# Fundamentals of Ecology

Week 6, Ecology Lecture 2

Cara Brook

February 9, 2023

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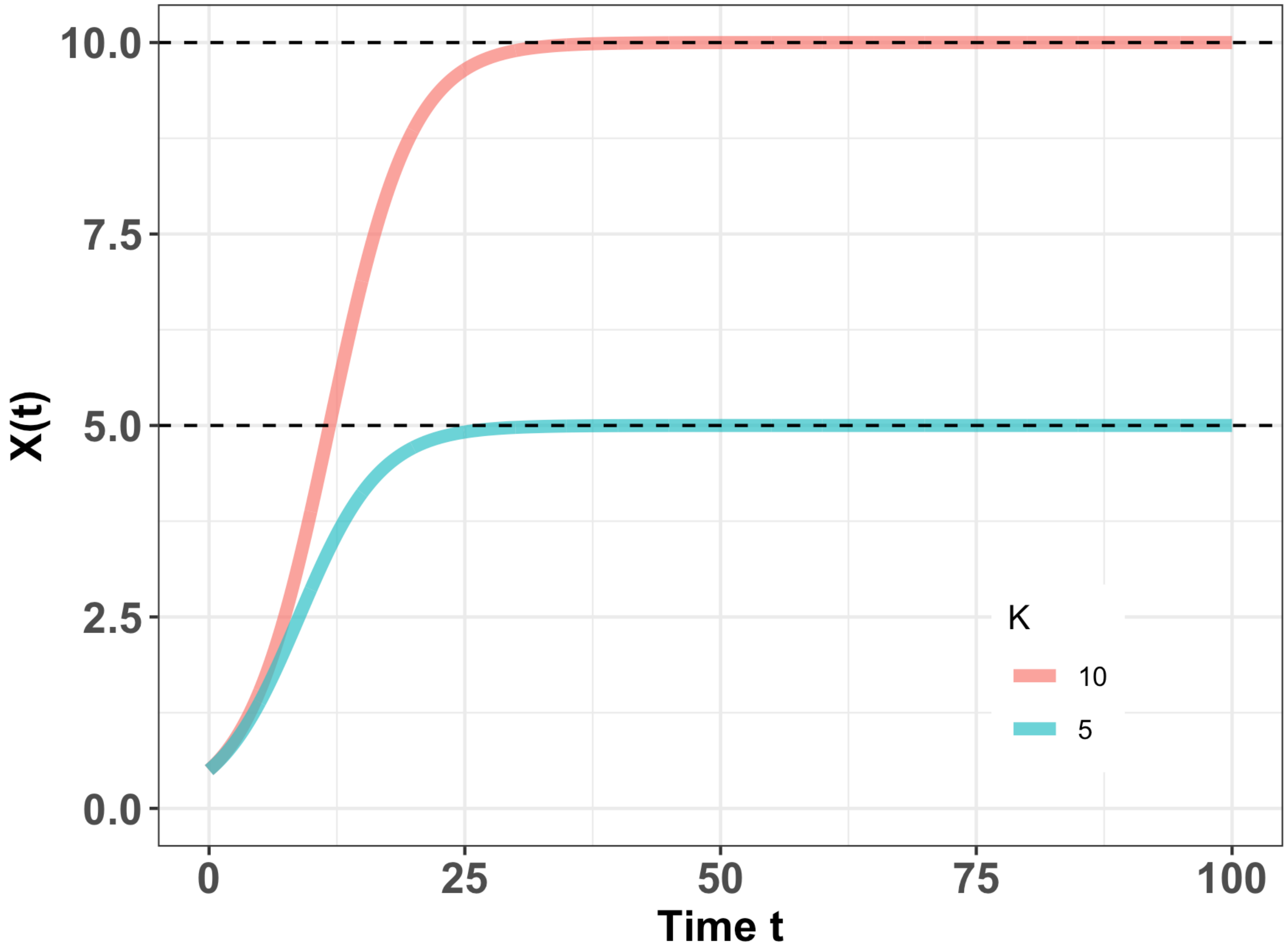
- Logistic growth models describe density-dependent growth rates that limit population growth as abundance approaches some specified carrying capacity
- Logistic growth models imply a stable equilibrium where the population size (N) is equal to the carrying capacity (K)
- Despite the dire predictions of Malthus in the late 1700s, most human populations do not appear to yet be approaching carrying capacity

# Logistic growth and equilibrium

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

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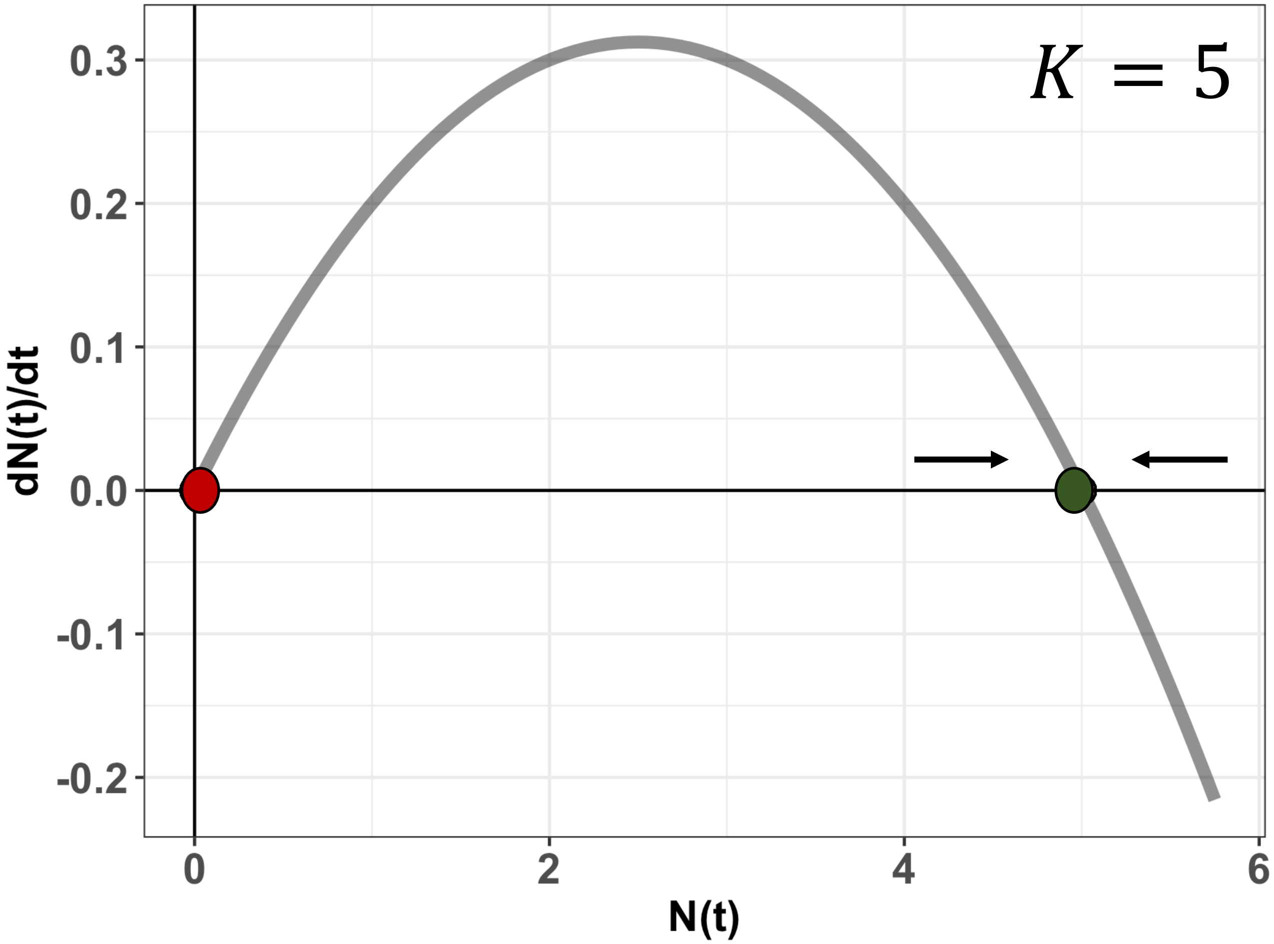


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When population size is not changing, the population is said to be at **equilibrium**.

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.

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population size

change in population size with time $\longrightarrow$ $$\frac{dN}{dt} = rN\underbrace{\left(1 - \frac{N}{K}\right)}_{\text{density-dependence}} - \boxed{H}$$ $\longleftarrow$ **harvesting rate**

carrying capacity

intrinsic growth rate

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.

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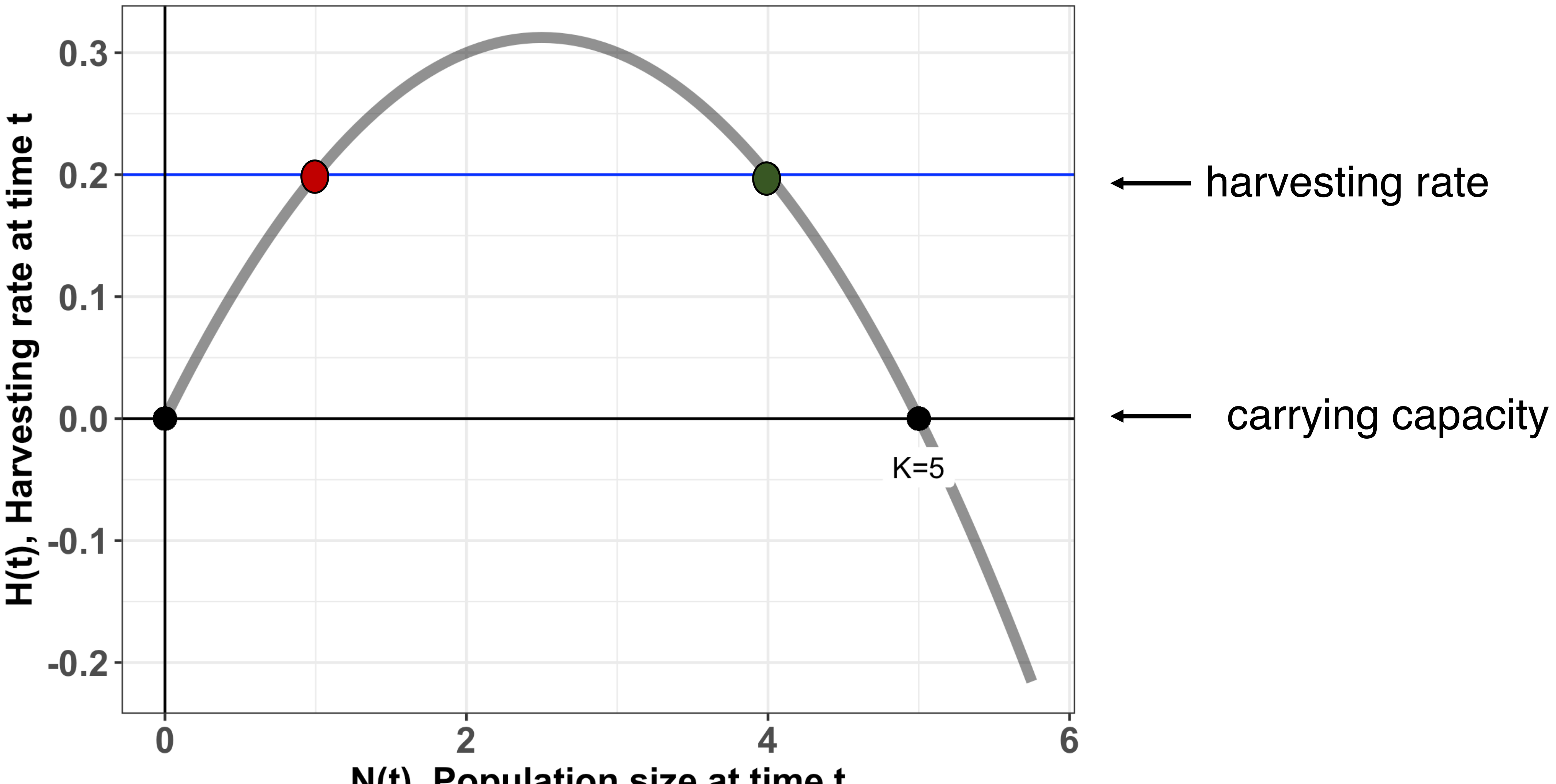

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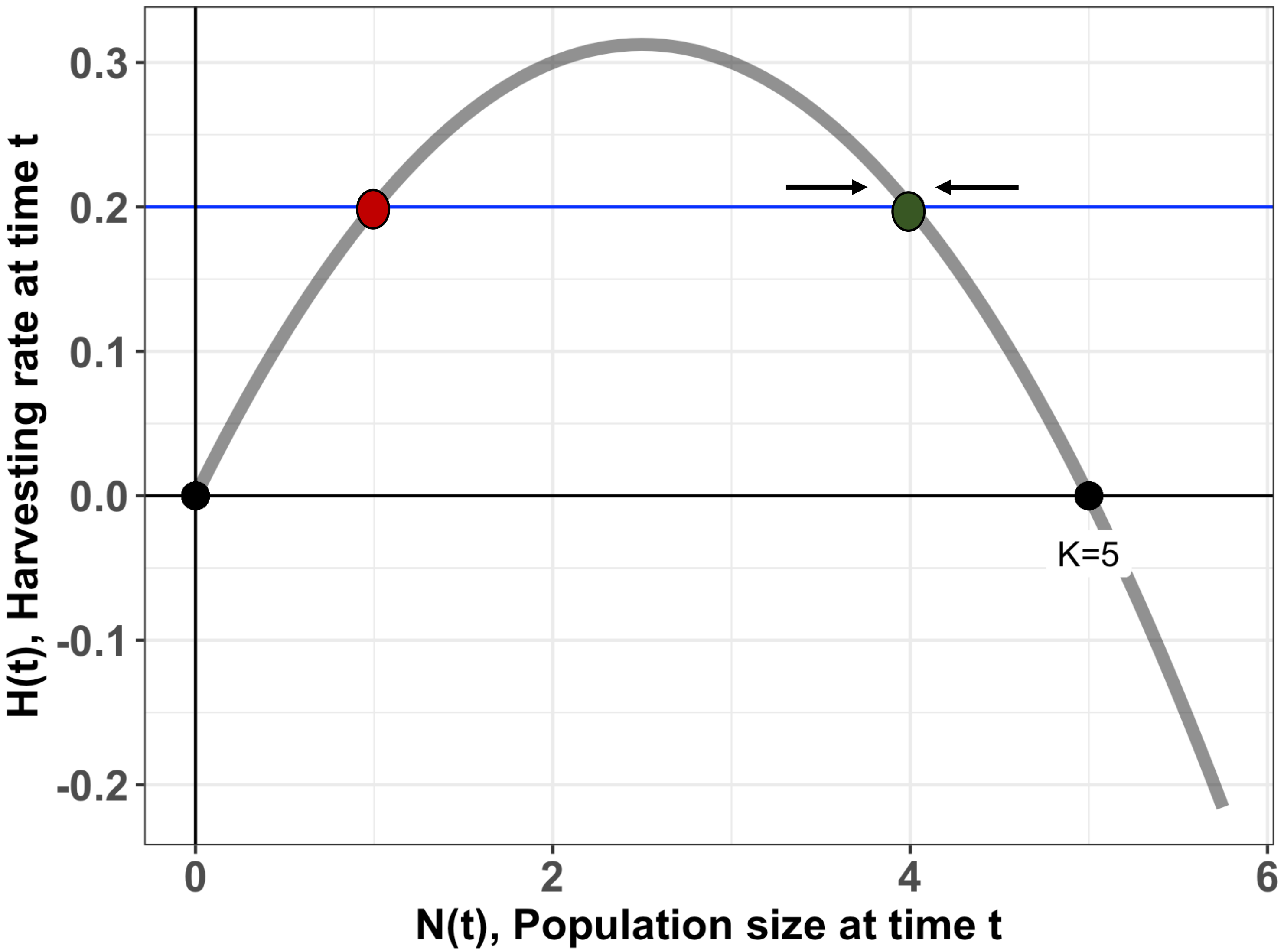


**stable equilibrium**
For a population of N=4, a harvest rate of 0.2 (animals/timestep) results in a stable equilibrium (**sustainable harvest**).

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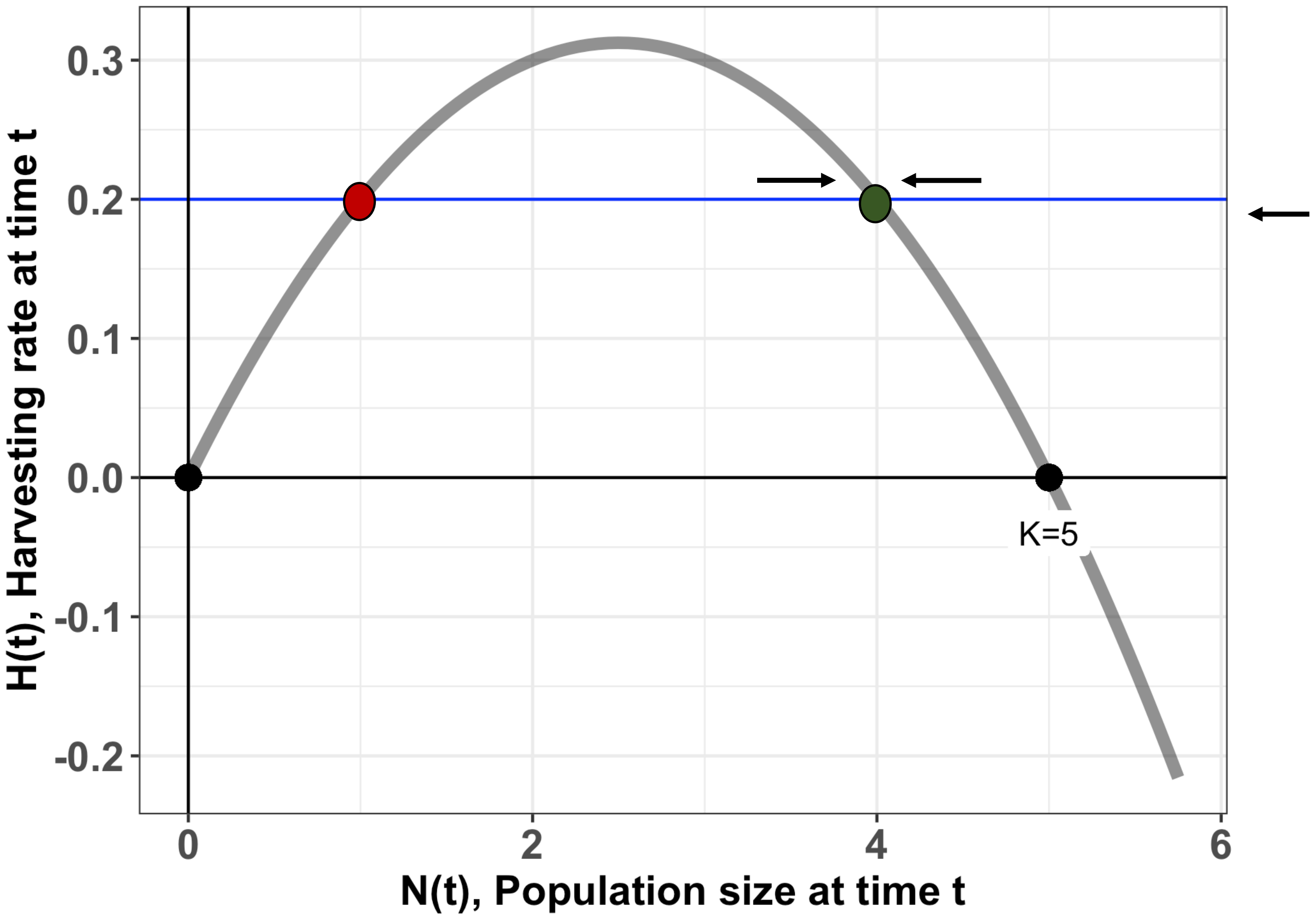


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Increases or decreases in population size will be compensated to return the system to N=4.

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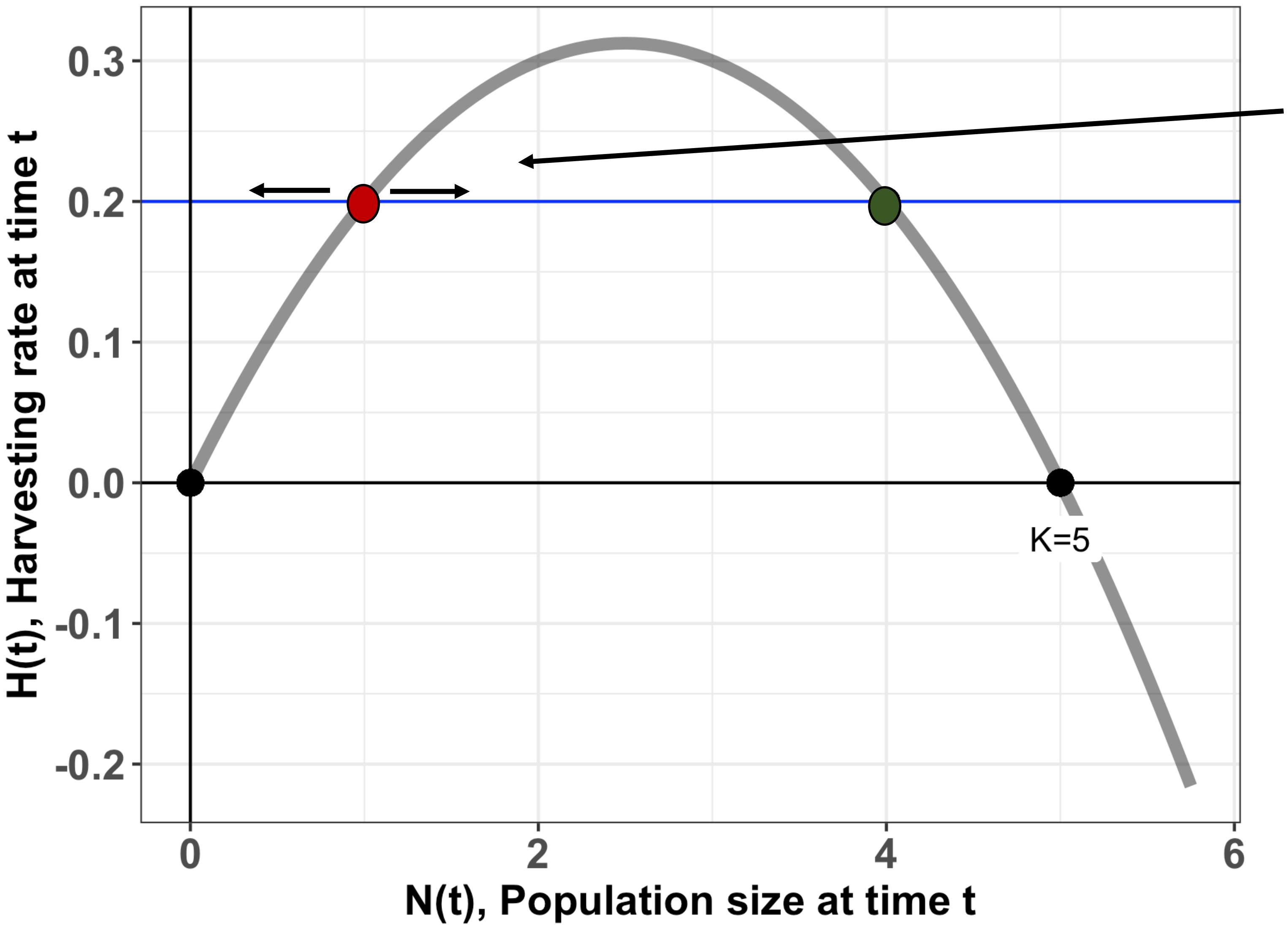


**unstable equilibrium**

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

# The stability of harvesting depends on population size.

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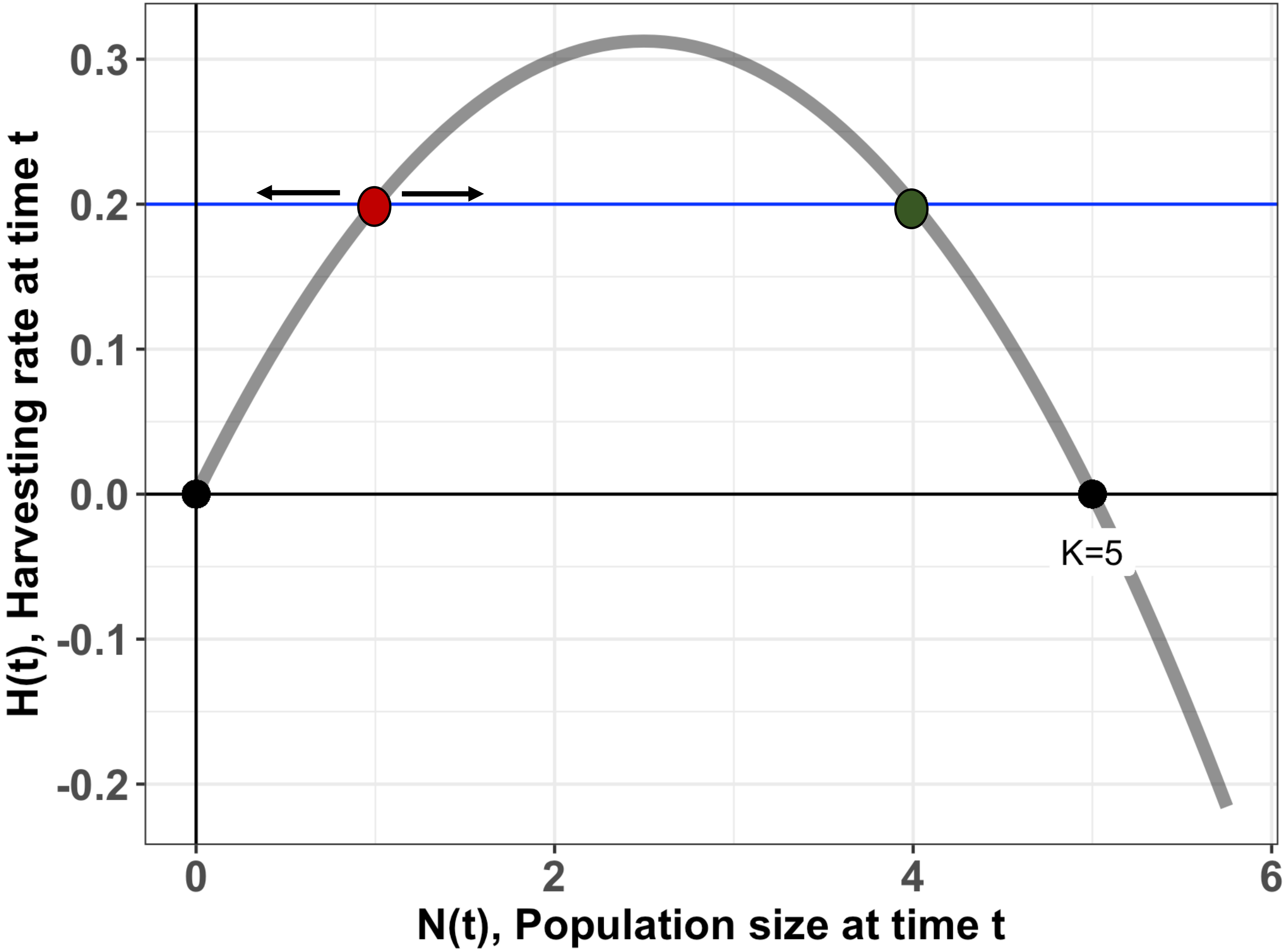


