

Life History Part I

EFB 370: Population Ecology

Dr. Elie Gurarie

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So far ...

We've studied this equation: $N_t = N_{t-1} + B_t - D_t$

with two assumptions:

Exponential Growth

Births and Deaths proportional to N

Analysis always relies on:

- difference and differential equations
- understanding randomness and stochasticity
- visualization and simulation
- statistics (esp. linear modeling)
- *natural history and biological intuition!*

Logistic Growth

Births decrease and/or Deaths decrease (linearly) with N

Coming up in the next weeks we blow up:

$$N_t$$

into:

sex / age classes:	structured populations
multiple sub-populations:	meta-populations
multiple species:	competitors / predator-prey
infected, susceptible, recovered:	disease dynamics

Always relying on:

- difference and differential equations
- probability and stochasticity
- visualization and simulation
- statistics (esp. linear modeling)
- *natural history and biological intuition!*

Drilling into structure of Birth and Death

$$N_t = N_{t-1} + B_t - D_t$$

B = Births

- **Fecundity** = # births / female / unit time

(unit time can be any unit of time, but is usually year)

D = Deaths

- **Mortality (rate)** = probability of death / unit time
- **Survival (rate)** = 1 - Mortality rate

Life History is the **pattern of survival and reproduction**.

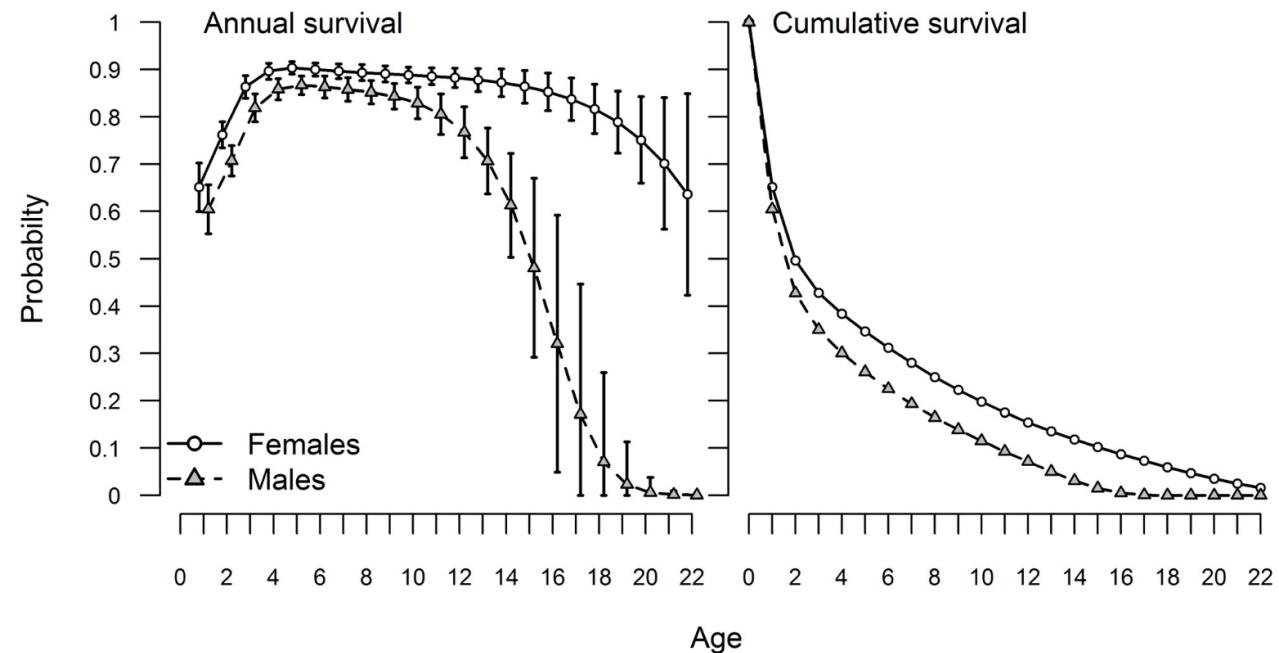
"pattern" means organized by:

Age | Size | Stage (larva / pupa / adult)

Reading:

- Gotelli - Chapter 3

Basic fact of life I: Survival varies with age!



