Fundamentals of Ecology

Week 5, Ecology Lecture 2

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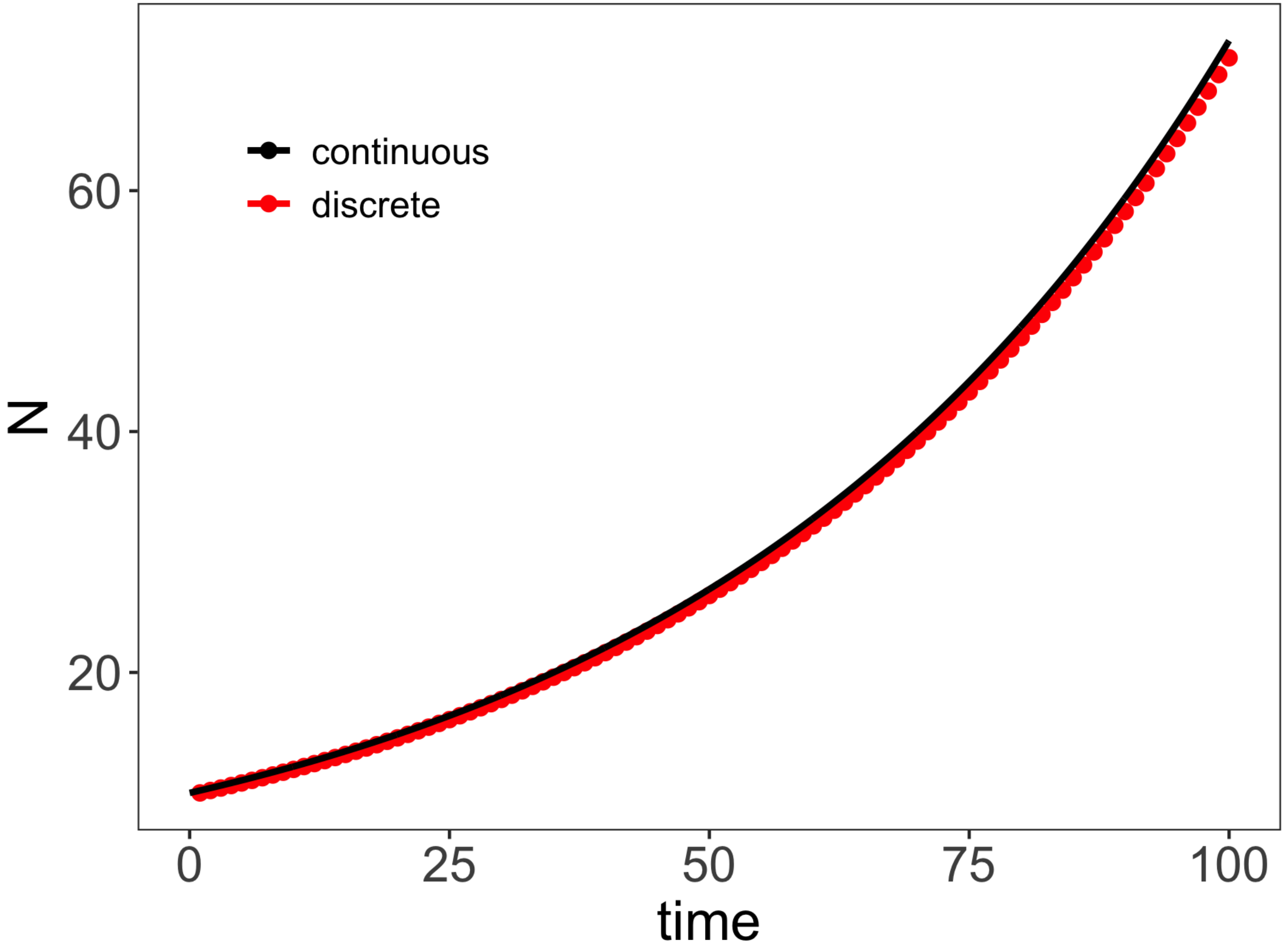
February 6, 2025

Learning objectives from Lecture 1

You should be able to:

- Define ecology as a science
- Distinguish a statistical model (pattern) from a population model (process)
- Construct a simple box plot for a population model
- Distinguish geometric and exponential growth – and know when to apply which model to which kinds of data
- Understand what it means to ‘fit’ a model to data
- Interpret whether growth is slowing, accelerating, or constant from lines ‘fit’ to different time points

Both geometric and exponential growth are unchecked.

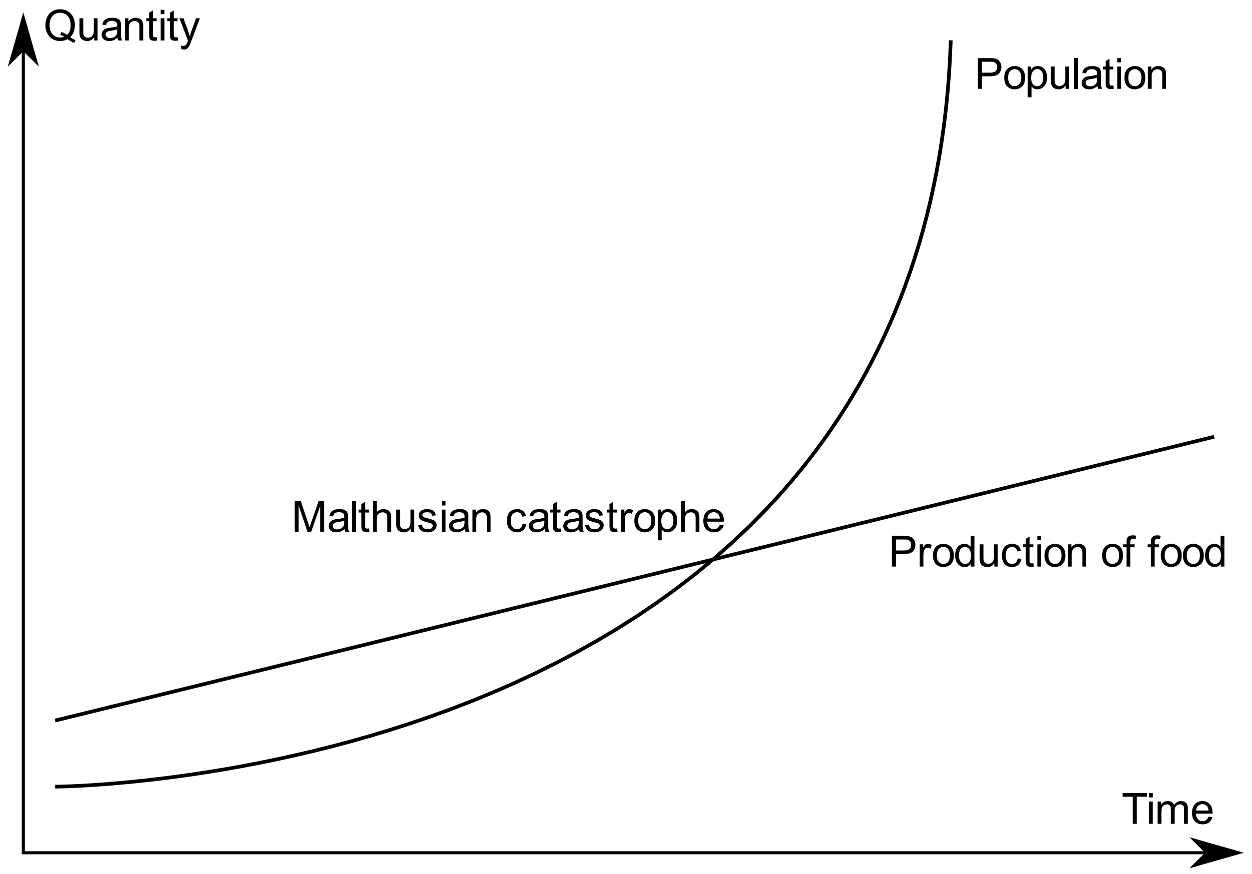


Malthus proposed some limits to population growth

"[. . .] the power of population is indefinitely greater than the power in the earth to produce subsistence for man. Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio. A slight acquaintance with numbers will shew the immensity of the first power in comparison of the second. By that law of our nature which makes food necessary to the life of man, the effects of these two unequal powers must be kept equal. This implies a strong and constantly operating check on population from the difficulty of subsistence. This difficulty must fall somewhere; and must necessarily be severely felt by a large portion of mankind."

- Thomas Malthus (1798)
An Essay on the Principle of Population as it Effects the Future Improvement of Society, With Remarks on the Speculations of Mr Godwin, Mr. Condorcet and Other Writers

Malthus proposed some limits to population growth



Problem!
No basis for assumption of arithmetical ratio for food.

- Thomas Malthus (1798)
An Essay on the Principle of Population as it Effects the Future Improvement of Society, With Remarks on the Speculations of Mr. Godwin, Mr. Condorcet and Other Writers

Logistic growth equation

change in population abundance per unit time

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

population size

intrinsic growth rate

carrying capacity

Population growth slows as abundance (**N**) approaches **carrying capacity** (**K**).

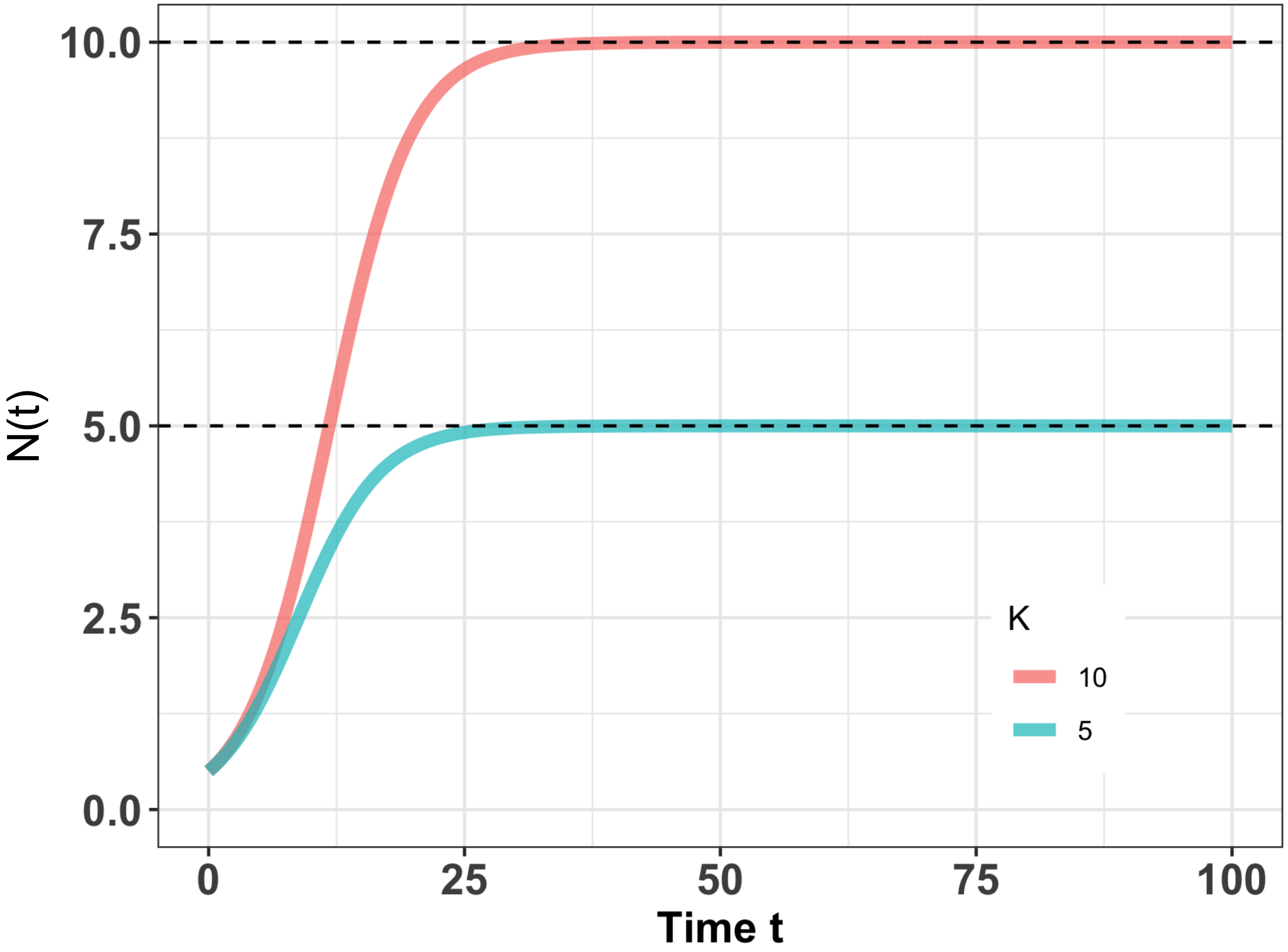
Population growth is **density-dependent**.

"We shall not insist on the hypothesis of geometric progression, given that it can hold only in very special circumstances; for example, when a fertile territory of almost unlimited size happens to be inhabited by people…"

- Pierre-Francois Verhulst (1838)

Logistic growth equation

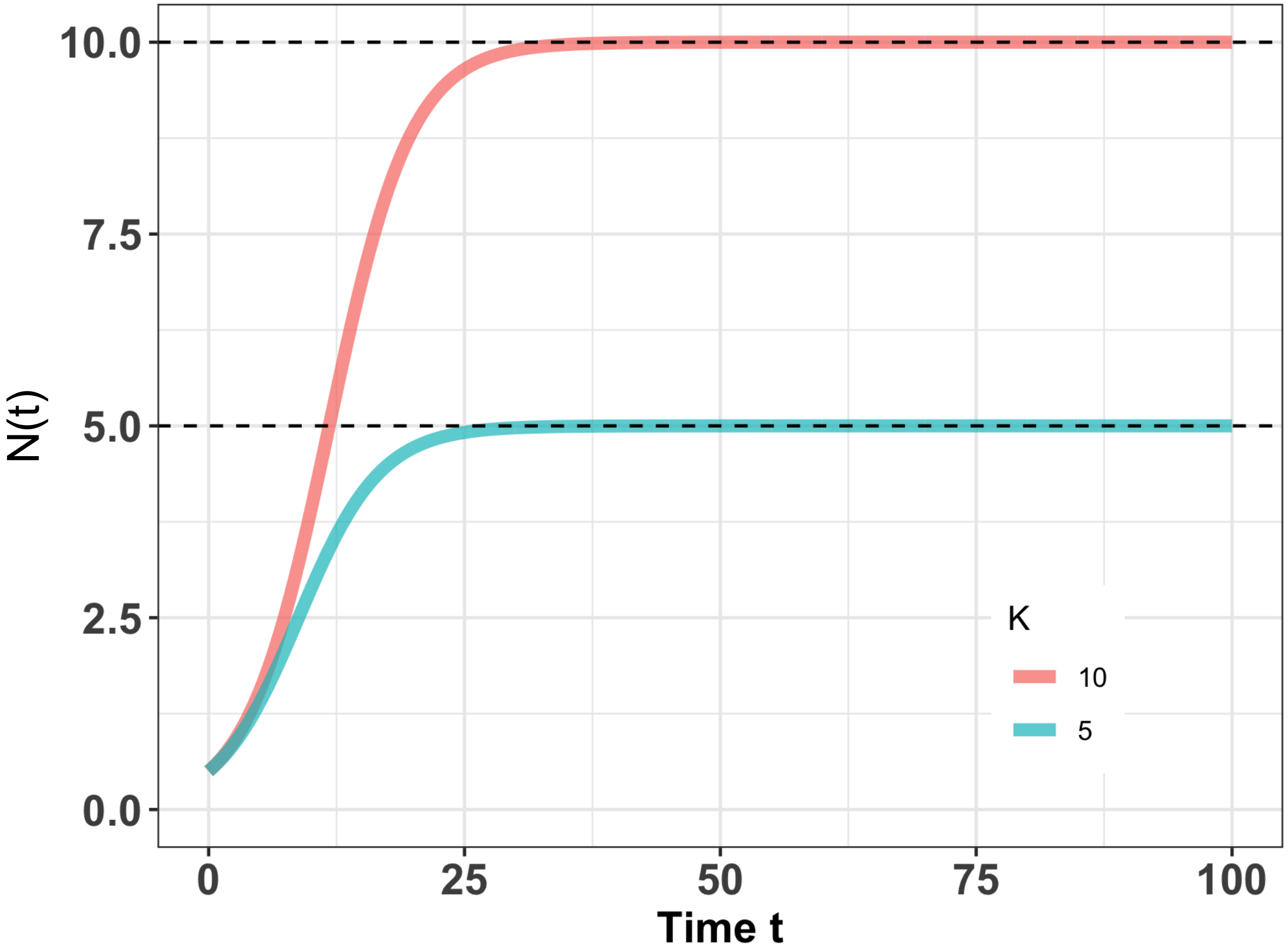
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$



Population growth slows to 0 as N approaches **K**, or – in other words – as the total population size approaches **carrying capacity**.

Logistic growth equation

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



Carrying capacity= maximum population size an environment can sustain indefinitely.

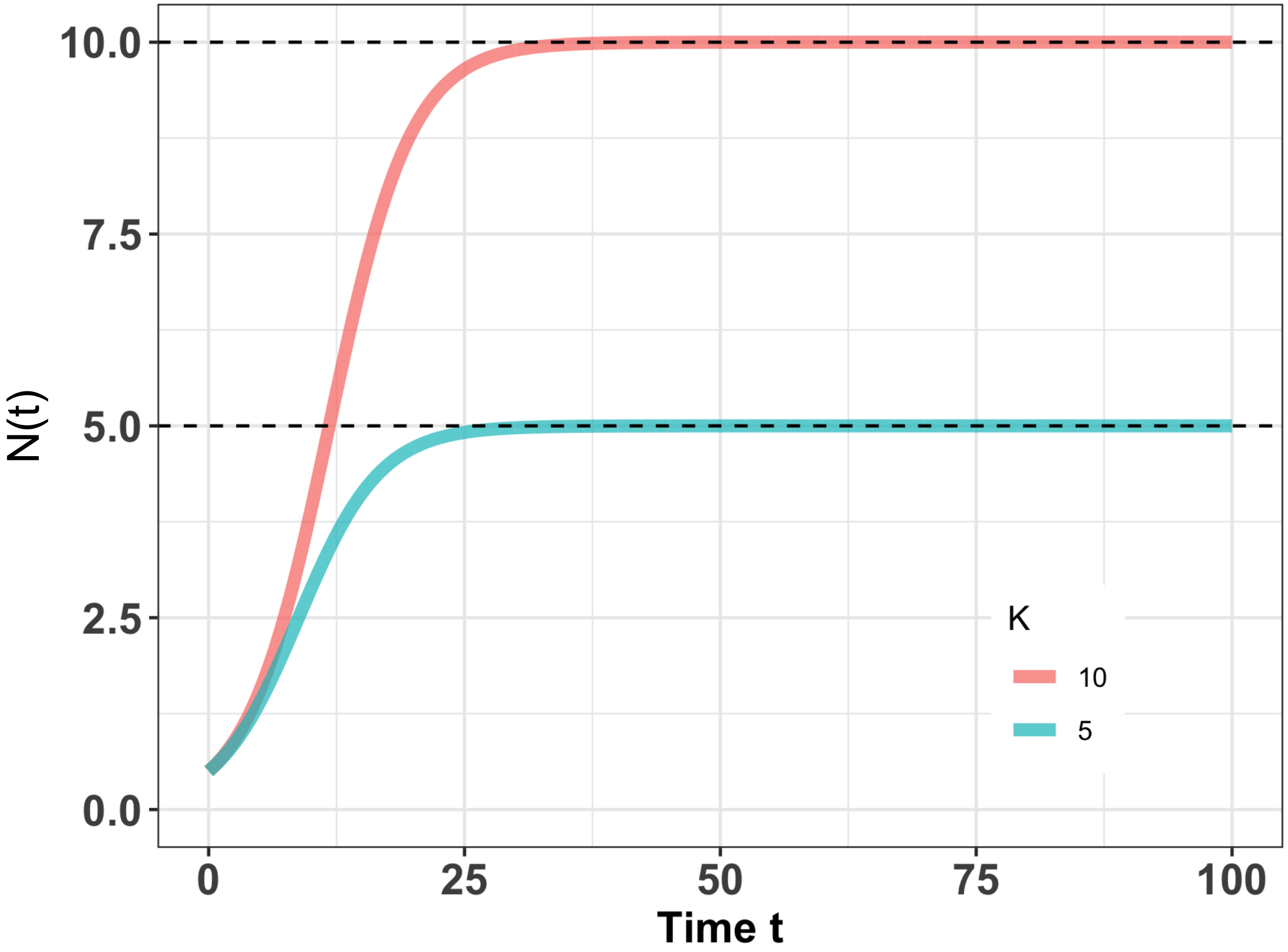
Ecology = organisms interacting with each other and the **environment**

K can change!

'**r**' vs. '**K**'-selected species

Logistic growth and equilibrium

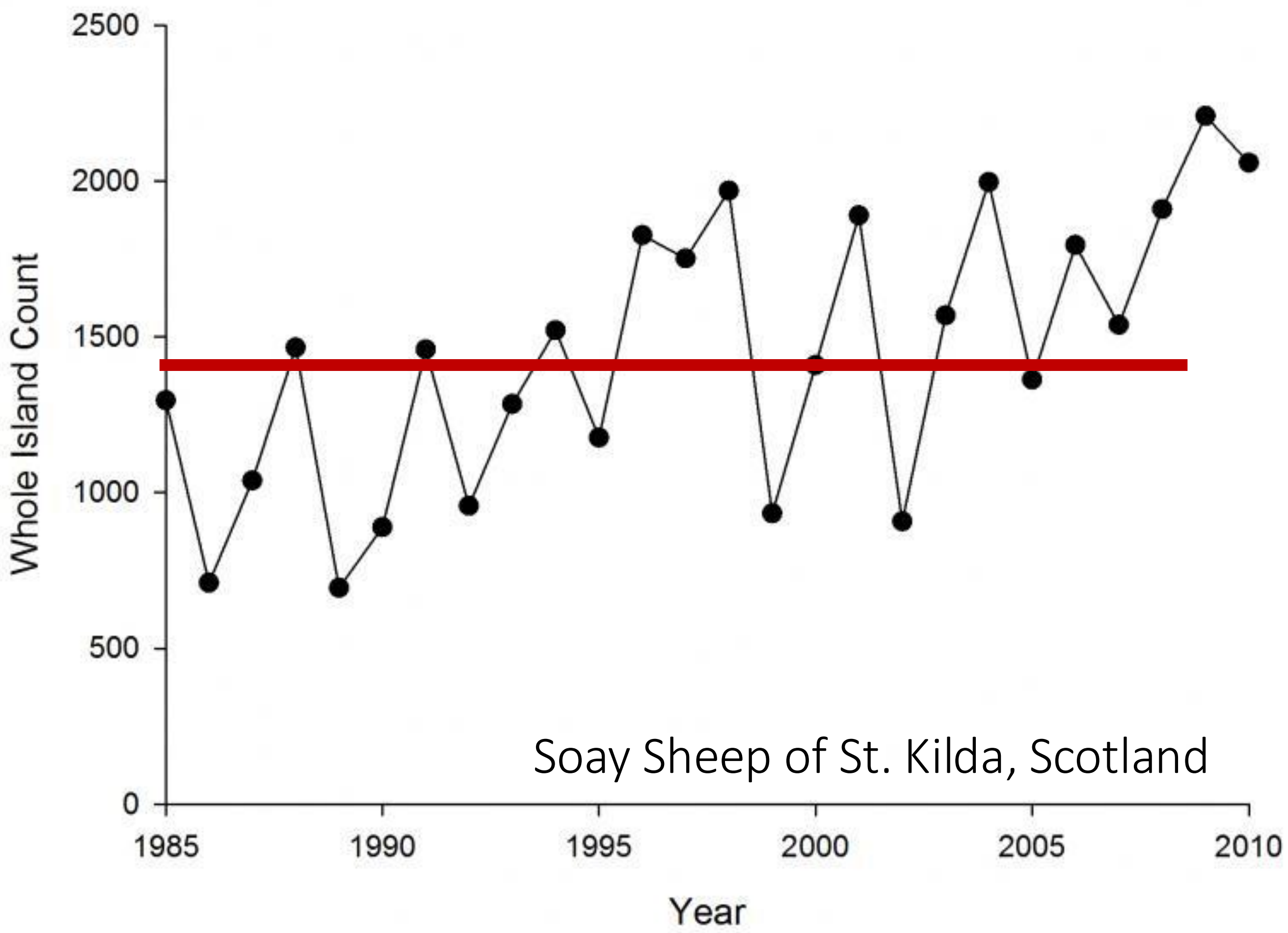
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$



$$\frac{dN}{dt} = 0$$

When population size is not changing, the population is said to be at **equilibrium**.

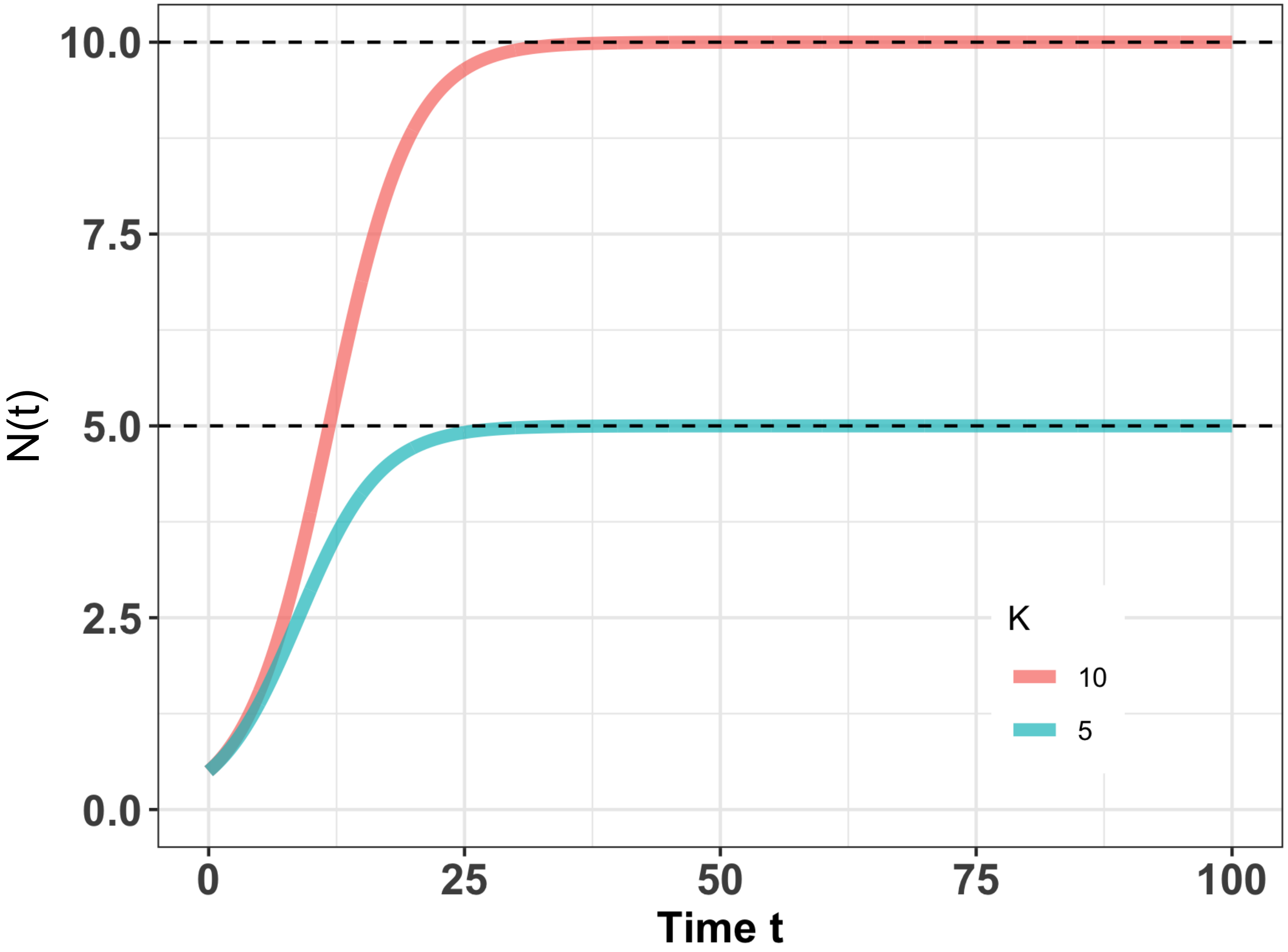
Many populations will fluctuate above or below carrying capacity.