**unstable equilibrium**

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)

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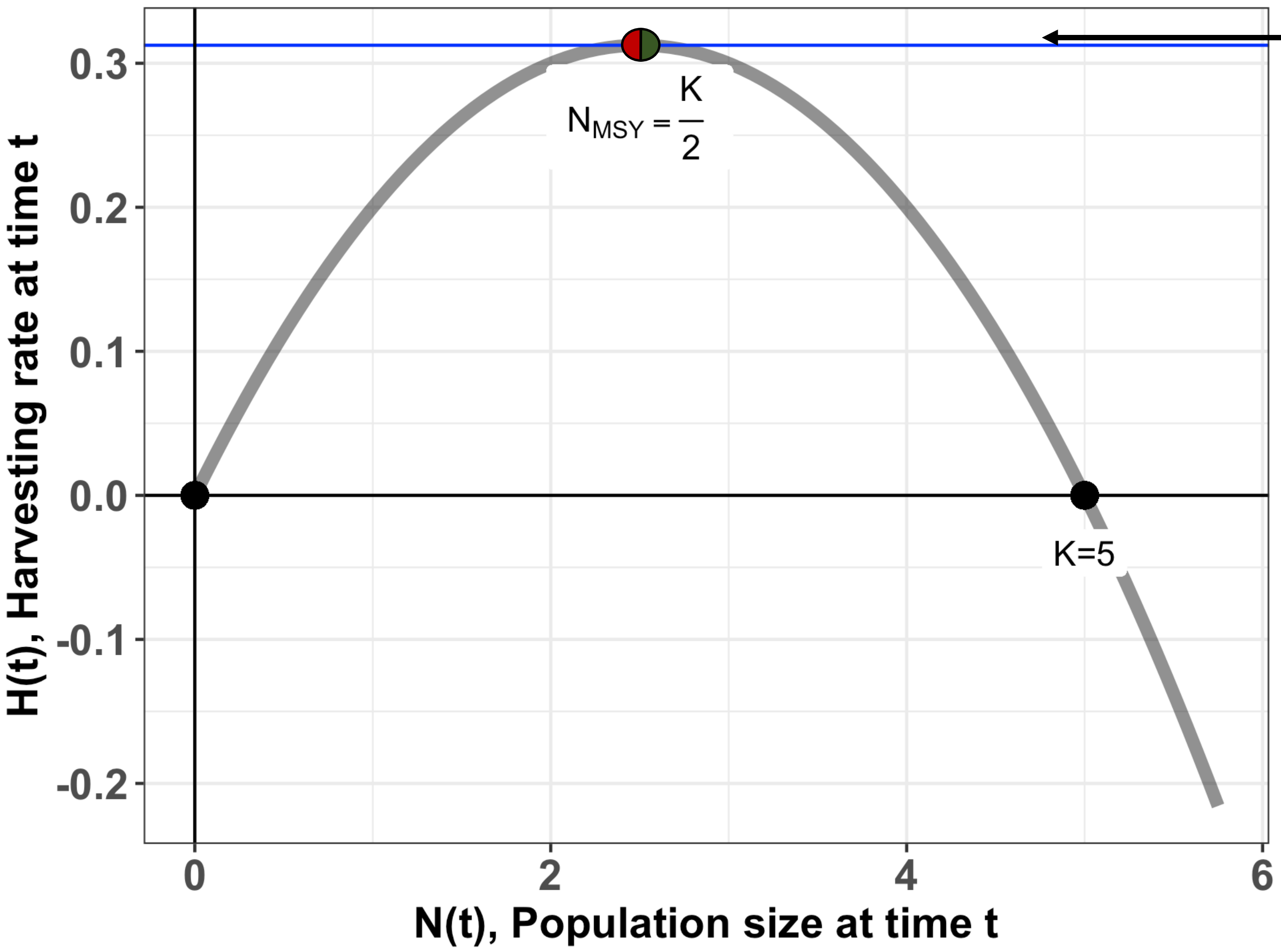


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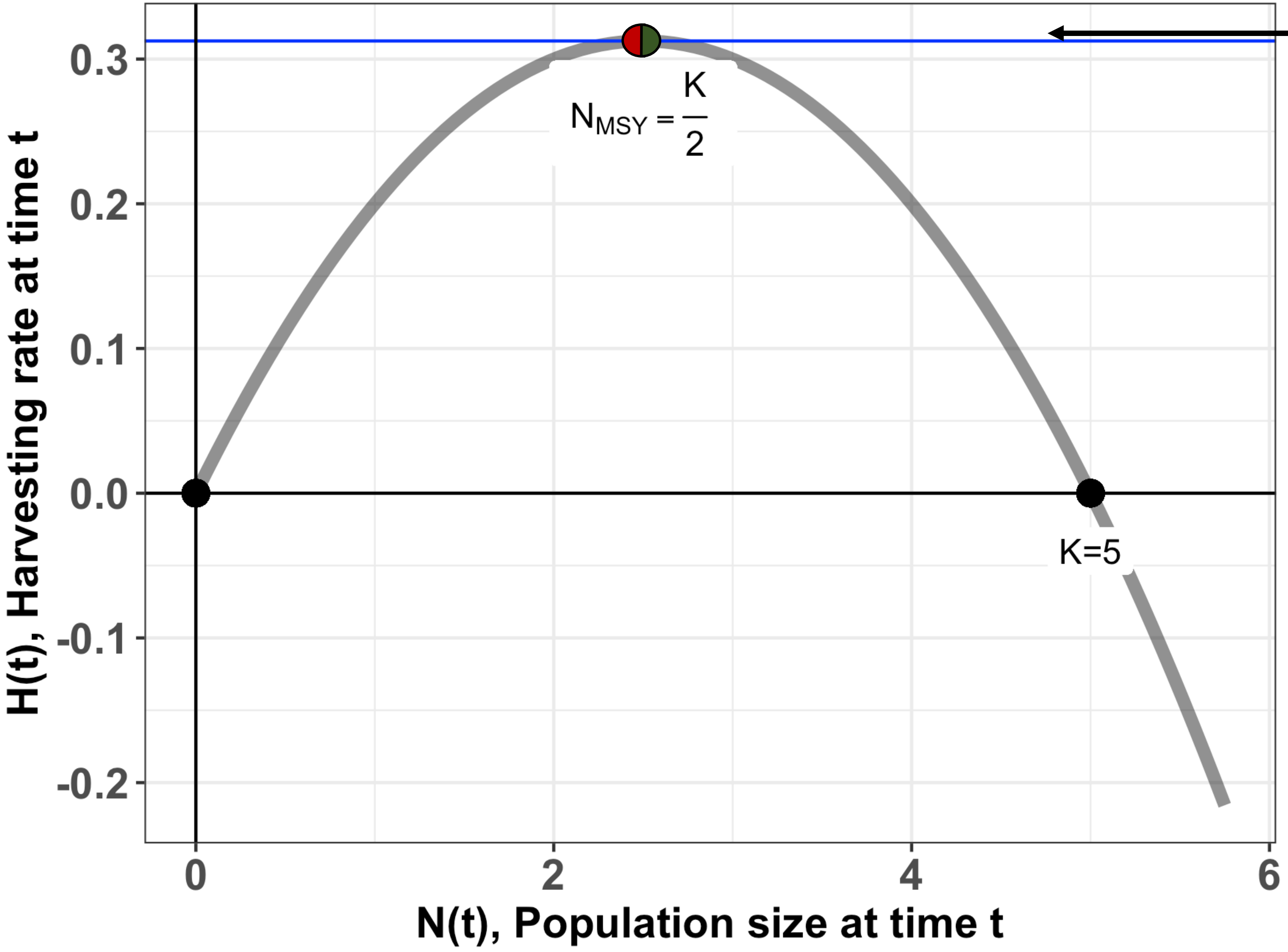


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Theoretically, harvest could be maximized here as well:

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

*take the derivative with respect to N*

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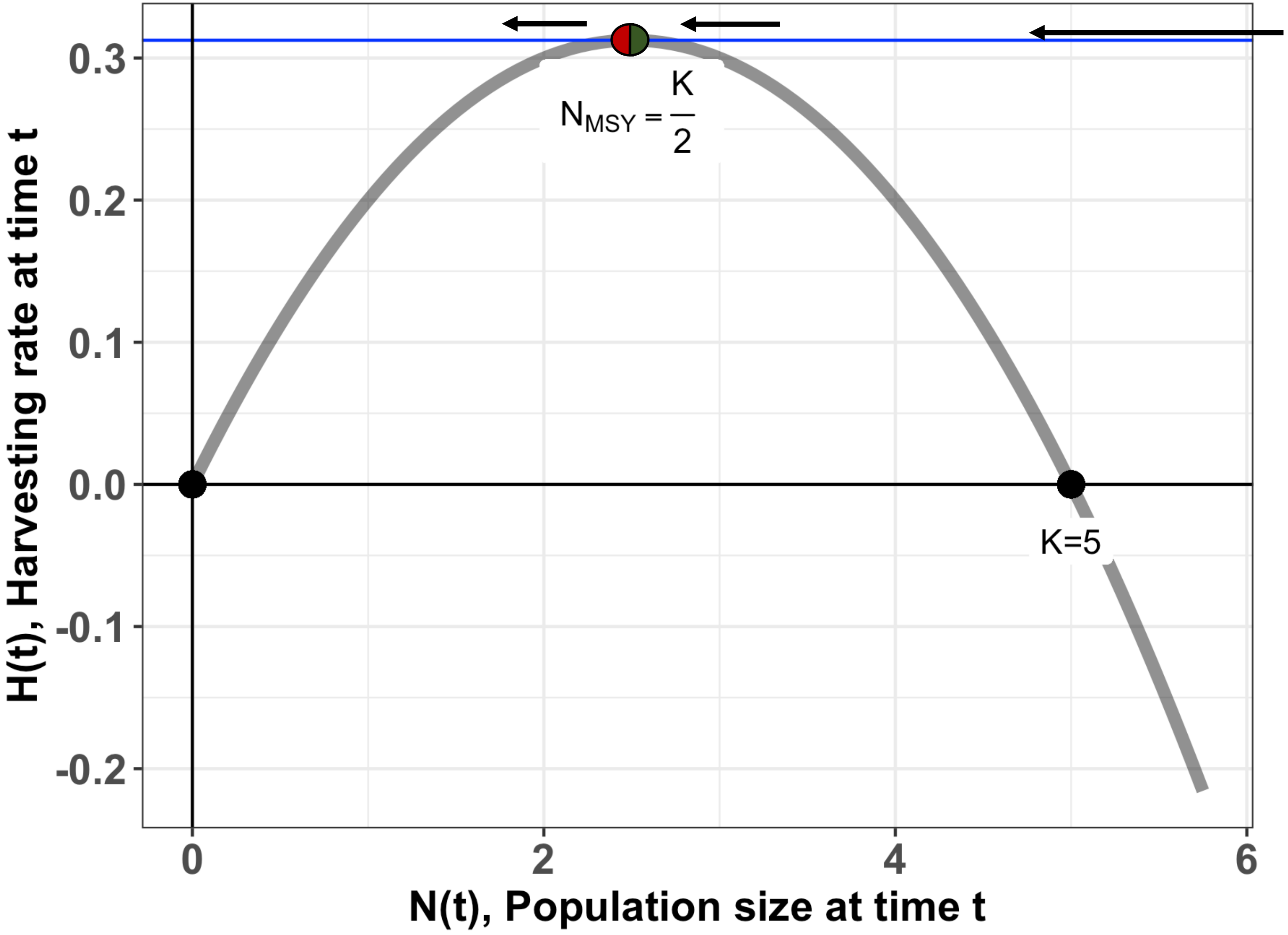
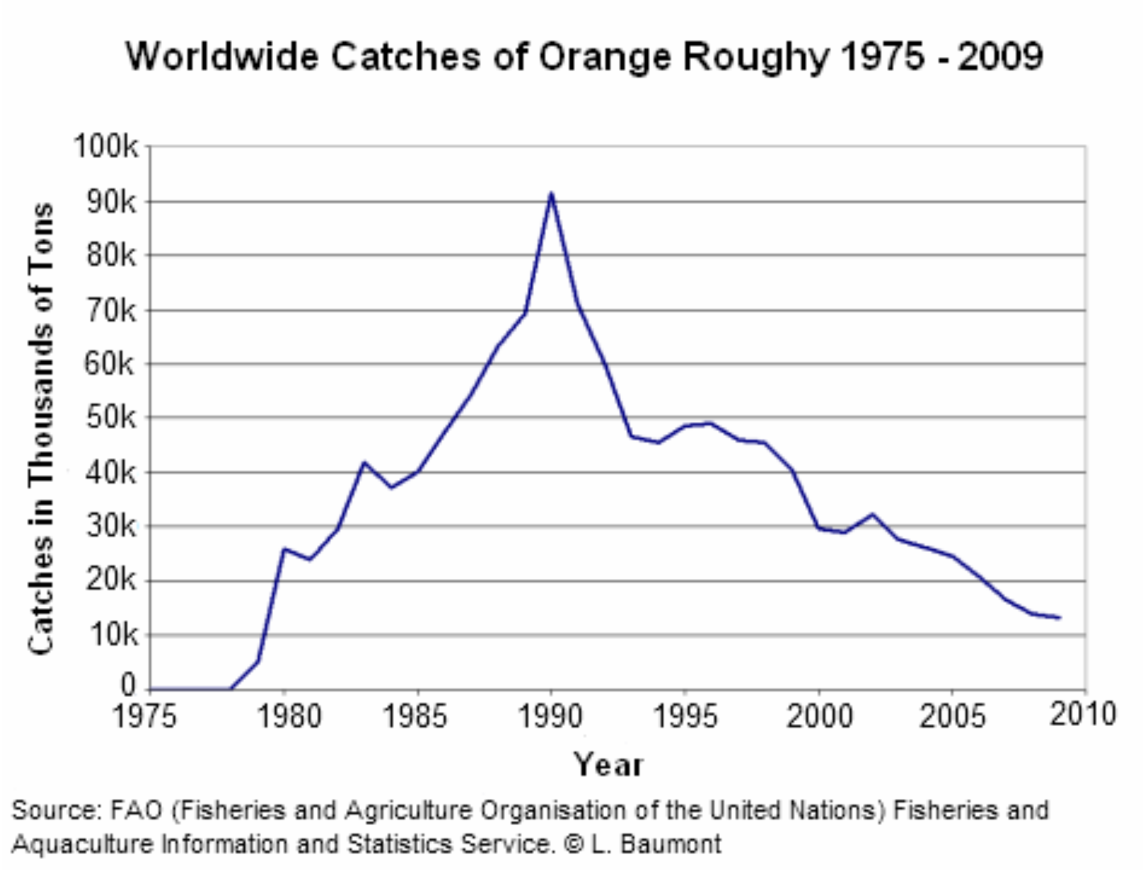



**MSY:** $H_{max} = \frac{rK}{4}$

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)



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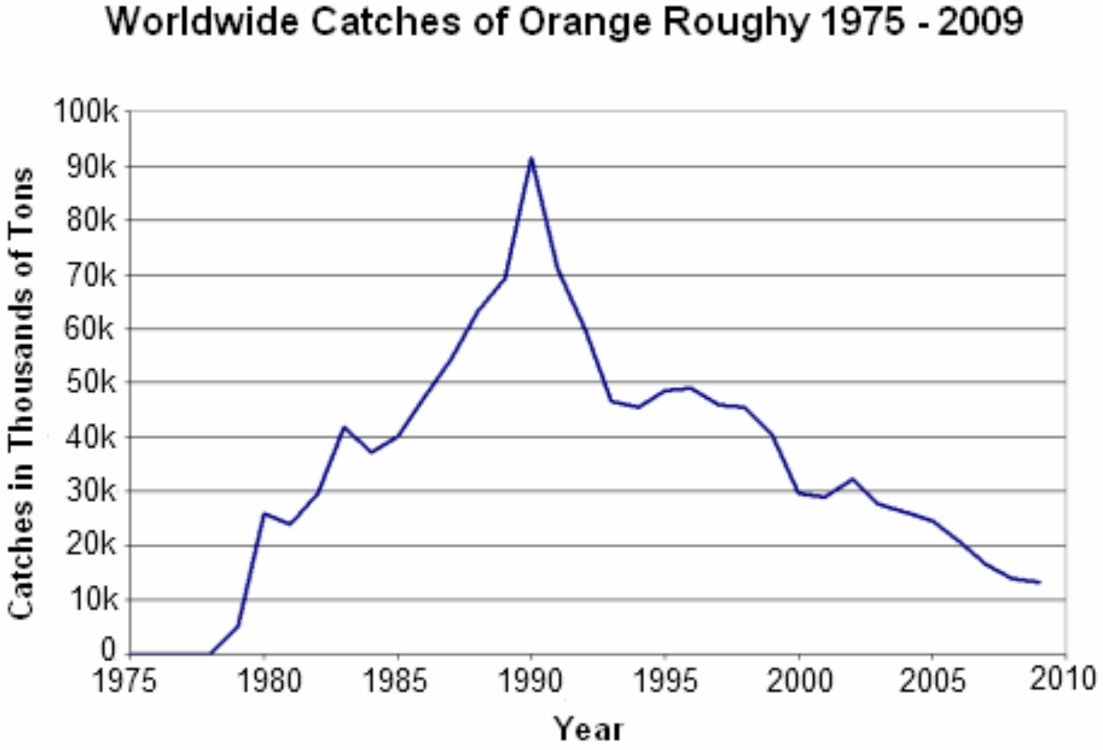


Source: FAO (Fisheries and Agriculture Organisation of the United Nations) Fisheries and Aquaculture Information and Statistics Service. © L. Baumont

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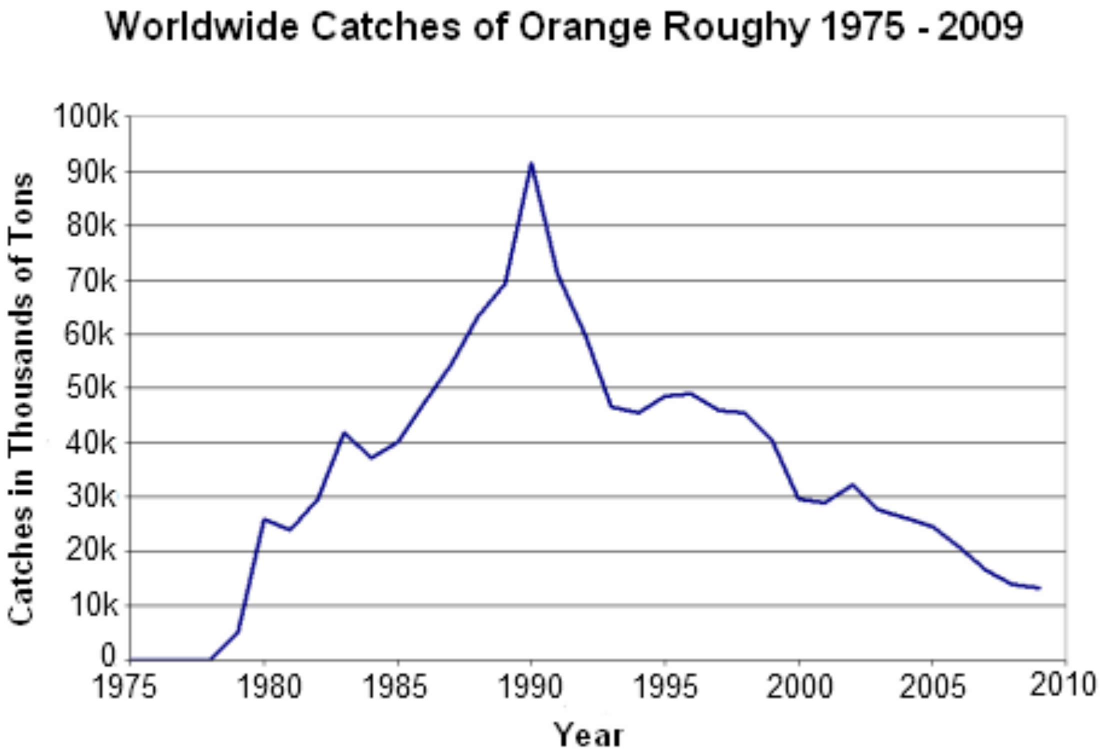


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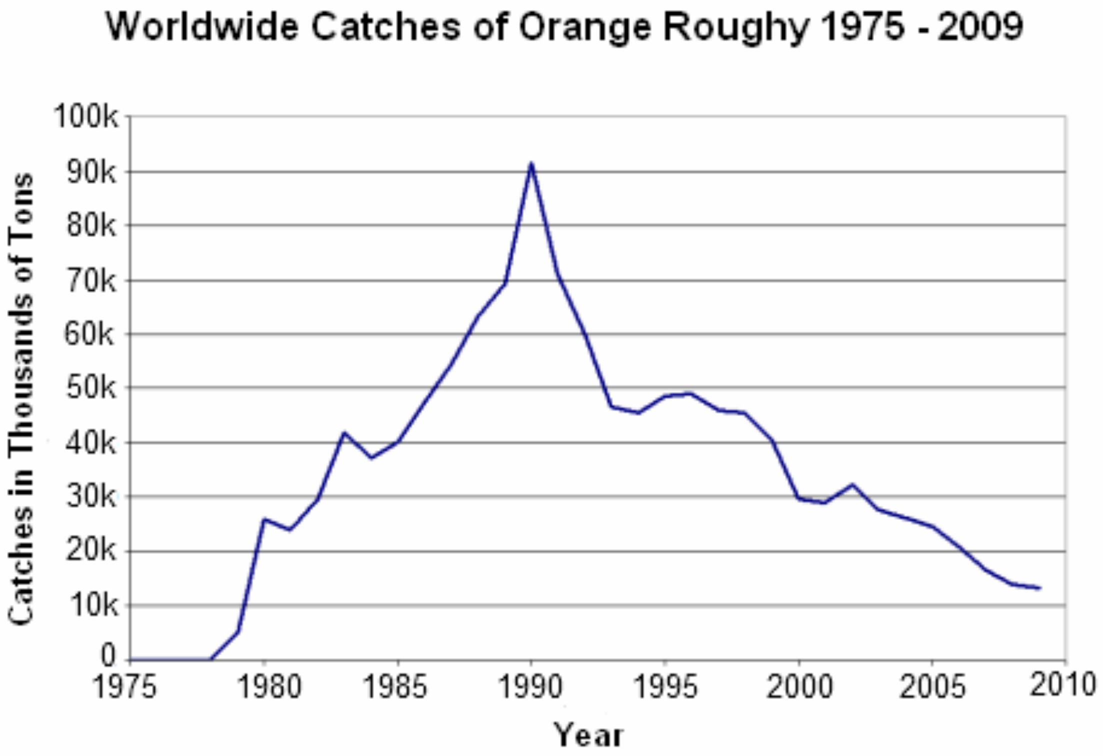


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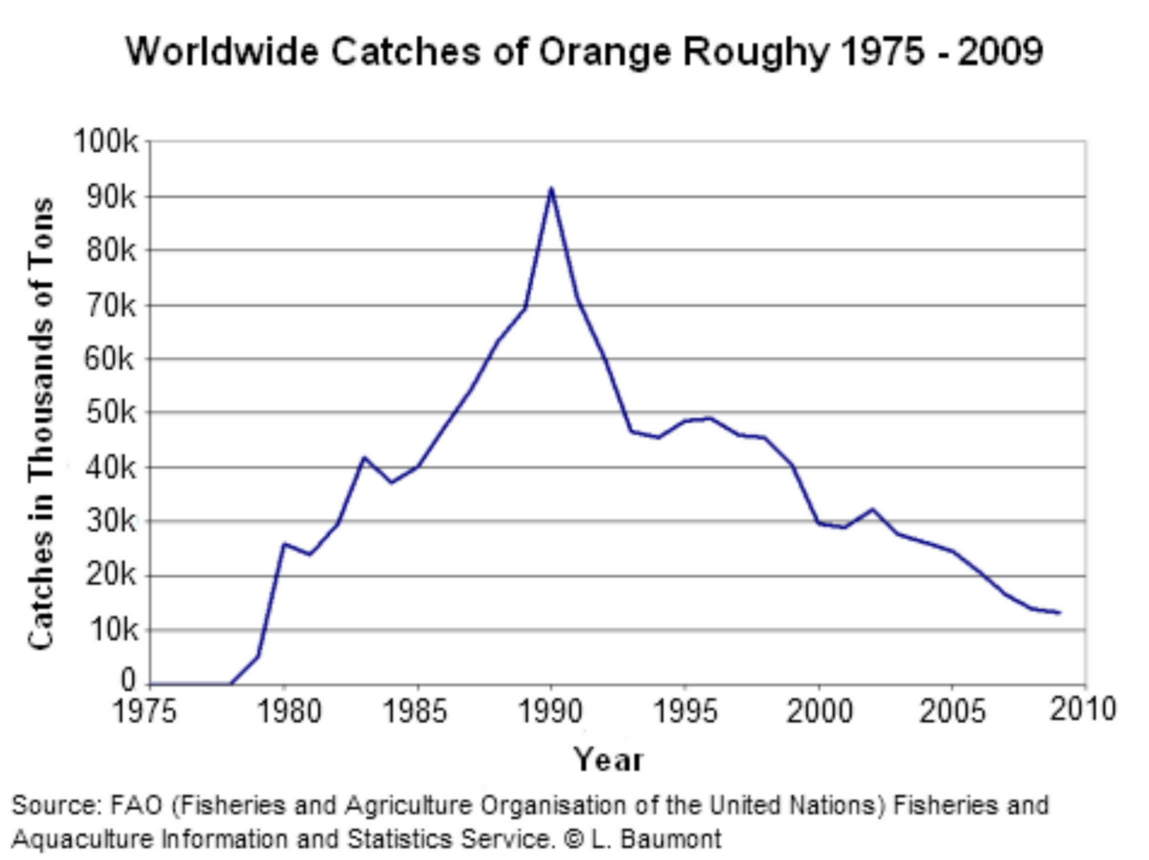
- High catch levels quickly decreased as stocks were fished down. By the late 1990s, three of the eight NZ orange roughy fisheries had collapsed and were closed.



