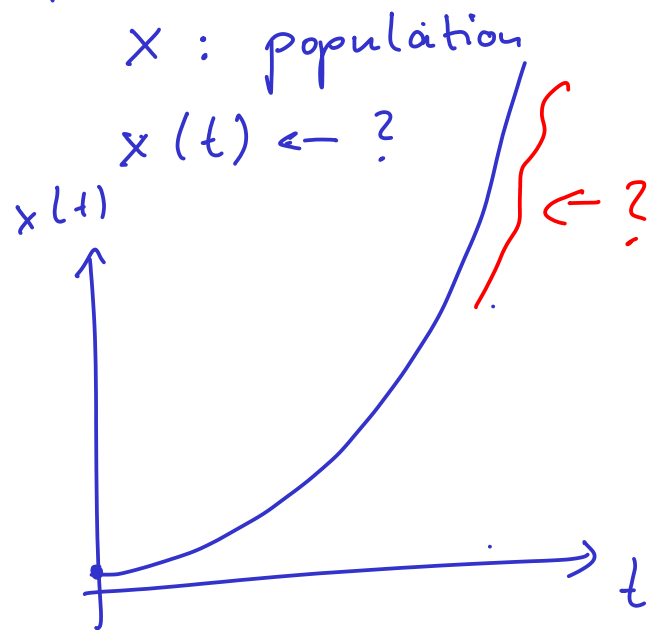


24-3-2020

Exponential growth: Growth rate is proportional to population



$$\frac{dx}{dt} = \dot{x} = r \cdot x$$

Differential equation

Initial Value Problem (IVP)

$$x(t) = \underbrace{x_0}_{\downarrow} \cdot e^{rt}$$

Initial condition

$$\rightarrow \boxed{x(0) = x_0}$$

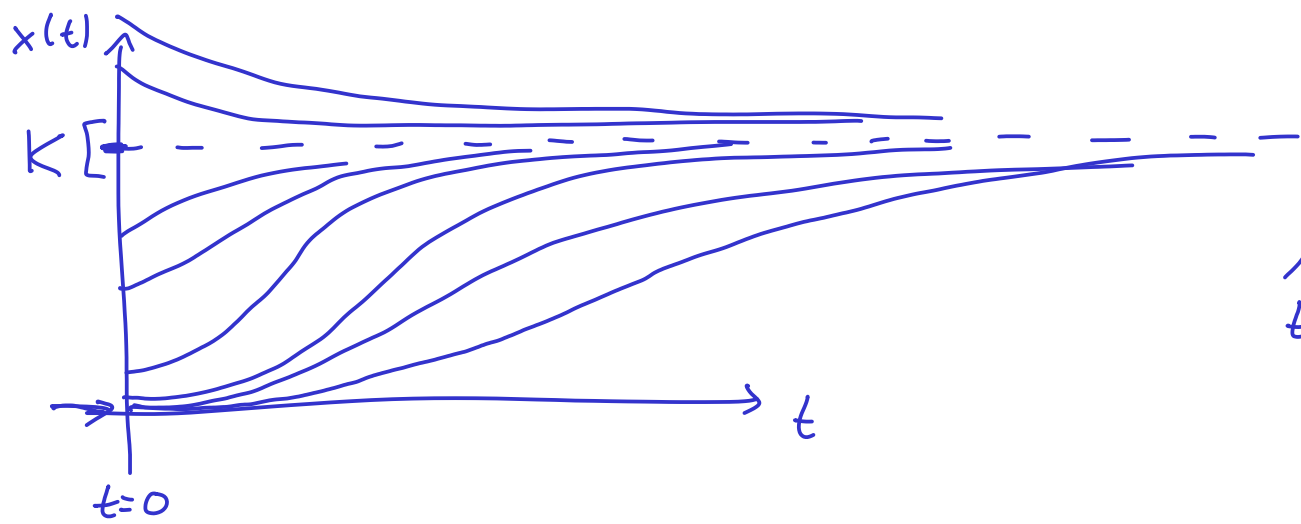
determined from initial conditions

Logistic growth (Verhulst 1838):

$$\rightarrow \dot{x} = r \cdot x \cdot \left(1 - \frac{x}{K}\right) \quad K: \text{capacity}$$

