

An Example

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

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

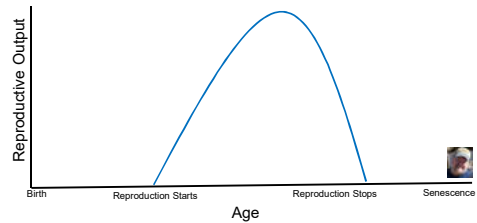
- $N_c = 8393$

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

- $SE = 3640$

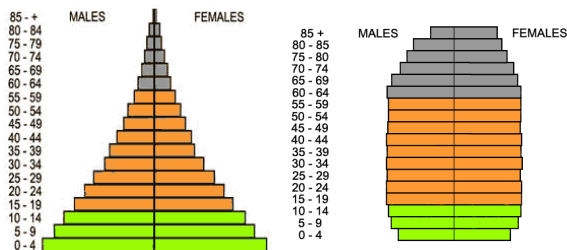
Senescence, Longevity and Fitness

- **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

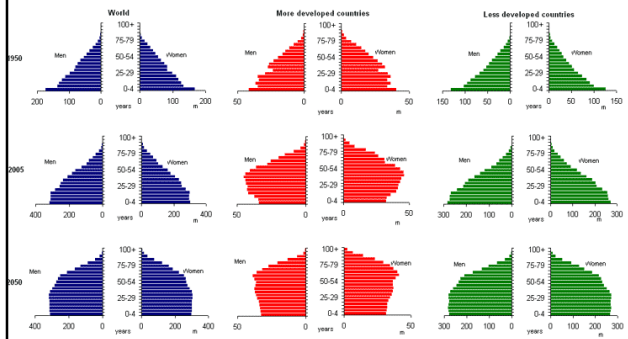


Life history and demographics

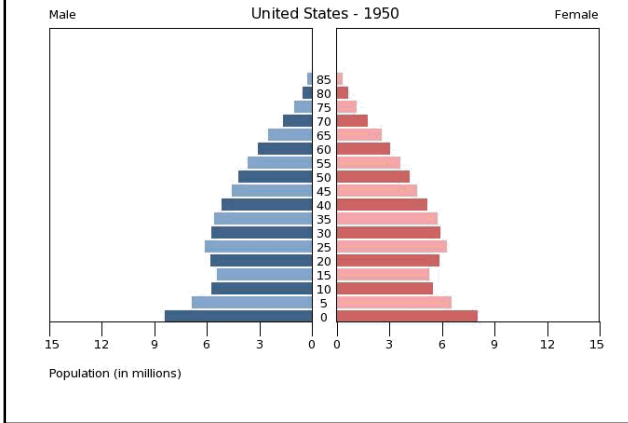
- Population size is more than # of individuals
- Must incorporate age categories (or life stages)



Human Population Demographic Trends



## Baby Boomers



### In Praise of China's One-Child Policy

By [Author Name]

In the ongoing debate over overpopulation, no country's experience has been more controversial than China's one-child policy. Many fight against it, but many also praise it. In the end, the policy is a necessary and prudent response to the environmental and economic challenges that the world faces.

**Reducing and controlling urban**

There are many other ways to control population. I thought it was time to recall. How what I learned this summer, during a visit to a leading professor of environmental policy at Beijing's prestigious Renmin University (Peking University). While some people, even Chinese, believe that the extreme governmental intervention was very important for the country's economic prosperity and environmental control, they also believe the policy is no longer necessary. They are right on all counts.

The one-child policy started in 1979. In September 1980, with population approaching 1 billion, a new progressive Chinese government led by Deng Xiaoping set a "one-child" target for all urban families. Exceptions were made for rural families and ethnic minorities, who were allowed two. The urbaners also, taking a second child was the world brought a range of incentives, including better housing, less unemployment and medical opportunities.

