lim_{k \to \infty} \rho(\Phi(t, y_k))$ exists uniformly for $t$ in all bounded subintervals of $\mathbb{R}_+$,

  then $\sigma(s) > \sigma(0)$ for some $s \geq 0$.

Notice $0 < \sigma(0) = \rho(y_0) \leq \epsilon_0$. 
state space

\[ X = \{(M, u); \ M \in \mathbb{R}_+, \ u \in L^1_+(\mathbb{R}_+), \ ||u|| \leq M\} \]

functional \( \rho(x, g) = ||g|| \) for \((x, g) \in X\),

semiflow \( \Phi(t, (\tilde{M}, \tilde{u})) = (M(t), u(t)) \)

composition \( \rho(\Phi(t, (\tilde{M}, \tilde{u}))) = ||u(t)|| \) total cell biomass

Recall \( M(t) \to R^\diamond \) for \( t \to \infty \),

\[ B_k = \{(M, g) \in X; |M - R^\diamond| < 1/k\}. \]

Use the Laplace transform and the Arzela-Ascoli theorem.
Conclusion

A compact attractor of points may not exist because

- the population can grow exponentially,

- the problem is infinite dimensional and there are no compactifying forces.

Still one can often prove persistence.