An Example

- *Lepomis sp.*
- 78 marked, 424 recapture, 3 recaptured

$$N_c = \frac{(78+1)(424+1)}{3+1} - 1$$

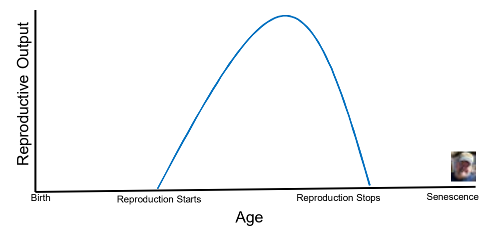
- N_c=8393

$$SE = \sqrt{\frac{(M+1)(n=1)(M-R)(n-r)}{(R+1)^2(R+2)}}$$

- SE=3640

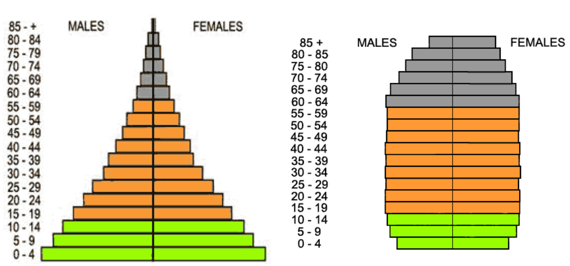
Senescence, Longevity and Fitness

- **physiological longevity** = average longevity of individuals of a population living under optimum conditions; organisms die of senescence
- **ecological longevity** = empirical average longevity of the individuals of a population under natural conditions
  - Few organisms in nature actually die of senescence; most die from disease, predation, or environmental stress
- Senescence of modular organisms

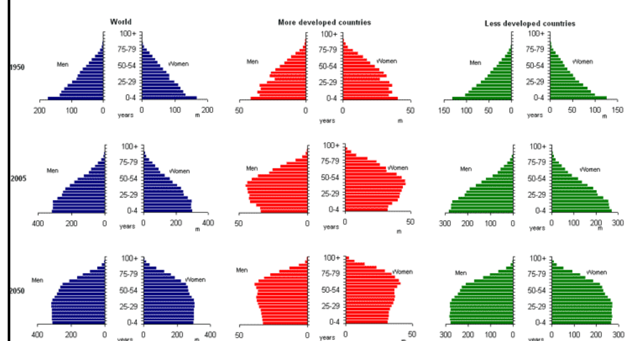


Life history and demographics

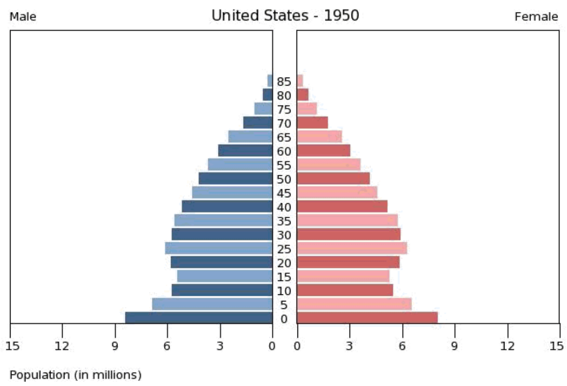
- Population size is more than # of individuals
- Must incorporate age categories (or life stages)

