

Fundamentals of Ecology

Week 6, Ecology Lecture 2

Cara Brook

February 6, 2024

Let's recap a bit!

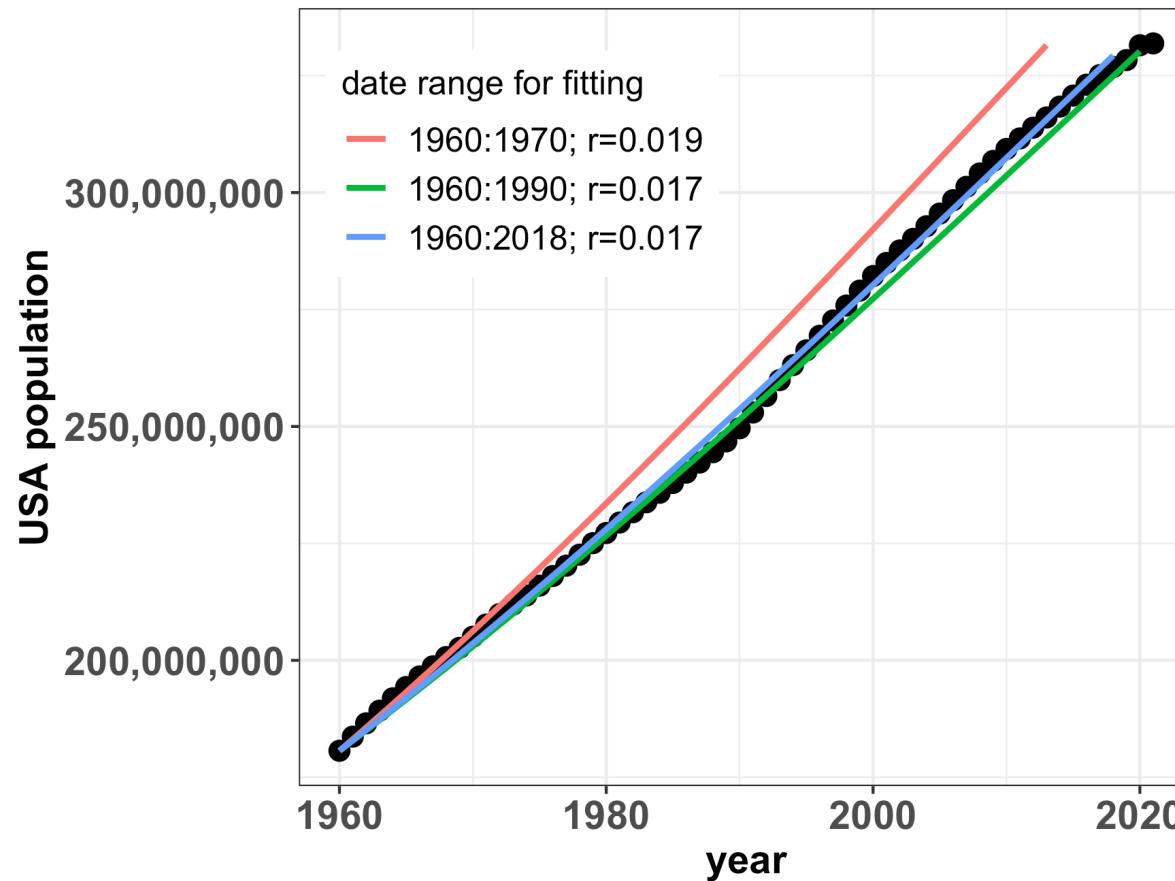
Ecology, generally

- Ecology is the study of organisms and their interactions with each other and the environment
- We use models (especially population models) to formalize hypotheses about these interactions and test those hypotheses against data
- We can ask questions at many ecological scales: individual, population, metapopulation, community, ecosystem

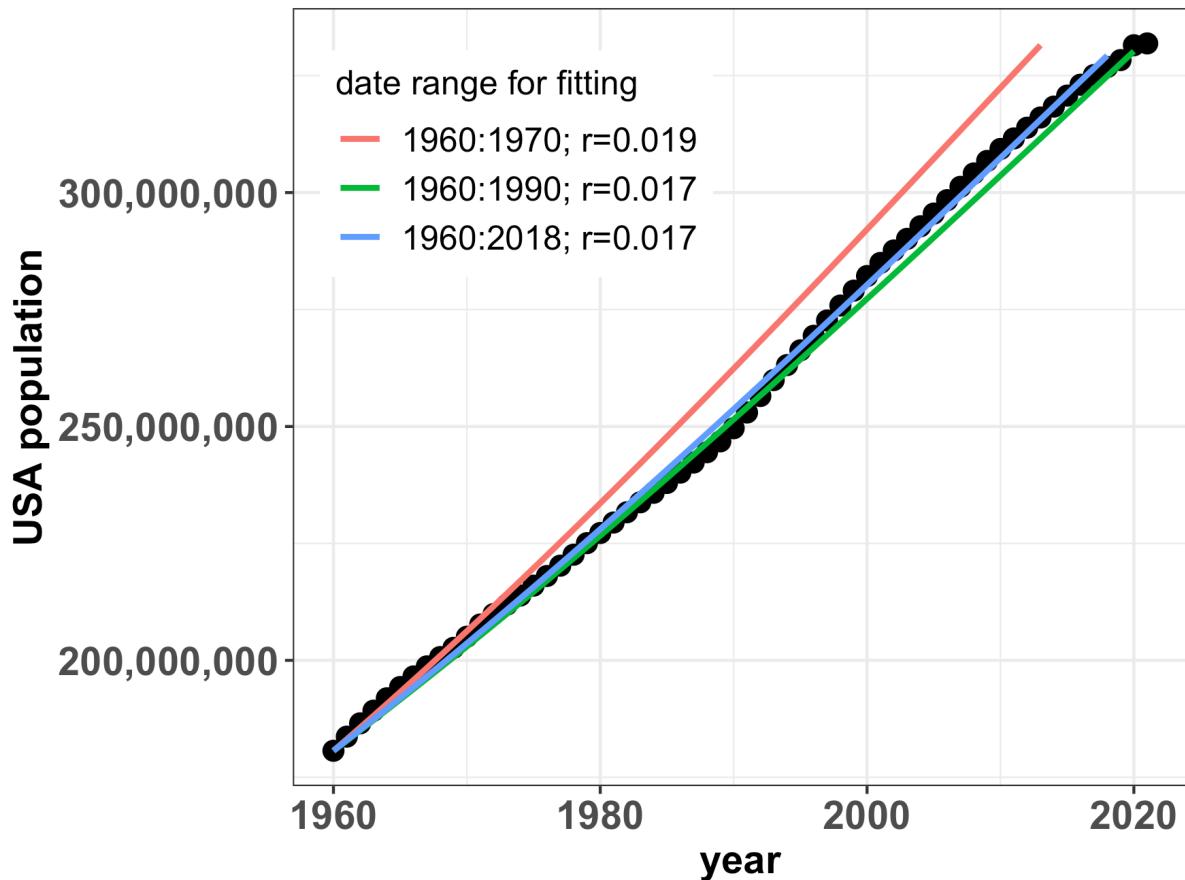
Population growth, specifically

- We can model population growth as geometric in discrete time or exponential in continuous time
- We can estimate growth rates by 'fitting' a model to data

We can estimate growth rates by ‘fitting’ a model to data



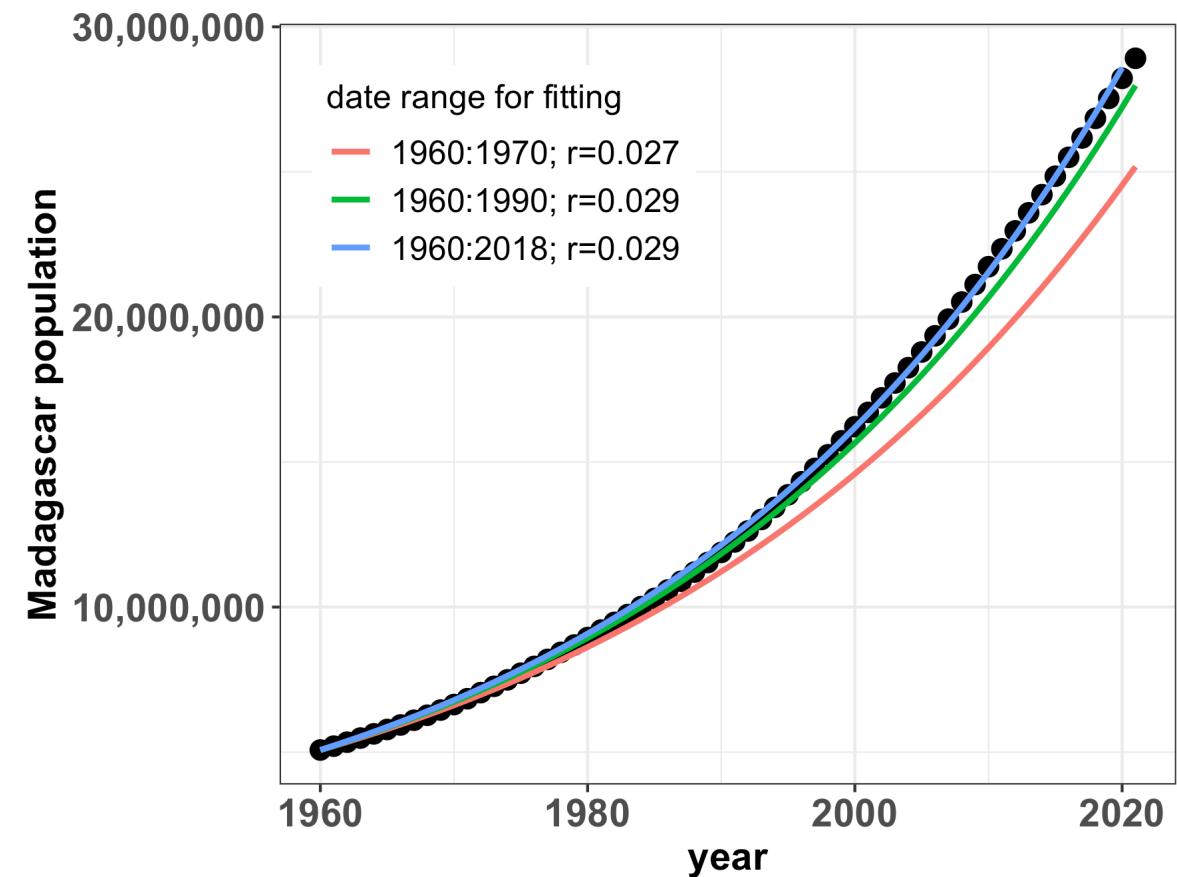
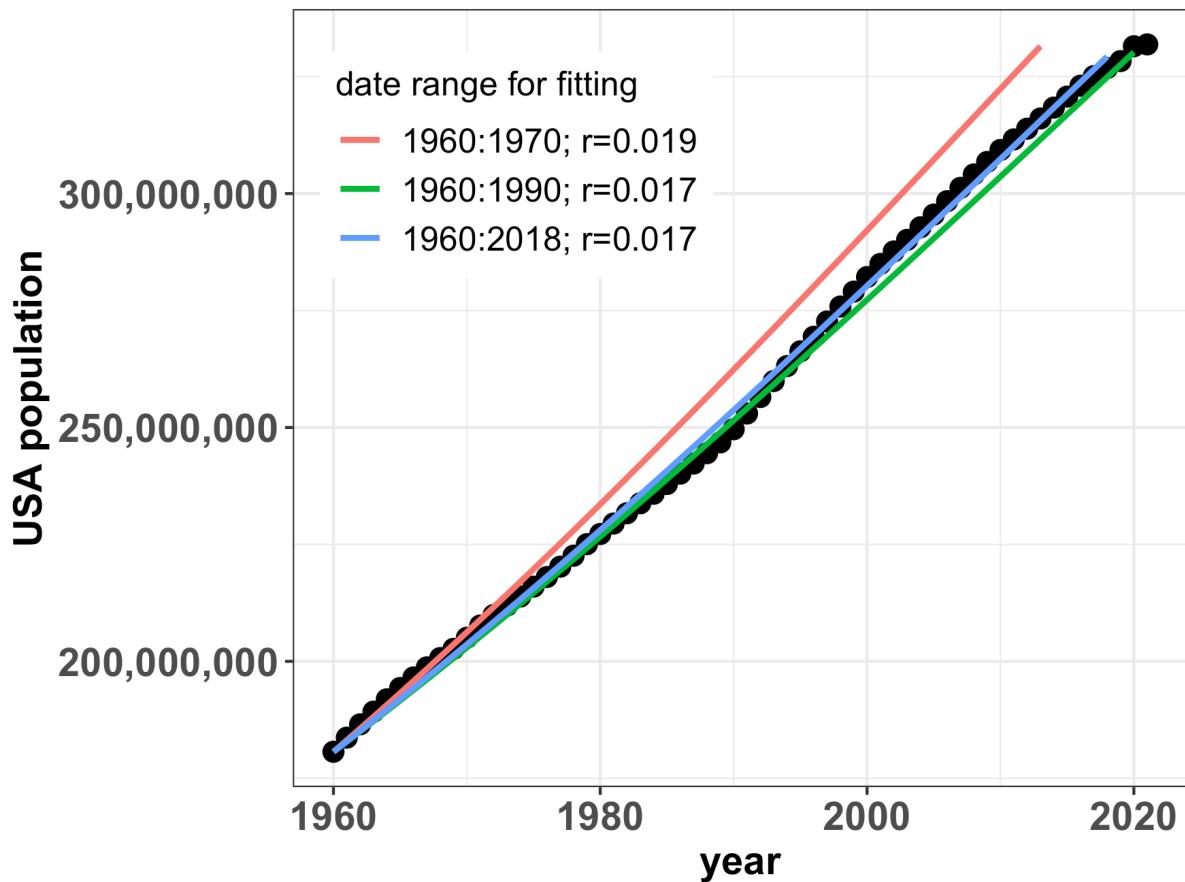
We can estimate growth rates by ‘fitting’ a model to data



US growth rates slowed over the time period!

Model fits to data from earlier years **overestimate** current population growth rates

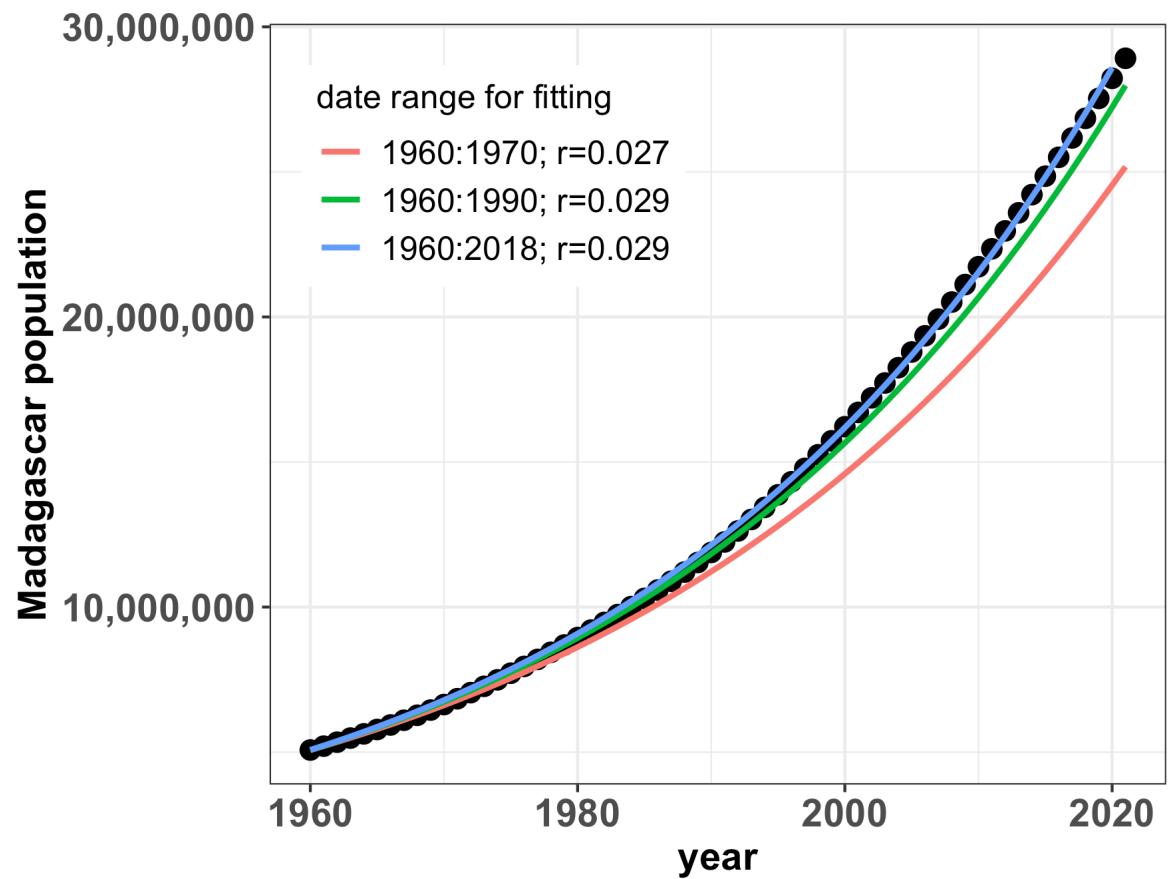
We can estimate growth rates by ‘fitting’ a model to data



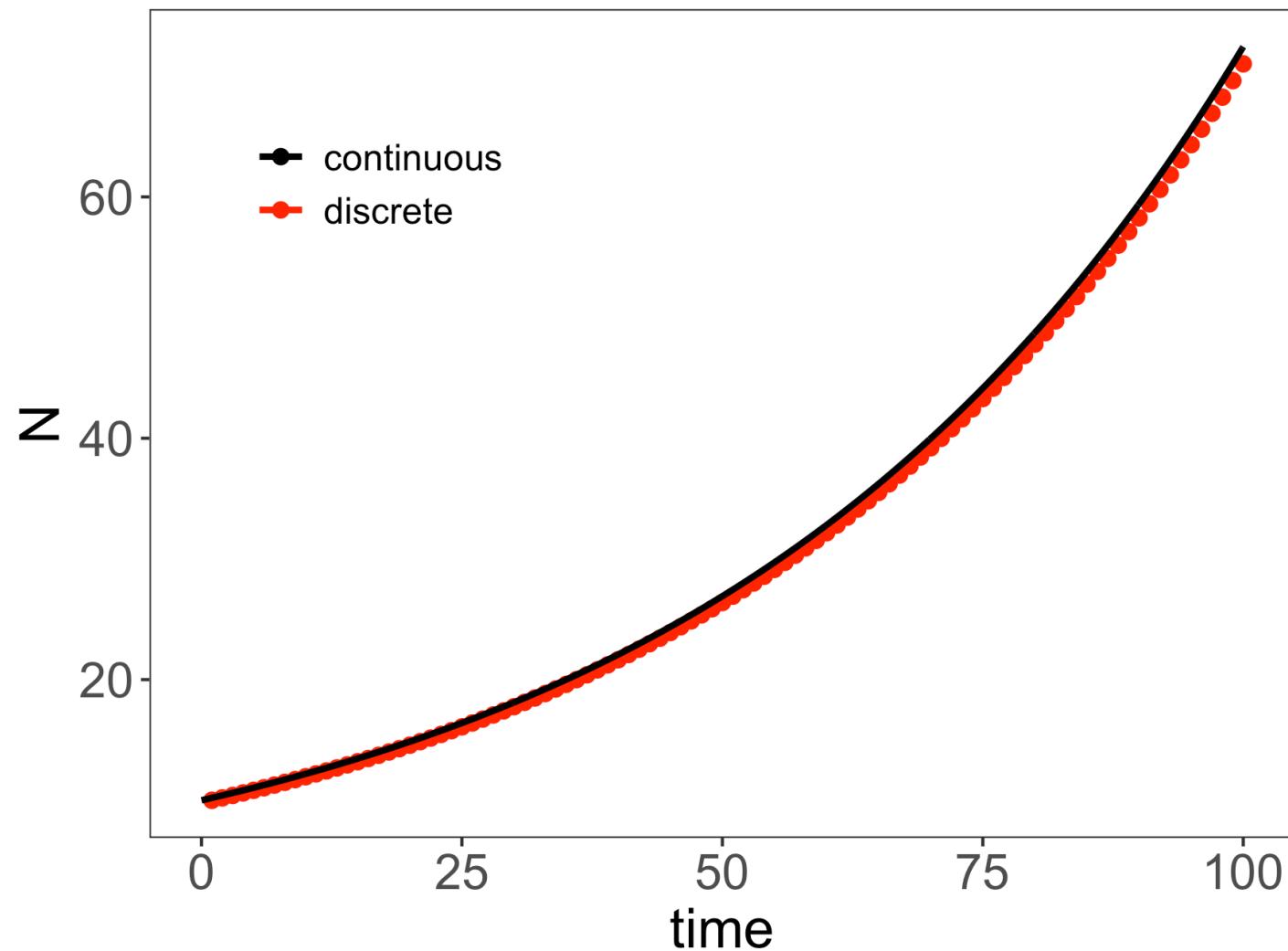
We can estimate growth rates by ‘fitting’ a model to data

Madagascar growth rates
accelerated over the time
period!

Model fits to data from earlier
years **underestimate** current
population growth rates



Both geometric and exponential growth are **unchecked**.



Malthus proposed some limits to population growth

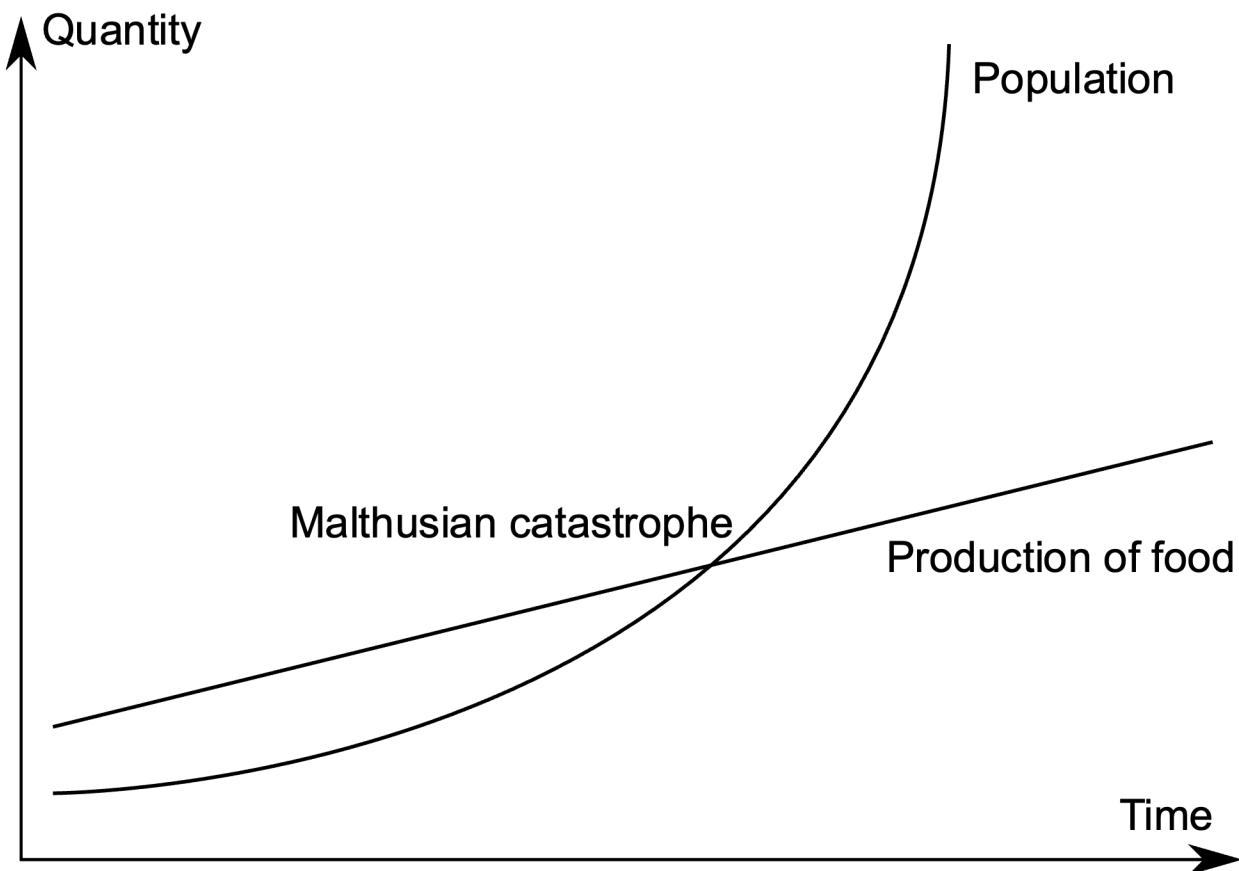
[. . .] the power of population is indefinitely greater than the power in the earth to produce subsistence for man. Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio. A slight acquaintance with numbers will shew the immensity of the first 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



- 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*

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



Logistic growth equation

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

↑ ↑

intrinsic growth rate **carrying capacity**

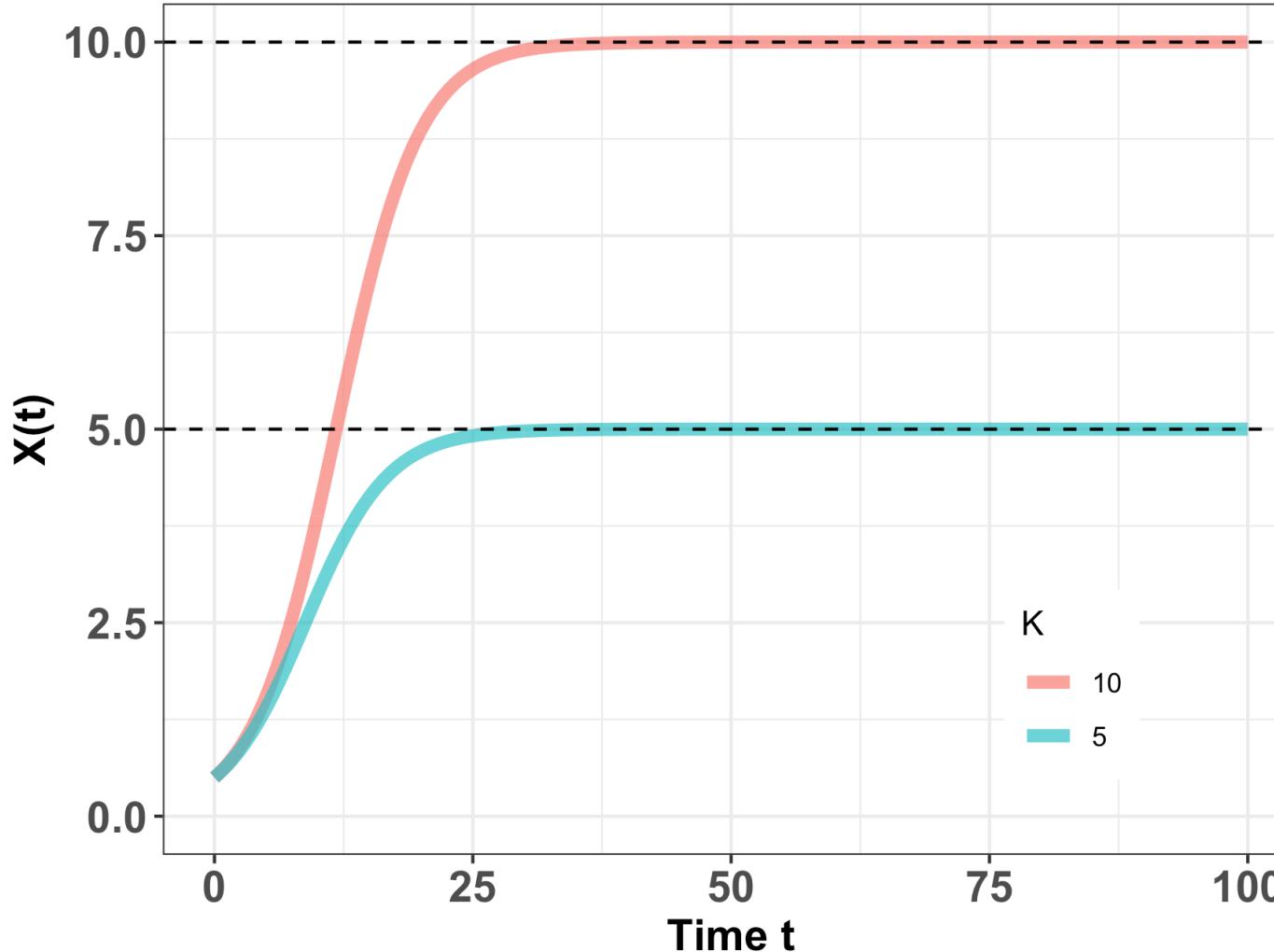
"We shall not insist on the hypothesis of geometric progression, given that it can hold only in very special circumstances; for example, when a fertile territory of almost unlimited size happens to be inhabited by people..."

- Pierre-Francois Verhulst (1838)

Population growth slows as abundance approaches **carrying capacity**.
Population growth is **density-dependent**.

