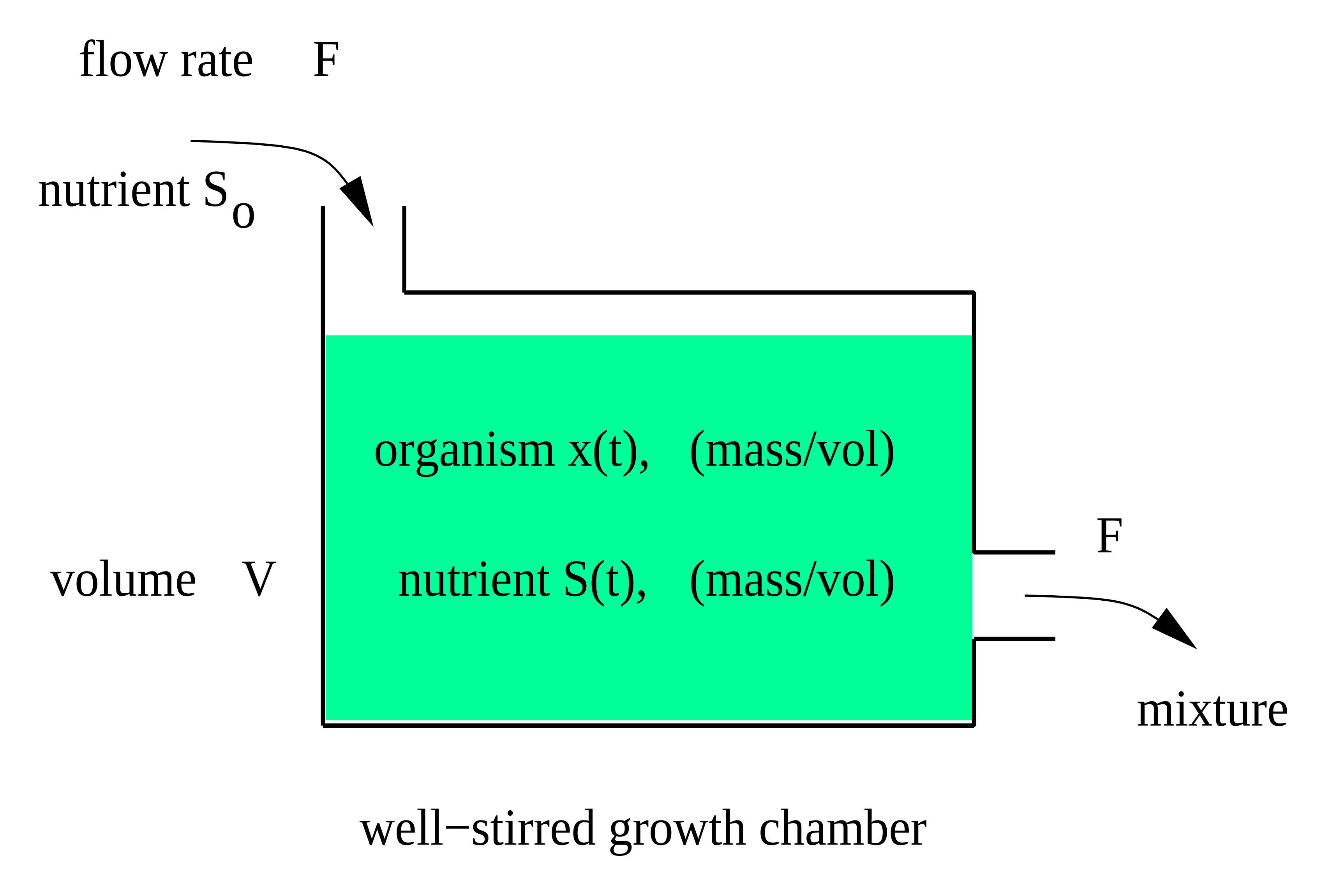
Chemostat Models



dx/dt = rate produced – rate out

dS/dt = rate in – rate out – rate consumed

Let $g(S)$ be the growth rate of the organism with units of 1/time and is an increasing function of nutrient. Let γ be the *yield* constant which is the mass of the organism produced per unit mass of nutrient, i.e.,