As a result, fertility rates began to drop precipitously, starting at 1.8 children per family and stabilizing at 1.6 on average today. Demographers call it a demographic dividend. Depending on assumptions, they believe the policy may have prevented an extra 400 million births.

Criticism of the policy began with the fact that Chinese birth rates were already falling in 1970s and fertility rates averaged 1.8. They claim that the drop in fertility had little to do with the policy and more to do with the sociology of urban living and family. In response, it can be argued that the phenomenal growth in India's population during the same period shows that China probably would not have avoided economic development stability without a one-child policy.

### Population Distribution for China in Year 2012

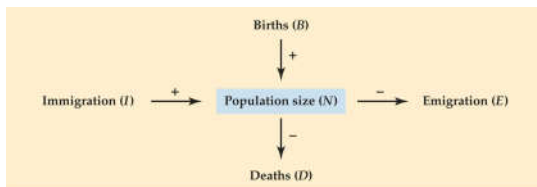
Population in Millions

Male (left side, blue bars) and Female (right side, red bars) population in millions. The x-axis ranges from 0 to 15 million on both sides. The y-axis shows age groups from 0 to 100. The pyramid is narrow at the base and wide at the top, indicating a low birth rate and an aging population.

## Population Size

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

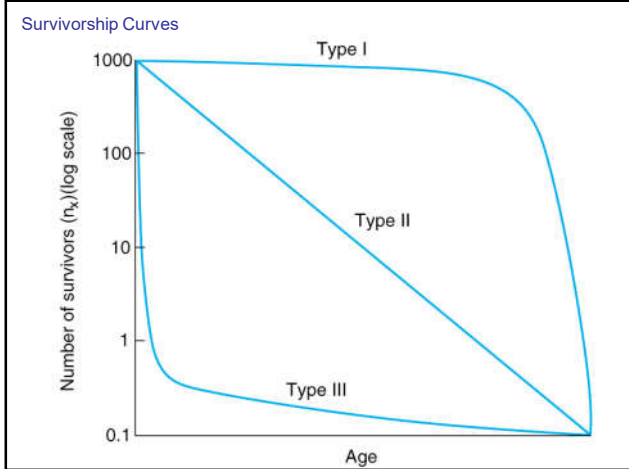
### Population size and dynamics



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.

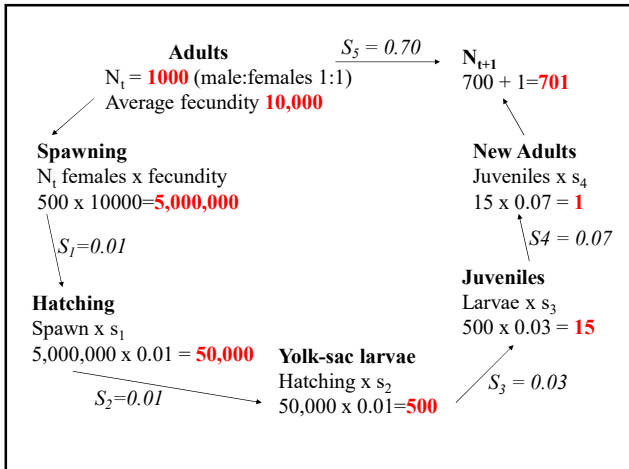


Research example

- 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.

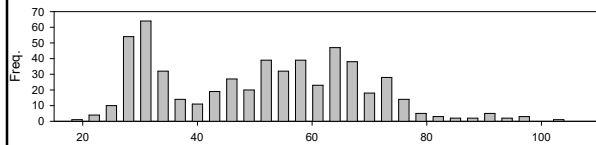


- Survival** (based on changes in age class abundance) averaged:
  - 1% : yolk-sac → post-yolk sac → YOY
  - 2.2-4.6% : post-yolk sac → YOY.
  - Daily **mortality** rates were 12-27% for larvae through time of yolk sac absorption; decreasing to 2-5% for juveniles.