$x \approx 0$ :  $1 - \frac{x}{K} \approx 1 \rightarrow$  approx. exponential growth

$x \approx K$ :  $1 - \frac{x}{K} \approx 0 \rightarrow$  no growth

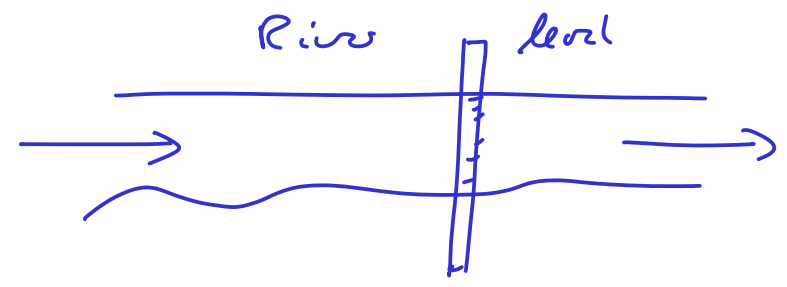


$$\lim_{t \rightarrow \infty} x(t) = K$$

unstable

Assume that  $x(0) = 0 : x(t) = 0$

Steady-state (stationary state)



Defined by  $\dot{x} = 0$

$$\dot{x} = r x \left( 1 - \frac{x}{K} \right) = 0$$

What are the steady states?

$x = 0$  or  $x = K$



General differential equation (1-dim):

$$\boxed{\dot{x} = f(x)} \text{ autonomous system}$$

$f(x) = r \cdot x \leftarrow$  exp. growth

$f(x) = r x \left(1 - \frac{x}{k}\right) \leftarrow$  log. growth

$\vdots$   
)

Steady-states:  $\dot{x} = 0$

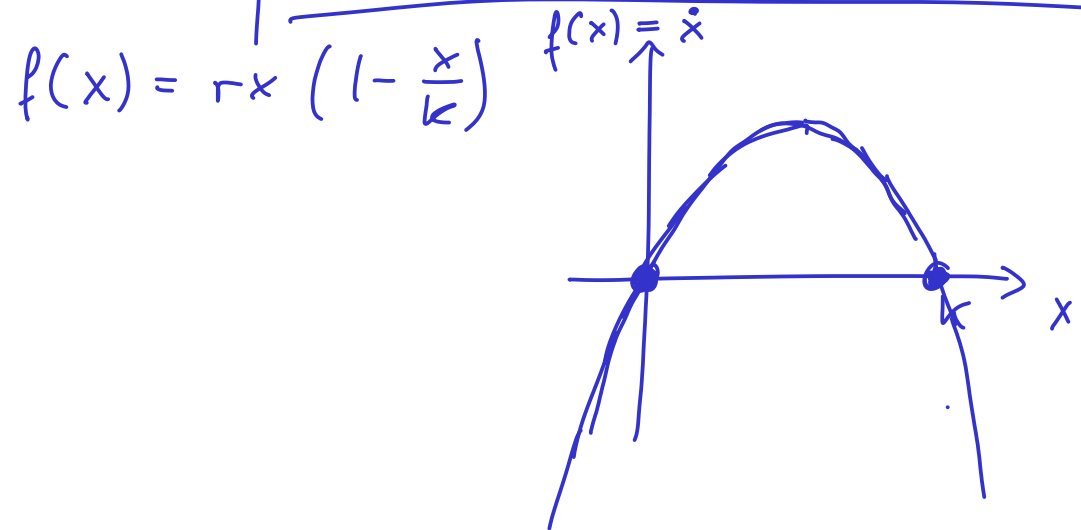
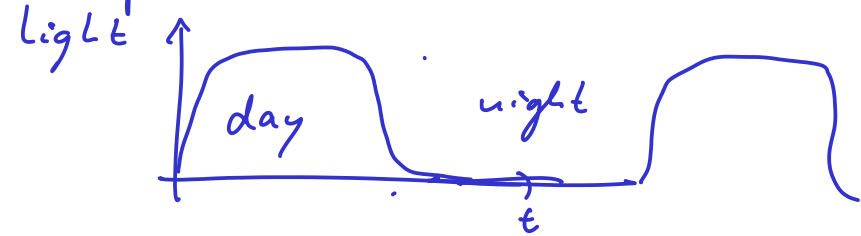
$$\Leftrightarrow f(x) = 0$$