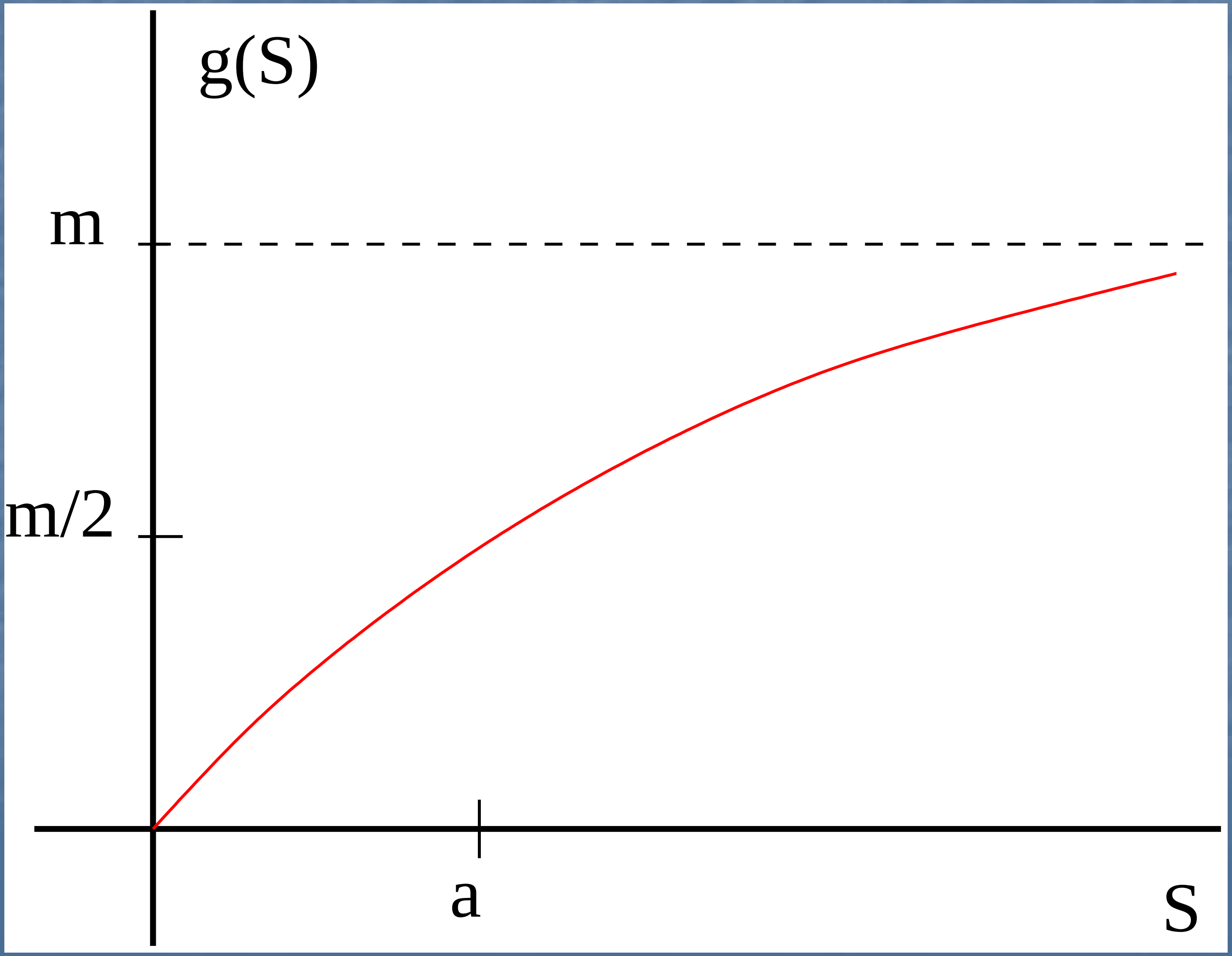
$$\gamma = \frac{\text{mass of organism produced}}{\text{mass of nutrient used}} .$$

Then the system of differential equations becomes:

$$\frac{dx}{dt} = g(S)\,x - \frac{F\,x}{V}$$

$$\frac{dS}{dt} = \frac{F\,S_0}{V} - \frac{F\,S}{V} - \frac{1}{\gamma}\,g(S)\,x .$$

Assume **g(S)=mS/(a+S)**, a Monod or Michaelis-Menton saturation function, which means that the organism is limited in its ability to consume nutrient. **m** is the maximal growth rate (units 1/t) and **a** is the half-saturation constant (units mass/vol).