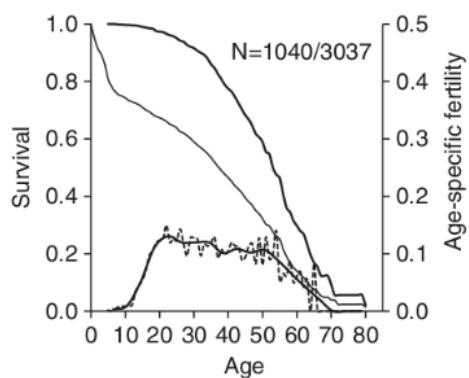
- **Survival Probability** (S_0, S_1, S_2, \dots) always between 0 and 1.
- **Cumulative Survival** ($1, S_0, S_0S_1, S_0S_1S_2, \dots$) always starts at 1 and goes to 0

(Altukhov et al. 2015)

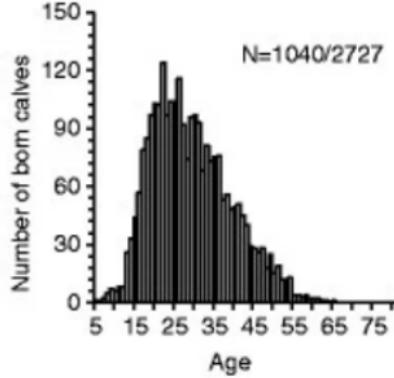


Basic fact of life II: Fecundity varies with age!

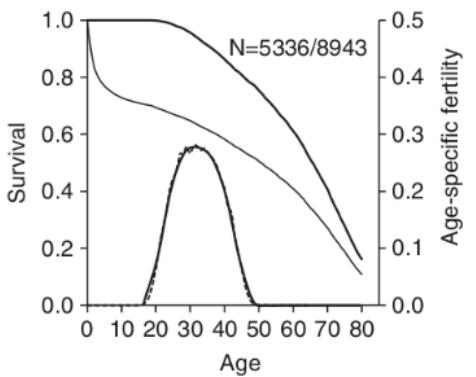
a Elephants



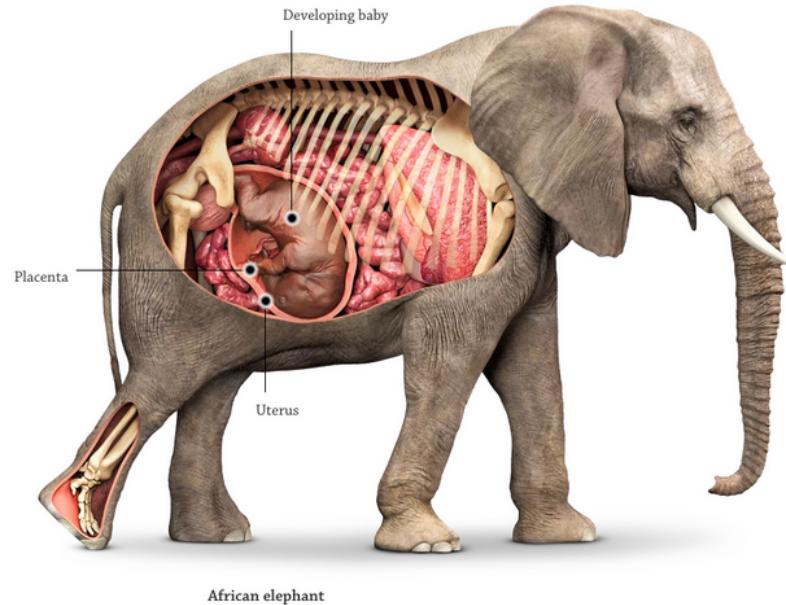
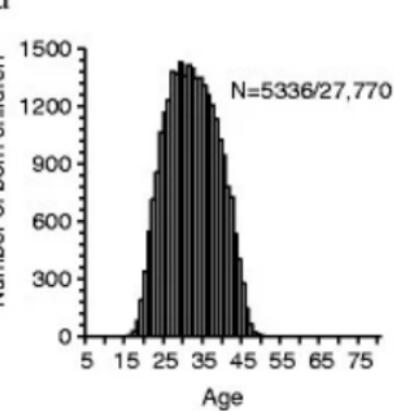
c



b Humans



d



African elephant

Research | Open Access | Published: 12 August 2014

Reproductive cessation and post-reproductive lifespan in Asian elephants and pre-industrial humans

Mirka Lahdenperä Khyne U Mar & Virpi Lummaa

Frontiers in Zoology, 11, Article number: 54 (2014) | Cite this article

8909 Accesses | 59 Citations | 45 Altmetric | Metrics

(Lahdenperä et al. 2015)

Monoceros academicus: Three Life Stages

.	Larva	Sophomore	Emeritus	.
				