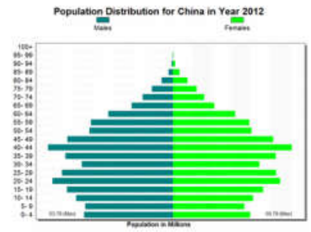


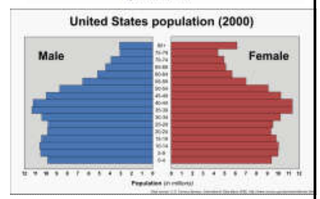
Human Population Demographic Trends



Baby Boomers



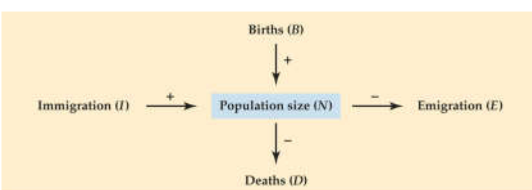




Population Size

- $N_{t+1} = N_t + B + I - D - E$

- Population size and dynamics



COMMUNITY ECOLOGY, Figure 4.1
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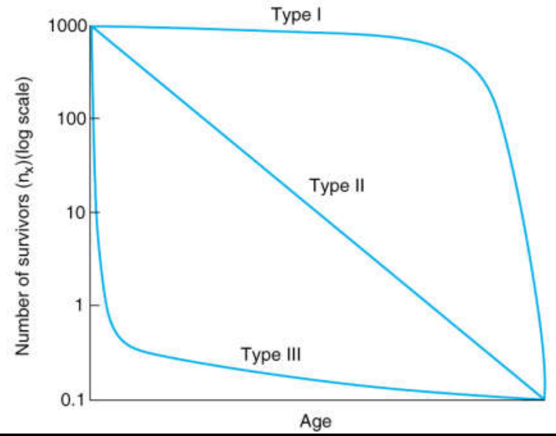
Natality

- Natality rate is equivalent to birth rate, but has broader meaning because it covers production of new individuals by hatching, germination, or fission
- Two basic aspects of natality:
  - **Fertility --** number of individuals born, hatched, etc.; the actual level of output
  - **Fecundity --** potential level of performance, physical capacity; often determined by counting the number of mature ova produced per female.

Survivorship Curves



Research example

- Mansfield and Jude 1986- Alewife (*Alosa pseudoharengus*) survival during the first growth season in southeastern Lake Michigan. Can. J. Fish. Aquatic Sci. 43:1318-1326.

- **Survival** (based on changes in age class abundance) averaged:
  - 1% : yolk-sac → post-yolk sac →YOY
  - 2.2-4.6% : post-yolk sac →YOY.
  - Daily **mortality** rates were 12-27% for larvae through time of yolk sac absorption; decreasing to 2-5% for juveniles.

Adults
N_t = **1000** (male:females 1:1)
Average fecundity **10,000**

S_5 = 0.70

N_{t+1}
700 + 1=**701**

Spawning
N_t females x fecundity
500 x 10000=**5,000,000**

S_1=0.01

Hatching
Spawn x s_1
5,000,000 x 0.01 = **50,000**

S_2=0.01

Yolk-sac larvae
Hatching x s_2
50,000 x 0.01=**500**

S_3 = 0.03

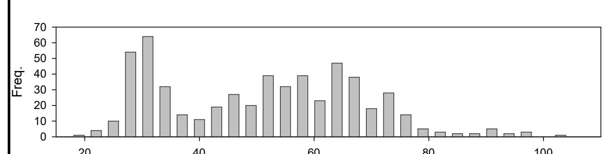
Juveniles
Larvae x s_3
500 x 0.03 = **15**

S4 = 0.07

New Adults
Juveniles x s_4
15 x 0.07 = **1**

Life Tables

- **Dynamic** (horizontal) **cohort**= cohort followed through time until all members have died
- **Static** (vertical or current) = one census period (day, season, etc.); only equivalent to dynamic if population does not change age distribution; assumes constant survivorship.



Life History Tables

- Time (x) = time interval used for separating age categories
- n_x = number alive at the beginning at age x
- L_x = proportion of individuals alive at age x

Age (x)	nx	lx
0	200	1.00
1	180	0.90
2	175	0.88
3	120	0.60
4	50	0.25
5	3	0.02
6	0	0.00

Life History Tables

- d_x = proportion of original population dying during the age interval x to x+1
- q_x = proportion of existing population dying during age interval x to x+1; $q_x = d_x/l_x$

Age (x)	nx	lx	dx	qx
0	200	1.000	0.100	0.100
1	180	0.900	0.025	0.028
2	175	0.875	0.275	0.314
3	120	0.600	0.350	0.583
4	50	0.250	0.235	0.940
5	3	0.015		
6	0	0.000		

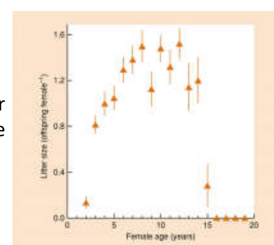
Life expectancy

- $L_x = (l_x+l_{x+1})/2$
- T_x = average life expectancy from current time not accounting for earlier mortality
  - $T_x=\Sigma(L_x)$; summed from x to last x
- $e_x = T_x / l_x$
  - Life expectancy accounting for earlier mortality. E.g. how much longer is an individual at age x expected to live.