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

- *r* and *K* and N are difficult to measure.

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# 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.
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  - 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

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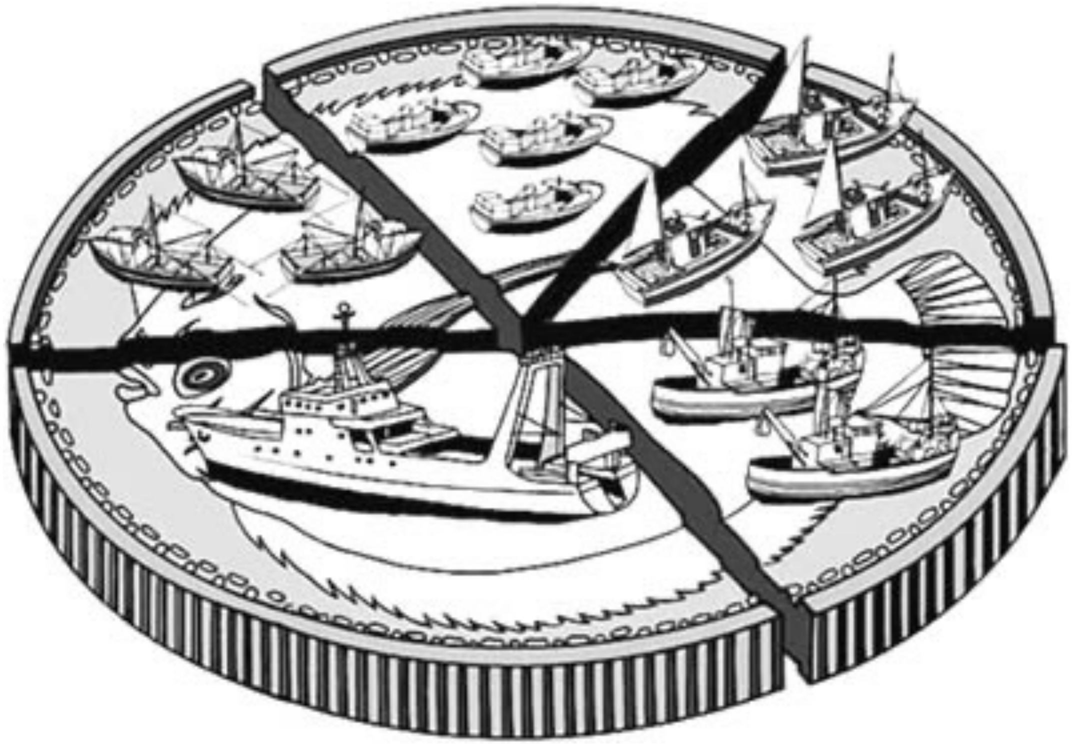
  - This practice can lead to intense pressure to fish all at once at the season's opening, sometimes overshooting the TAC.



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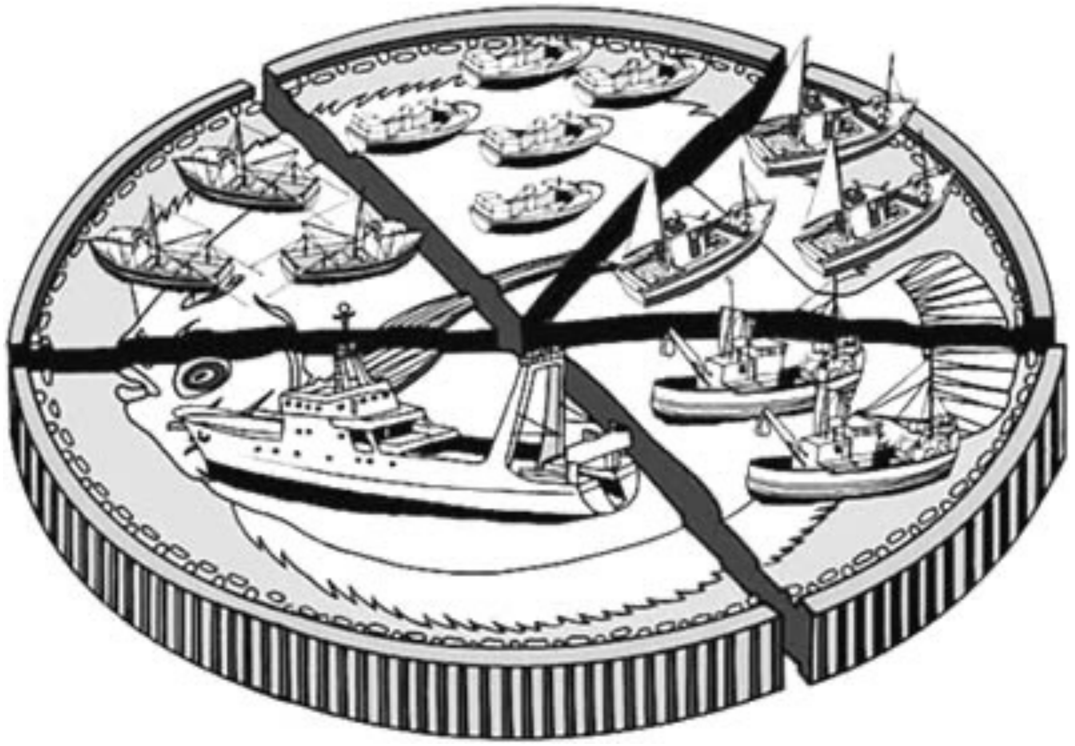

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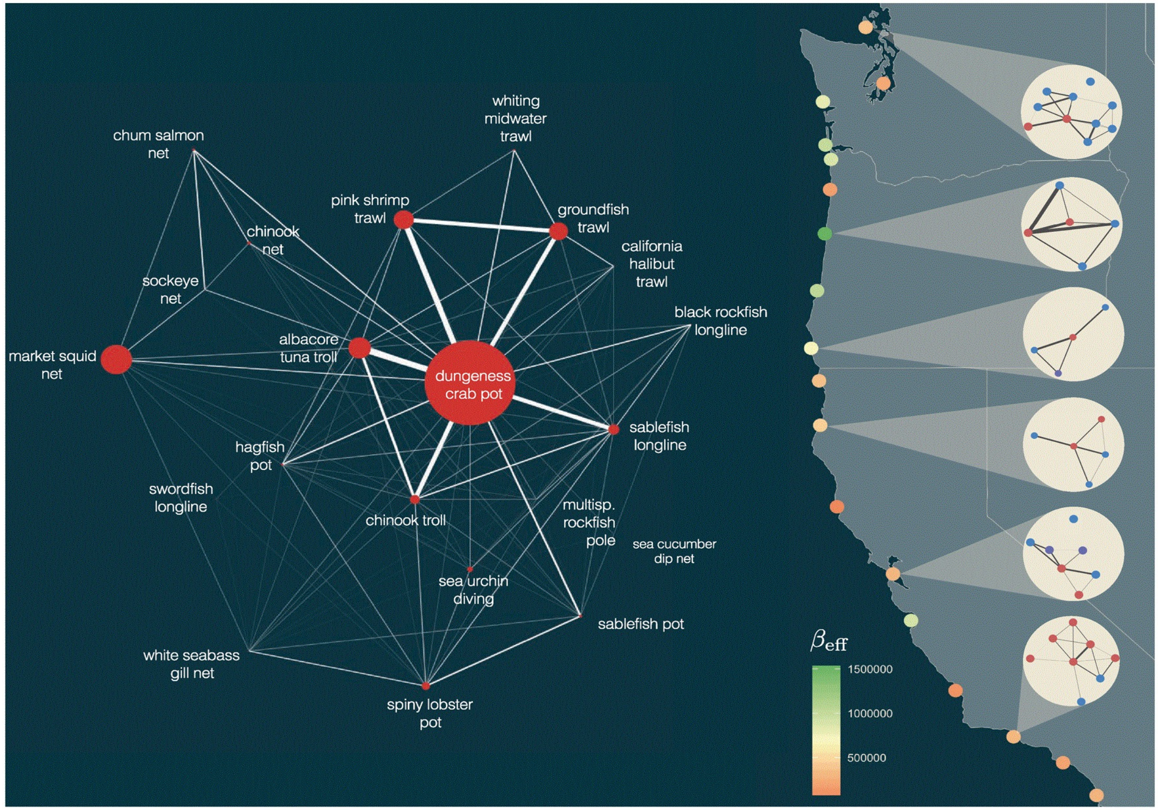
- The work of Elinor Ostrom showed that some of these challenges can be overcome when the limits of a resource are clearly defined, when the group of stakeholders is small, and when communication is high.




Dr. Emma Fuller, Fractal Agriculture

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

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- 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**

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# Deterministic vs. Stochastic

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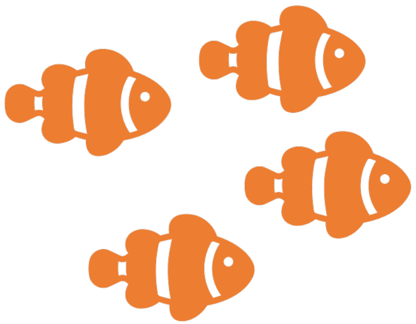

annual survival rate = 0.5

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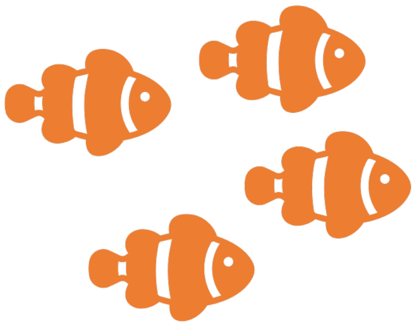

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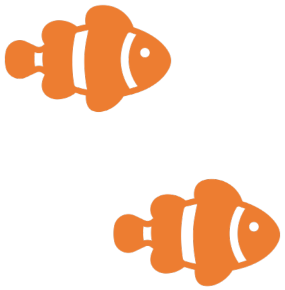

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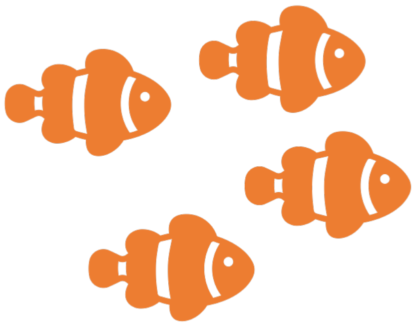

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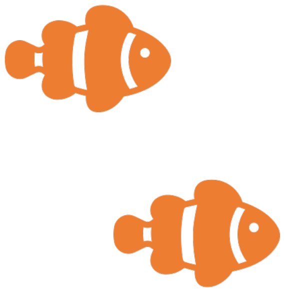

All the models we have looked at so far have been deterministic!

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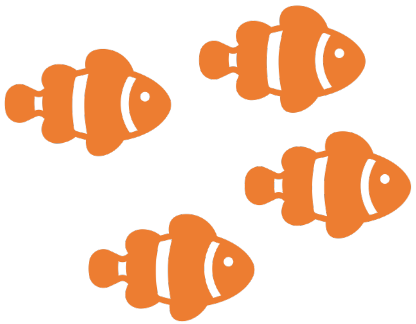

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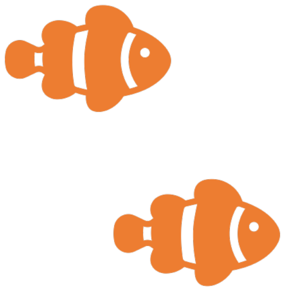

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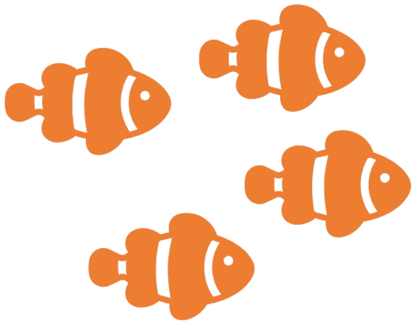

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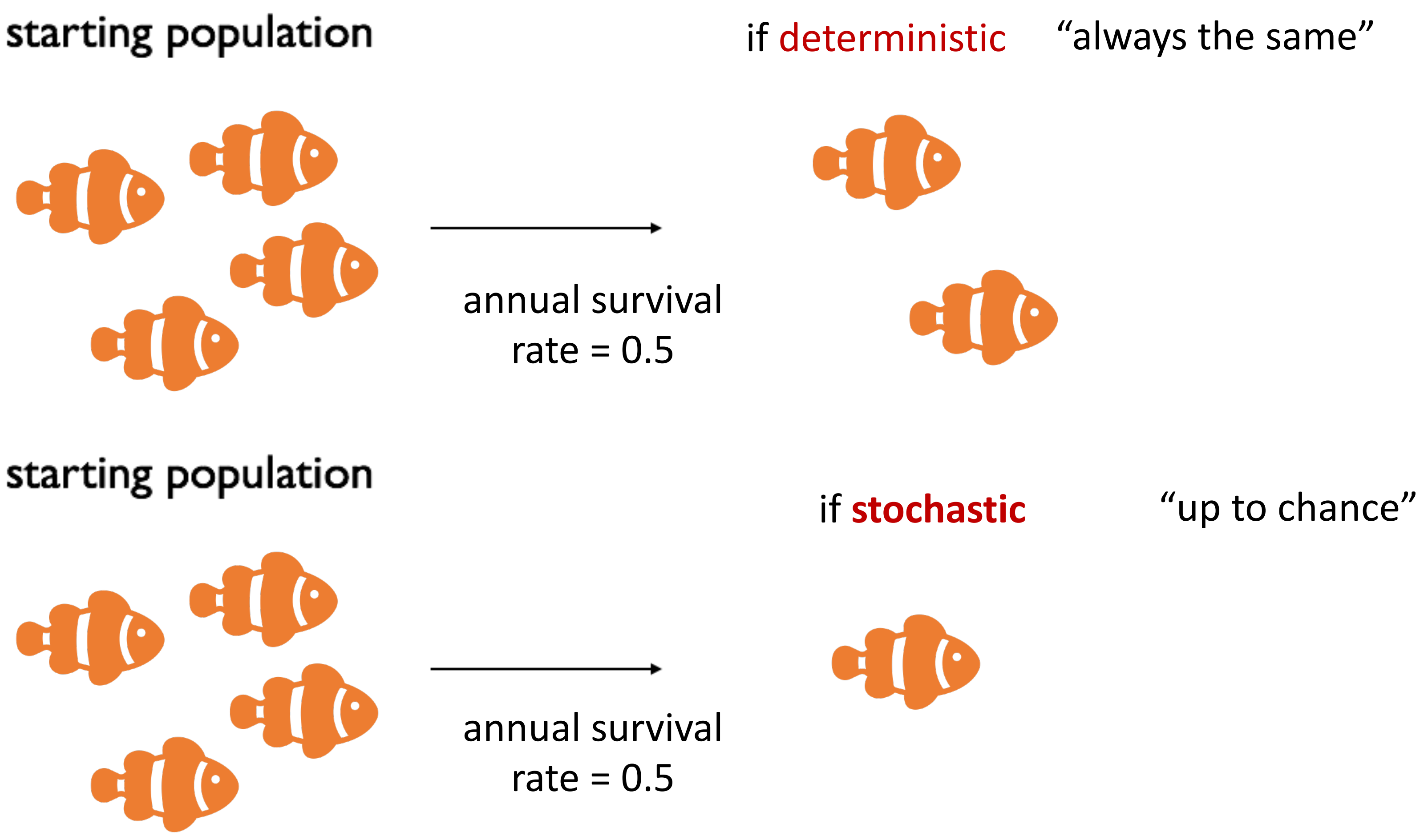

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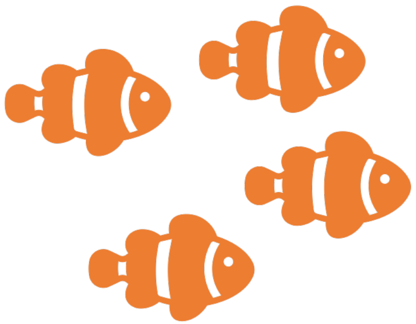

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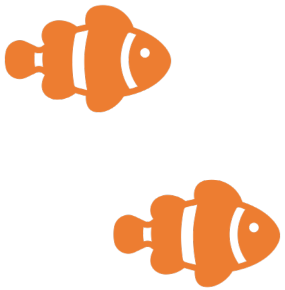

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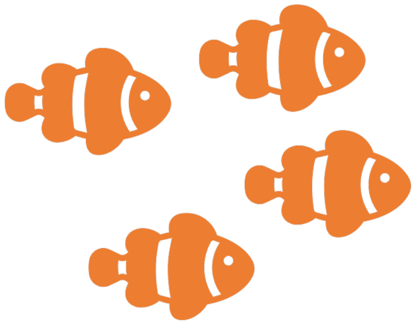

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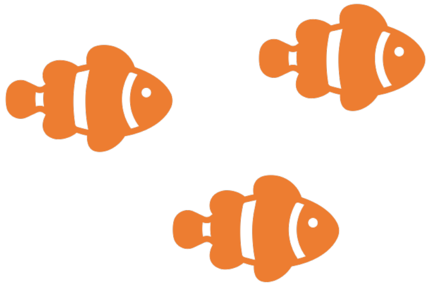
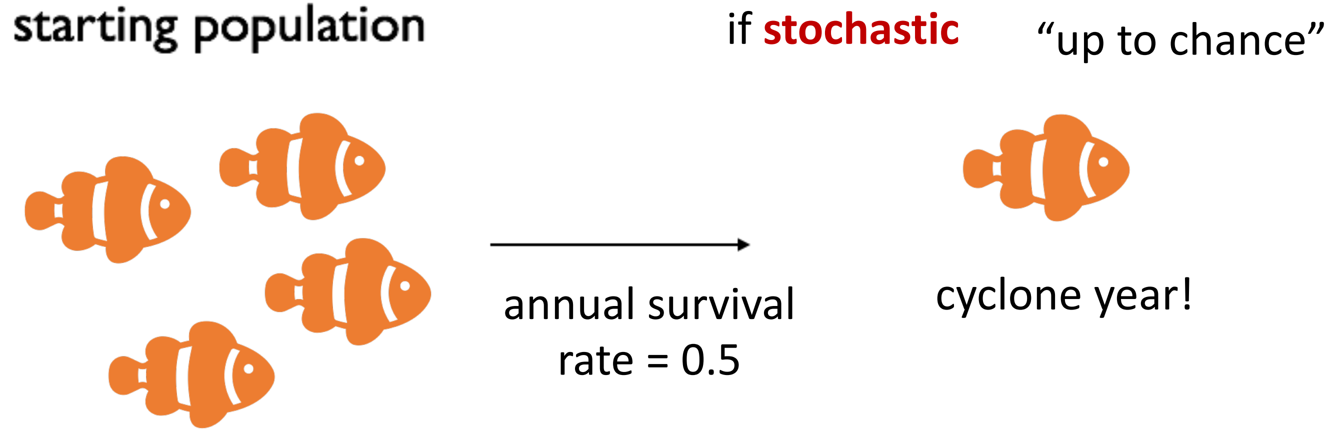


# The case of the orange roughy highlights many of the **inherent problems with MSY**

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- 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)

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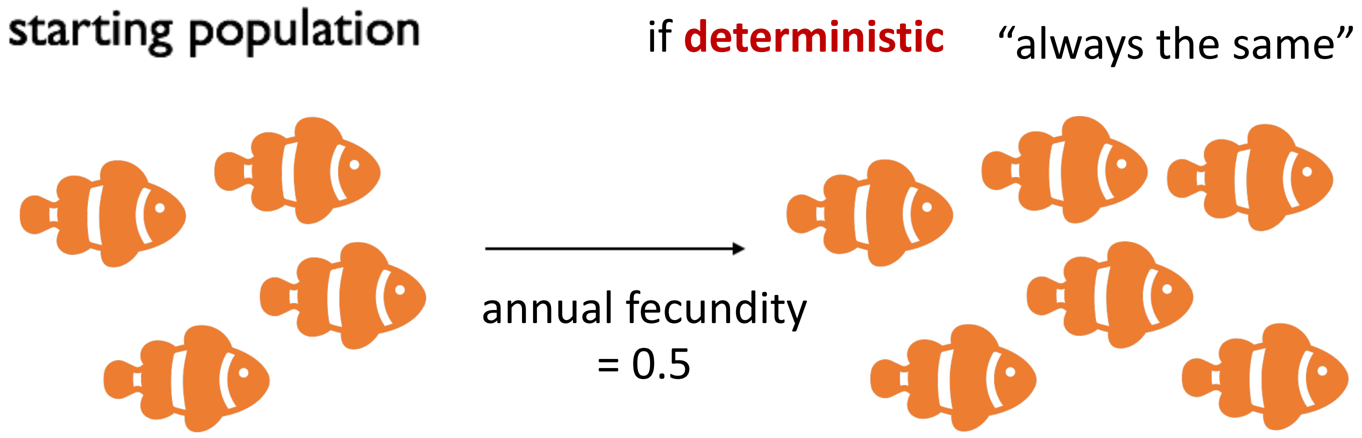


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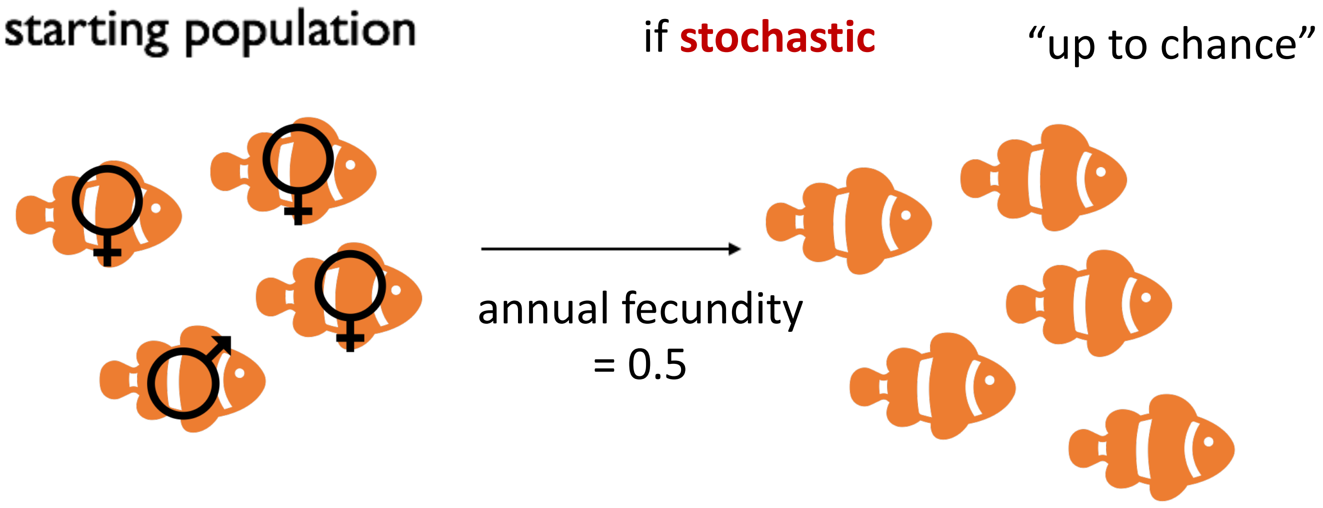


Only one male encounters only one female, so only 1 new fish is born!