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)	$n_x$	$l_x$
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)	$n_x$	$l_x$	$d_x$	$q_x$
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		

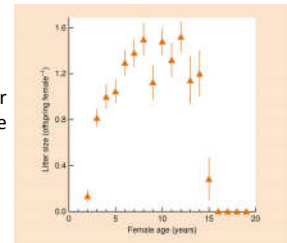
### Life expectancy

- $L_x = (l_x + l_{x+1})/2$
- $T_x$  = average life expectancy from current time not accounting for earlier mortality
  - $T_x = \sum(L_x)$ ; 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)	$n_x$	$l_x$	$d_x$	$q_x$	$L_x$	$T_x$	$e_x$
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	$a_x$	$l_x$	$d_x$	$q_x$	$\text{Log}_{10} a_x$	$\text{Log}_{10} l_x$	$k_x$	$M_x$	$f_x$	$l_{m_x}$	$x l_{m_x}$	$-rx$	$e^{-rx}$	$l_{m_x} e^{-rx}$	$L_x$	$T_x$	$e_x$
0	200	1.00	0.10	0.10	2.30	0.00	0.04	0	0.00	0.00	0.00	1.00	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	-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	-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	-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	-3.50	0.03	0.04	0.13	0.13	0.52	
5	2	0.01	0.30	-2.00			0		0.00	0.00	-4.38	0.01	0.00	0.00			
6	0						0		0.00	0.00	-5.26	0.01	0.00				
7	0						0		0.00	0.00	-6.13	0.00	0.00				
8	0						0		0.00	0.00	-7.01	0.00	0.00				
9	0						0		0.00	0.00	-7.89	0.00	0.00				
$R_0$	$\sum l_x m_x$		8.075														
	$\sum x l_x m_x$		19.250														
	$\sum l_x m_x e^{-rx} = 1$														1.415		

**Defining R**

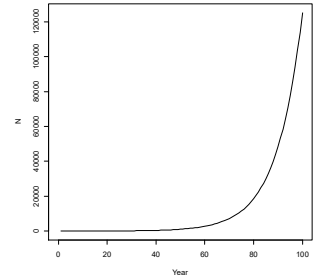
$R_0$  is a multiplier allowing us to determine population size at future generation.

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

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	
<b>sum</b>			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	81	
pct 1	0	100	0	28	13	16	17	15	17	16	16	16	16	16	
pct 2	0	0	5	0	4	2	3	3	3	3	3	3	3	3	
pct 3	0	0	0	-1	0	1	0	0	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	1.50	0.00	
$R_0=5.25$															