Survival	0.5	1	0	
Fecundity	0	1.5	0.5	

- Survival is a probability (unitless)
- Fecundity is an expected number of offspring (n. ind.).

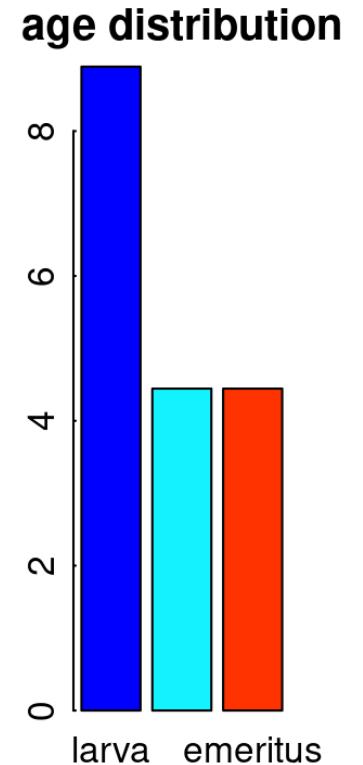
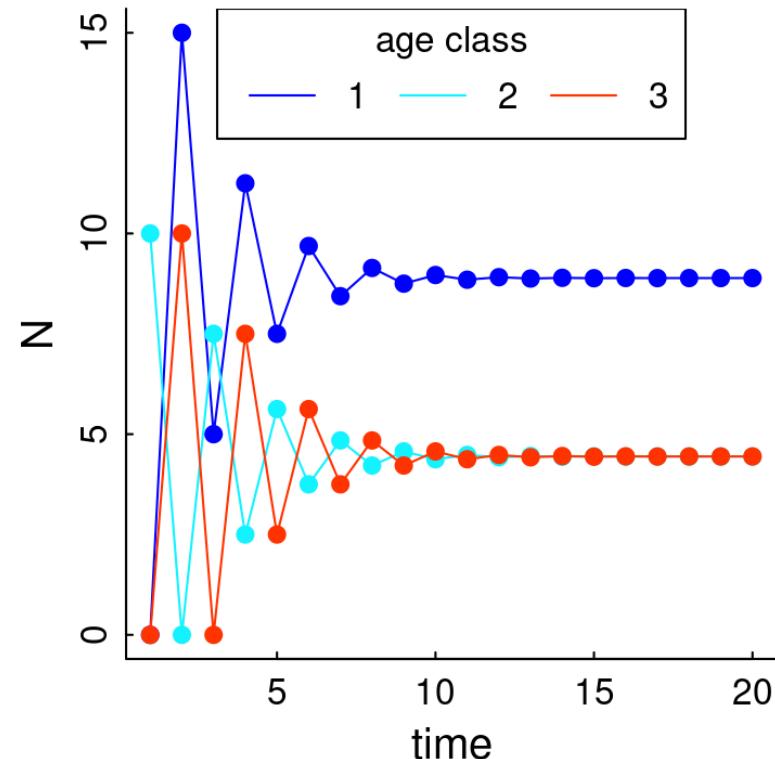
Human experiment: 16 volunteers please.

Experiment: results

Stage	Survival	Fecundity
1. larvae	0.5	0
2. sophomore	1	1
3. emeritus	0	.5

See numerical experiment:

