

Population persistence without a compact attractor

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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**, Φ .

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 : $\mathbb{R}_+ = [0, \infty)$ or $\mathbb{Z}_+ = \mathbb{N} \cup \{0\} = \{0, 1, \dots\}$.

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

Semiflow (map) $\Phi : J \times X \rightarrow X$.

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,

$$I(t) = I_1(t) + I_2(t).$$

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

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

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

β and μ 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 $S(t) = e^{(\beta - \mu)t} S(0)$, $\beta > \mu$.

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

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)

May, Anderson, McLean (1988, 1989)

Busenberg, Haderl (1990)

Busenberg, van den Driessche (1990)

Haderl, Ngoma (1990)

Busenberg, Cooke, Thieme (1991)

Mena-Lorca, Hethcote (1992)

Thieme (1992, 1993, 2007)

Gao, Mena-Lorca, Hethcote (1996)

Ma, Takeuchi (1999, 2004)

Iannelli, Martcheva (2000)

Hethcote (2000)

Inaba (2005, 2006, 2007)

Inaba, Nishiura (2008)

Mostly **frequency-dependent** rather than **density-dependent** incidence.

Endemic equilibrium

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

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

\mathcal{R} can be interpreted as the **reproduction ratio** of infected hosts.

Instability of the endemic equilibrium

The endemic equilibrium is unstable if q_1 and q_2 are sufficiently small and

$$0 < \kappa_1(\alpha_2 - \alpha_1) + (\kappa_2 - \kappa_1)\gamma. \quad (1)$$

(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**

$$\rho : X \rightarrow \mathbb{R}_+.$$

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 Φ is **uniformly ρ -persistent** if there exists some $\epsilon > 0$ s.t.

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

Φ **uniformly weakly ρ -persistent** if (2) holds with \limsup replacing \liminf .

Overall assumptions

- X is a metric space.
- ρ is continuous
- $\rho \circ \Phi$ is continuous.

Theorem

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

- $\Phi(t, x) \rightarrow A$ as $t \rightarrow \infty$ for every $x \in X$ with $\rho(x) > 0$
- there are no $y \in A$, $s, t \in J$:

$$\rho(y) > 0, \quad \rho(\Phi(s, y)) = 0, \quad \text{and } \rho(\Phi(t + s, y)) > 0.$$

Then Φ is uniformly persistent if it is uniformly weakly persistent.

$\Phi(t, x) \rightarrow A$: for every **open** set $U \supseteq A$ there exists some $r \in J$
s.t. $\Phi(t, x) \in U$ for all $t \in J, t \geq r$.

Hale, Waltman (1989), Freedman, Moson (1990), Thieme (1993)

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 $q_1 = q_2$, $\kappa_1 = \kappa_2$, $\alpha_1 = \alpha_2$.

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

If $q = 0$, **Lotka-Volterra predator-prey model**

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

unif. weakly but not uniformly persistent, no compact attracting set A .

Pedagogic transition to a simpler model

$$\begin{aligned}S' &= \beta S + \beta q I - \mu S - \kappa S I, \\I' &= \kappa S I - (\mu + \alpha) I.\end{aligned}$$

Rewrite in term of $N = S + I$ and I ,

$$\begin{aligned}N' &= \beta(N - I) - \mu N + (\beta q - \alpha) I, \\I' &= \kappa(N - I) I - (\mu + \alpha) I.\end{aligned}$$

Rewrite in terms of N and $y = I/N$,

$$\begin{aligned}N' &= N \left(\beta(1 - y) - \mu + (q\beta - \alpha)y \right), \\y' &= y \left((\kappa N - \alpha - \beta)(1 - y) - q\beta y \right).\end{aligned}$$

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

$$N' = -N(\mu + \alpha).$$

$$\begin{aligned}N' &= N\left(\beta(1-y) - \mu + (q\beta - \alpha)y\right), \\y' &= y\left((\kappa N - \alpha - \beta)(1-y) - q\beta y\right).\end{aligned}$$

Lemma

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

$$\limsup_{t \rightarrow \infty} N(t) \geq \epsilon$$

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 on $J = \mathbb{R}$.

Theorem

Assume there exists a **closed** set A in X s.t.

- $\Phi(t, x) \rightarrow A$ as $t \rightarrow \infty$ 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 Φ is uniformly persistent if it is uniformly weakly persistent.

Host persistence if $q > 0$:

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

$$A \cap \{\epsilon_1 \leq \rho \leq \epsilon_2\} = \{(N, y); \epsilon_1 \leq N \leq \epsilon_2, 0 \leq y \leq 1\}.$$

Theorem

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

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

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

Uniform weak disease persistence

Infected proportion $y(t)$

$$\begin{aligned}N' &= N\left(\beta(1-y) - \mu + (q\beta - \alpha)y\right), \\y' &= y\left((\kappa N - \alpha - \beta)(1-y) - q\beta y\right).\end{aligned}$$

Lemma

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

$$\limsup_{t \rightarrow \infty} y(t) \geq \epsilon$$

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

$\rho(N, y) = y$. ρ does not control N .

Persistence à la Baron von Münchhausen

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



Persistence Theorem à la Baron von Münchhausen

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 $D \subseteq X$, $\delta > 0$:

◆ $B \cap D \cap \{\rho = \varepsilon\}$ is **compact**.

