

## *Population ecology*

### **Lab 3: Population life tables**

#### **I. Introduction to ecological populations, life tables, and population growth models**

This week we begin a new unit on population ecology. A population is a set of individuals of the same species living in a given region or habitat. Populations are examples of ecological systems. As such, they exhibit both structural and functional properties. The total number of individuals in a population, the age distribution of those individuals, the sex ratio of adults, probabilities of survival (or mortality), and rates of fecundity are key traits of **population structure**. Ecologists employ a variety of methods to study the structure of populations.

Life history tables, or **life tables**, are a method of quantifying population structure that addresses all of the above population traits. Life tables provide age-specific information on survival and fecundity rates for a particular population. An ecologist can collect two very different types of life history data for individuals in a population, which can lead to two kinds of life tables. **Horizontal** (dynamic or cohort) life tables require ecologists to follow all the individuals of a single cohort in a population from birth to death. Construction of horizontal life tables frequently depends on the recapture of marked individuals for mobile species or repeated, representative samples of sessile species. Since individuals must be followed from birth to death, the horizontal life table technique is not well-suited for the study of long-lived individuals. **Vertical** (static or time-specific) life tables consist of data on individuals of all ages in a population from a single point in time. In vertical life table studies, it is important to work with a large, random sample of individuals to ensure that the data is representative of the entire population. For example, the age distribution of your sample of individuals should reflect the age distribution of the whole population. Non-destructive sampling methods are particularly useful for the construction of vertical life tables as they minimize the impact of large sampling efforts on population dynamics.

Both dynamic and static observations of population structure can be used 1) to quantify the age structure of a population; 2) to estimate an optimal age of sexual maturity; and 3) to predict population growth rates. Population growth projections are based on mathematical models such as the exponential growth model...

$$N_t = N_0 (e^{rt}).$$

In the exponential growth model, the number of individuals at any time (t) can be predicted using the number of individuals at the starting time ( $N_0$ ), the base of the natural logarithm ( $e = 2.7182818$ ), the intrinsic rate of population growth (r), and the time (t) since  $N_0$ . The intrinsic rate of population growth (r) is a direct consequence of the age structure of a population. Environmental conditions, seasonal effects, and population densities also shape population growth rates. In general, populations only

exhibit exponential growth when resources are not limited. Therefore, ecologists developed **density-dependent growth models** to simulate the effects of environmental stress on population growth. Other population growth model alternatives include the **Leslie matrix** and **Lotka-Volterra model**.

## II. Anatomy of life tables

A life history table contains information on age classes ( $x$ ), the total number of individuals in each age class ( $n(x)$ ), survival rates for each age class ( $l(x)$ ), fecundity rates for each age class ( $b(x)$ ), and the number of offspring produced per individual at each age class ( $l(x)*b(x)$  and  $l(x)*b(x)*x$ ). The following is an example of a horizontal life table:

### Example 1: Horizontal Life Table

Age class (months)	Number/age class	Survival rate	Fecundity	Offspring/ind	Age-weighted fecundity
$x$	$n(x)$	$l(x)$	$b(x)$	$l(x)*b(x)$	$l(x)*b(x)*x$
0	134	1.000	0.00	0.00	0.00
1	117	0.873	0.00	0.00	0.00
2	82	0.612	6.28	3.84	7.69
3	64	0.478	9.60	4.59	13.77
4	52	0.388	12.10	4.70	18.78
5	43	0.321	13.60	4.37	21.83
6	23	0.172	17.40	2.99	17.96
7	13	0.097	14.50	1.41	9.85
8	3	0.022	15.00	0.33	2.64
9	2	0.015	0.00	0.00	0.00
10	1	0.007	8.30	0.06	0.58
11	0	0.000	5.00	0.00	0.00
<b>Sum</b>				22.28	93.09
			<b>R<sub>0</sub></b>	22.28 offspring	
			<b>G</b>	4.18 months	
			<b>r</b>	0.743 ind/month	
			<b>Optimal age for sexual maturity</b>	5 months	

You will be provided with fecundity rates and pre-determined age classes for life tables in this lab. Calculation of the other parameters depends on the type of life table you are constructing. **The important differences between horizontal and vertical life tables relate to their respective sampling approaches (described above) and calculations of survivorship.**

### 1. Horizontal (dynamic or cohort) life tables

When using cohort information, calculate the survival rate for an age class ( $l(x)$ ) as the number of individuals in that age class ( $n(x)$ ) divided by the number of

individuals alive in the first age class ( $n(0)$ ). In the above table, survival at age class 0 ( $l(0)$ ) is  $n(0)/n(0)$  or  $134/134 = 1.000$ . At age class 1,  $l(1) = n(1)/n(0)$  or  $117/134 = 0.873$ .

