Lecture 5 – Density-independent deterministic growth

Note: Probably won't finish MSY section.

Concepts:
  Population vs. Per capita growth rate
  Negative vs. Positive density-dependence
  Stable vs. Unstable fixed point equilibria
  Maximum Sustainable Yield (MSY)

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

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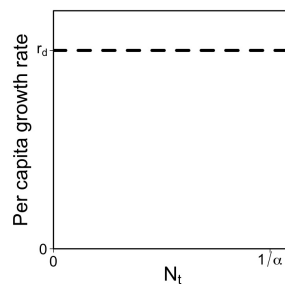 r_d is discrete growth factor

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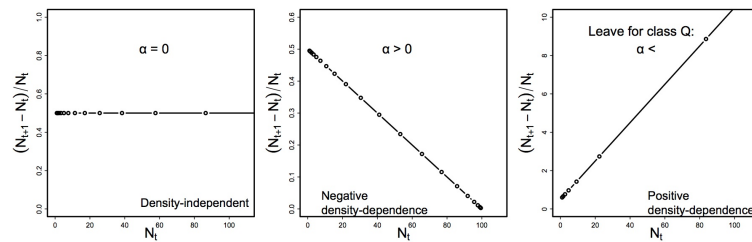
$$\lim_{N_t \to 0} (r_d - \alpha N_t) = r_d$$

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?
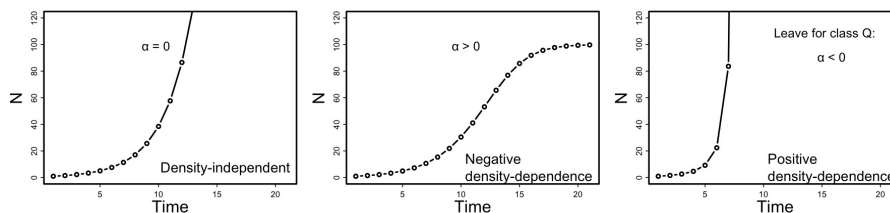Plug into equation for population growth rate by replacing r_d with $r_d - \alpha N_t$

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

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:

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

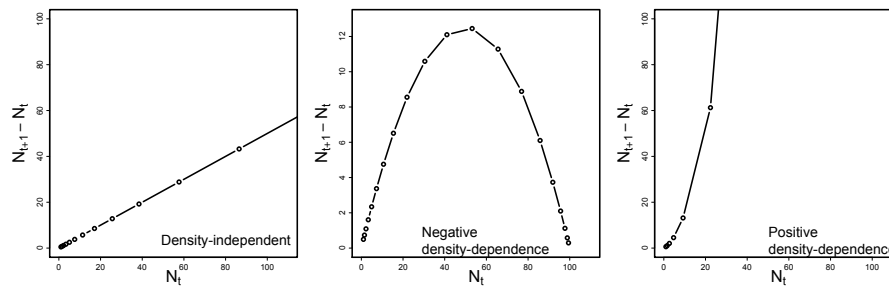   *Trivial point equilibrium:*

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

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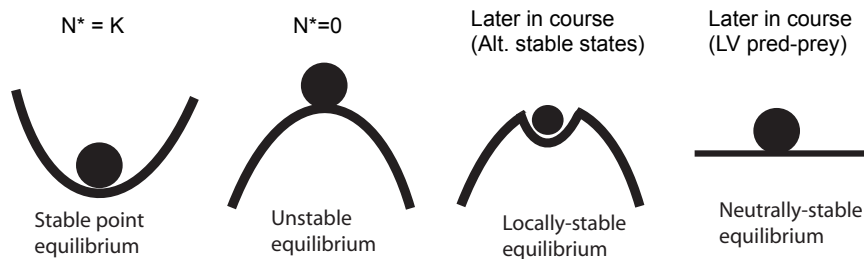
Class Q: What does $N_{t+1} - N_t$ vs. N_t look like?

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:

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

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

$$\text{or equivalently} \quad N_t = \frac{KN_0}{N_0 + (K - N_0)e^{-rt}}$$

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 $= 0$

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

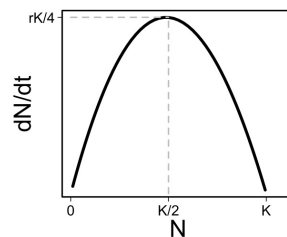Step #3: Solve for N

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

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-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...

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

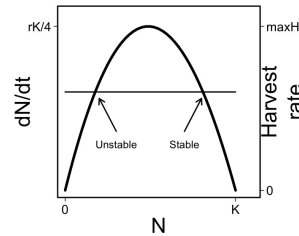...whose solution is...

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

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!

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

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - hN = 0$$
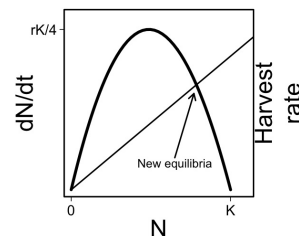
Step #2: Solve for N^*
    Trivial solution is $N^* = 0$

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

Thus model as *one* trivial and *one* non-trivial solution.
Visualize as slope $= h$

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 ...

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

and logistic growth corresponds to...

$$\beta_0 = 0, \quad \beta_1 = r, \quad \beta_2 = -\frac{r}{K}, \quad \beta_{n>2} = 0$$