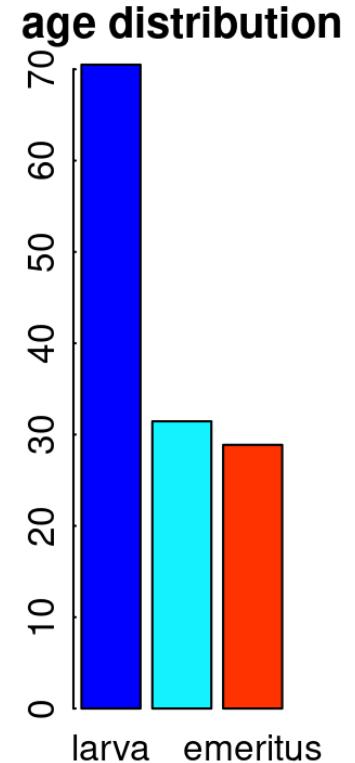
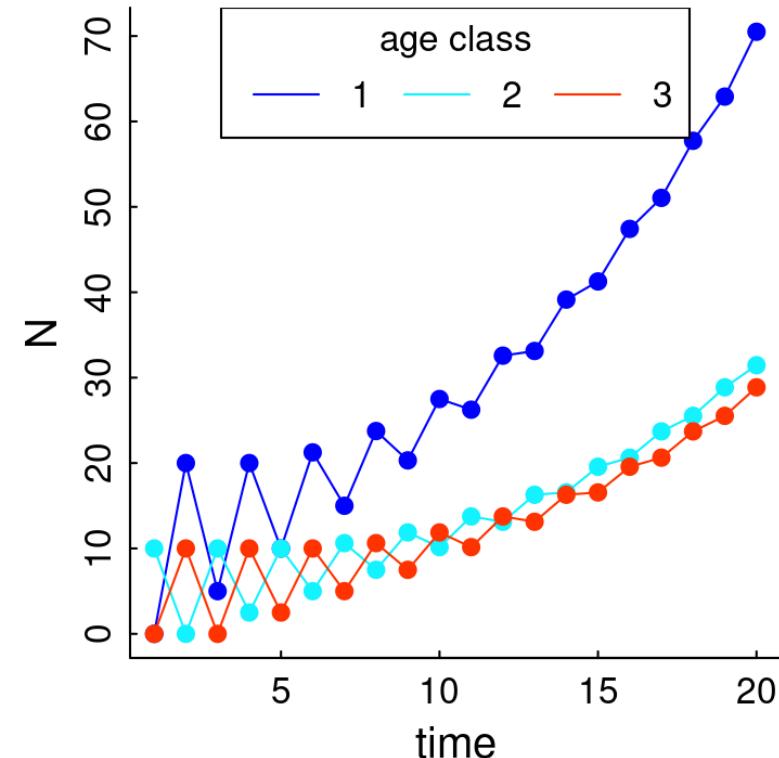
<https://egurarie.shinyapps.io/AgeStructuredGrowth/>



- Eventually obtains a 2:1:1 stable age distribution
- Overall growth = 1

Change one value

Stage	Survival	Fecundity
1. larvae	0.5	0
2. sophomore	1	2
3. emeritus	0	.5



This time, population grows.
And the stable age distribution is a bit different.

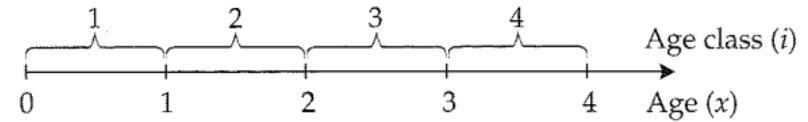
Life Table analysis

A "schedule" of all births and deaths in our population

- **Fecundity schedule:** how many offspring are born by age
- **Survivorship schedule:** with what probability individuals by age

With those (& some tedious calculations) you can compute:

- Life expectancy
- Population growth rate λ
important note: ALL of these models are *discrete exponential* growth models
- Age structure: Are there lots of: young individuals? Old individuals? Reproductive age individuals?
- Survivorship patterns Does most mortality occur in the very young? The very old? Or equally across all ages?



Life history *strategy*

Often - beyond a description - the real question is what influences or explains these parameters?

- evolutionary
- environmental
- density dependent
- human impacts

Life Tables - some "encouragement"

perennial plants, that do not exhibit simple age structure.

Many students find the analysis of life tables to be one of the most confusing topics in ecology. Admittedly, the calculations in this chapter are tedious; we have to keep track of the birth rate, death rate, and number of individuals in each age class of the population. Be careful with your subscripts, but try

Two main pieces:

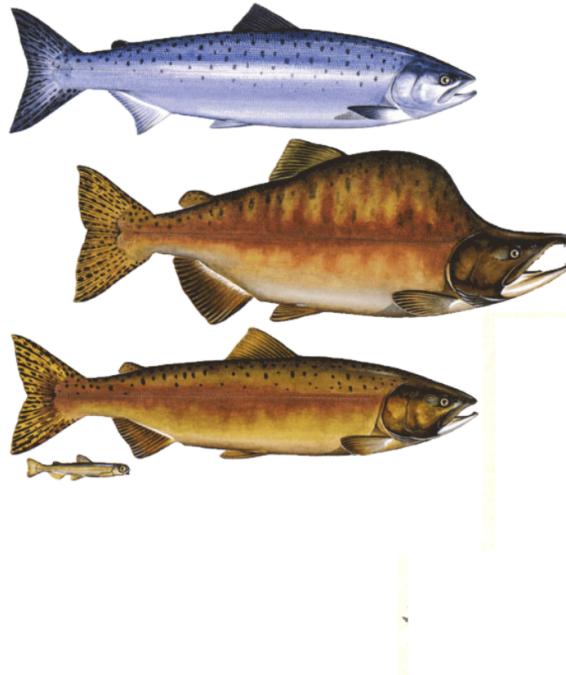
- **Fecundity schedules:** Number of births per age class - i.e. reproductive contribution of females
- **Survivorship schedules:** Number of deaths or probability of death per age class.