But they can still be stable populations if they return to **equilibrium**.

Logistic growth and equilibrium

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



$$\frac{dN}{dt} = 0$$

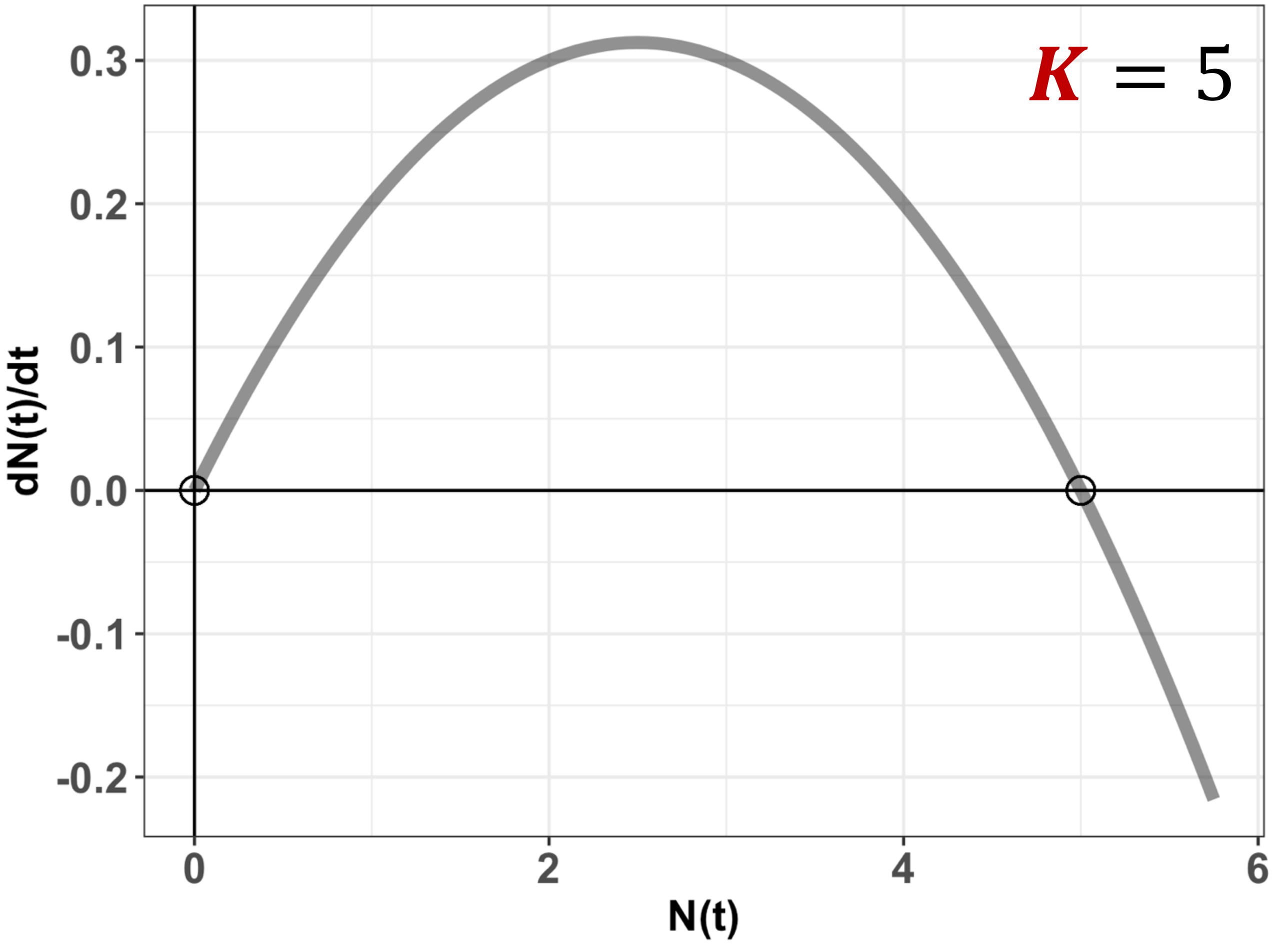
$$0 = rN\left(1 - \frac{N}{K}\right)$$

$$N = K$$

A little algebra shows that the population at carrying capacity is at **equilibrium**.

Logistic growth and equilibrium

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



$$\frac{dN}{dt} = 0$$

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

$$\left.\begin{array}{l} N = K \text{ or} \\ N = 0 \end{array}\right\}$$

logistic growth **equilibria**

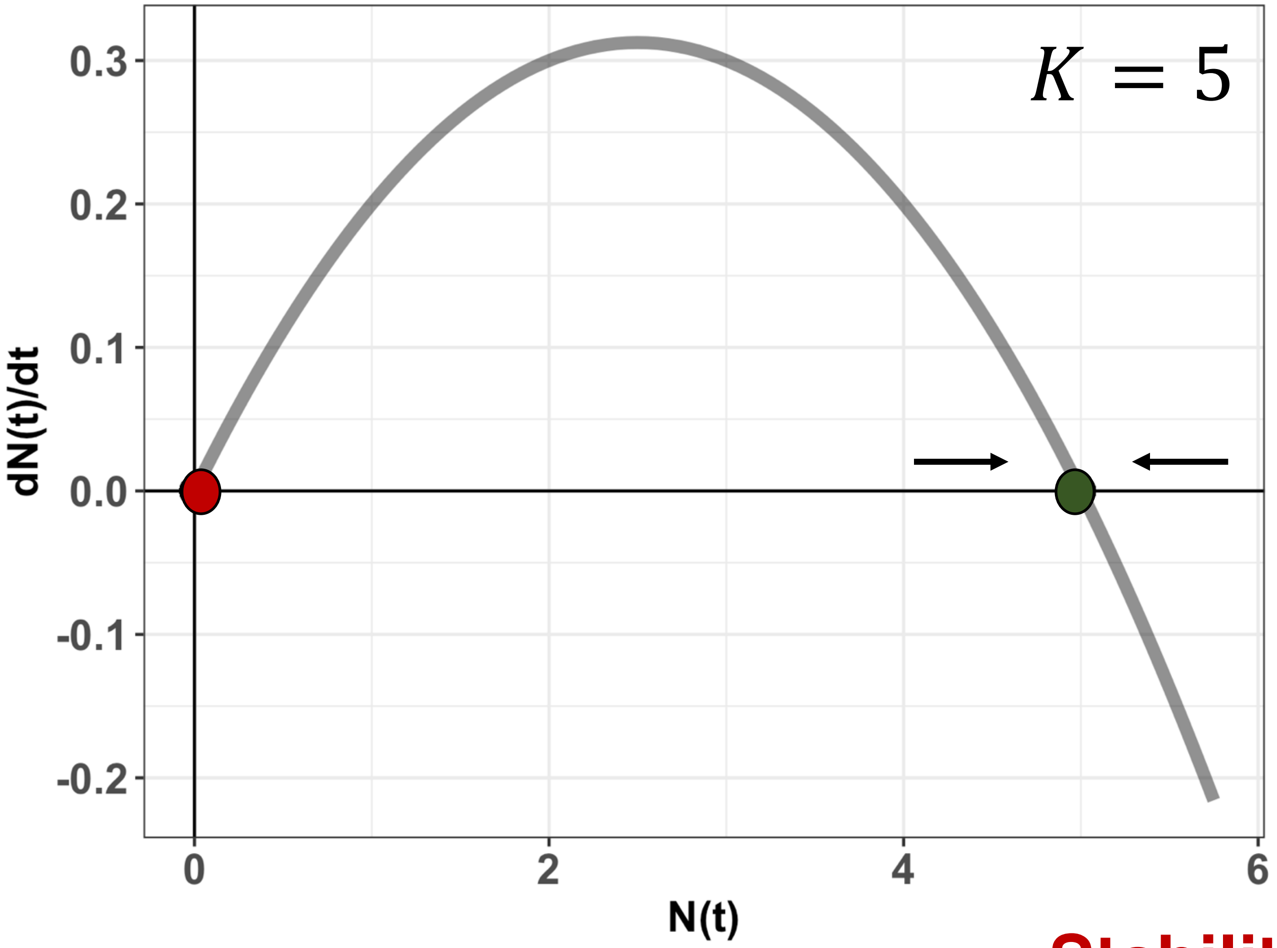
What is **K**?

Logistic growth and equilibrium

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

$$\frac{dN}{dt} = 0$$

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



$$\left.\begin{array}{l} N = K \text{ or} \\ N = 0 \end{array}\right\}$$

logistic growth **equilibria**

Stability: If the population is perturbed, will it return to equilibrium?

Logistic growth and equilibrium

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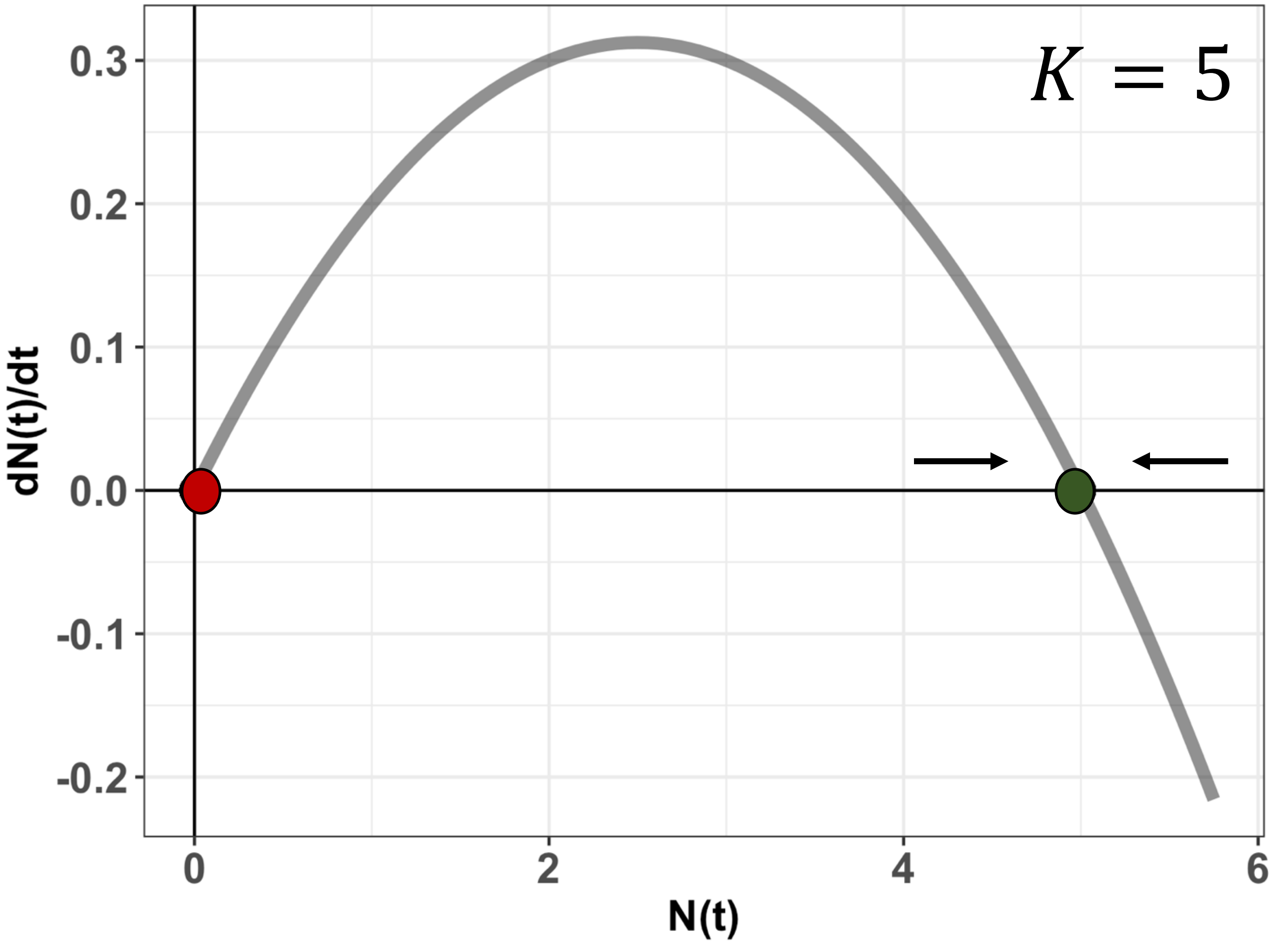
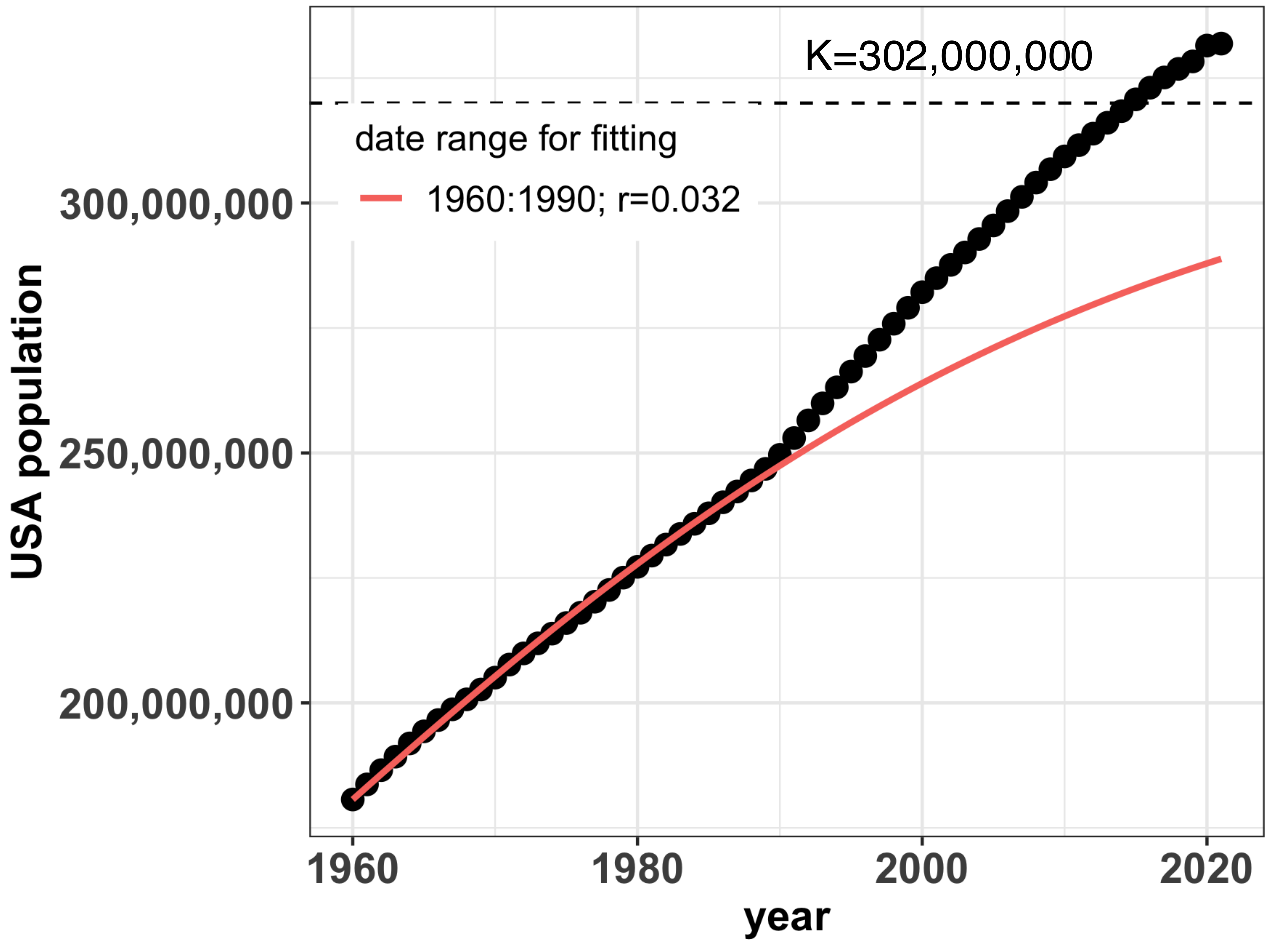
$$\frac{dN}{dt} = 0$$

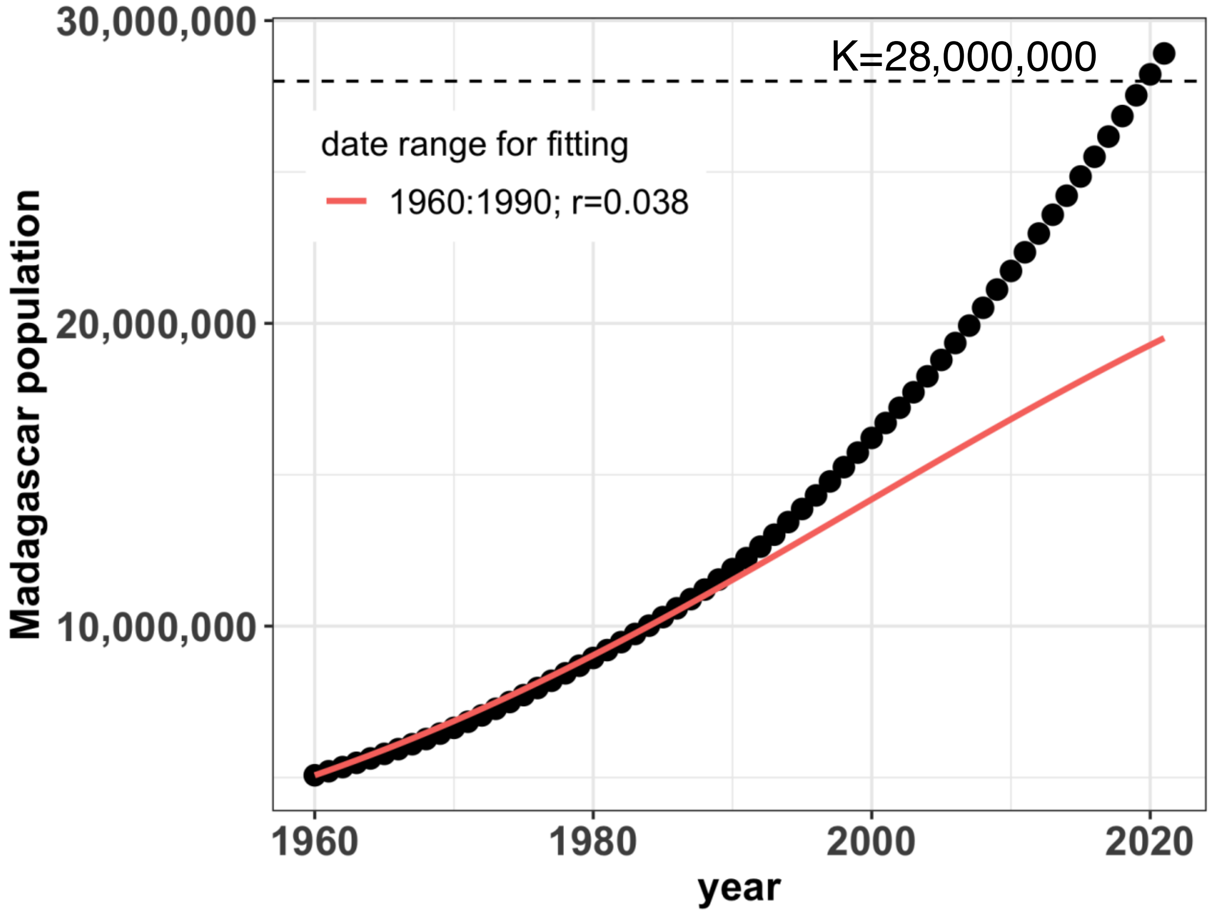


When population size is not changing, the population is said to be at **equilibrium**.

Mathematically, the carrying capacity (K) can be shown to be a **stable equilibrium**, meaning that if the system is perturbed, growth will accelerate or decelerate to return the population to K.

Despite Malthus' predictions, logistic growth still does not describe human populations well.





Logistic growth and harvesting

Humans have attempted to leverage density-dependent growth rates for **sustainable harvesting**, which refers to the offtake of individuals within a population's capacity for replenishment. Frequently, this refers to the harvesting of animals for human consumption.

The science of sustainable harvest is used extensively in fisheries management.

$$\underbrace{\frac{dN}{dt}}_{\text{change in population size with time}} = \underbrace{r}_{\text{intrinsic growth rate}} N \underbrace{\left(1 - \frac{\overbrace{N}^{\text{population size}}}{\underbrace{K}_{\text{carrying capacity}}}\right)}_{\text{density-dependence}} - \underbrace{\boxed{H}}_{\text{harvesting rate}}$$

Logistic growth and harvesting

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

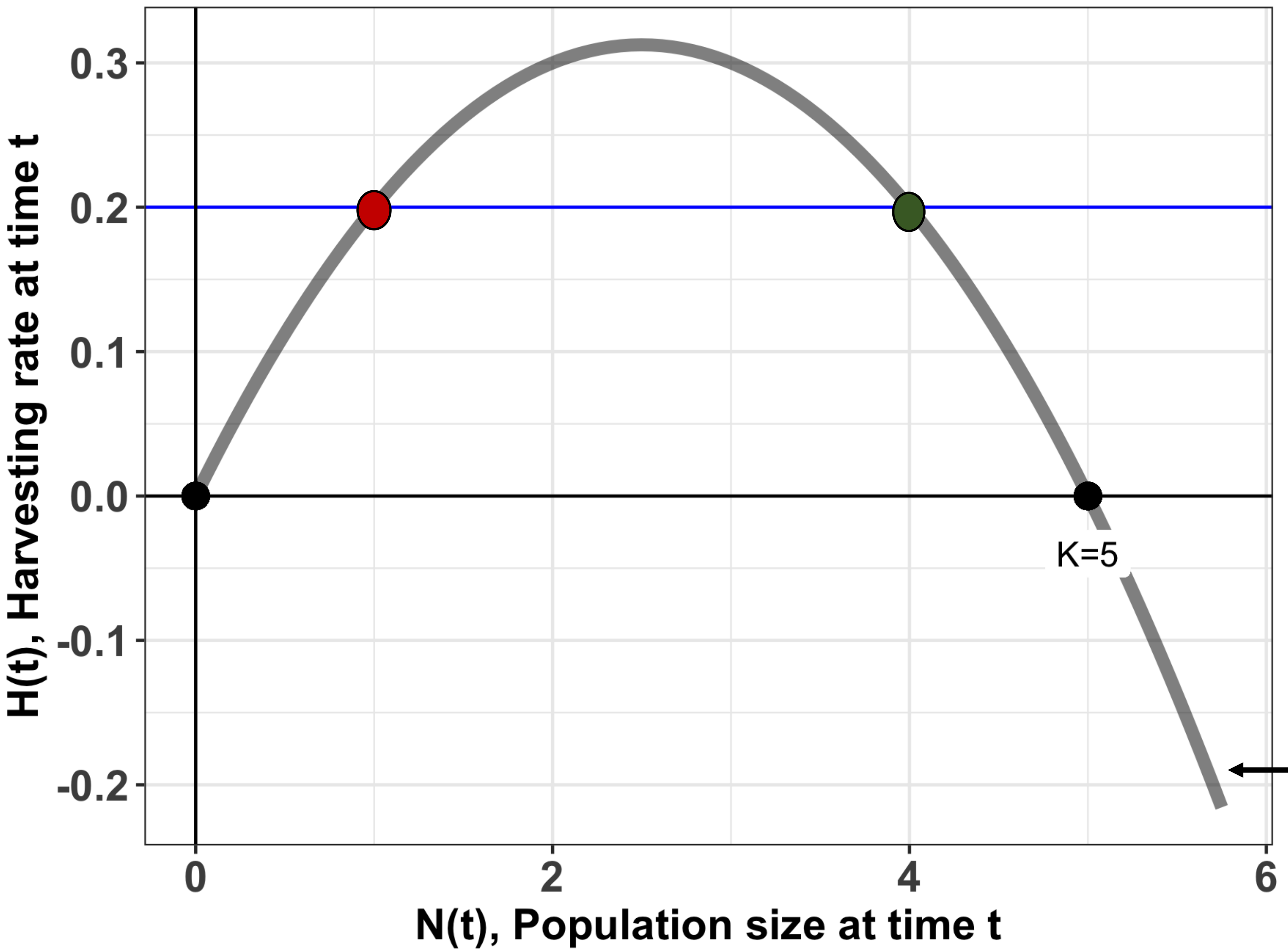
$$0 = rN\left(1 - \frac{N}{K}\right) - H$$

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

For a harvested population, **theoretically**, the population size is at equilibrium if the **harvest rate equals the population change**.

The stability of harvesting depends on population size.