Logistic growth equation

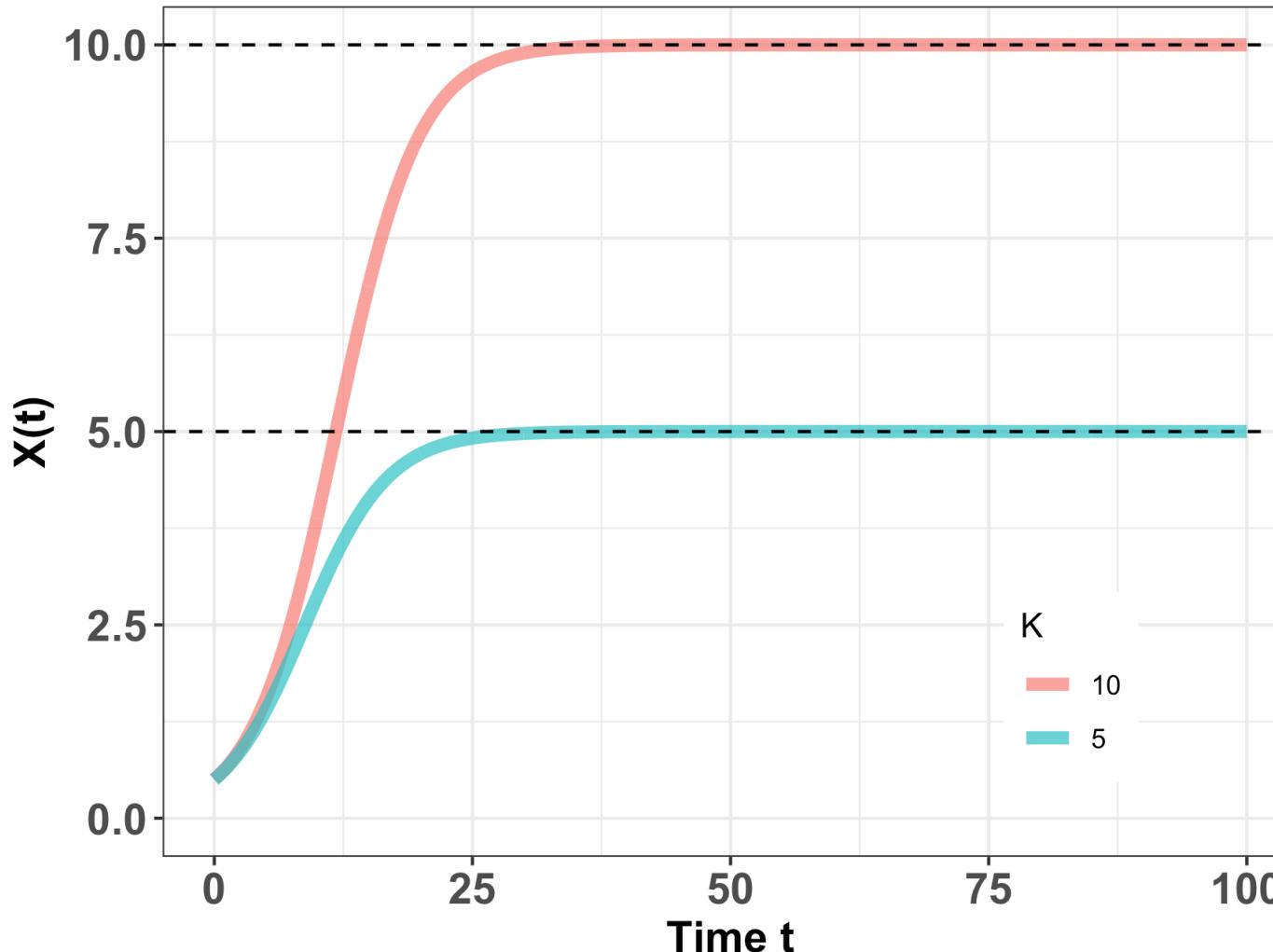
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$



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!

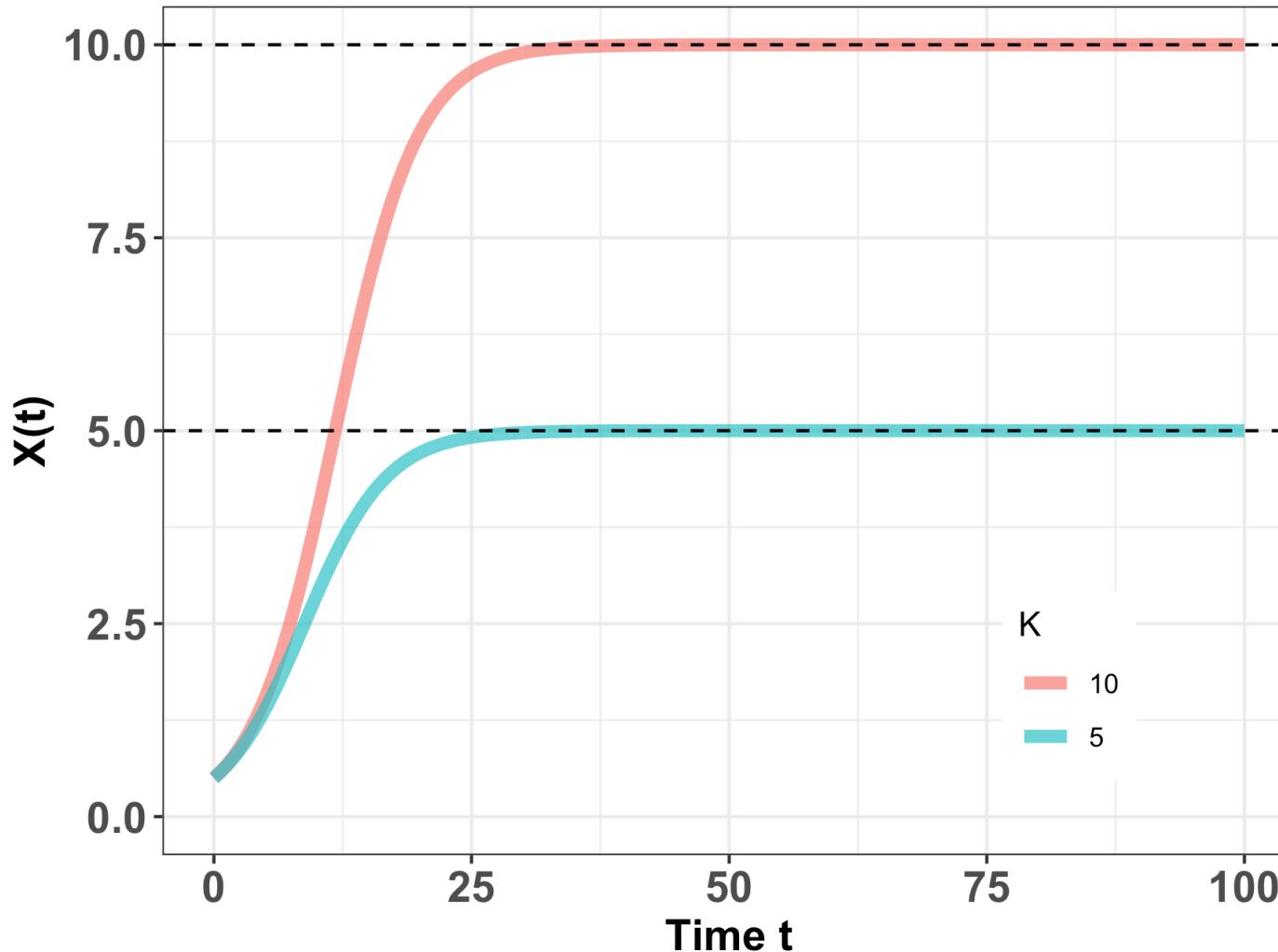
'r' vs. **'K'**-selected species

Logistic growth and equilibrium

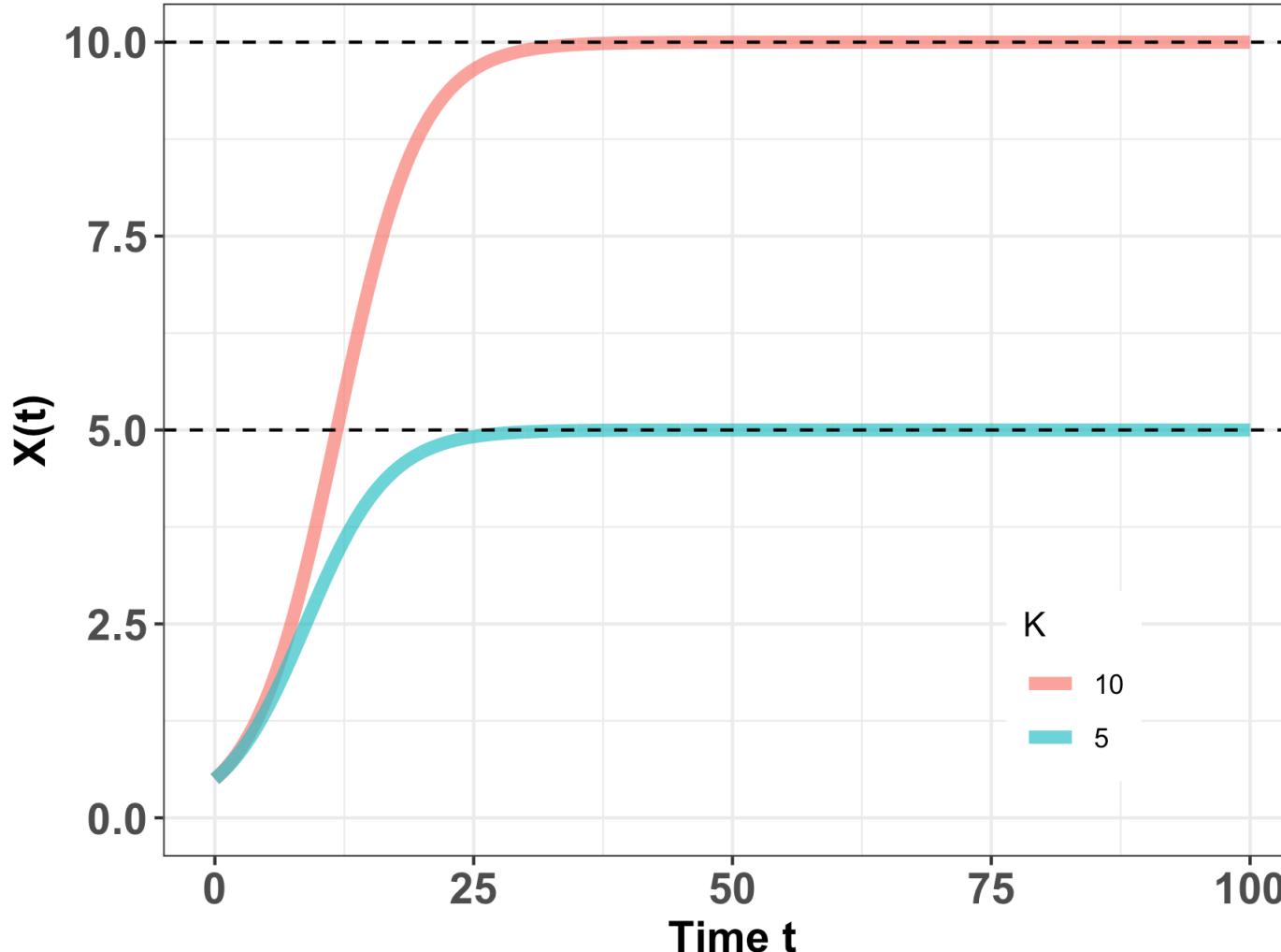
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

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

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



Logistic growth and equilibrium



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

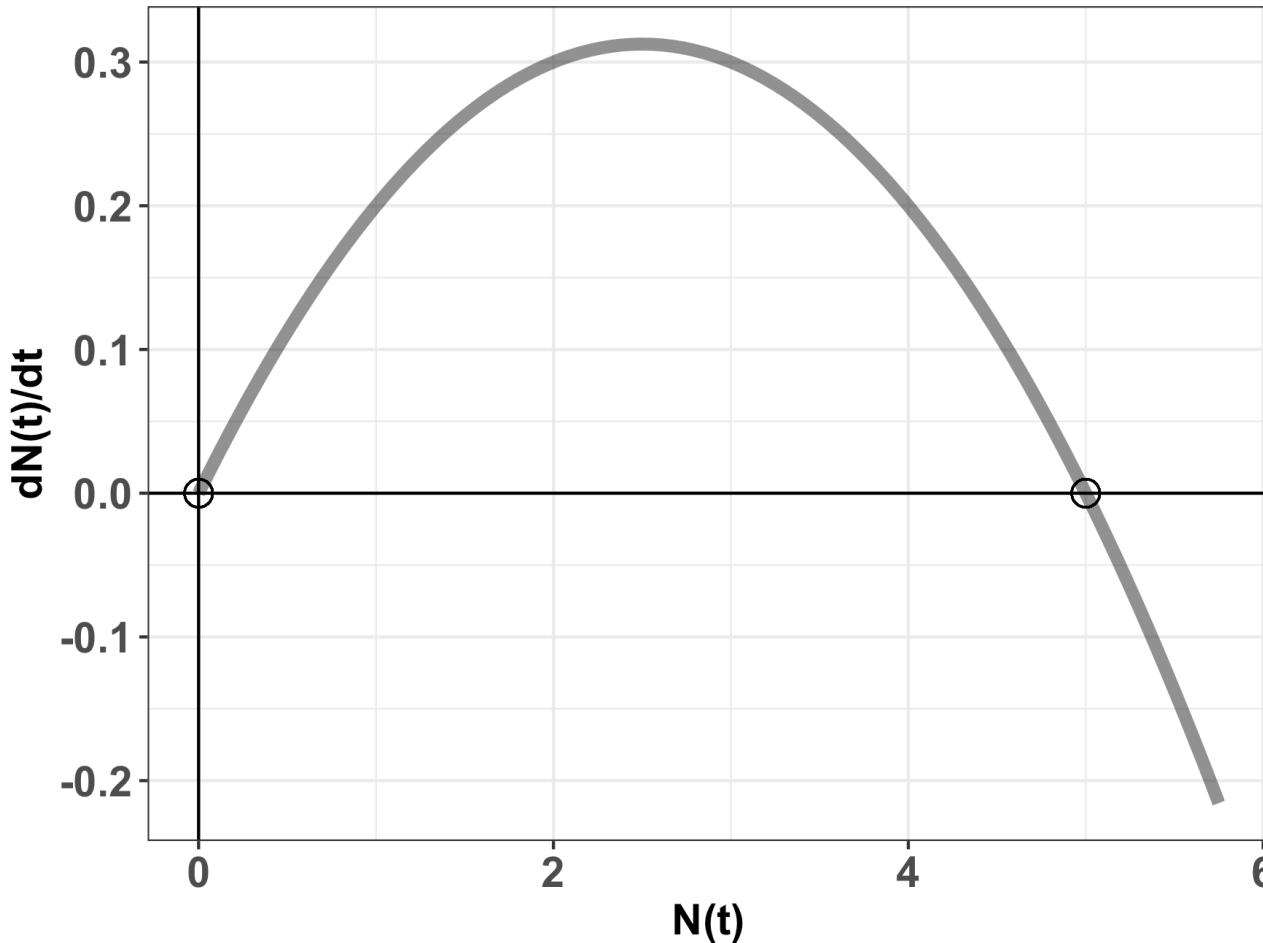
$$\frac{dN}{dt} = 0$$

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

$$N = K$$

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

Logistic growth and equilibrium



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

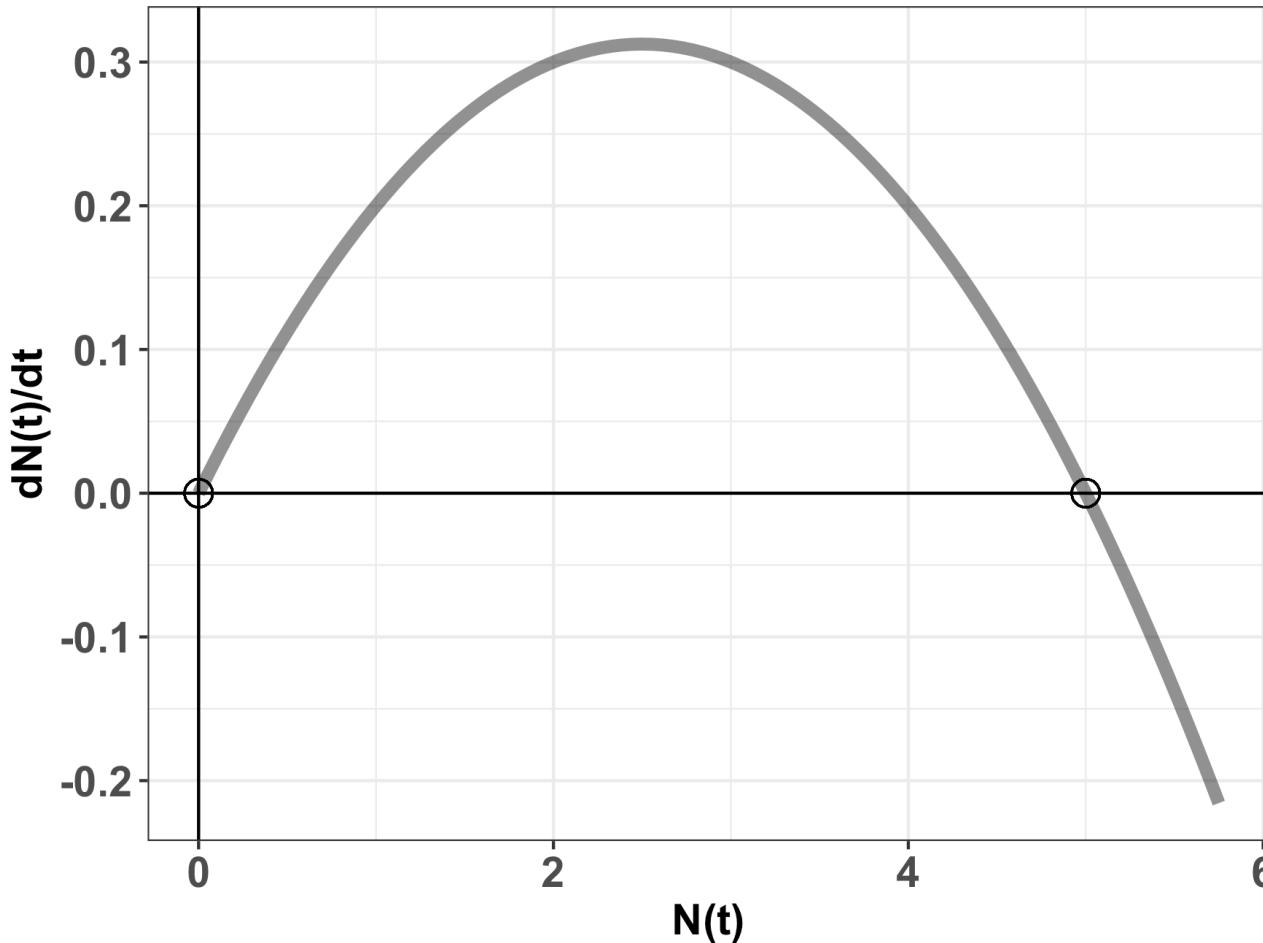
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$N = K$ or
 $N = 0$

logistic
growth
equilibria

Logistic growth and equilibrium



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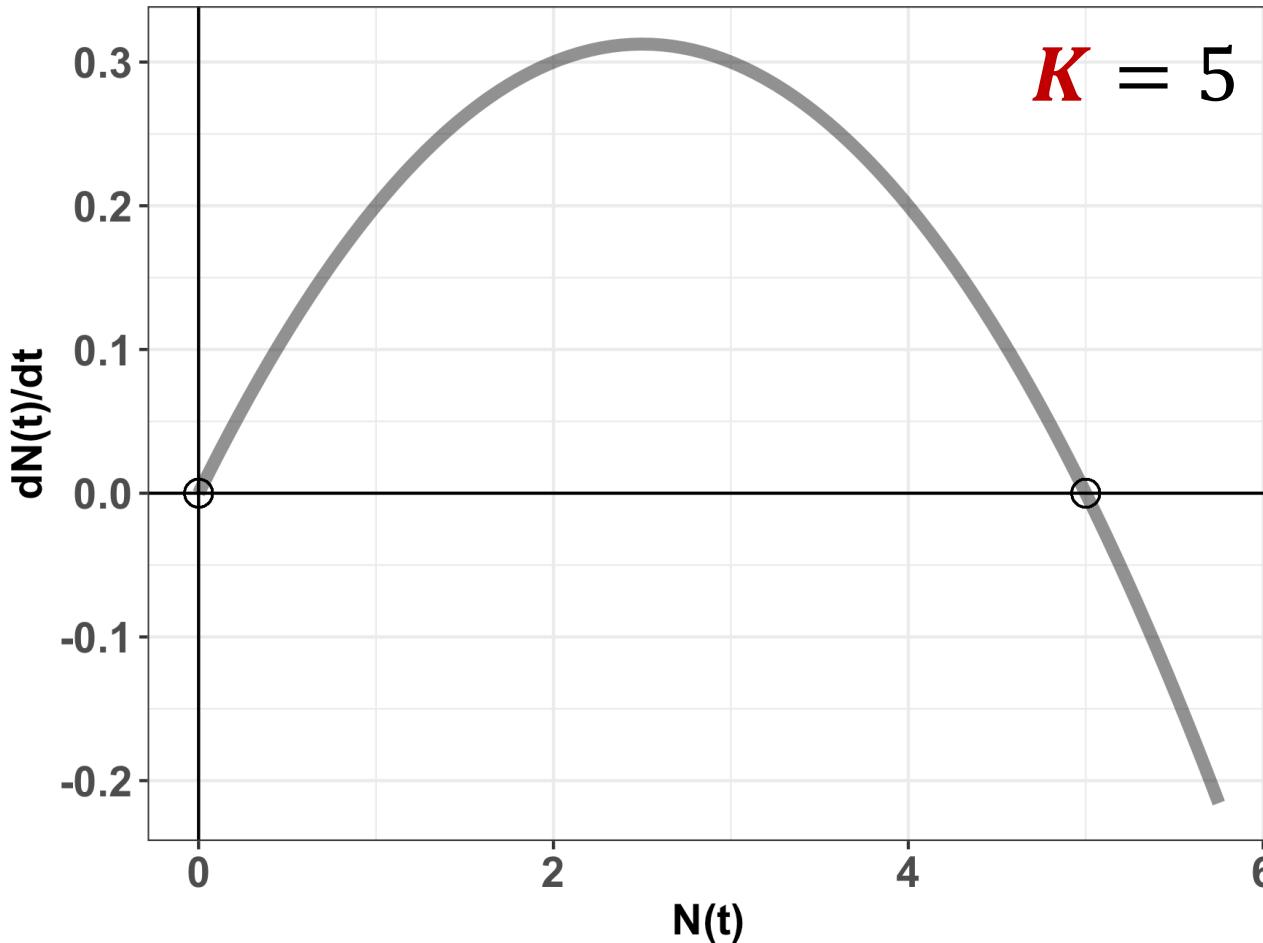
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logistic
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What is **K**?

Logistic growth and equilibrium



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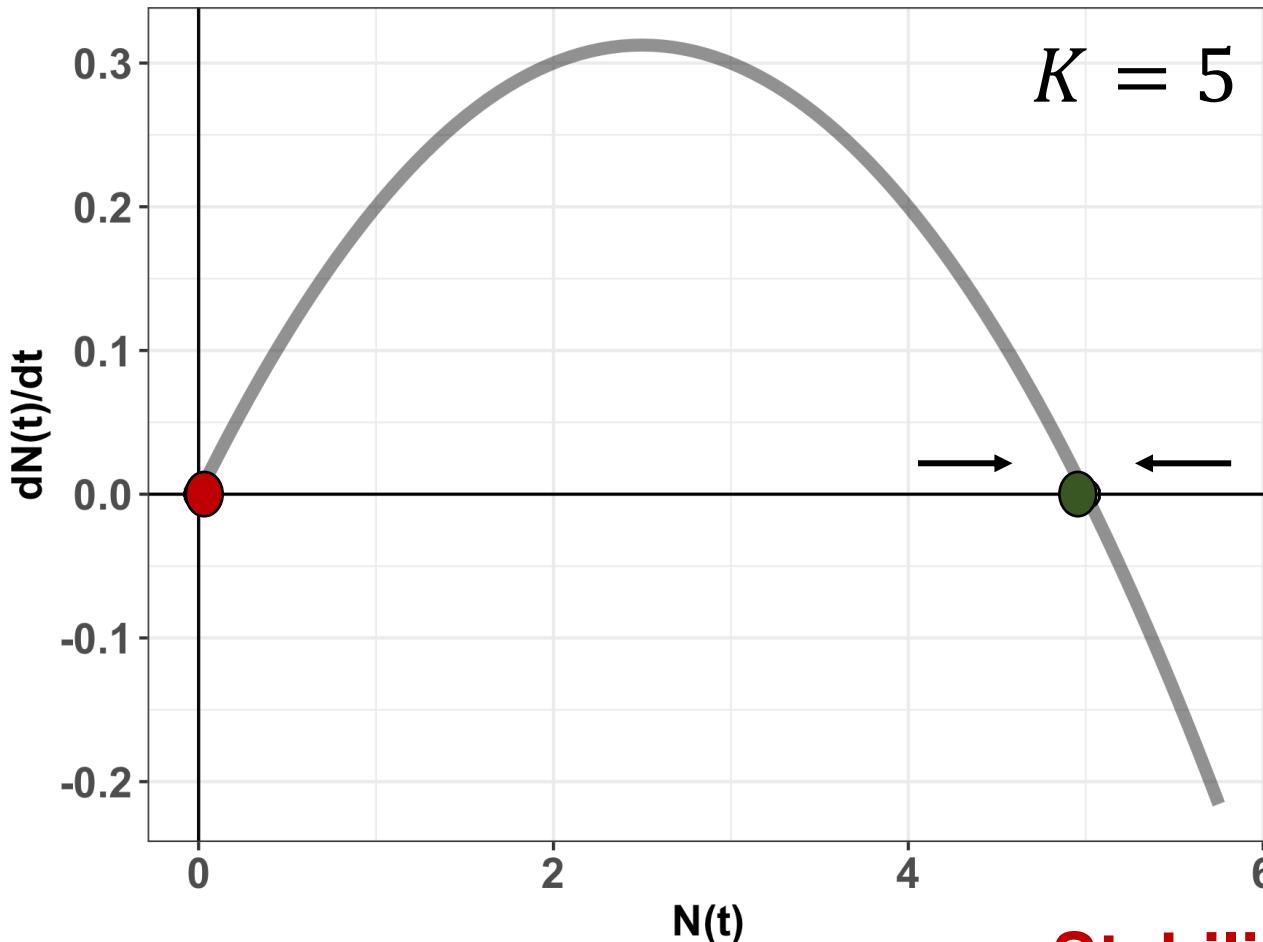
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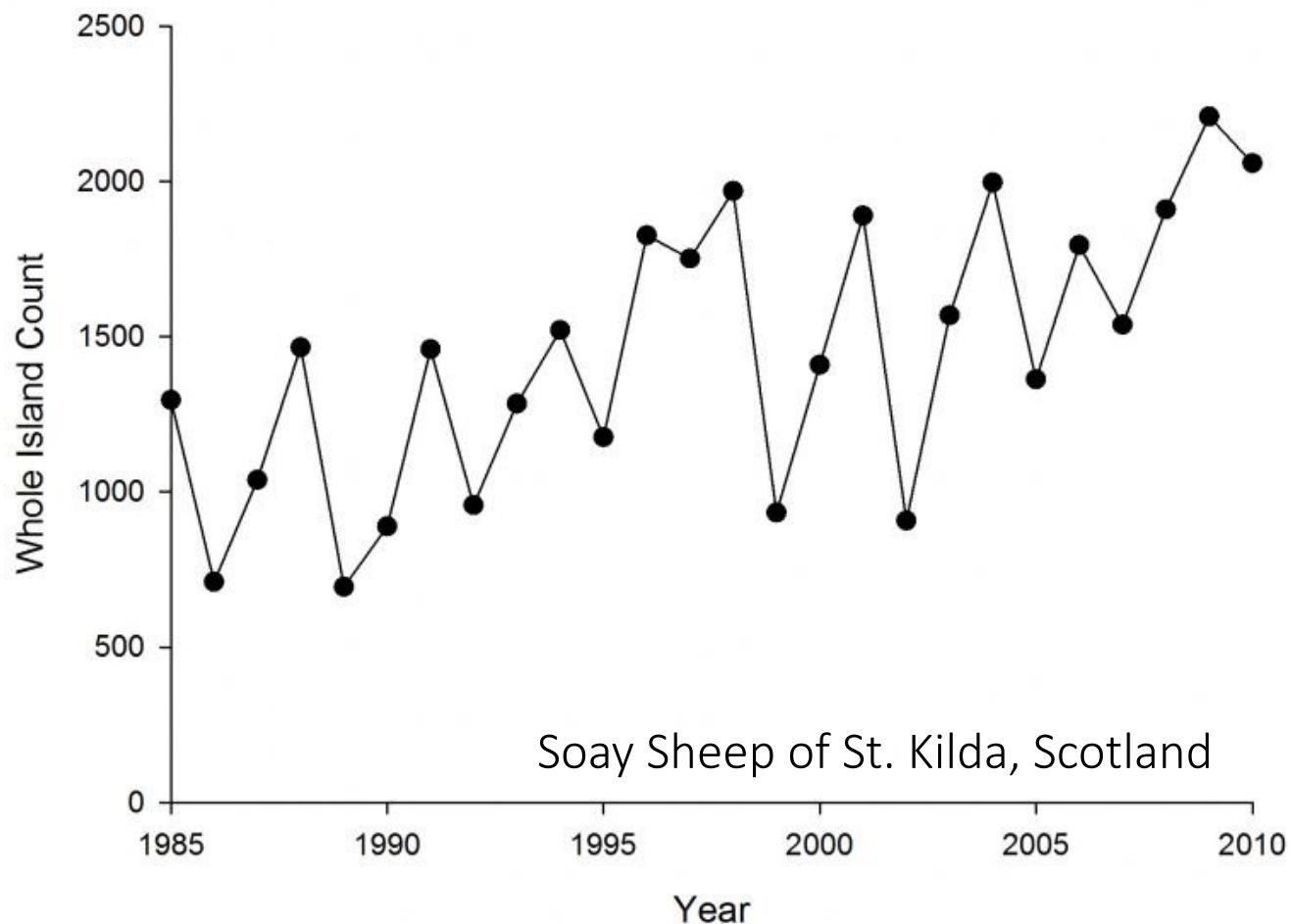
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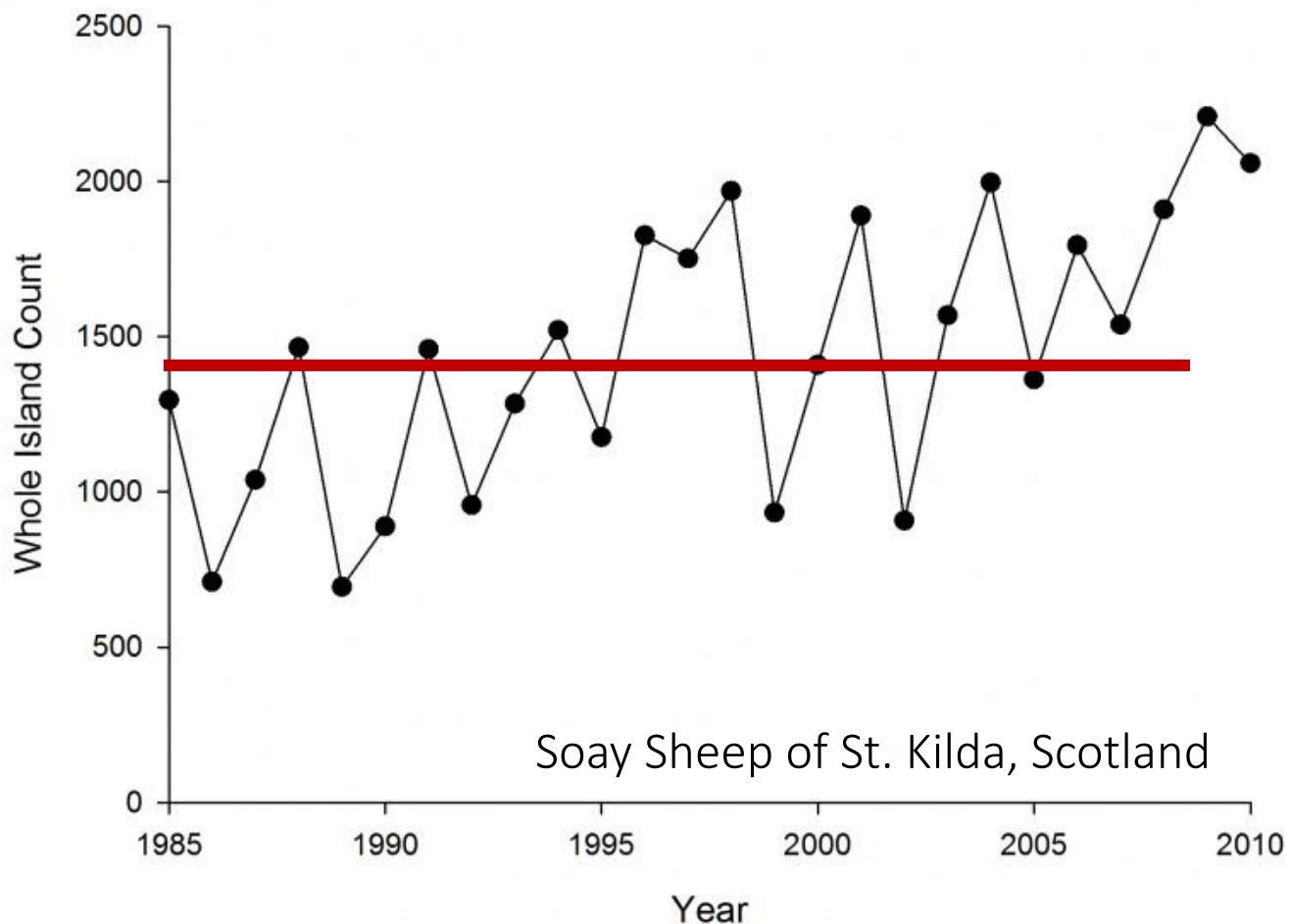
logistic
growth
equilibria

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

Many populations will fluctuate above or below carrying capacity.