g(a)=m/2

Divide the first equation by γ and both equations by $S_0 F/V$:

$$\frac{V}{\gamma F S_0}\frac{dx}{dt} = \left[\frac{m\,\frac{V}{F}\,\frac{S}{S_0}}{\frac{a}{S_0} + \frac{S}{S_0}}\right]\frac{x}{\gamma S_0} - \frac{x}{\gamma S_0}$$

$$\frac{V}{F S_0}\frac{dS}{dt} = \frac{S_0}{S_0} - \frac{S}{S_0} - \left[\frac{m\,\frac{V}{F}\,\frac{S}{S_0}}{\frac{a}{S_0} + \frac{S}{S_0}}\right]\frac{x}{\gamma S_0}\,.$$

Scaling x by γS_0, S by S_0 and t by V/F and replacing parameters a/S_0 by a and mV/F by m gives:

$$\frac{dx}{dt} = \left[\frac{m\,S}{a+S}\right]x - x$$

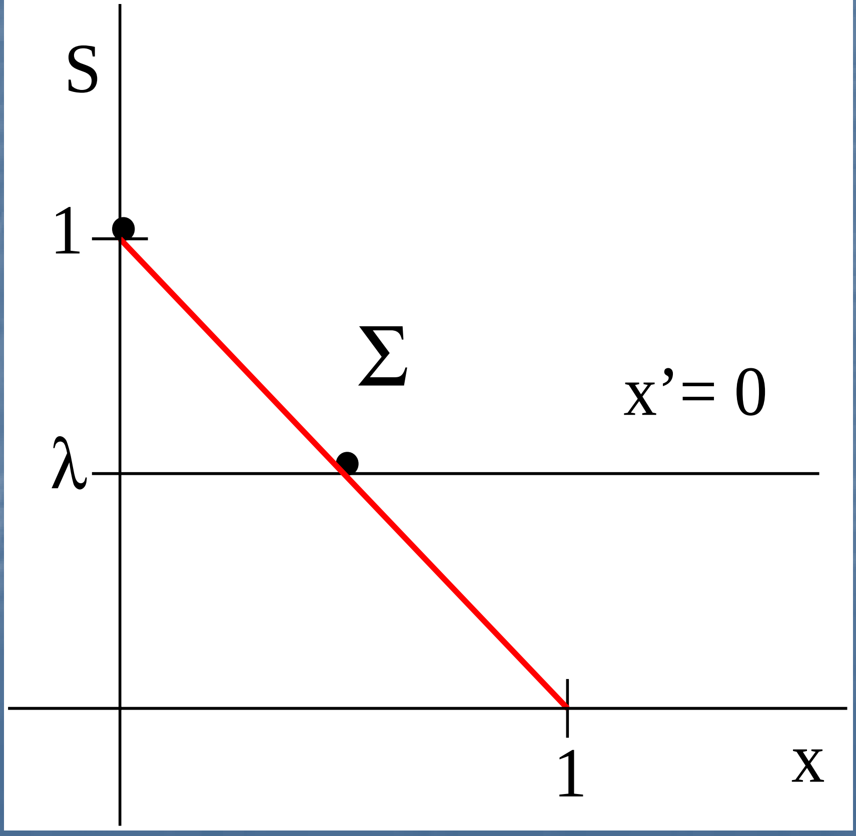
$$\frac{dS}{dt} = 1 - S - \left[\frac{m\,S}{a+S}\right]x\,. \qquad \text{(Ch)}$$

Model Analysis

Define $T = x + S$ and let "$'$" denote differentiation with respect to t. Clearly, $T' = x' + S' = 1 - T$ so $T(t) = 1 + (T(0) - 1)\, e^{-t}$ and solutions to (Ch) asymptotically approach the invariant unit simplex $\Sigma = \{(x, S) : x + S = 1\}$.