Age (x)	nx	lx	dx	qx	Lx	Tx	ex
0	200	1.000	0.100	0.100	0.950	3.130	3.130
1	180	0.900	0.025	0.028	0.888	2.180	2.422
2	175	0.875	0.275	0.314	0.738	1.293	1.477
3	120	0.600	0.350	0.583	0.425	0.555	0.925
4	50	0.250	0.240	0.960	0.130	0.130	0.520
5	2	0.010					
6	0	0.000					

Natality

- **f_x** = total natality; number of fertilized eggs produced in a given year by individuals surviving to age x
- **m_x** = age specific natality; average number of fertilized eggs produced per individual surviving to beginning of age x
- Lotka proved that any pair of unchanging l_x and m_x values will eventually give rise to a population with a **stable age distribution**



Reproductive Rates

R_0 = net reproductive rate; Net number of offspring produced per individual. Also, a multiplier allowing us to determine population size in the next generation. For simplicity, assume discrete generations.

$$R_0=\sum(l_x m_x)$$

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$	k_x	M_x	f_x	$l_x m_x$	$xl_x m_x$	-rx	e^{-rx}	$l_x m_x e^{-rx}$	L_x	T_x	e_x
0	200	1.00	0.10	0.10	2.30	0.00	0.04	0		0.00		0.00		0.00	0.95	3.13	3.13
1	180	0.90	0.03	0.03	2.26	-0.05	0.01	2	360.00	1.80	1.80	-0.88	0.42	0.75	0.89	2.18	2.42
2	175	0.88	0.28	0.31	2.24	-0.06	0.16	3	525.00	2.63	5.25	-1.75	0.17	0.46	0.74	1.29	1.48
3	120	0.60	0.35	0.58	2.08	-0.22	0.37	4	480.00	2.40	7.20	-2.63	0.07	0.17	0.43	0.56	0.93
4	50	0.25	0.24	0.96	1.70	-0.60	1.22	5	250.00	1.25	5.00	-3.50	0.03	0.04	0.13	0.13	0.52
5	2	0.01			0.30	-2.00		0		0.00		-4.38	0.01	0.00		0.00	
6	0							0		0.00		-5.26	0.01	0.00			
7	0							0		0.00		-6.13	0.00	0.00			
8	0							0		0.00		-7.01	0.00	0.00			
9	0							0		0.00		-7.89	0.00	0.00			

R_o	$\sum l_x m_x$	8.075	$\sum l_x m_x e^{-rx}=1$
	$\sum xl_x m_x$	19.250	1.415

Defining R

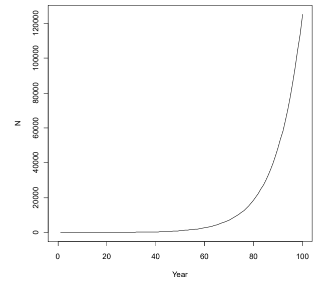
R_0 is a multiplier allowing us to determine population size at future generation.

$$N_{t+1} = N_t * R_0$$

General formula for population size at time t is:

$$N_t = N_0 * R_0^{\,t}$$

Predicts exponential growth



			time											
age	fecund	Survive	1	2	3	4	5	6	7	8	9	10	11	12
0	0	1	50	0	75	56	113	169	232	380	538	831	1,234	1,851
1	5	0.3	0	15	0	23	17	34	51	70	114	161	249	370
2	15	0.25	0	0	4	0	6	4	8	13	17	28	40	62
3	0	0.2	0	0	0	1	0	1	1	2	3	3	6	8
sum			50	15	79	80	135	208	292	464	672	1,024	1,529	2,292
pct 0			100	0	95	71	83	81	79	82	80	81	81	81
pct 1			0	100	0	28	13	16	17	15	17	16	16	16
pct 2			0	0	5	0	4	2	3	3	3	3	3	3
pct 3			0	0	0	1	0	1	0	0	0	0	0	0
				5.25	1.01	1.70	1.54	1.40	1.59	1.45	1.52	1.49	1.50	0.00