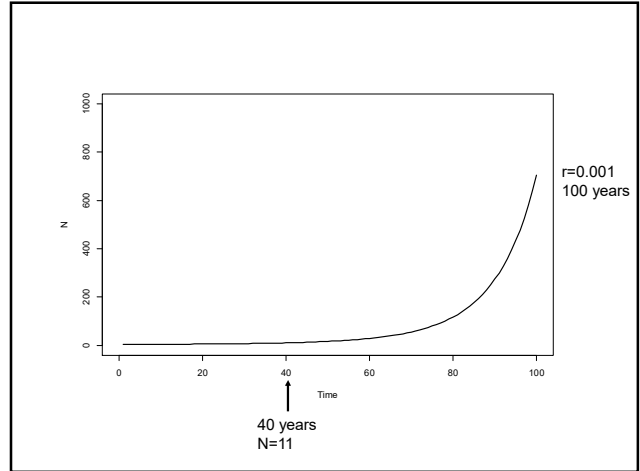
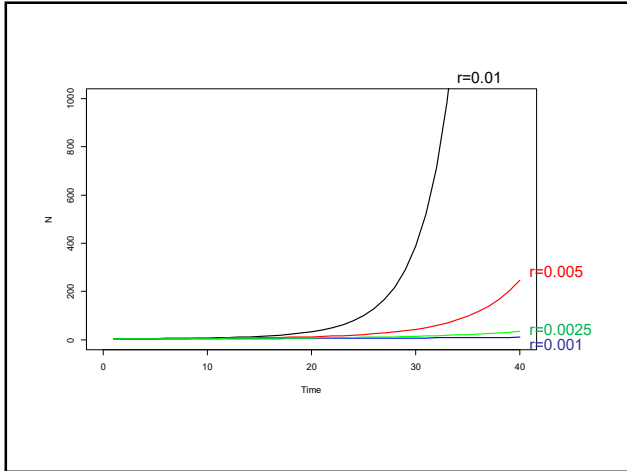
		time													
age	fecund	Survive	1	2	3	4	5	6	7	8	9	10	11	12	
0	1	1	50	50	110	226	415	810	1,562	3,000	5,786	11,141	21,457	41,335	
1	4	0.3	0	15	15	33	68	124	243	469	900	1,735	3,342	6,437	
2	15	0.25	0	0	4	4	8	17	31	61	117	225	434	836	
3	0	0.2	0	0	0	1	1	2	3	6	12	23	45	87	
<b>sum</b>			50	65	129	264	491	953	1,839	3,535	6,814	13,125	25,279	48,694	
pct 0	100		77	65	86	84	65	65	65	65	65	65	65	65	
pct 1	0	23	12	13	14	13	13	13	13	13	13	13	13	13	
pct 2	0	0	3	1	2	2	2	2	2	2	2	2	2	2	
pct 3	0	0	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	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 > 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	$a_x$	$l_x$	$d_x$	$q_x$	$\text{Log}_{10} a_x$	$\text{Log}_{10} l_x$
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					

$R_0$	$\sum l_x m_x$	8.075
	$\sum x l_x m_x$	19.250
	$T_x$	2.384
	$r$	0.876
	Double	0.787



Determining  $r$ ...

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

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

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	$a_x$	$l_x$	$d_x$	$q_x$	$\text{Log}_{10} a_x$	$\text{Log}_{10} l_x$
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					
$R_0$	$\sum l_x m_x$	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 $a_x$	Log $q_x$	$k_x$	$M_x$	$f_x$	$l_m x$	$x l_m x$	$-rx$	$e^{-rx}$	$l_m x e^{-rx}$	$L_x$
0	200	1.00	0.10	0.10	2.30	0.00	0.04	0	0.00	0.00	0.00	0.00	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	0.00	-4.38	0.01	0.00	0.00	
6	0							0	0.00	0.00	-5.26	0.01	0.00	0.00	
7	0							0	0.00	0.00	-6.13	0.00	0.00	0.00	
8	0							0	0.00	0.00	-7.01	0.00	0.00	0.00	
9	0							0	0.00	0.00	-7.89	0.00	0.00	0.00	

$R_0$	$\sum l_m x$	8.075	$\sum l_m x e^{-rx}$	1
	$\sum x l_m x$	19.250		1.415
	$T_c$	2.384		
	$r$	0.876		
	Double	0.787		

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 $a_x$	Log $q_x$	$k_x$	$M_x$	$f_x$	$l_m x$	$x l_m x$	$-rx$	$e^{-rx}$	$l_m x e^{-rx}$	$L_x$
0	200	1.00	0.10	0.10	2.30	0.00	0.04	0	0.00	0.00	0.00	0.00	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	0.00	-4.38	0.01	0.00	0.00	
6	0							0	0.00	0.00	-5.26	0.01	0.00	0.00	
7	0							0	0.00	0.00	-6.13	0.00	0.00	0.00	
8	0							0	0.00	0.00	-7.01	0.00	0.00	0.00	
9	0							0	0.00	0.00	-7.89	0.00	0.00	0.00	

$R_0$	$\sum l_m x$	8.075	$\sum l_m x e^{-rx}$	1
	$\sum x l_m x$	19.250		1.415
	$T_c$	2.384		
	$r$	0.876		
	Double	0.787		

- 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.