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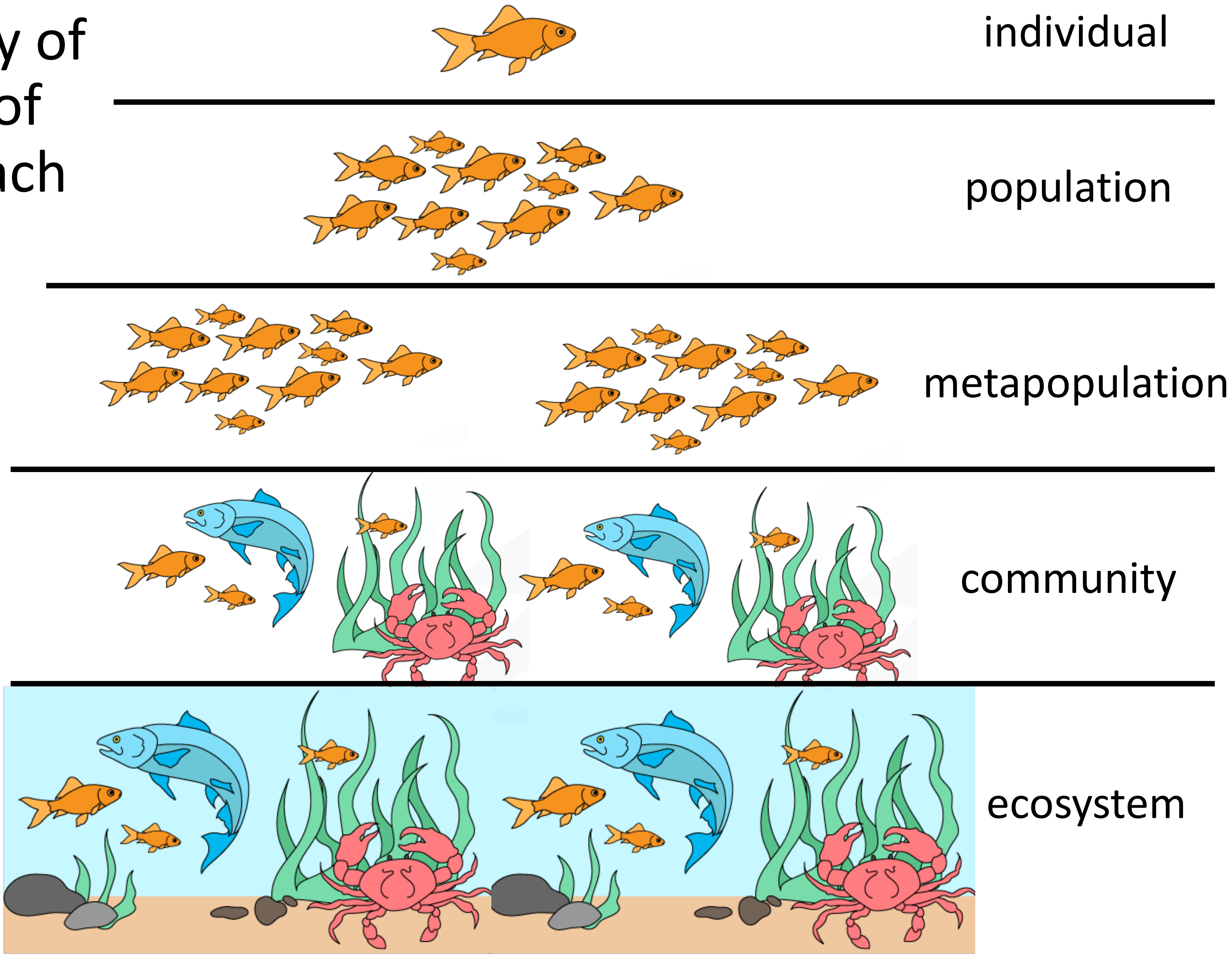
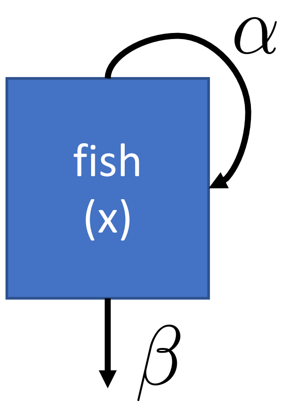
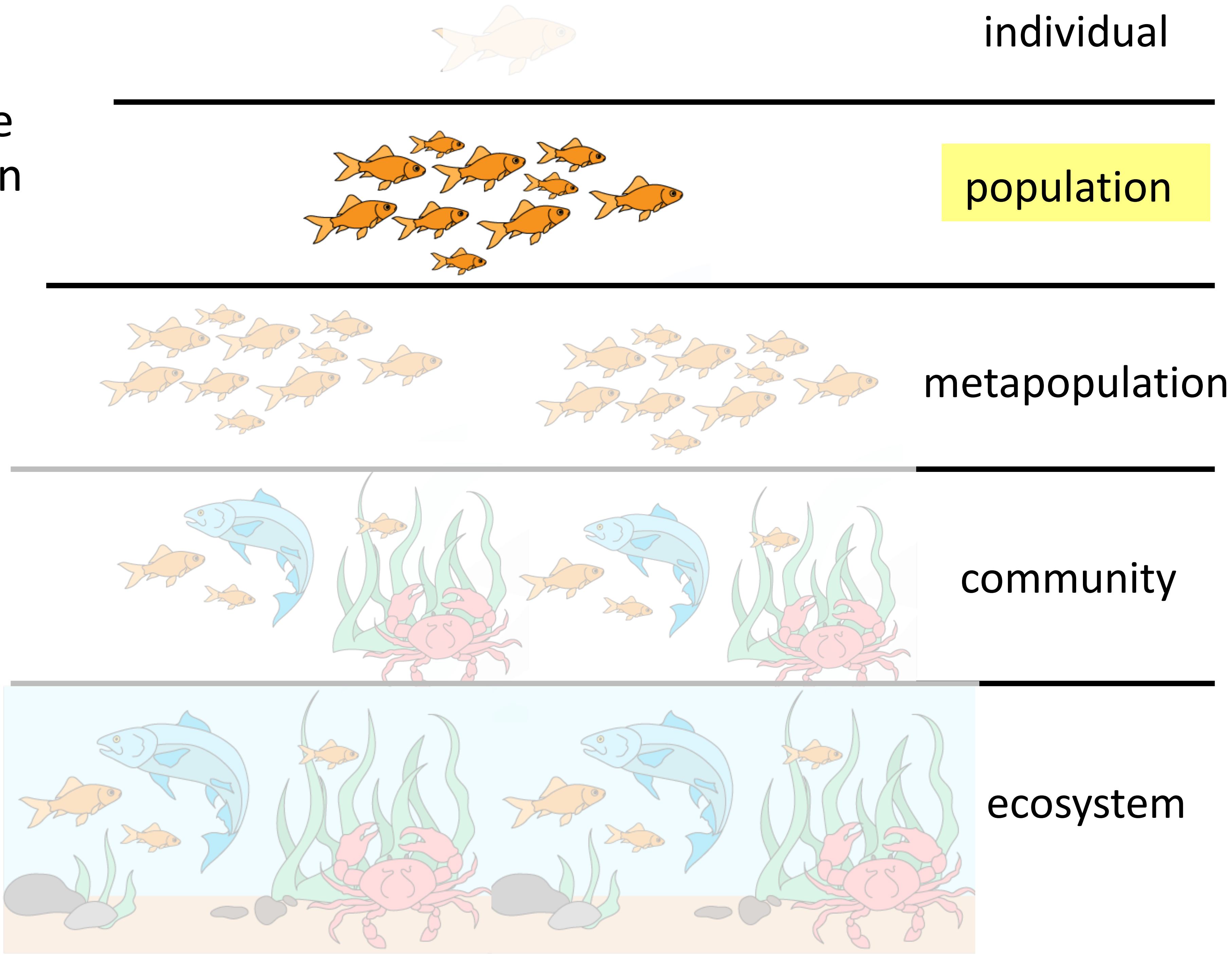


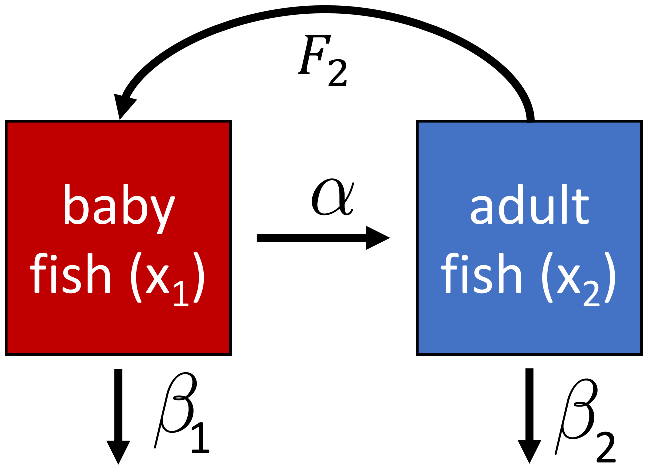
**Population** = multiple individuals of the same species (**conspecifics**) in the same habitat

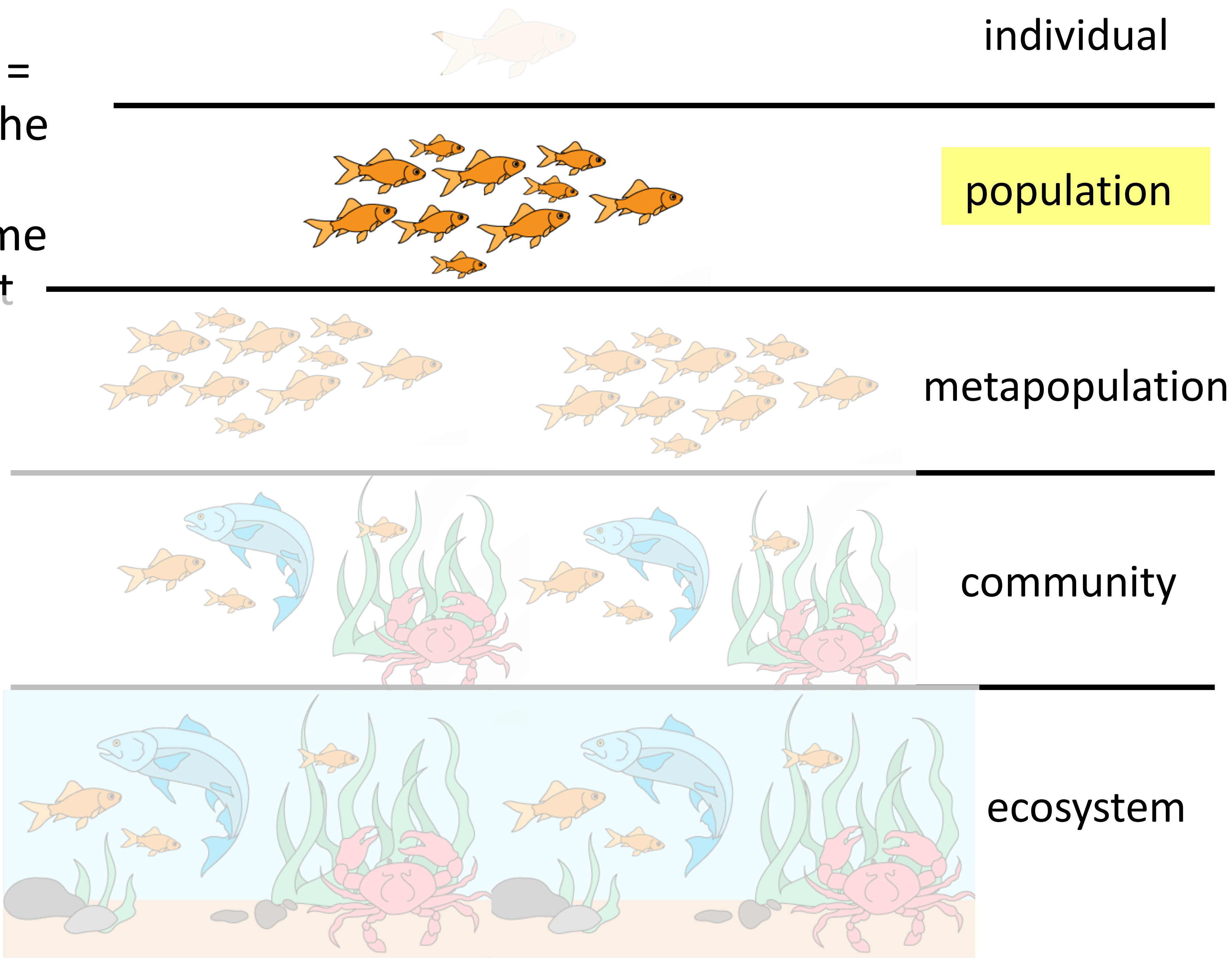



*How does the abundance of fish **change** through time?*



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



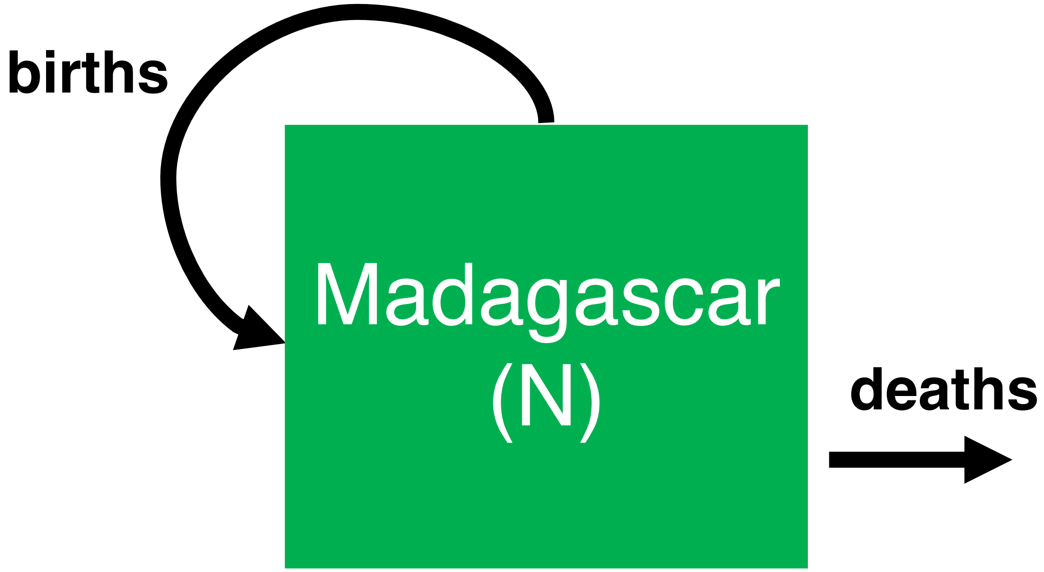




*How does the abundance of fish **change** through time?*

# Modeling demographic complexity

# 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**

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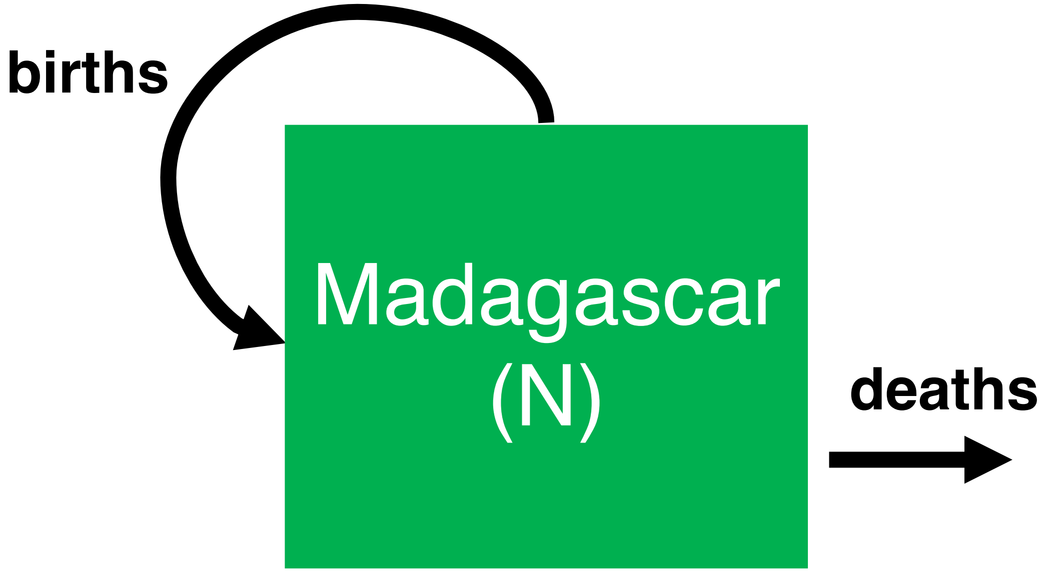


**What is wrong about this model?**

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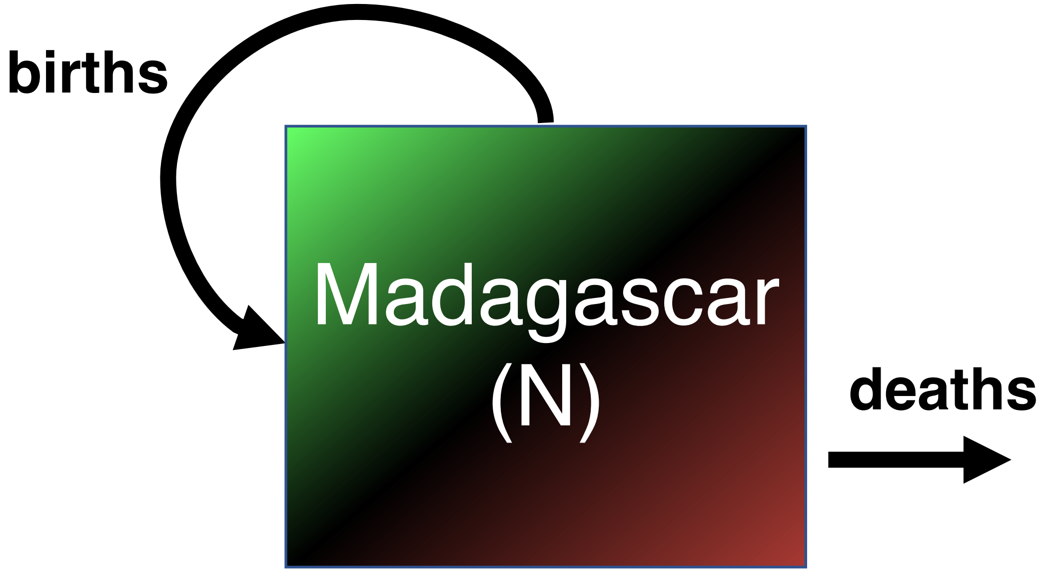


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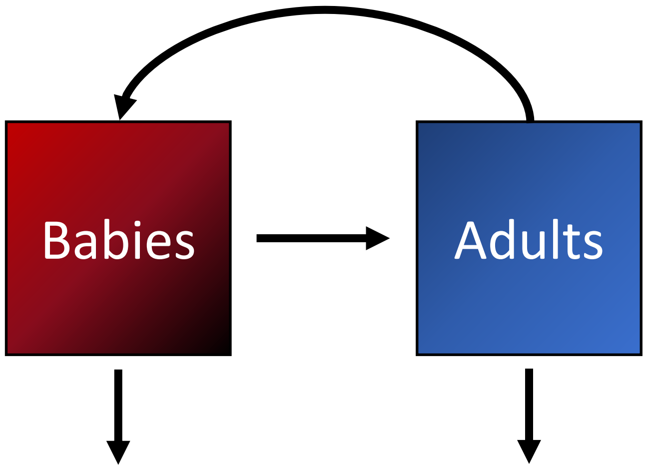


**The structured population model**

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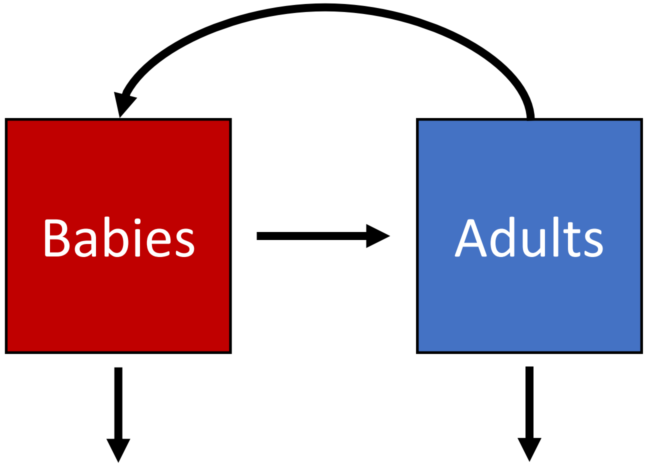


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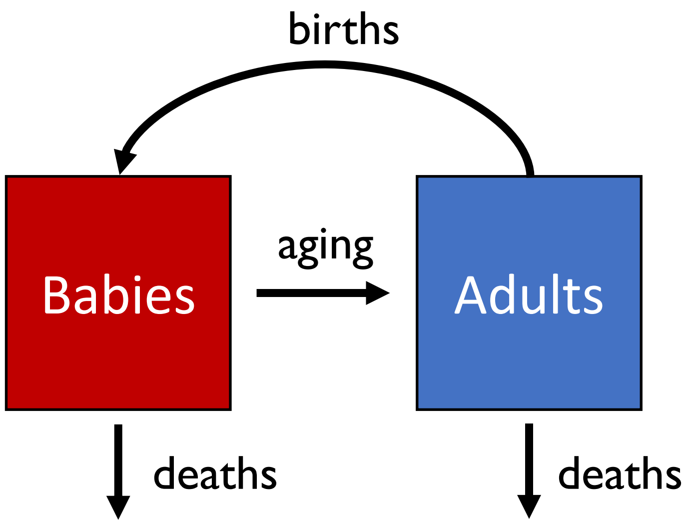



**The structured population model**

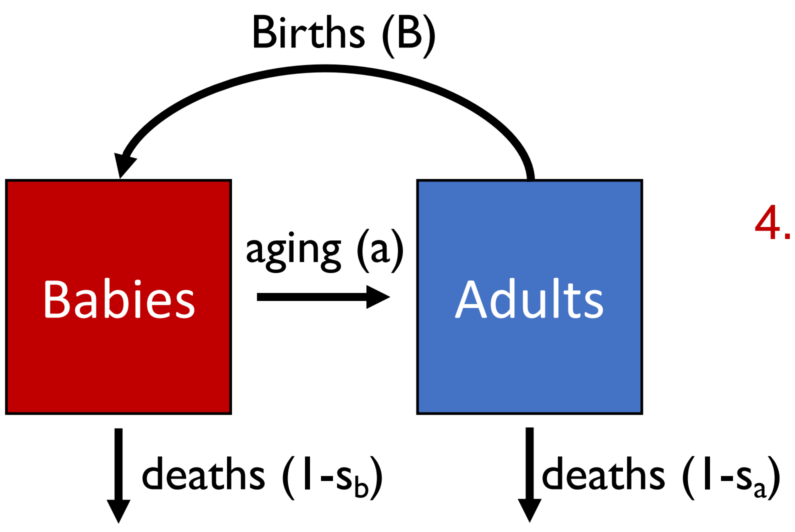
# The structured population model

Population rate of increase

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

pop size at t + 1

pop size at t

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

matrix of survival and fecundity rates

vector of population sizes

| | |
|---|---|
| $s_b(1\text{-}a)$ | $B$ |
| $s_b a$ | $s_a$ |

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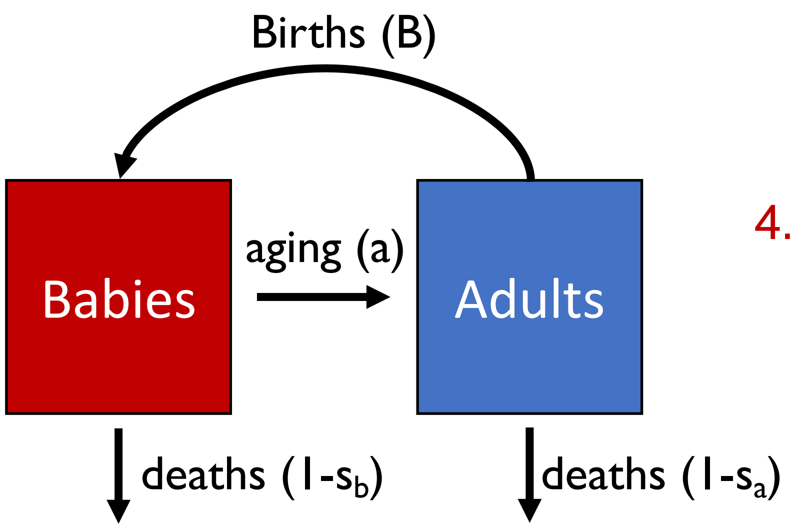


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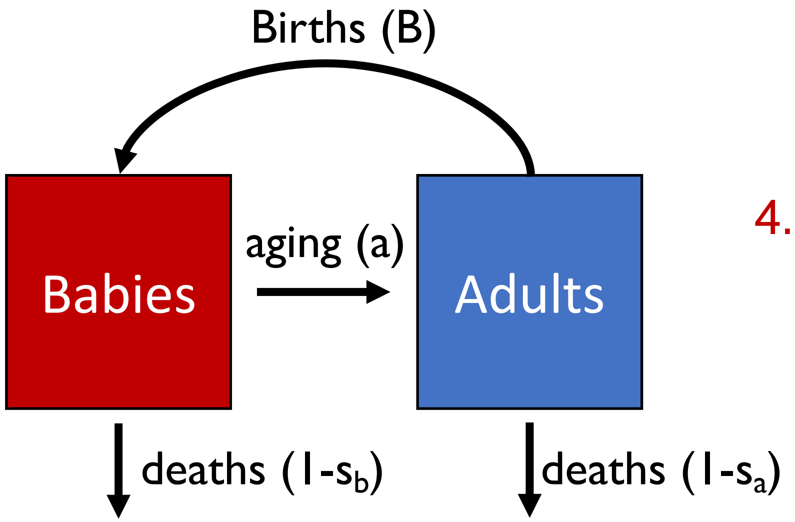
***Discrete time**

# The structured population model

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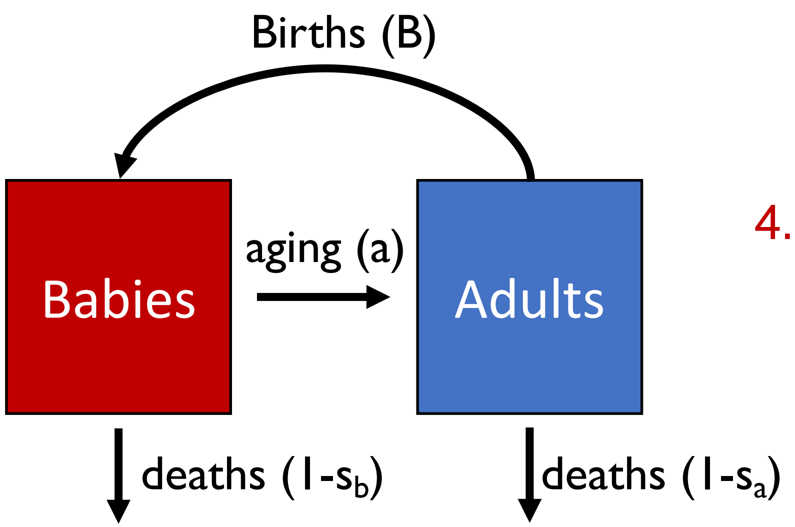
$$N_{t+1} = A^* \, N_t$$