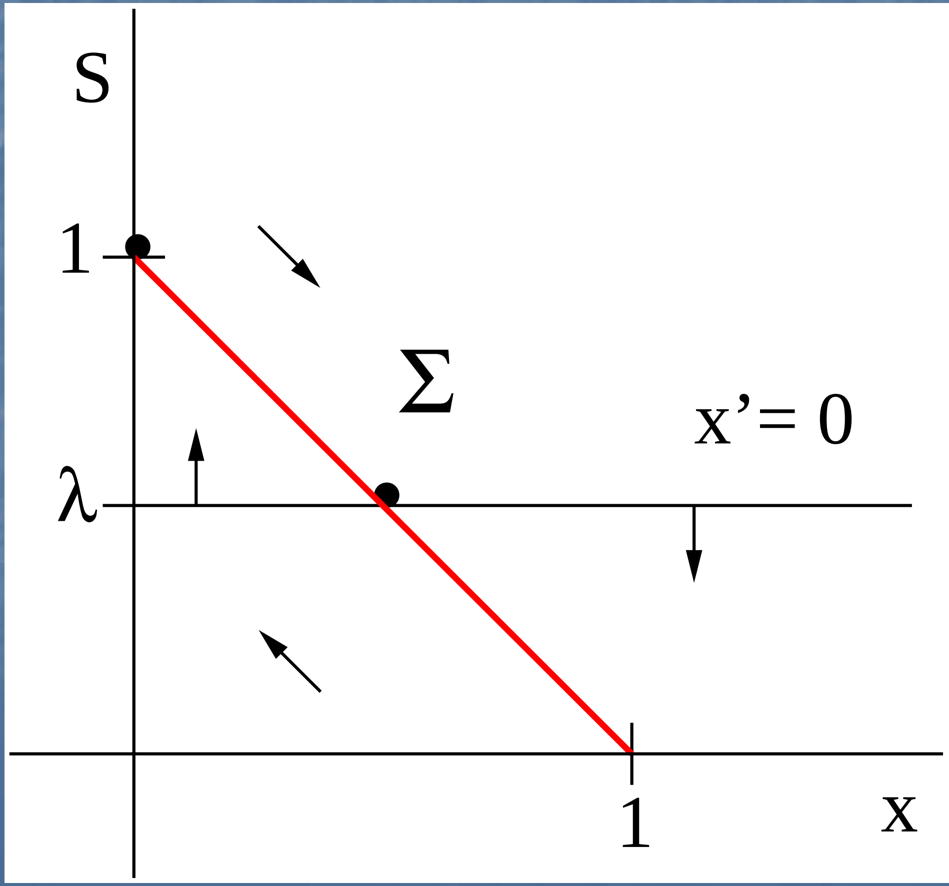
$$\frac{dx}{dt} = x\left[\frac{mS}{a+S} - 1\right]$$

If $m < 1$ then $x' < 0$ and the equilibrium $(x, S) = (0, 1)$ is a global attractor, i.e., the organism dies out. If $m > 1$ then the x-nullcline is the horizontal line $S = a/(m-1)$. Define $\lambda = a/(m-1)$ and note that $x' > 0$ if $S > \lambda$ and $x' < 0$ if $S < \lambda$.