Fecundity Schedule

semelparous | monocarpic

Reproduce ONCE (e.g. [Pacific salmon](#) / [desert flower](#) / [annual plant](#))

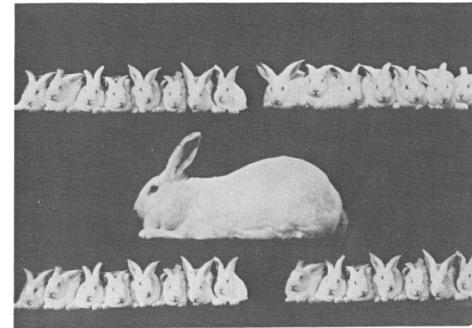
Typical Schedule: **0-0-0-0-0-1000**



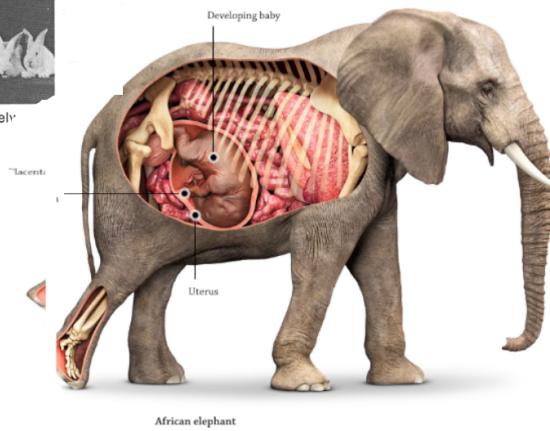
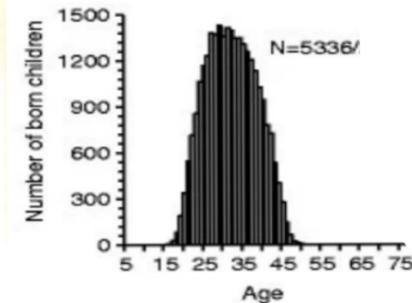
iteroparous | polycarpic

Reproduce many times (e.g. [rabbit](#) / [elephant](#) / [human](#) / [oak](#))

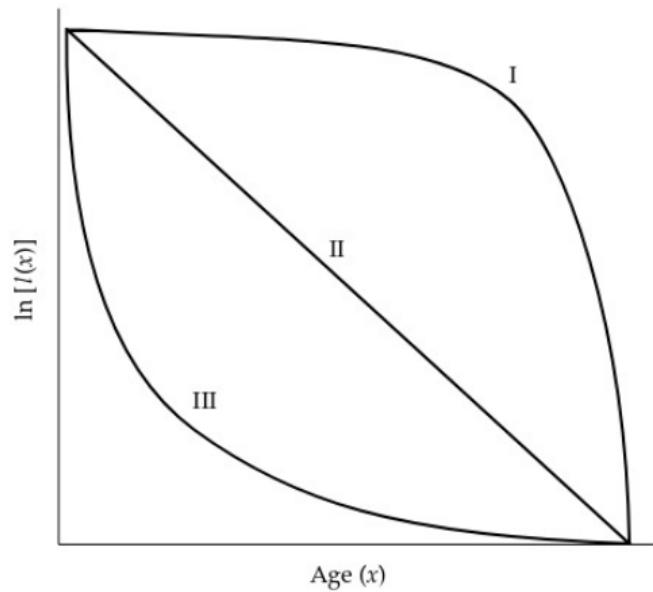
Typical schedule: **0-10-10-10-10-10**



A New Zealand doe and the progeny she produced in one twelve-month period.



Survivorship schedules



- **TYPE I:** high survivorship for juveniles; most mortality late in life
- **TYPE II:** survivorship (or mortality) is relatively constant throughout life
- **TYPE III:** low survivorship for juveniles; survivorship high once older ages are reached

Figure 3.2 Type I, II, and III survivorship curves. Note the logarithmic transformation of the y axis.