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



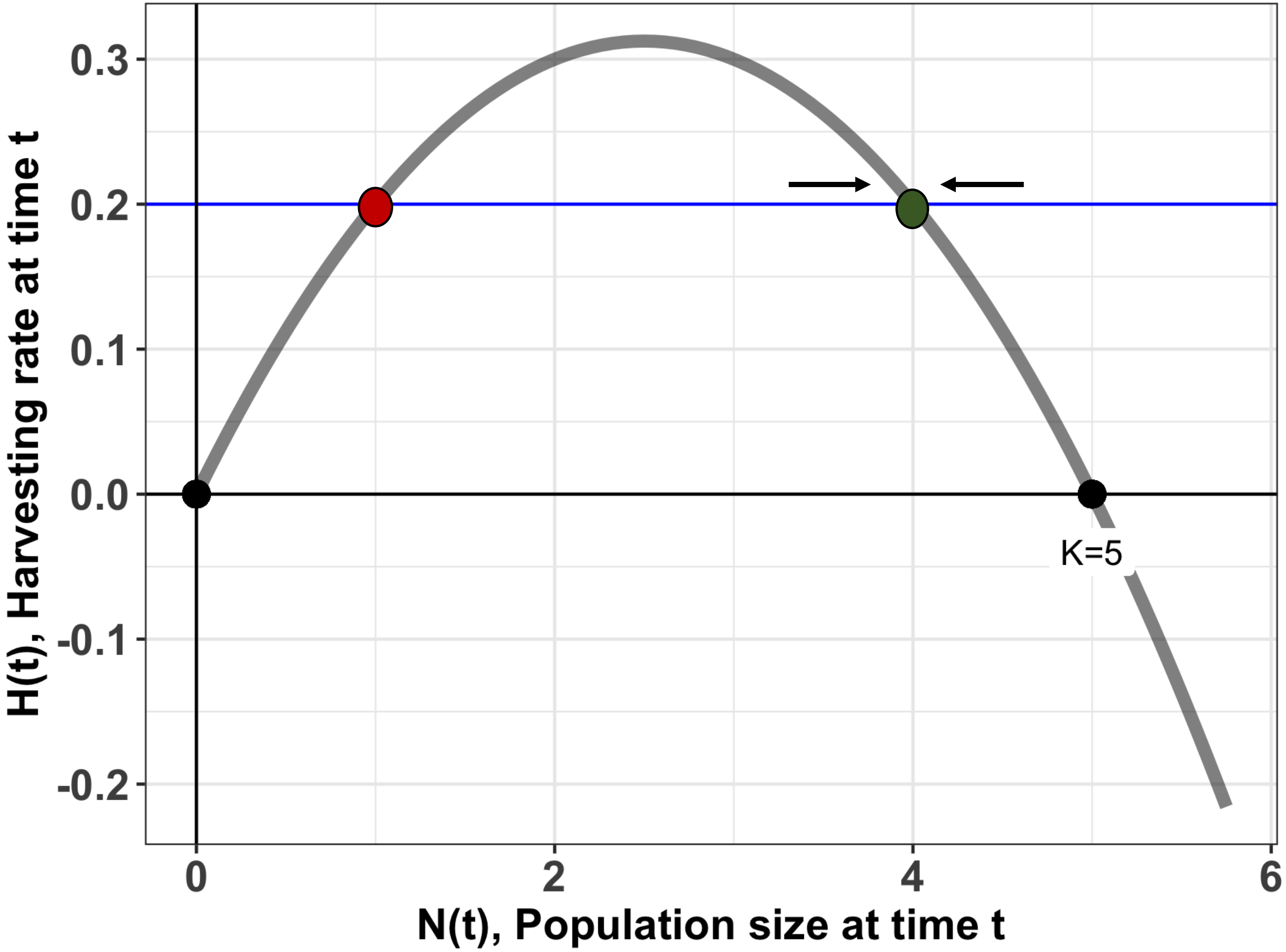
harvesting rate

carrying capacity

Curve shows equilibrium solutions to harvesting equation, with r= 0.25 & K=5. Some equilibria are **stable**, and some are **unstable**.

The stability of harvesting depends on population size.

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

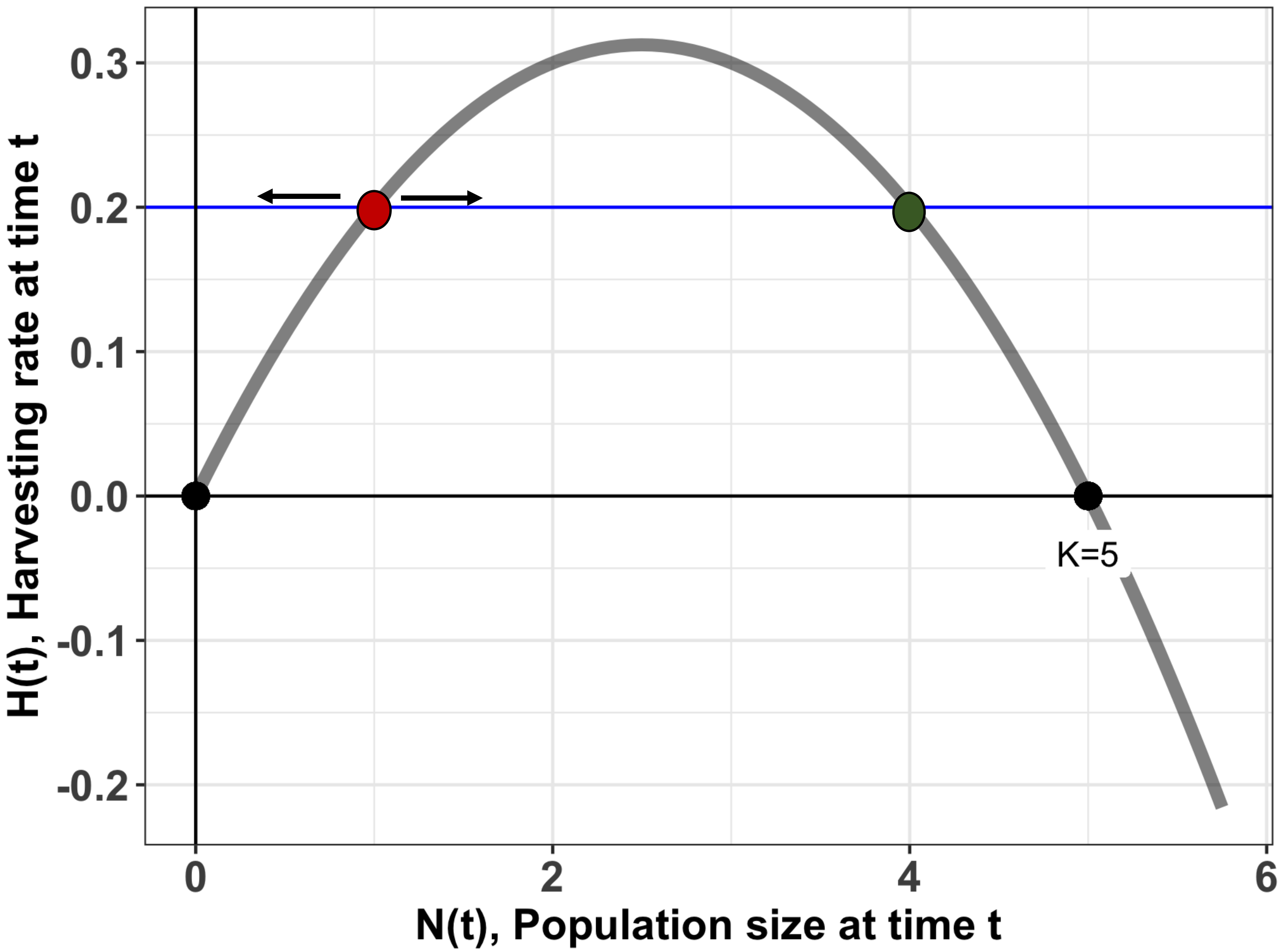


stable equilibrium
For a population of N=4, a harvest rate of 0.2 (animals/timestep) results in a stable equilibrium (**sustainable harvest**).

Increases or decreases in population size will be compensated to return the system to N=4.

The stability of harvesting depends on population size.

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



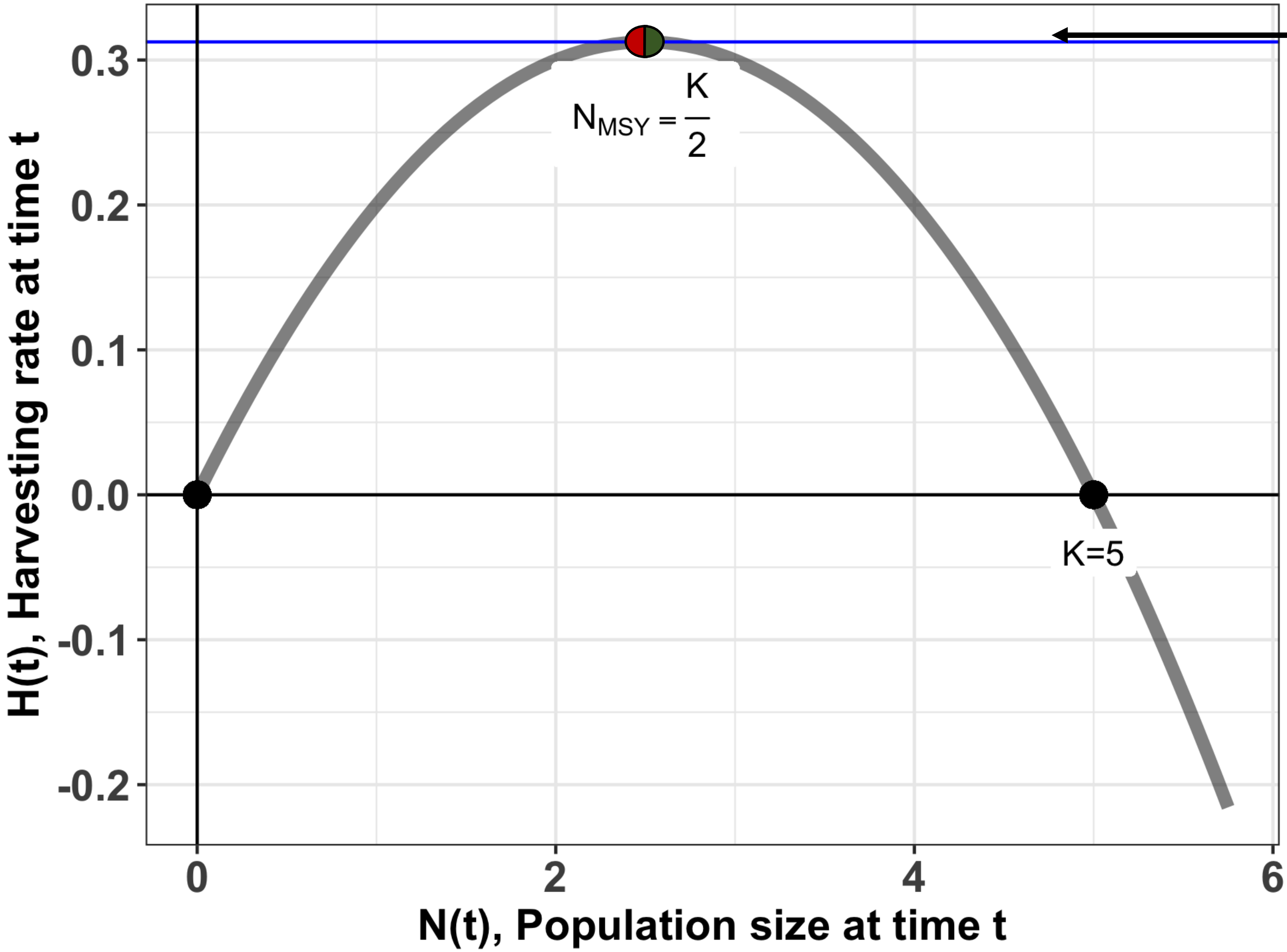
unstable equilibrium

For a population of N=1, a harvest rate of 0.2 (animals/timestep) results in an unsustainable equilibrium.

Random increases or decreases in population size will result in the population moving away from N=1 to, respectively, N=4 or N=0 (the latter is a **population collapse**).

Maximum sustainable yield (MSY)

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



In the logistic growth equation, population growth (dN/dt) is maximized at half the carrying capacity $N = \frac{K}{2}$

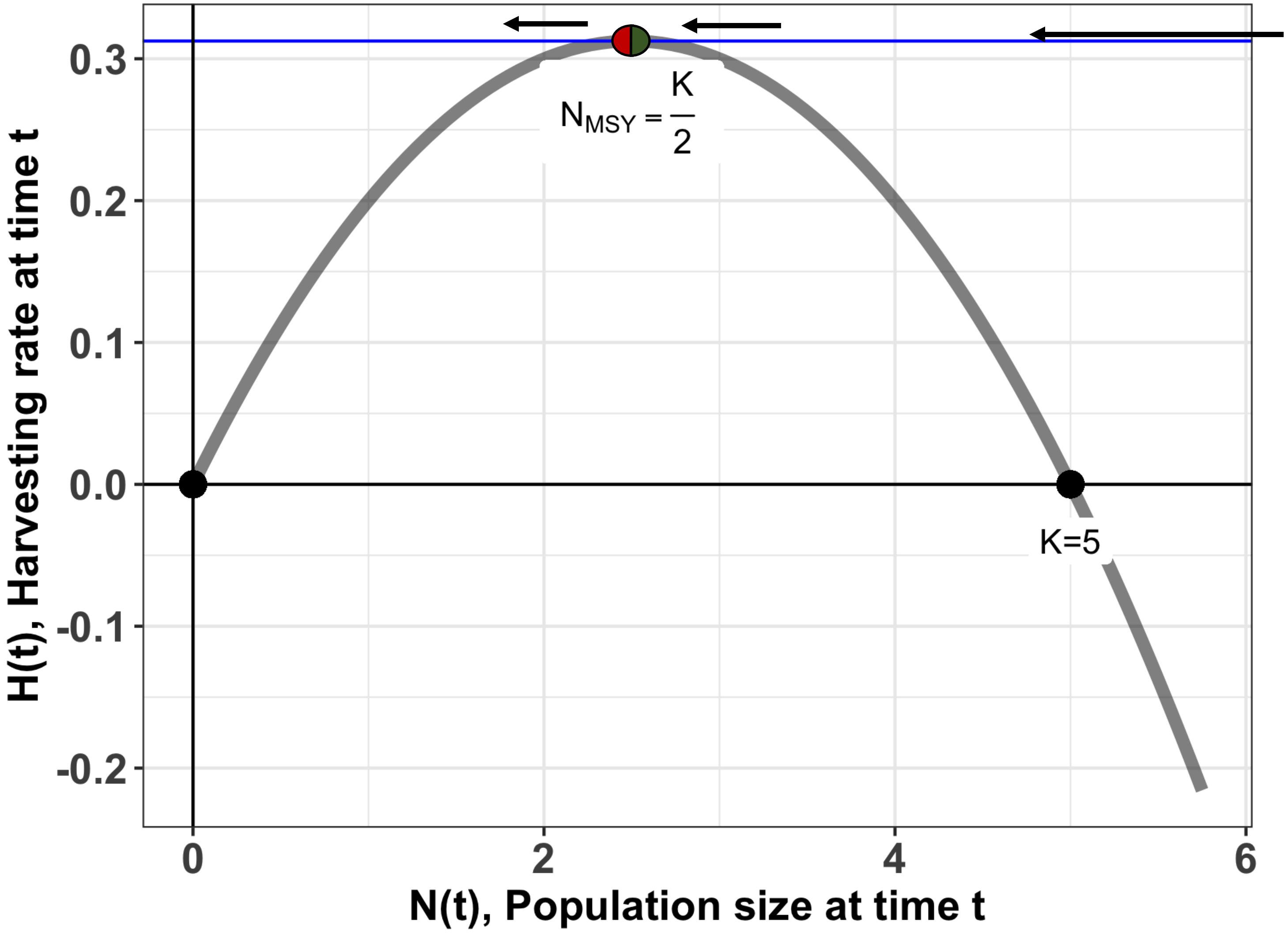
Theoretically, harvest could be maximized here as well:

MSY: $H_{max} = \frac{rK}{4}$

take the derivative with respect to N

Maximum sustainable yield (MSY)

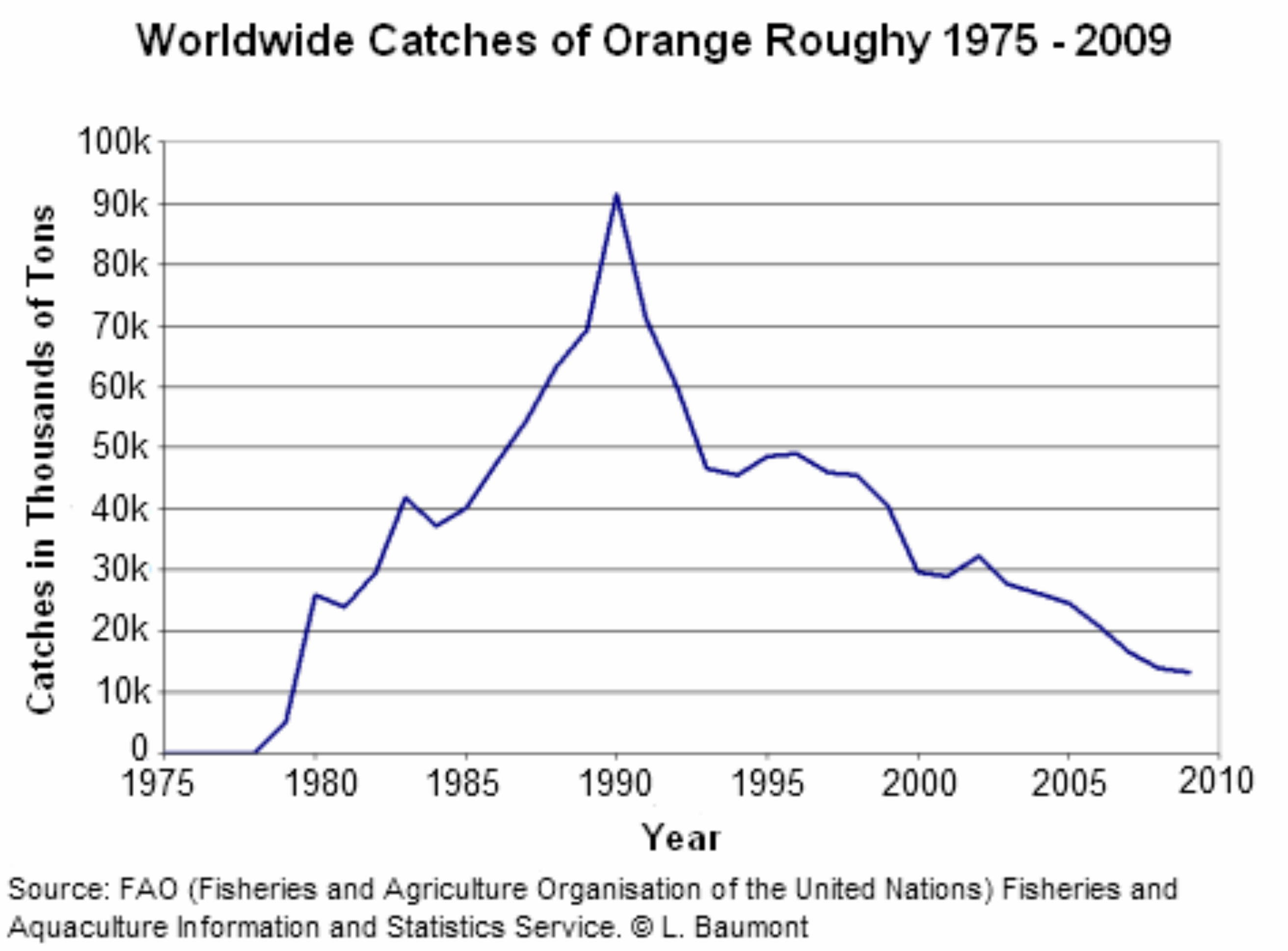
$$H = rN\left(1 - \frac{N}{K}\right)$$



MSY: $H_{max} = \frac{rK}{4}$

The MSY is a **semi-stable equilibrium**, meaning that small gains in population size (N) will be compensated to return the system to N_{MSY}, while small losses will result in the system collapsing to N=0.

Case Study: Orange Roughy



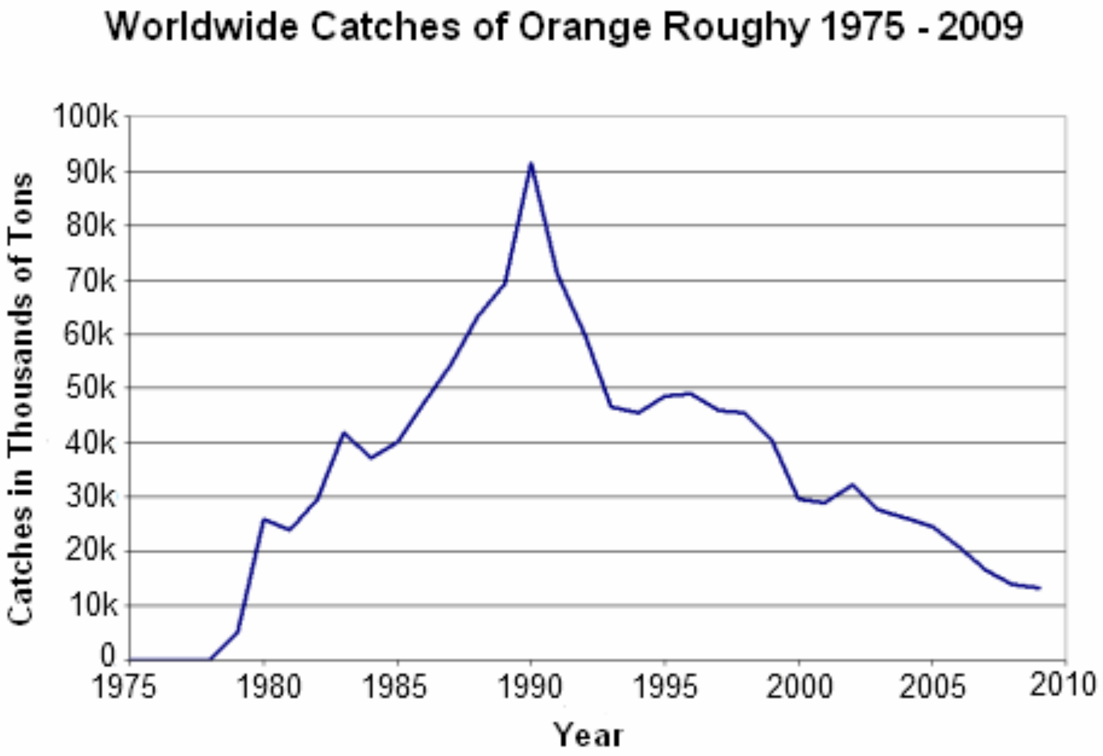
Many populations will fluctuate above or below carrying capacity.

But they can still be stable populations if they return to **equilibrium**.

In some cases, it is not possible to recover.

Case Study: Orange Roughy

- Found in deep waters of eastern Pacific (Chile), western Pacific (Australia/NZ), and southeastern Atlantic (Namibia to South Africa)
- Can live up to 200 years! Matures at 20-30 yrs
- Fished via trawling, originally thought to have only a 30-year lifespan
- Annual global catches began in 1979 and increased to over 90,000 tons in the late 1980s.
- High catch levels quickly decreased as stocks were fished down. By the late 1990s, three of the eight NZ orange roughy fisheries had collapsed and were closed.



Source: FAO (Fisheries and Agriculture Organisation of the United Nations) Fisheries and Aquaculture Information and Statistics Service. © L. Baumont

The case of the orange roughy highlights many of the **inherent problems with MSY**

- *r* and *K* and N are difficult to measure.
- Many harvesting models neglect population structure or model only a single species in isolation.
- Simple harvesting models assume constant harvest.
- MSY fails to acknowledge the reality of **overfishing**.

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

Overfishing:
A Tragedy of the Commons

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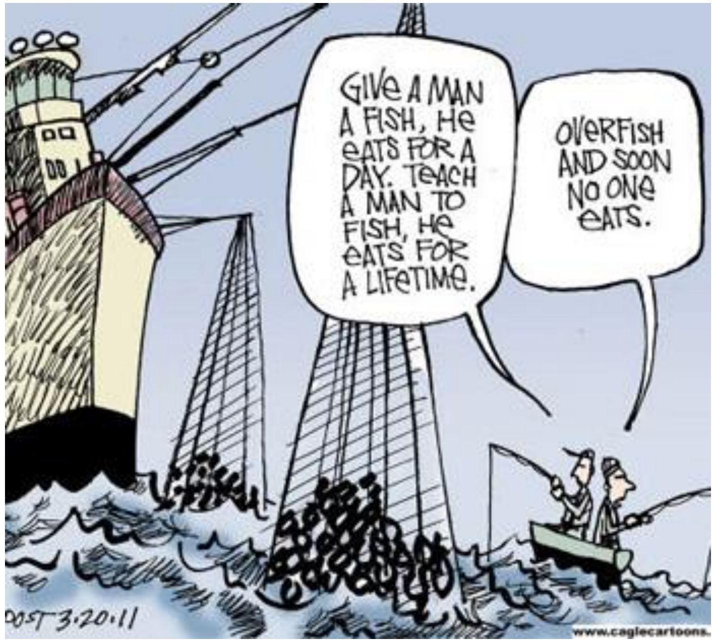
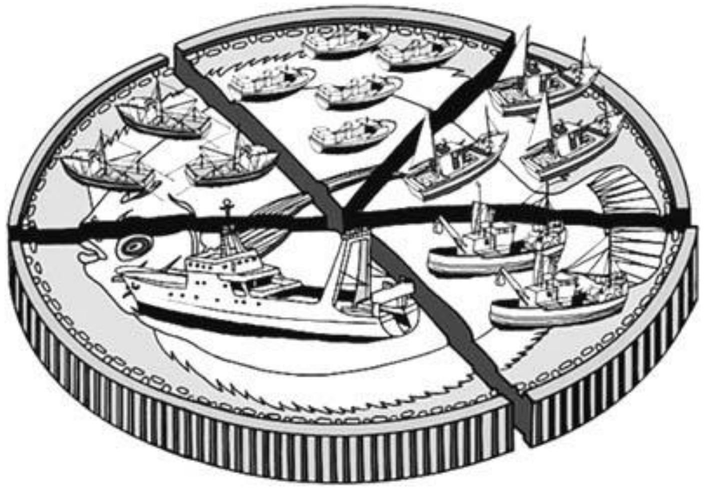


- ***Tragedy of the Commons:***
  - Individuals incentivized to use as much of a **shared, open access resource** as possible to maximize their own benefit.
  - The **cost of depleting the resource** (e.g., overgrazing the pasture, overfishing, polluting the air) **is borne by the entire group**, not just by the individual who is using it heavily.
  - Each individual's actions can negatively impact everyone.
  - Tragedy results: Too many fish are removed, the pasture is overgrazed
- Idea was popularized by ecologist Garret Hardin in 1968, a Malthus-like reference to the overpopulation of the Earth
- Fisheries provide a classic example of Tragedy of the Commons because property rights are incomplete and access is open. Many examples of fisheries collapse:
  - Sturgeon in Caspian sea in 2000s
  - Atlantic cod in Canada & elsewhere in 1990s
  - Orange roughy in NZ in 1990s
- Despite its dangers, MSY is still highlight as a policy in many **international treaties**.

