Lecture 5 – Density-dependent deterministic growth

Announcements:
PS1 due
Handout Q2

Concepts:
Population vs. Per capita growth rate
Negative vs. Positive density-dependence
Stable vs. Unstable fixed point equilibria
Maximum Sustainable Yield (MSY) Probably won't finish this section

$$N_{t+1} = \lambda \cdot N_t = (1 + r_d)N_t = N_t + r_d N_t$$

Next year = previous year plus some per capita increment (proportion r_d of previous year)
r_d is discrete growth factor

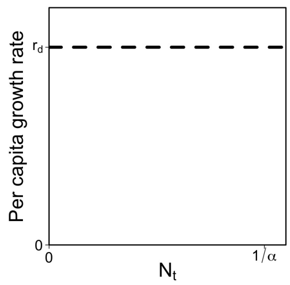
Per capita increment is density-independent:

$$\frac{N_{t+1}}{N_t} = \lambda = 1 + r_d$$

or equivalently...

$$\frac{N_{t+1} - N_t}{N_t} = r_d$$

When drawing, leave room for 3x3 = 9 graphs!



Now make per capita growth rate density-dependent:
Realized per capita growth increment = $r_d - \alpha N_t$

$$\frac{N_{t+1}}{N_t} = 1 + r_d - \alpha N_t$$

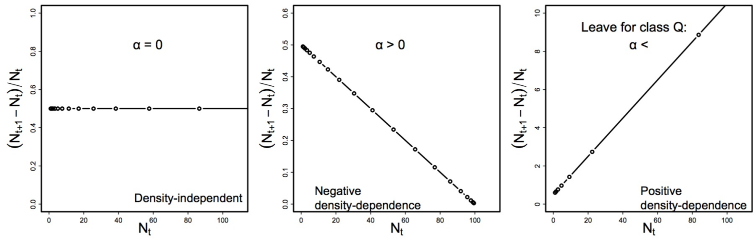
α - per capita strength of density-dependence (self-limitation rate)

$$\lim_{N_t \to 0} (r_d - \alpha N_t) = r_d$$

At what population size does realized per capita growth increment = 0?

$$0 = r_d - \alpha N_t$$
$$\alpha N_t = r_d$$
$$N_t = \frac{r_d}{\alpha}$$

Class Q: Using $r_d - \alpha N_t$, plot realized per capita growth rate vs. N_t for:
density-independece   positive density-dependence   negative density-dependence.



What do population dynamics look like?
Plug into equation for population growth rate by replacing r_d with $r_d - \alpha N_t$

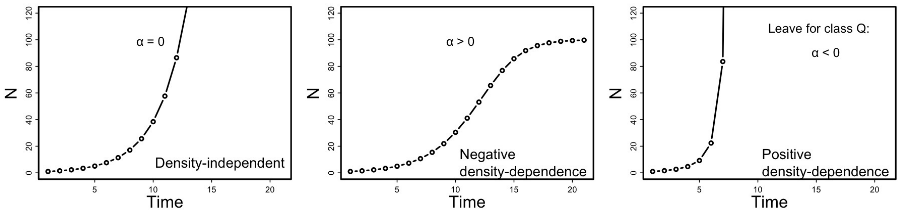
$$N_{t+1} = N_t + (r_d - \alpha N_t) N_t \qquad (\textit{Discrete logistic growth eqn.})$$

Typically written with $K = \dfrac{r_d}{\alpha}$ for 'carrying capacity':

$$= N_t + \left(r_d - \frac{r_d}{K} N_t\right) N_t$$

$$= N_t + r_d \left(1 - \frac{N_t}{K}\right) N_t$$

Draw one after the other:
Class Q: What would positive density dependence look like?



Class Q: Have you read Mark Kot's *'Historical hiatus'*?
With what kind of density-dependence has the global human population been growing?
How is that possible?

Definition:
The *equilibrium* (a.k.a. steady state) abundance for the difference equation $N_{t+1} = F(N_t)$, is the value N_t^* where $N_{t+1} = F(N_t^*) = N_t^*$ (i.e. population growth rate is zero.)
(We will use N^* to denote an equilibrium/steady-state.)

Class exercise 1: Simulating logistic growth
Walk through Part A of *'Class5-Ex-LogisticGrowth.R'*

Allow students to explore.

Class Qs: Where are the point equilibria?
A:

Non-trivial point equilibrium:

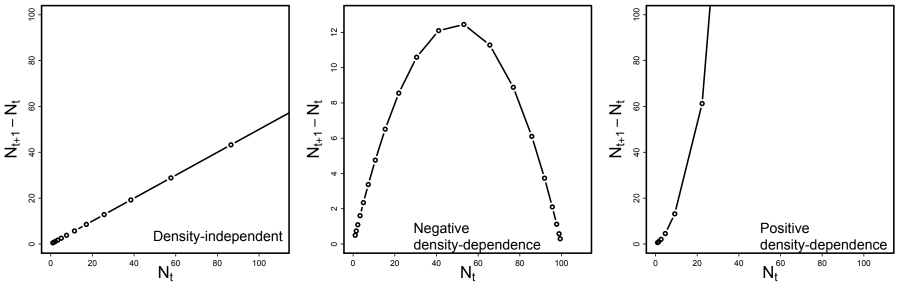
When $N_t^* = K$, growth rate $= 0$, thus $N_{t+1} = N_t$.