The pieces (columns):

Age class (x)	Number at Start (S_x)	Cum. Prob. of survival ($l_x = S_x/S_1$)	births/ind (b_x)	Surv. prob ($g_x = l_x - l_{x+1}$)	Rep. rate: ($l \times b$)	$g = lbx$
1. larva	16			0		
2. sophomore	8			1.5		
3. emeritus	8			.5		
4. beyond	0	0	--	--	--	--
totals:	$\Sigma S_i = 32$	$\Sigma D_i = S_1 = 16$			$R_0 = \sum lb$	$G = \frac{\sum(lbx)}{\sum(lb)}$

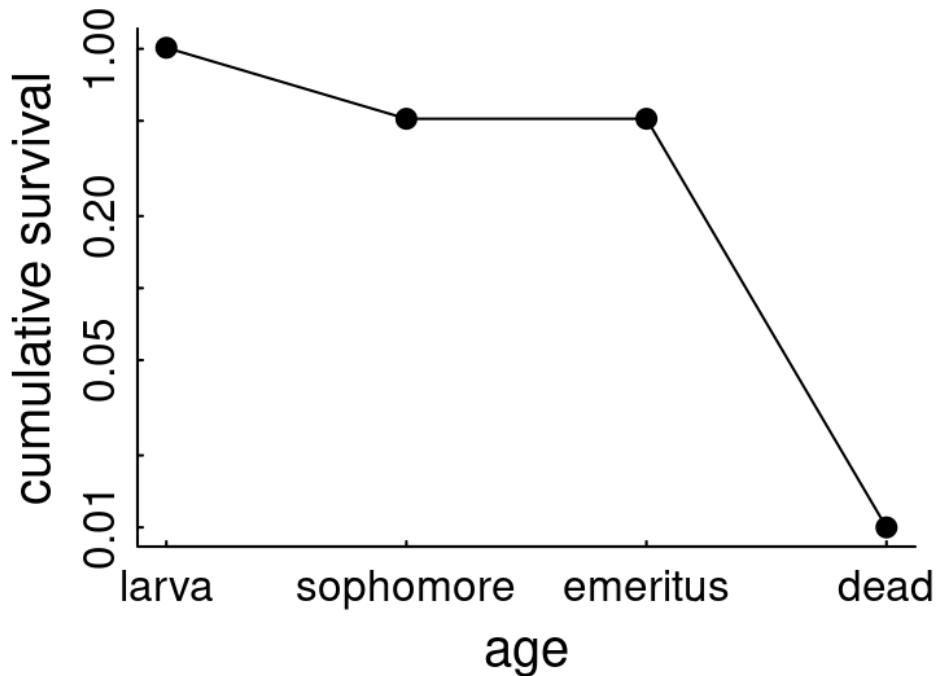
Goals:

1. Fill out table
2. compute reproductive rate: R_0 - mean number of offspring / female
3. compute generation time: G - mean age of mother

The pieces (columns):

Age class (x)	Number at Start (S_x)	Cum. Prob. of survival ($l_x = S_x/S_1$)	births/ind (b_x)	Surv. prob ($g_x = l_x - l_{x+1}$)	Rep. rate: ($l \times b$)	$g = lbx$
1. larva	16	1.0	0	0.5	0	0
2. sophomore	8	0.5	1.5	1	0.75	1.5
3. emeritus	8	0.5	.5	0	0.25	.75
4. beyond	0	0	--	--	--	--
totals:	$\Sigma S_i = 32$	$\Sigma D_i = S_1 = 16$			$R_0 = 1$	$G = 2.25$