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

# The structured population model

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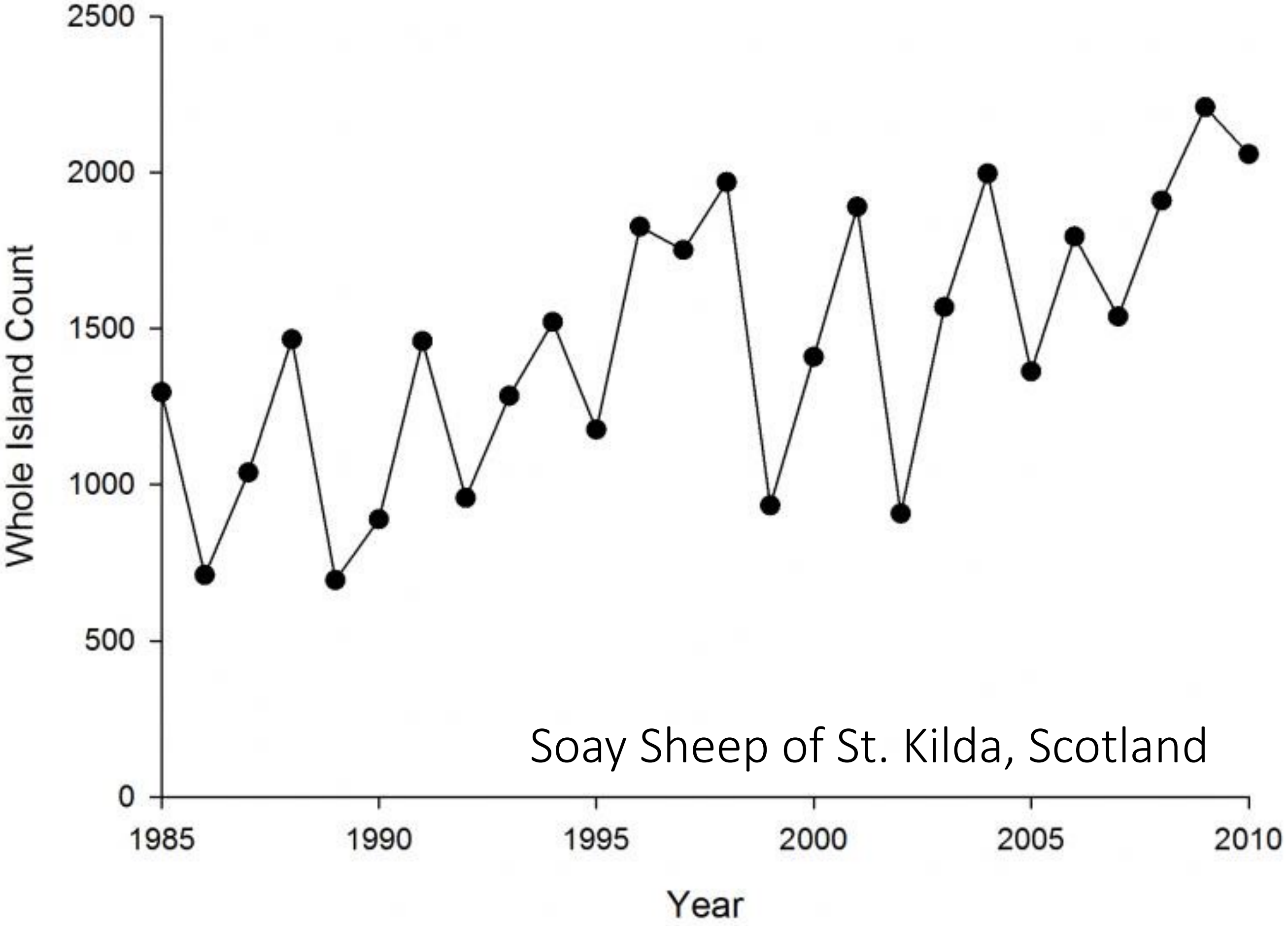
$\lambda$=dominant eigenvalue of transition matrix →

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

**Population growth will depend on population structure!**

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

# Structured populations in practice




Soay Sheep of St. Kilda, Scotland

# Structured populations in practice

Model compared against data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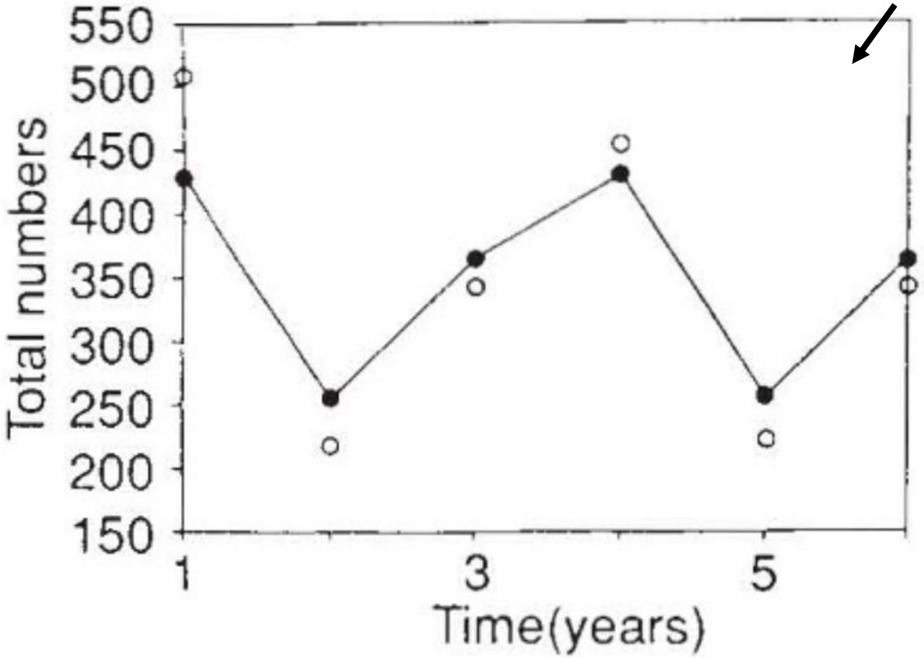



## Overcompensation and population cycles in an ungulate

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.

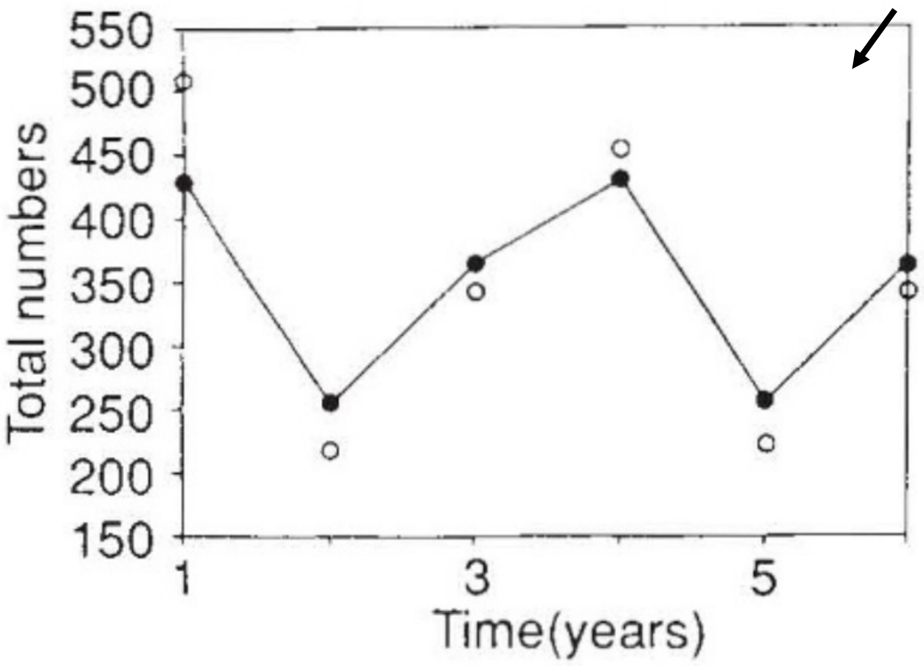
population at t+1

average fecundity

growth rate

population at t

Model compared against data

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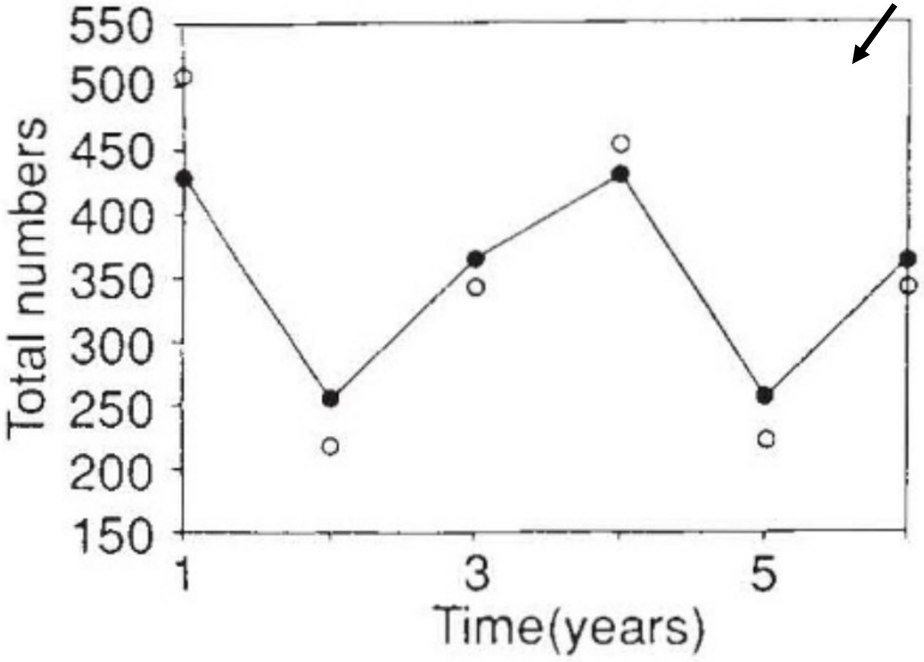


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Similar to the simple logistic growth equation!

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

# 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

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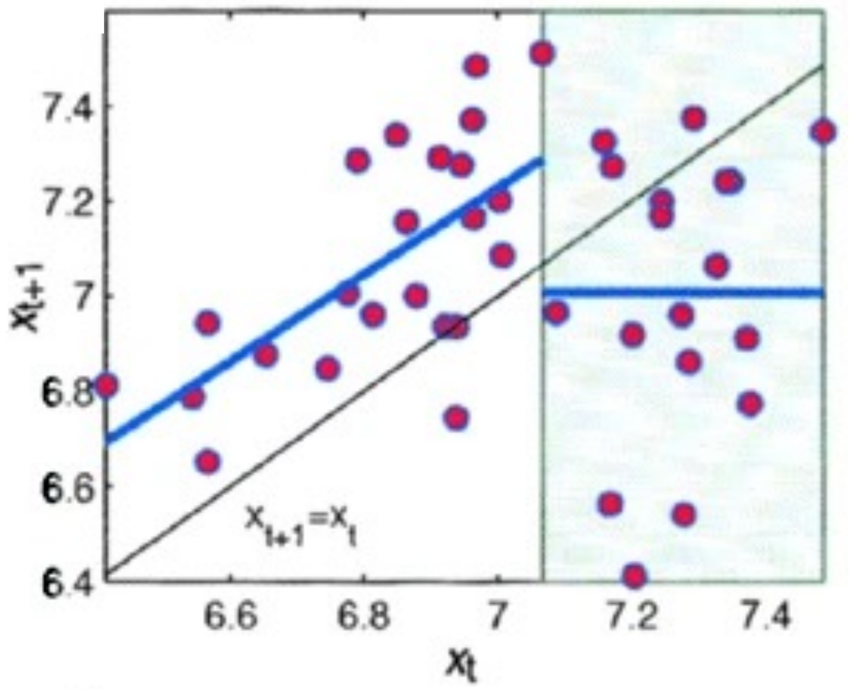

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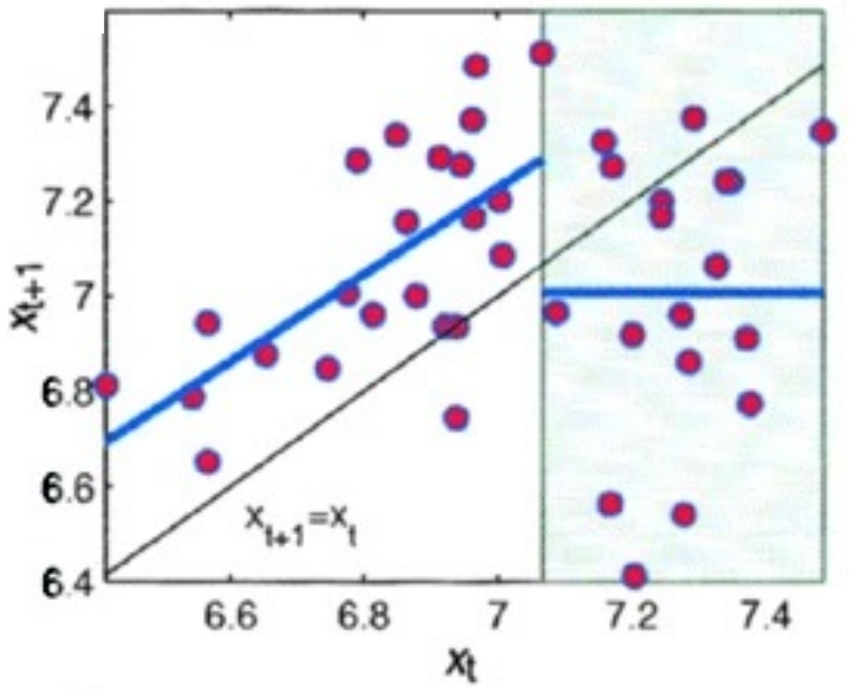


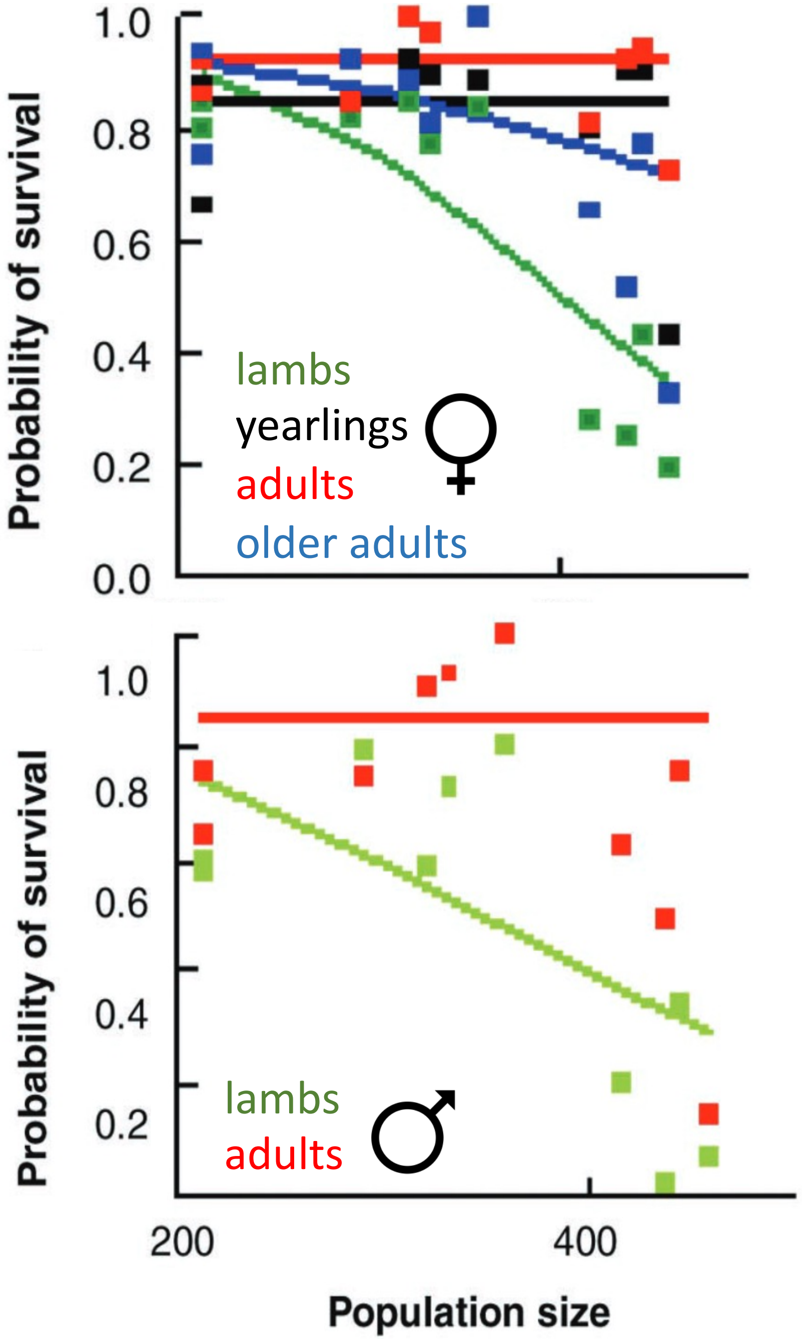
# Structured populations in practice

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

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

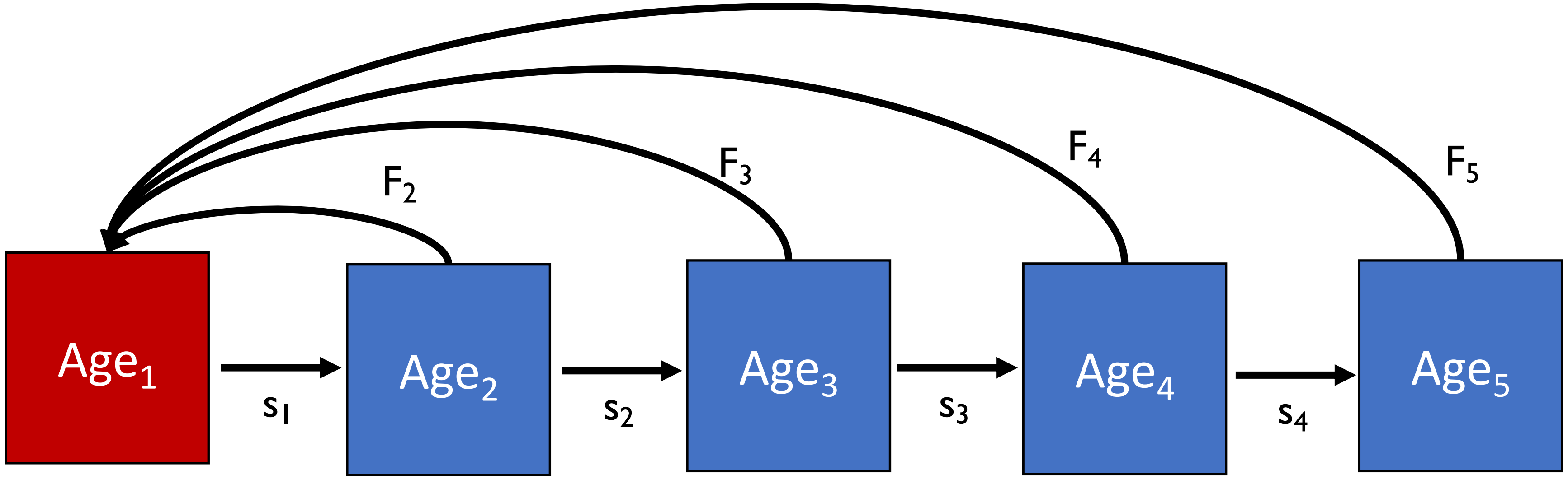
T. Coulson,[1*†] E. A. Catchpole,[2] S. D. Albon,[3] B. J. T. Morgan,[4] J. M. Pemberton,[5] T. H. Clutton-Brock,[6] M. J. Crawley,[6] B. T. Grenfell[7]

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.*

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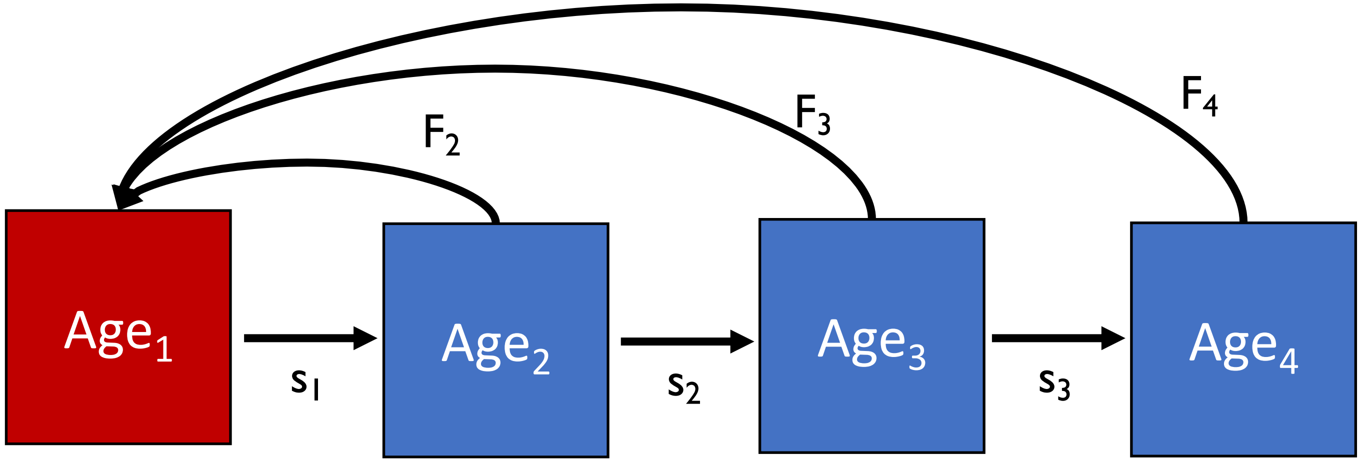


$\lambda$=dominant eigenvalue of transition matrix $\longrightarrow$

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

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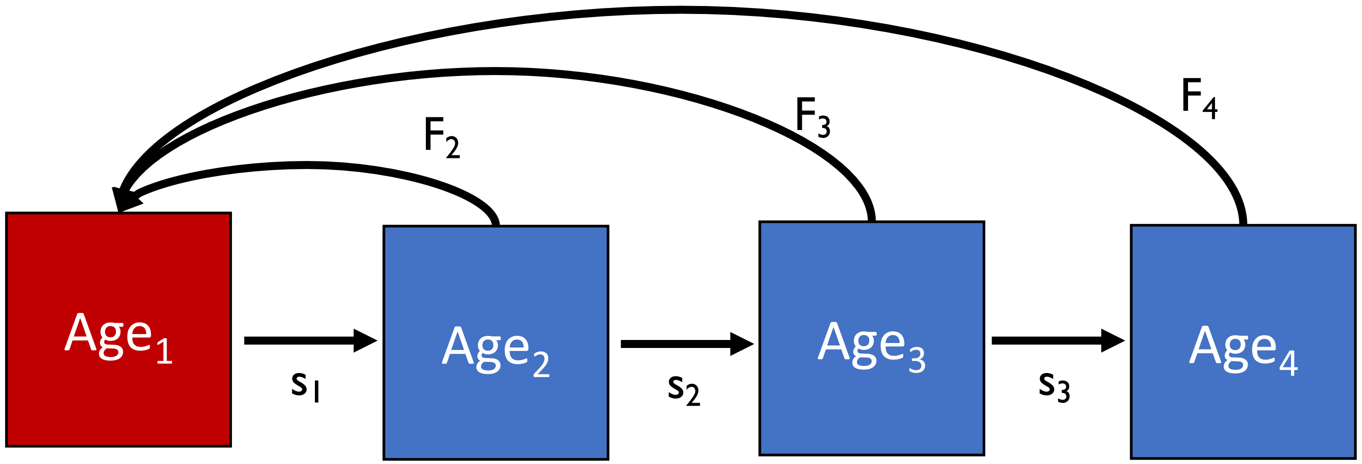
# The structured population model

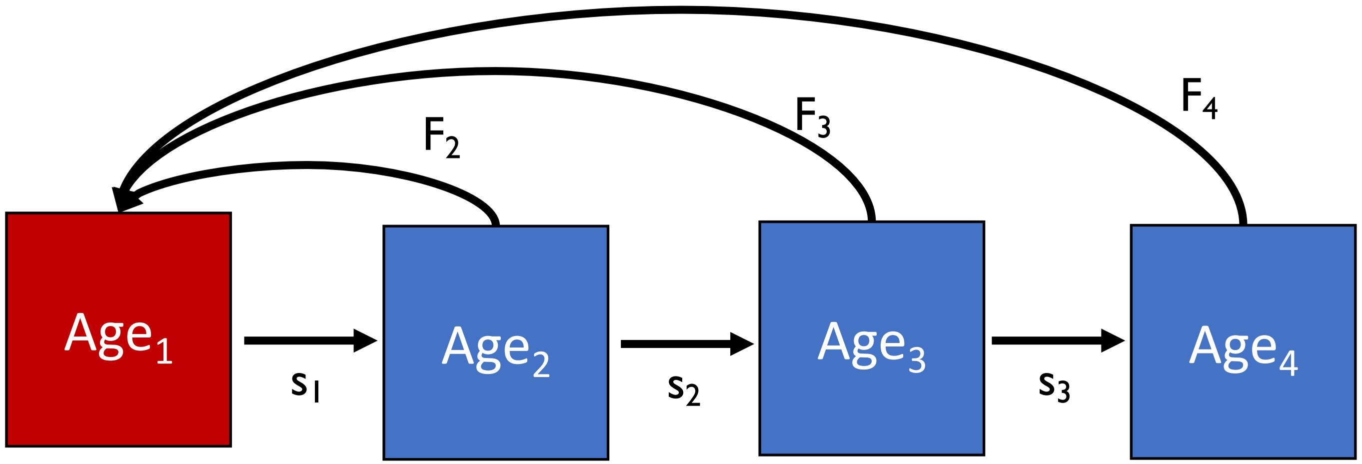



Demographers collect these rates in life tables

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

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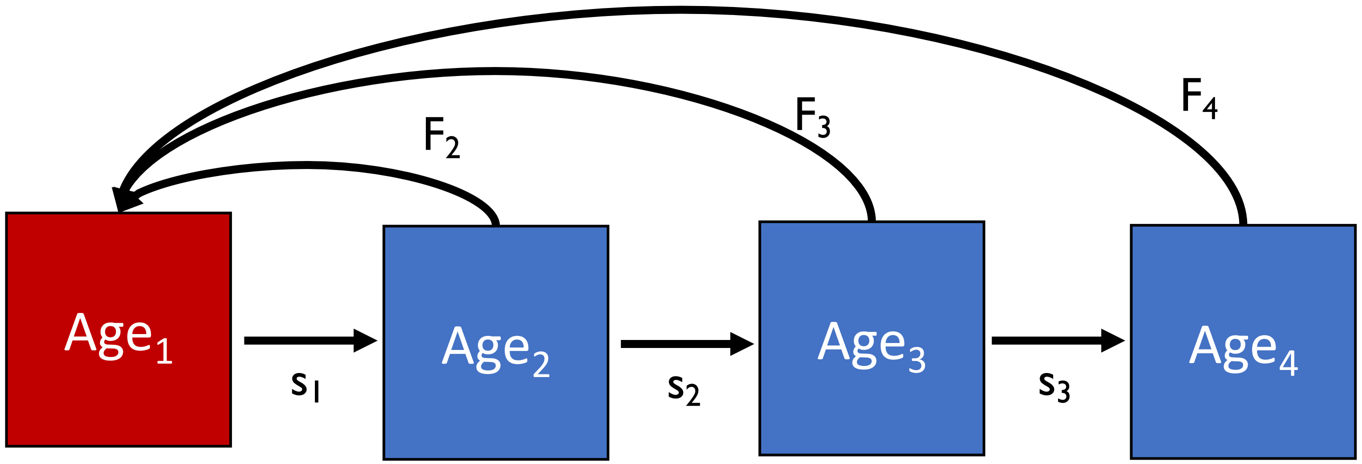