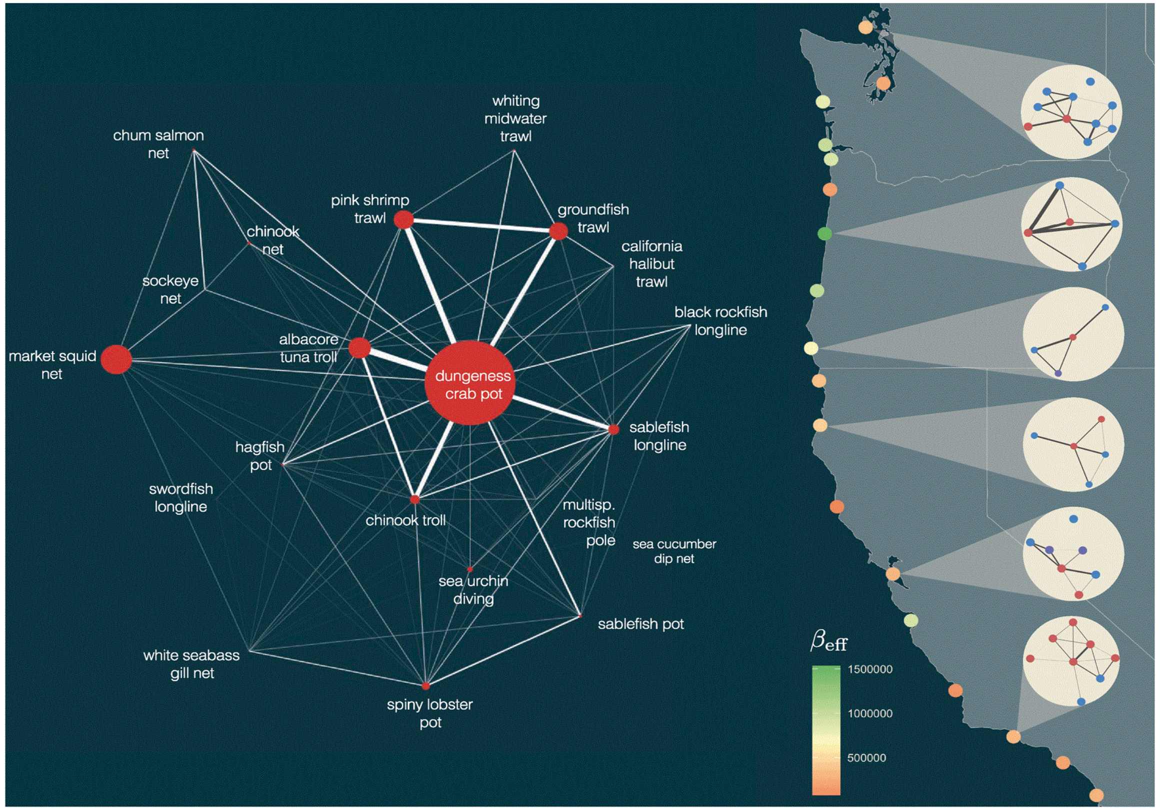
Managing the Commons - Internationally

- **Total Allowable Catch (TAC)** = total number of fish allowed to be caught in each fishery each year
  - Government coordination attempt to set international management goals
  - Can lead to intense pressure to fish all at once at the season's opening, sometimes overshooting the TAC.
- **Individual Fishing Quotas (IFQs)** = allocation by country or individual fisher
  - Can mitigate TAC challenges
  - **Individual Transferrable Quotas (ITQs)** = can be traded or transferred
  - allocation is still a challenge



Managing the Commons - Locally

- The work of Elinor Ostrom showed that **some of these challenges can be overcome** when:
  - resource limits are clearly defined
  - the group of stakeholders is small
  - communication is high



Dr. Emma Fuller,
Fractal Agriculture

Fuller et al. 2017. *ICES Journal of Marine Science*

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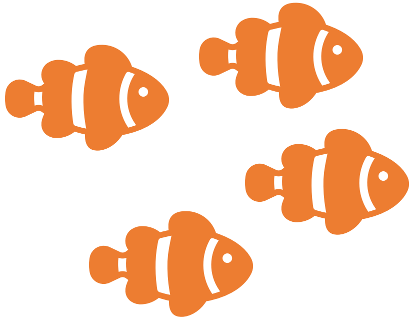
- r and K and N are difficult to measure.
- Many harvesting models neglect population structure or model only a single species in isolation.
- Simple harvesting models assume constant harvest.
- MSY fails to acknowledge the reality of **overfishing**.
- Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in N can be devastating
  - environmental **stochasticity**
  - demographic **stochasticity**

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

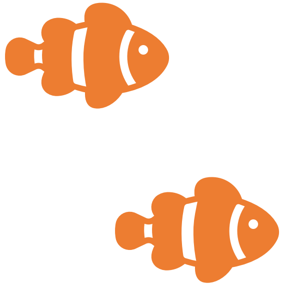
Deterministic vs. Stochastic

starting population



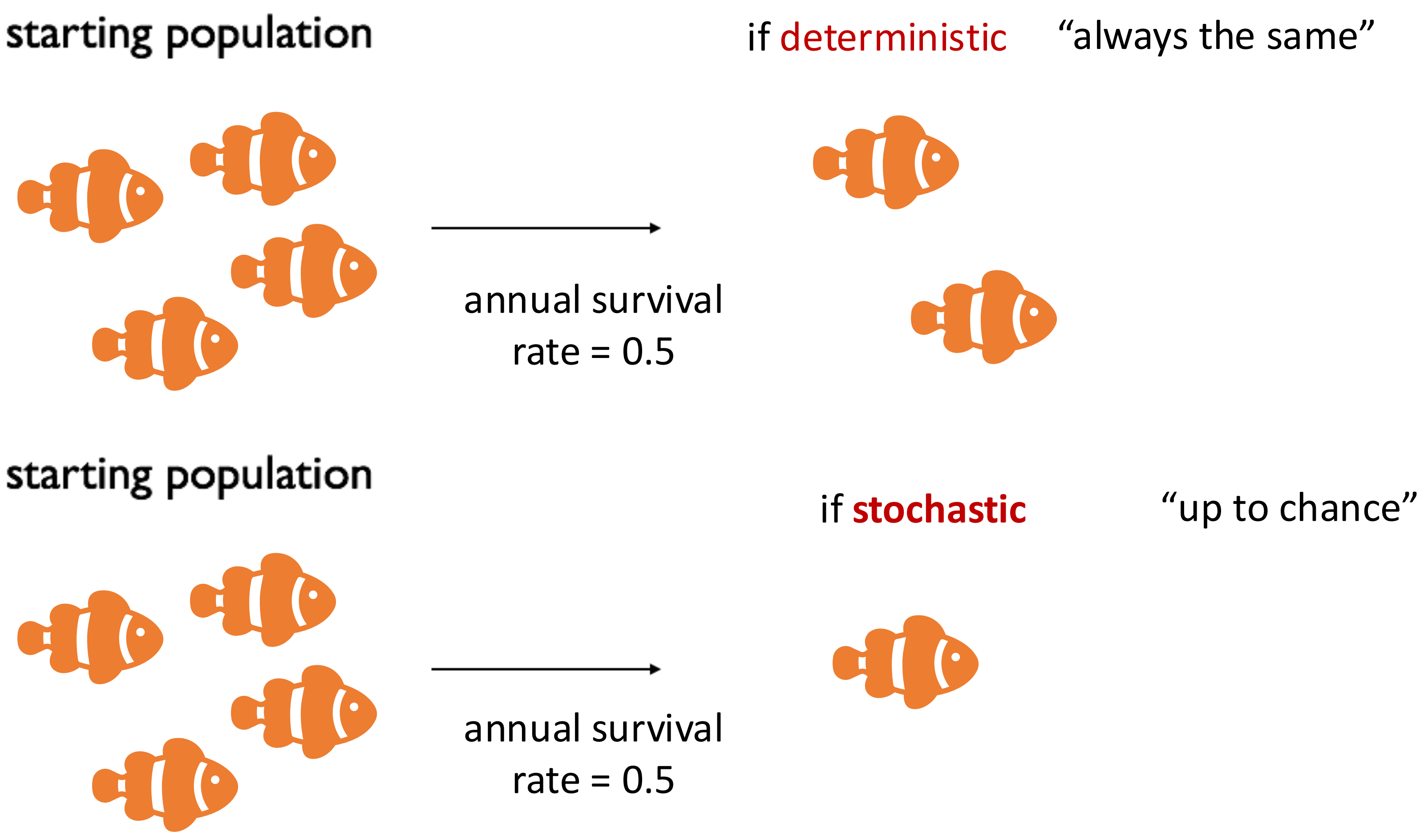
annual survival
rate = 0.5

if **deterministic** “always the same”

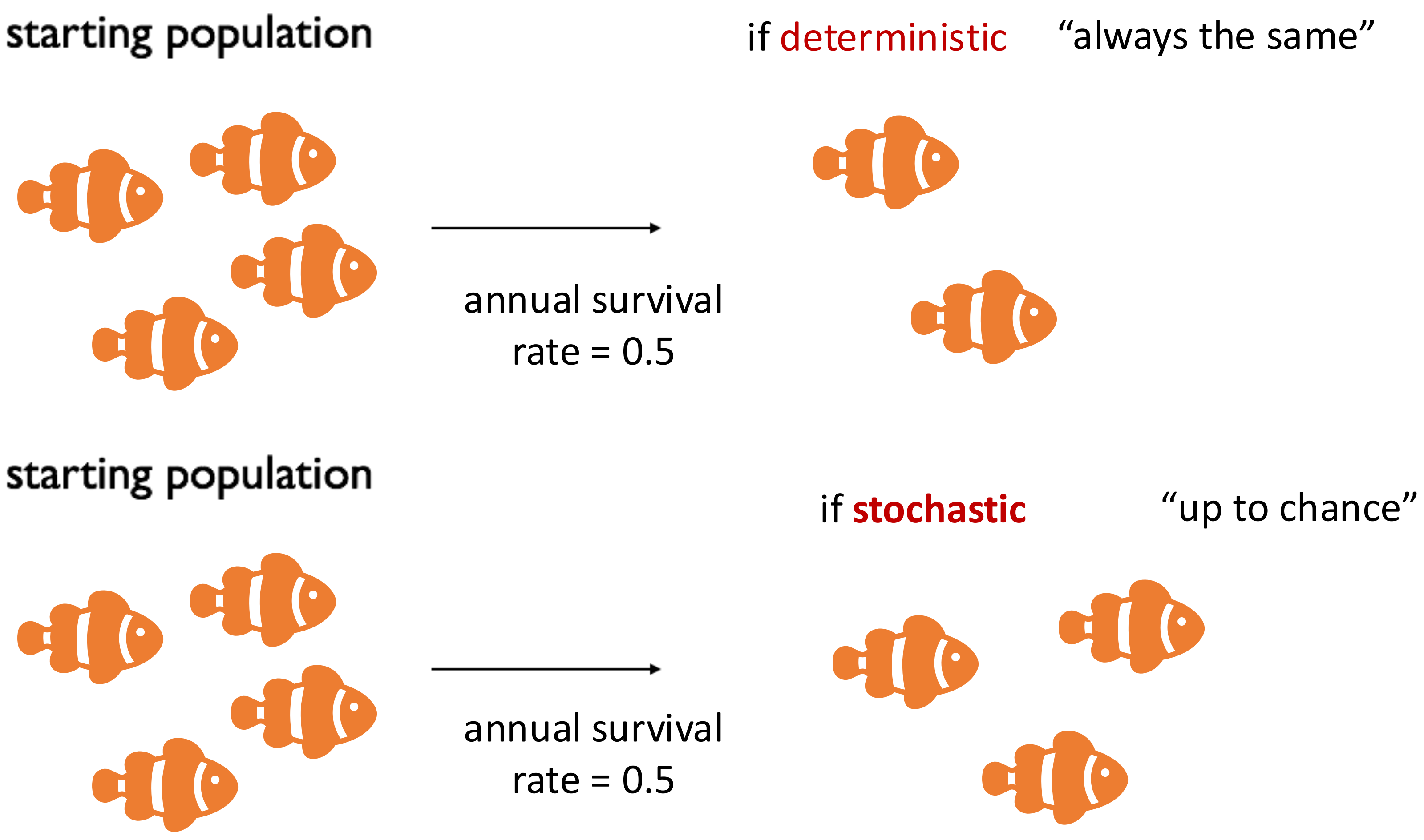


All the models we have looked at so far have been deterministic!

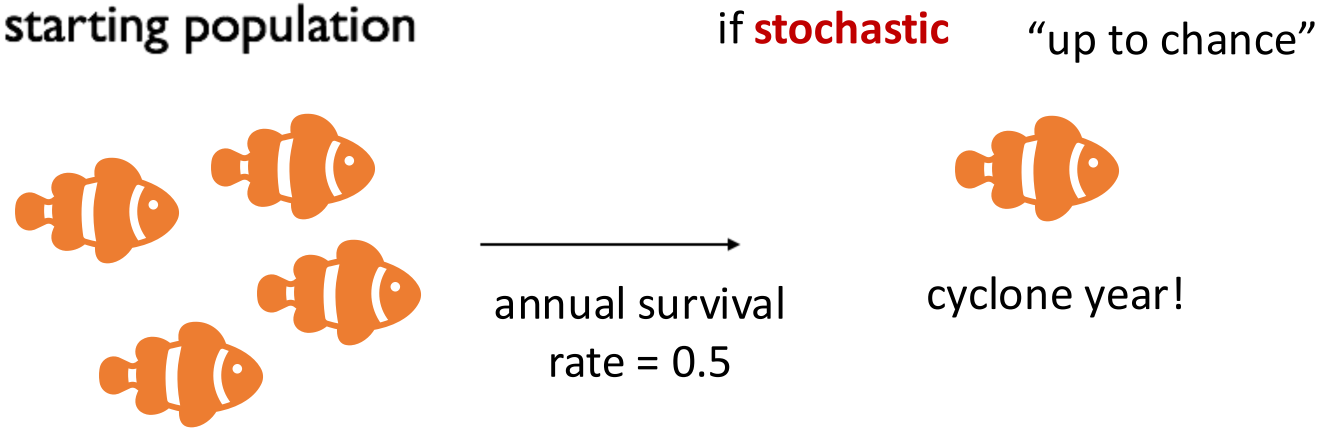
Deterministic vs. Stochastic



Deterministic vs. Stochastic

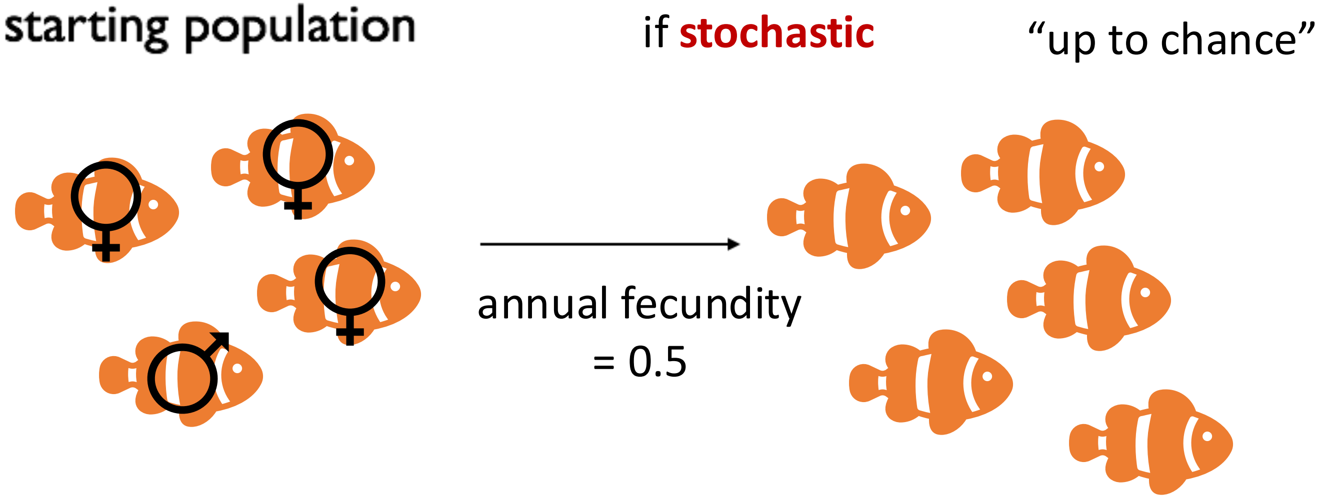


The case of the orange roughy highlights many of the **inherent problems with MSY**



- *r* and *K* and N = difficult to measure.
- Neglect population structure.
- Single species models.
- Assumes constant harvest.
- Ignores reality of overfishing.
- Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in N can be devastating
  - **environmental stochasticity**
    - temporal changes in mortality or reproductive rate (e.g. due to climate)

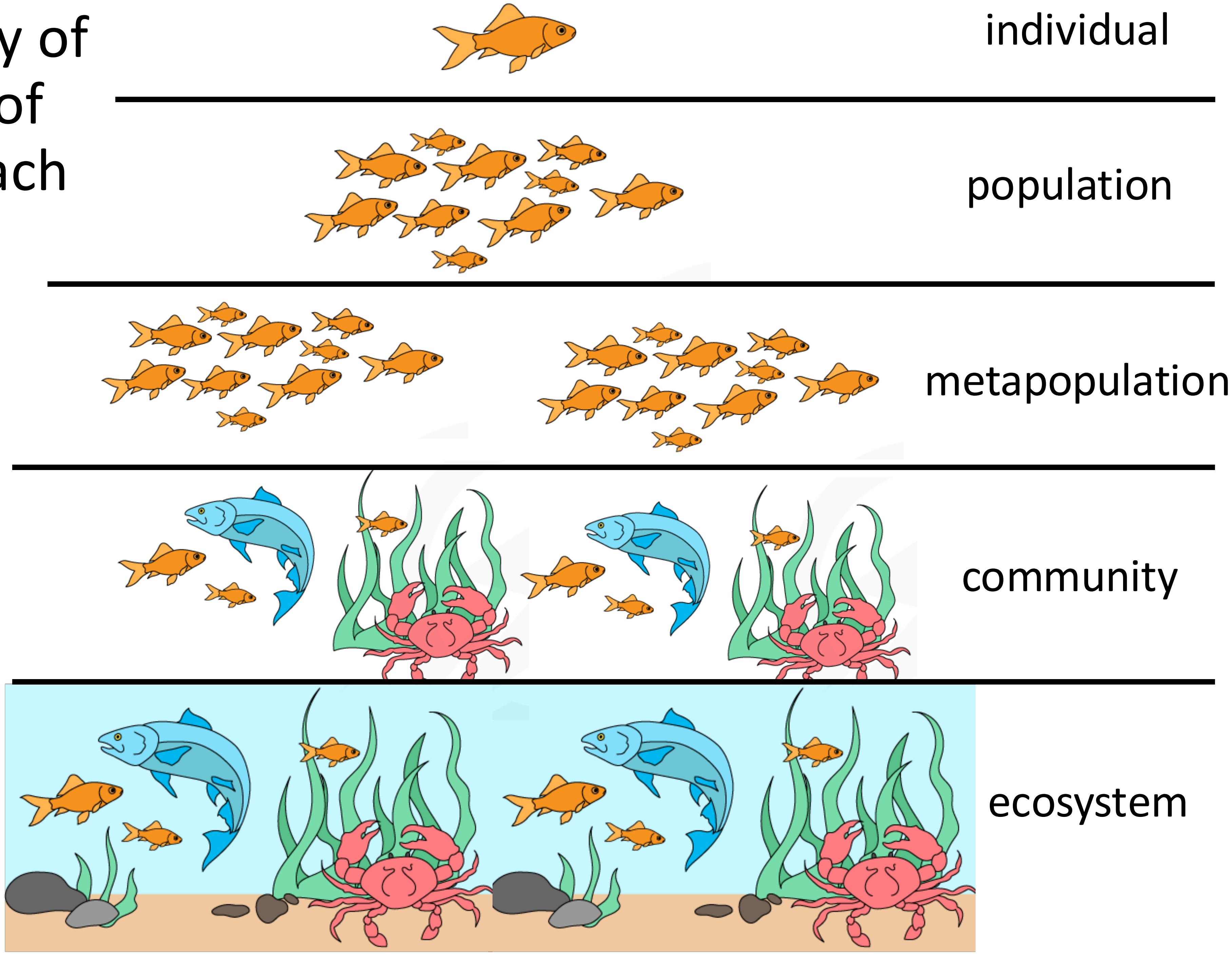
The case of the orange roughy highlights many of the **inherent problems with MSY**



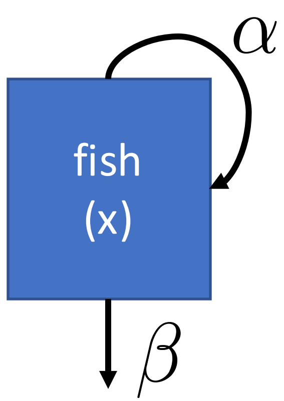
Only one male encounters only one female, so only 1 new fish is born!

- *r* and *K* and N = difficult to measure.
- Neglect population structure.
- Single species models.
- Assumes constant harvest.
- Ignores reality of overfishing.
- Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in N can be devastating
  - **environmental stochasticity**
    - temporal changes in mortality or reproductive rate (due to climate)
  - **demographic stochasticity**
    - individual-level differences in mortality and reproduction, esp. at small pop size

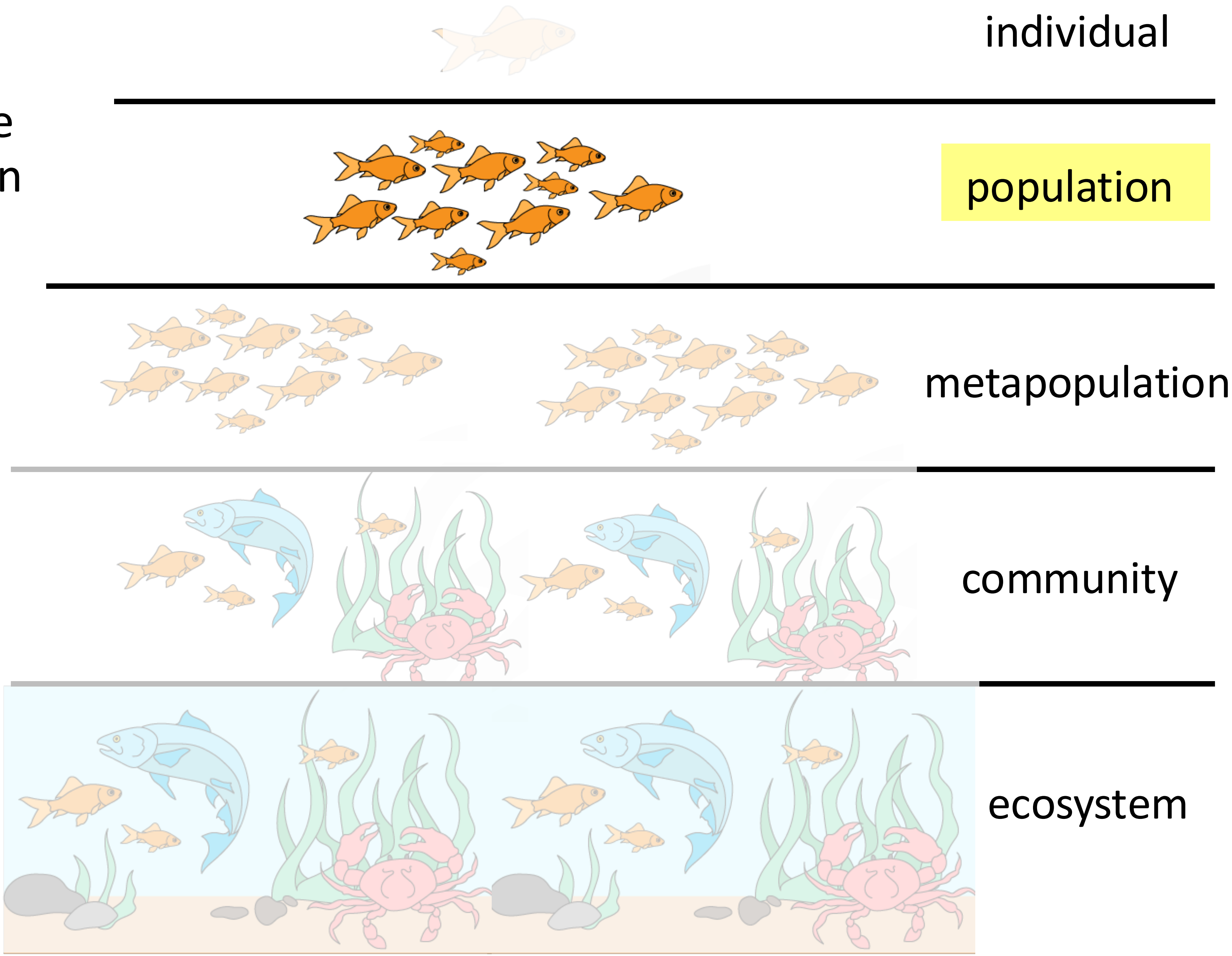
Ecology is the study of the **interactions** of **organisms** with each other and their **environment.**



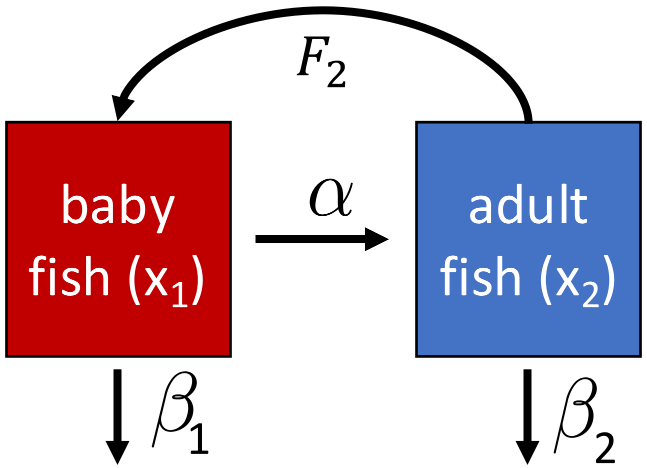
Population = multiple individuals of the same species (**conspecifics**) in the same habitat