R_0=5.25

			time											
age	fecund	Survive	1	2	3	4	5	6	7	8	9	10	11	12
0	1	1	50	50	110	226	415	810	1,562	3,000	5,785	11,141	21,457	41,335
1	4	0.3	0	15	15	33	68	124	243	469	900	1,735	3,342	6,437
2	15	0.25	0	0	4	4	8	17	31	61	117	225	434	836
3	0	0.2	0	0	0	1	1	2	3	6	12	23	45	87
sum			50	65	129	264	491	953	1,839	3,535	6,814	13,125	25,279	48,694
pct 0			100	77	85	86	84	85	85	85	85	85	85	85
pct 1			0	23	12	13	14	13	13	13	13	13	13	13
pct 2			0	0	3	1	2	2	2	2	2	2	2	2
pct 3			0	0	0	0	0	0	0	0	0	0	0	0
				1.98	2.05	1.86	1.94	1.93	1.92	1.93	1.93	1.93	1.93	0.00

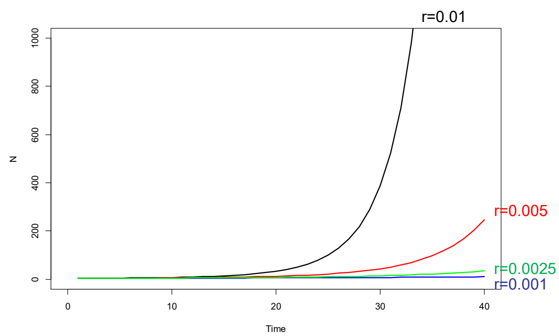
R_0=5.95

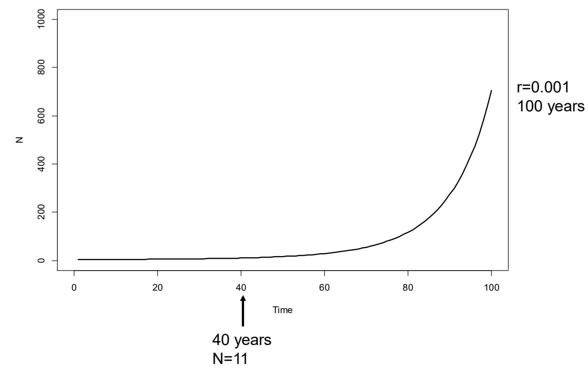
Reproductive Rates

- **r = intrinsic rate of increase**; per capita rate of increase; also **Malthusian Parameter**. When r is >0 populations will increase, when it is <0 populations will decrease; a population that is not increasing or decreasing will have an r of 0. Units – number of new individuals per unit time.

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$
0	200	1.00	0.10	0.10	2.30	0.00
1	180	0.90	0.03	0.03	2.26	-0.05
2	175	0.88	0.28	0.31	2.24	-0.06
3	120	0.60	0.35	0.58	2.08	-0.22
4	50	0.25	0.24	0.96	1.70	-0.60
5	2	0.01			0.30	-2.00
6	0					
7	0					
8	0					
9	0					

R_o	$\sum l_x m_x$	8.075
	$\sum xl_x m_x$	19.250
	T_c	2.384
	r	0.876
	Double	0.787





Determining r…

If generation time (T) is known, can determine r from Lotka's Equation:

$$1 = \sum e^{-rx} l_x m_x$$ using iteration

This is difficult, and the equation is not biologically meaningful…

r can be estimated by:

$$r = \frac{\ln(R_0)}{T_c}$$

where **T_c is generation time**.