Trivial point equilibrium:

When $N_t^* = 0$, growth rate $= 0$, thus $N_{t+1} = N_t$.

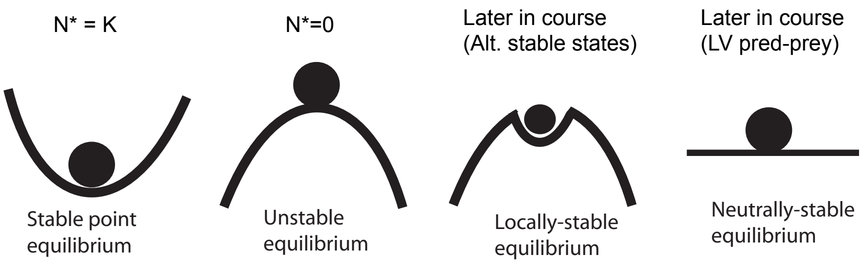
What happens with $N_t > K$?
Best way to see where equilibria is:
Plot population-level growth rate, $(N_{t+1} - N_t)$ or $\frac{dN}{dt}$, as function of N

Class Q: What does $N_{t+1} - N_t$ vs. N_t look like?



At low N, few individuals to reproduce $\implies$ low population growth rate.
At high N, strong self-limitation $\implies$ low population growth rate.

Ball & Cup analogy:



Continuous logistic
Recall: **Discrete geometric growth to continuous exponential growth**

$$N_{t+1} = (1 + r_d)N_t \text{ converted to } N_t = N_0 e^{rt}$$

Differential equation solution:

$$\frac{d(N_0 e^{rt})}{dt} = \frac{dN}{dt} = rN$$

Discrete logistic:

$$N_{t+1} = N_t + r_d(1 - \alpha N_t)N_t$$

$$\text{converts to} \quad N_t = \frac{N_0 e^{rt}}{1 + \alpha N_0(e^{rt} - 1)}$$

$$\text{or equivalently} \quad N_t = \frac{K N_0}{N_0 + (K - N_0)e^{-rt}}$$

Class Q: See if you can prove these equalities at home.
Hint: To go from 2nd to 1st, divide once by $\frac{K}{K}$ and multiply once by $\frac{N_0 e^{rt}}{N_0 e^{rt}}$.

Differential solution:

$$\frac{dN}{dt} = rN - \alpha N^2 = rN\left(1 - \frac{N}{K}\right)$$

the latter being attributed to Verhulst (1838)

NOTE: There are a number of other ways to represent density-dependent growth:
Ricker model (and extensions):

$$N_{t+1} = N_t e^{r(1 - N_t/K)}$$

...which is a special case of the Beverton-Holt model ...which is a special case of the Hassell model.

Definition:
The steady state abundance for a differential equation $\frac{dN}{dt} = f(N)$ is the value N^* where $f(N^*) = 0$. Population growth rate is zero. System is at equilibrium.

For the logistic, there are two equilibria:
 Trivial equilibrium, $N^* = 0$
 Non-trivial equilibrium, $N^* = K$.

Solving for equilibria analytically:

$$\text{Step 1: Set } f(N) = \frac{dN}{dt} = 0$$
$$\text{Step 2: Solve for } N^*$$
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) = 0$$
$$rN - \frac{rN^2}{K} = 0$$
$$rN = \frac{rN^2}{K}$$
$$N = \frac{N^2}{K}$$
$$NK = N^2$$
$$N^* = K$$

Class Exercise 2 ODE-solvers and continuous logistic
Walk through code
Class Q: How do values of r, K, and N_0 affect the maximum value of $\frac{dN}{dt}$?

Parameter	**Max.** $\frac{dN}{dt}$
N_0	doesn't affect
r	increases
K	increases

With this knowledge you should be able to take Quiz 2. So take it!

Maximum Sustainable Yield
Where is maximum $\frac{dN}{dt}$?