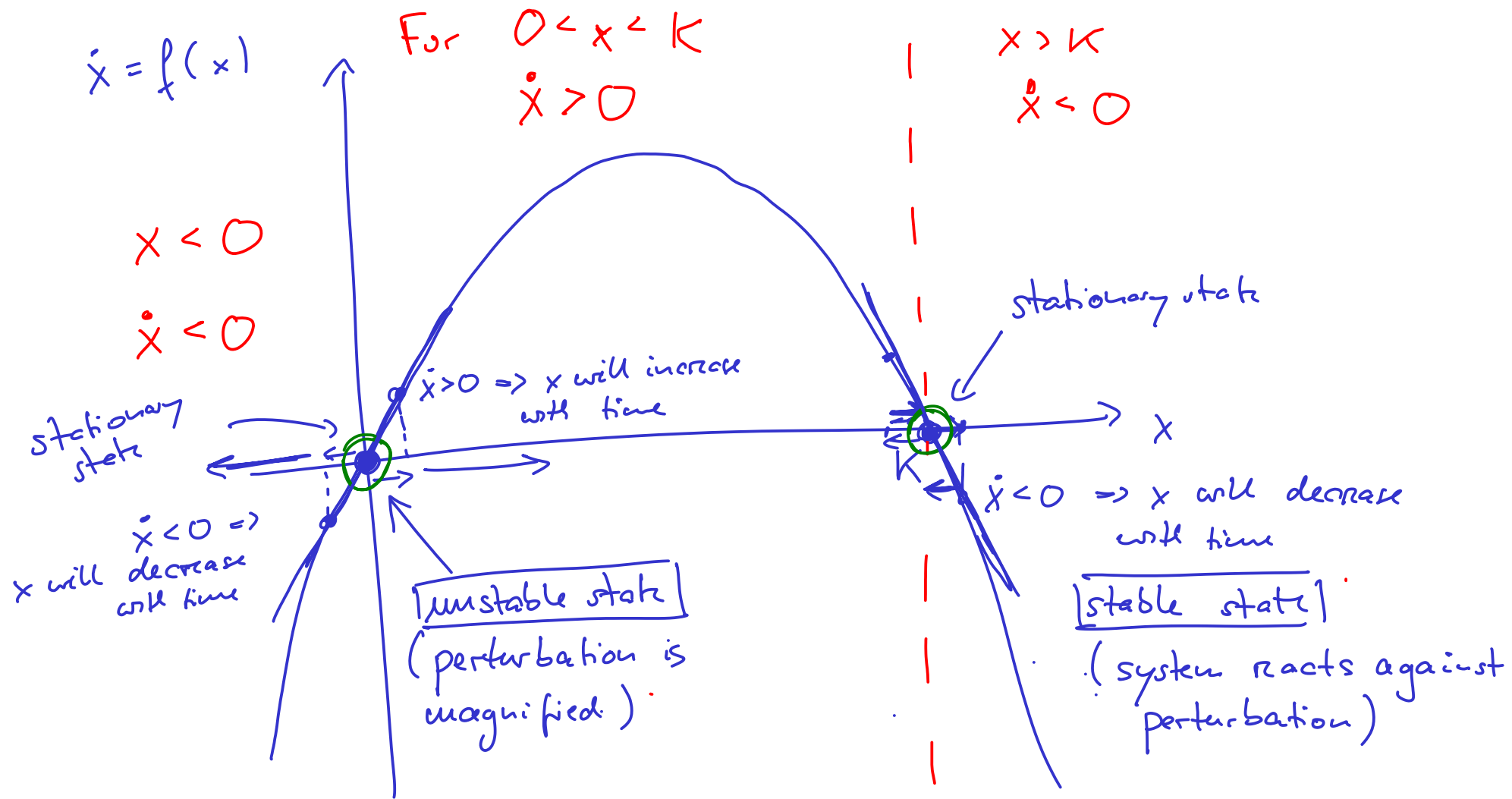
non-autonomous system

$$\boxed{\dot{x} = f(x, t)}$$

↑  
time

e.g. circadian clock  
dependence on time





$$\dot{x} = f(x)$$

Stability of a steady state is determined by the sign of the derivative of  $f(x)$

$f'(x) > 0$  : unstable

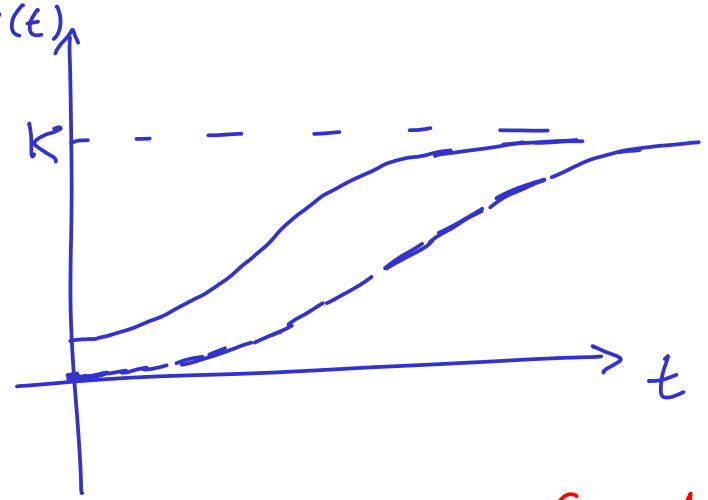