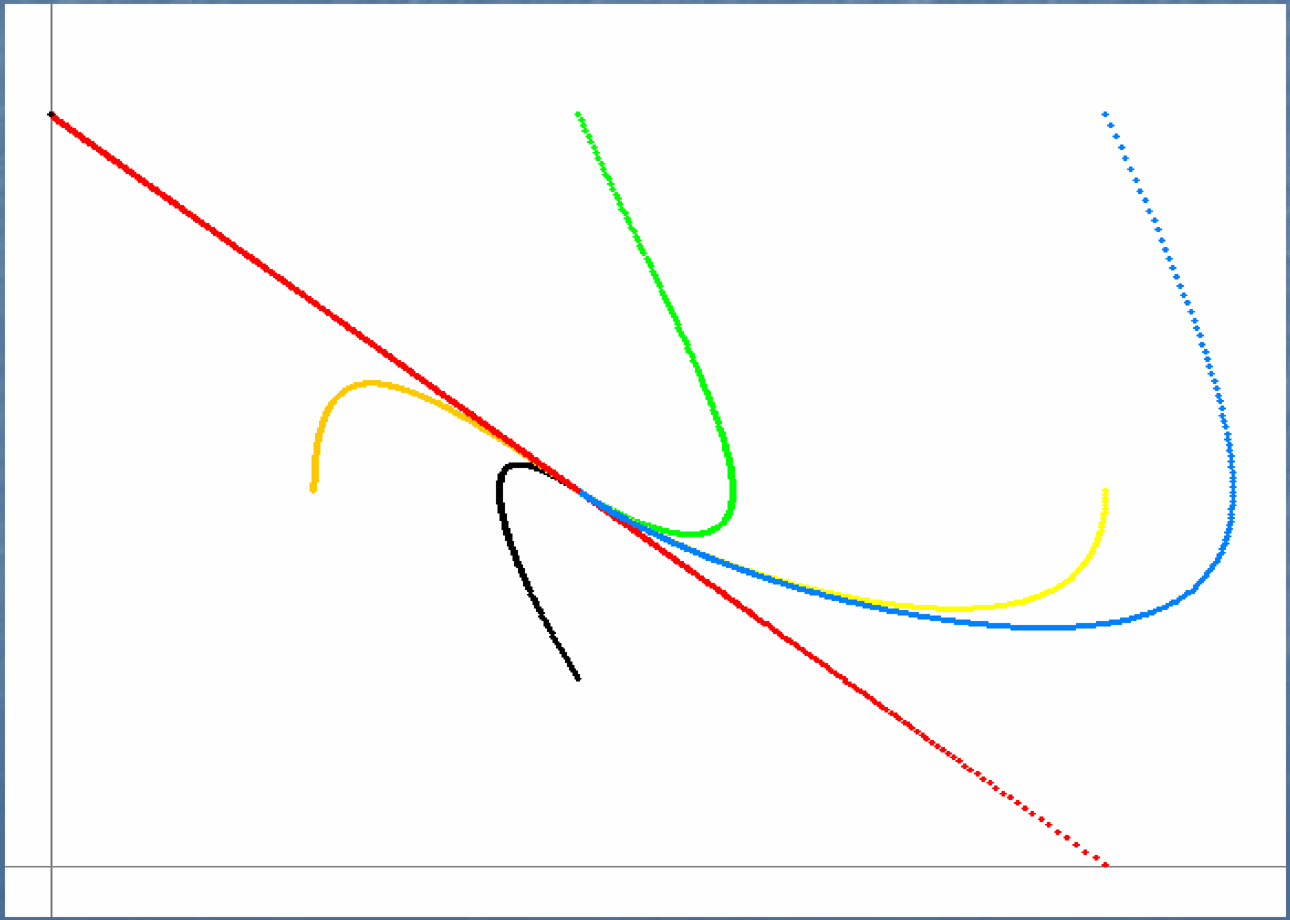
Model Analysis

λ is called the *breakeven* concentration because it is the minimum for S so that x will grow. As λ decreases through 1 a new equilibrium $E = (1 - \lambda, \lambda)$ bifurcates from $(0, 1)$. Assume that $\lambda < 1$.



Model Analysis

When **m>1** and **λ<1,** the equilibrium **(0,1)** is a saddle and **E=(1-λ,λ)** is globally stable. If **m=3** and **a=1** then **E=(.5,.5).**



Competition

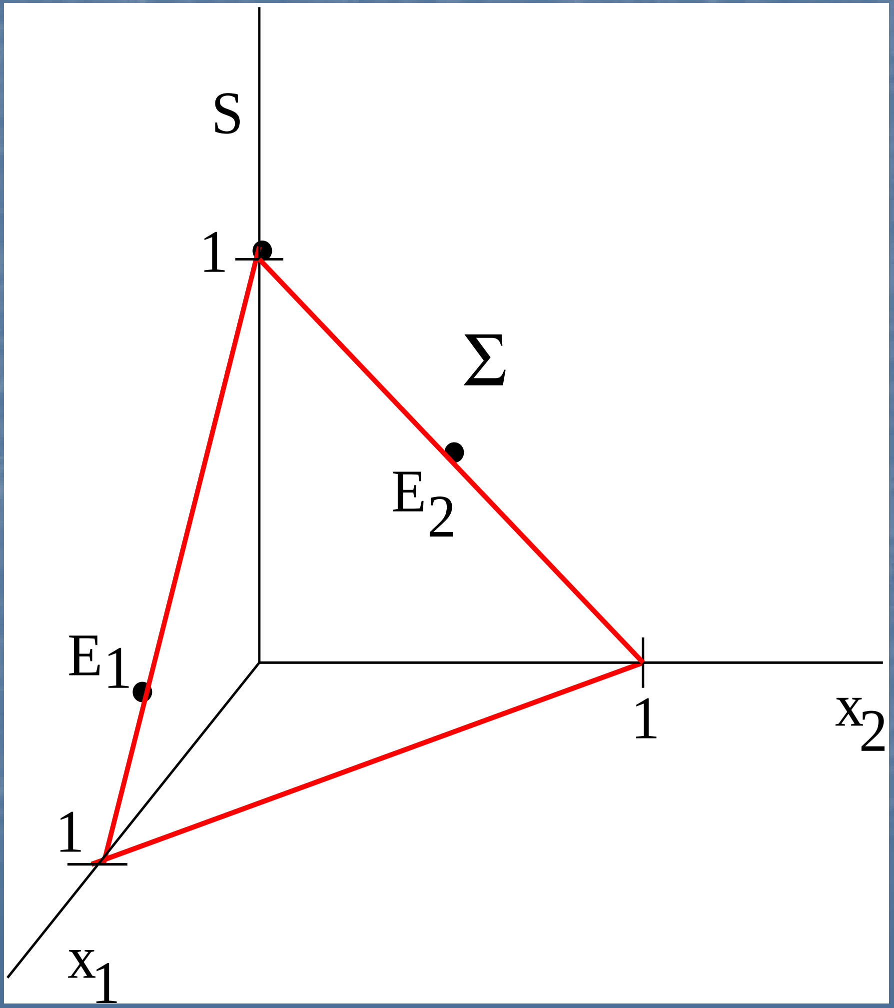
Assume two organisms x_1 and x_2 compete for the common nutrient S. The system of o.d.e's becomes:

$$x_1' = \frac{m_1 S x_1}{a_1 + S} - x_1$$

$$x_2' = \frac{m_2 S x_2}{a_2 + S} - x_2$$

$$S' = 1 - S - \frac{m_1 S x_1}{a_1 + S} - \frac{m_2 S x_2}{a_2 + S}.$$

Solutions approach the simplex $S + x_1 + x_2 = 1$. If $m_i > 1$ and $\lambda_i = a_i/(m_i - 1) < 1$ then the equilibria are (0,0,1), $E_1 = (1 - \lambda_1, 0, \lambda_1)$ and $E_2 = (0, 1 - \lambda_2, \lambda_2)$.



Competition

Since $S = 1 - x_1 - x_2$ on the attracting simplex Σ, the following 2-dim. system describes the behavior on Σ where $x_1 + x_2 \leq 1$:

$$x_1' = x_1 \left[\frac{m_1 (1 - x_1 - x_2)}{a_1 + 1 - x_1 - x_2} - 1 \right]$$

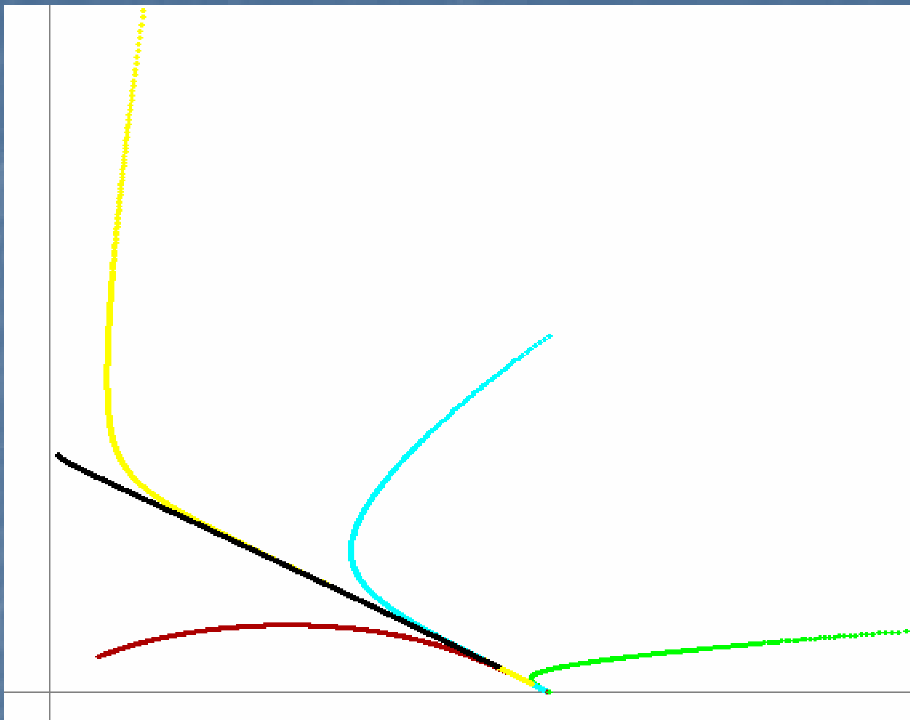
$$x_2' = x_2 \left[\frac{m_2 (1 - x_1 - x_2)}{a_2 + 1 - x_1 - x_2} - 1 \right]$$

Using topological results like the Poincaré-Bendixson theorem and the Butler-McGehee lemma, it follows that:

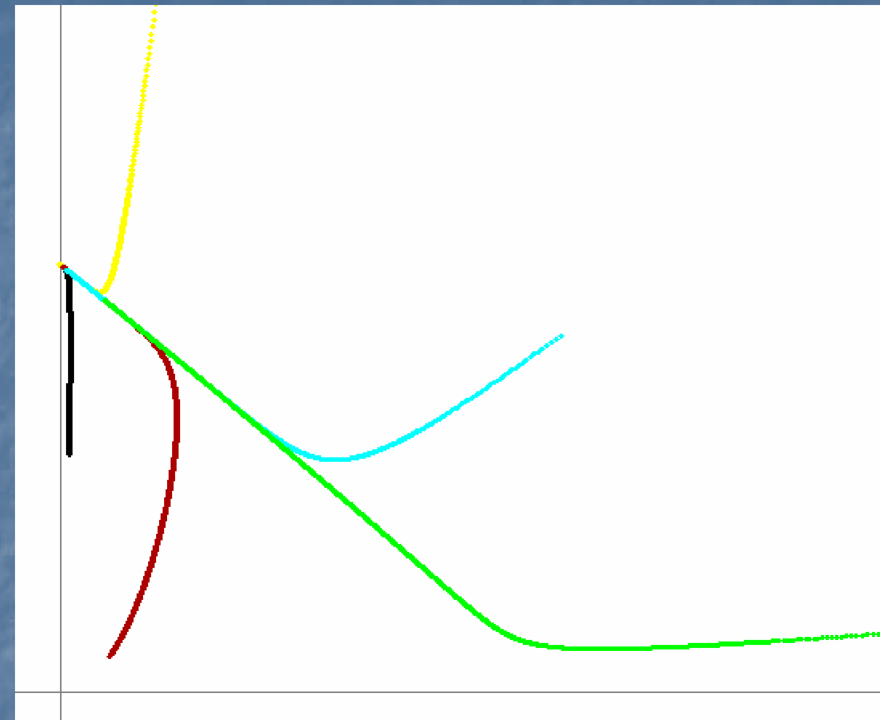
Theorem (Hsu, Hubbell, and Waltman, 1977). If $m_i > 1$ and $0 < \lambda_1 < \lambda_2 < 1$ then each solution with $x_i(0) > 0$ has $S(t) \to \lambda_1$, $x_1(t) \to 1 - \lambda_1$ and $x_2(t) \to 0$.