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) = rN - \frac{rN^2}{K}$$

Maximum occurs where slope = 0, $\implies$ derivative with respect to N.
Step #1: Differentiate with respect to N

$$\frac{d\left(rN - \frac{rN^2}{K}\right)}{dN} = r - \frac{2rN}{K}$$

Step #2: Set = 0

$$r - \frac{2rN}{K} = 0$$

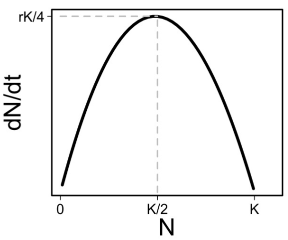
Step #3: Solve for N

$$2rN = rK$$
$$N = \frac{K}{2}$$

A: Maximum population growth rate occurs at half the carrying capacity

Q: What is maximum possible population growth rate?
A: Plug in $\frac{K}{2}$ for N...

$$\frac{dN}{dt} = r\frac{K}{2}\left(1 - \frac{K/2}{K}\right) = r\frac{K}{2}\left(1 - \frac{1}{2}\right) = \frac{rK}{4}$$



Context of harvest:
$\frac{dN}{dt}$ vs. N = Stock-recruitment function. Replace axis labels on graph.
Maximum Sustainable Yield (MSY)
Occurs when $N = \frac{K}{2}$ and produces harvestable biomass at rate $\frac{rK}{4}$.
Over-fished when $N < \frac{K}{2}$
Not over-fished when $N > \frac{K}{2}$.

Fixed-quota harvest scenario

$$\frac{dN}{dt} = f(N) = rN\left(1 - \frac{N}{K}\right) - H$$

Class Q: What are units of H? A: Individuals per time.

Solve for equilibria:
Step #1: Set $f(N)$ to 0

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - H = 0$$

Step #2: Solve for N^*
Trivial solution is $N^* = 0$
Rearrange to:

$$-\frac{r}{K}N^2 + rN - H = 0$$

This is just like the quadratic equation...

$$ax^2 + bx + c = 0$$

...whose solution is...

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

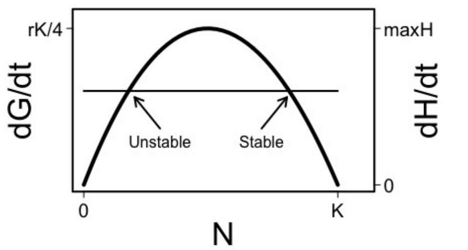
Thus:

$$N^* = \frac{-r \pm \sqrt{r^2 - 4rH/K}}{-2r/K} = \frac{rK \pm \sqrt{r^2K^2 - 4rKH}}{2r}$$

Thus model contains *two* non-trivial solutions and *one* trivial solution!

Graphical representation:

$$\frac{dN}{dt} = \underbrace{rN\left(1 - \frac{N}{K}\right)}_{\frac{dG}{dt}} \underbrace{-H}_{\frac{dH}{dt}} = 0$$



Right-hand equilibrium is a stable fixed point.

Stochastic fluctuations always return to feasible (positive) equilibrium.

Left-hand equilibrium is unstable.

Positive fluctuation will send system to stable fixed point.

Negative fluctuation will send system to extinction.

Problem for inferring MSY from real data: Show Fisheries figure.

Fixed-effort harvest scenario

$$\frac{dN}{dt} = f(N) = rN\left(1 - \frac{N}{K}\right) - hN$$

Class Q: What are units of h? A: Individuals per individual (fraction of population) per time.

Solve for equilibria

Step #1: Set $f(N)$ to 0

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - hN = 0$$

Step #2: Solve for N^*

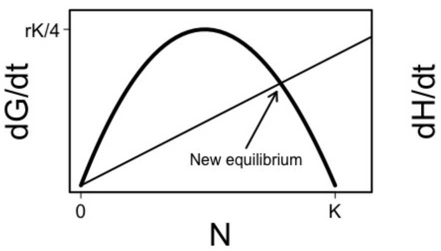
Trivial solution is $N^* = 0$

$$N^* = \frac{rK - hK}{r} = \frac{(r-h)K}{r}$$

Thus model as *one* trivial and *one* non-trivial solution.

Graphical representation:

$$\frac{dN}{dt} = \underbrace{rN\left(1 - \frac{N}{K}\right)}_{\frac{dG}{dt}} \underbrace{-hN}_{\frac{dH}{dt}} = 0$$



Non-trivial solution is always stable!
Also note intuitive interpretation:

$$N^* > 0 \text{ as long as } r > h$$

Polynomial representation of $\frac{dN}{dt}$
Recall: population size as function of time as polynomial

$$N(t) = \sum_{n=0}^{\infty} \beta_n t^n = \beta_0 + \beta_1 t + \beta_2 t^2 + ...$$

Could also think of in terms of population growth

$$\frac{dN}{dt} = f(N) = \sum_{n=0}^{\infty} \beta_n N^n$$

such that exponential growth corresponds to ...

$$\beta_0 = 0, \;\; \beta_1 = r, \;\; \beta_{n>1} = 0$$

and logistic growth corresponds to...

$$\begin{aligned} \beta_0 &= 0 \\ \beta_1 &= r \\ \beta_2 &= -\alpha = -\frac{r}{K} \\ \beta_{n>2} &= 0 \end{aligned}$$