$f'(x) < 0$  : stable

$$\dot{x} = r \cdot x \cdot \left(1 - \frac{x}{K}\right)$$

$$K > x > 0 : \dot{x} > 0$$

Application to macroscopic ecosystems  
(sexually reproducing species):

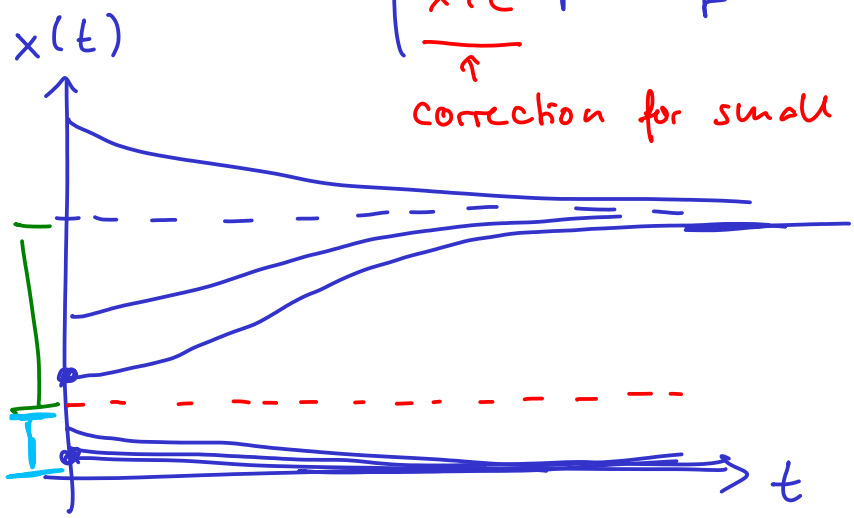
• the behaviour for small population sizes is unrealistic