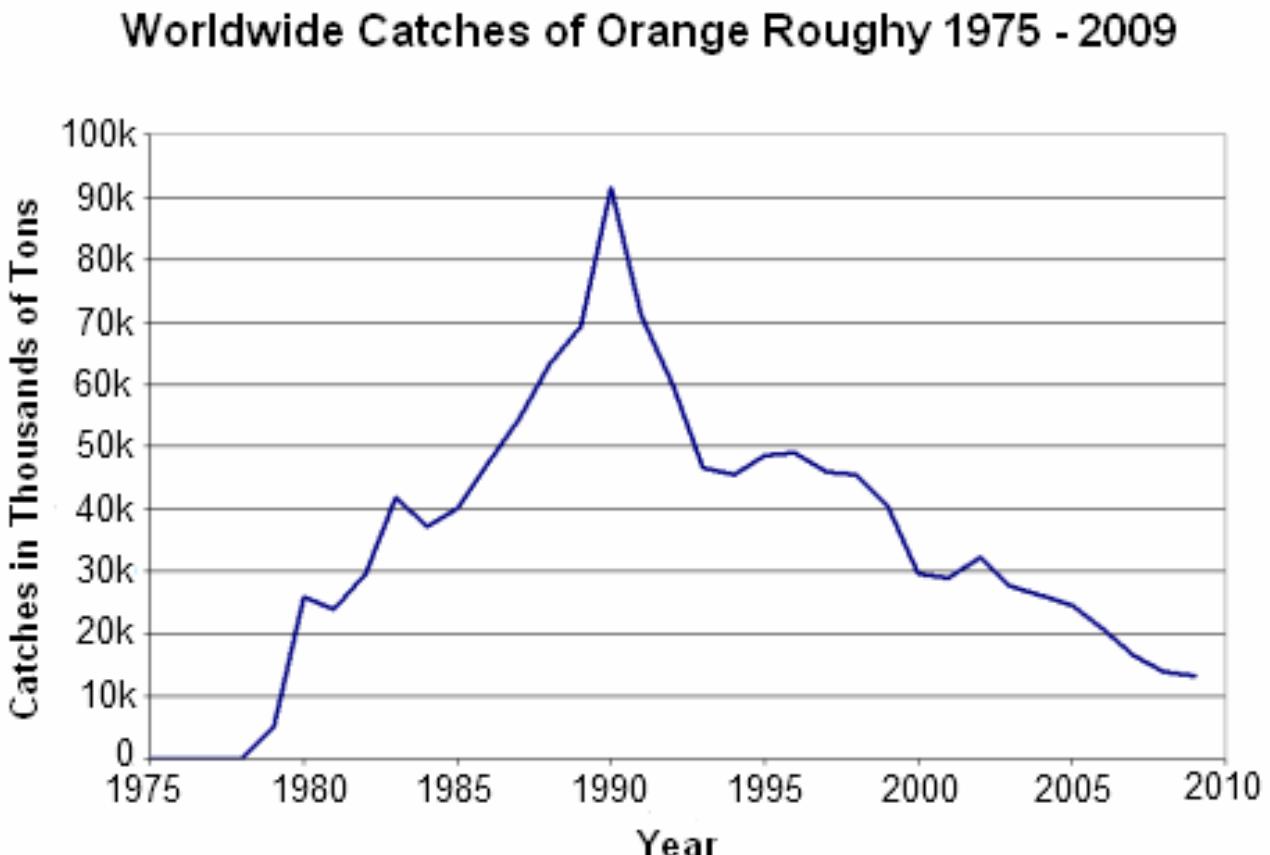
Many populations will fluctuate above or below carrying capacity.



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

In some cases, it is not possible to recover.

Many populations will fluctuate above or below carrying capacity.



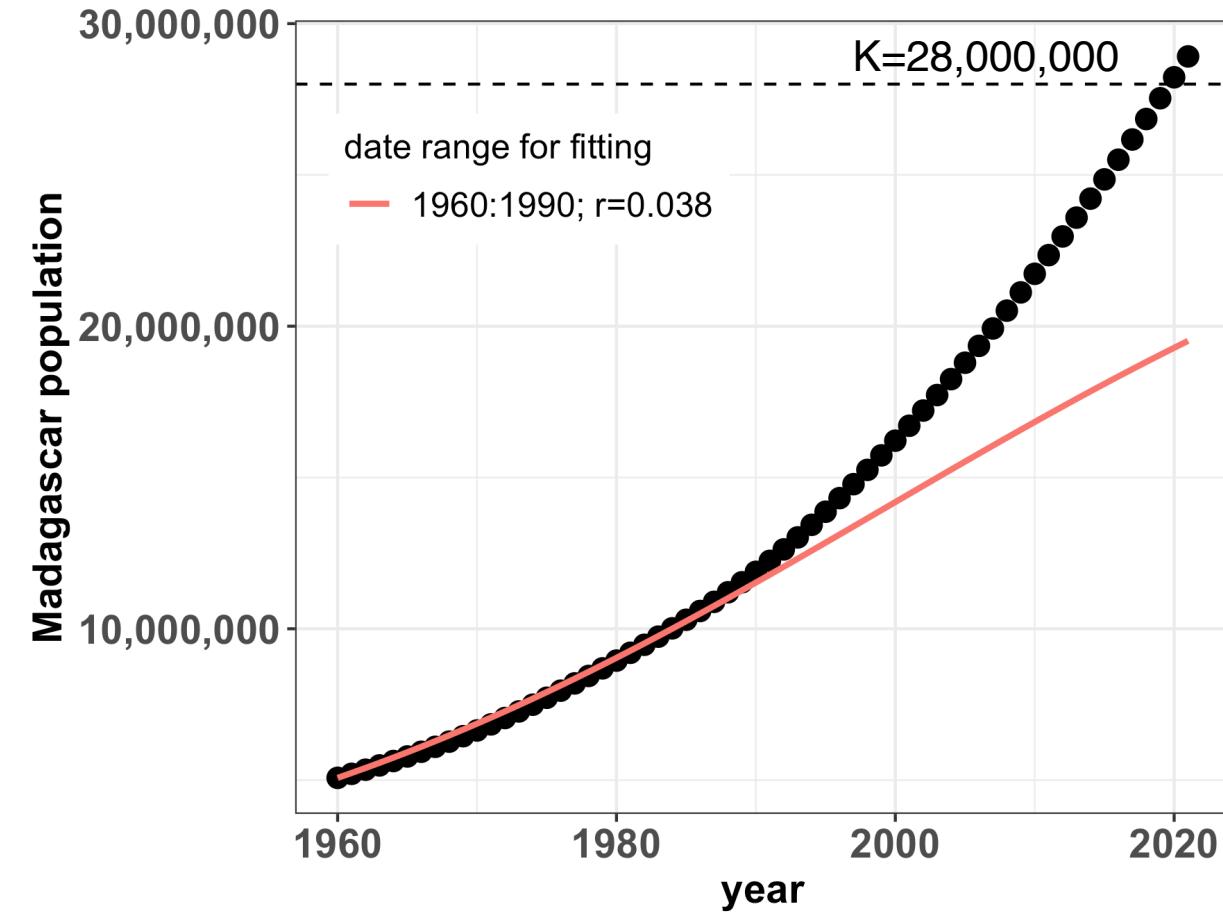
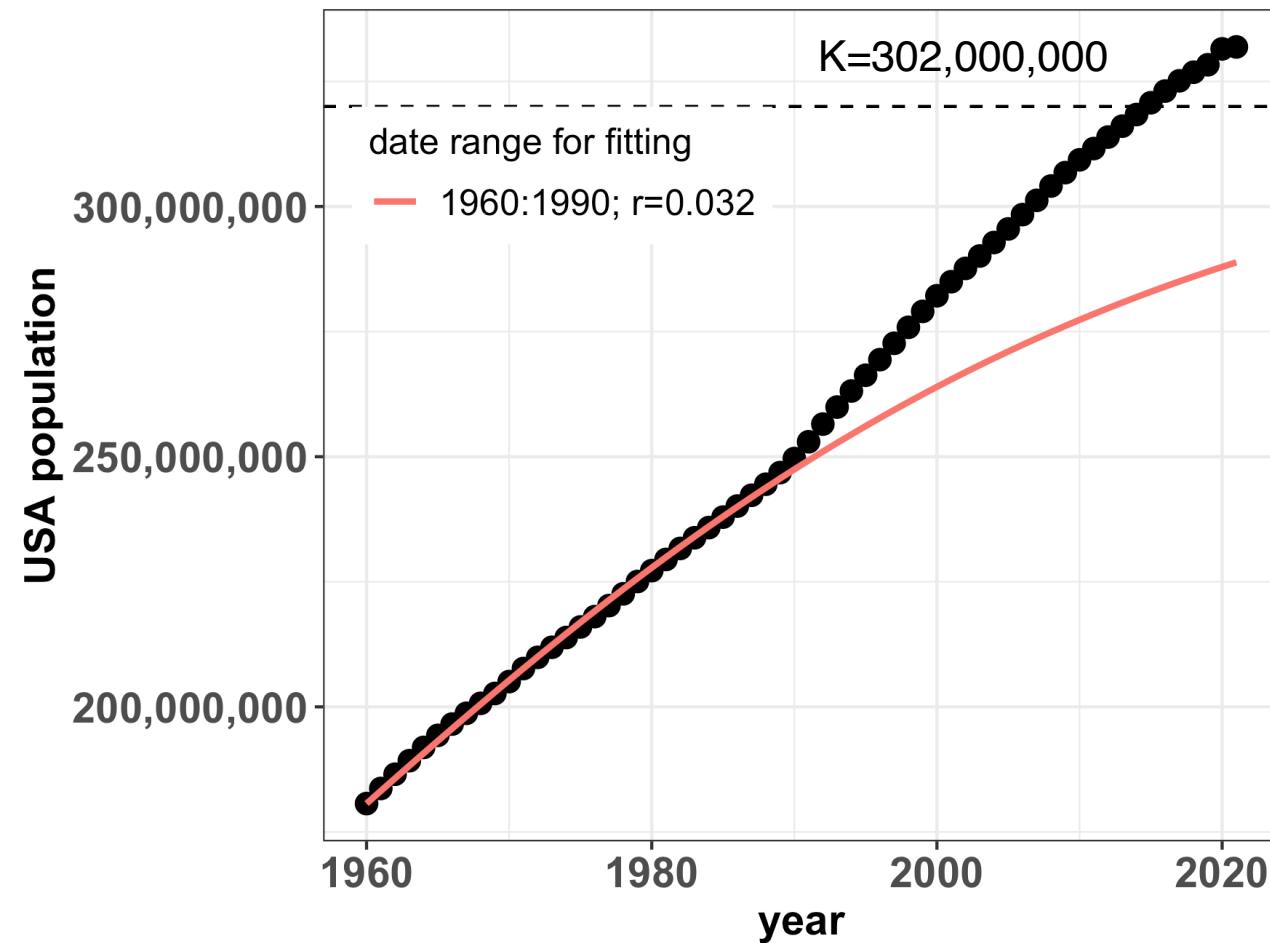
Source: FAO (Fisheries and Agriculture Organisation of the United Nations) Fisheries and Aquaculture Information and Statistics Service. © L. Baumont



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

In some cases, it is not possible to recover.

Logistic growth still does not describe human populations well.

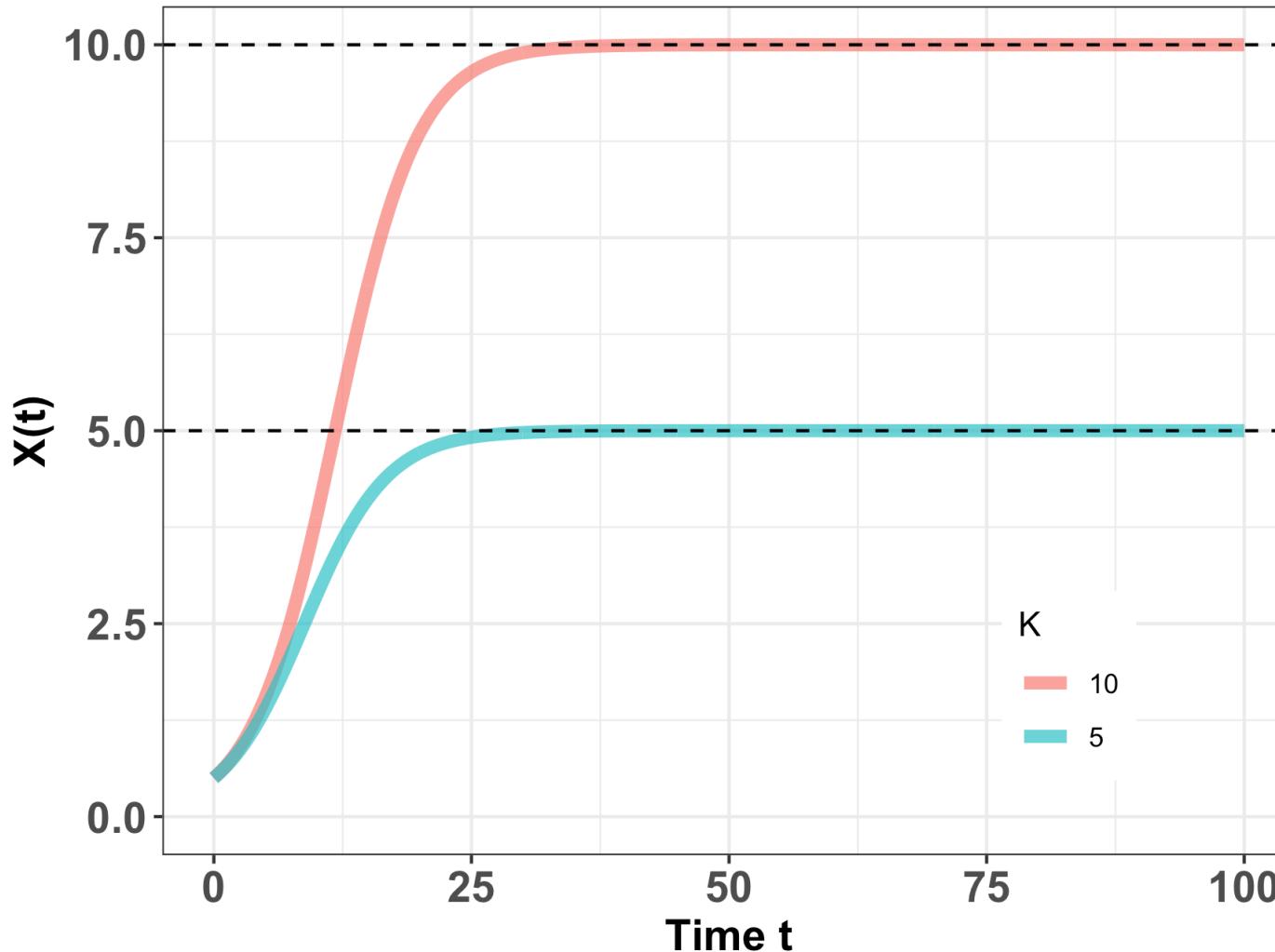


Logistic growth and equilibrium

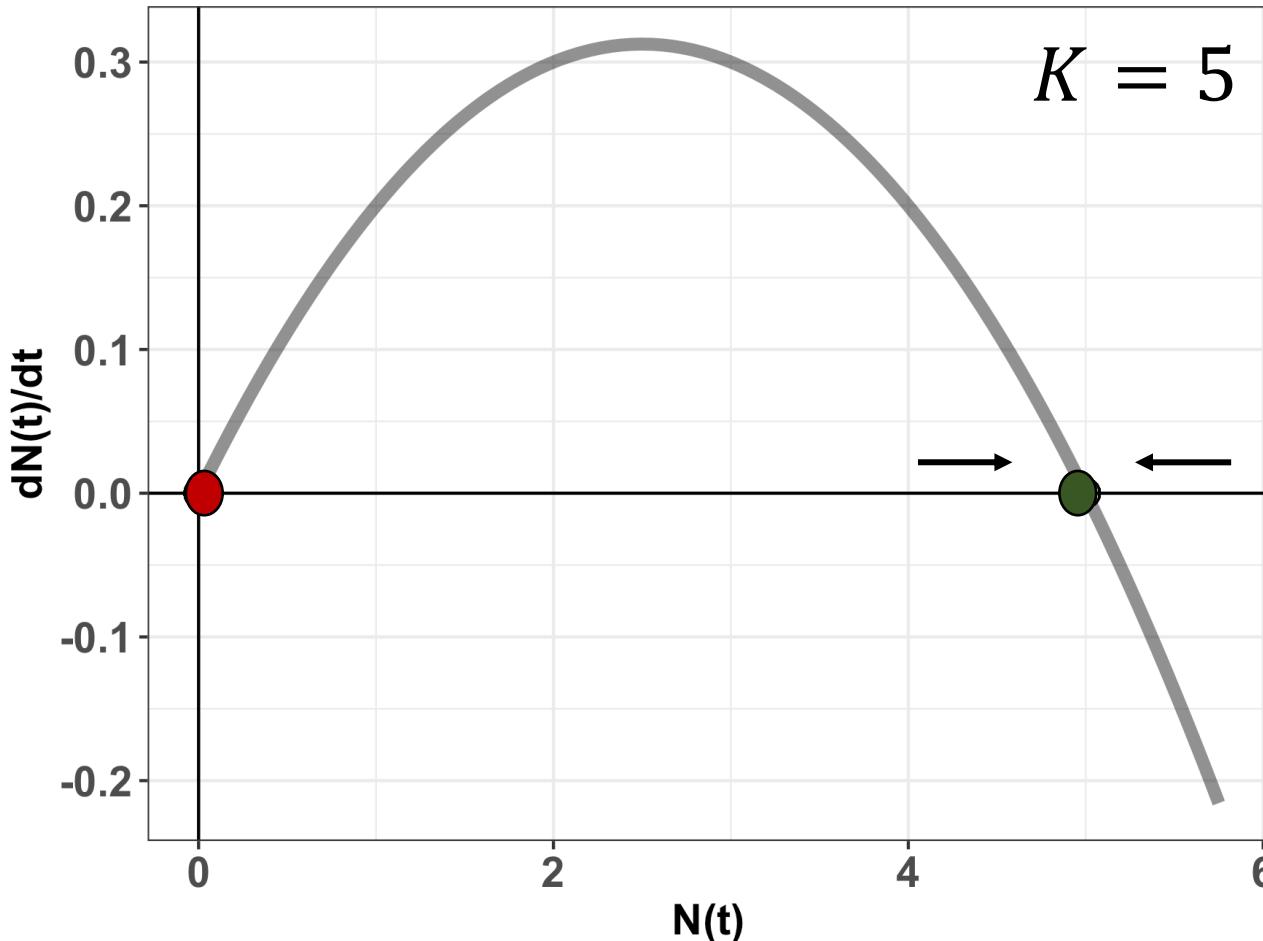
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

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



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**.

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 .

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.

$$\text{change in population size with time} \longrightarrow \frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - H$$

Diagram illustrating the logistic growth equation with annotations:

- change in population size with time** → $\frac{dN}{dt}$ (intrinsic growth rate)
- population size** → N (density-dependence)
- carrying capacity** → K (density-dependence)
- harvesting rate** → H (density-dependence)

Logistic growth and harvesting

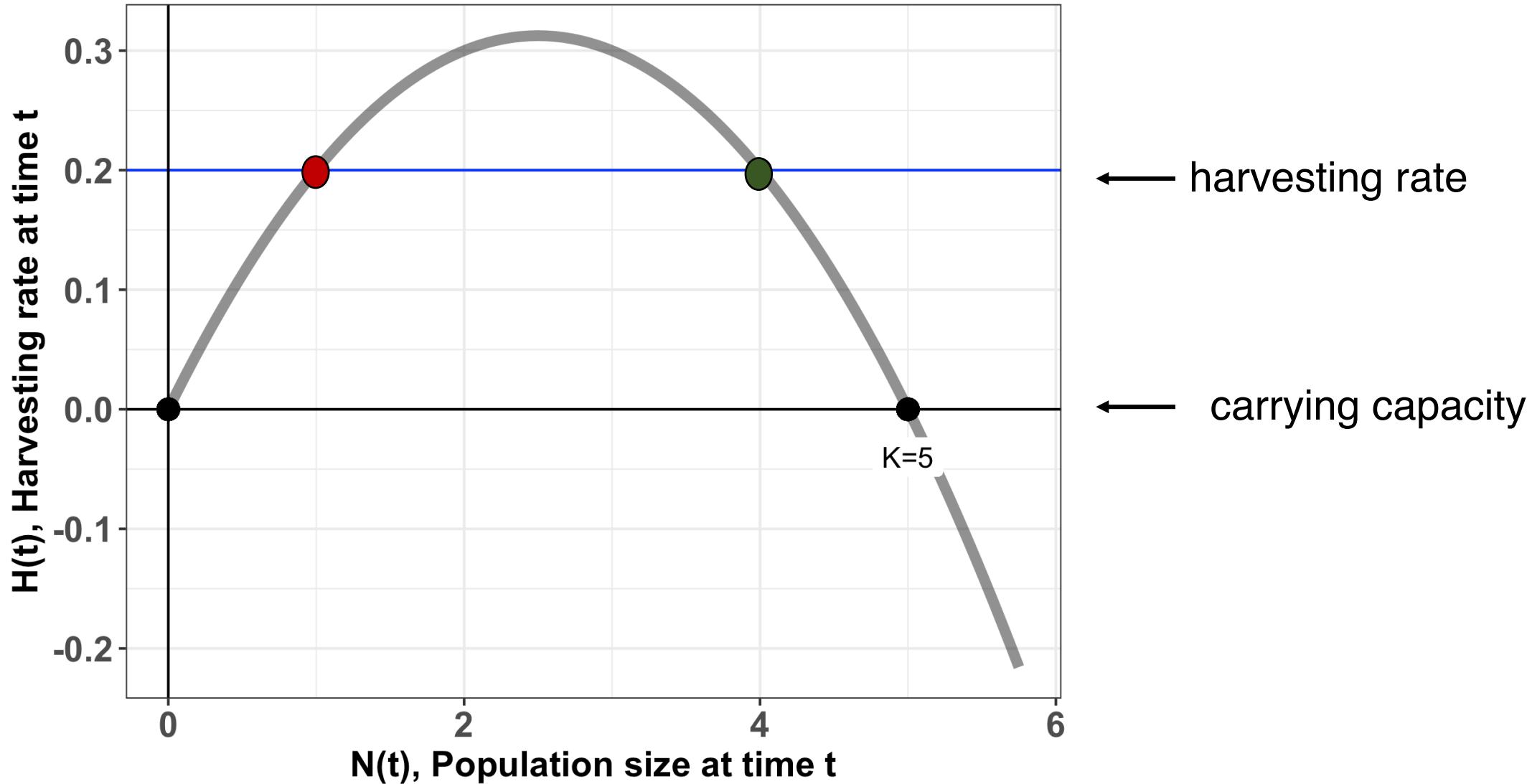
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - H$$

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

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

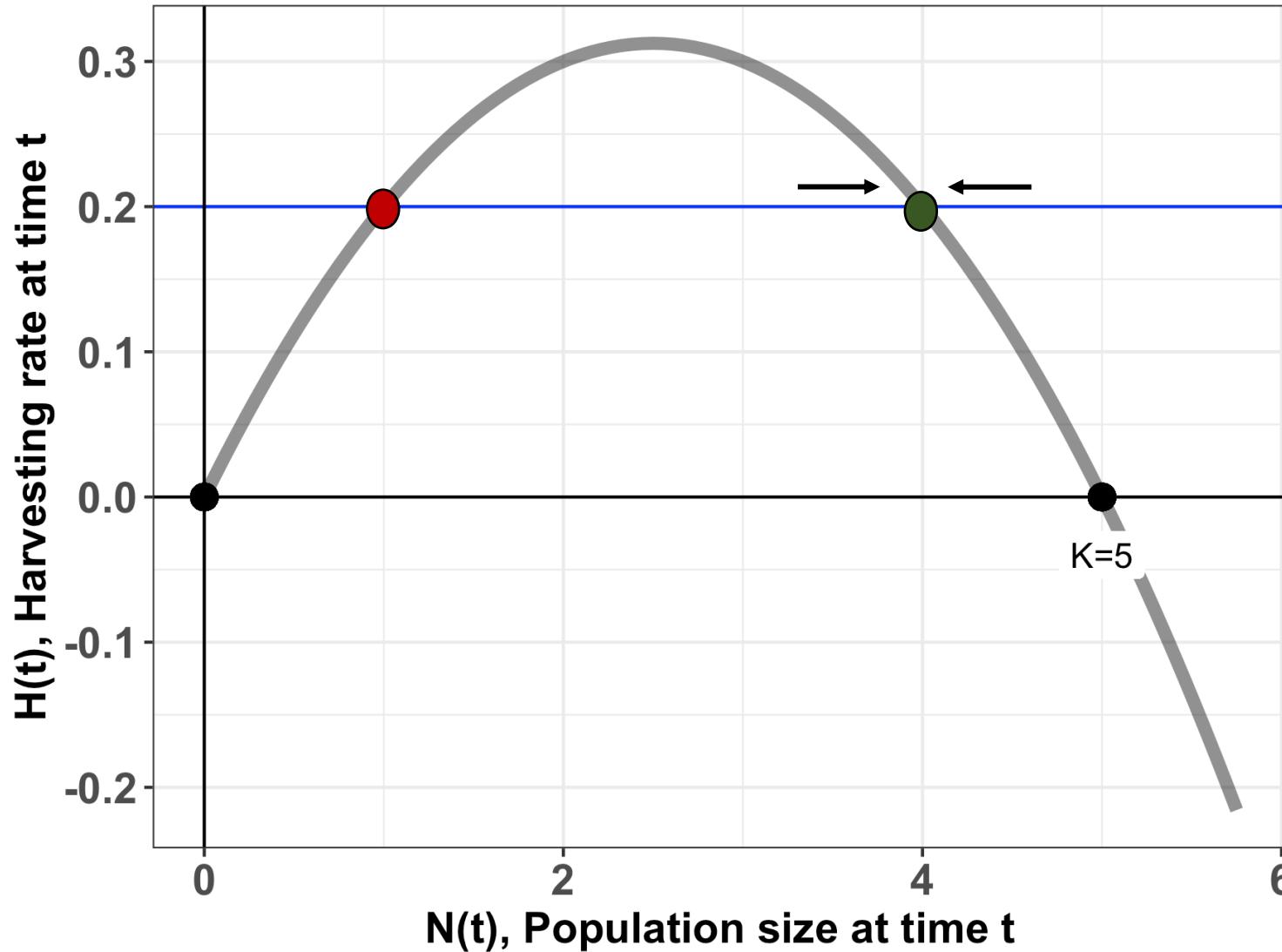
The stability of harvesting depends on population size.

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



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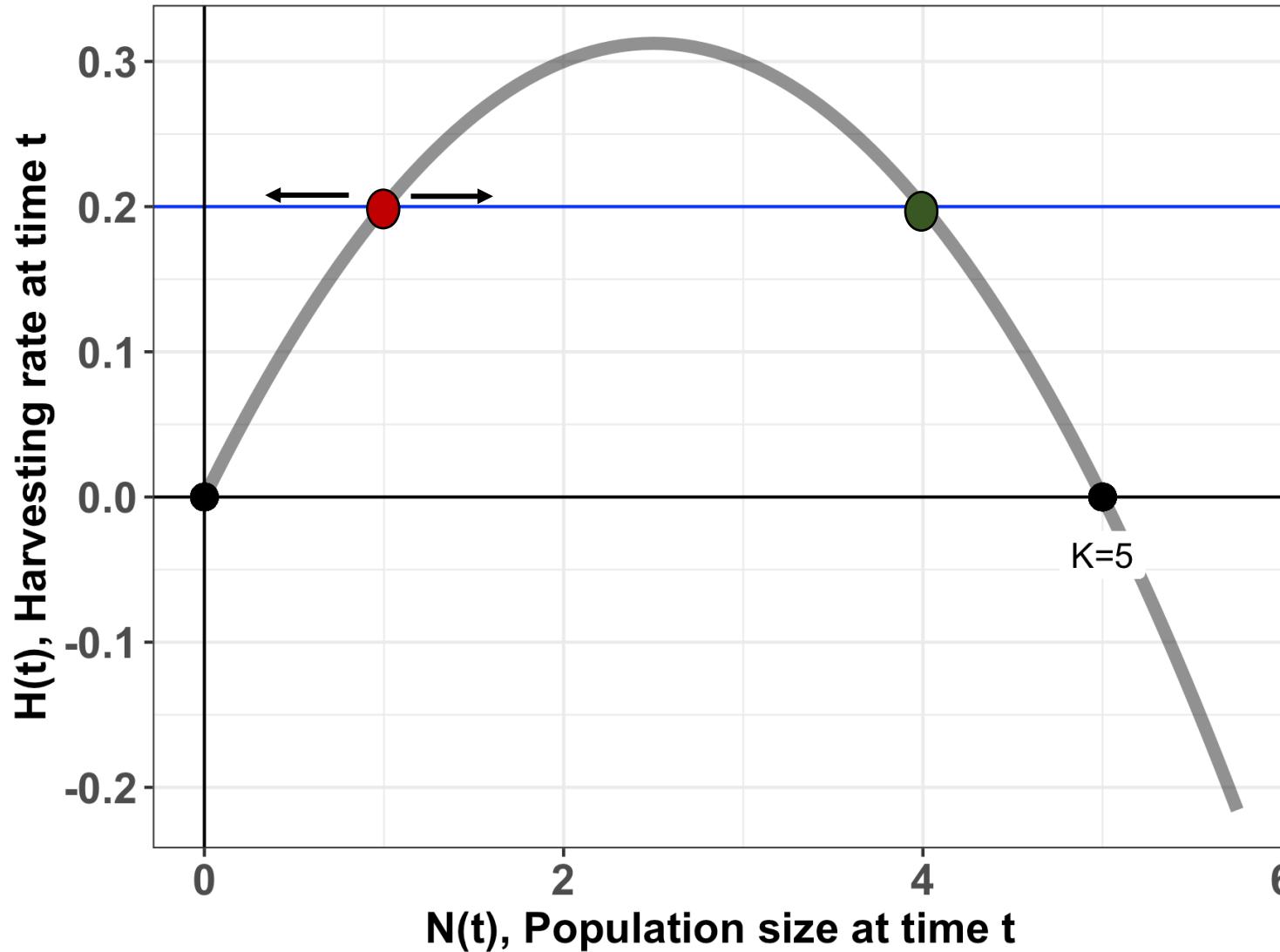


stable equilibrium
For a population of $N=4$,
a harvest rate of 0.2
(animals/timestep)
results in a stable
equilibrium (**sustainable
harvest**).