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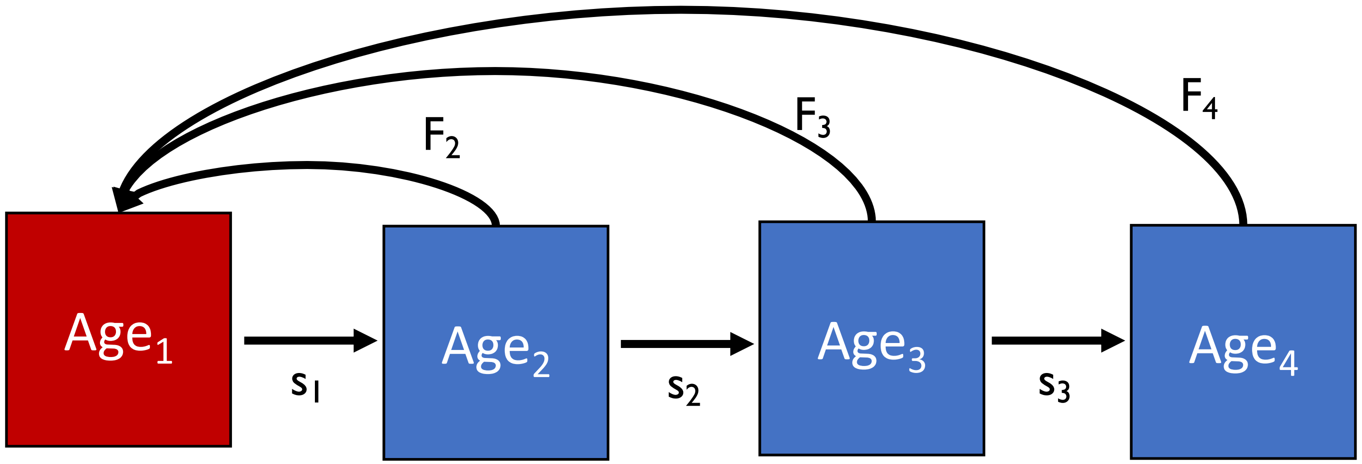
**Net reproductive rate ($R_0$)**: $\sum l_x m_x = 2.21$

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

# The structured population model

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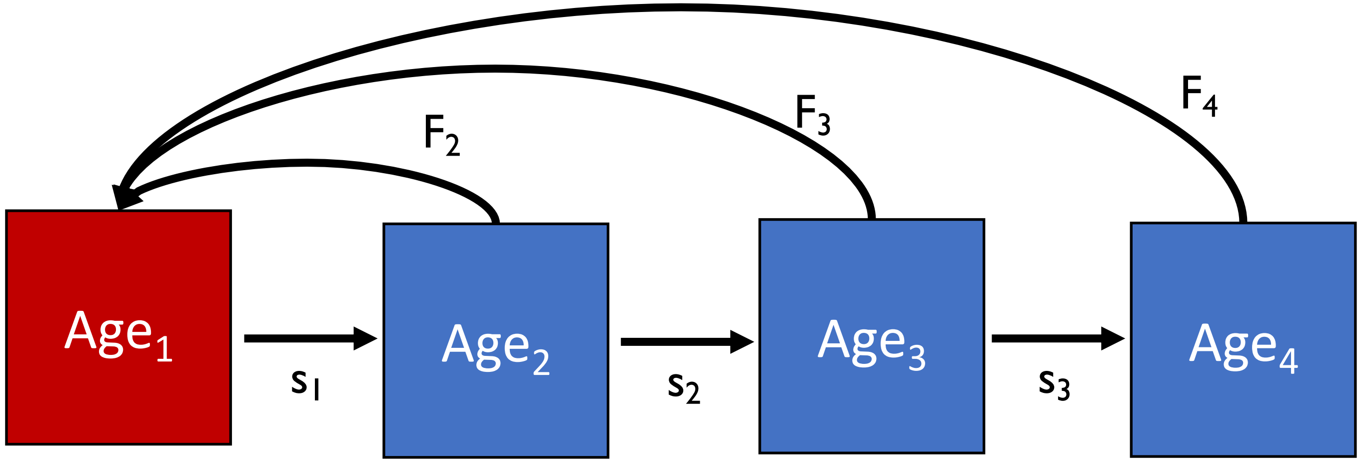
**Net reproductive rate ($R_0$):** $\sum l_x m_x = 2.21$

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

# The structured population model

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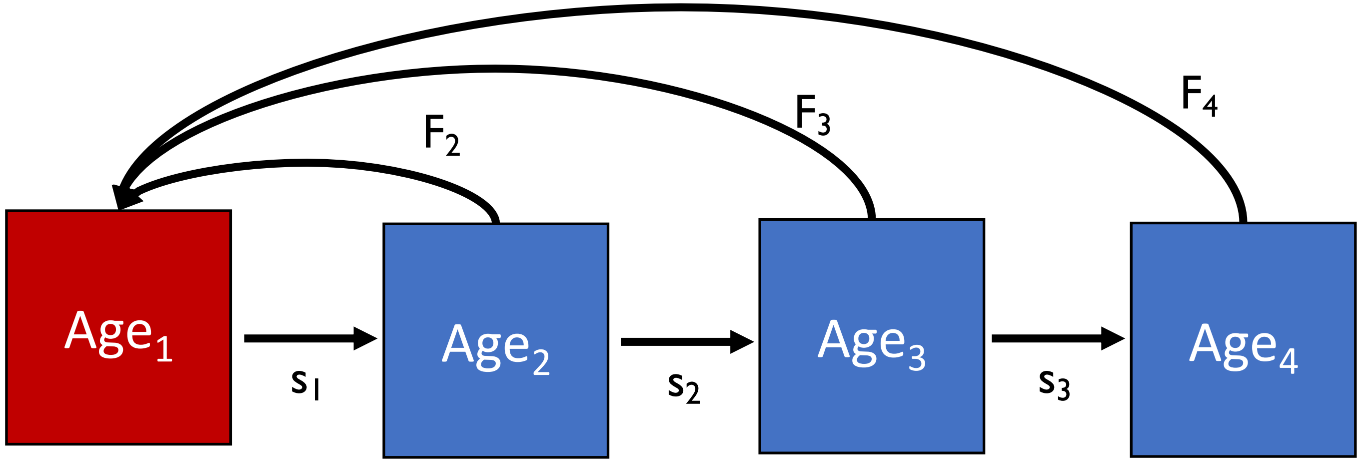
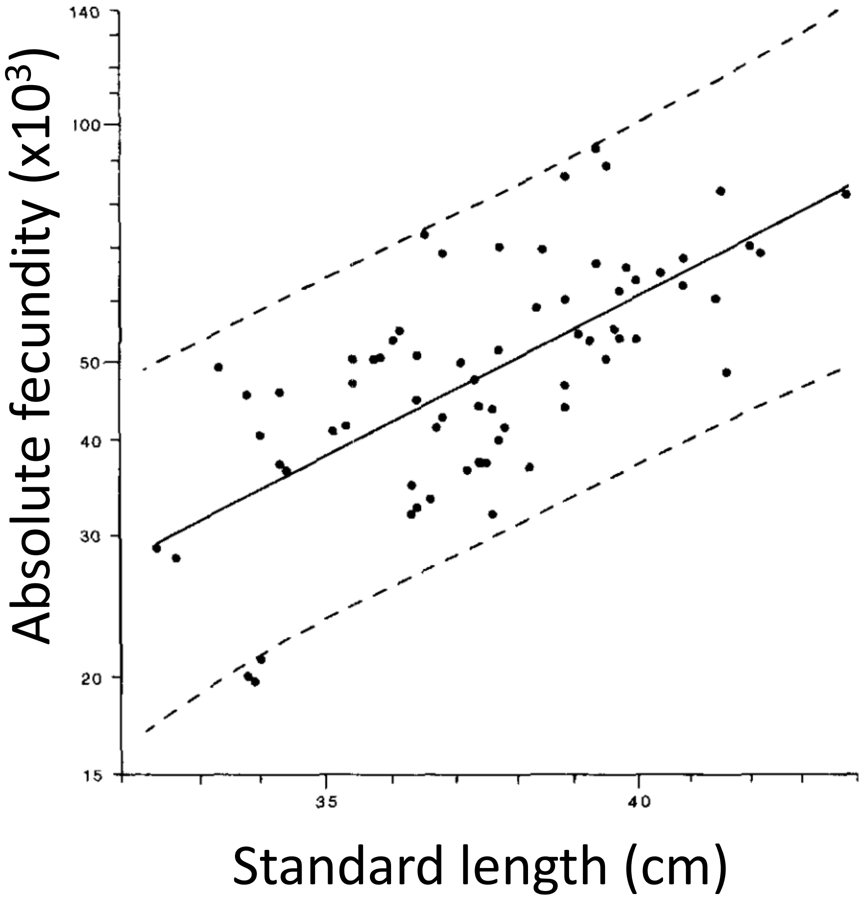
| | | | | ⋮ |

Orange roughy can live up to 200 years!

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

# The structured population model

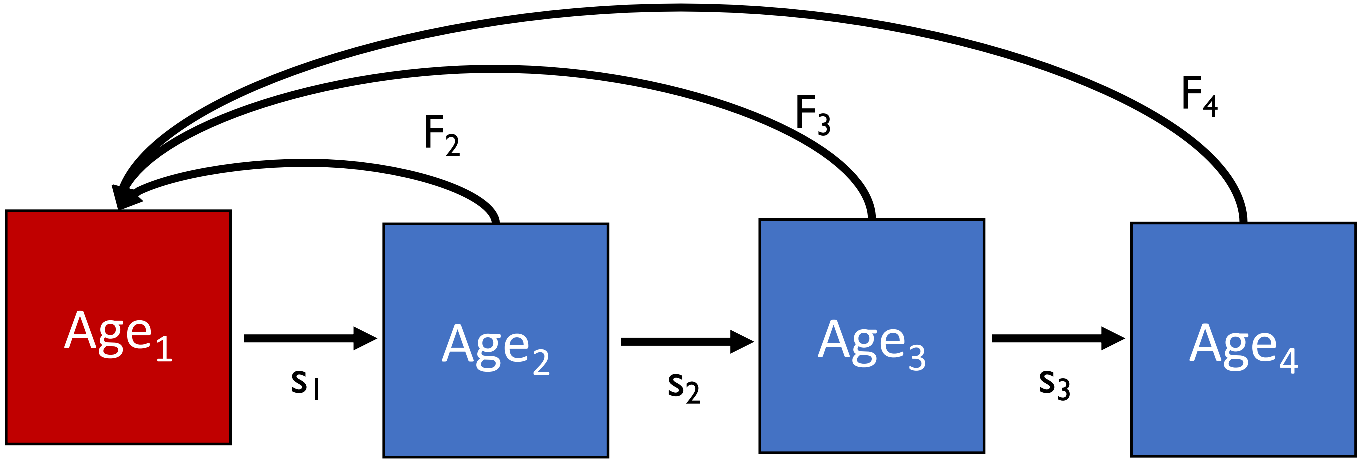


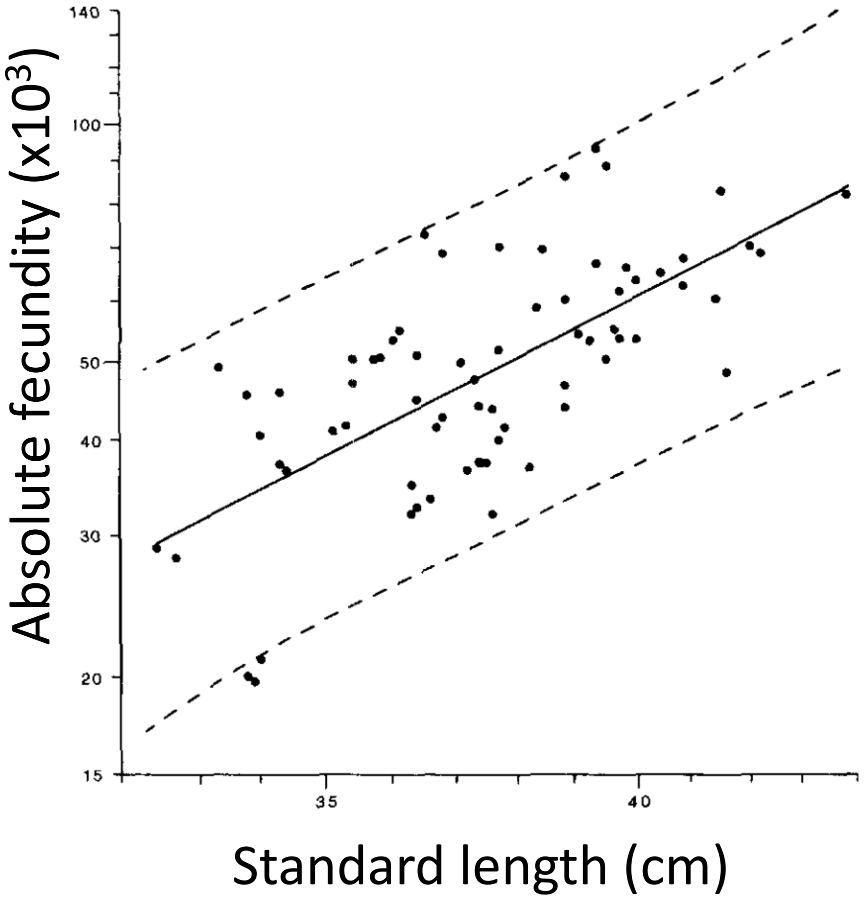




Fecundity (eggs) increases in older, bigger fish!

Pankhurst & Conroy 1987
*NZ J of Marine & Freshwater Res*

# The structured population model



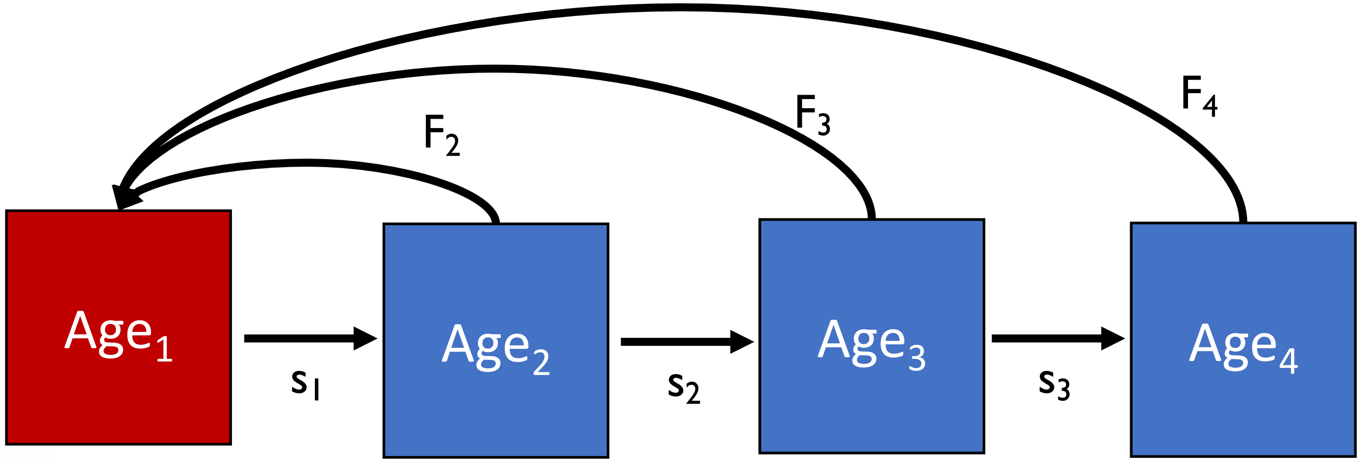



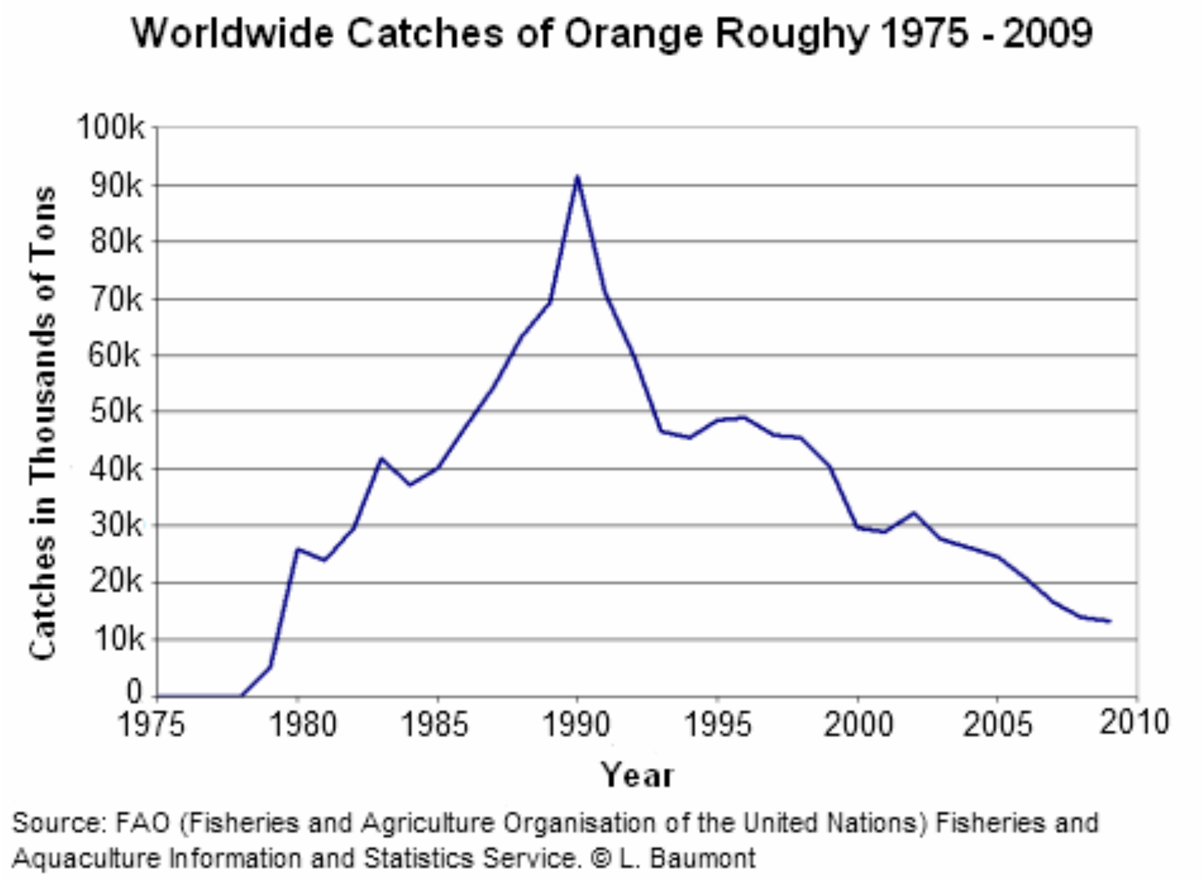

Fecundity (eggs) increases in older, bigger fish!

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

Norway 1910
(Norsk folkemuseum)

# The structured population model

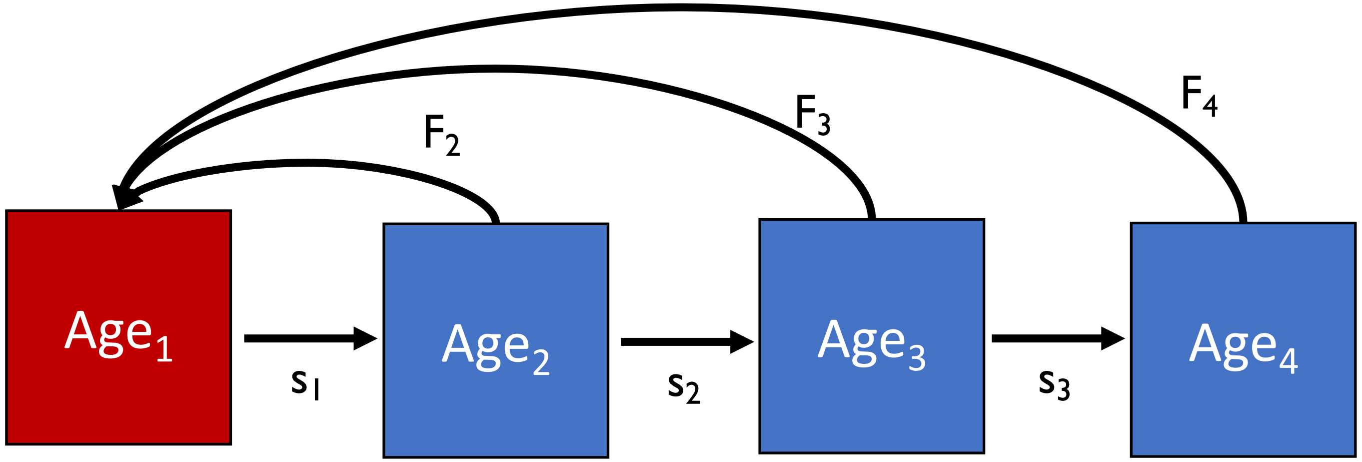



Poor modeling projections has led to severe overexploitation, a common problem in fisheries…

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**.

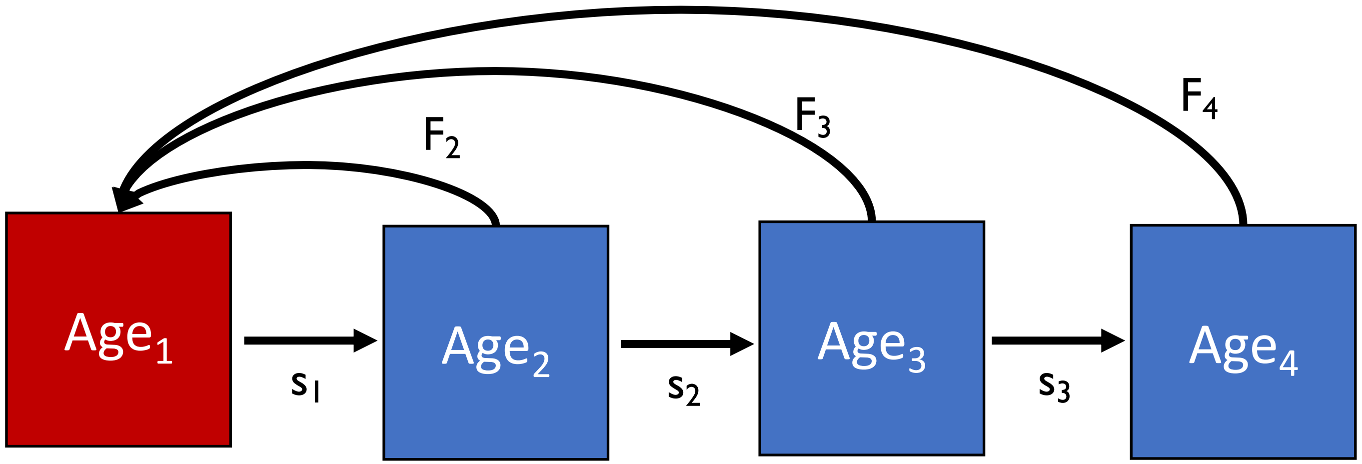
| Age. Curt. | Per-sons. | Age. Curt. | Per-sons | Age. Curt. | Per-sons | Age. Curt. | Per-sons | Age. Curt. | Per-sons | Age. Curt. | Per-sons |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1000 | 8 | 680 | 15 | 628 | 22 | 585 | 29 | 539 | 36 | 481 |
| 2 | 855 | 9 | 670 | 16 | 622 | 23 | 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. | Per-sons. | Age. Curt. | Per-sons | Age. Curt. | Per-sons | Age Curt. | Per-sons | Age. Curt. | Per-sons | Age. Curt. | Per-sons |
| 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. | |