Net growth rate (constant):  $r = b - d$   
 ↑ net growth      ↑ birth      ↓ death

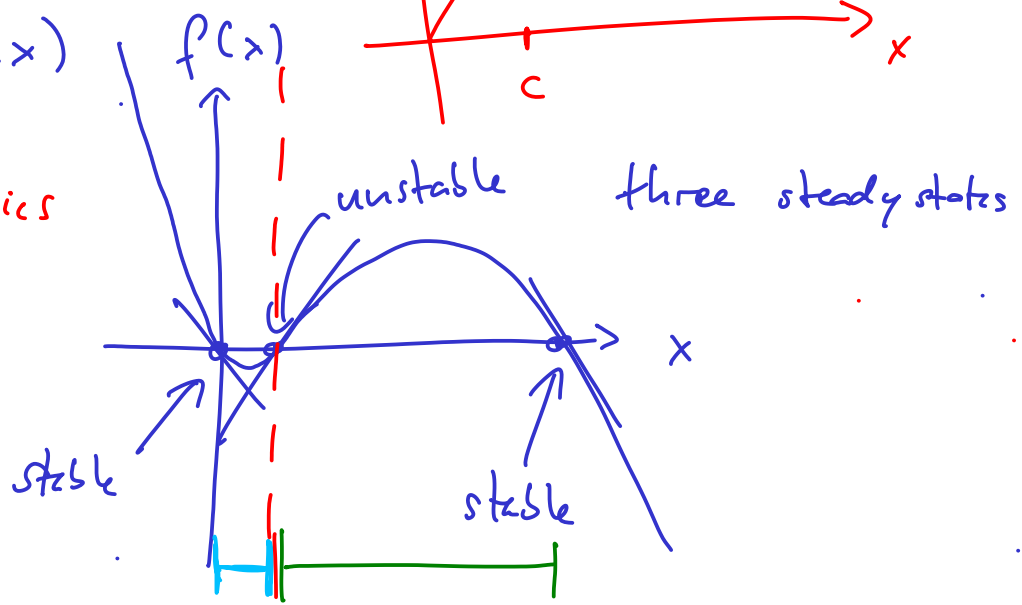
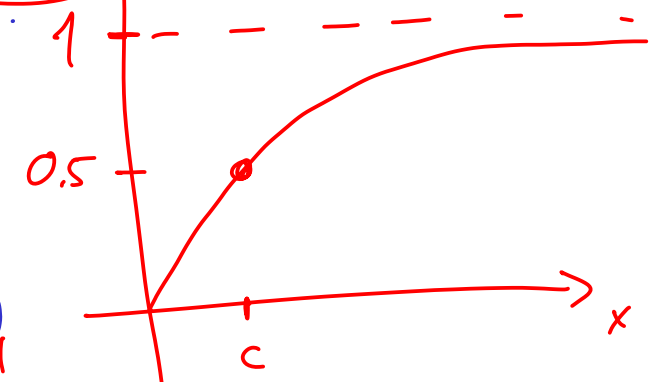
$$\dot{x} = r \cdot x \cdot \left( \frac{x}{x+c} \cdot \frac{b}{r} - \frac{d}{r} - \frac{x}{K} \right) = f(x)$$