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

The stability of harvesting depends on population size.

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



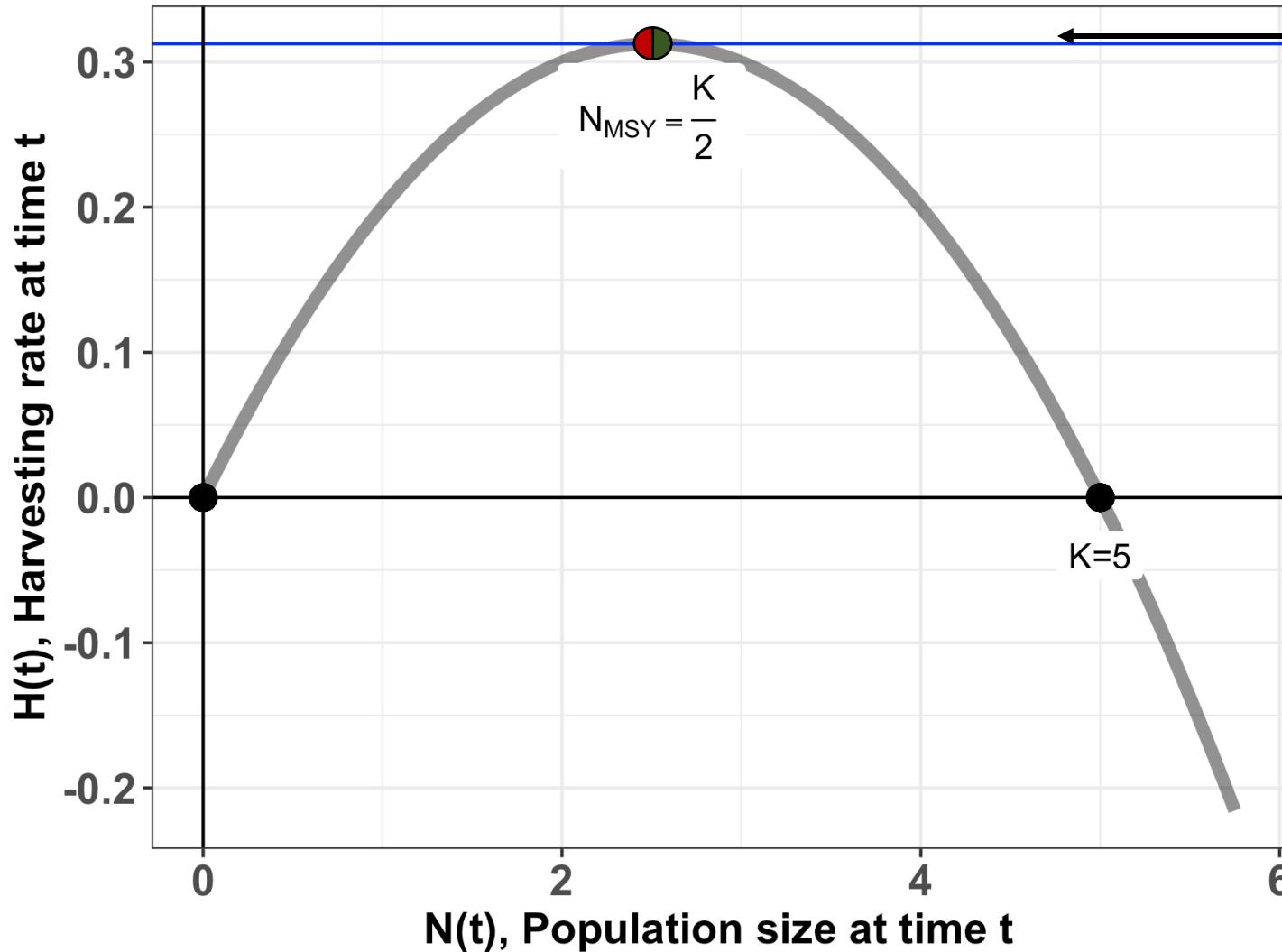
unstable equilibrium

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)

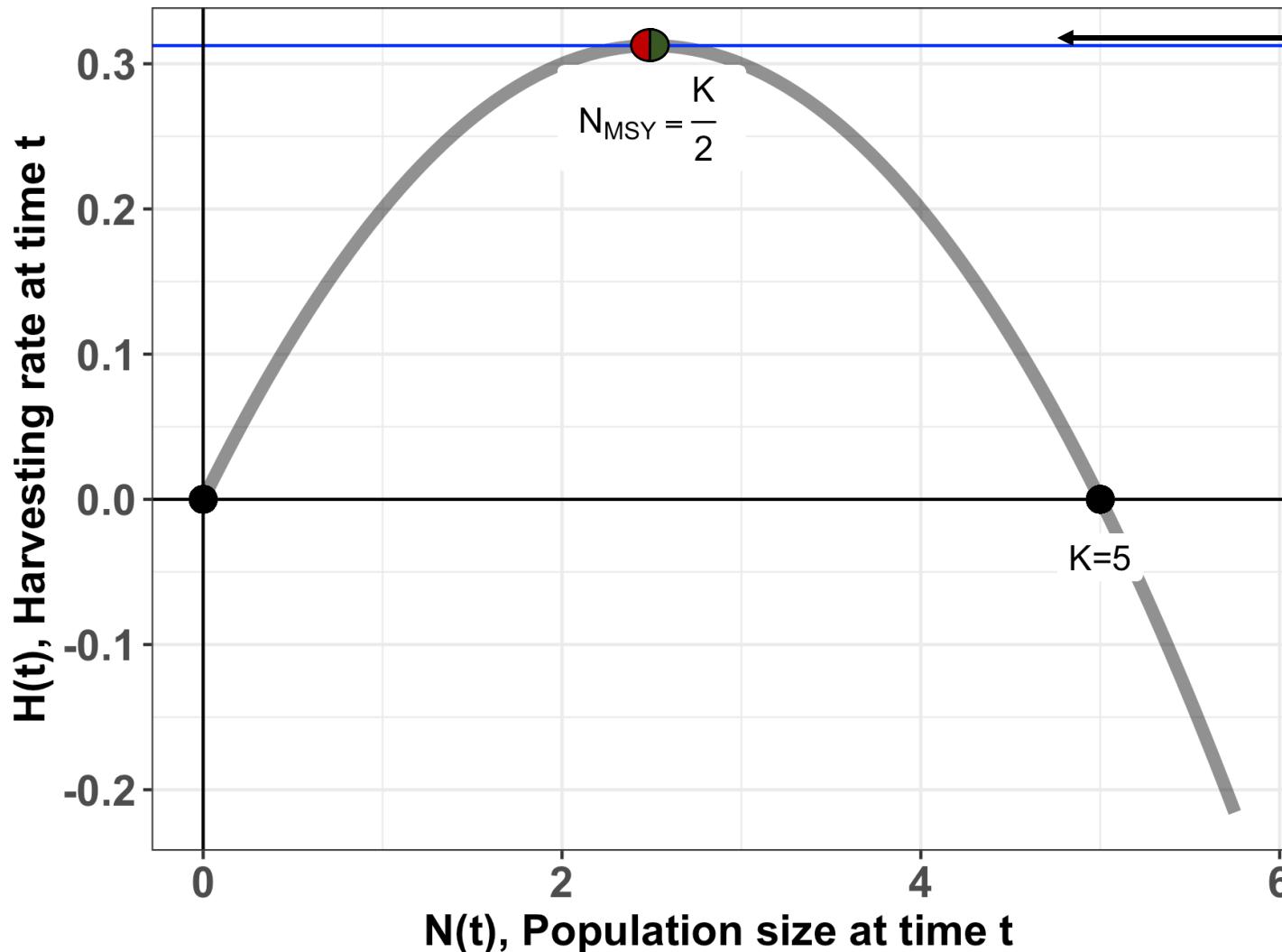
$$H = rN \left(1 - \frac{N}{K}\right)$$



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

Maximum sustainable yield (MSY)

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

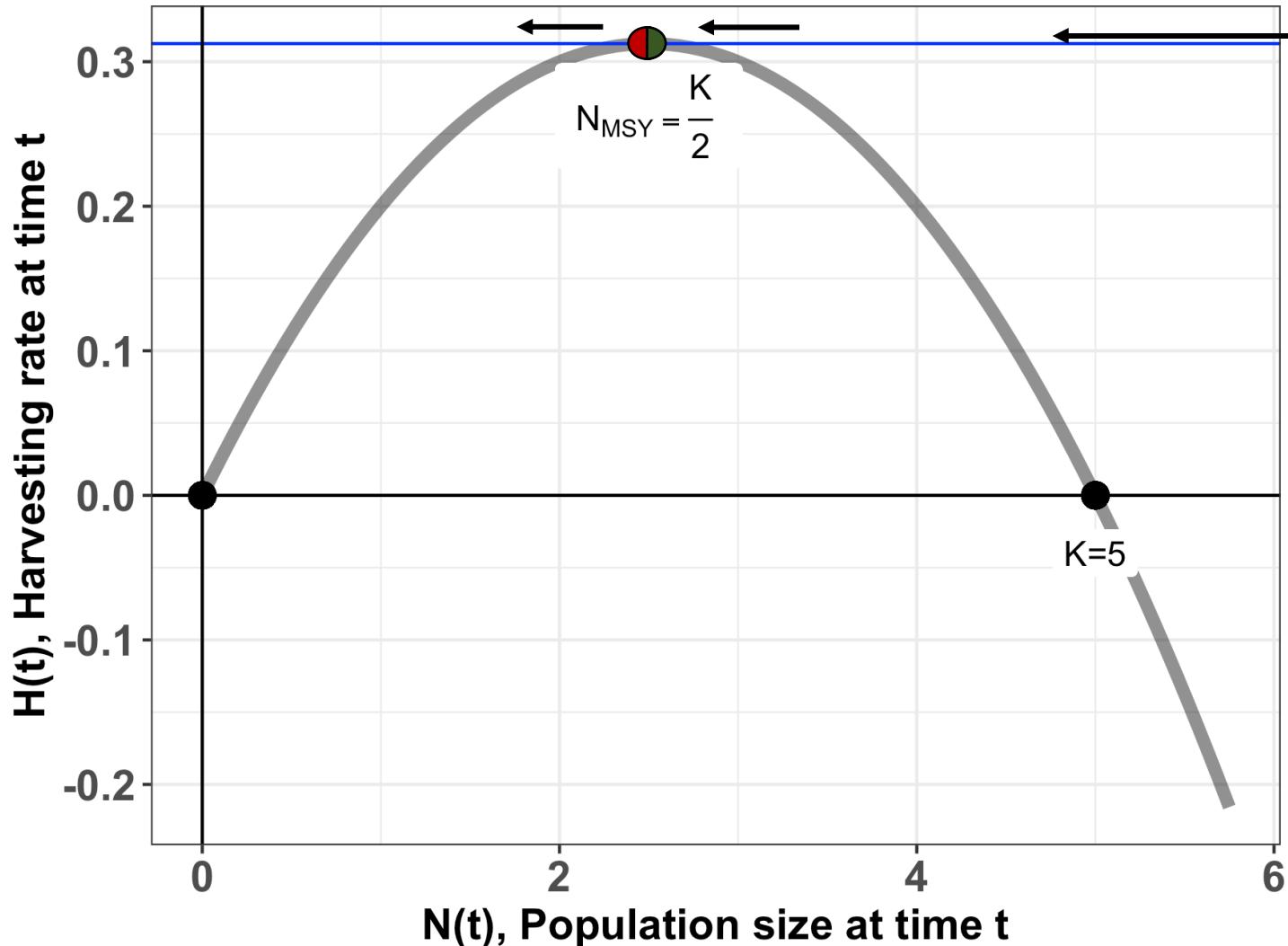
Theoretically, harvest could be maximized here as well:

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

take the derivative with respect to N

Maximum sustainable yield (MSY)

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



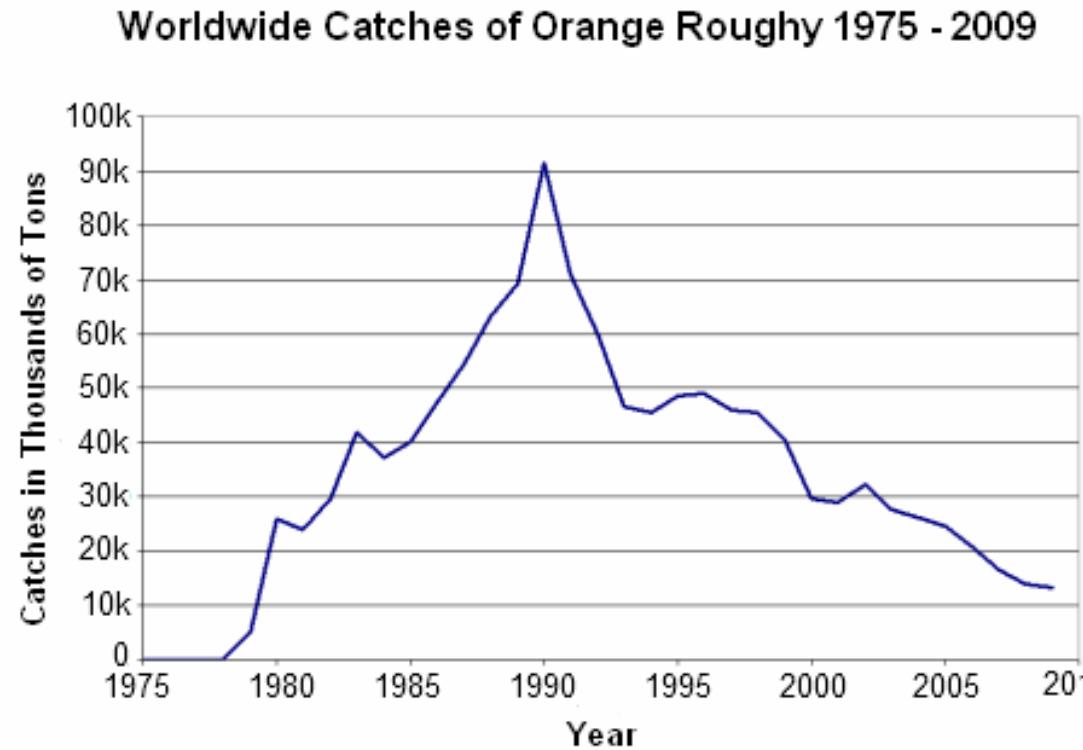
$$\text{MSY: } H_{max} = \frac{rK}{4}$$

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



- 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**.

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

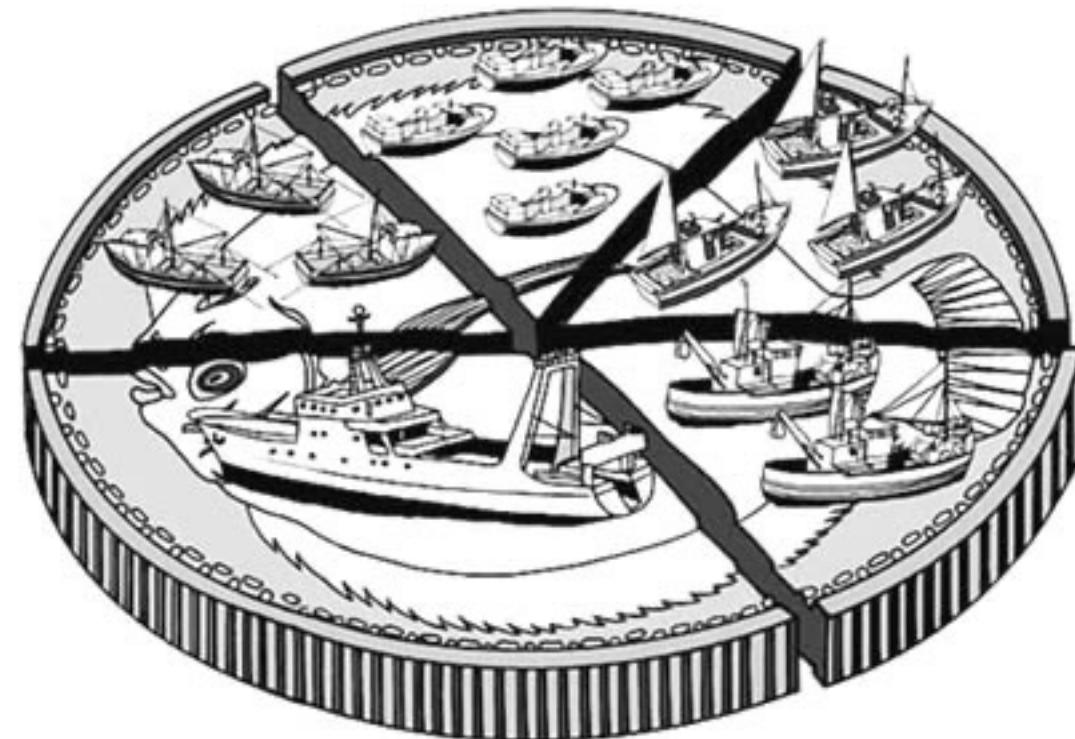
Overfishing: A Tragedy of the Commons



- Tragedy of the Commons: A situation in which individual users, who have open access to a common pool resource, cause depletion of the resource through their uncoordinated actions.
 - 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

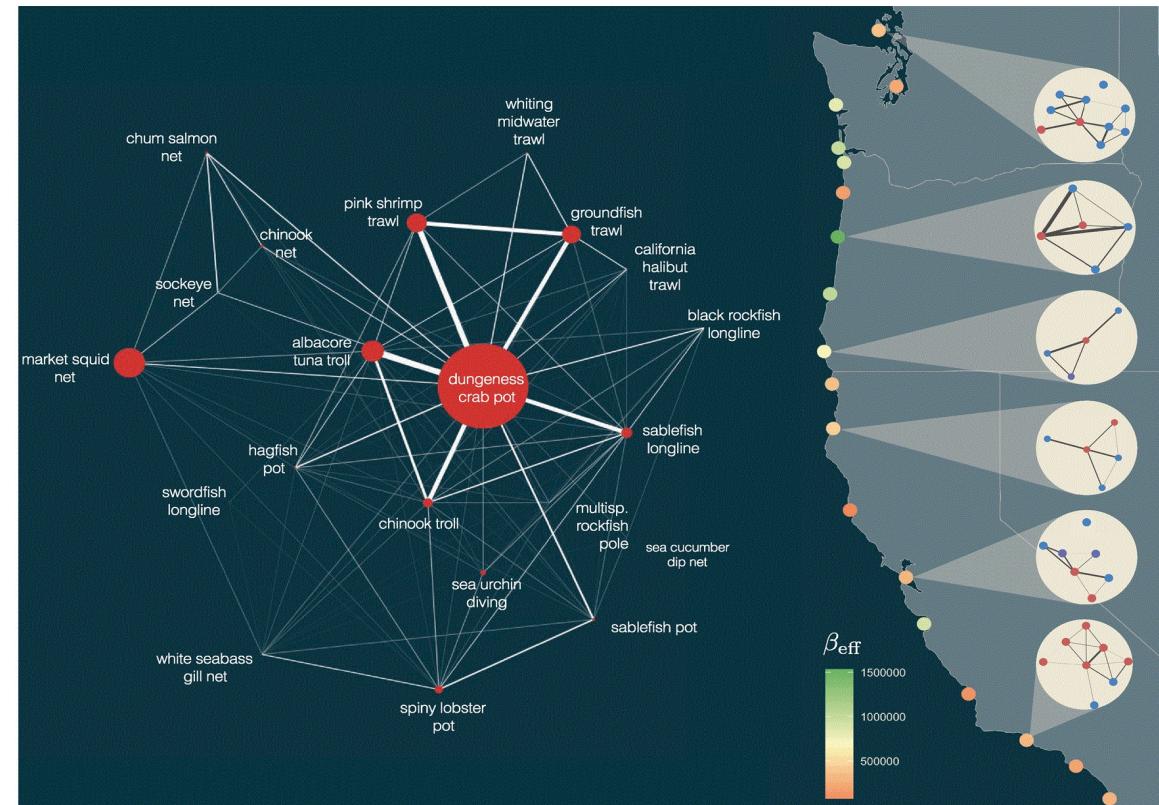
Overfishing: A Tragedy of the Commons

- International management of fisheries has been attempted through government coordination to set a **Total Allowable Catch (TAC)** for each fishery each year.
 - This practice can lead to intense pressure to fish all at once at the season's opening, sometimes overshooting the TAC.
 - This challenge can be mitigated by the use of **Individual Fishing Quotas (IFQs)** or **Individual Transferrable Quotas (ITQs)**, but allocation is still an issue.



Overfishing: A Tragedy of the Commons

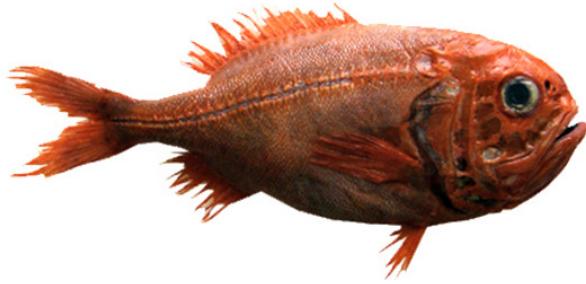
- International management of fisheries has been attempted through government coordination to set a **Total Allowable Catch (TAC)** for each fishery each year.
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 - This challenge can be mitigated by the use of **Individual Fishing Quotas (IFQs)** or **Individual Transferrable Quotas (ITQs)**, but allocation is still an issue.
- The work of Elinor Ostrom showed that some of these challenges can be overcome when the limits of a resource are clearly defined, when the group of stakeholders is small, and when communication is high.



Dr. Emma Fuller,
Fractal Agriculture



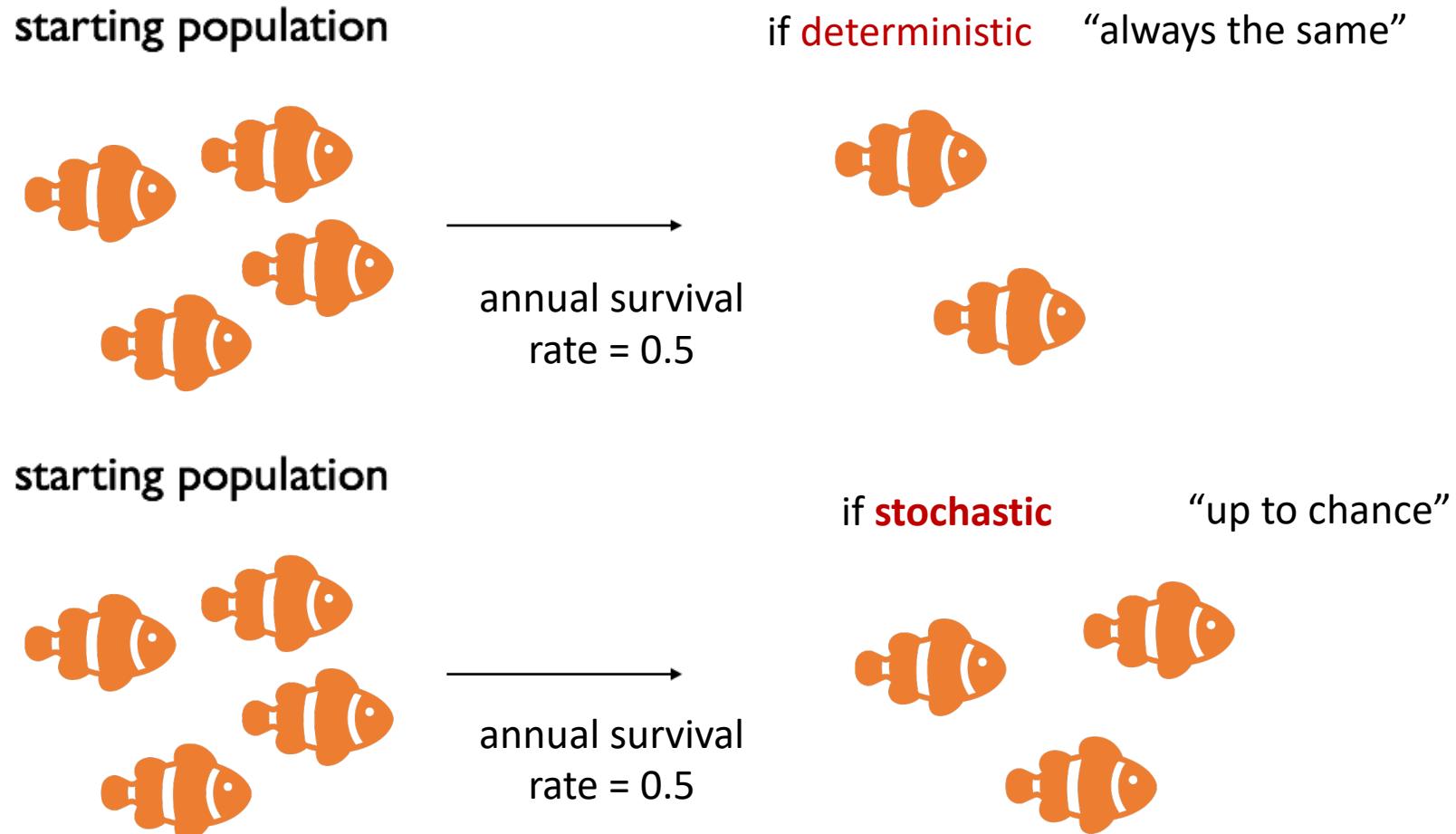
The case of the orange roughy highlights many of the **inherent problems with MSY**



- 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**.
- Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in N can be devastating
 - environmental **stochasticity**
 - demographic **stochasticity**

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

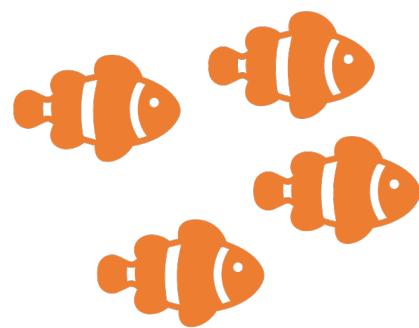
Deterministic vs. Stochastic



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



starting population



if **stochastic**

“up to chance”



cyclone year!

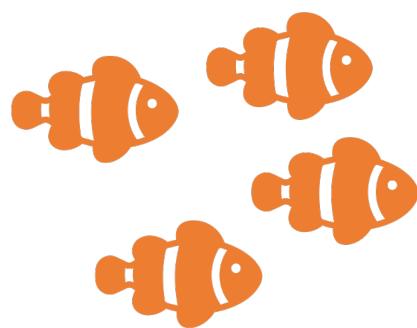
annual survival
rate = 0.5

- r and K and N = difficult to measure.
- Neglect population structure.
- Single species models.
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- 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**

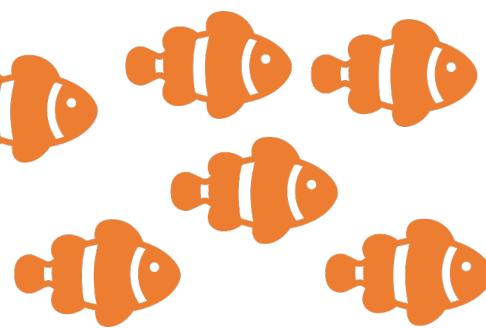


starting population



if **deterministic** “always the same”

annual fecundity
= 0.5

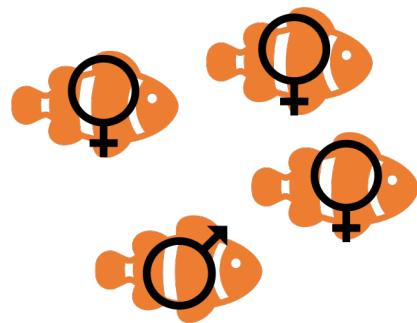


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 - individual-level differences in mortality and reproduction, esp. at small pop size

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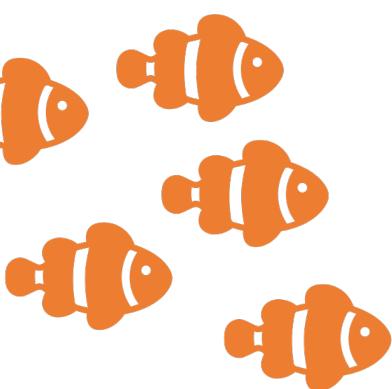
starting population



if stochastic

annual fecundity
= 0.5

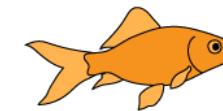
“up to chance”



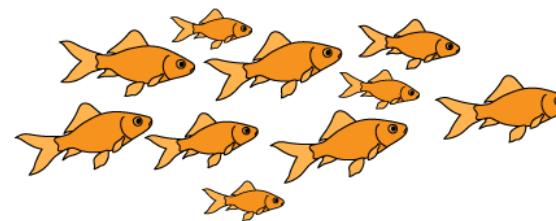
Only one male encounters only one female, so only 1 new fish is born!

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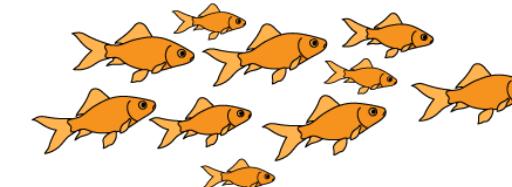
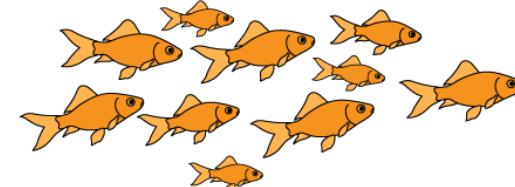
Ecology is the study of
the **interactions** of
organisms with each
other and their
environment.