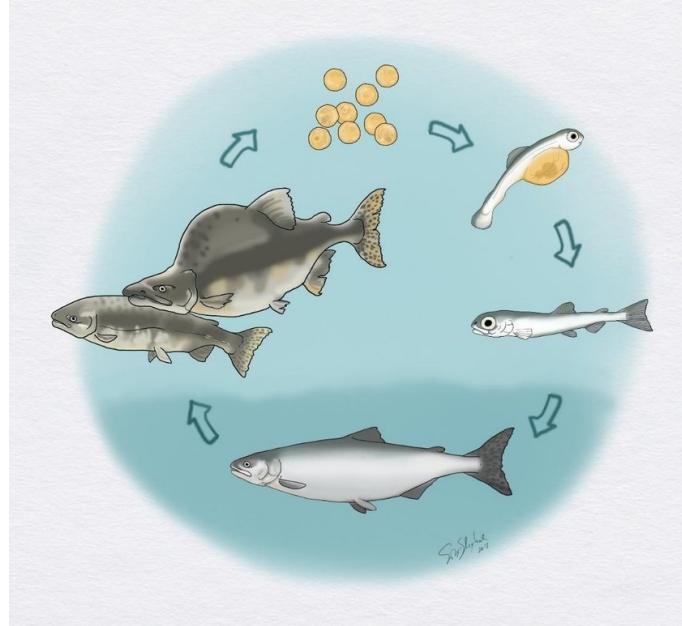
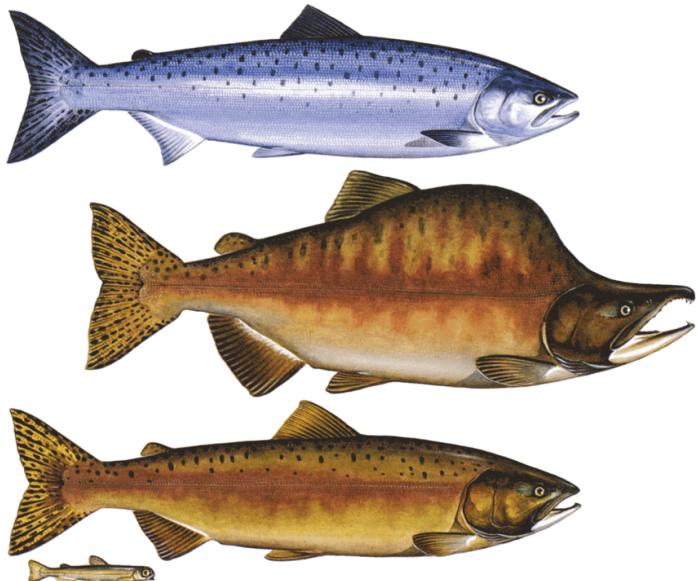
Monoceros academicus: Type I



- **TYPE I:** high survivorship for juveniles; most mortality late in life. Investment in young and survival. Typical of long-lived species.

Stage	Survival	Fecundity
1. larvae	0.5	0
2. sophomore	1	1.5
3. emeritus	0	.5

Pink Salmon (*Onchorynchus gorbuscha*)



Strict 2-year life cycle

Year 0:

- Spawn in late-summer
- Hatch in winter
- Emerge in spring

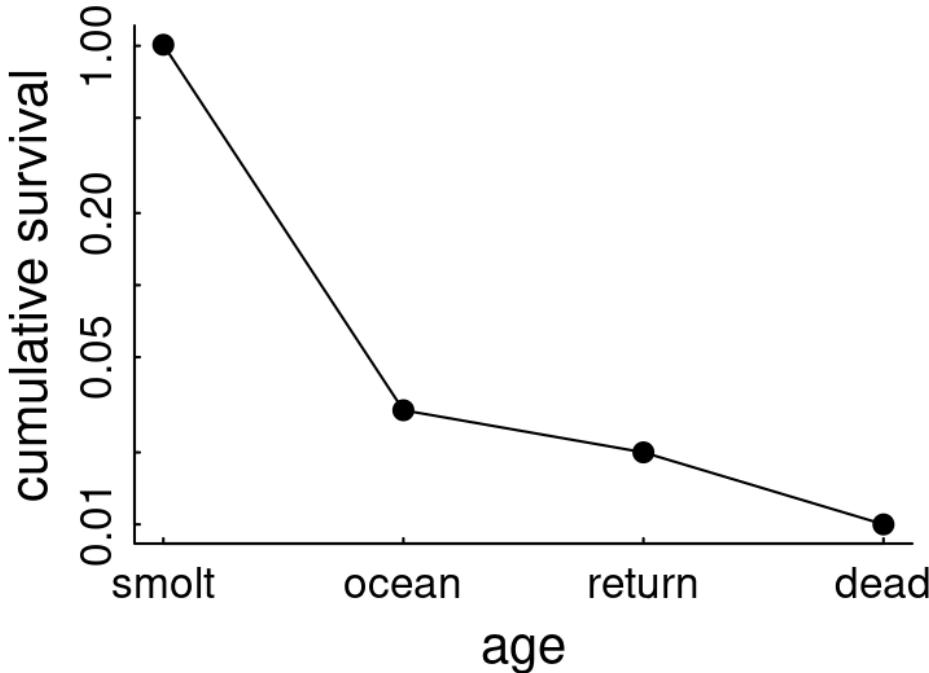
Year 1:

- Ocean phase

Year 2.