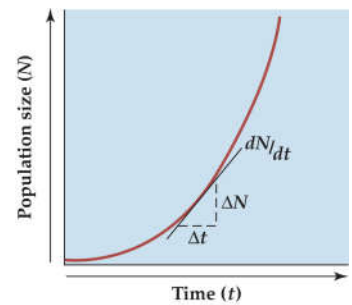
$$\frac{dN}{dt} = rN$$

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).

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



COMMUNITY ECOLOGY Figure 4.2

More about r

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

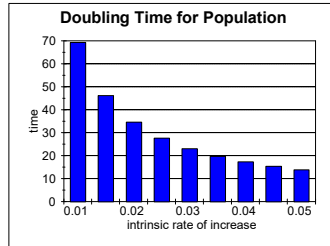
$$N_t = N_0 e^{rt}$$

$N_t=2$  and  $N_0=1$   $t=?$

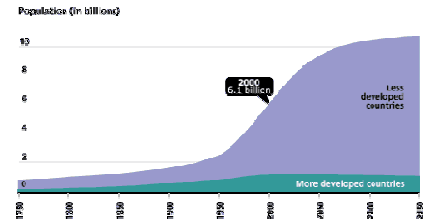
$$\frac{N_t}{N_0} = e^{rt}$$

$$\ln 2 = rt$$

$$t = 0.69/r$$



Human Population Growth



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

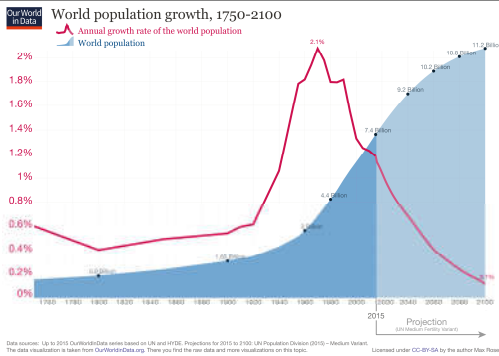
Given current growth rates, what will the world population be in 30 years??

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

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

$$9,349,922,439$$

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	$a_i$	$M_i$
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? ( $f_3$ )
  - $f_x = m_x \cdot a_x$
  - $f_3 = m_3 \cdot a_3 = 6 \cdot 100 = 600$

stage	$a_x$	$l_x$	$d_x$	$q_x$	$M_x$	$f_x$
0	1500	1.00	0.80	0.80	0	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	$a_x$	$l_x$	$d_x$	$q_x$	$\log_{10} a_x$	$\log_{10} l_x$	$k_x$	$M_x$	$f_x$	$l_x m_x$	$x l_x m_x$
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)
- $T = \sum(x l_x m_x) / \sum(l_x m_x)$
- $T = 2.7 / 1.27 = 2.12$

stage	$a_x$	$l_x$	$d_x$	$q_x$	$\log_{10} a_x$	$\log_{10} l_x$	$k_x$	$M_x$	$f_x$	$l_x m_x$	$x l_x m_x$
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? ( $r$ )
- $r = \ln R_0 / T$
- $r = \ln(1.27) / 2.12 = 0.1127438$
- $N_t = N_0 e^{rt}$
- $N_{243} = 1500 e^{0.1127 \cdot 243}$
- $N_{243} = 1500 e^{27.3861}$
- $1.17 \times 10^{15}$

stage	$a_x$	$l_x$	$d_x$	$q_x$	$\log_{10} a_x$	$\log_{10} l_x$	$k_x$	$M_x$	$f_x$	$l_x m_x$	$x l_x m_x$
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	$a_x$	$l_x$	$d_x$	$q_x$	$\log_{10} a_x$	$\log_{10} l_x$	$k_x$	$M_x$	$f_x$	$l_x m_x$	$x l_x m_x$
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