◆ If $t \in \mathbb{R}_+$ and $x \in B$ and $\rho(x) = \varepsilon = \sigma(t, x)$ and $\sup_{0 < s < t} \sigma(s, x) \leq \varepsilon$,

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

Then, Φ is uniformly ρ -persistent if it is uniformly weakly ρ -persistent.

More about disease persistence

$$\begin{aligned}N' &= N\left(\beta(1-y) - \mu + (q\beta - \alpha)y\right), \\y' &= y\left((\kappa N - \alpha - \beta)(1-y) - q\beta y\right).\end{aligned}$$

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

Use host persistence: $\liminf_{t \rightarrow \infty} N(t) > \epsilon_0$.

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

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

where $c > 0$ is chosen large enough.

Theorem

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

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

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

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

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

$$\begin{aligned} N' &= N \left(\beta(1 - y) - \mu + (q\beta - \alpha)y \right), \\ y' &= y \left((\kappa N - \alpha - \beta)(1 - y) - q\beta y \right). \end{aligned}$$

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

Uniform limitation of the host through the disease

Theorem

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

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

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 ρ -persistent on X .

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

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

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

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, $R(t)$,

$$R' = D(R^{\diamond} - R(t)) - f(R(t)) \int_0^{\infty} \kappa(a) c(t, a) da,$$

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

$$c(t, 0) = \int_0^{\infty} \beta(a) c(t, a) da,$$

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

O.Arino, Sánchez, Webb (1997)

Dyson, Villella-Bressan, Webb (1999, 2000)

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 $b(t) = c(t, 0)$,

$$c(t, a) = \left\{ \begin{array}{ll} b(t-a)\mathcal{F}(a), & t > a, \\ g(a-t)\frac{\mathcal{F}(a)}{\mathcal{F}(a-t)}, & t < a, \end{array} \right\} = [S(t)g](a)$$

where b is the unique solution of

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

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

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

$S(t)g$ 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 $\check{u} = \check{c}(\cdot)$.

Introduce the bounded linear operator B ,

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

Abstract integral equation

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

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

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,

$$\begin{aligned}\|u(t)\| &= \|S(t)\check{u}\|e^{-Dt} + \int_0^t e^{-D(t-r)} f(R(r)) \|S(t-r)Bu(r)\| dr \\ &= \|\check{u}\|e^{-Dt} + \int_0^t e^{-D(t-r)} f(R(r)) \|Bu(r)\| dr.\end{aligned}$$

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**,

$$\begin{cases} M' = D(R^\diamond - M), & M(0) = \check{M} := \check{R} + \|\check{u}\|, \\ R(t) = M(t) - \|u(t)\|, \\ u(t) = e^{-Dt}S(t)\check{u} + \int_0^t S(t-r)e^{-D(t-r)}f(R(r))Bu(r)dr. \end{cases}$$

We integrate the first equation,

$$M(t) = \check{M}e^{-Dt} + R^\diamond(1 - e^{-Dt}),$$

$$M(t) \rightarrow R^\diamond, \quad t \rightarrow \infty.$$

The basic production ratio

\mathcal{P}_0 **basic biomass production number**,

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

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

$$\exp\left(\int_0^a \kappa(s)f(R^\diamond)ds\right)$$

amplification factor of a cell's biomass from age 0 to age a .

e^{-Da} probability of not being washed out before age a .

Theorem

Let $\mathcal{P}_0 < 1$ and

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

Then the cell population goes extinct: $\int_0^\infty \int_0^\infty c(t, a) dt da < \infty$ and $\int_0^\infty c(t, a) da \rightarrow 0$ as $t \rightarrow \infty$.

Condition (3) means that, at high cell-age, cell division is faster than biomass acquisition.

Uniform weak persistence via Laplace transform

Theorem

Let

$$1 < \mathcal{P}_0 = \int_{\mathbb{R}_+} \exp\left(\int_0^a \kappa(s) f(R^\diamond) ds - Da\right) m(da).$$

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

$$\limsup_{t \rightarrow \infty} \int_0^\infty c(t, a) da \geq \epsilon$$

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 $\lambda > 0$.

Uniform persistence theorem

Theorem

Let $\mathcal{P}_0 > 1$. Then the cell population persists uniformly (i.e. there exists some $\epsilon > 0$ such that $\liminf_{t \rightarrow \infty} \int_0^\infty c(t, a) da \geq \epsilon$ for every solution with $\int_0^\infty c(0, a) da > 0$) if

(i) $\frac{\mathcal{F}(a+s)}{\mathcal{F}(s)} \rightarrow 0$ as $s \rightarrow \infty$ 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 Φ is uniformly ρ -persistent if it is uniformly weakly ρ -persistent and there exist some $\epsilon_0 > 0$ and a sequence (B_k) of subsets of X :

♥ 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 $\rho \circ \Phi$.)

- ♠ 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
- the continuity of $\rho(\Phi(t, y_k))$ in $t \geq 0$ holds uniformly in k (possibly after choosing subsequences).

Abstract persistence theorem continued

- if $\tau \in (0, \infty)$ and

$$\sigma(t) = \lim_{k \rightarrow \infty} \rho(\Phi(t, y_k)) \quad \text{exists uniformly for } t \in [0, \tau]$$

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

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

Notice $0 < \sigma(0) = \rho(y_k) \leq \epsilon_0$.

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 $\Phi(t, (\check{M}, \check{u})) = (M(t), u(t))$.

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

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

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

Use the Laplace transform and the Arzela-Ascoli theorem.

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.