Cohort Generation Time

T_c is the average birth-to-birth time for a generation.

$$T_c = \frac{\sum x l_x m_x}{R_0}$$

Recall that $R_0 = \sum l_x m_x$

Thus

$$T_c = \frac{\sum x l_x m_x}{\sum l_x m_x}$$

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$
0	200	1.00	0.10	0.10	2.30	0.00
1	180	0.90	0.03	0.03	2.26	-0.05
2	175	0.88	0.28	0.31	2.24	-0.06
3	120	0.60	0.35	0.58	2.08	-0.22
4	50	0.25	0.24	0.96	1.70	-0.60
5	2	0.01			0.30	-2.00
6	0					
7	0					
8	0					
9	0					

R_o	$\sum l_x m_x$	8.075
	$\sum x l_x m_x$	19.250
	T_c	2.384
	r	0.876
	Double	0.787

Lotka's Solution to r, solve for Tc first, then r

$T_c = (19.25/8.075) = 2.3839$

$r = \ln(8.075)/2.3839 = 0.876$

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$	k_x	M_x	f_x	l_xm_x	xl_xm_x	-rx	e^{-rx}	$l_xm_xe^{-rx}$	L_x
0	200	1.00	0.10	0.10	2.30	0.00	0.04	0		0.00		0.00		0.00	0.95
1	180	0.90	0.03	0.03	2.26	-0.05	0.01	2	360.00	1.80	1.80	-0.88	0.42	0.75	0.89
2	175	0.88	0.28	0.31	2.24	-0.06	0.16	3	525.00	2.63	5.25	-1.75	0.17	0.46	0.74
3	120	0.60	0.35	0.58	2.08	-0.22	0.37	4	480.00	2.40	7.20	-2.63	0.07	0.17	0.43
4	50	0.25	0.24	0.96	1.70	-0.60	1.22	5	250.00	1.25	5.00	-3.50	0.03	0.04	0.13
5	2	0.01			0.30	-2.00		0		0.00		-4.38	0.01	0.00	
6	0							0		0.00		-5.26	0.01	0.00	
7	0							0		0.00		-6.13	0.00	0.00	
8	0							0		0.00		-7.01	0.00	0.00	
9	0							0		0.00		-7.89	0.00	0.00	

R_o	$\sum l_xm_x$	8.075
	$\sum xl_xm_x$	19.250
	T_c	2.384
	r	0.876
	Double	0.787

$\sum l_xm_xe^{-rx}=1$

1.415

How good is our estimate of r?

- True value of r difficult to get:

$$1 = \sum e^{-rx} l_x m_x$$

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$	k_x	M_x	f_x	l_xm_x	xl_xm_x	-rx	e^{-rx}	$l_xm_xe^{-rx}$	L_x
0	200	1.00	0.10	0.10	2.30	0.00	0.04	0		0.00		0.00		0.00	0.95
1	180	0.90	0.03	0.03	2.26	-0.05	0.01	2	360.00	1.80	1.80	-0.88	0.42	0.75	0.89
2	175	0.88	0.28	0.31	2.24	-0.06	0.16	3	525.00	2.63	5.25	-1.75	0.17	0.46	0.74
3	120	0.60	0.35	0.58	2.08	-0.22	0.37	4	480.00	2.40	7.20	-2.63	0.07	0.17	0.43
4	50	0.25	0.24	0.96	1.70	-0.60	1.22	5	250.00	1.25	5.00	-3.50	0.03	0.04	0.13
5	2	0.01			0.30	-2.00		0		0.00		-4.38	0.01	0.00	
6	0							0		0.00		-5.26	0.01	0.00	
7	0							0		0.00		-6.13	0.00	0.00	
8	0							0		0.00		-7.01	0.00	0.00	
9	0							0		0.00		-7.89	0.00	0.00	

R_o	$\sum l_xm_x$	8.075
	$\sum xl_xm_x$	19.250
	T_c	2.384
	r	0.876
	Double	0.787

$\sum l_xm_xe^{-rx}=1$

1.415

- Value > 1 means estimate of r is too small
- Value < 1 means estimate is too large
- In this case, actual r slightly greater than 0.876

How do we use this?

$$N_{t+1} = N_t * R_0$$

- However, r is much more useful as a continuous measure of population growth.

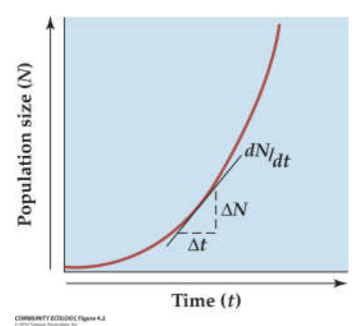
$$\frac{dN}{dt} = rN$$

Differential equation of logistic growth. Can only tell you the rate (dN/dt) of growth, can't project population size.

$$N_t = N_0 e^{rt}$$

Integrate the first equation, and it is written in a form where you can project population size given a time period (t).