How does the abundance of fish ***change*** *through time?*



Structured Population = multiple individuals of the same species (**conspecifics**) in the same habitat but in different life history stages



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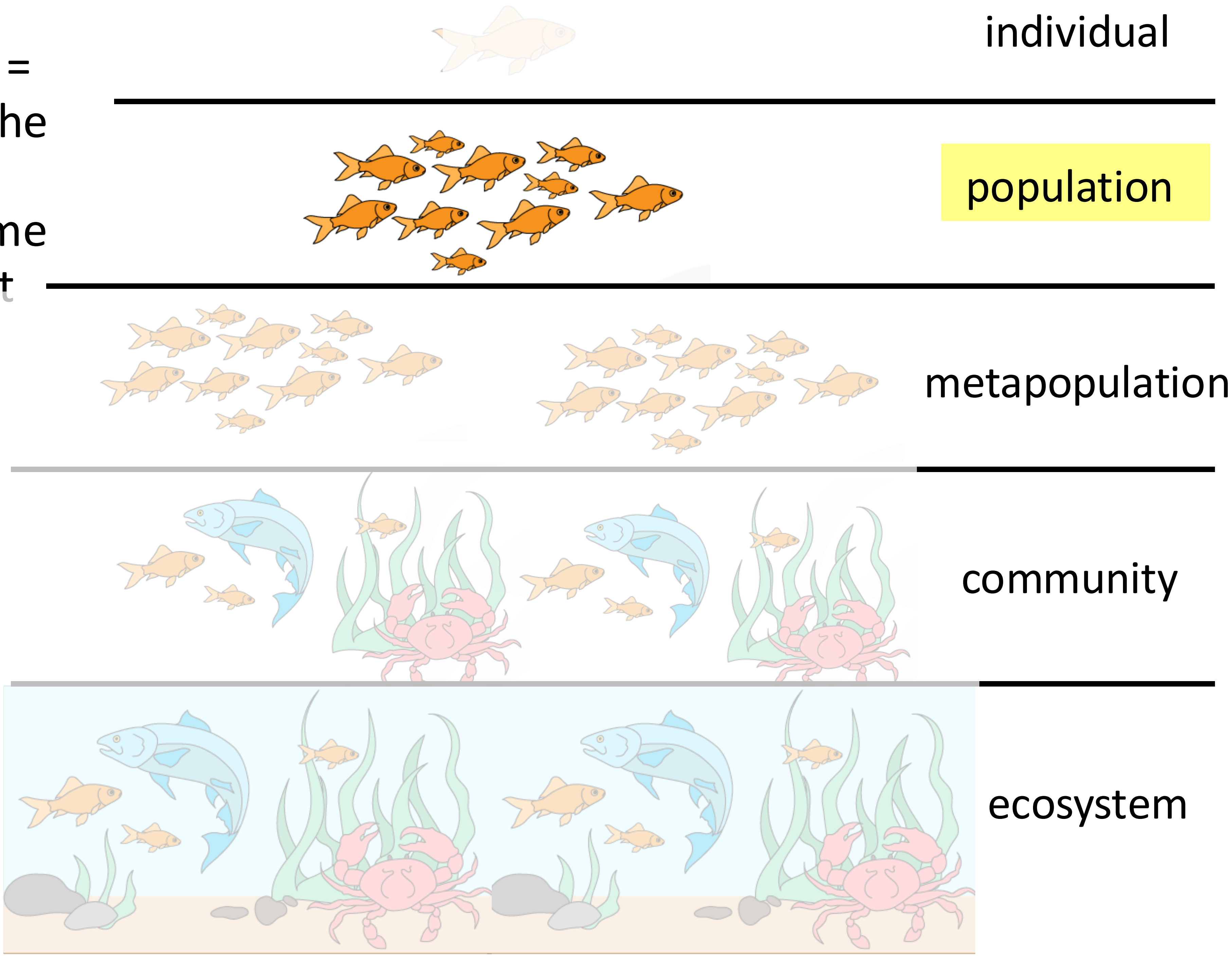
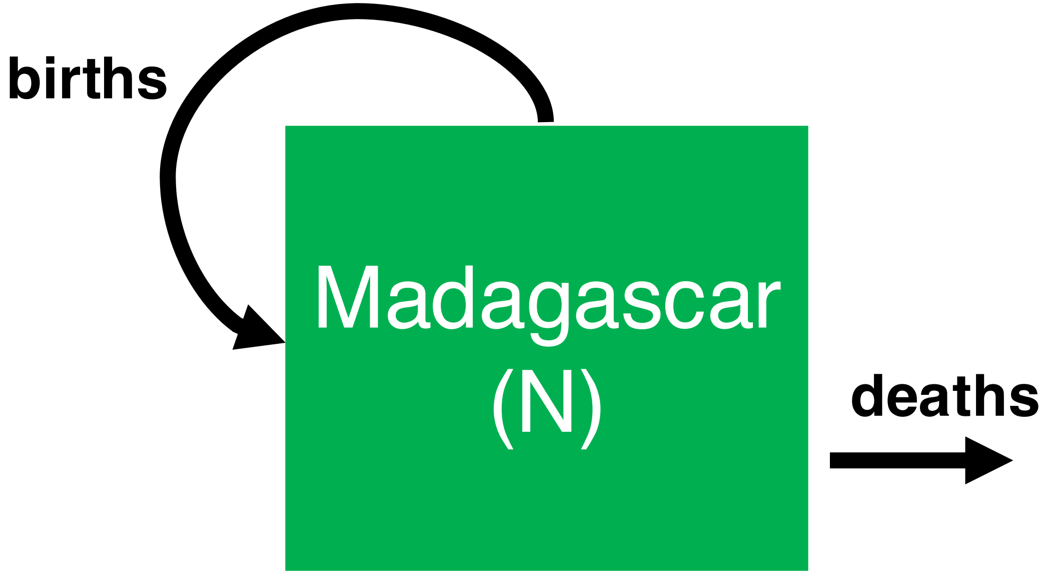


Modeling demographic complexity

1. Populations are divided into compartments
2. Individuals within a compartment are homogenously mixed
3. Compartments and transition rates are determined by biological systems
4. Rates of transferring between compartments are expressed mathematically



The simplest population model

Modeling demographic complexity

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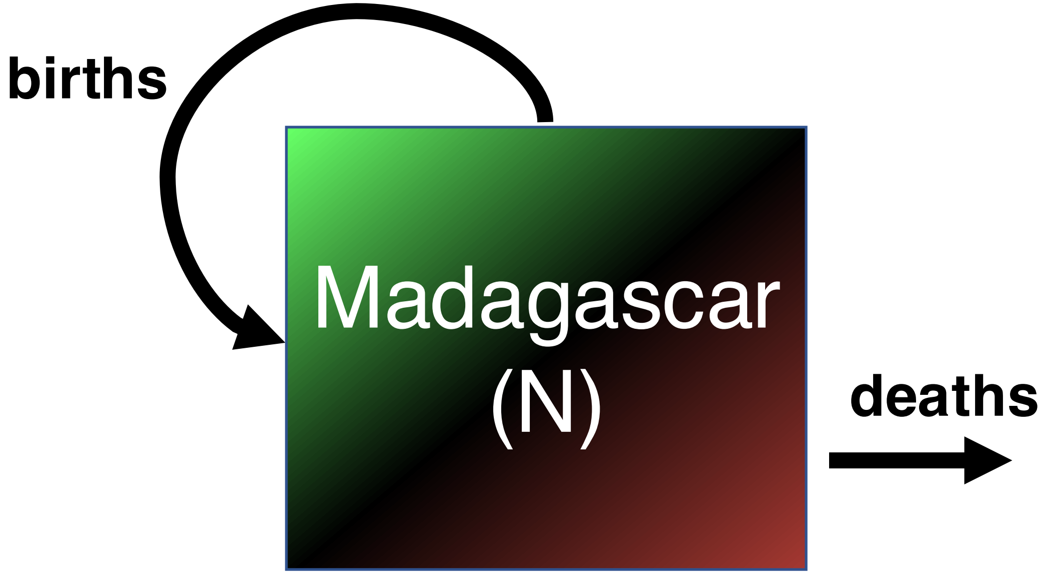

What is wrong about this model?

Modeling demographic complexity

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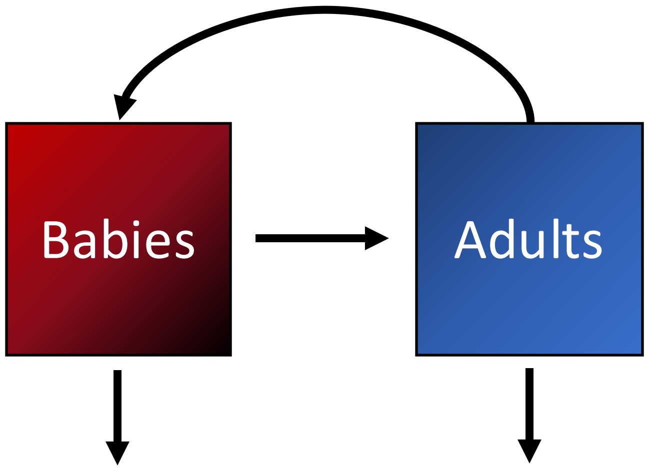

The structured population model

Modeling demographic complexity

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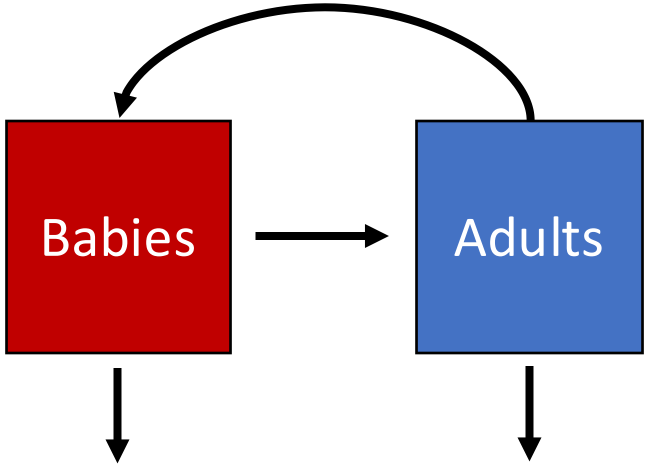

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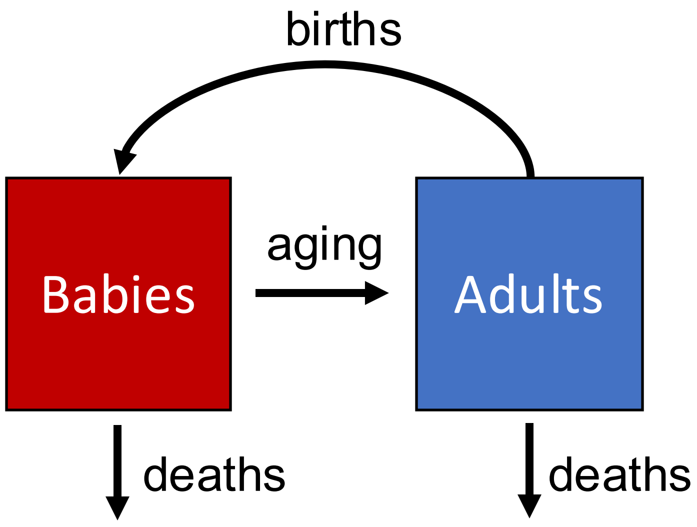

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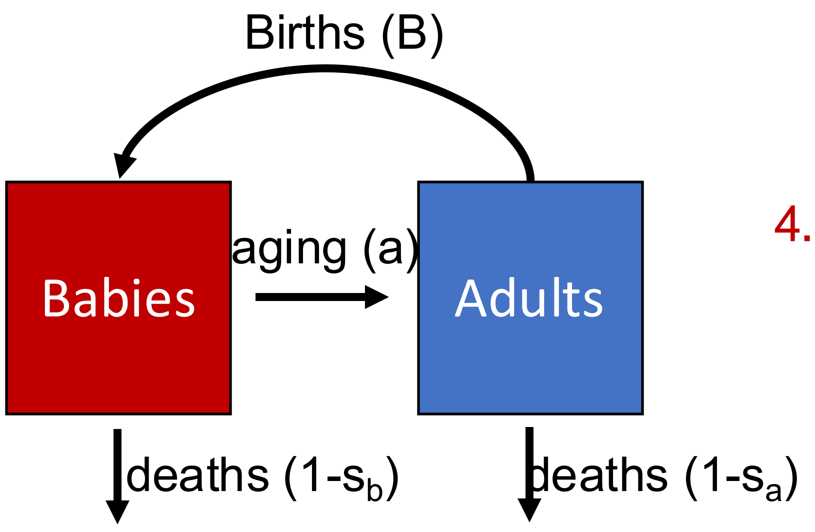


Population rate of increase

$$\lambda = N_{t+1}/N_t$$

pop size at t + 1

pop size at t

$$N_{t+1} = A^* \, N_t$$

matrix of survival and fecundity rates

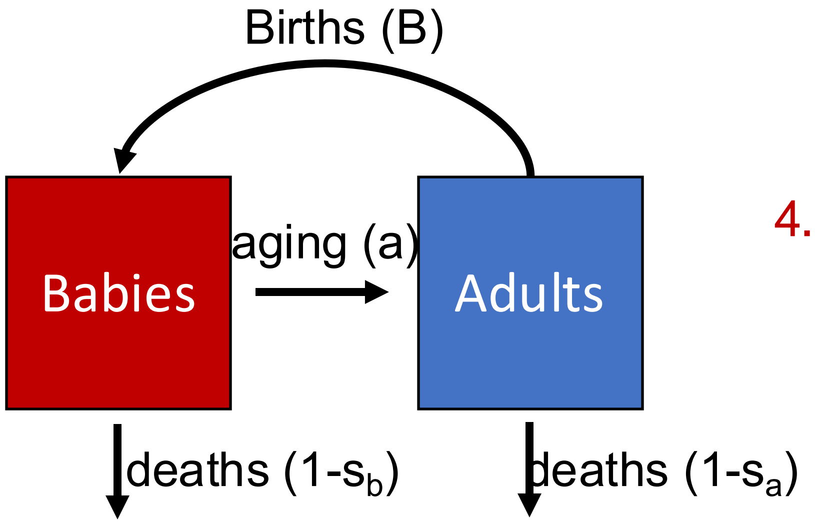
vector of population sizes

$$\begin{bmatrix} s_b(1-a) & B \\ s_b a & s_a \end{bmatrix}$$

***Discrete time**

The structured population model

1. Populations are divided into compartments
2. Individuals within a compartment are homogenously mixed
3. Compartments and transition rates are determined by biological systems
4. Rates of transferring between compartments are expressed mathematically



$$N_{t+1} = A^* \, N_t$$

Population rate of increase – can be derived from the transition matrix!

λ

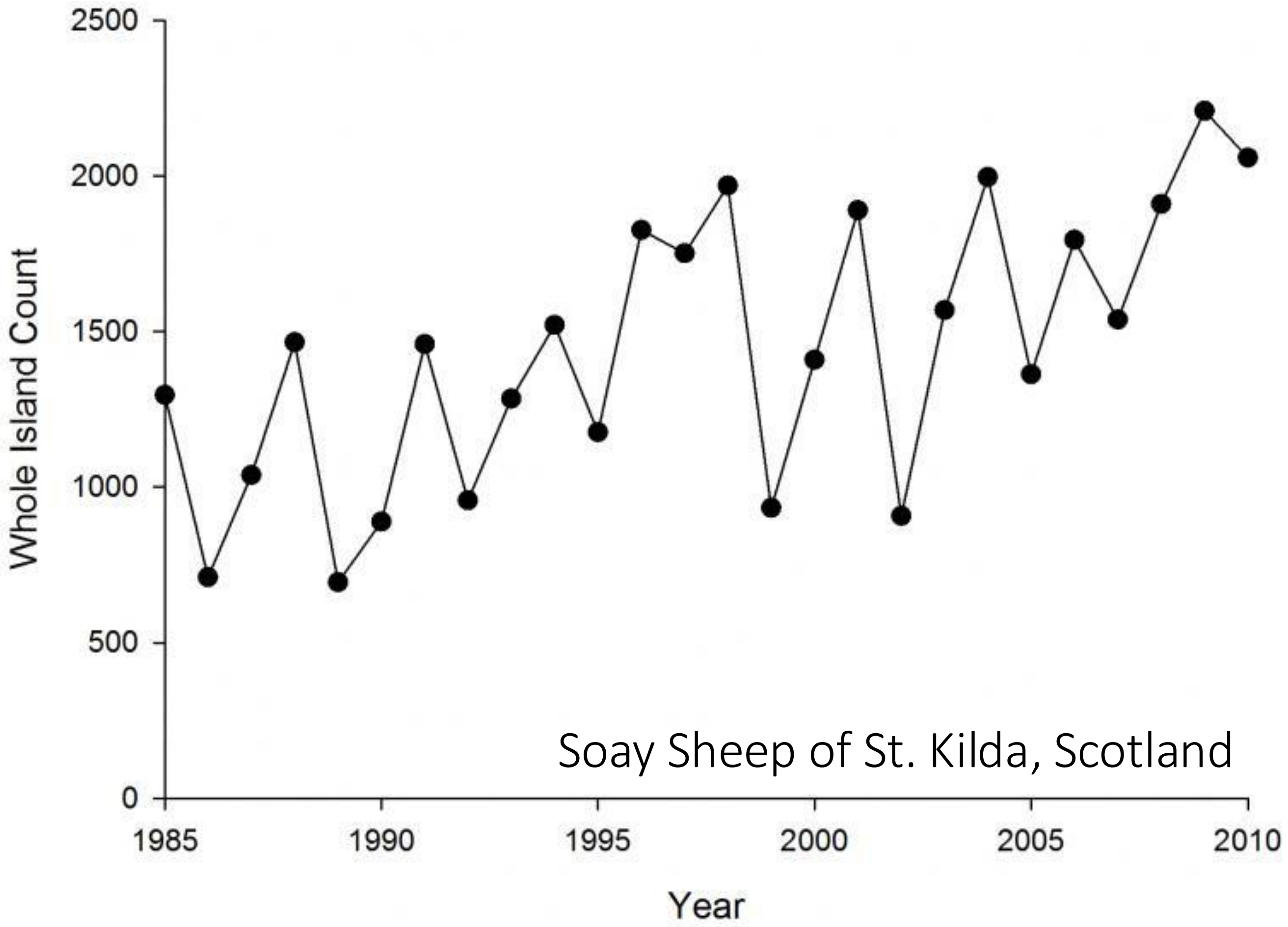
$$\underset{\mathbf{A}}{\begin{bmatrix} s_b(1-a) & B \\ s_b a & s_a \end{bmatrix}} \times \underset{\mathbf{N_t}}{\begin{bmatrix} N_b \\ N_a \end{bmatrix}} = \underset{\mathbf{N_{t+1}}}{\begin{bmatrix} s_b(1-a)\,N_b + BN_a \\ s_b\,a\,N_b + s_aN_a \end{bmatrix}}$$

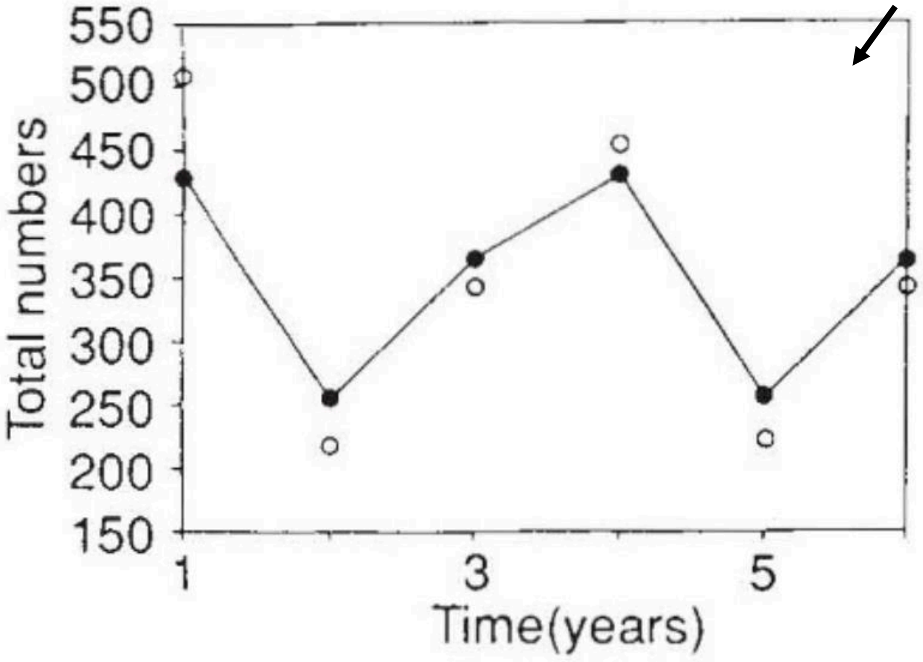
Population growth will depend on population structure!

(pop grows @ λ >1 & declines @ λ < 1)

Structured populations in practice

Model compared against data





Overcompensation and population cycles in an ungulate

B. T. Grenfell, O. F. Price, S. D. Albon & T. H. Glutton-Brock

Nature **355**, 823–826 (1992) | Cite this article

Structured populations in practice

These results used a simple **density-dependent** model only!

$$N_{t+1} = \lambda d N_t / (1 + (a N_t)^b)$$

a and *b* control the strength of density dependence.

population at t+1

average fecundity

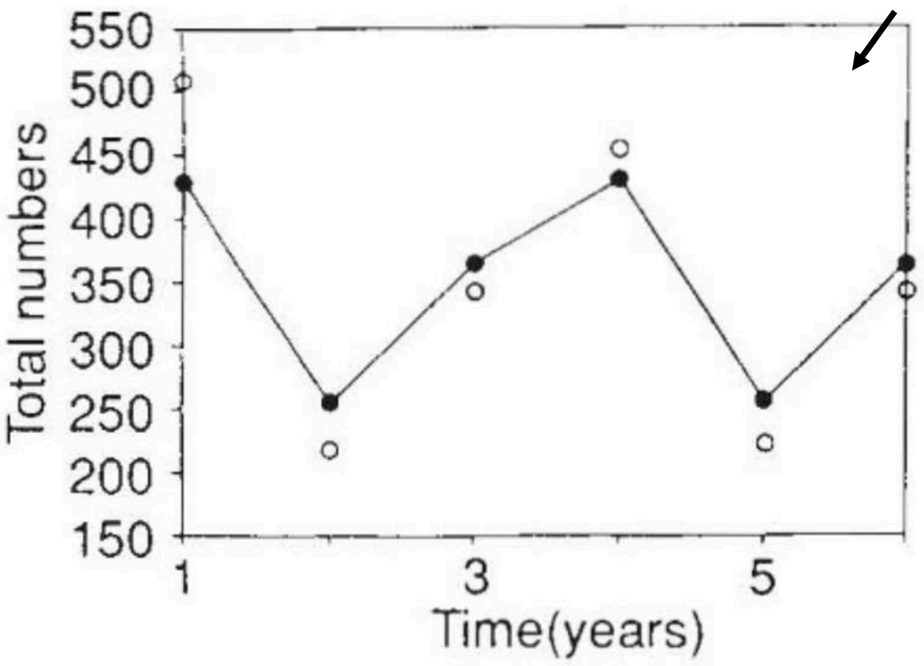
growth rate

population at t

Similar to the simple logistic growth equation!

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

Model compared against data



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Structured populations in practice

In later work, the authors added **environmental stochasticity** (bad weather) to **better represent** the data……

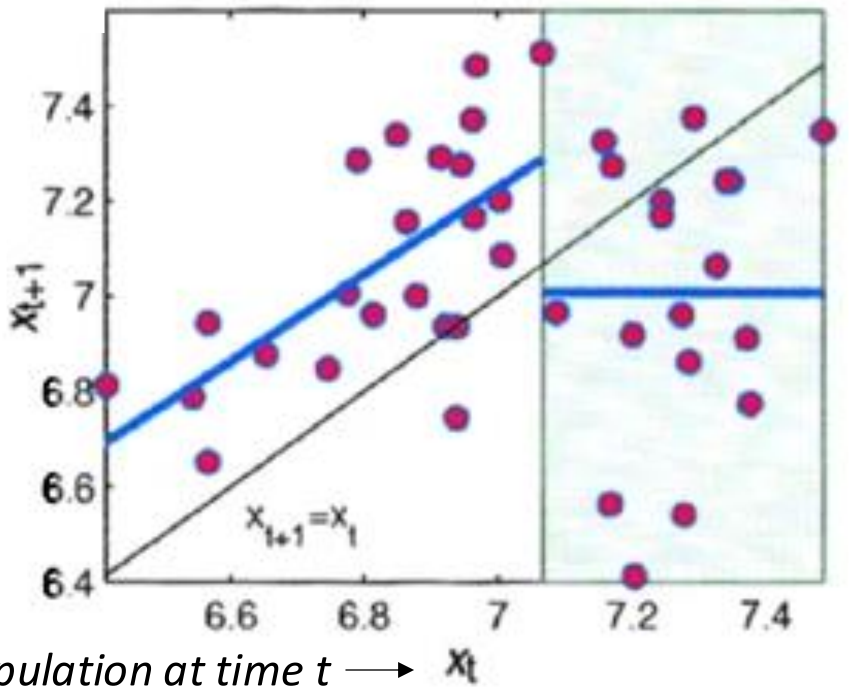
Noise and determinism in synchronized sheep dynamics

B. T. Grenfell, K. Wilson, B. F. Finkenstädt, T. N. Coulson, S. Murray, S. D. Albon, J. M. Pemberton, T. H. Clutton-Brock & M. J. Crawley

Nature **394**, 674–677 (1998) | Cite this article

At high population sizes, population crashes can occur due to density dependence – but these happen preferentially in bad weather!

sheep population at time t+1



sheep population at time t

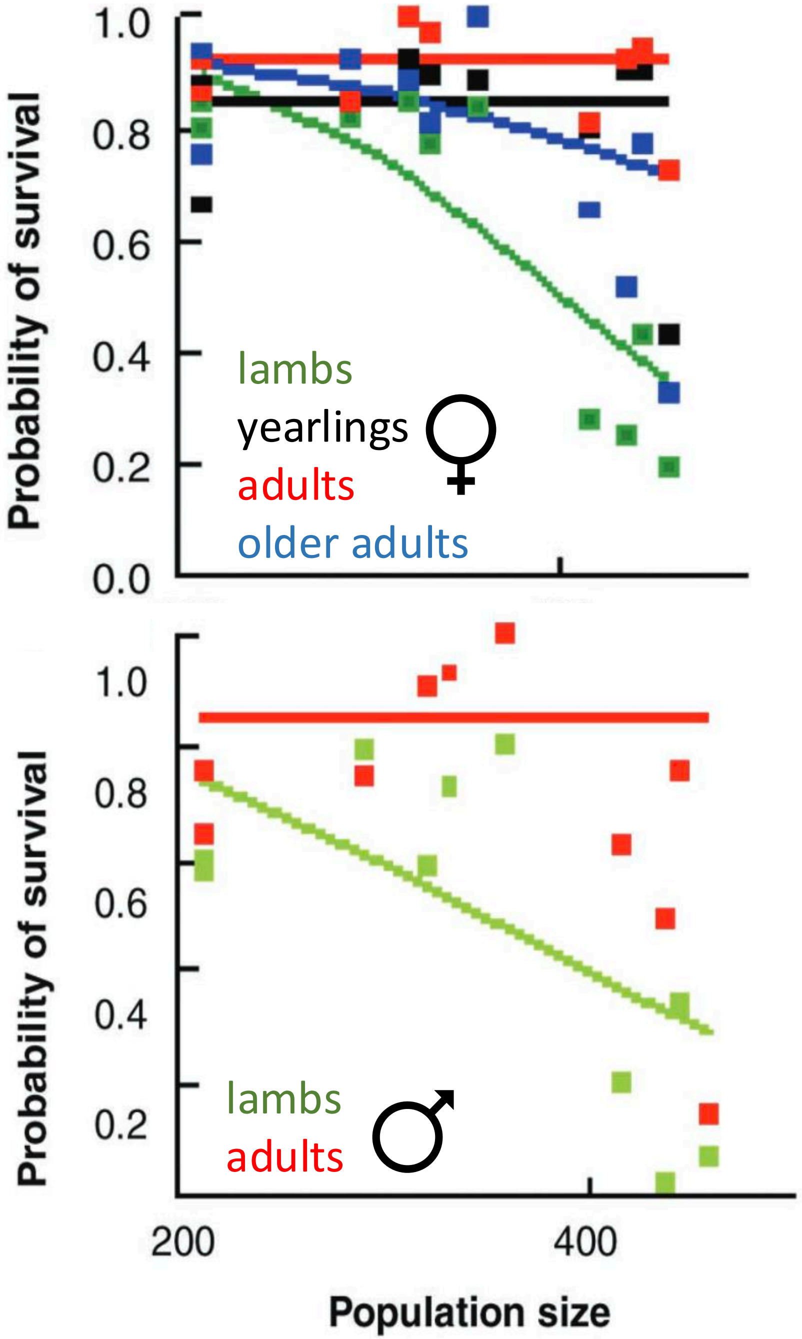
Structured populations in practice

And, finally, they added in **population structure** as well!

Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep

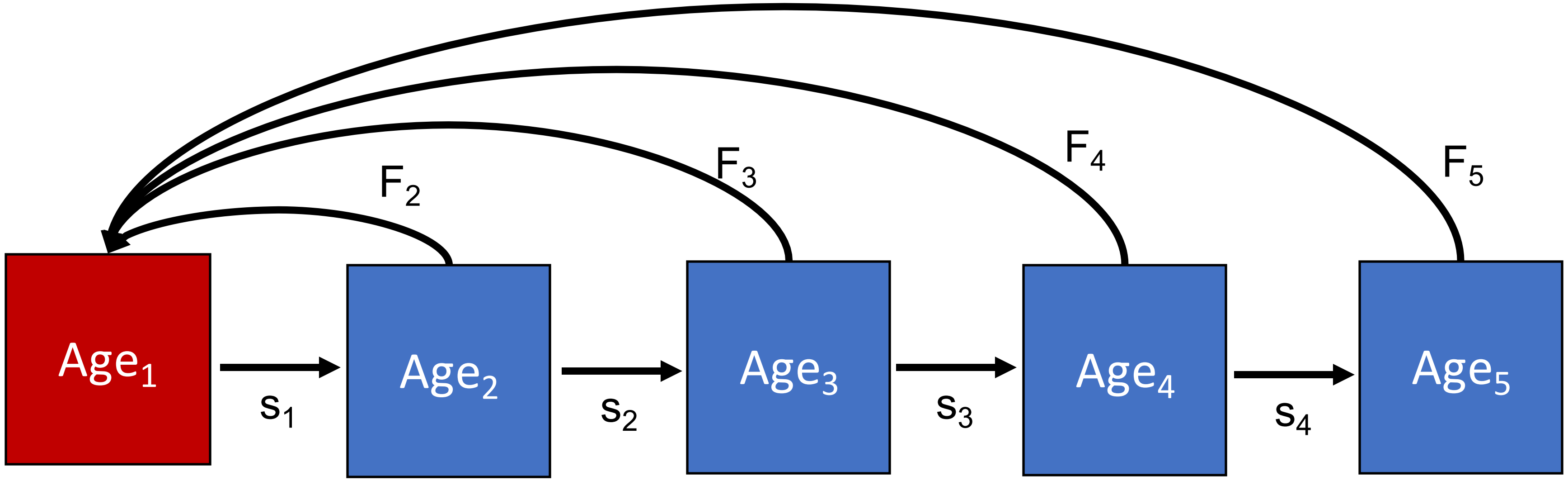
T. Coulson,[1*†] E. A. Catchpole,[2] S. D. Albon,[3] B. J. T. Morgan,[4] J. M. Pemberton,[5] T. H. Clutton-Brock,[6] M. J. Crawley,[6] B. T. Grenfell[7]

25 MAY 2001 VOL 292 SCIENCE www.sciencemag.org



The structured population model

If data are available, we can model much more detailed population structures using the same approach.

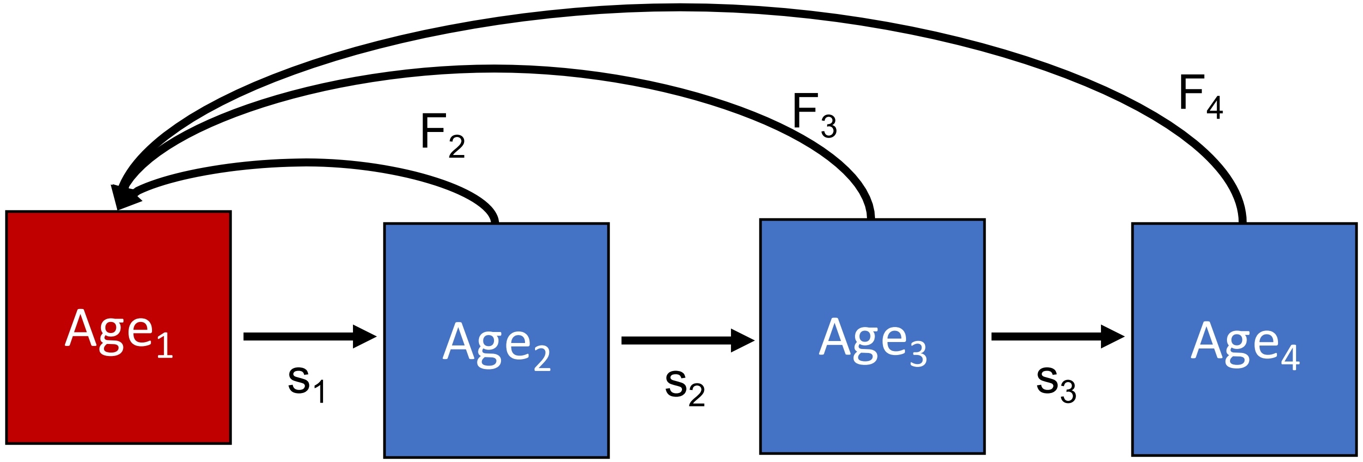


The **Leslie matrix** model divides classes based on age.
The **Lefkovitch matrix** model divides classes based on life stage.

Leslie 1945 *Biometrika.* Leslie 1948 *Biometrika.*
Lefkovitch 1965 *Biometrics.*

The structured population model

If data are available, we can model much more detailed population structures using the same approach.



λ=can be derived from transition matrix $\rightarrow$

$$\begin{array}{ccccc} \mathbf{A} & & \mathbf{N_t} & & \mathbf{N_{t+1}} \\ \begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} & \mathbf{x} & \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix} & \mathbf{=} & \begin{bmatrix} N_{1\ t+1} \\ N_{2\ t+1} \\ N_{3\ t+1} \\ N_{4.t+1} \end{bmatrix} \end{array}$$

$$N_{t+1} = A^* N_t$$

Leslie 1945 *Biometrika.* Leslie 1948 *Biometrika.*
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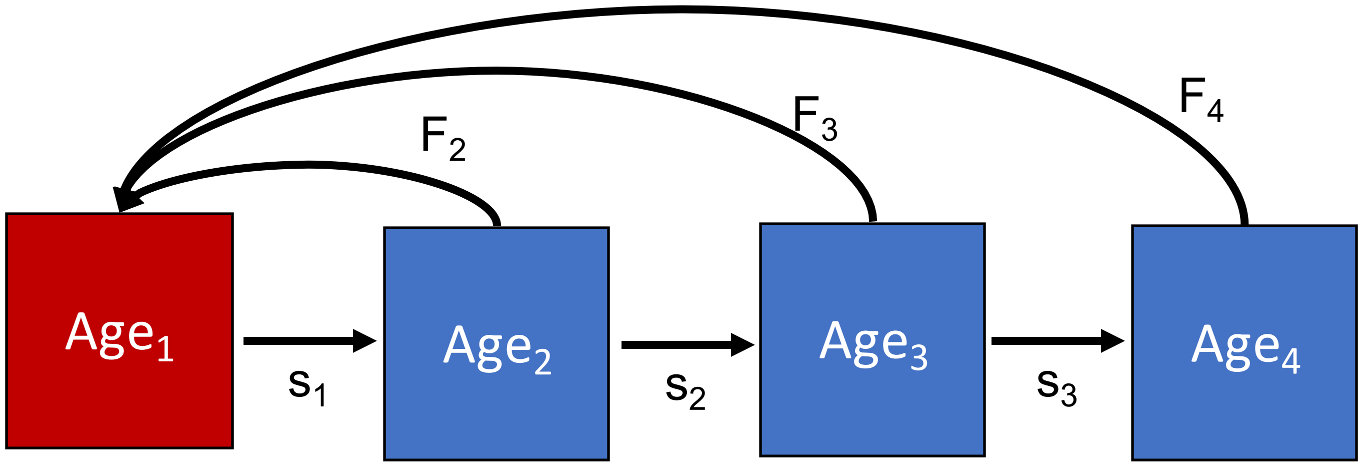
The structured population model

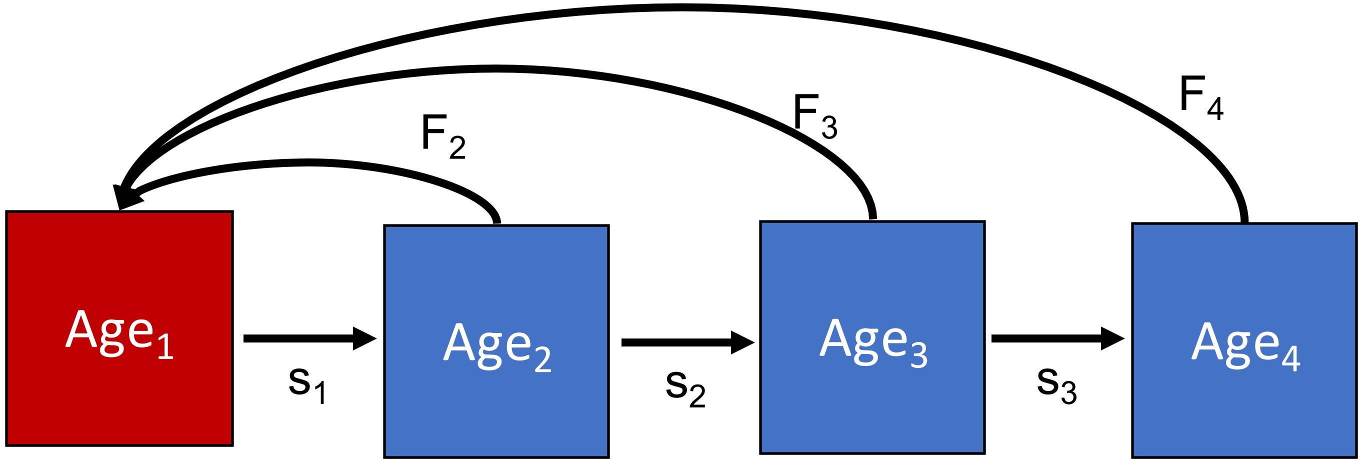


Demographers collect these rates in life tables

x (age)	N_x (number in cohort)	l_x (survivorship to age x)	m_x (fecundity)	$l_x m_x$
0	100	1	0	0
1	60	.6	2	1.2
2	30	.3	3	0.9
3	10	.1	1	0.1
4	1	.01	1	0.01

Gross reproductive rate (GRR): $\sum m_x = 7$

The structured population model



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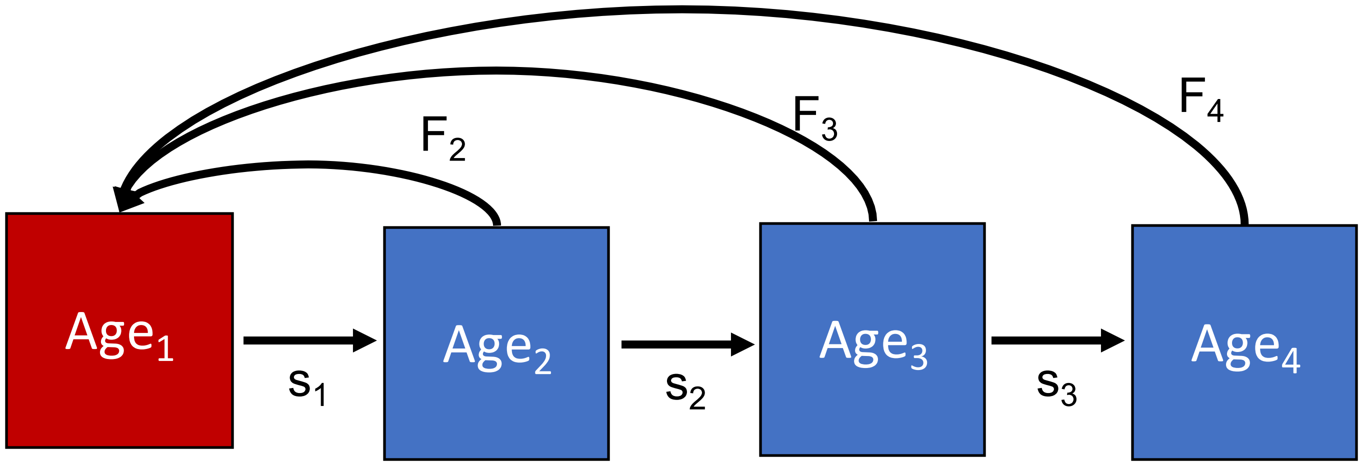
4	1	.01	1	0.01

Net reproductive rate (R_0): $\sum l_x m_x = 2.21$

(pop grows at $\boldsymbol{R_0}$ >1 and declines at $\boldsymbol{R_0} < 1$)

The structured population model



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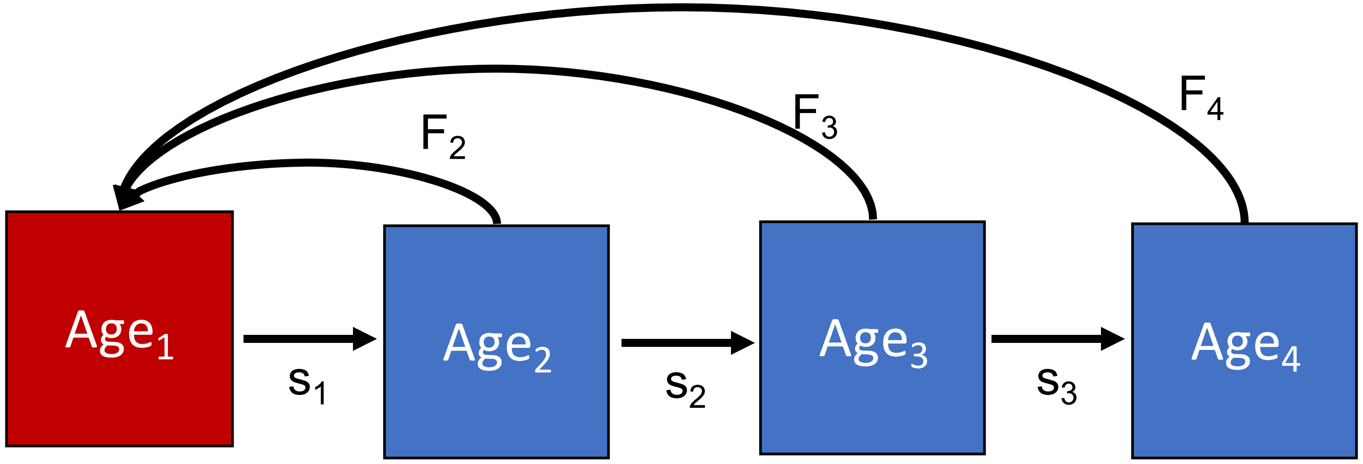
Net reproductive rate (R_0): $\sum l_x m_x = 2.21$

$\lambda = \boldsymbol{R_0}^{1/G}$ where G = length of a generation (often 1 year)

The structured population model



x (age)	N_x (number in cohort)	l_x (survivorship to age x)	m_x (fecundity)	$l_x m_x$
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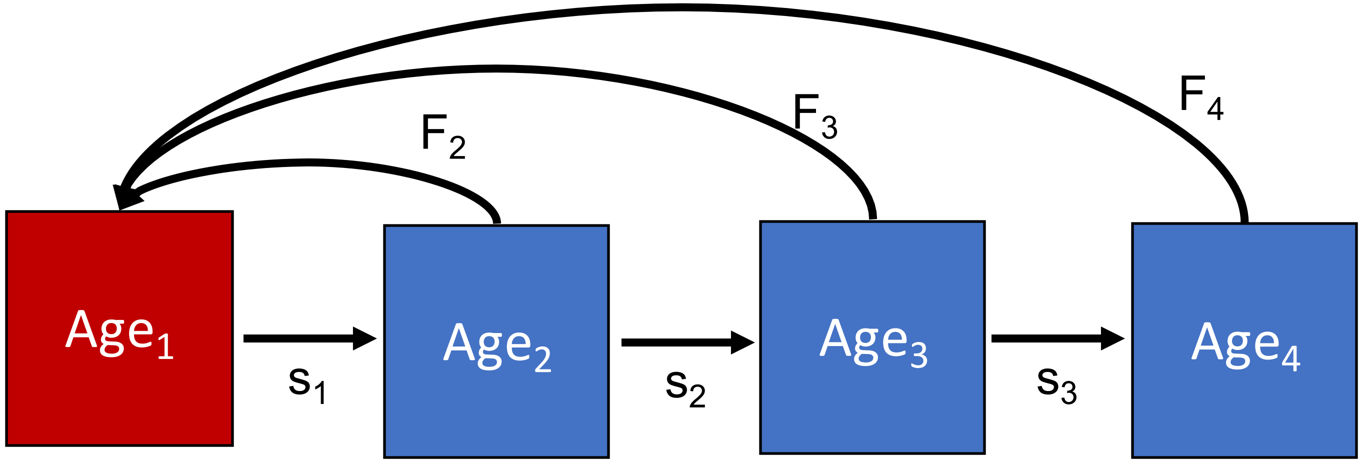
1	60	.6	2	1.2
2	30	.3	3	0.9
3	10	.1	1	0.1
4	1	.01	1	0.01

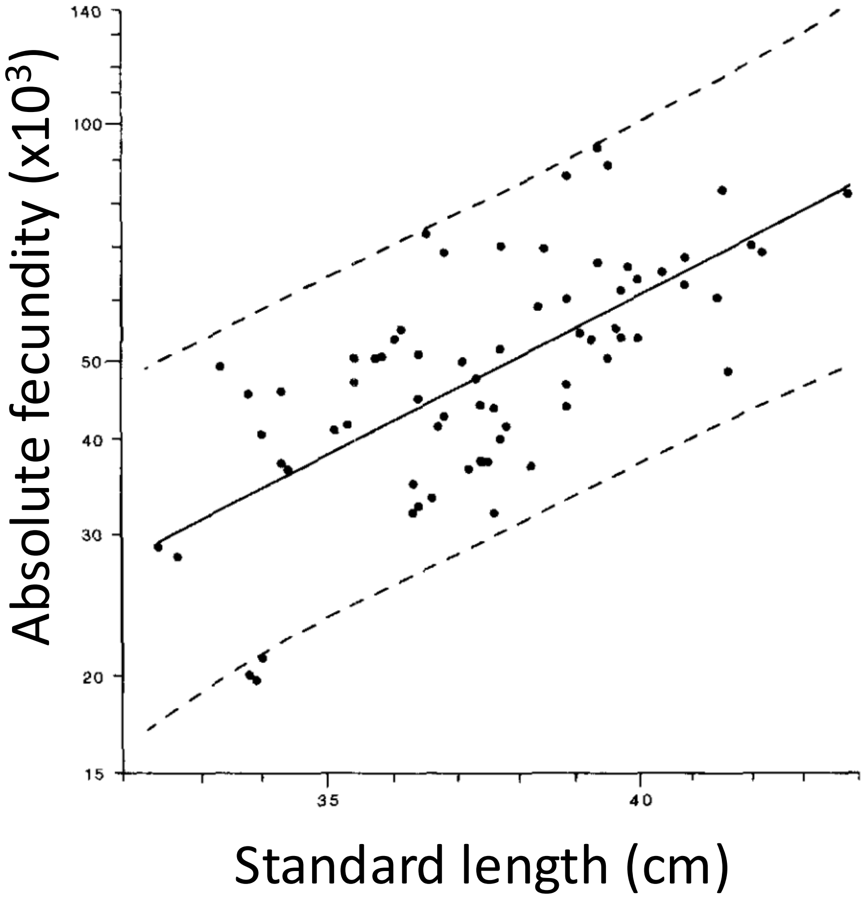
⋮

Orange roughy can live up to 200 years!

Net reproductive rate (R_0): $\sum l_x m_x = \cdots$

The structured population model



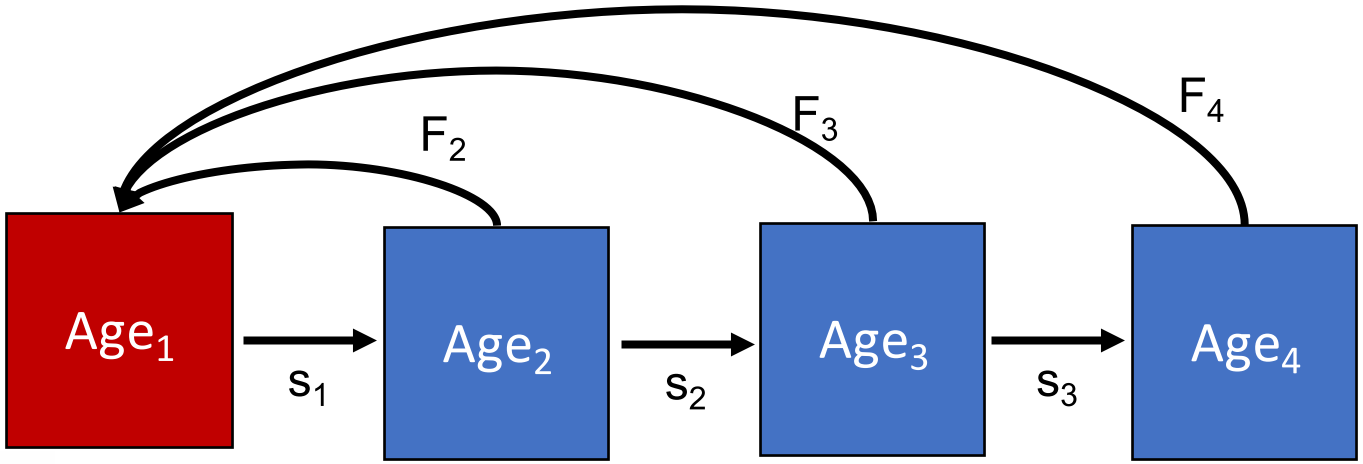


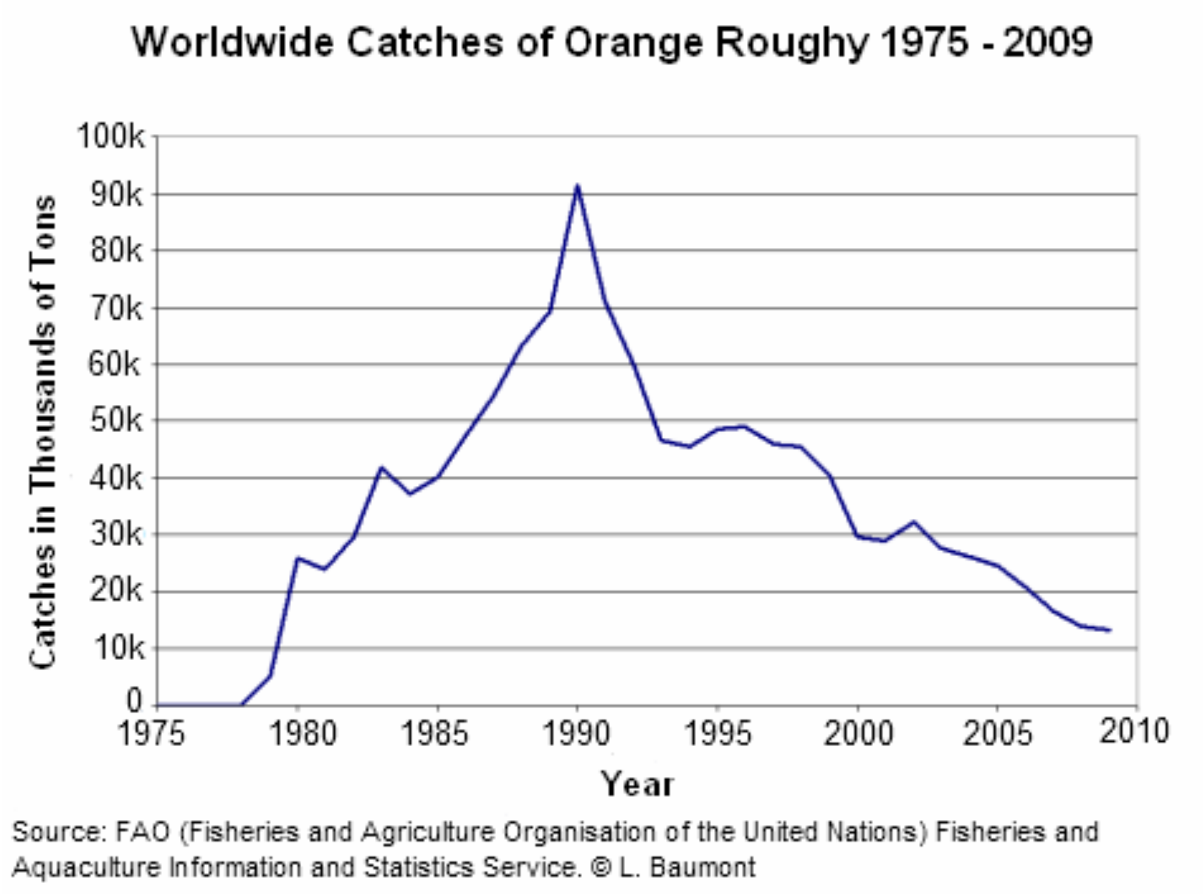
Fecundity (eggs) increases in older, bigger fish!