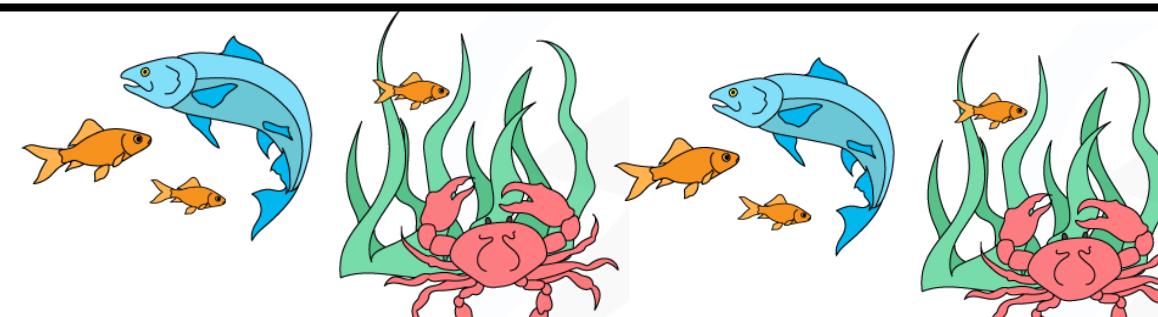
individual



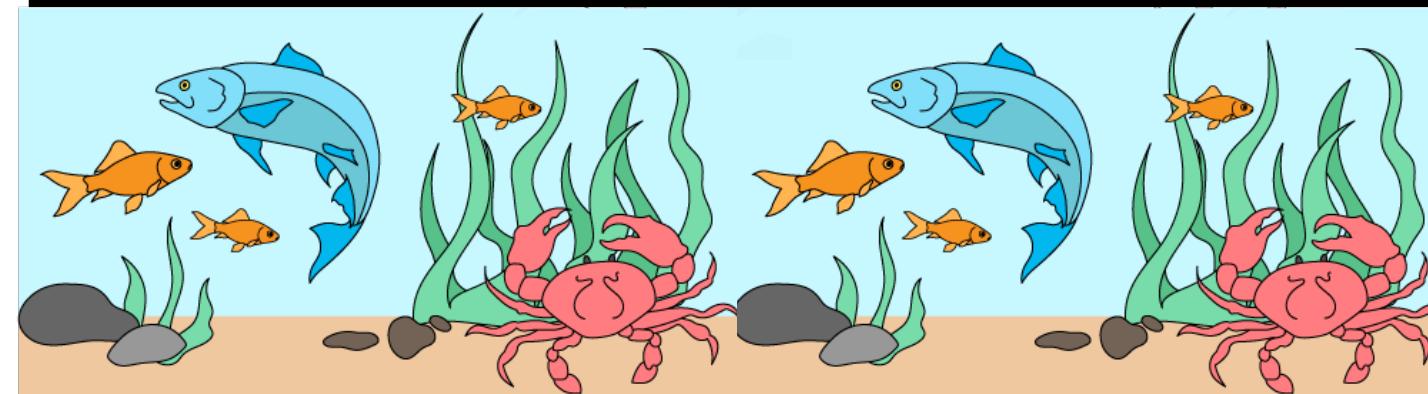
population



metapopulation

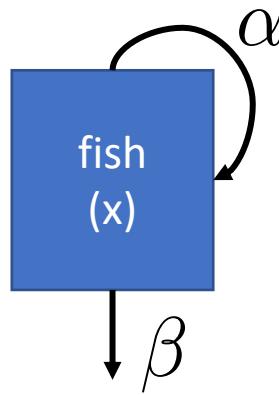


community

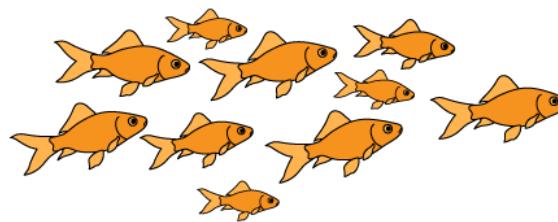


ecosystem

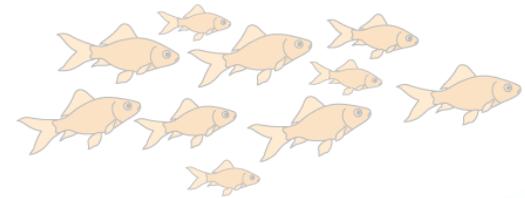
Population = multiple individuals of the same species (**conspecifics**) in the same habitat



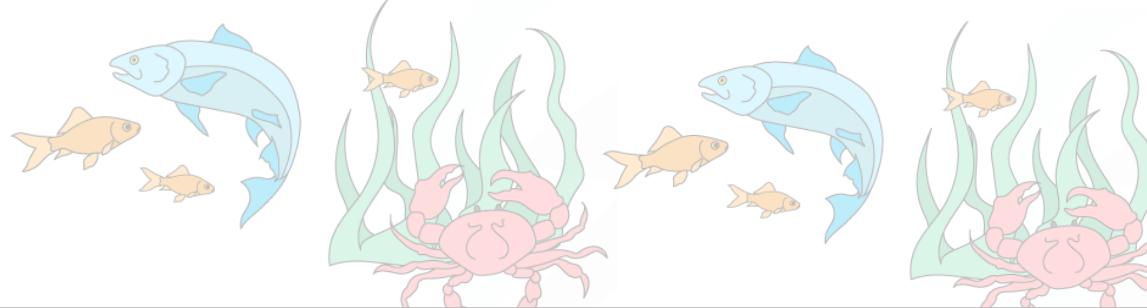
individual



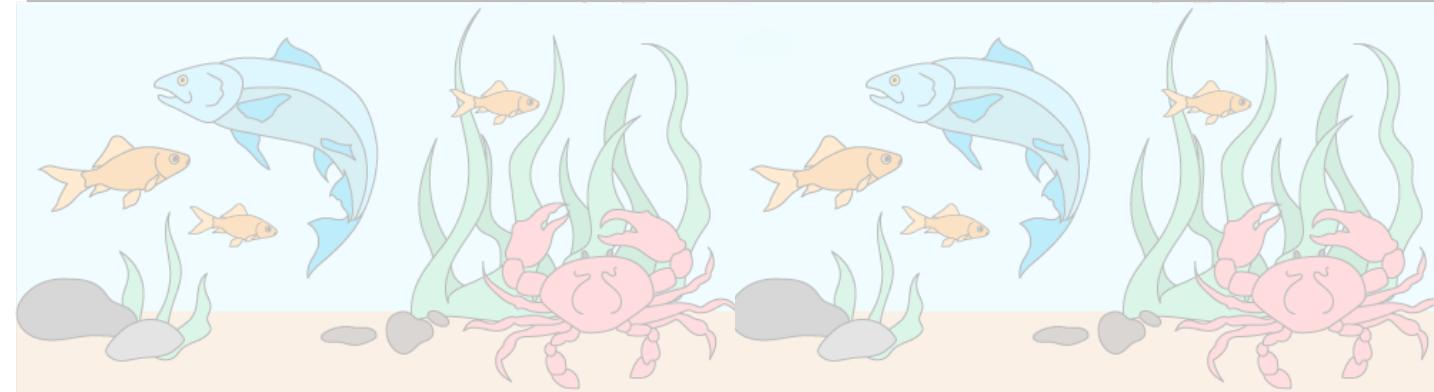
population



metapopulation



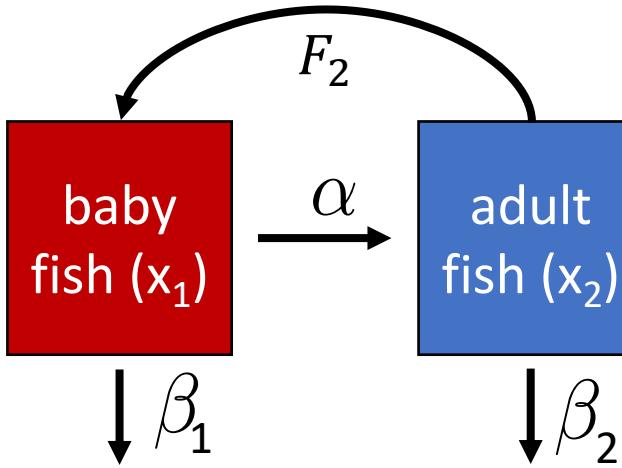
community



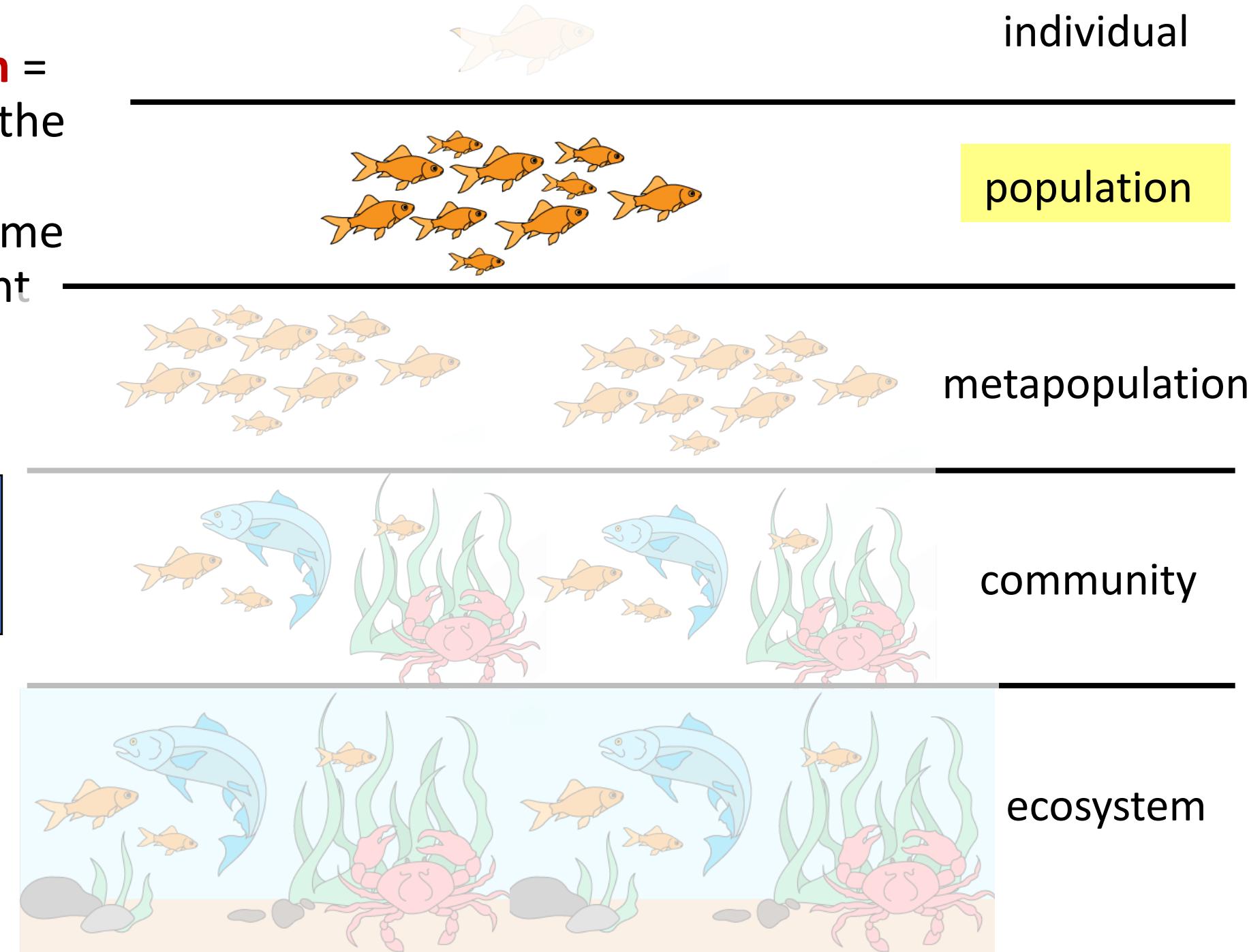
ecosystem

*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

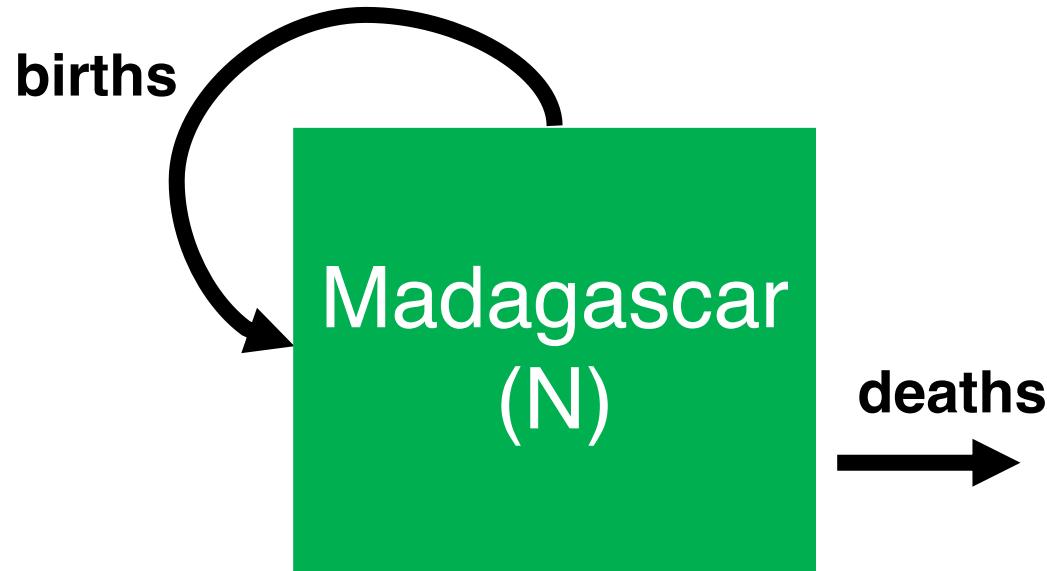


*How does the
abundance of fish
change through time?*



Modeling demographic complexity

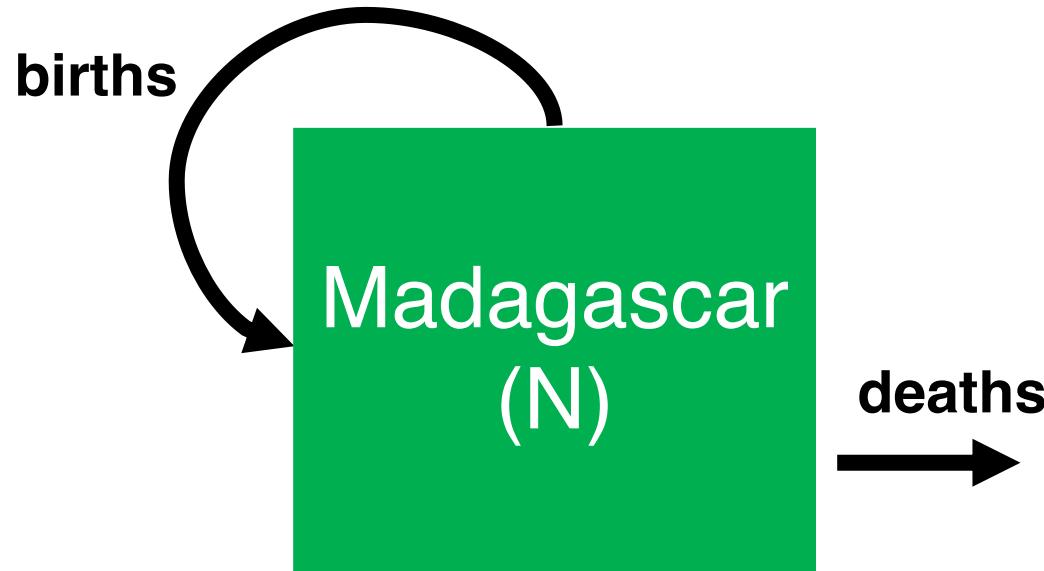
1. Populations are divided into compartments
2. Individuals within a compartment are homogeneously mixed
3. Compartments and transition rates are determined by biological systems
4. Rates of transferring between compartments are expressed mathematically



The simplest
population model

Modeling demographic complexity

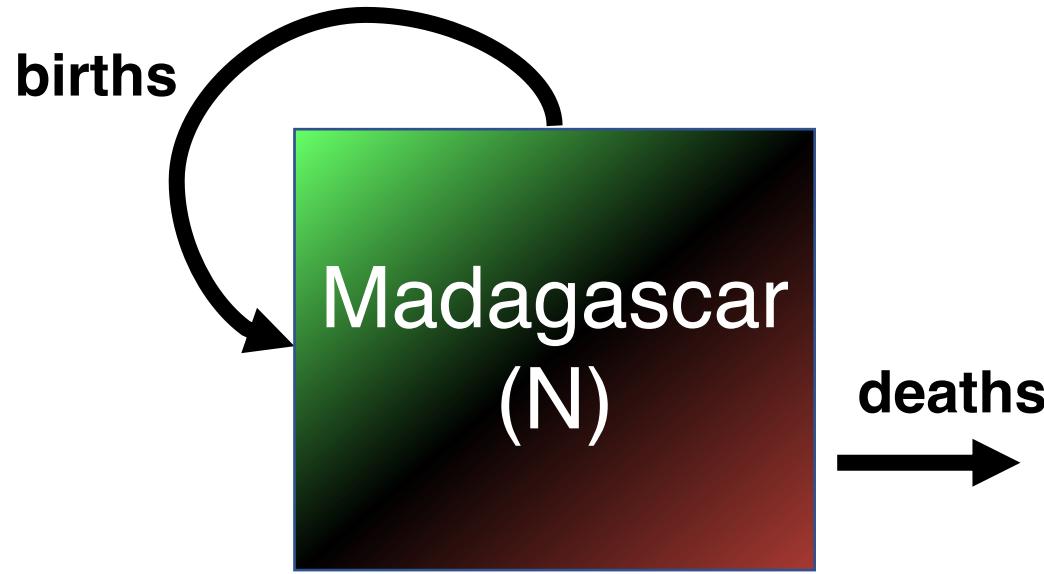
1. Populations are divided into compartments
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3. Compartments and transition rates are determined by biological systems
4. Rates of transferring between compartments are expressed mathematically



What is wrong about this model?

Modeling demographic complexity

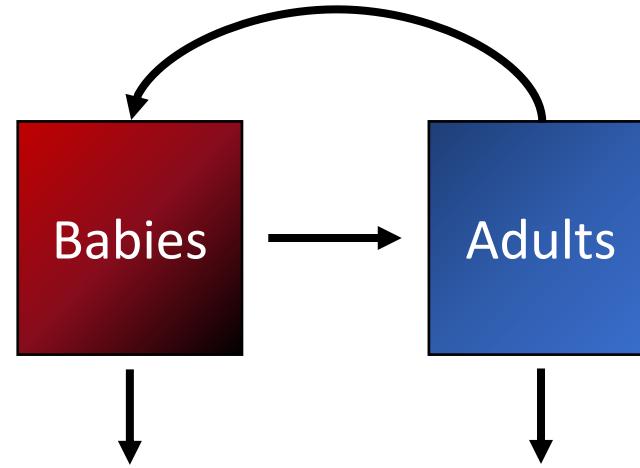
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What is wrong about this model?

Modeling demographic complexity

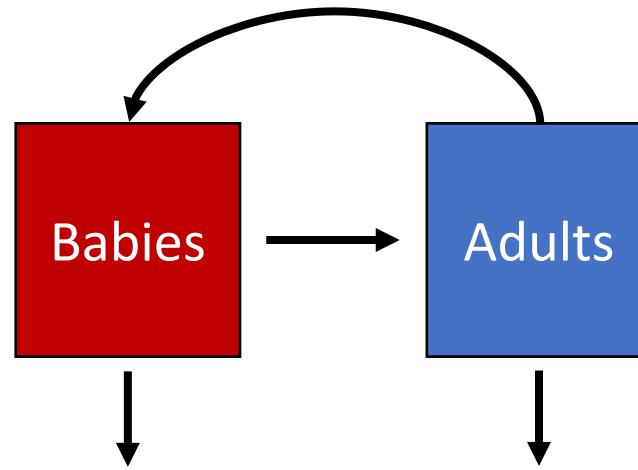
1. Populations are divided into compartments
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The structured population model

Modeling demographic complexity

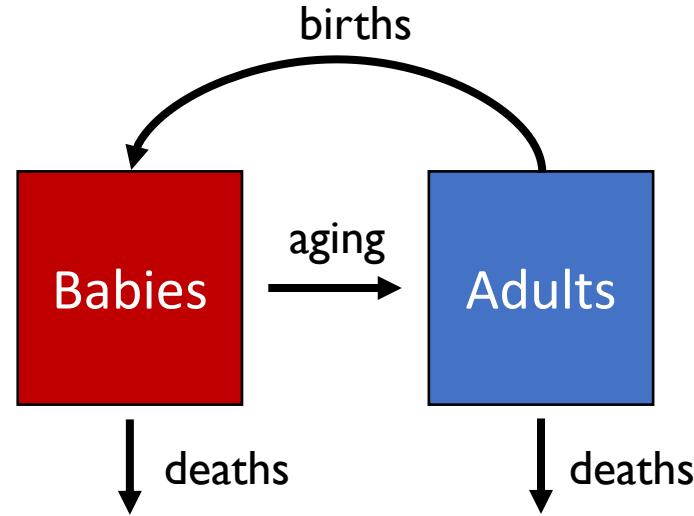
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The structured population model

Modeling demographic complexity

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The structured population model

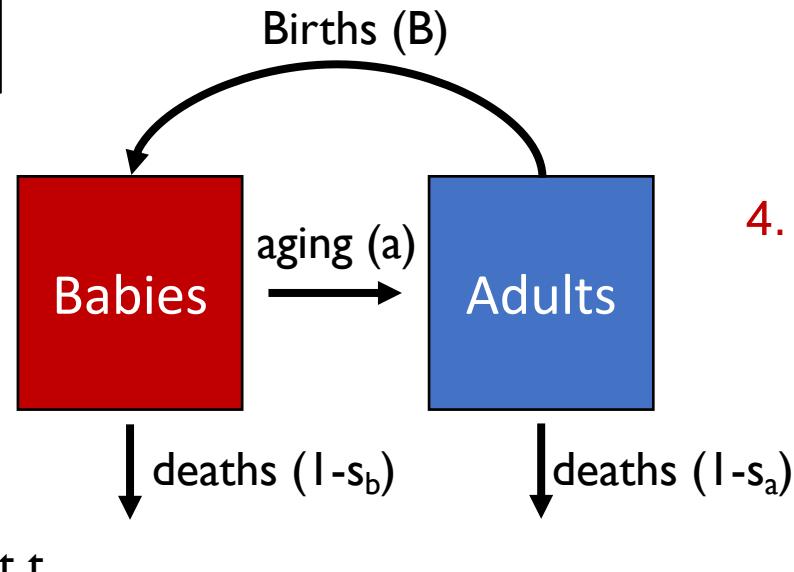
The structured population model

Population rate of increase

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

pop size at $t + 1$

pop size at t



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

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

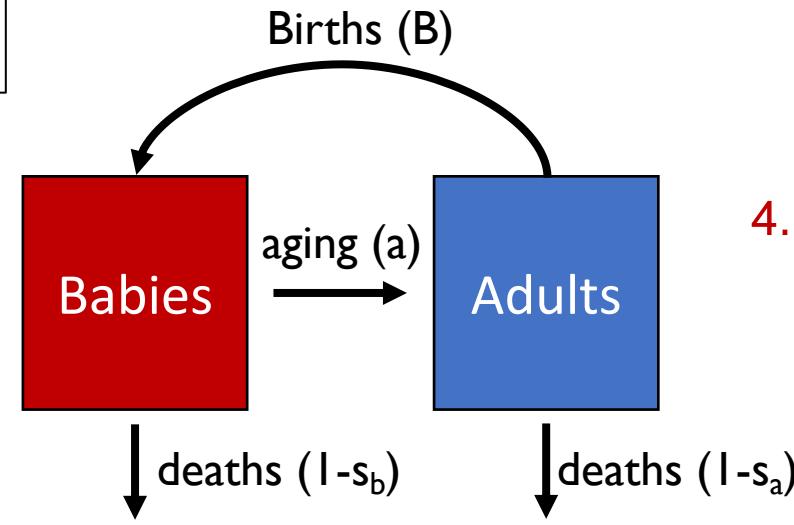
matrix of survival and fecundity rates

$s_b(1-a)$	B
$s_b a$	s_a

vector of population sizes

*Discrete time

The structured population model



1. Populations are divided into compartments
2. Individuals within a compartment are homogeneously 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

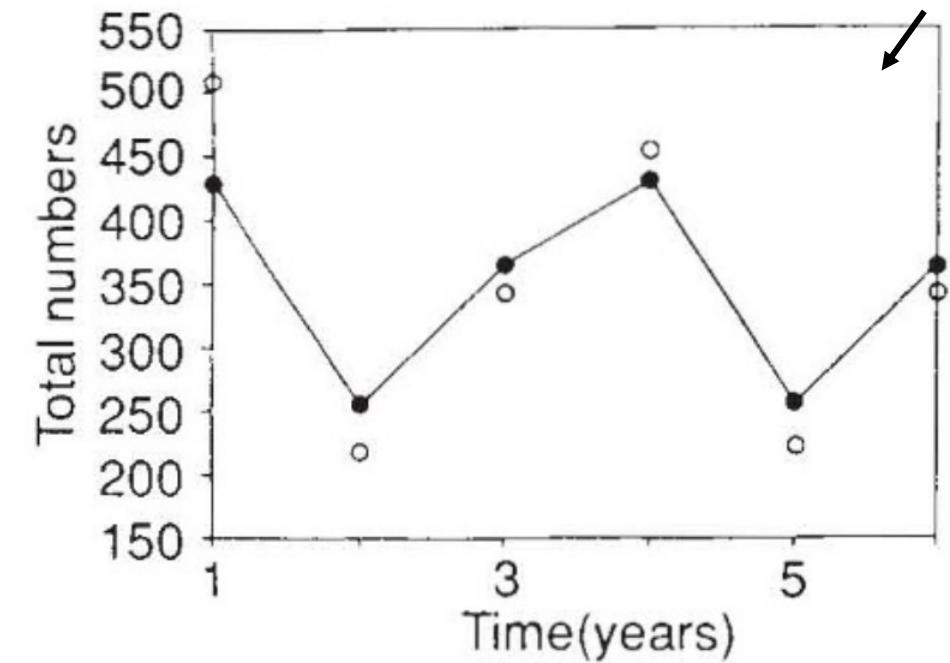
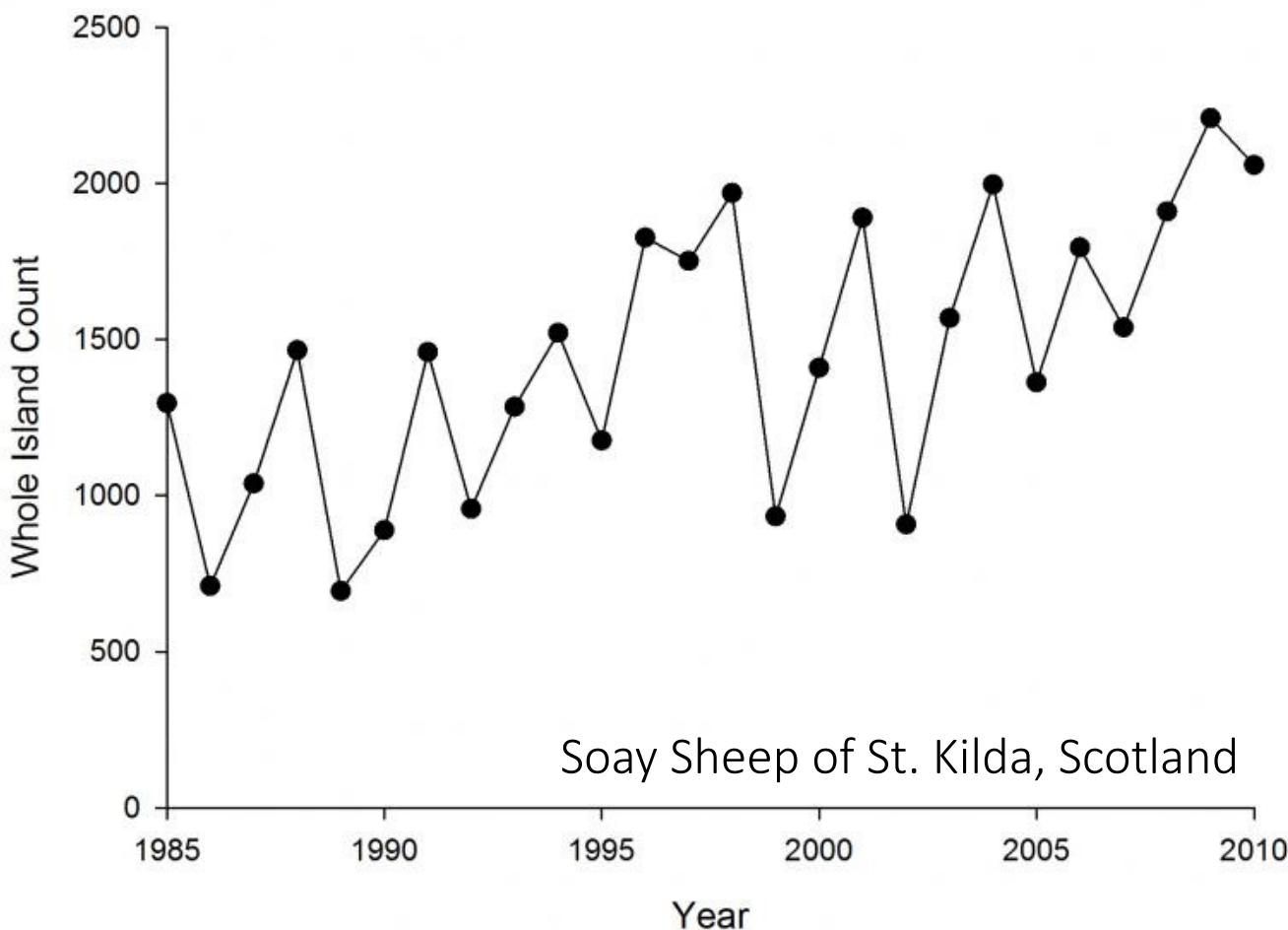
λ =dominant eigenvalue of transition matrix

$$\begin{array}{c} \mathbf{A} \\ \xrightarrow{\hspace{1cm}} \\ \begin{matrix} s_b(1-a) & B \\ \hline s_b a & s_a \end{matrix} \end{array} \times \begin{array}{c} \mathbf{N}_t \\ \xrightarrow{\hspace{1cm}} \\ \begin{matrix} N_b \\ \hline N_a \end{matrix} \end{array} = \begin{array}{c} \mathbf{N}_{t+1} \\ \xrightarrow{\hspace{1cm}} \\ \begin{matrix} s_b(1-a) N_b + B N_a \\ \hline s_b a N_b + s_a N_a \end{matrix} \end{array}$$

Population growth will depend on population structure!