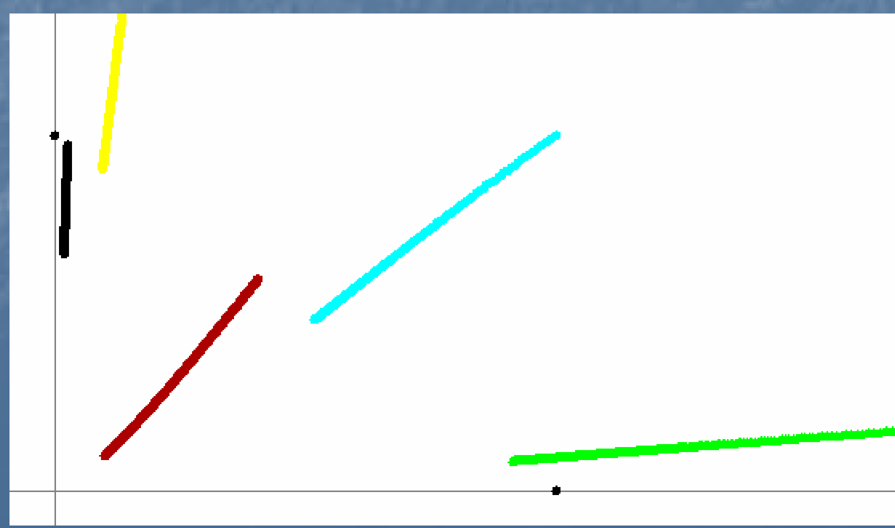
Competition

$\lambda_1=.5,\ \lambda_2=.667$



$\lambda_1=.5,\ \lambda_2=.4$





$\lambda_1=.5,\ \lambda_2=.5$

$x_1,\ x_2$ on Σ

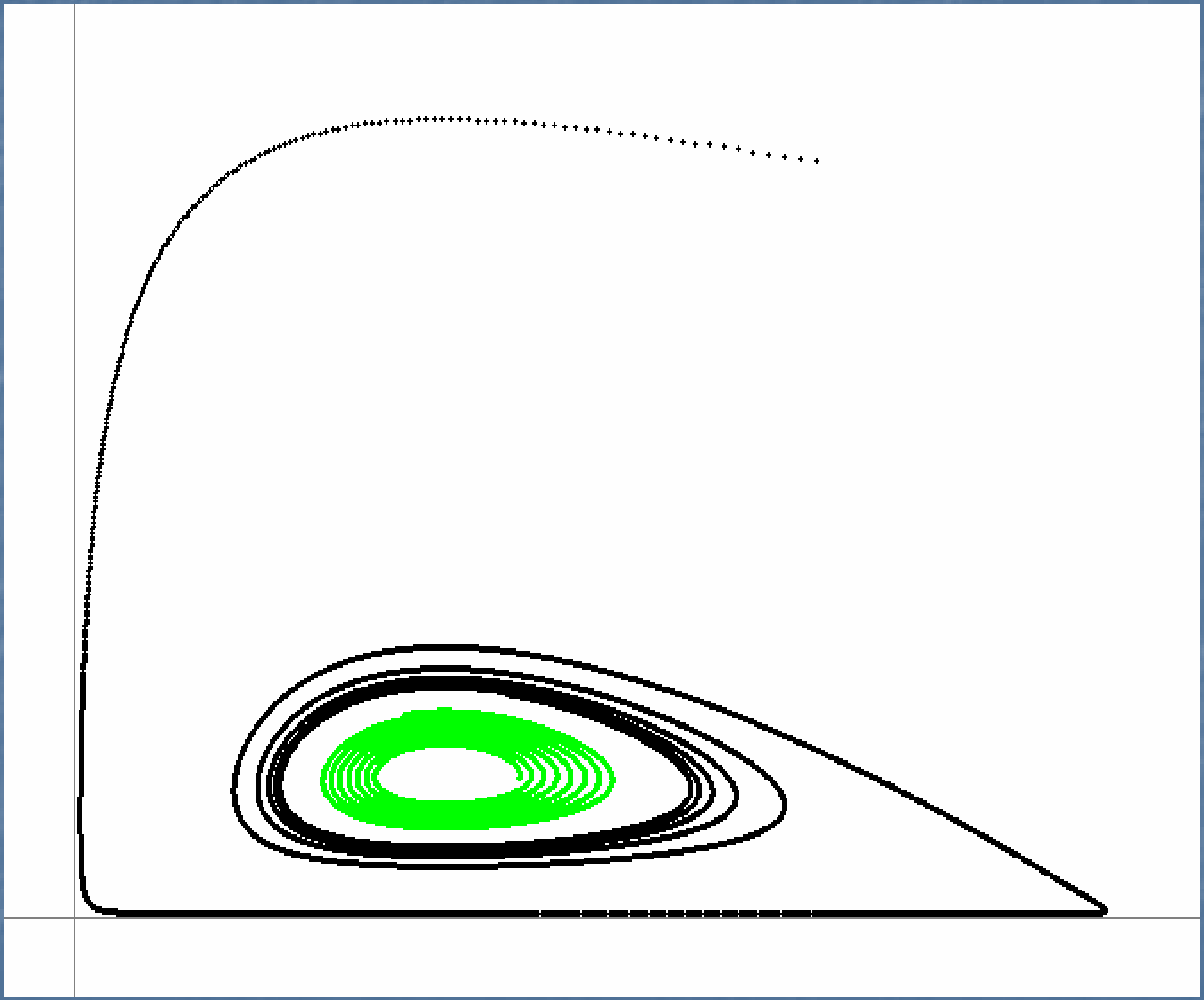
Prey-Predator

If x_1 is a prey and x_2 is a predator with a Michaelis-Menton interaction term then the system becomes:

$$\begin{aligned} x_1' &= \frac{m_1 S x_1}{a_1 + S} - \frac{m x_1 x_2}{a + x_1} - x_1 \\ x_2' &= \frac{m_2 S x_2}{a_2 + S} + \frac{m x_1 x_2}{a + x_1} - x_2 \\ S' &= 1 - S - \frac{m_1 S x_1}{a_1 + S} - \frac{m_2 S x_2}{a_2 + S} . \end{aligned}$$

Solutions approach the simplex Σ where $S + x_1 + x_2 = 1$. A Hopf bifurcation occurs in Σ at $a_1 \approx 0.35$, $m_1 = 2$, $a_2 = 0.5$, $m_2 = 0.05$, $a = 0.25$ and $m = 2$ resulting in a globally stable periodic solution.

Prey-Predator



$a_1=0.3$

References

- L. Edelstein-Kesket, *Mathematical Models in Biology*, Random House, New York, 1988.
- S.B. Hsu, S.P. Hubbell and P. Waltman, A mathematical theory for single nutrient competition in continuous cultures of micro-organisms, *SIAM Jour. Appl. Math*. **32**, 366-383, 1977.
- H.L. Smith and P. Waltman, *The Theory of the Chemostat: Dynamics of Microbial Competition*, Cambridge University Press, 1995.