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



More about r

How long does it take a population to double in size??

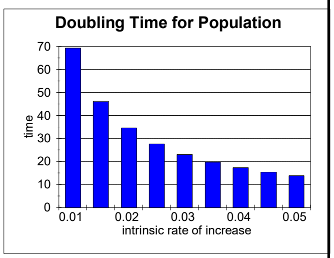
$$N_t = N_0 e^{rt}$$

N_t=2 and N_o=1 t=?

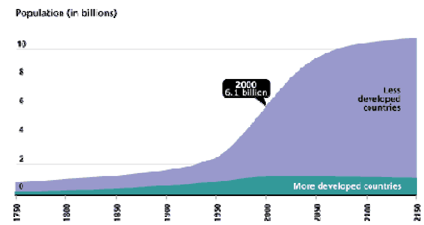
$$\frac{N_t}{N_0} = e^{rt}$$

ln 2=rt

t=0.69/r



Human Population Growth



year	r	doubling time
1970	0.02	35
1991	0.018	39
2000	0.0125	55

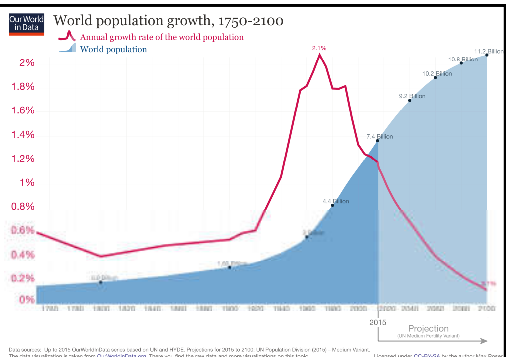
Given current growth rates, what will the world population be in 30 years??

N_t=N_0e^{rt}

N_t=6,426,101,450 $e^{0.0125(30)}$

9,349,922,439

Variability in r



- Clearly, r is variable through time
- The maximum rate of increase obtainable by a population is r_{max}
- Difference between r_{max} and r is due to environmental resistance
- r_{max} - quality of food, space, etc. are optimum, no competition or predation.

An example

stage	a_x	M_x
0	1500	0
1	300	2
2	200	3
3	100	6
4	50	2
5	10	1

- Given these data, answer the following
  - What proportion of individuals survive to age 2? (l_2)
  - What proportion of 2 year olds die before reaching age 3? (q_2)
  - What is the expected lifespan? (e_0)
  - How many total offspring are produced by the third year class? (f_3)
  - Is the population growing or shrinking? (r/R_0)
  - What is the generation time? (T)
  - How large will the population be in 243 years? (r)
  - How long before the population doubles? (r)

An example

- What proportion of individuals survive to age 2? (l_2)
  - $l_x = a_x/a_0$ = 200/1500 =13.3%

stage	a_x	l_x
0	1500	1.00
1	300	0.20
2	200	0.13
3	100	0.07
4	50	0.03
5	10	0.01

An example

- What proportion of 2 year olds die before reaching age 3? (q_2)
- $q_x = a_{x+1}/a_x$ = 100/200 =50%

stage	a_x	l_x	d_x	q_x
0	1500	1.00	0.80	0.80
1	300	0.20	0.07	0.33
2	200	0.13	0.07	0.50
3	100	0.07	0.03	0.50
4	50	0.03	0.03	0.80
5	10	0.01		

An example

- What is the expected lifespan? (e_0)
  - $L_x = (a_x + a_{x+1})/2$
  - $e_x = \text{Sum}(L_x)/a_x$
  - e_0=(900+150+150+75+30)/1500 = 1405/1500 = 0.94

stage	a_x	l_x	d_x	q_x	L_x	e_x
0	1500	1.00	0.80	0.80	900.00	0.94
1	300	0.20	0.07	0.33	250.00	1.68
2	200	0.13	0.07	0.50	150.00	1.28
3	100	0.07	0.03	0.50	75.00	1.05
4	50	0.03	0.03	0.80	30.00	0.60
5	10	0.01				