These are precisely the fish we like to catch! One of the problems with MSY…

Norway 1910
(Norsk folkemuseum)

The structured population model



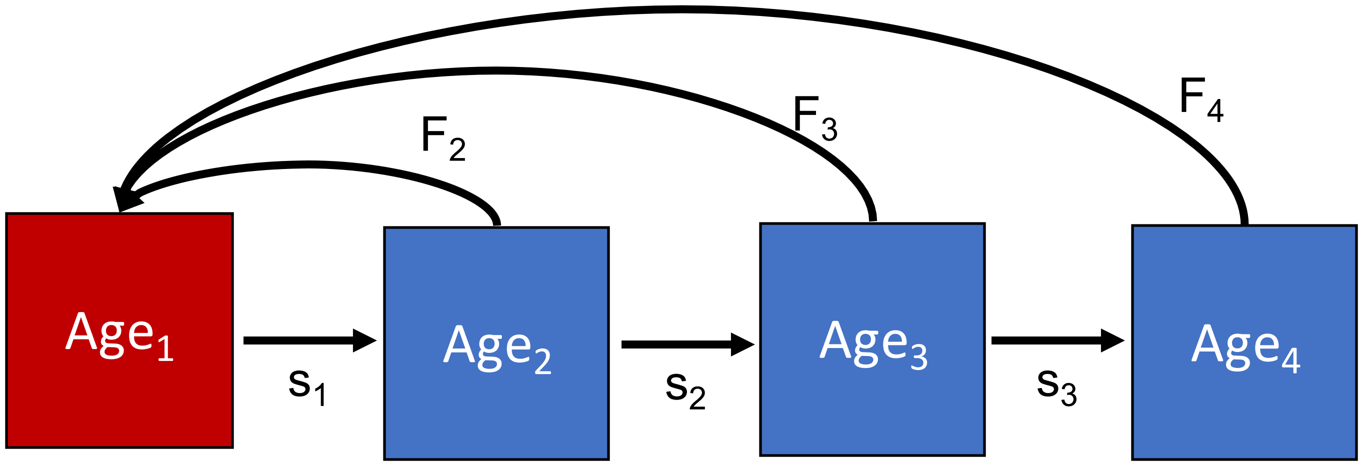


Poor modeling projections has led to severe overexploitation, a common problem in fisheries…

In 2008, the international TAC for orange roughy was reduced from 1470 tons to 914 tons… down from over 90,000 tons in the early 1990s…

The structured population model

Life table analysis is also used extensively in **human demography**.



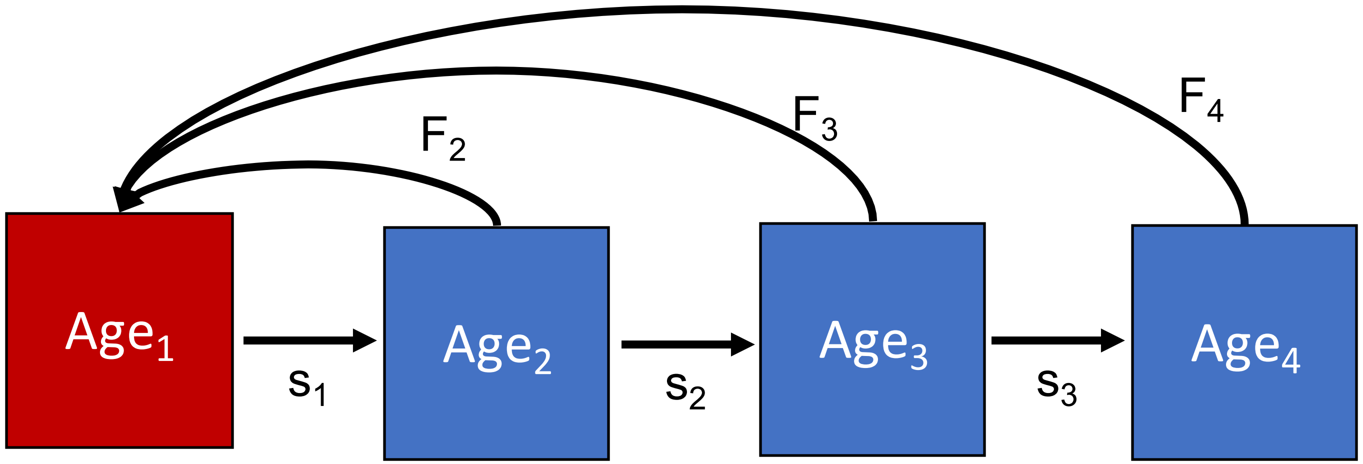
Age. Curt.	Persons.	Age. Curt.	Persons	Age. Curt.	Persons	Age. Curt.	Persons	Age. Curt.	Persons	Age. Curt.	Persons	Age. Curt.	Persons
1	1000	8	680	15	628	22	586	29	539	36	481
2	855	9	670	16	622	23	579	30	531	37	472
3	798	10	661	17	616	24	573	31	523	38	463
4	760	11	653	18	610	25	567	32	515	39	454
5	732	12	646	19	604	26	560	33	507	40	445
6	710	13	640	20	598	27	553	34	499	41	436
7	692	14	634	21	592	28	546	35	490	42	427
Age. Curt.	**Persons.**	**Age. Curt.**	**Persons**	**Age. Curt.**	**Persons**	**Age. Curt.**	**Persons**	**Age. Curt.**	**Persons**	**Age. Curt.**	**Persons**	**Age. Curt.**	**Persons**
43	417	50	346	57	272	64	202	71	131	78	58
44	407	51	335	58	262	65	192	72	120	79	49
45	397	52	324	59	252	66	182	73	109	80	41
46	387	53	313	60	242	67	172	74	98	81	34
47	377	54	302	61	232	68	162	75	88	82	28
48	367	55	292	62	222	69	152	76	78	83	23
49	357	56	282	63	212	70	142	77	68	84	20

Age.	Persons.
7	5547
14	4584
21	4270
28	3964
35	3604
42	3178
49	2709
56	2194
63	1694
70	1204
77	692
84	253
100	107
	34000
	Sum Total.

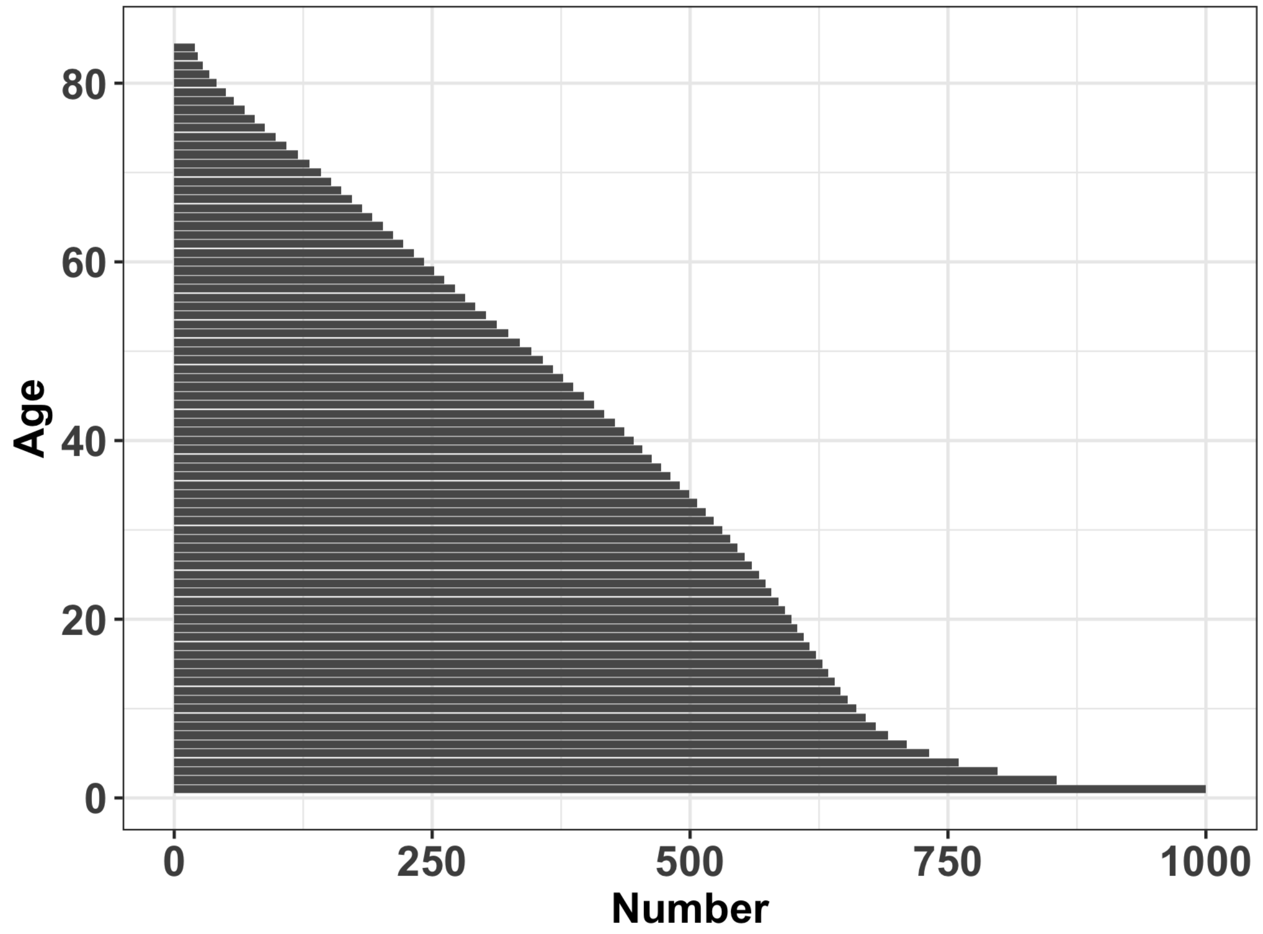
Edmond Halley, 1693

"An estimate of the degrees of the mortality of mankind, drawn from curious tables of the births and funerals at the city of Breslau, with an attempt to ascertain the price of annuities upon lives…"

The structured population model



Population pyramid for Breslau



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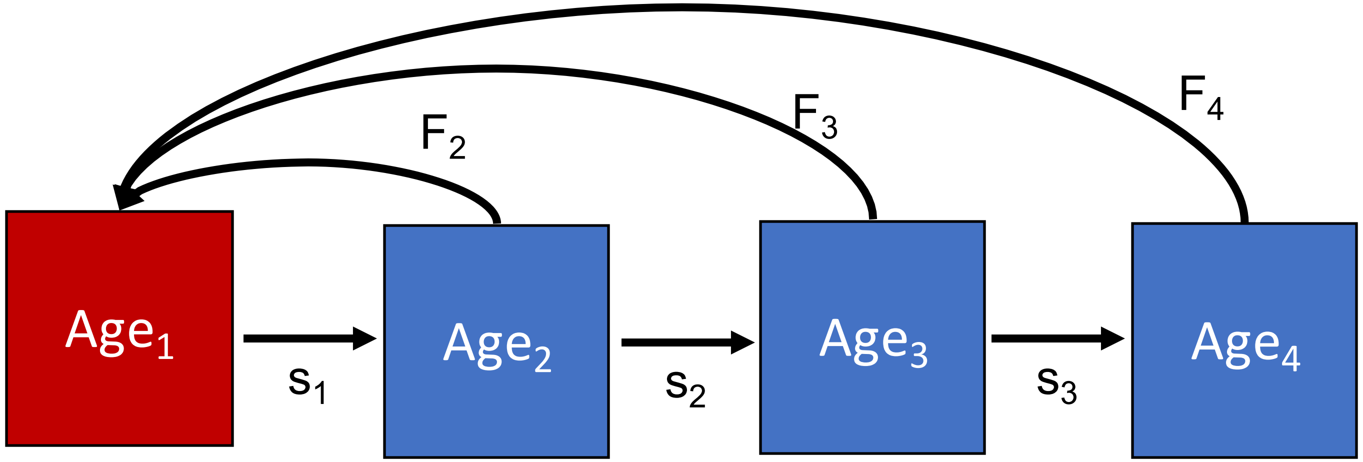
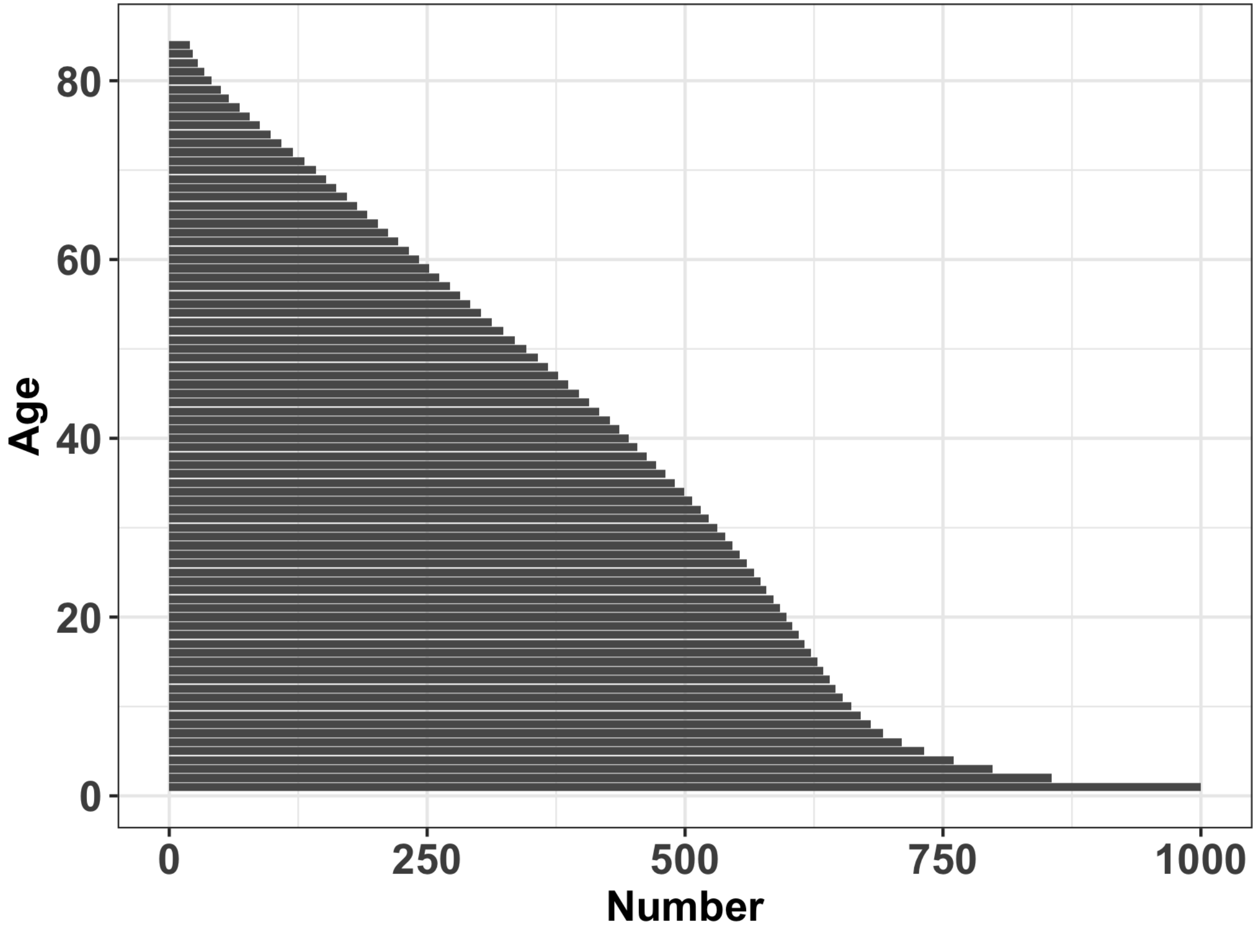


Population pyramid for Breslau

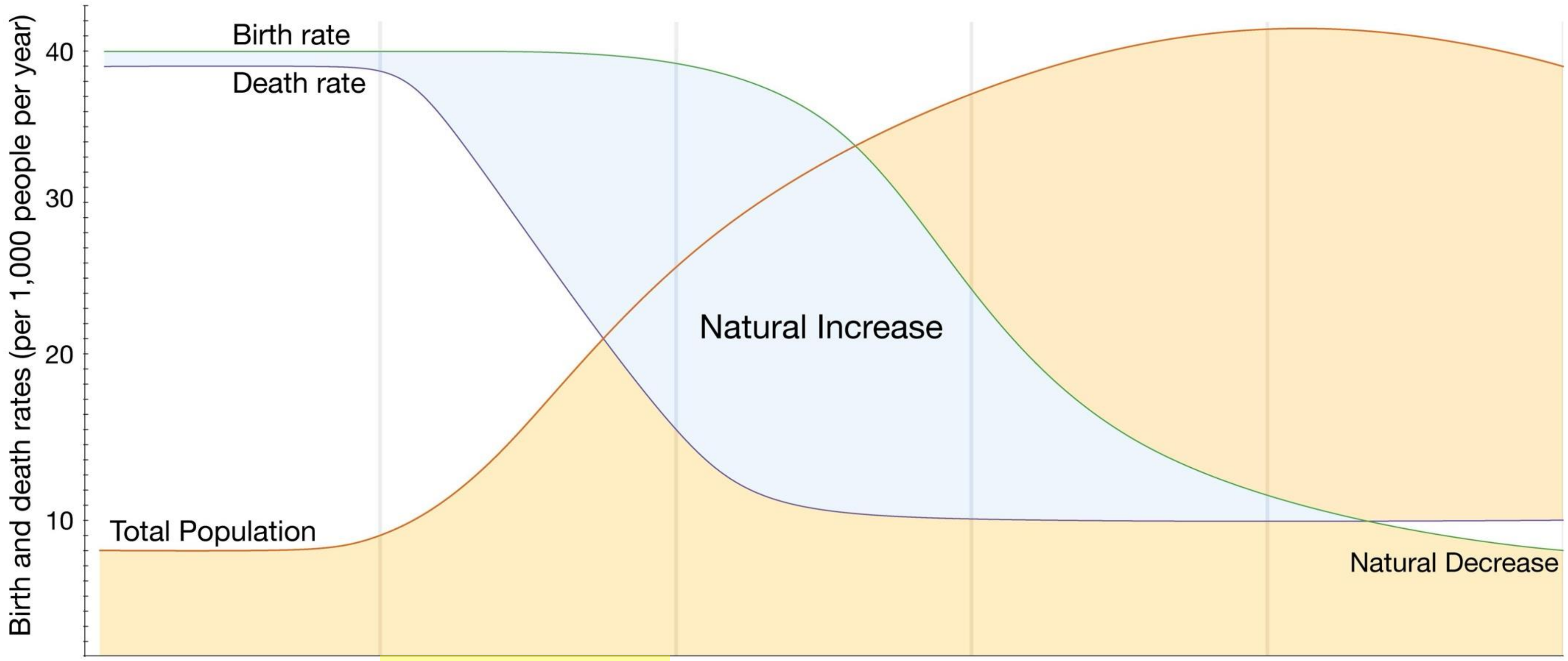


Humans are not like fish!
Fecundity tends to decrease in older age classes due to **reproductive senescence**.

Younger human populations that start <u>giving birth earlier</u> grow faster!

$$\underbrace{\begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix}}_{\mathbf{A}} \times \underbrace{\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}}_{\mathbf{N_t}} = \underbrace{\begin{bmatrix} N_{1\ t+1} \\ N_{2\ t+1} \\ N_{3\ t+1} \\ N_{4.t+1} \end{bmatrix}}_{\mathbf{N_{t+1}}}$$

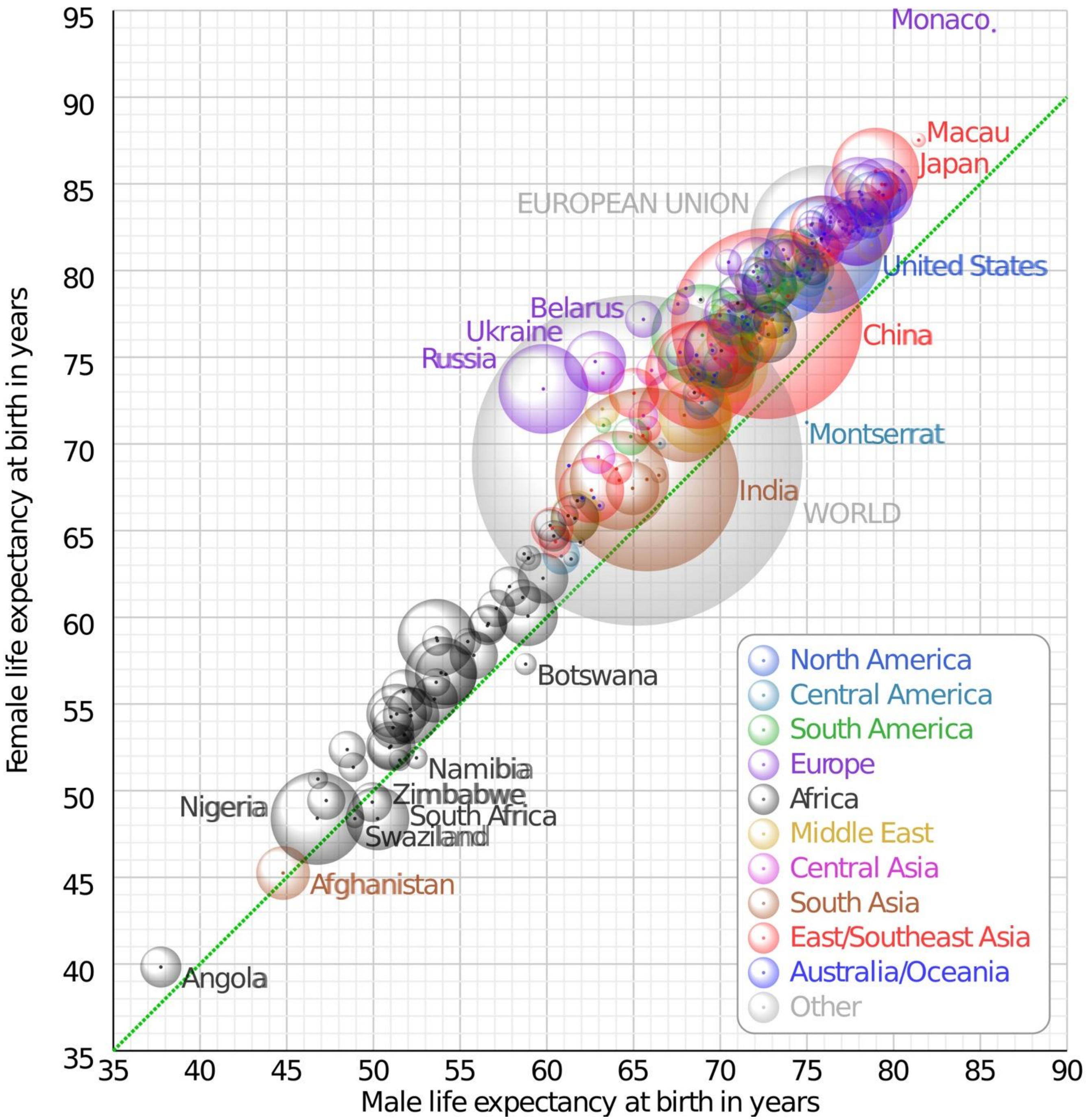
Demographic transition



	Stage 1	*Stage 2*	*Stage 3*	*Stage 4*	*Stage 5*
Birth rate	*High*	*High*	*Falling*	*Low*	*Very low*
Death rate	*High*	*Falls rapidly*	*Falls more slowly*	*Low*	*Low*
Natural increase	*Stable or slow increase*	*Very rapid increase*	*Increase slows down*	*Stable or slow increase*	*Stable or slow decrease*