(pop grows @ $\lambda > 1$ & declines @ $\lambda < 1$)

Structured populations in practice



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](#)

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Model
compared
against
data

Model
compared
against
data

Structured populations in practice

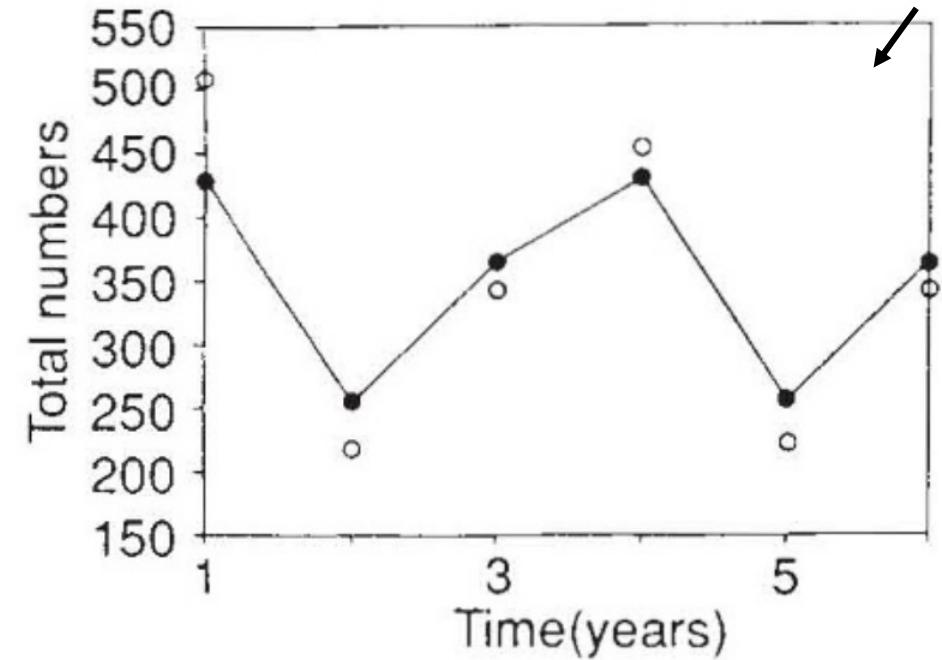
These results used a simple **density-dependent** model only!

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

↑ ↑ growth rate

population at $t+1$ average fecundity population at t

a and b control the strength of density dependence.



Overcompensation and population cycles in an ungulate

[B. T. Grenfell](#), [O. F. Price](#), [S. D. Albon](#) & [T. H. Glutton-Brock](#)

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Model
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against
data

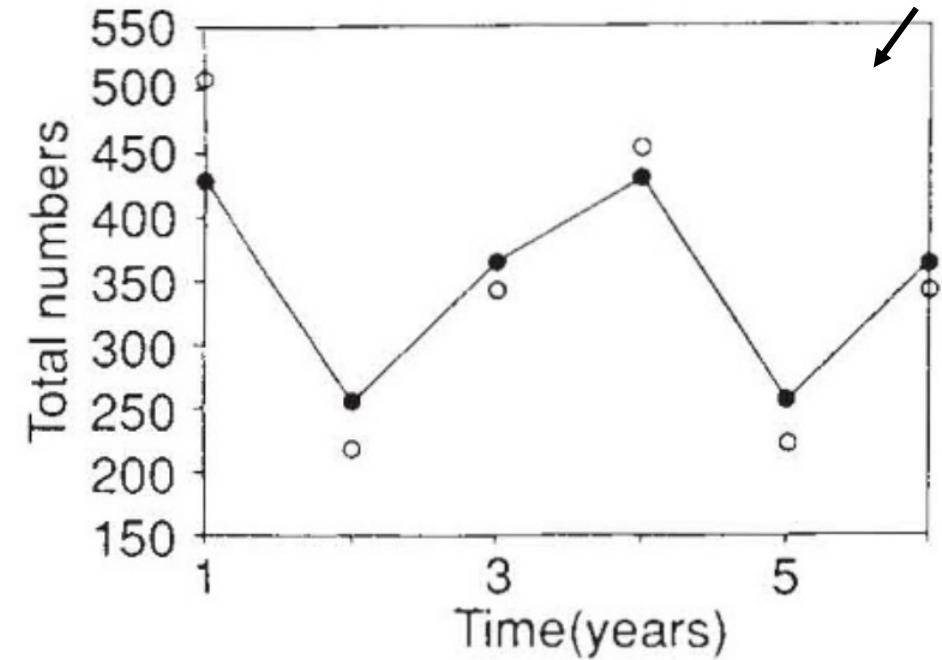
Structured populations in practice

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

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

↑ ↑ ↑
population average growth
at t+1 fecundity rate
 ↑
 population at t

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



Similar to the simple logistic growth equation!

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

Overcompensation and population cycles in an ungulate

[B. T. Grenfell, O. F. Price, S. D. Albon & T. H. Glutton-Brock](#)

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589 Accesses | 107 Citations | [Metrics](#)

Structured populations in practice

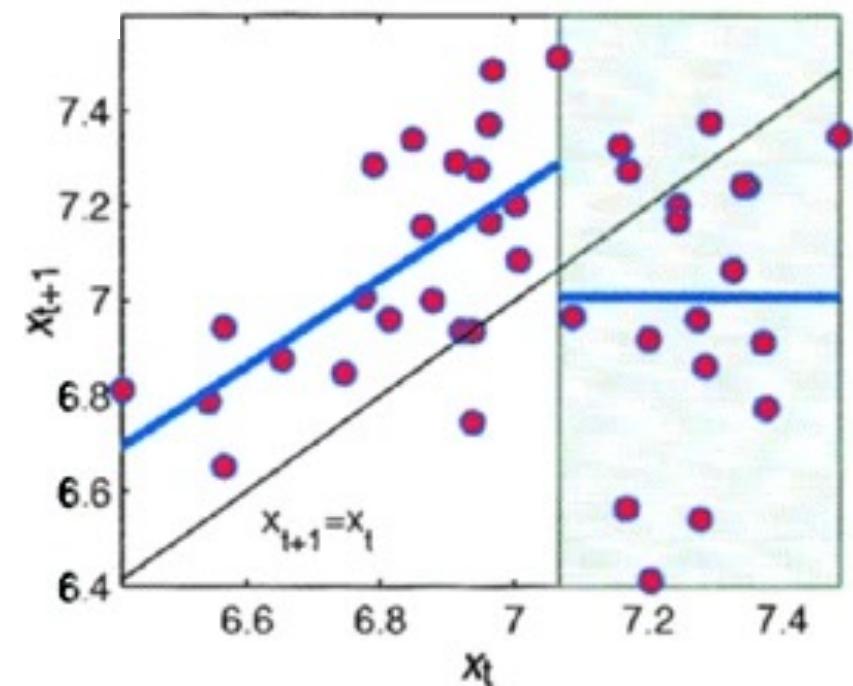
In later work, the authors added **environmental stochasticity** (bad weather) to **better represent** the data.....

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](#)

1746 Accesses | 414 Citations | 4 Altmetric | [Metrics](#)



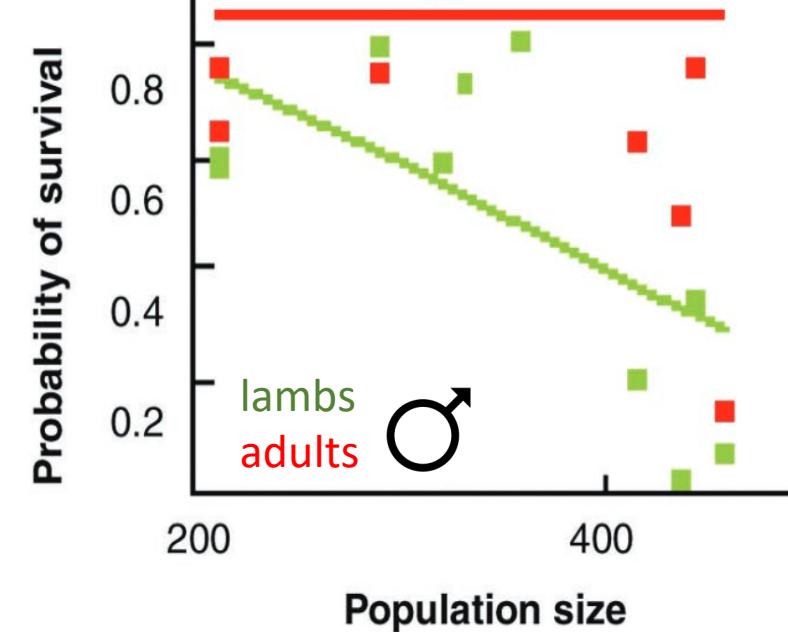
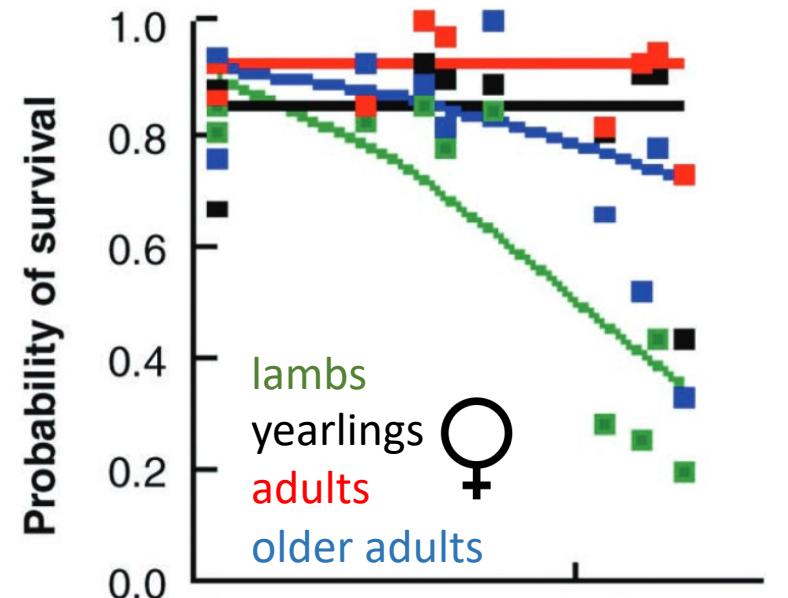
Structured populations in practice

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

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

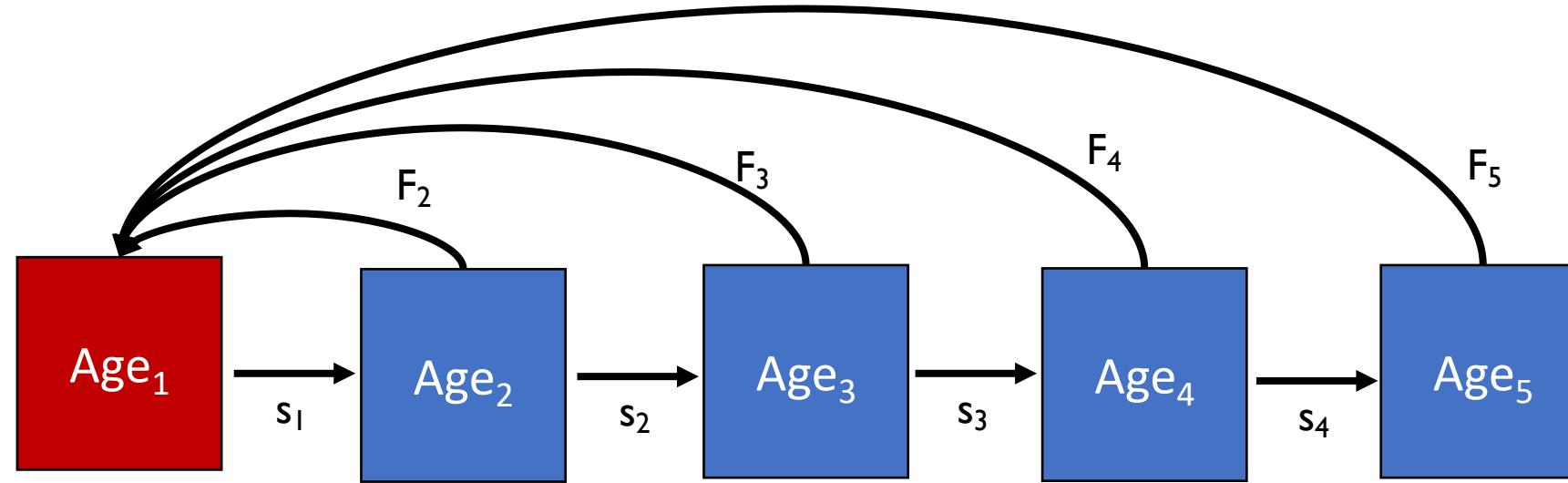
T. Coulson,^{1*}† E. A. Catchpole,² S. D. Albon,³ B. J. T. Morgan,⁴
J. M. Pemberton,⁵ T. H. Clutton-Brock,⁶ M. J. Crawley,⁶
B. T. Grenfell⁷

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.

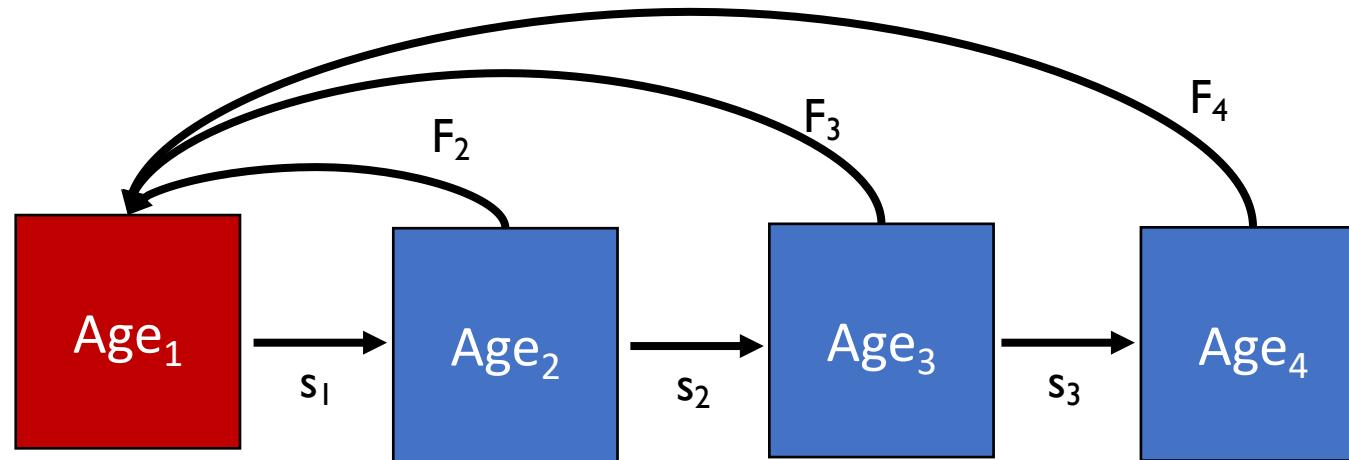


The **Leslie matrix** model divides classes based on age.

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

The structured population model

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



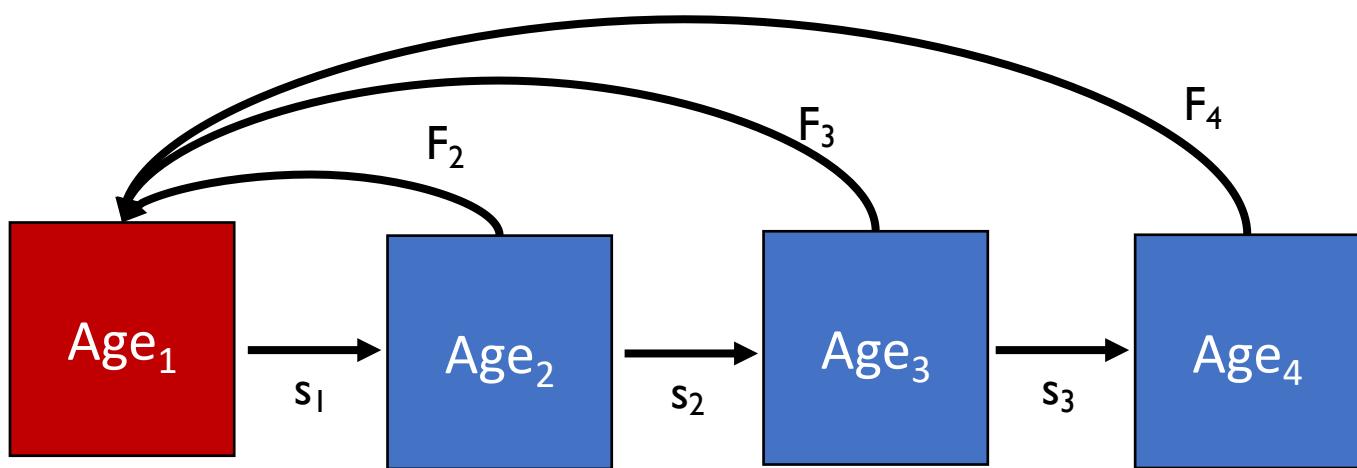
$$\lambda = \text{dominant eigenvalue of transition matrix} \rightarrow \begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} \times \begin{bmatrix} N_t \\ N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix} = \begin{bmatrix} N_{t+1} \\ N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix}$$

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

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

The structured population model

Demographers collect these rates in life tables



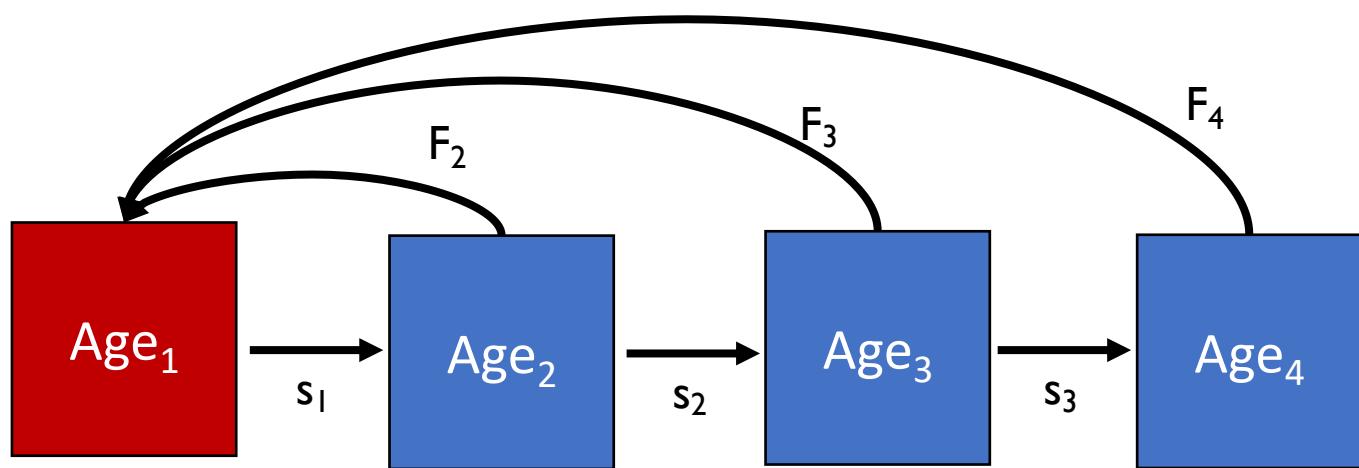
x (age)	N _x (number in cohort)	I _x (survivorship to age x)	m _x (fecundity)	I _x m _x
0	100	1	0	0
1	60	.6	2	1.2
2	30	.3	3	0.9
3	10	.1	1	0.1
4	1	.01	1	0.01



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

The structured population model

Demographers collect these rates in life tables



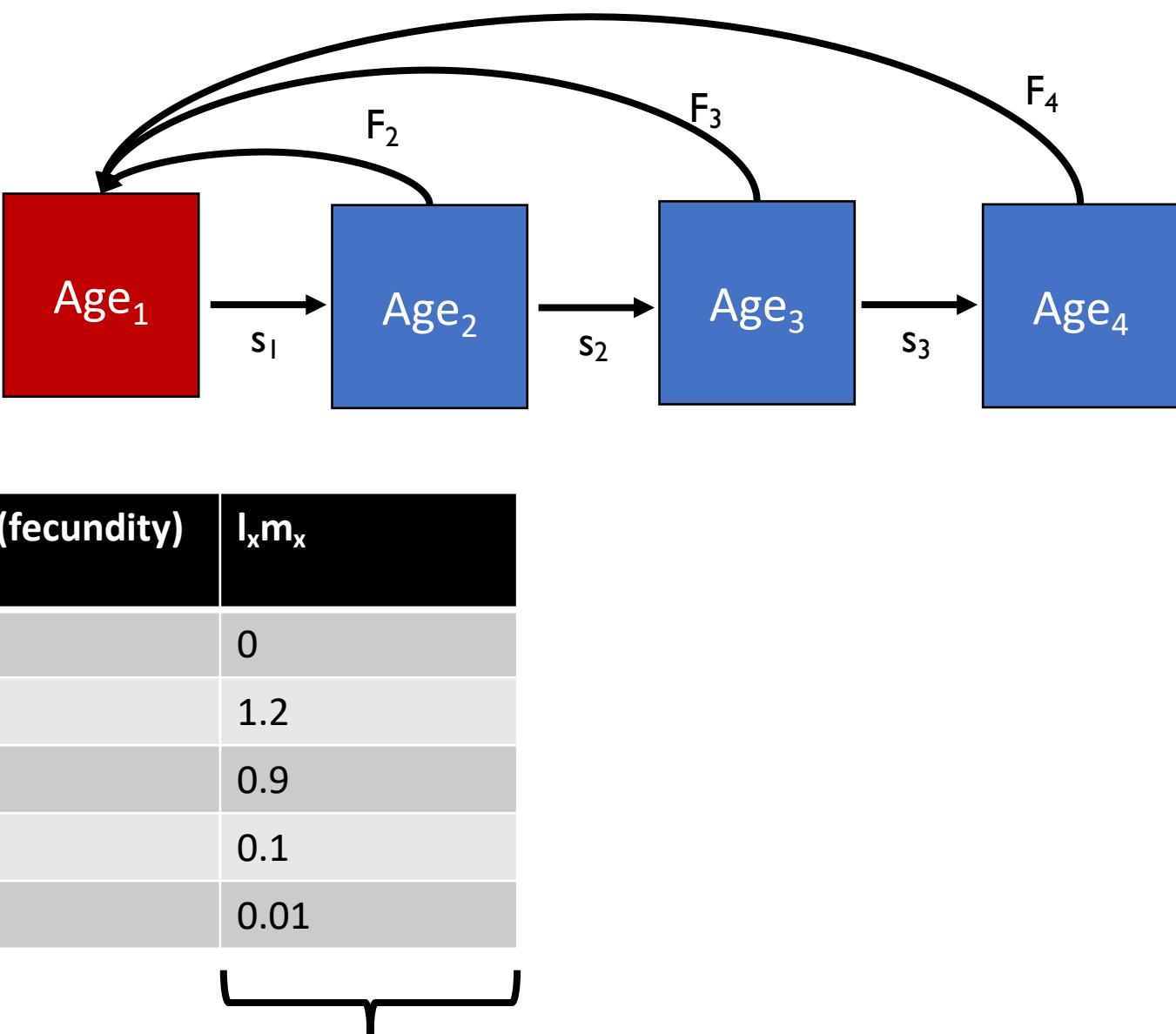
x (age)	N _x (number in cohort)	I _x (survivorship to age x)	m _x (fecundity)	I _x m _x
0	100	1	0	0
1	60	.6	2	1.2
2	30	.3	3	0.9
3	10	.1	1	0.1
4	1	.01	1	0.01



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

The structured population model

Demographers collect these rates in life tables

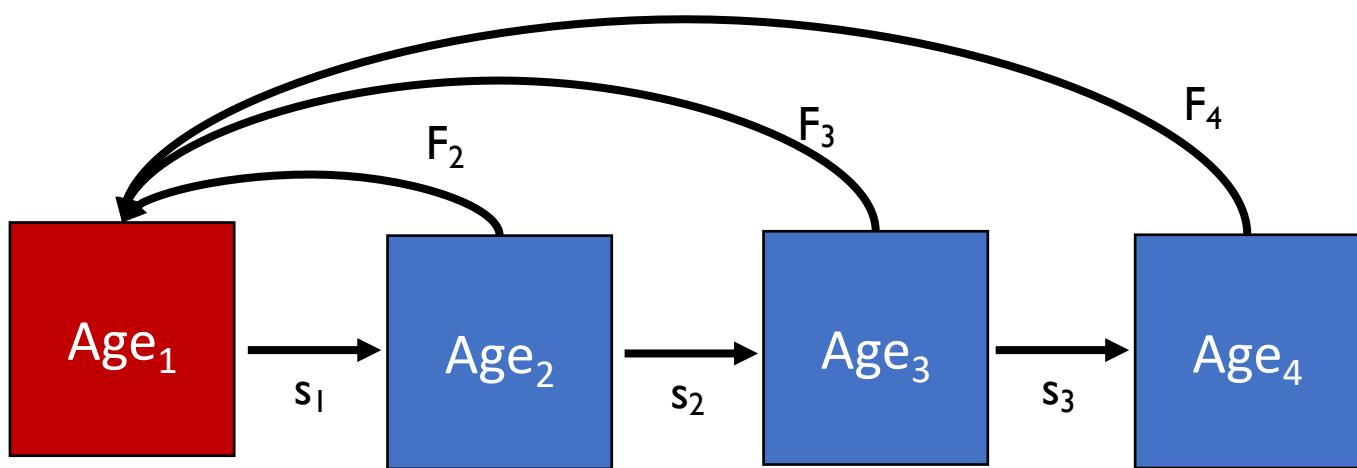


Net reproductive rate (R_0): $\sum l_x m_x = 2.21$

(pop grows at $R_0 > 1$ and declines at $R_0 < 1$)

The structured population model

Demographers collect these rates in life tables



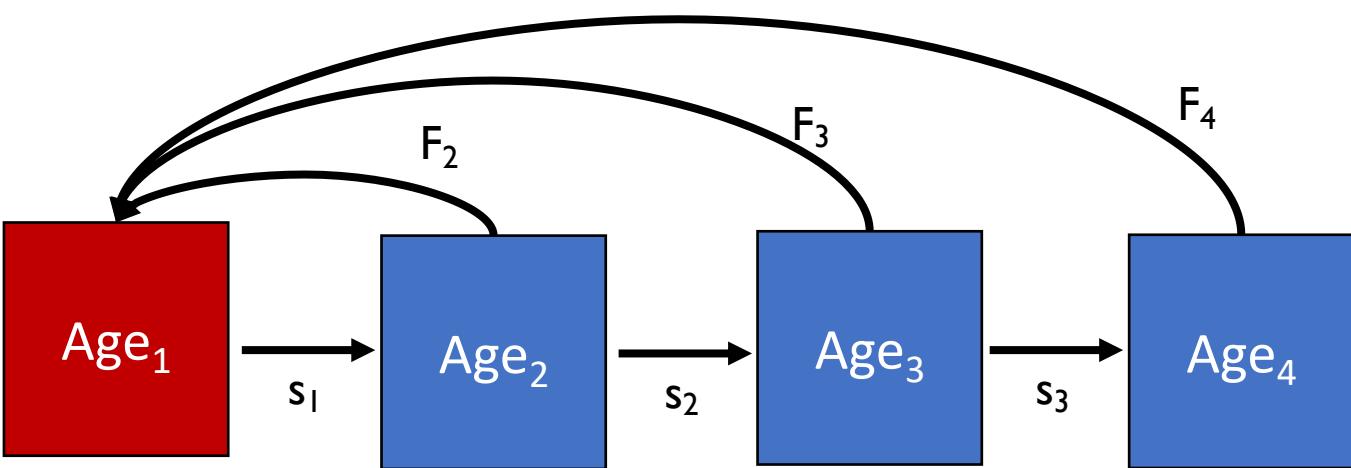
x (age)	N _x (number in cohort)	l _x (survivorship to age x)	m _x (fecundity)	l _x m _x
0	100	1	0	0
1	60	.6	2	1.2
2	30	.3	3	0.9
3	10	.1	1	0.1
4	1	.01	1	0.01



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

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

The structured population model



x (age)	N _x (number in cohort)	I _x (survivorship to age x)	m _x (fecundity)	I _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

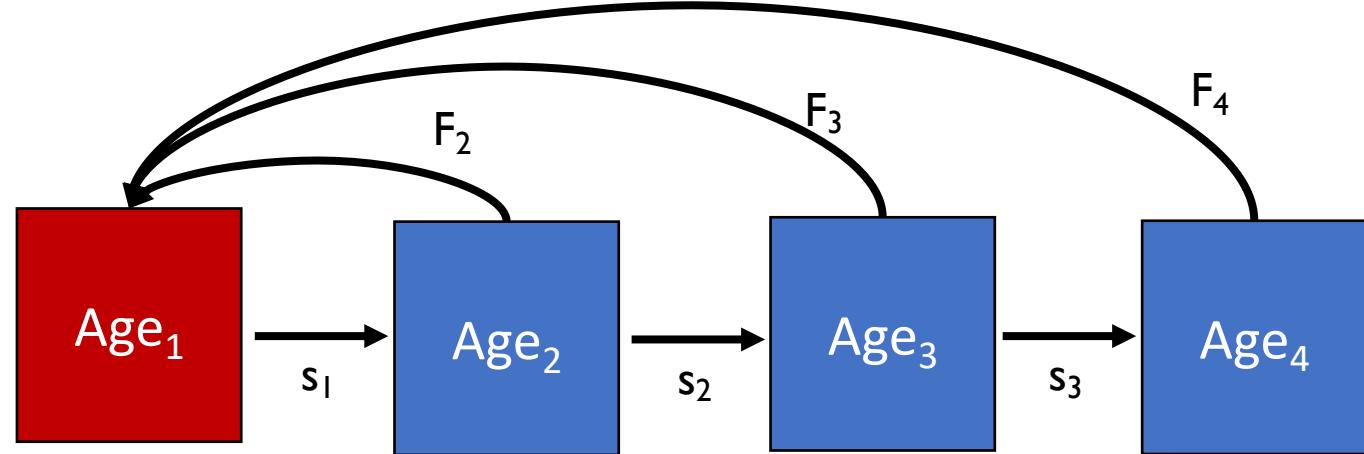
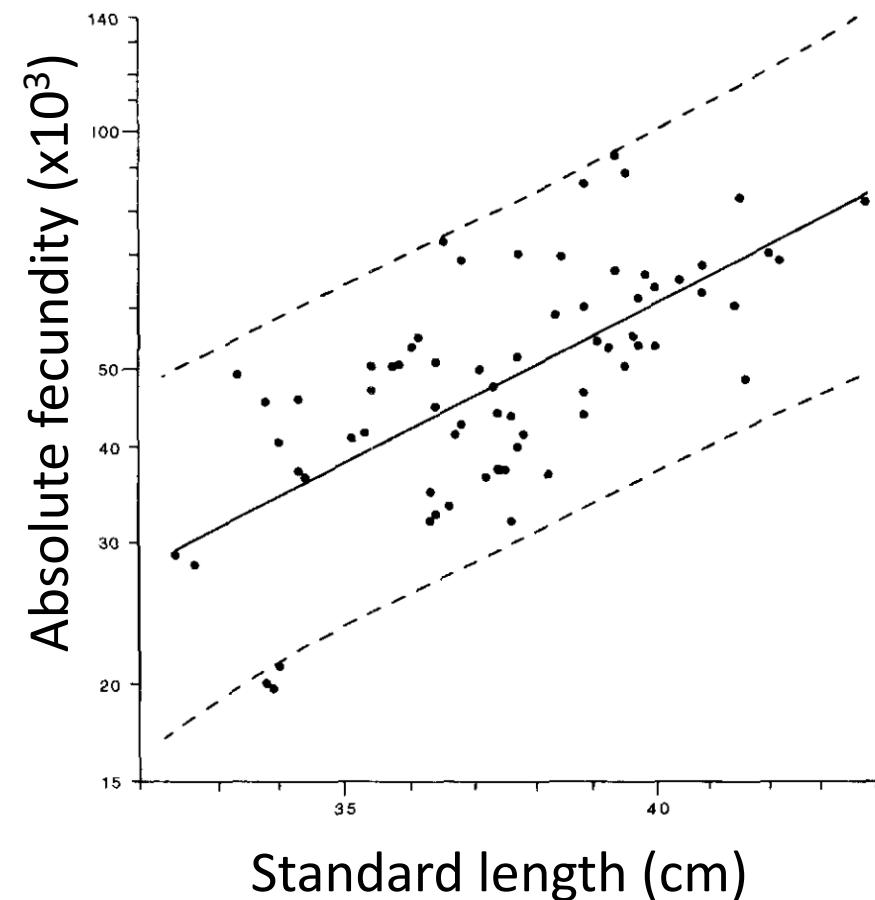


⋮

Orange roughy can live up to 200 years!