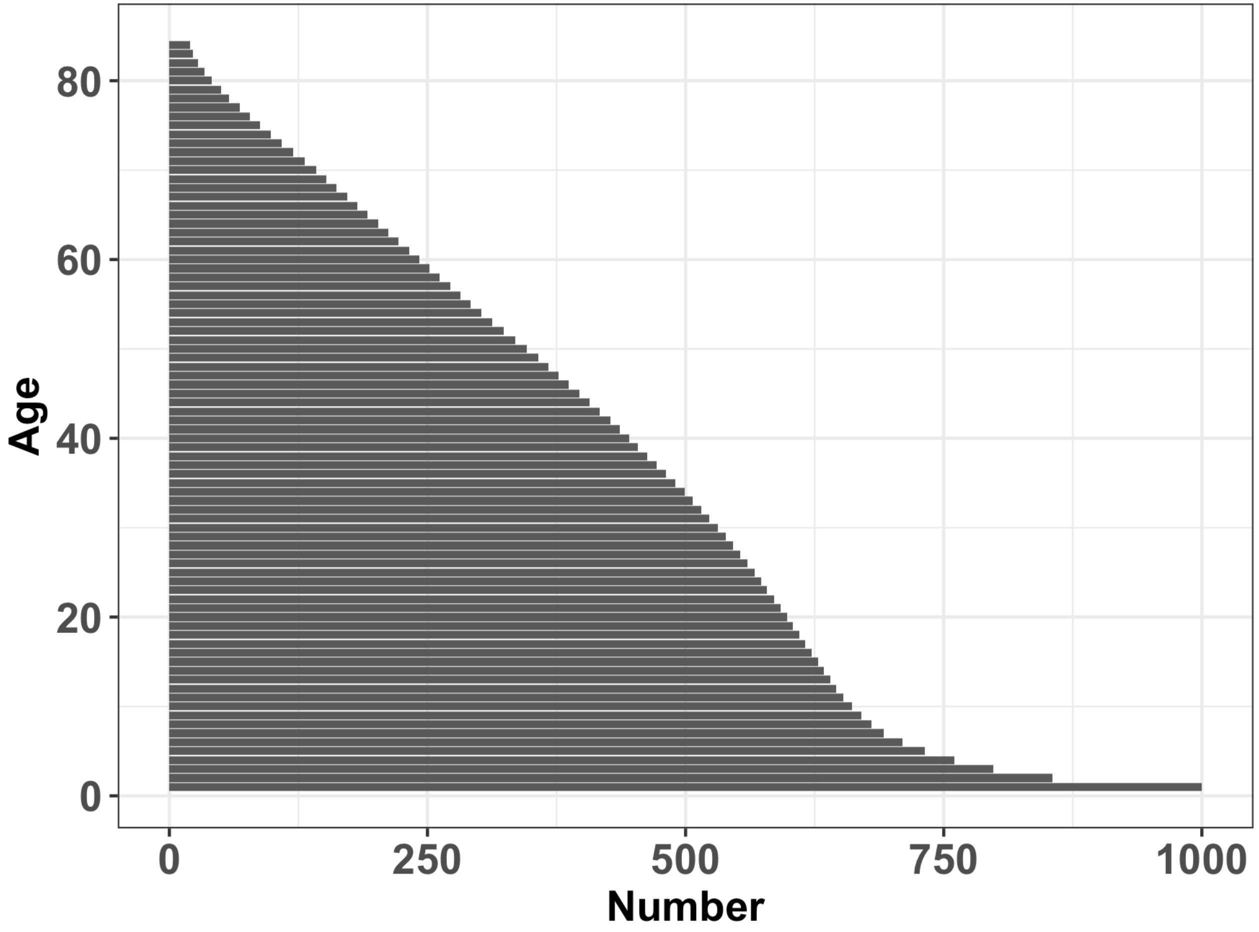
Edmond Halley, 1693

*"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




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…"*

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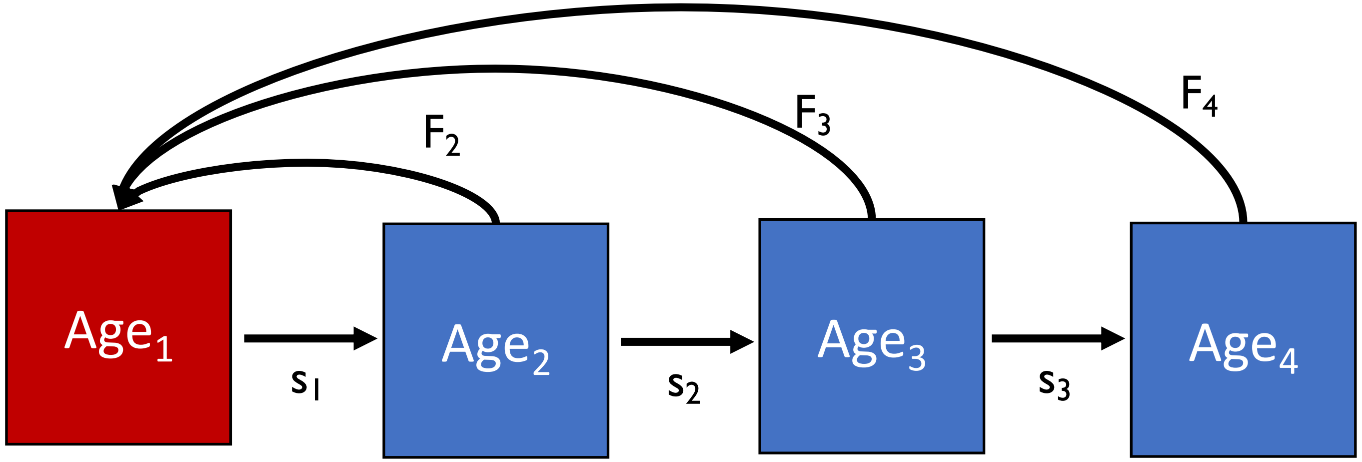
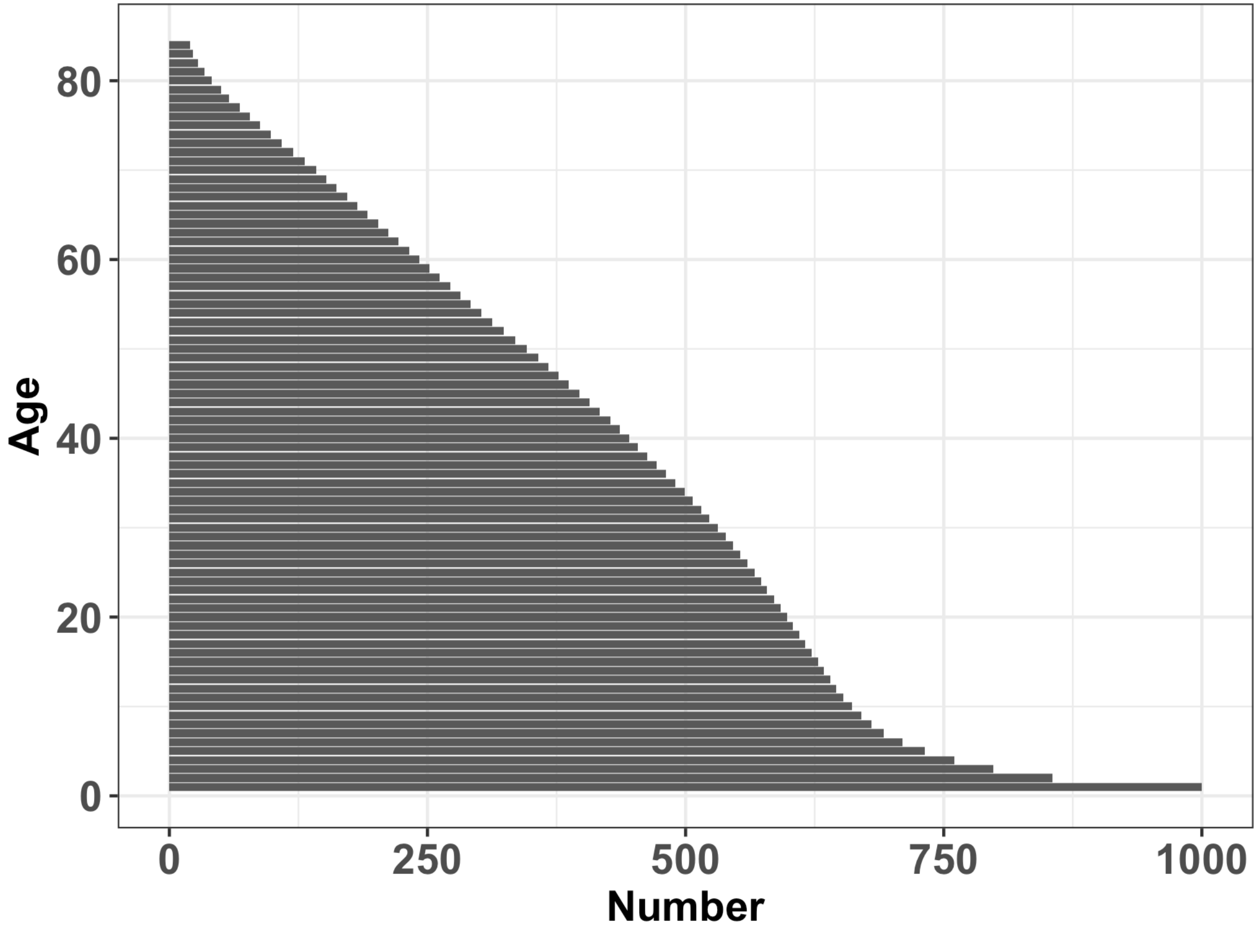



**Population pyramid for Breslau**



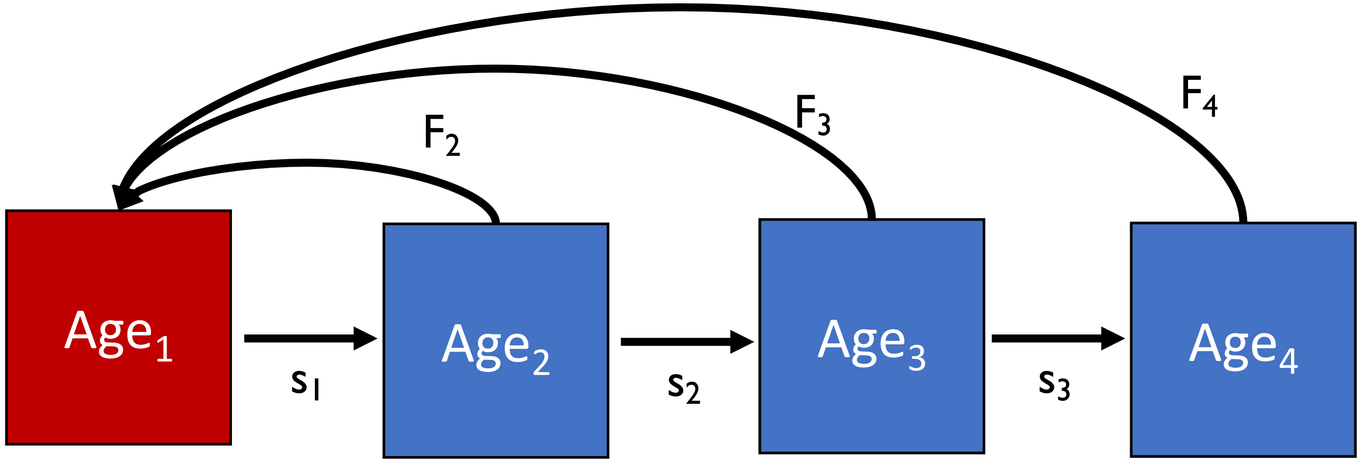

Humans are not like fish!

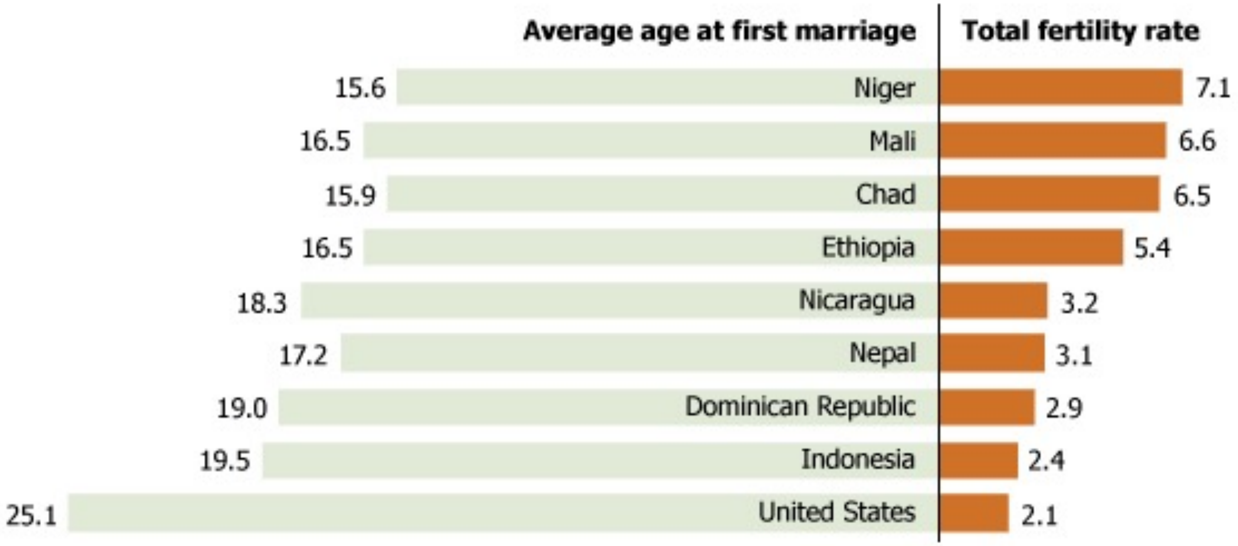
Fecundity tends to decrease in older age classes due to **reproductive senescence**.

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

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

# The structured population model

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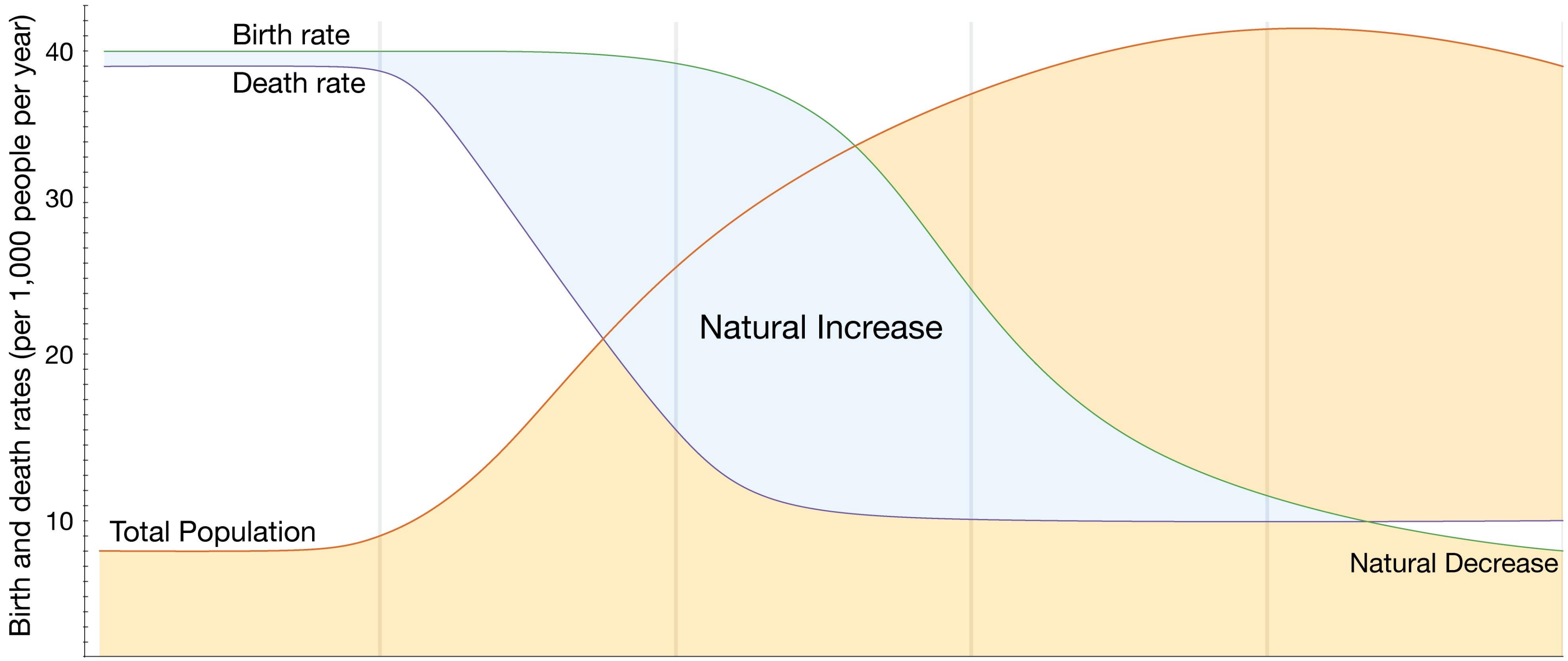
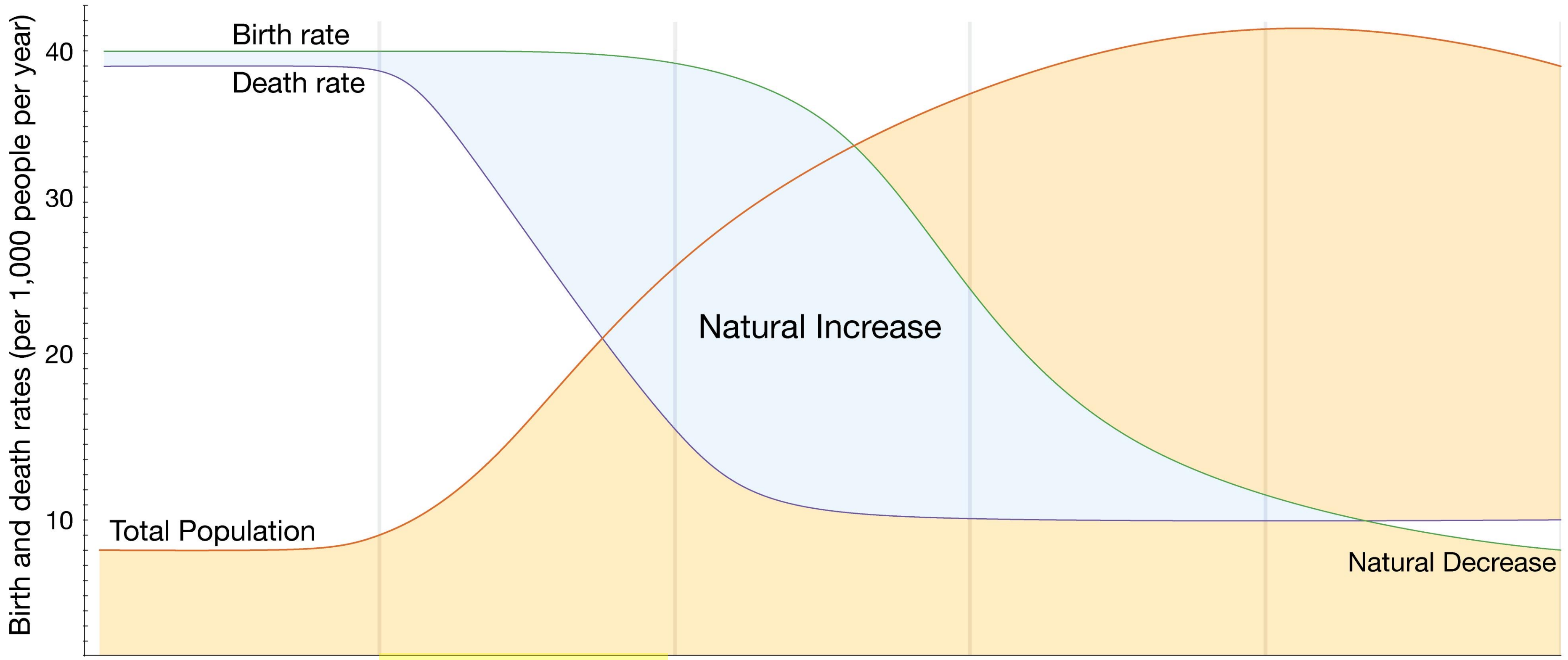
# Demographic transition




| | *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

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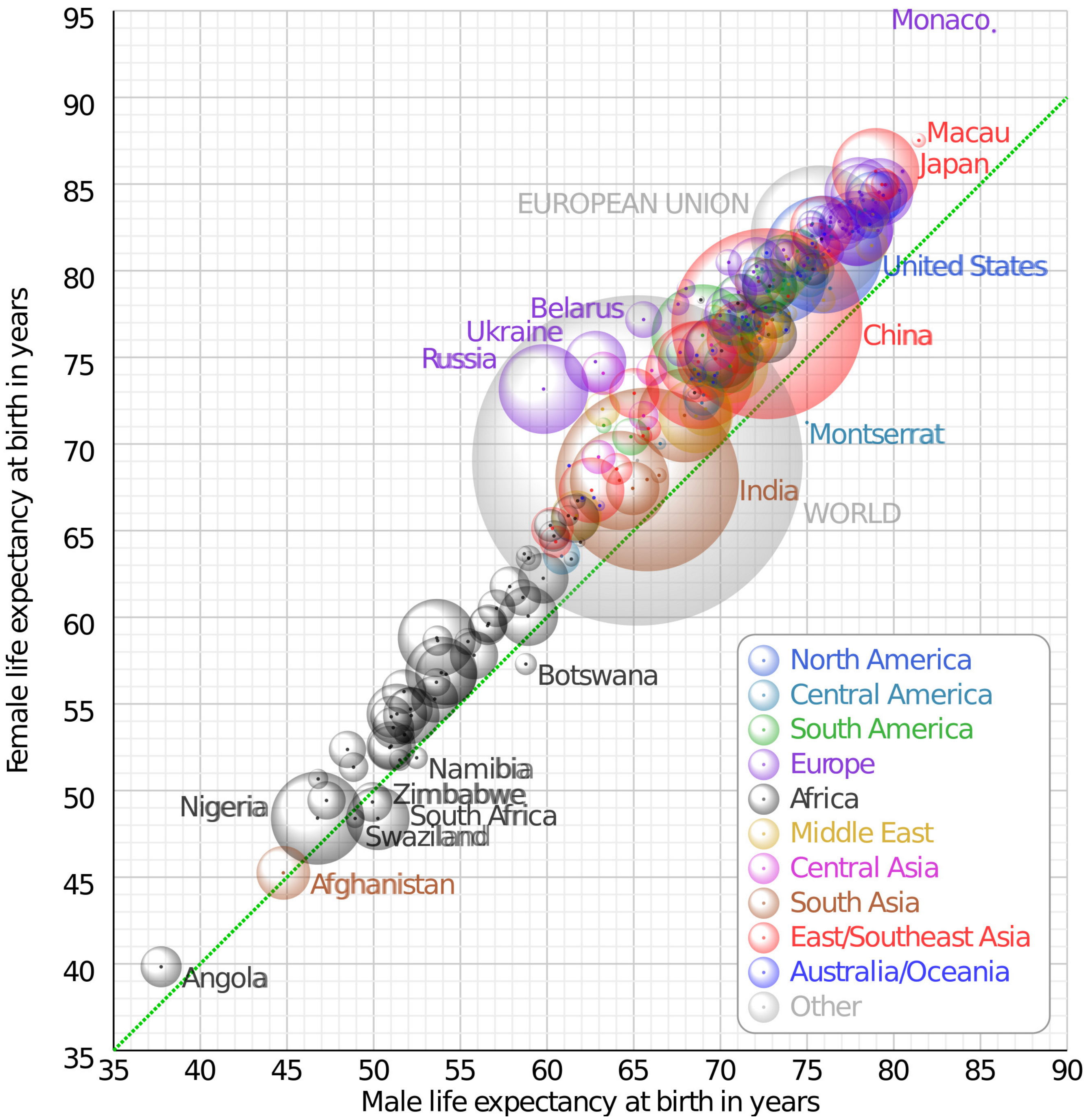
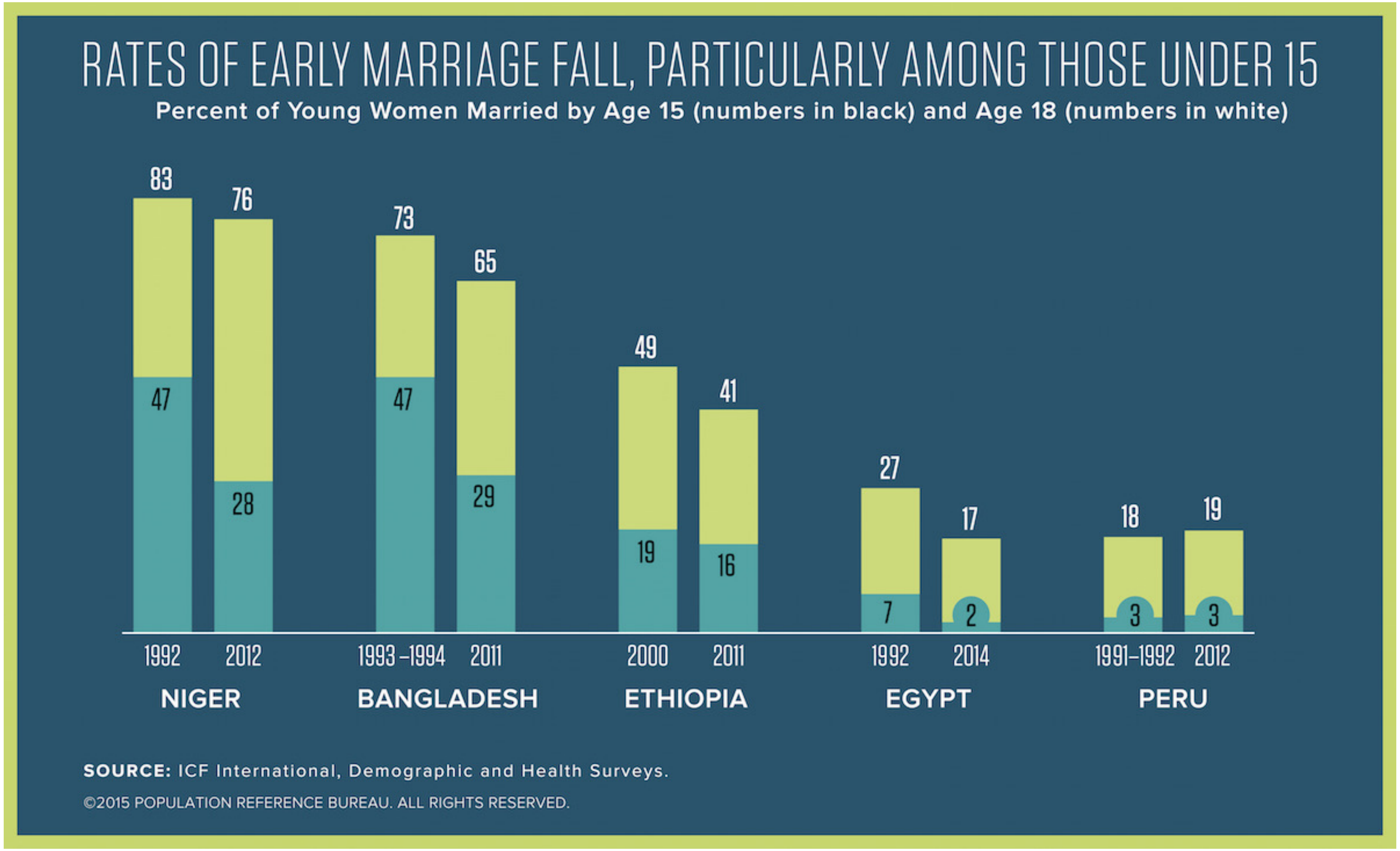
# Demographic transition