Next, use the provided fecundity data to calculate the offspring produced per individual in each age class ( $l(x)*b(x)$ ) and the age-weighted number of offspring for each age class ( $l(x)*b(x)*x$ ). Once the horizontal life table is completed, you can calculate the net reproductive rate ( $R_0$ ), mean generation time ( $G$ ), and intrinsic growth rate ( $r$ ) of the population.

Net reproductive rate ( $R_0$ ) is the sum of the  $l(x)*b(x)$  column. It represents the expected number of offspring an individual will produce over its lifetime in the population. If  $R_0 > 1$ , then population size increases. If  $R_0 < 1$ , then population size decreases. And, if  $R_0 = 1$ , then population size does not change. In the population described by the horizontal life table above, an individual is expected to produce 22.28 offspring over its lifetime. Mean generation time ( $G$ ) is the sum of the  $l(x)*b(x)*x$  column divided by the net reproductive rate ( $R_0$ ). The intrinsic growth rate ( $r$ ) is an estimate of population growth; it is equal to the natural log of the net reproductive ( $R_0$ ) divided by the mean generation time ( $G$ ), or....

$$r = \ln (R_0) / G.$$

The optimal age for sexual maturity in the population corresponds to the age class with the greatest age-weighted fecundity ( $l(x)*b(x)*x$ ).

## 2. Vertical (static or time-specific) life table

When using time-specific information, you need to count all of the individuals you sampled. First, record the number of individuals at each age class in your sample ( $s(x)$ ). See the following vertical life table example.

*Example 2: Vertical Life Table for a Gambusia holbrooki population*

Age class (days)	Sample/age class	Number/age class	Survival rate	Fecundity	Offspring/ind	Age-weighted fecundity
x	s(x)	n(x)	L(x)	b(x)	l(x)*b(x)	l(x)*b(x)*x
0	130	759	1.000	0.00	0.00	0.00
30	190	629	0.829	0.00	0.00	0.00
60	240	439	0.578	0.00	0.00	0.00
90	120	199	0.262	24.00	6.29	565.92
120	60	79	0.104	0.00	0.00	0.00
150	15	19	0.025	29.00	0.73	109.13
180	3	4	0.005	32.00	0.16	28.80
210	1	1	0.001	0.00	0.00	0.00
240	0	0	0.000	0.00	0.00	0.00
<b>Sum</b>	759				7.18	703.85
				<b>R<sub>0</sub></b>	7.18 offspring	
				<b>G</b>	98.08 days	
				<b>r</b>	0.114 ind/day	
				<b>Optimal age for sexual maturity</b>	90 days	

Next, you must determine how many individuals are alive in each age class ( $n(x)$ ) using data you collect at a single time in the field. The assumption stands that each individual you sampled was alive in the first age class ( $x = 0$ ). For example, if you sample 759 individuals, all of them had to have been alive at the first age class ( $x = 0$ ). So,  $n(0) = 759$  or the sum of the  $s(x)$  column (see the above vertical life table example). If 130 of the individuals in your total sample were between 0 and 29 days old (age class 0), then 629 individuals in your sample were alive at the second age class ( $x = 30$ ). Once you have calculated the number alive at each age class ( $n(x)$ ), you can determine the survival rate ( $l(x)$ ) for each age class. Survival rate for a specific age class ( $l(x)$ ) is the number alive in that age class ( $n(x)$ ) divided by the number alive in the first age class ( $n(0)$ ), or  $l(x) = n(x) / n(0)$ . In the above vertical life table example, the survival rate at age class 0 ( $l(0)$ ) =  $759/759 = 1.000$ ,  $l(30) = 629/759 = 0.829$ , and so on.

All other calculations for vertical life tables are the same as described above for horizontal life tables.