- Enter freshwater late spring
- Spawn
- Die

Pink Salmon (*Onchorrhynchus gorbuscha*): Type III



- **TYPE III:** low survivorship for juveniles; survivorship high once older ages are reached. Basically - produce a whole boatload of offspring and hope for the best. Typically short-lived species.

Stage	Survival	Fecundity
1. smolt	0.05	0
2. ocean	0.9	0
3. return	0	21

You can use life-history tables to compute:

Stable Age Distributions:

$$c(x) = \frac{e^{-rx}l(x)}{\sum_{x=0}^k e^{-rx}l(x)}$$

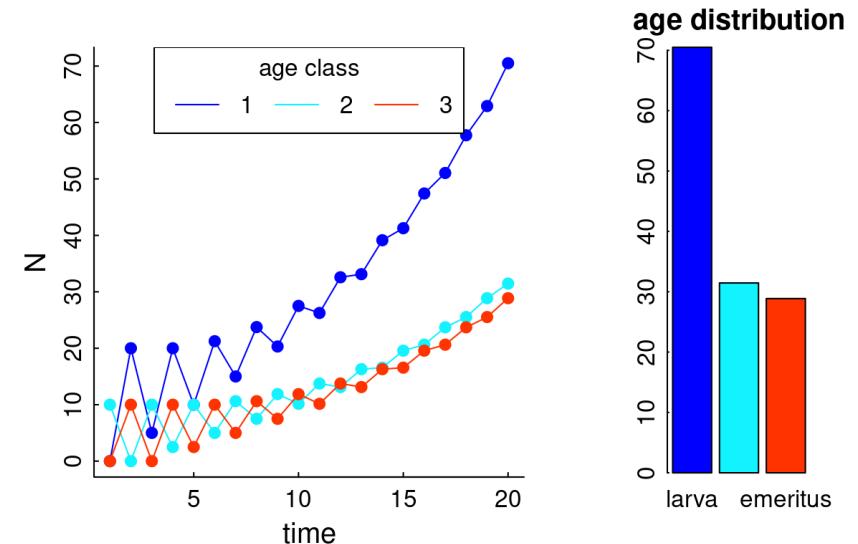
Reproductive value (Number of offspring YET to be born.)

$$v(x) = \frac{e^{rx}}{l(x)} \sum_{y=x+1}^k e^{-ry} l(y)b(y)$$

Growth rate approximately: $r \approx \log(R_0)/G$, or exactly solve this:

$$1 = \sum_{x=1}^n e^{-rx}l(x)b(x)$$

for r .



Note how growth rate affects **stable age distribution!**

Assumptions ...

are the same as exponential growth:

1. Closed population
2. No genetic structure (or individual variability)
3. No time lags
4. Stationarity:
 - Exp. growth: b and d (birth and death rates) constant
 - Stage structured growth: $l(x)$ and $b(x)$ schedules are invariant in time.

The really interesting ecological questions ask what happens when conditions change

Ways of calculating ...

1. Through time: **Cohort analysis** - follow a cohort (or several cohorts) through time
2. Snapshot: **Age distribution** - almost always something weird turns up!
3. Mark-recapture, observational analysis of survival and reproduction

If you have **N-1 variables** you can often infer the **missing one!**

Age	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6	Yr7
0	<u>1000</u>	1005	1010	995	1007	990	1002
1	800	<u>801</u>	799	789	810	805	802
2	600	598	<u>601</u>	609	601	595	603
3	400	406	403	<u>401</u>	390	399	400
4	200	202	202	196	<u>205</u>	198	199
5	100	105	101	103	99	<u>96</u>	97

Age	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6	Yr7
0	1000	1005	<u>1010</u>	995	1007	990	1002
1	800	801	<u>799</u>	789	810	805	802
2	600	598	<u>601</u>	609	601	595	603
3	400	406	<u>403</u>	401	390	399	400
4	200	202	<u>202</u>	196	205	198	199
5	100	105	<u>101</u>	103	99	96	97

SO much easier to just use matrices!

... next week we learn *A POWERFUL, EASY-ISH TRICK* to get both the **intrinsic growth rate** and **stable distribution** and **reproductive value** from a life table using the:



Expectation

Reality

Given

$$A = \begin{bmatrix} 2 & 3 & 0 \\ 4 & 3 & 7 \end{bmatrix} \quad B = \begin{bmatrix} 5 & 7 \\ 6 & 4 \end{bmatrix}$$

Find AB and BA.