correction for small population densities

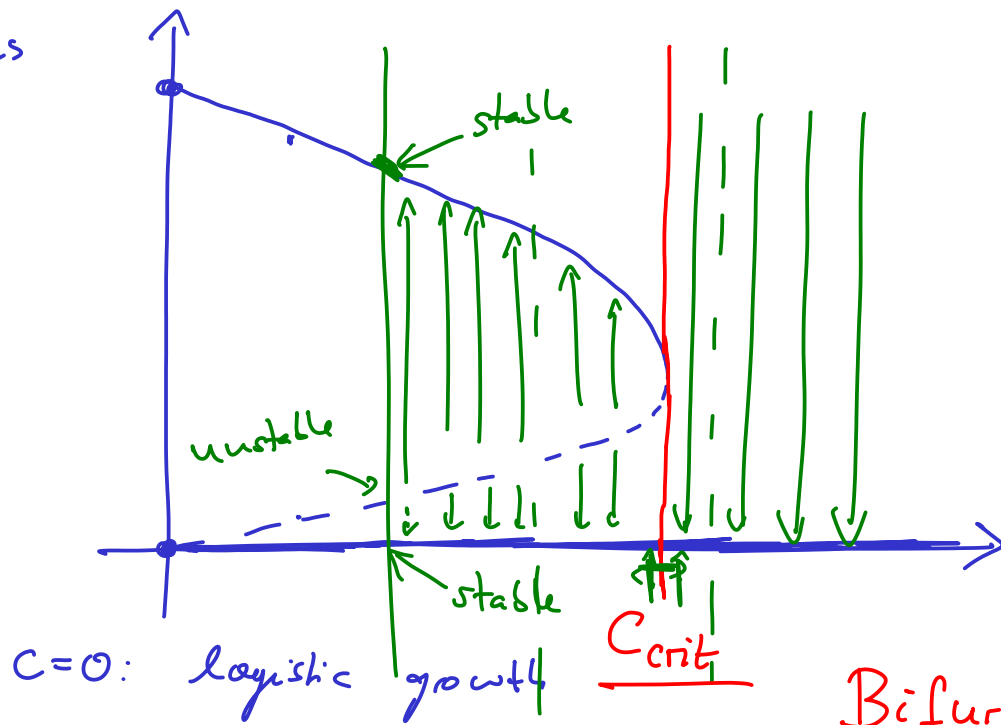


$$x=c: \frac{c}{c+c} = \frac{1}{2}$$

$$\frac{x}{x+c}$$



steady states



$C=0$ : logistic growth  $C_{crit}$

bistable

$C < C_{crit}$  :