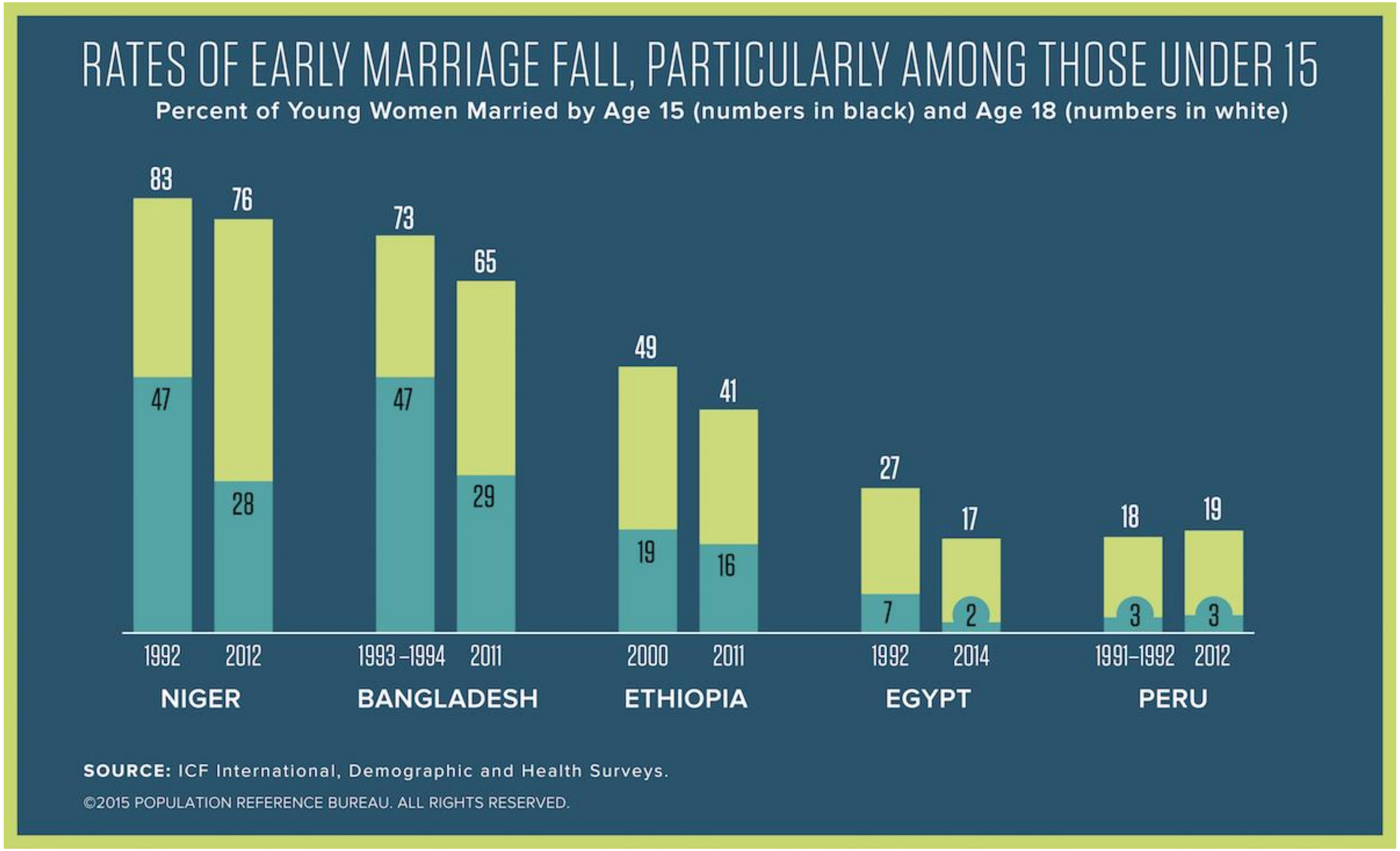
Demographic transition

Death rates are falling globally…

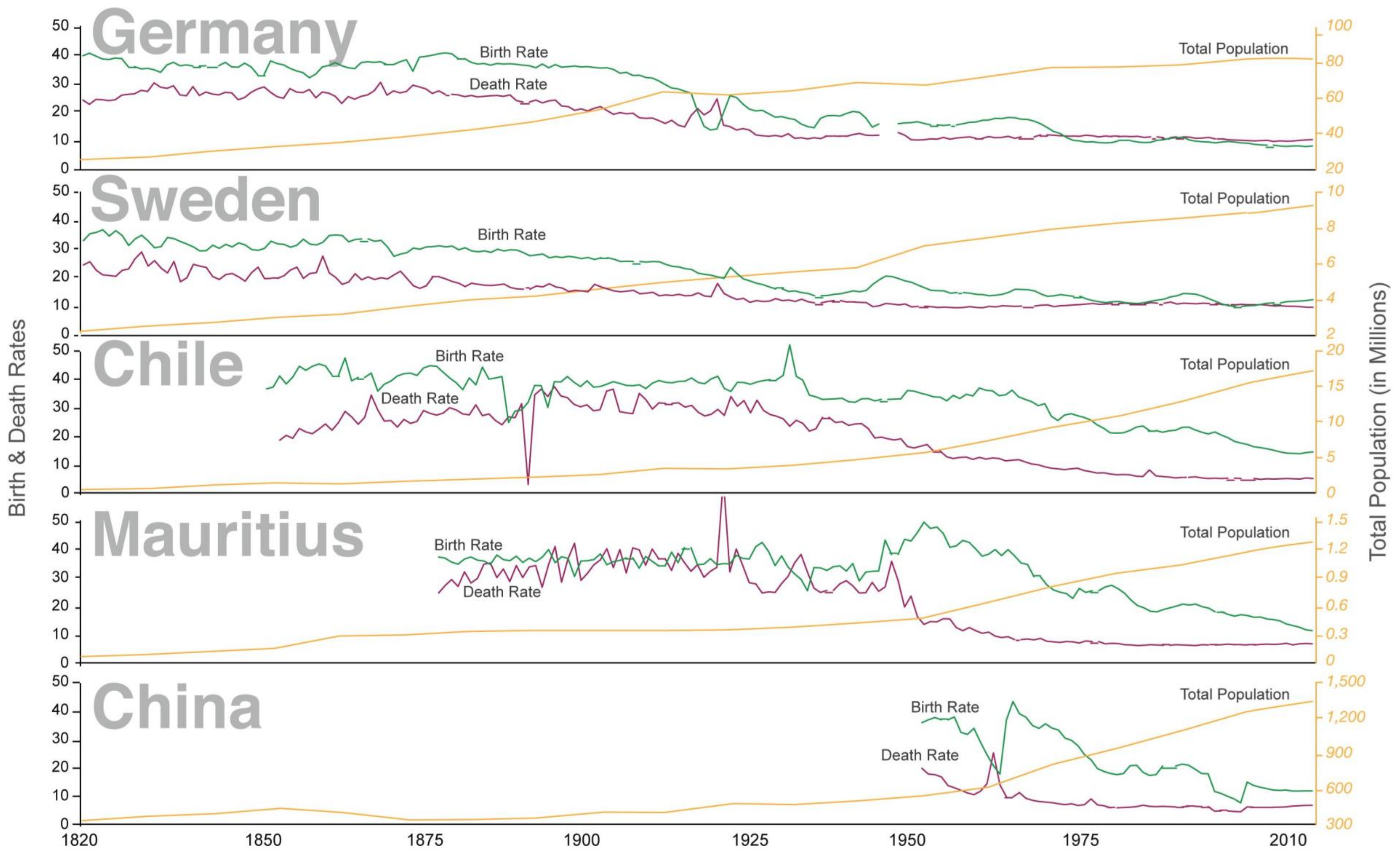


Demographic transition

And birth rates are also falling…



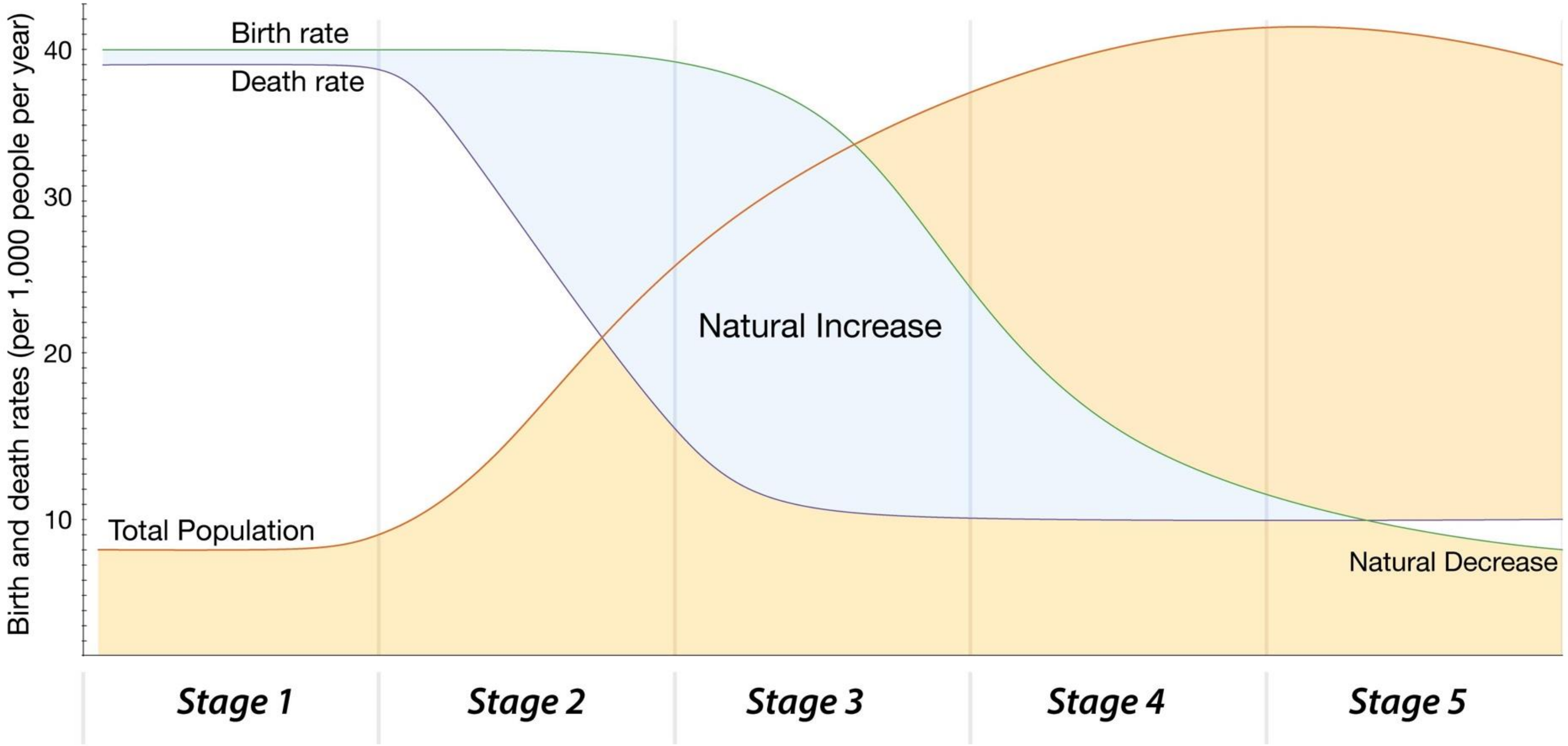
Demographic transition



Data source: The data on birth rates, death rates and the total population are taken from the International Historical Statistics, edited by Palgrave Macmillan (April 2013).
The interactive data visualisation is available at OurWorldinData.org. There you find the raw data and more visualisations on this topic.

Demographic transition

How does age structure predict population growth?



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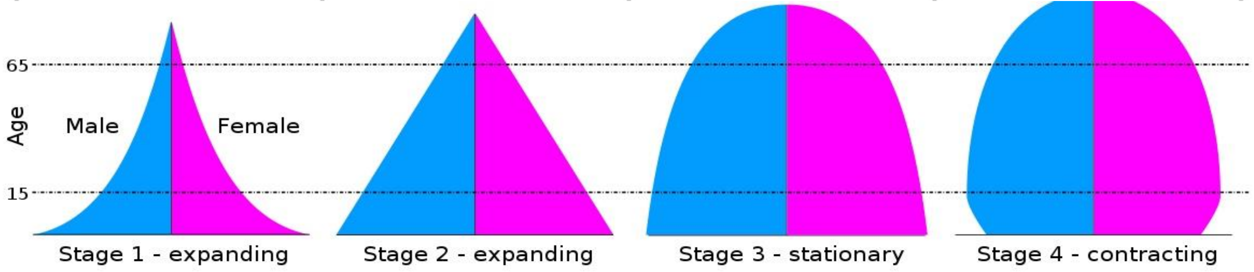
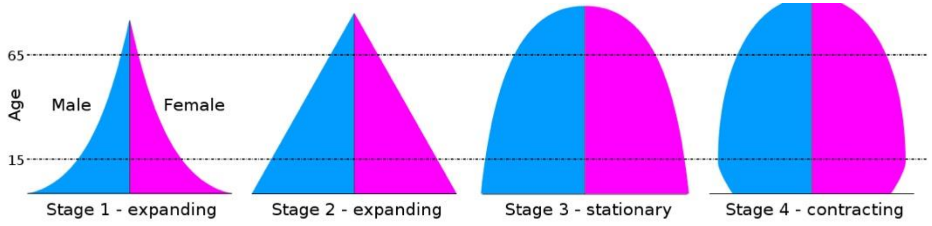
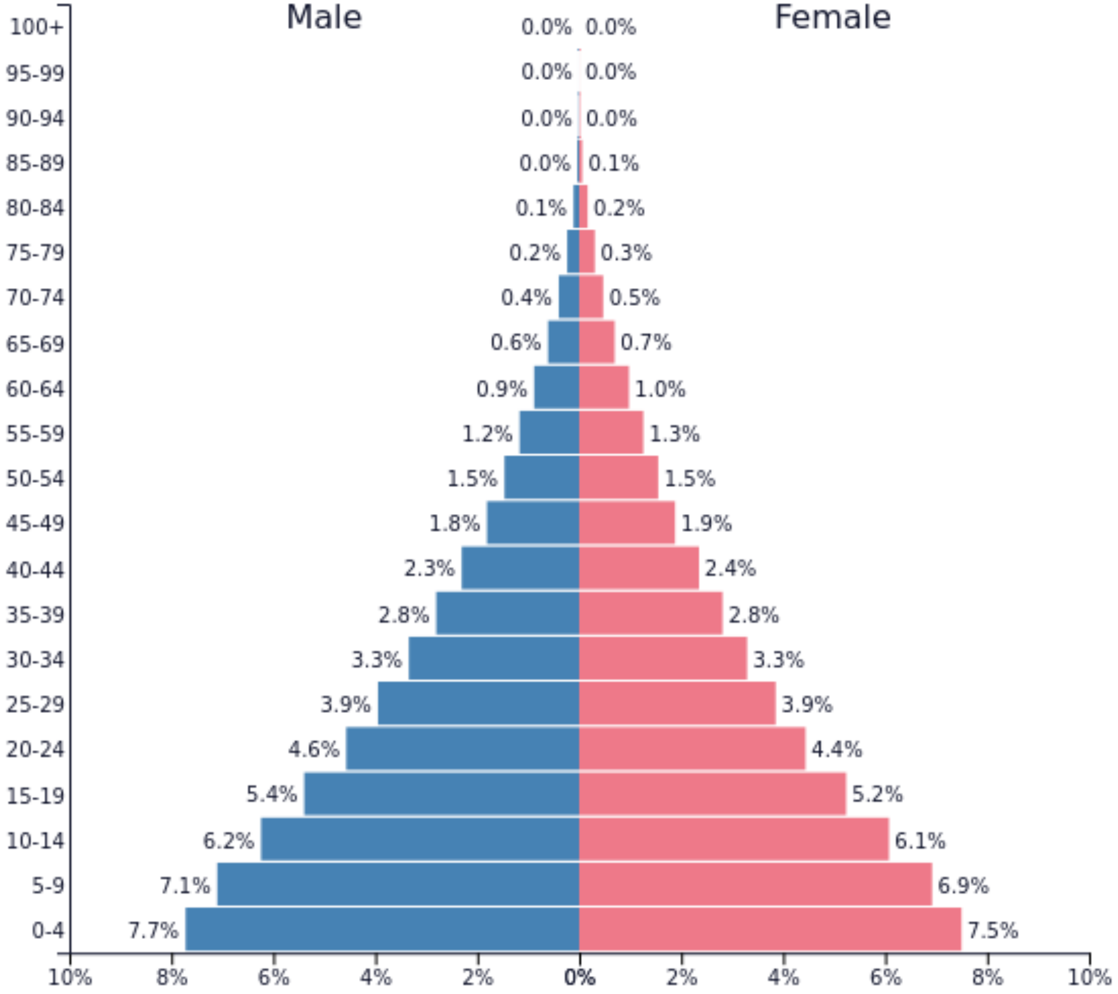
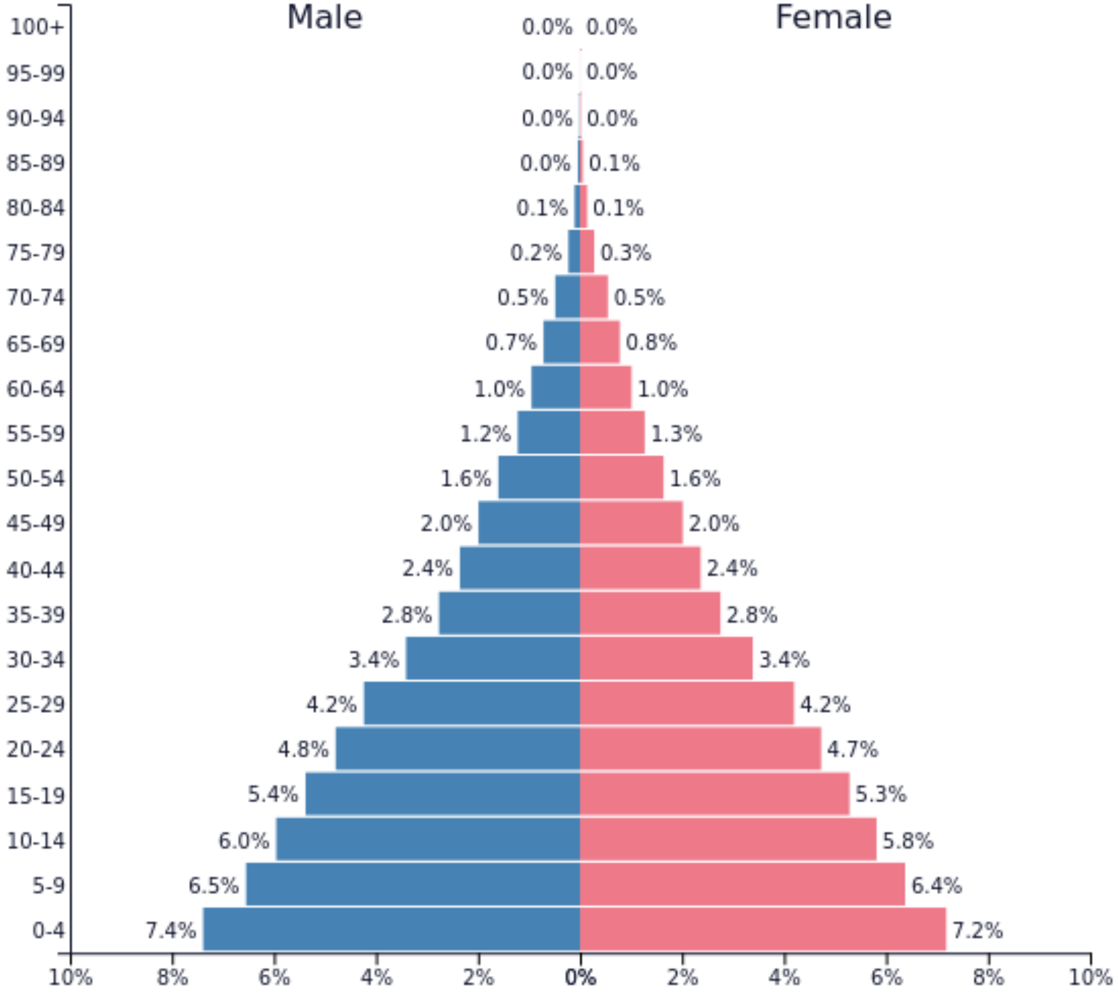


Where are we globally?





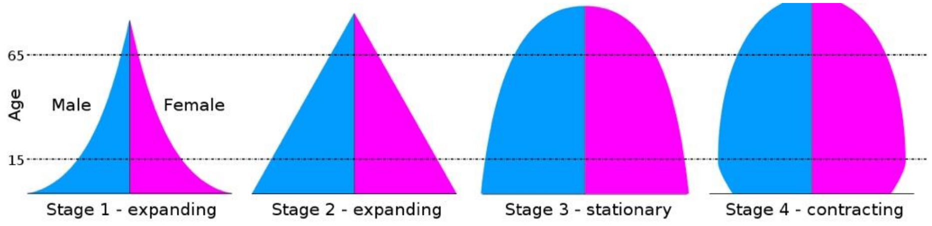
Benin - 2024
Population: **14,462,724**

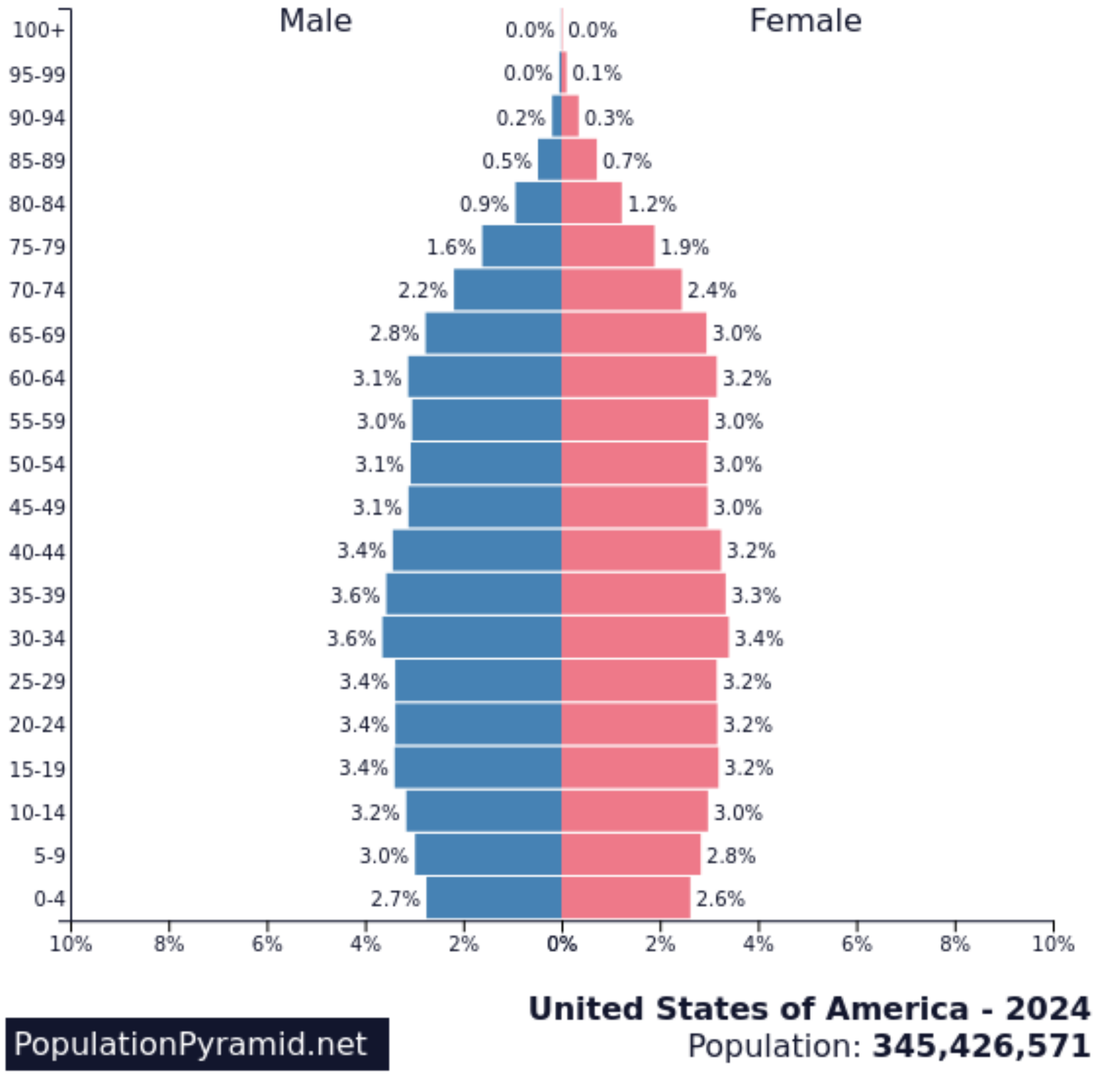


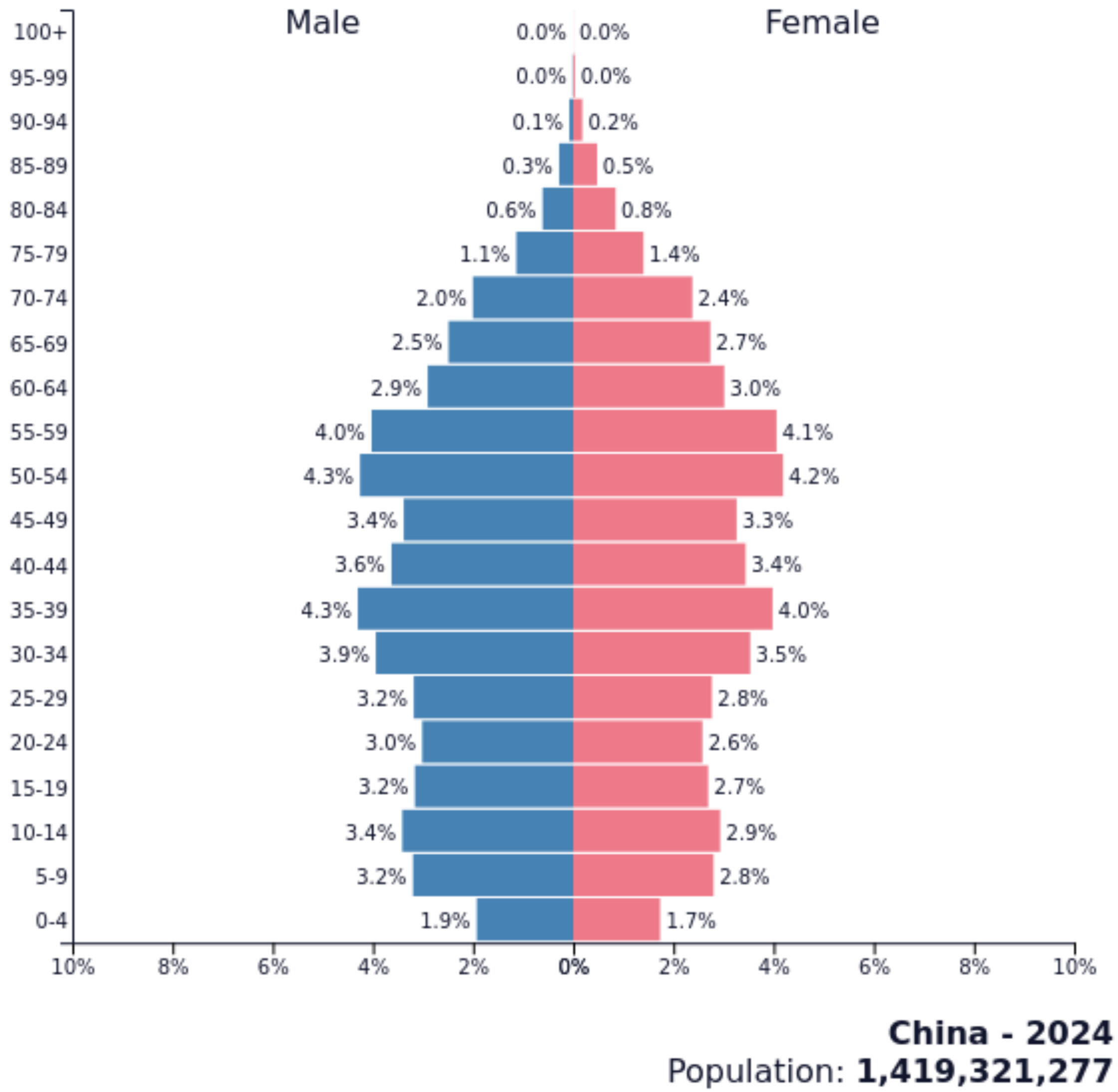
Madagascar - 2024
Population: **31,964,956**

PopulationPyramid.net

Where are we globally?







Where are we globally?