Death rates are falling globally…

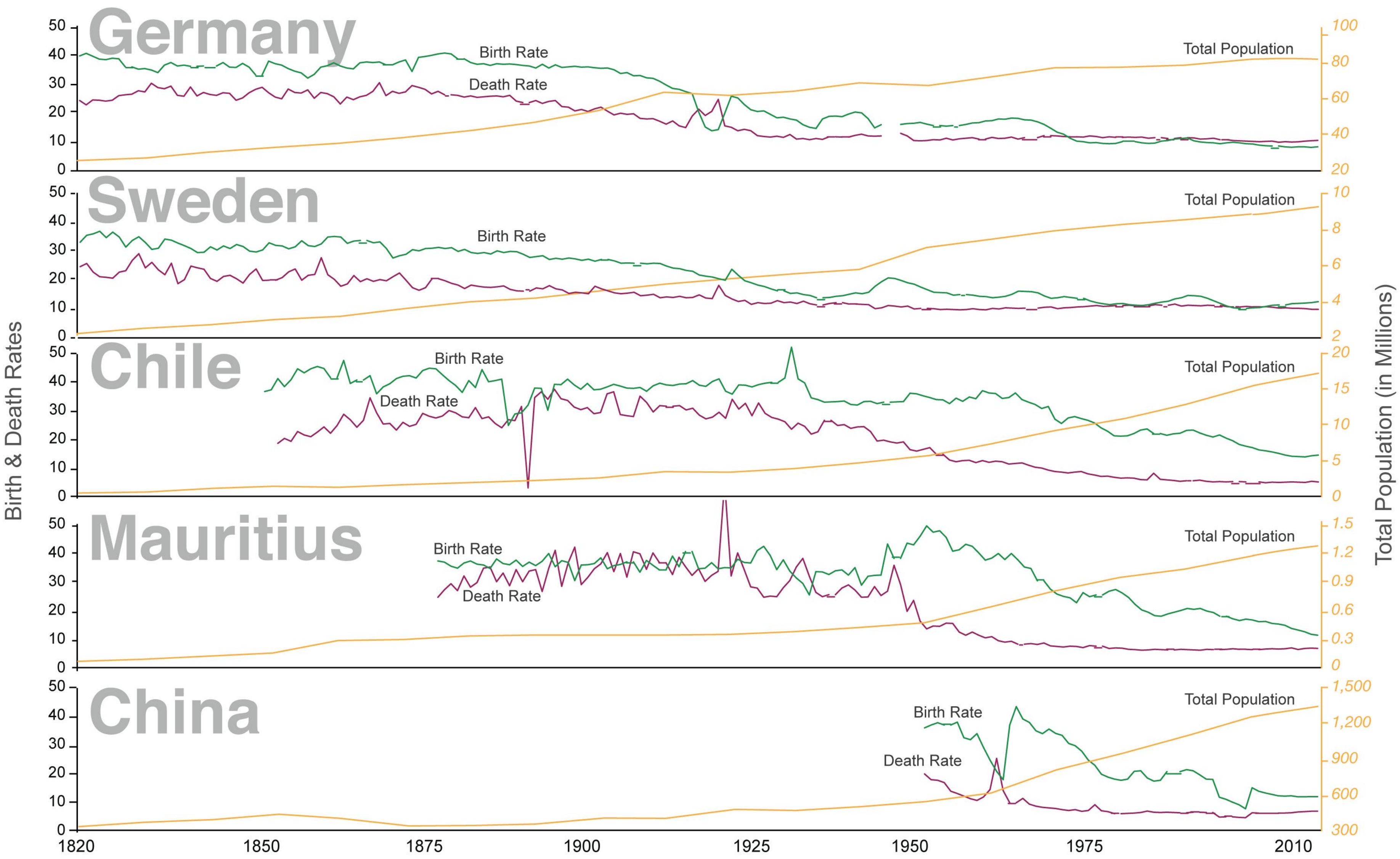


# Demographic transition

And birth rates are also falling…



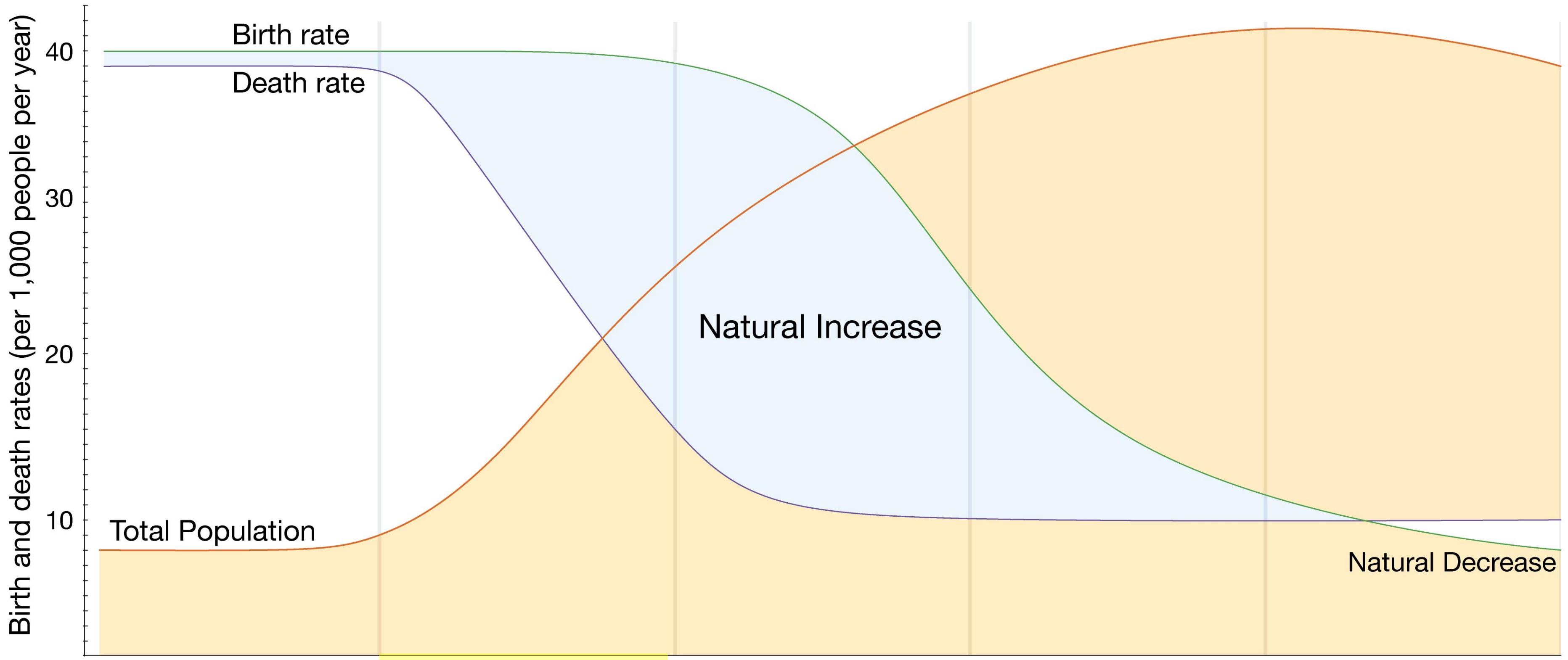
# Demographic transition




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?




| | Stage 1 | Stage 2 | Stage 3 | Stage 4 | Stage 5 |
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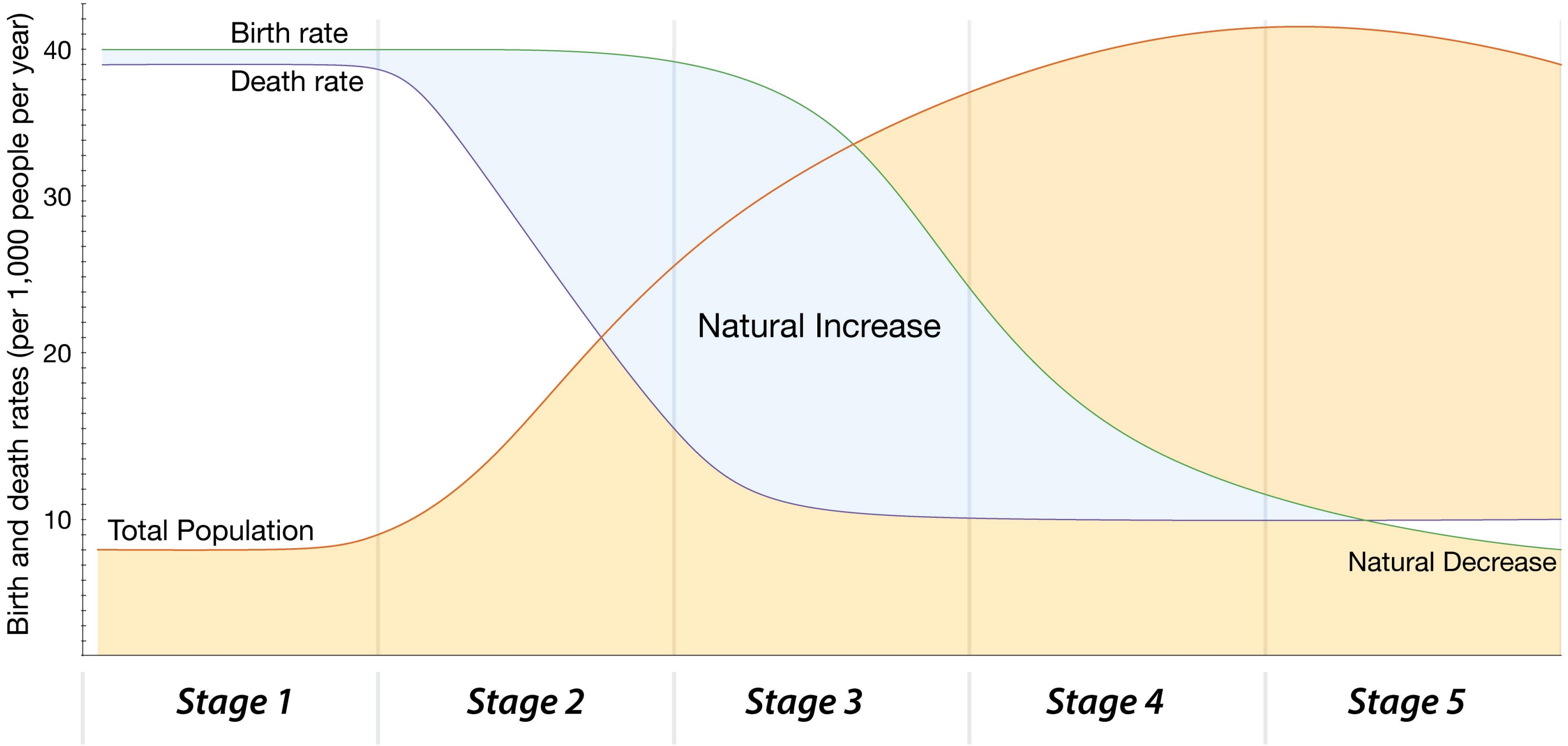


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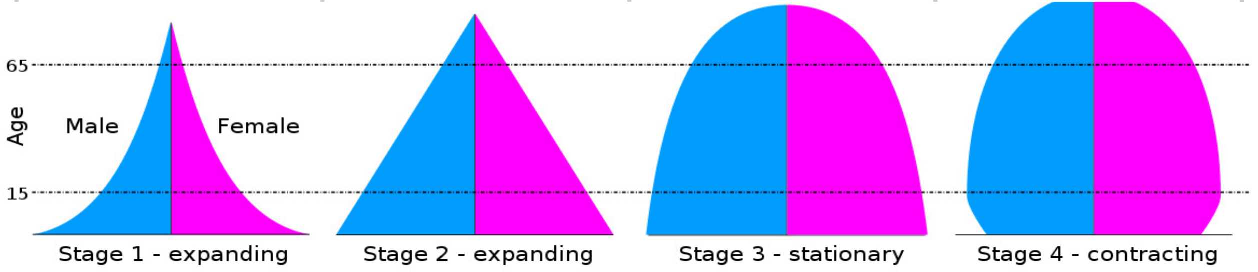
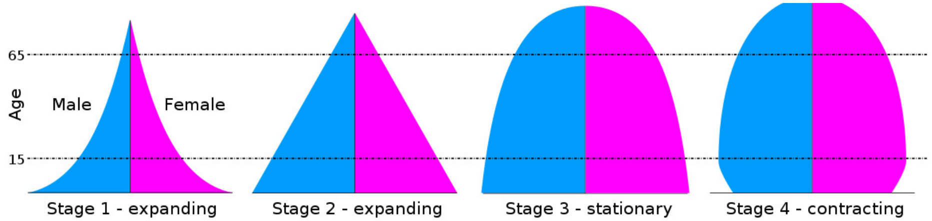
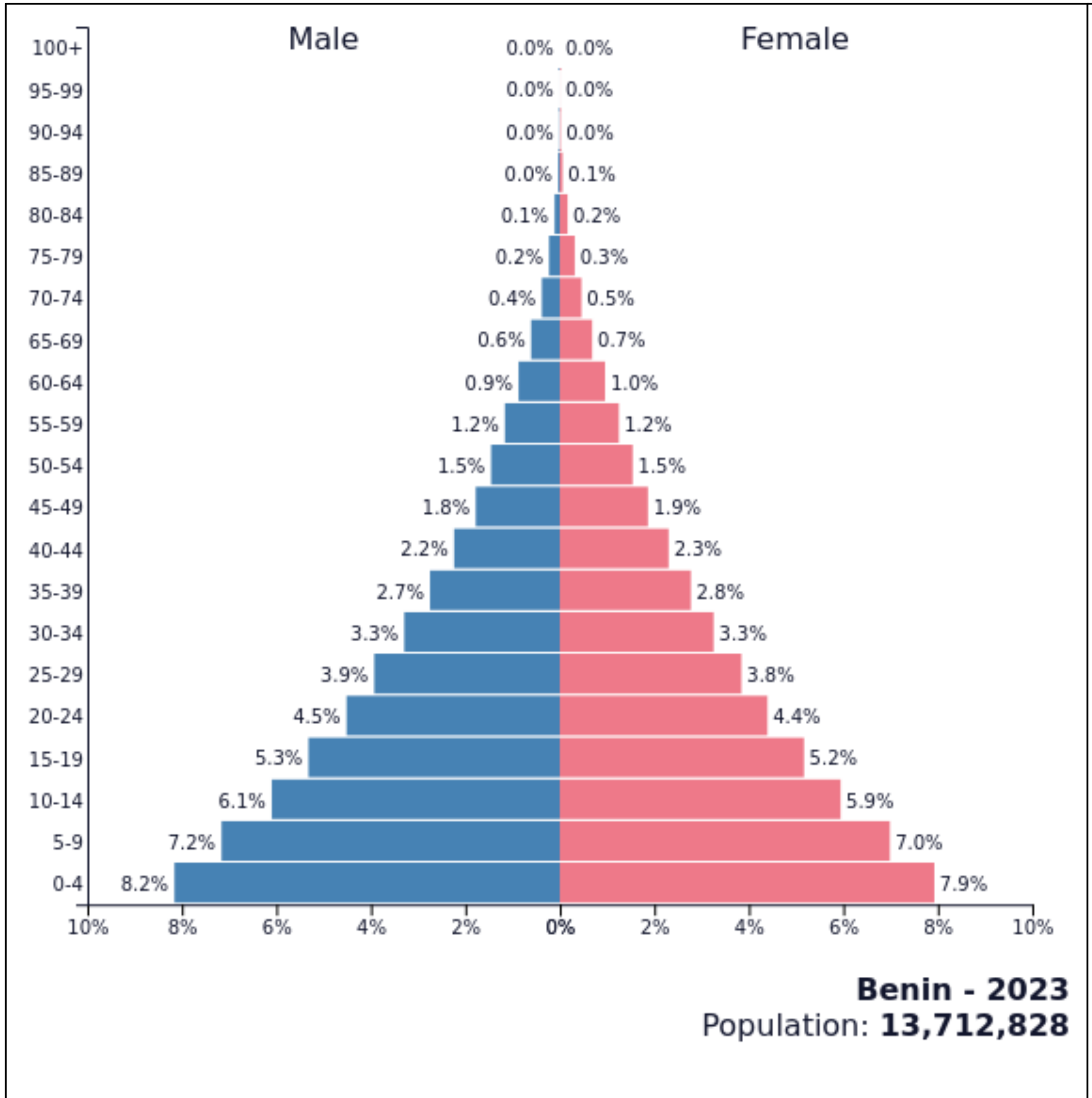
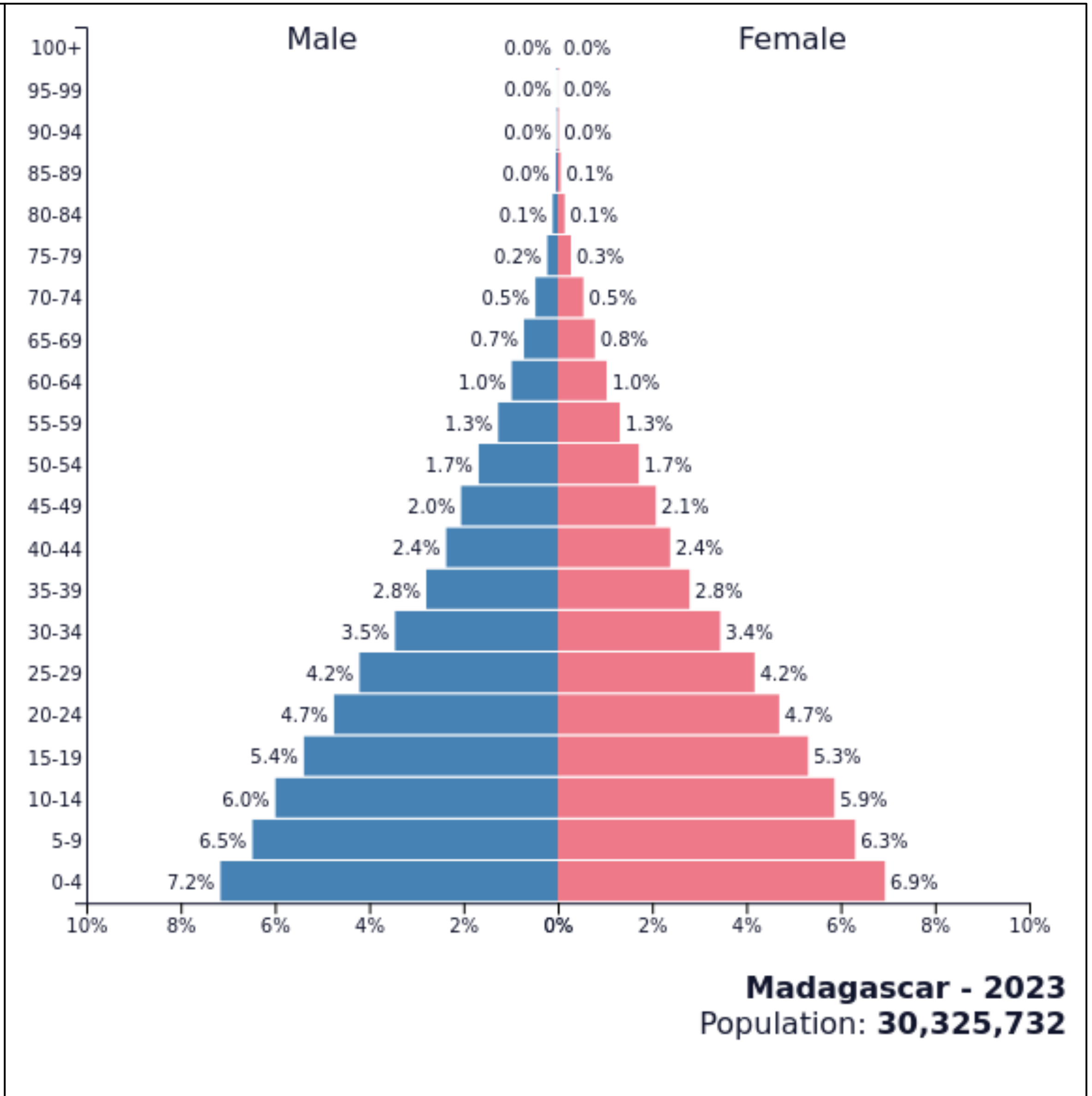


# Where are we globally?



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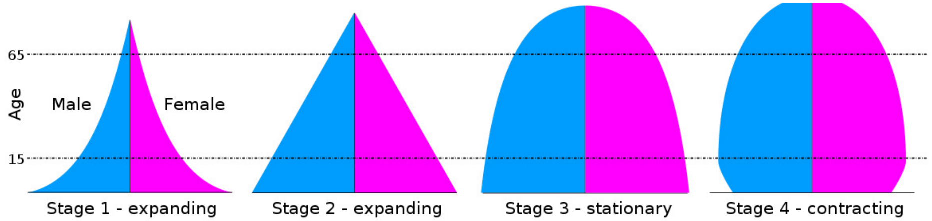


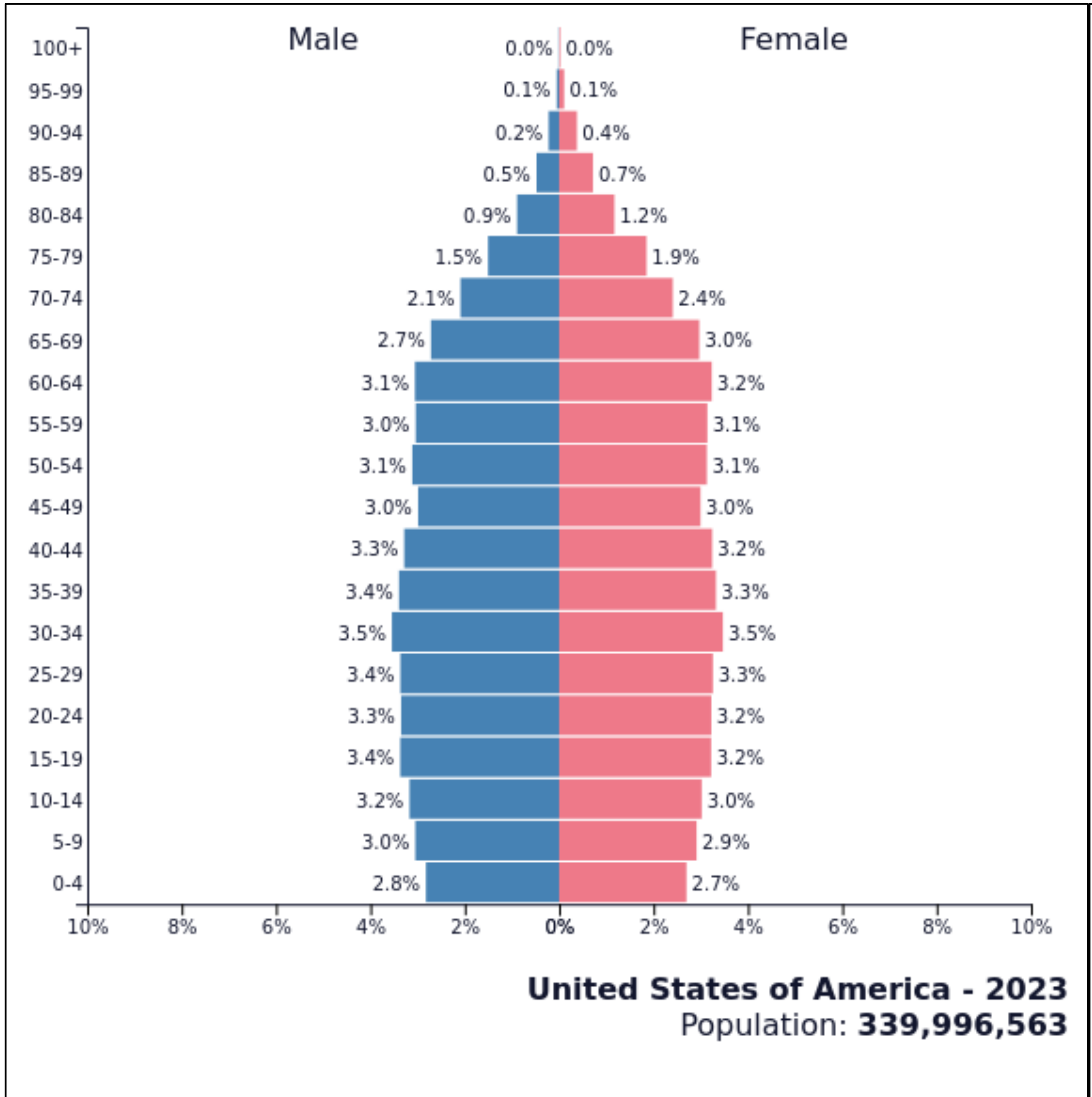


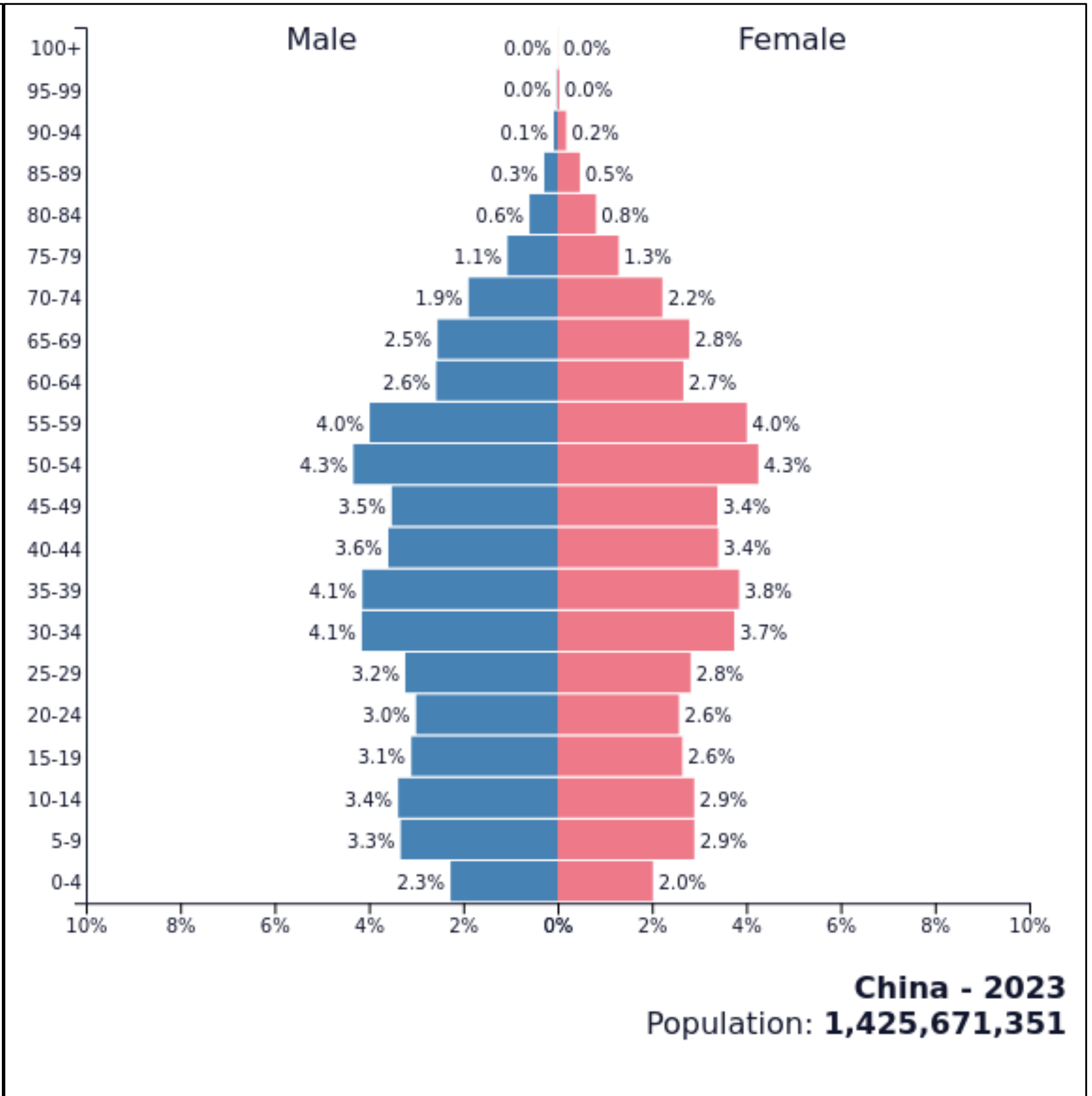

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