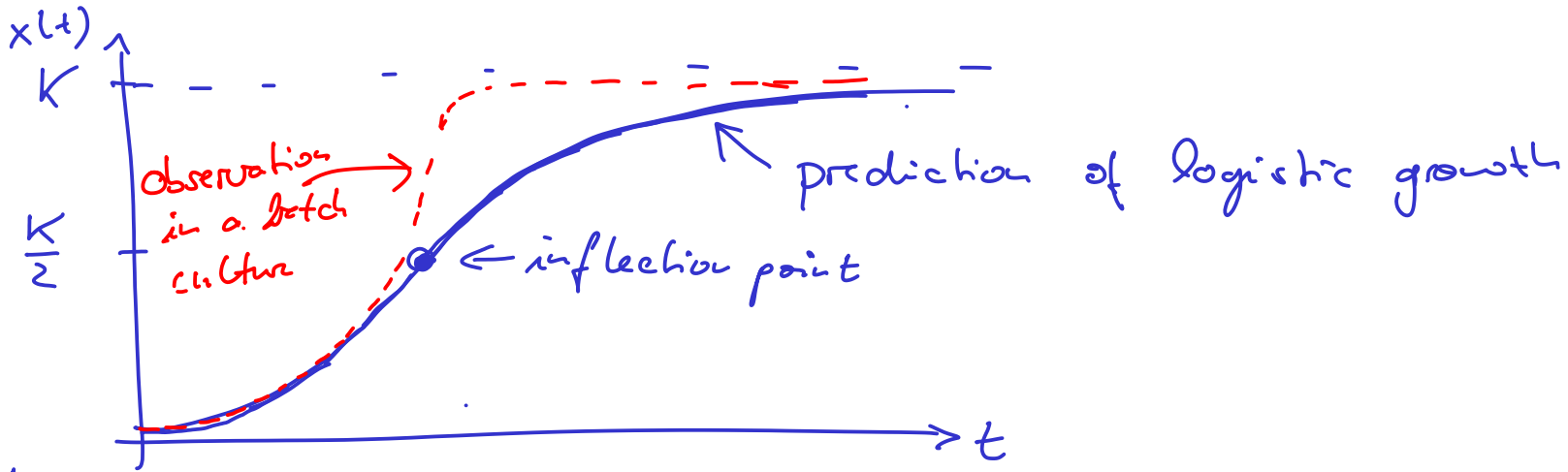
2 stable steady-states  
1 unstable

$C > C_{crit}$  :

1 stable steady-state  
( $x=0$ , extinction)

Bifurcation :

A small change of a parameter leads to a global change of the system's behaviour



Jacques

Monod (1950) : bacterial growth law

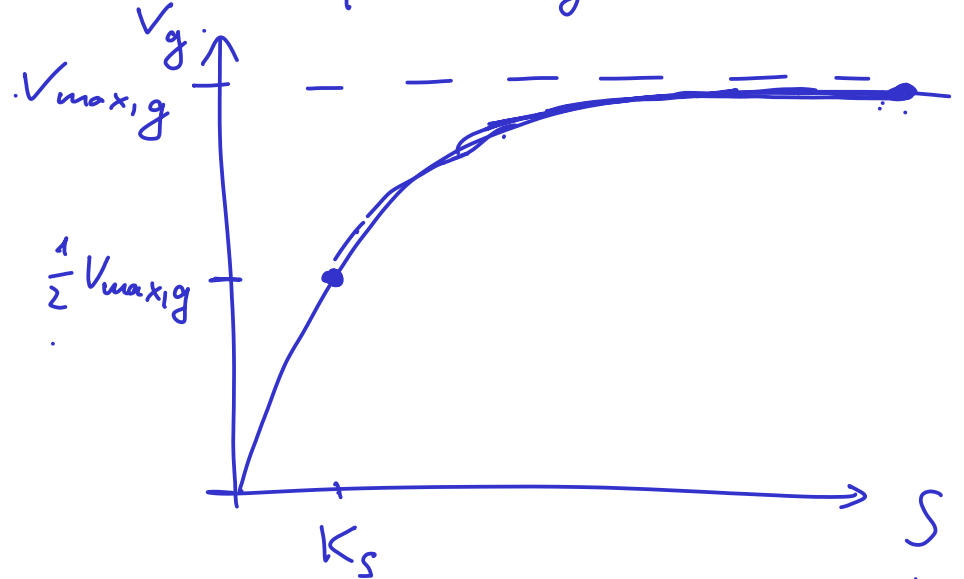
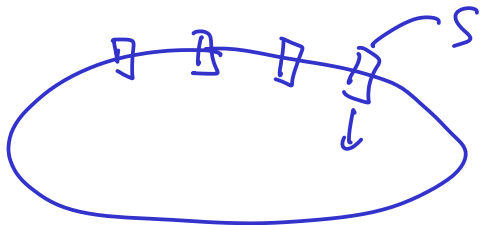
Growth rate of microbes depends on the concentration of a "limiting nutrient"

$$V_g = V_{max,g} \cdot \frac{S}{K_s + S}$$

↑  
growth rate

↑  
Monod-constant

← concentration of limiting substrate



$$\dot{x} = \frac{dX}{dt} = V_g = \tau_g \cdot X$$

$$\tau_g = \tau_{max,g} \cdot \frac{S}{K_s + S}$$

X: population of bacteria

S: substrate

↳  $\dot{S} = ?$

a common unit for biomass  
and nutrient is

C-mol

$$\dot{X} = r_g \cdot X = r_{max,g} \cdot X \cdot \frac{S}{K_s + S}$$

growth rate of bacteria depends on  
a) population x, b) substrate concentration

$$\dot{S} = - \frac{1}{Y_{X/S}} r_g \cdot X$$

yield factor:  
how much biomass do you get  
from the nutrients..?