### III. Objectives

The field portion of today's lab will involve collecting data on mosquitofish (*Gambusia*) populations in campus ponds. *Gambusia holbrooki* is a small, live-bearing fish found throughout south Florida, including the Everglades. In this lab exercise, you will also analyze previously published data on the structure of clam (*Musculium*) populations. *Musculium partumeium* is a freshwater clam from Virginia.

The objectives of Lab 3 are:

- 1) To generate life history tables for *Gambusia* and *Musculium*; and...
- 2) To compare and contrast the life history tables you generate for both organisms.

#### IV. Instructions

Before setting out to sample mosquitofish, complete the following pre-field instructions.

- 1) Generate several testable hypotheses as a class that you can test with today's exercise (Hint: the objectives, above, may help with this).
- 2) Discuss how to keep track of the population data. Set up field data sheets for your *Gambusia* sampling.
- 3) Divide into groups and work as teams in the field. Work should be divided up so that all team members get to experience each aspect of the exercise.
- 4) Be sure you have all the field sampling equipment that you will need.
- 5) Each team should participate in sampling. Your TA will pool data from all teams to generate a larger dataset. Use the complete dataset for your analysis.

We will work in ponds on campus where we will collect sample specimens of *G. holbrooki*. For each collected specimen, we will non-destructively measure its standard length (in mm) and then release it (handle the fish carefully). The age of each fish (in days) will be calculated using the relationship:

$$\text{Age} = 8 * (\text{Standard Length}) - 68 \quad [r^2=0.702, P=0.001]$$

Fish smaller than 9 mm will have ages < 0 days in the above formula. Therefore, exclude all fish with standard lengths < 9 mm. Use the fecundity values provided in Example 2 above to complete a vertical life table for the mosquitofish population that we study.

Hornbach and Childers (1986) collected data on a *Musculium partumeium* population in a stream near the University of Virginia campus in the early 1980s. They collected age-specific data on 4 cohorts of the freshwater clam over 16 months. Population and fecundity data for two of these cohorts, one beginning in the fall of 1981 and the other in the spring of 1982, are provided in the tables below. Use these two incomplete tables to generate a horizontal life history table for each cohort.

*Horizontal life table for Musculium partumeium (Fall 1981)*

Age class (months)	Number/age class	Survival rate	Fecundity	Offspring/ind	Age-weighted fecundity
x	n(x)	l(x)	b(x)	l(x)*b(x)	l(x)*b(x)*x
1	313		0.00		
2	310		0.00		
3	293		0.00		
4	146		0.00		
5	111		0.00		
6	101		20.80		
7	27		9.70		
8	26		15.40		
9	25		8.00		
10	1		9.00		
11	1		27.00		
12	0		0.00		
<b>Sum</b>					
			<b>R<sub>0</sub></b>		
			<b>G</b>		
			<b>r</b>		
			<b>Optimal age for sexual maturity</b>		

*Horizontal life table for Musculium partumeium (Spring 1982)*

Age class (months)	Number/age class	Survival rate	Fecundity	Offspring/ind	Age-weighted fecundity
x	n(x)	l(x)	b(x)	l(x)*b(x)	l(x)*b(x)*x
1	134		0.00		
2	117		0.00		
3	82		6.28		
4	64		9.60		
5	52		12.10		
6	43		13.60		
7	23		17.40		
8	13		14.50		
9	3		15.00		
10	2		0.00		
11	1		8.30		
12	0		5.00		
<b>Sum</b>					
			<b>R<sub>0</sub></b>		
			<b>G</b>		
			<b>r</b>		
			<b>Optimal age for sexual maturity</b>		

## Literature Cited

Hornbach, D. J., and D. L. Childers. 1986. Life history variation in a stream population of *Musculium partumeium* (Bivalvia: Pisidiidae). *Journal of the North American Benthological Society* **5**:263-271.

This paper is included in the Ecology Lab manual.

## Further Reading

Caswell, H., R. Lensink, M. G. Neubert. 2003. Demography and dispersal: Life table response experiments for invasion speed. *Ecology* **84**(8):1968-1978.

Stolen, M, K., and J. Barlow. 2003. A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon system, Florida, U.S.A. *Marine Mammal Science* **19**(4):630-649.

Floater, G. J., and M. P. Zalucki. 1999. Life tables of the processionary caterpillar *Ochrogaster lunifer* Herrich-Schaeffer (Lepidoptera: Thaumetopoeidae) at local and regional scales. *Australian Journal of Entomology* **38**(4):330-339.