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

The structured population model



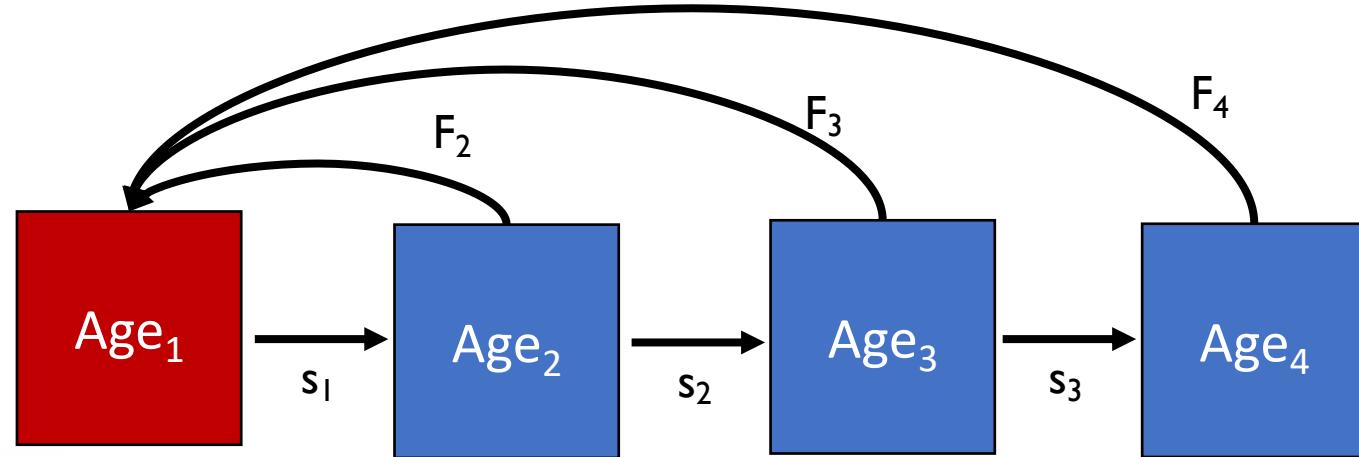
Fecundity (eggs)
increases in older,
bigger fish!

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

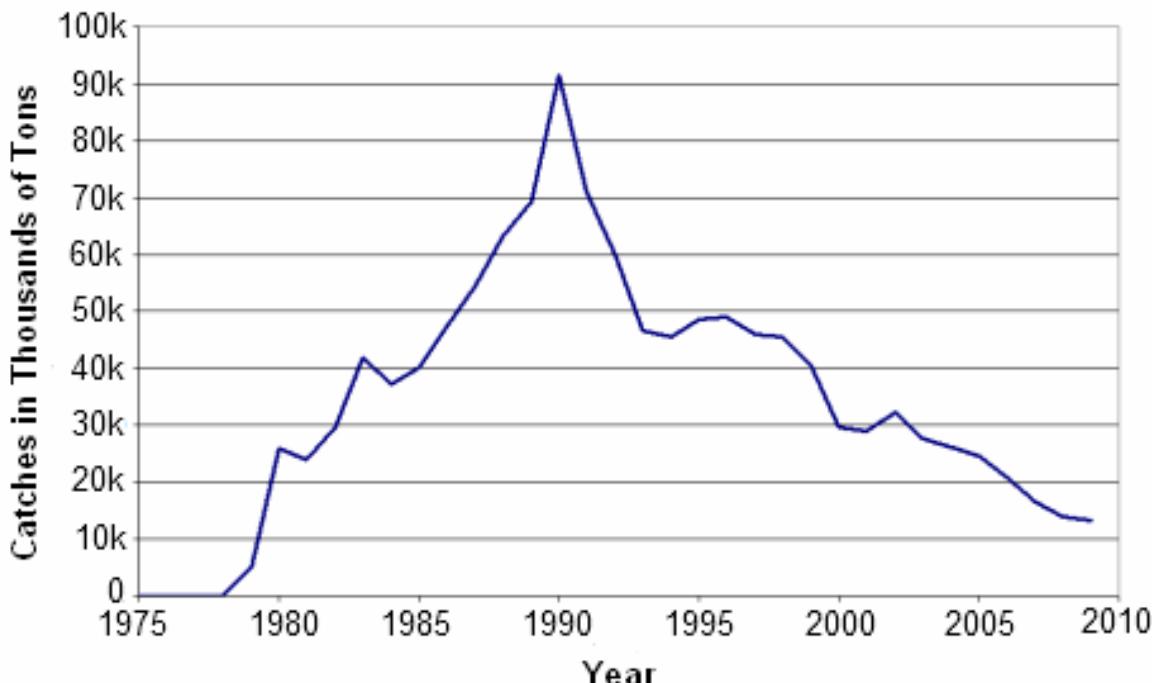


Norway 1910
(Norsk folkemuseum)

The structured population model

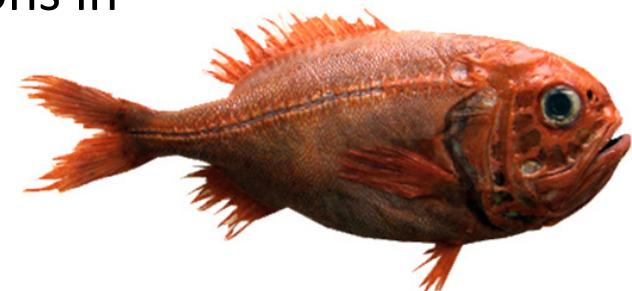


Worldwide Catches of Orange Roughy 1975 - 2009



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

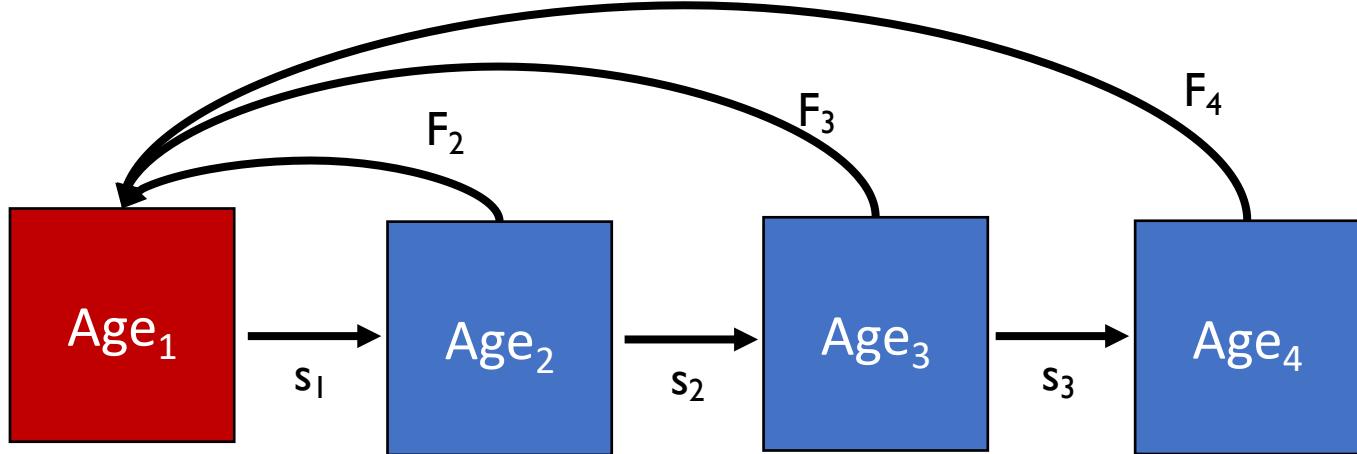
In 2008, the international TAC for orange roughy was reduced from 1470 tons to 914 tons... down from over 90,000 tons in the early 1990s...



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

The structured population model

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

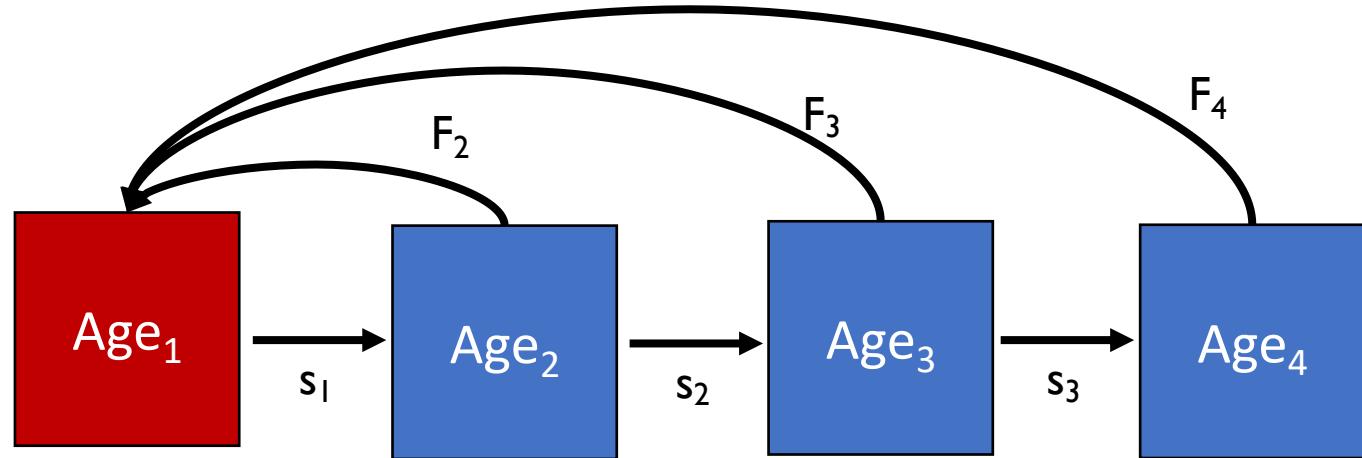
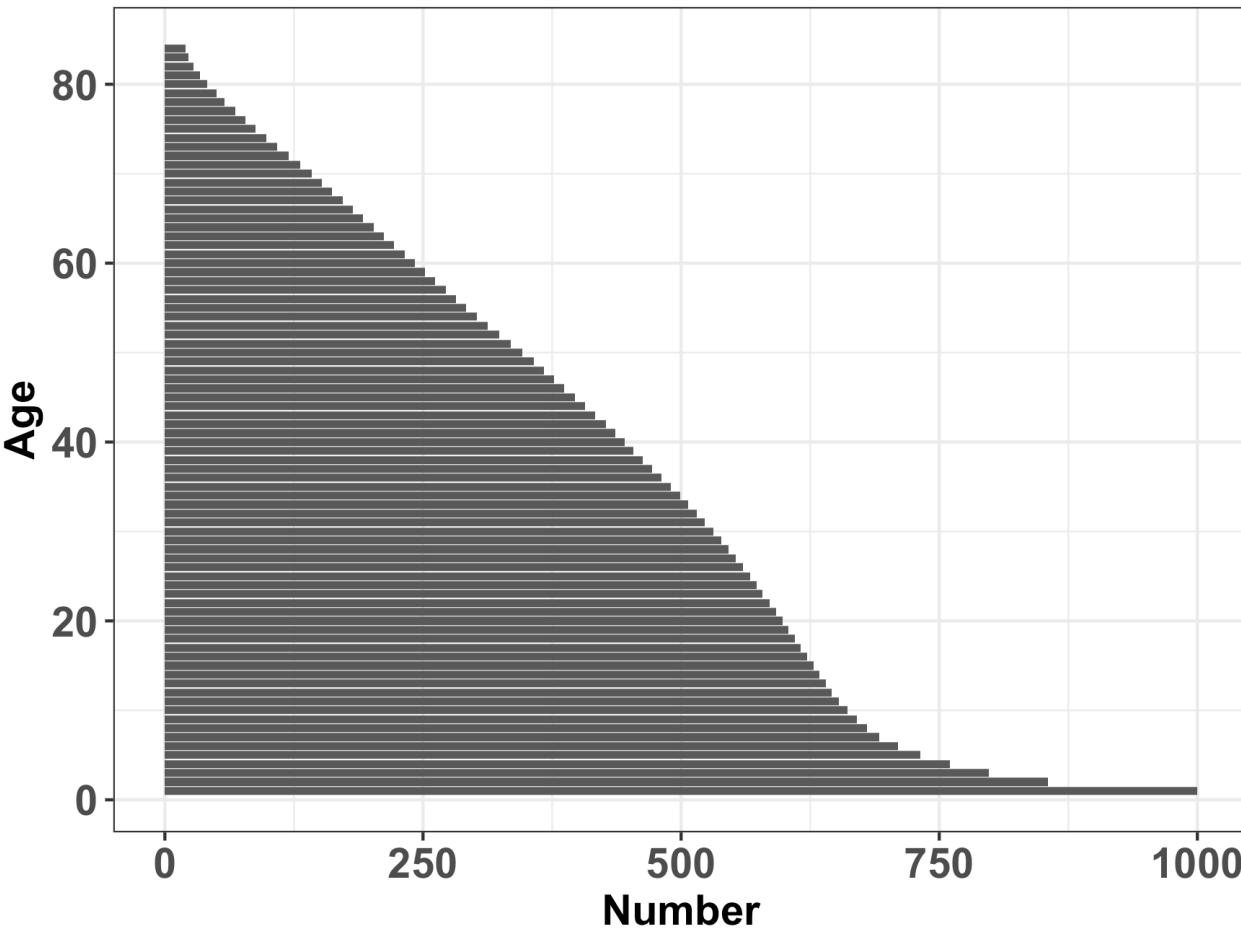


Age. Year.	Per- sons.	Age. Cur.	Per- sons.								
1	1000	8	680	15	623	22	585	29	539	35	481
2	855	9	570	16	612	23	579	30	531	37	472
3	798	10	651	17	615	24	573	31	523	38	453
4	750	11	553	18	610	25	567	32	515	39	454
5	732	12	546	19	604	26	560	33	507	40	445
6	710	13	640	20	593	27	555	34	495	41	436
7	652	14	634	21	592	28	546	35	490	42	427
Age. Cur.	Per- sons.	Age. Cur.	Per- sons.	Age. Cur.	Per- sons.	Age. Cur.	Per- sons.	Age. Cur.	Per- sons.	Age. Cur.	Per- sons.
43	417	50	345	57	272	64	202	71	131	78	58
44	407	51	333	58	252	65	192	72	120	79	49
45	397	52	324	59	252	65	182	73	105	80	41
46	387	53	313	60	242	67	172	74	98	81	34
47	377	54	302	61	232	68	162	75	90	82	28
48	367	55	292	62	222	69	152	76	82	83	23
49	357	56	282	63	212	70	142	77	68	84	20
											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

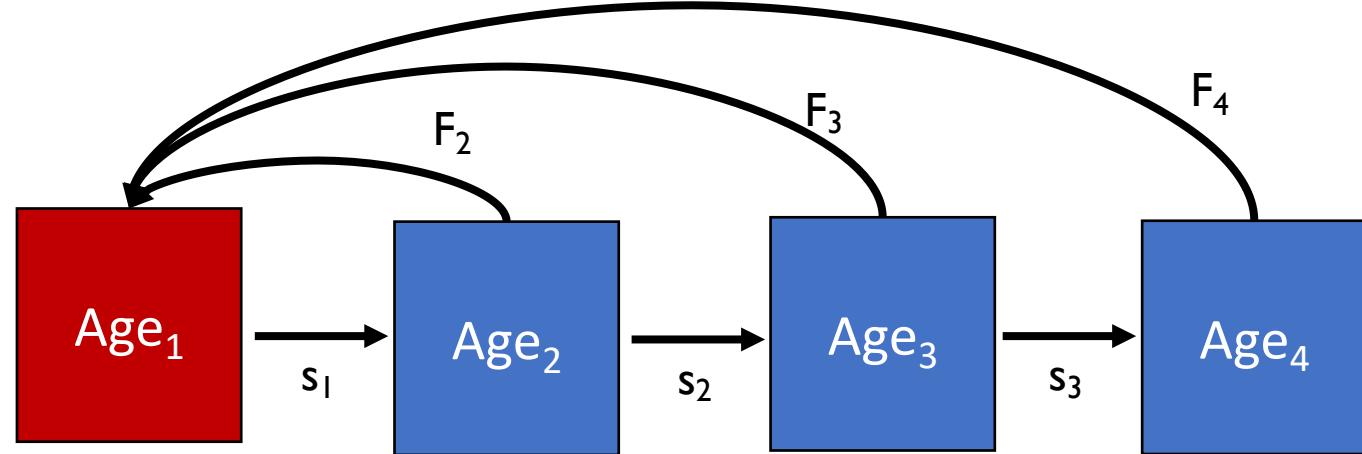
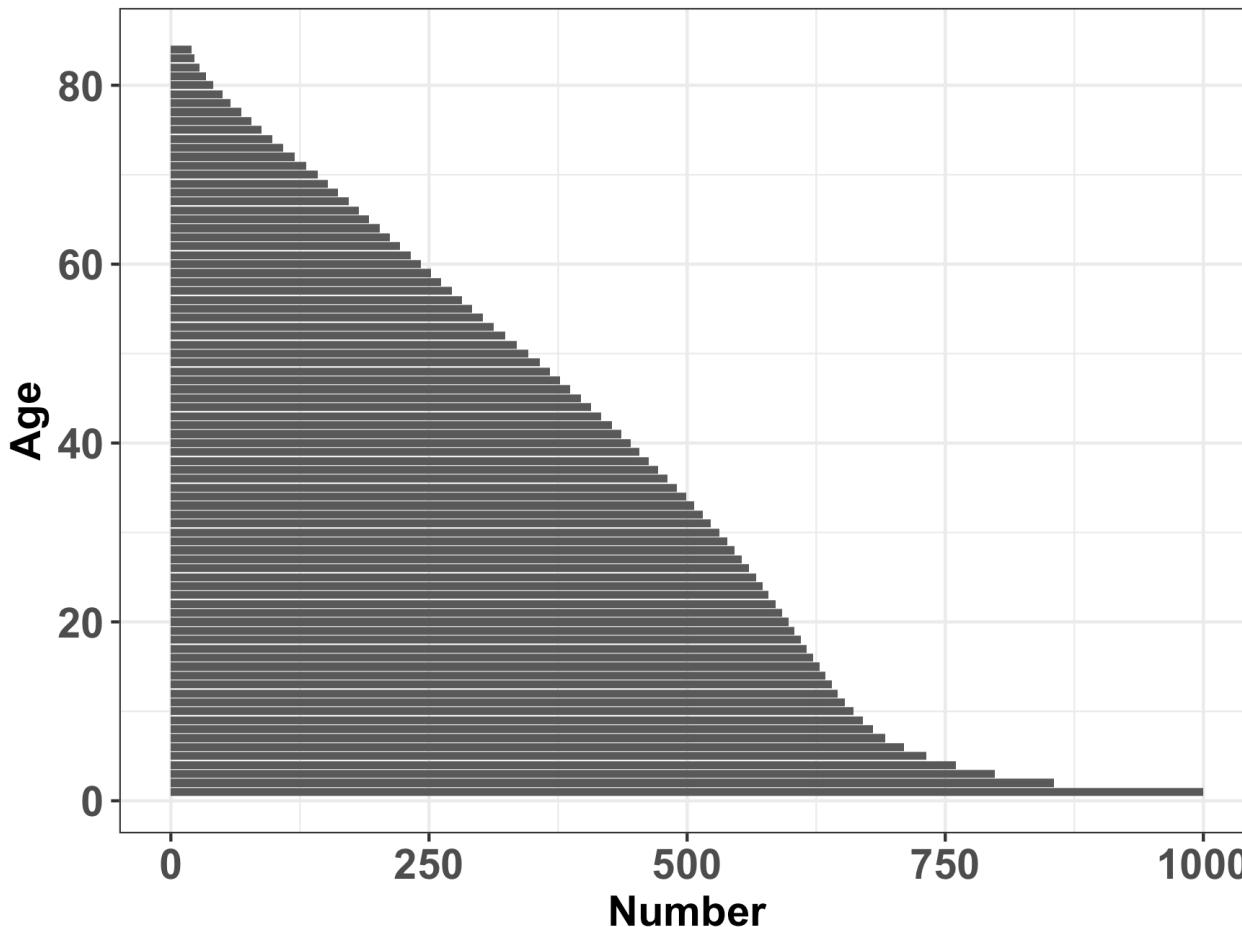
Population pyramid for Breslau



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

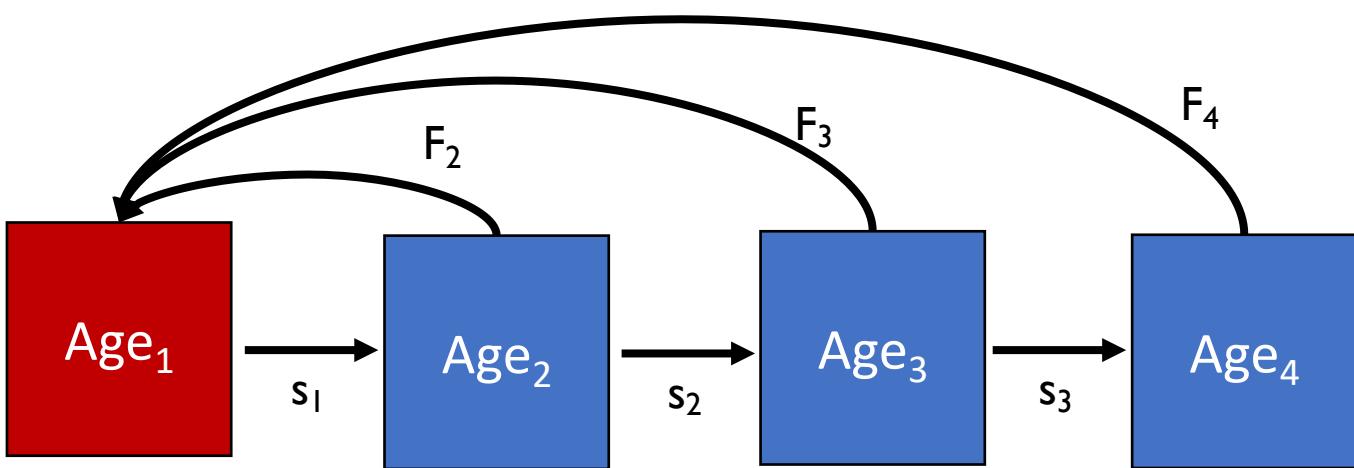


Humans are not like fish!
Fecundity tends to decrease in older age classes due to **reproductive senescence**.

Younger human populations that start giving birth earlier grow faster!

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

The structured population model

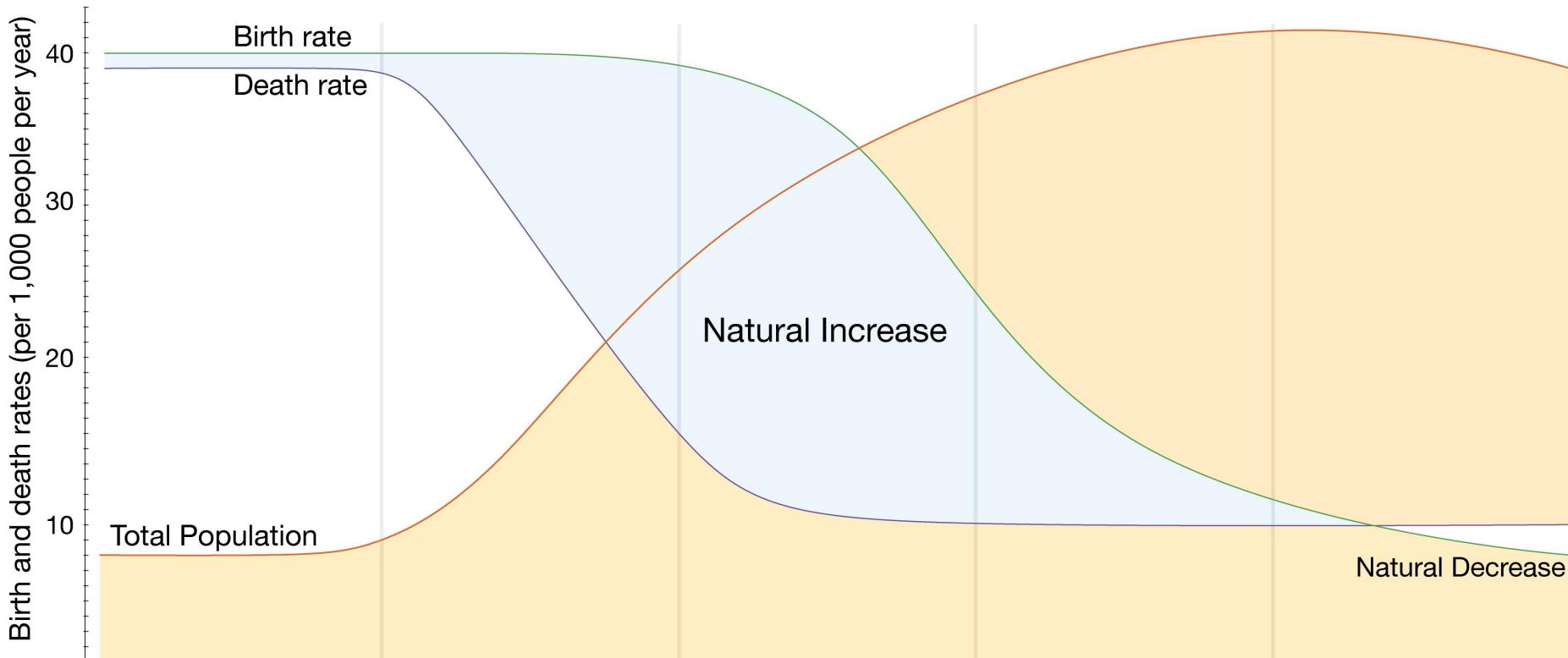


Humans are not like fish!
Fecundity tends to decrease in older age classes due to **reproductive senescence**.