Common yield factors for E.coli / yeast under  
aerobic growth exceed 0.5 (0.5-0.7)

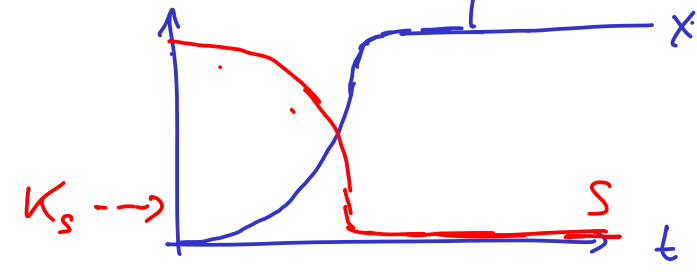
Two coupled differential equations!

Species  
Resource

$$\begin{aligned} \dot{X} &= r_{max,g} \cdot X \cdot \frac{S}{K_s + S} \\ \dot{S} &= - \frac{1}{Y_{X/S}} \cdot r_{max,g} \cdot X \cdot \frac{S}{K_s + S} \end{aligned}$$

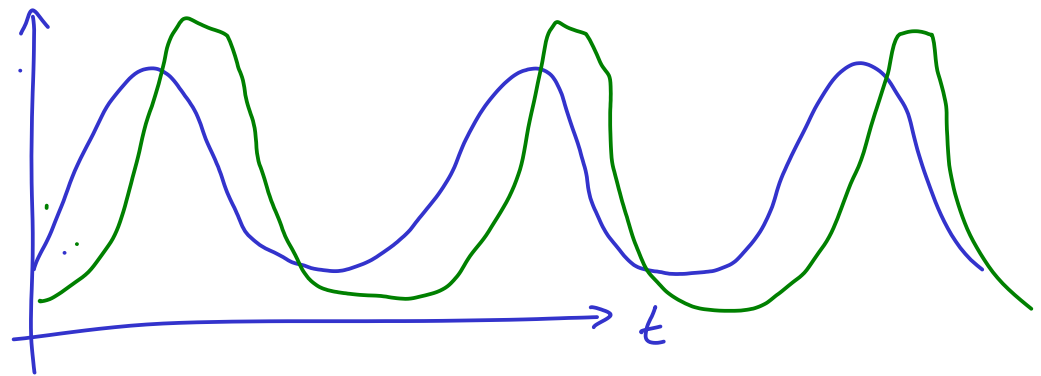
}

2-dimensional system





# Lotka-Volterra System (1920) (1926).



Predator - Prey model

$X$  : prey (e.g. rabbit)

$Y$  : predator (e.g. fox)

$$\begin{aligned} \dot{X} &= r_1 X - a_1 X \cdot Y \\ \dot{Y} &= a_2 X \cdot Y - r_2 Y \end{aligned} \quad \text{2-dim}$$

## Generalised Lotka-Volterra Systems

$X_i$ ,  $i = 1 \dots n$  :  $n$  different species

Generalisation

$$\dot{X}_i = r_i \cdot X_i + \sum_{j=1}^n a_{ij} X_i X_j$$

$n$ -dim

interaction term

$r_i$  can be positive or negative

$a_{ij}$  : interaction terms / interaction matrix  
can be positive or negative

# Consumer - Resource Models (MacArthur, 1970)

$X_i$ ,  $i = 1..n$  : species

$R_j$ ,  $j = 1..m$  : resources

$$\dot{X}_i = b_i X_i \left( \sum_{j=1}^m c_{ij} w_j R_j - m_i \right)$$

yield

"capture rate"

"value of resource j"

"maintenance"

$$\dot{R}_j = R_j \left( \tau_j \left( 1 - \frac{R_j}{K_j} \right) - \sum_{i=1}^n c_{ij} X_i \right)$$

influx

consumption