An example

- How many total offspring are produced by the third year class? (f_3)
- $f_x = m_x * a_x$
- $f_3 = m_3 * a_3$ = 6*100 = 600

stage	a_x	l_x	d_x	q_x	M_x	f_x
0	1500	1.00	0.80	0.80	0	
1	300	0.20	0.07	0.33	2	600.00
2	200	0.13	0.07	0.50	3	600.00
3	100	0.07	0.03	0.50	6	600.00
4	50	0.03	0.03	0.80	2	100.00
5	10	0.01			1	10.00

An example

- Is the population growing or shrinking? (r/R_0)
- R_0=Sum($l_x m_x$)
- R_0=0+0.4+0.4+0.4+0.07+0.01 = 1.28

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$	k_x	M_x	f_x	$l_x m_x$	$xl_x m_x$
0	1500	1.00	0.80	0.80	3.18	0.00	0.70	0		0.00	
1	300	0.20	0.07	0.33	2.48	-0.70	0.17	2	600.00	0.40	0.40
2	200	0.13	0.07	0.50	2.30	-0.88	0.30	3	600.00	0.40	0.80
3	100	0.07	0.03	0.50	2.00	-1.18	0.29	6	600.00	0.40	1.20
4	50	0.03	0.03	0.80	1.70	-1.48	0.66	2	100.00	0.07	0.27
5	10	0.01			1.00	-2.18		1	10.00	0.01	0.03

An example

- What is the generation time? (T)
- T=sum($xl_x m_x$)/sum($l_x m_x$)
- T=2.7/1.27 = 2.12

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$	k_x	M_x	f_x	$l_x m_x$	$xl_x m_x$
0	1500	1.00	0.80	0.80	3.18	0.00	0.70	0		0.00	
1	300	0.20	0.07	0.33	2.48	-0.70	0.17	2	600.00	0.40	0.40
2	200	0.13	0.07	0.50	2.30	-0.88	0.30	3	600.00	0.40	0.80
3	100	0.07	0.03	0.50	2.00	-1.18	0.29	6	600.00	0.40	1.20
4	50	0.03	0.03	0.80	1.70	-1.48	0.66	2	100.00	0.07	0.27
5	10	0.01			1.00	-2.18		1	10.00	0.01	0.03

An example

- How large will the population be in 243 years? (r)
- $r=\ln R_0/T$
- r=ln(1.27)/2.12 = 0.1127438
- $N_t=N_0e^{rt}$
- $N_{243}=1500\ e^{0.1127*243}$
- $N_{243} = 1500\ e^{27.3861}$
- 1.17×10^{15}

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$	k_x	M_x	f_x	$l_x m_x$	$xl_x m_x$
0	1500	1.00	0.80	0.80	3.18	0.00	0.70	0		0.00	
1	300	0.20	0.07	0.33	2.48	-0.70	0.17	2	600.00	0.40	0.40
2	200	0.13	0.07	0.50	2.30	-0.88	0.30	3	600.00	0.40	0.80
3	100	0.07	0.03	0.50	2.00	-1.18	0.29	6	600.00	0.40	1.20
4	50	0.03	0.03	0.80	1.70	-1.48	0.66	2	100.00	0.07	0.27
5	10	0.01			1.00	-2.18		1	10.00	0.01	0.03

An example

- How long before the population doubles? (r)
- Double time = 0.69/r = 0.69/0.114 = 6.05 years

stage	a_x	l_x	d_x	q_x	$Log_{10}a_x$	$Log_{10}l_x$	k_x	M_x	f_x	$l_x m_x$	$xl_x m_x$
0	1500	1.00	0.80	0.80	3.18	0.00	0.70	0		0.00	
1	300	0.20	0.07	0.33	2.48	-0.70	0.17	2	600.00	0.40	0.40
2	200	0.13	0.07	0.50	2.30	-0.88	0.30	3	600.00	0.40	0.80
3	100	0.07	0.03	0.50	2.00	-1.18	0.29	6	600.00	0.40	1.20
4	50	0.03	0.03	0.80	1.70	-1.48	0.66	2	100.00	0.07	0.27
5	10	0.01			1.00	-2.18		1	10.00	0.01	0.03