Younger human populations that start giving birth earlier grow faster!

$$\begin{matrix}
 & \mathbf{A} & \mathbf{N}_t & \mathbf{N}_{t+1} \\
 \left[\begin{array}{cccc}
 0 & F_2 & F_3 & F_4 \\
 s_1 & 0 & 0 & 0 \\
 0 & s_2 & 0 & 0 \\
 0 & 0 & s_3 & 0
 \end{array} \right] & \times & \left[\begin{array}{c} N_1 \\ N_2 \\ N_3 \\ N_4 \end{array} \right] & = \left[\begin{array}{c} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{array} \right]
 \end{matrix}$$

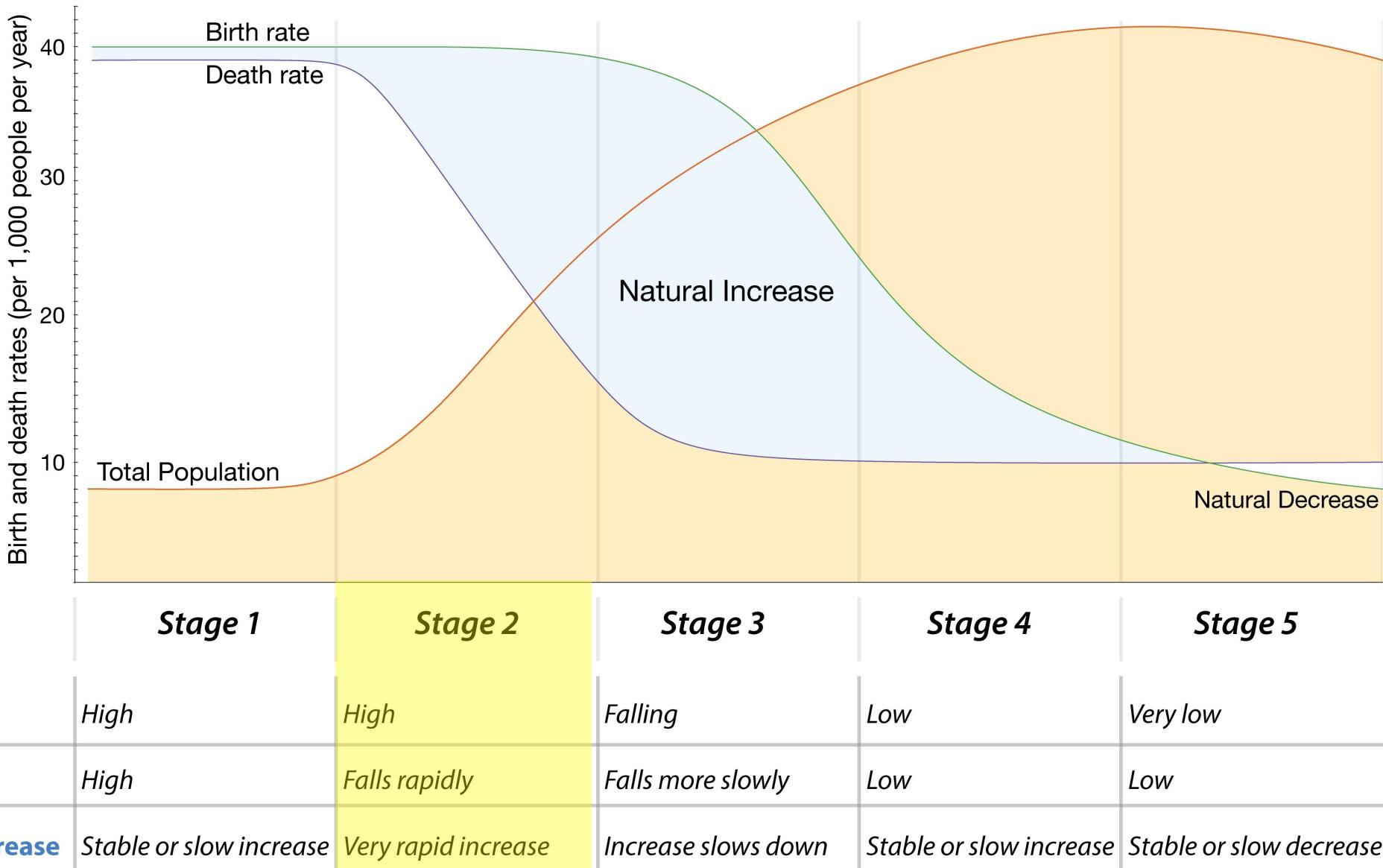
Demographic transition



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

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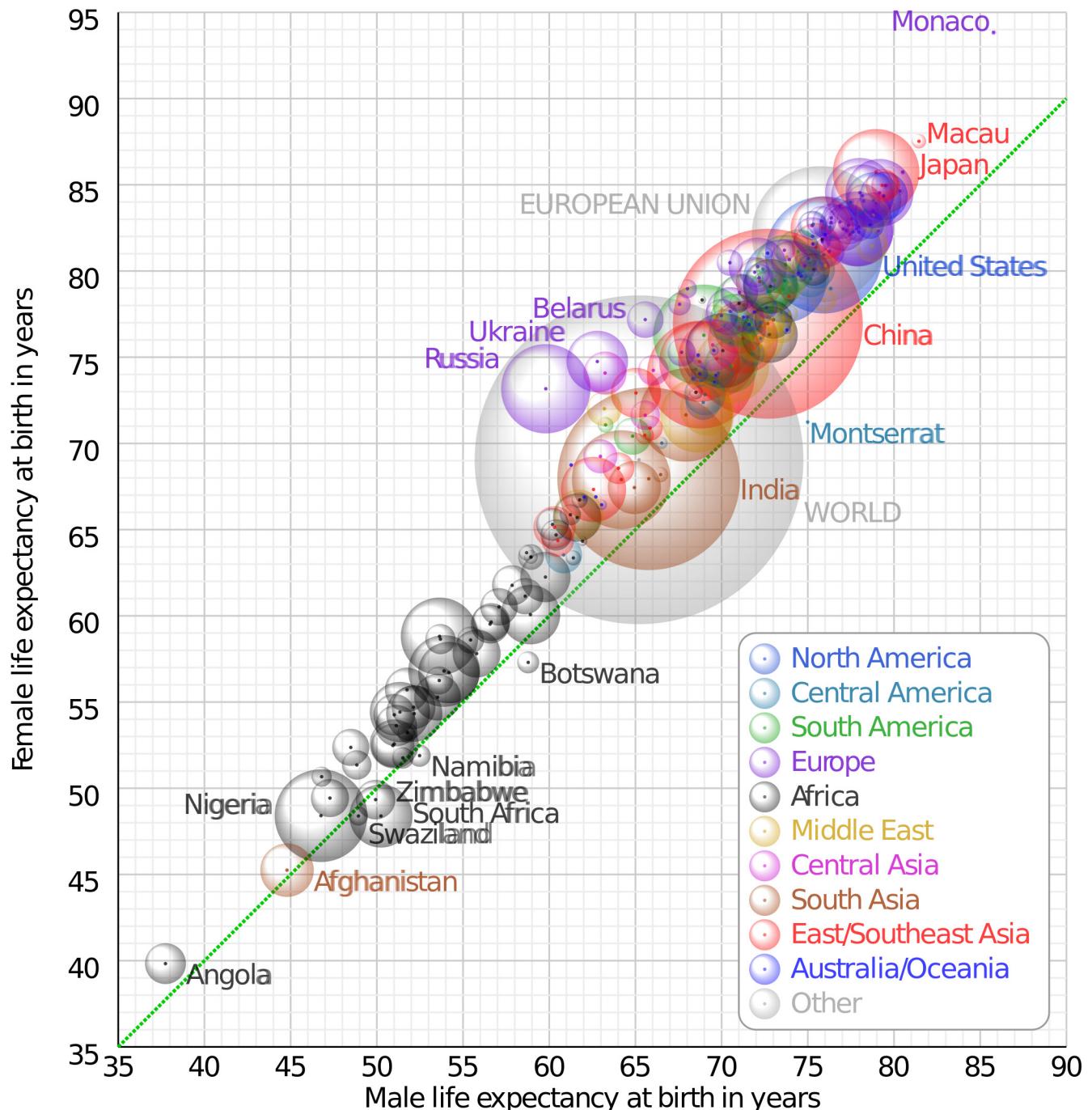
Demographic transition



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Demographic transition

Death rates are falling globally...

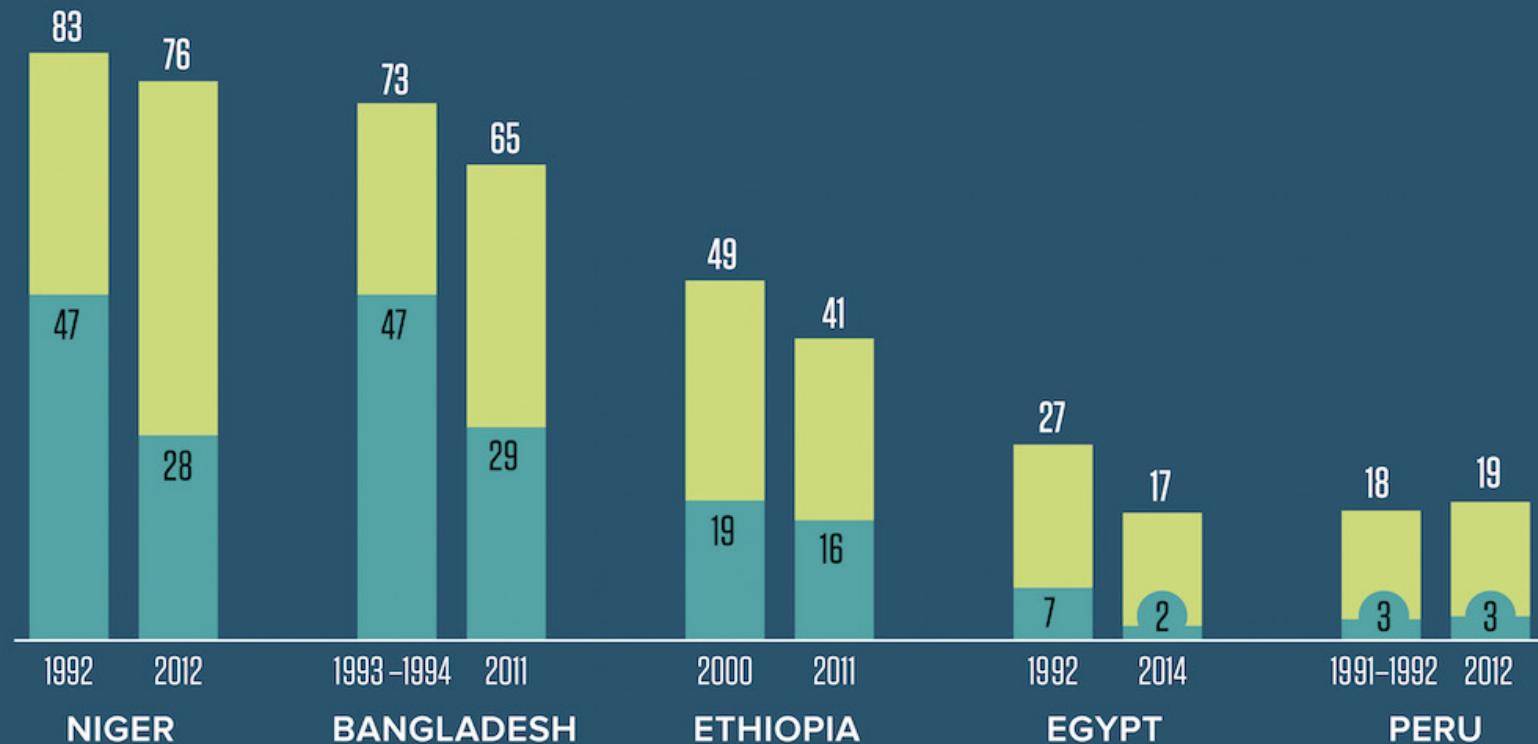


Demographic transition

And birth rates
are also falling...

RATES OF EARLY MARRIAGE FALL, PARTICULARLY AMONG THOSE UNDER 15

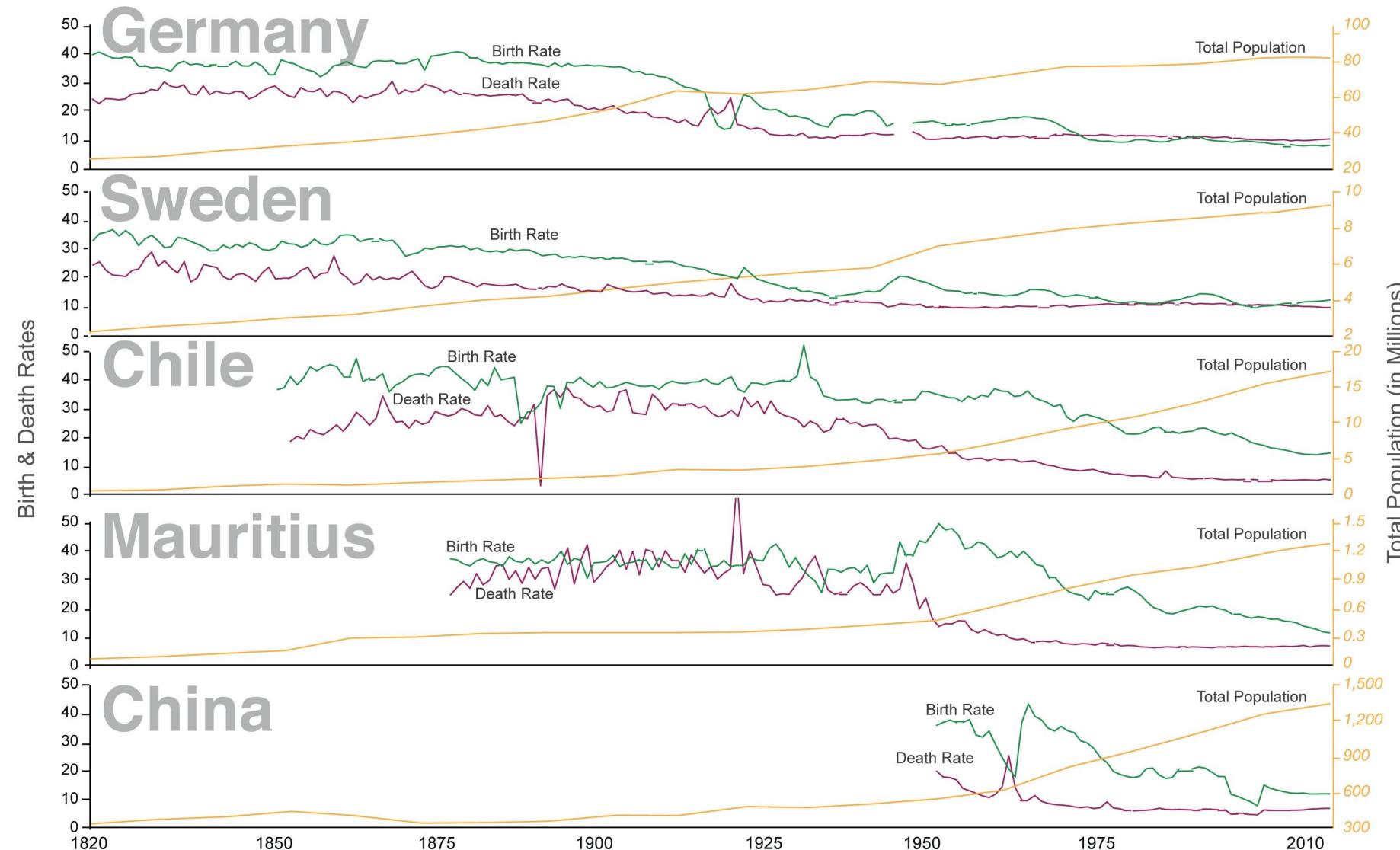
Percent of Young Women Married by Age 15 (numbers in black) and Age 18 (numbers in white)



SOURCE: ICF International, Demographic and Health Surveys.

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Demographic transition



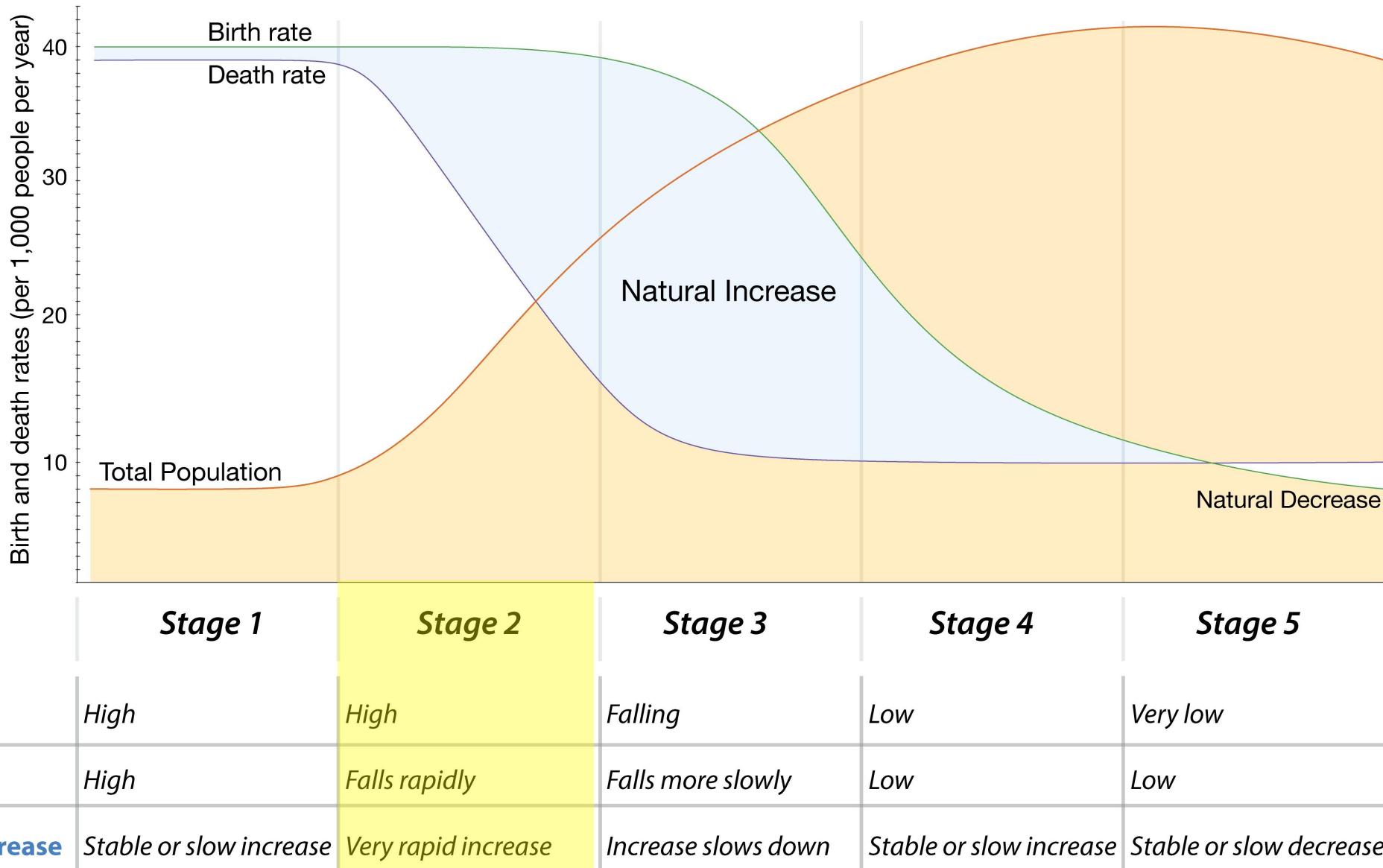
Data source: The data on birth rates, death rates and the total population are taken from the International Historical Statistics, edited by Palgrave Macmillan (April 2013).

The interactive data visualisation is available at OurWorldInData.org. There you find the raw data and more visualisations on this topic.

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Demographic transition

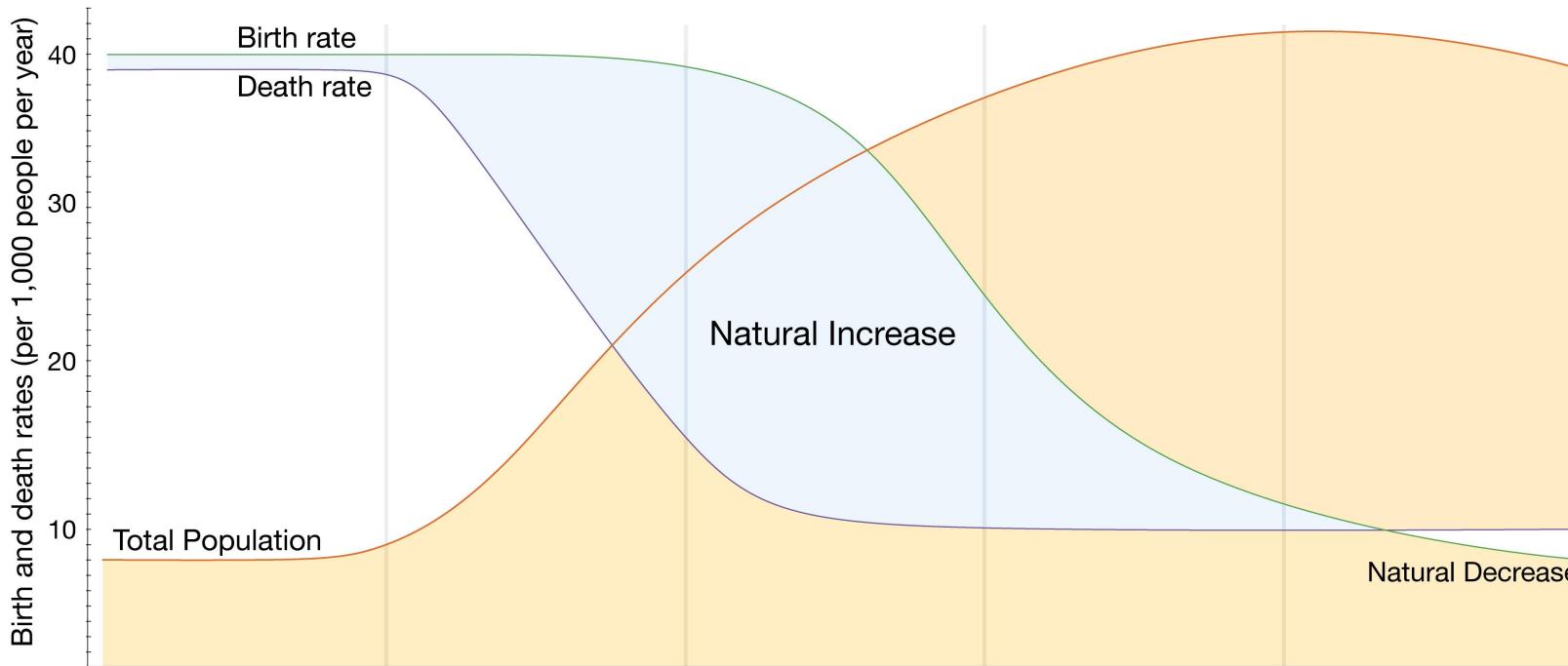
How does age structure predict population growth?



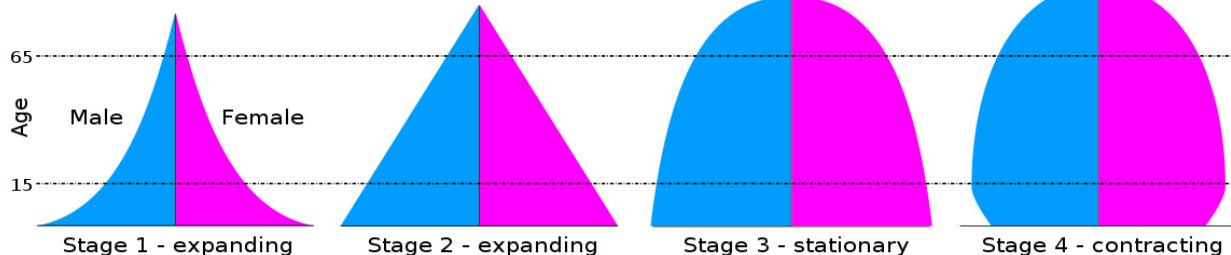
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Demographic transition

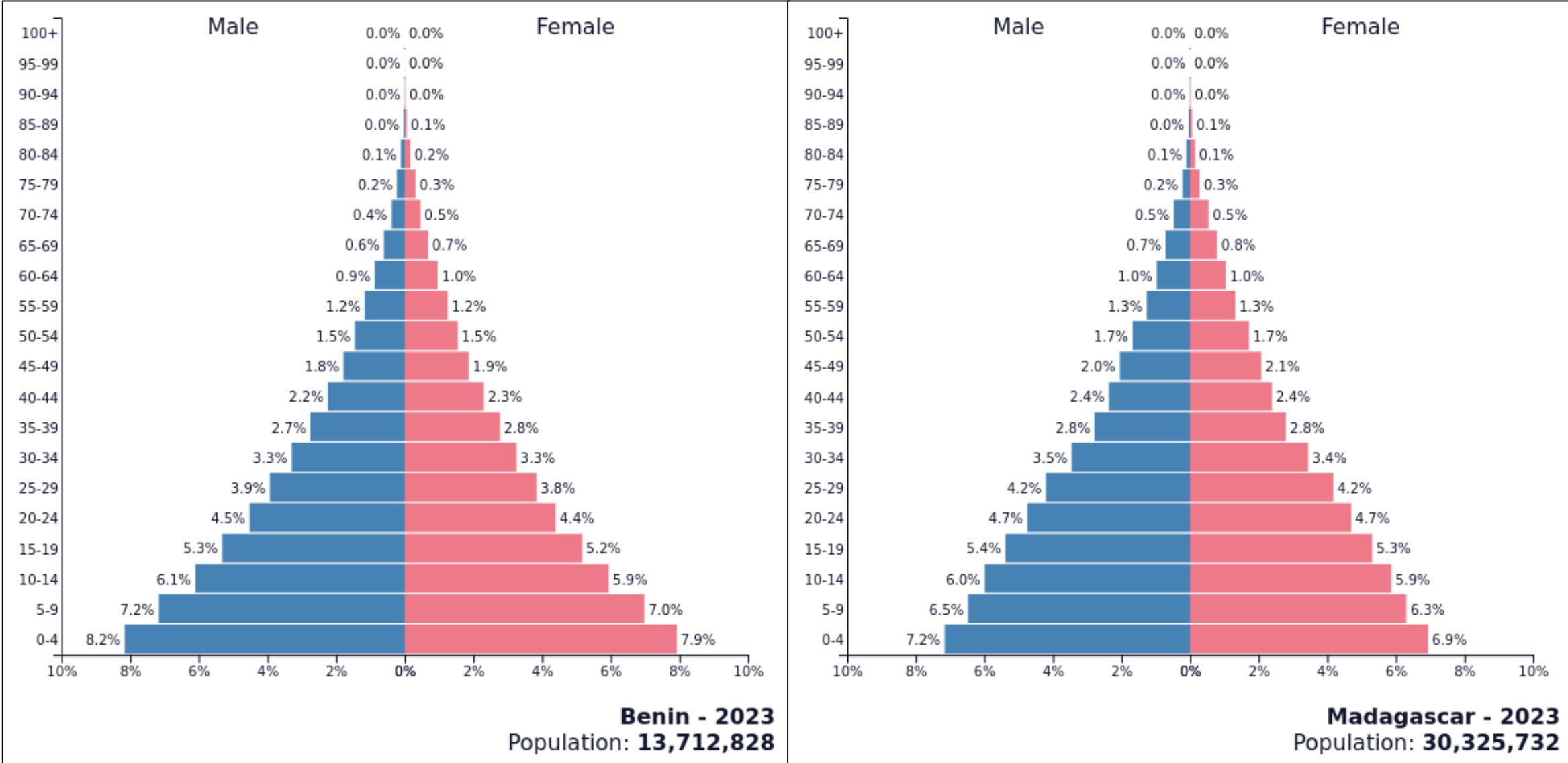
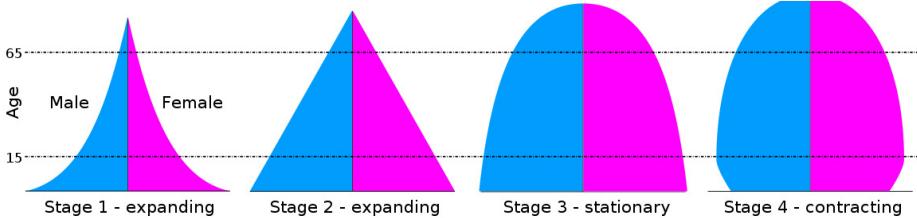
How does age structure predict population growth?



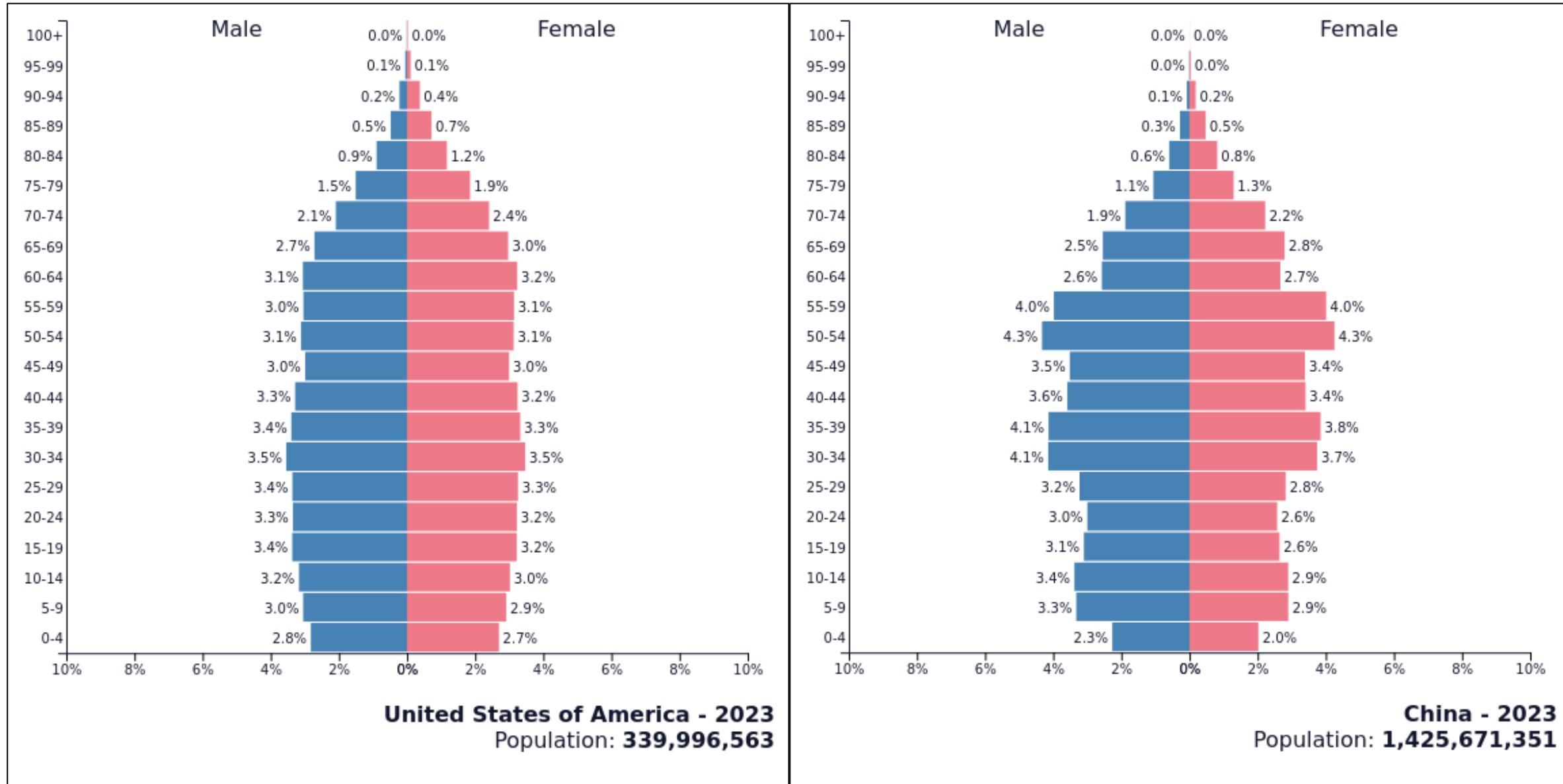
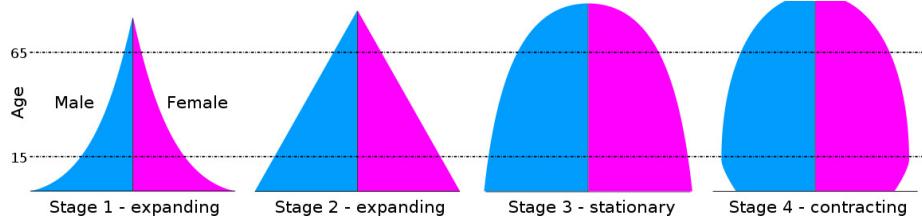
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Birth rate	High	High	Falling	Low	Very low
Death rate	High	Falls rapidly	Falls more slowly	Low	Low
Natural increase	Stable or slow increase	Very rapid increase	Increase slows down	Stable or slow increase	Stable or slow decrease



Where are we globally?



Where are we globally?



Where are we globally?

