Population Biology: Life Tables & Theoretical Populations

The purpose of this lab is to introduce the basic principles of population biology and to allow you to manipulate and explore a few of the most common equations using some simple Mathcad© wooksheets. A good introduction of this subject can be found in a general biology text book such as Campbell (1996), while a more complete discussion of population biology can be found in an ecology text (e.g., Begon et al. 1990) or in one of the references listed at the end of this exercise.

Exercise Objectives:

After you have completed this lab, you should be able to:

1. Give definitions of the terms in **bold** type.
2. Estimate population size from capture-recapture data.
3. Compare the following sets of terms: semelparous vs. iteroparous life cycles, cohort vs. static life tables, Type I vs. II vs. III survivorship curves, density dependent vs. density independent population growth, discrete vs. continuous breeding seasons, divergent vs. dampening oscillation cycles, and time lag vs. generation time in population models.
4. Calculate l_x, d_x, q_x, R_0, T_c, and e_x; and estimate r from life table data.
5. Choose the appropriate theoretical model for predicting growth of a given population.
6. Calculate population size at a particular time (N_{t+1}) when given its size one time unit previous (Nt) and the corresponding variables (e.g., r, K, T, and/or L) of the appropriate model.
7. Understand how r, K, T, and L affect population growth.

Population Size

A **population** is a localized group of individuals of the same species. Sometimes populations have easily defined boundaries (e.g., the White-footed Mouse population of Sandford Natural Area or Hungerford's Crawling Water Beetles of the East Branch Maple River); whereas, in other instances, the boundaries are almost impossible to define so they are arbitrarily set by the investigator's convenience (e.g., Eastern Chipmunks around Holmes Hall). Once the boundaries are set, the next challenge is determining a population's size. While it may be most straightforward to actually count all the individuals of a population, this is rarely done. Usually population size is estimated by counting all the individuals from a smaller sample area, then extrapolated to the set boundaries. Another common method is **capture-recapture**. Using this method, a small random sample of the population is captured, marked, then released to disperse within the general population. Next a subsequent random sample of the population is recaptured. The ratio of marked to recaptured individuals in the second sample can be used to estimate the general poplation's size. Here is a simple formula for estimating population size (*N*) from capture–recapture data:

$$N = \frac{\text{Total individuals marked in first sample} \times \text{Size of second sample}}{\text{Number recaptured individuals in second sample}}$$

The field of population biology is concerned with how a population's size changes with time and what factors control those changes, such as birth, mortality, reproductive success, and individual growth. There are many mathematical models and analysis tools that are helpful in understanding population dynamics. In this lab, we hope to explore and manipulate some of the fundamental tools available.

Semelparous vs Iteroparous Life Cycles

A population's growth potential has much to with how often individual members reproduce. Some species (e.g., most invertebrates) have only one reproductive event in their lifetime, while others (e.g., most birds and mammals) are capable of multiple events over an extended portion of their lives. The former are called **semelparous** and the latter, **iteroparous** life cycles. There is a large amount of variation, however, within these broad categories. For example, some semelparous species have overlapping generations of young so that, at any one time, there may one-, two-, and three-year-old individuals present in the population. A common form of semelparity in insects of temperate regions is an annual species. In this case, the insect overwinters as an egg or larval resting stage until spring, then grows throughout the warm months and emerges into the reproductive adult. Adults mate and lay eggs that, again, remain dormant throughout the winter. Still other semelparous species complete several generations each summer. It is easy to imagine, then, how the frequency of reproductive events, the number of young produced in each event, and the length of each generation can greatly influence how fast a population can grow.

Life Tables

Constructing a **life table** is often a simple method for keeping track of births, deaths, and reproductive output in a population of interest. Basically, there are three methods of constructing such a table: 1) the **cohort life table** follows a group of same-aged individuals from birth (or fertilized eggs) throughout their lives, 2) a **static life table** is made from data collected from all ages at one particular time — it assumes the age distribution is stable from generation to generation, and 3) a life table can be made from mortality data collected from a specified time period and also assumes a stable age distribution. Note: For organisms that have seperate sexes, life tables frequently follow only female individuals.

Constructing a Cohort (Horizontal) Life Table for a Semelparous, Annual Organism:

Let's begin with a animal that has an **annual life cycle**, only one breeding season in its life time (it's semelparous), and no overlap between generations. A cohort life table can be constructed from counts of all the individuals of a population (or estimate the population size from samples) as it progresses through the growing season. The easiest way to think of this to consider an insect with a determinant number of instars; for example, a typical caddisfly with a life history of eight distinct stages (egg, 1st–5th instar larva, pupa, and adult).

To make a life table for this simple life history, we need only count (or estimate) the population size at each life history stage and the number of eggs produced by the adults. The first column (x) specifies the age classification and the second column (a_x) gives the number alive at the beginning of each age. From these data we can calculate several life history features. First, the **proportion surviving** to each life stage (l_x) can be found by dividing the number of indivuals living at the beginning of each age (a_x) by the initial number of eggs (a_0). Conversely, the proportion of the original cohort dying during each age (d_x) is found by subtracting l_{x+1} from l_x. The **age-specific mortality rate** (q_x), the fraction of the population dying at each stage age, is helpful in locating points where mortality is most intense and is calculated by divding d_x by l_x.

The next three columns of the life table are used to assess the population's reproductive output. The number of eggs produced at each age, is tabulated in the F_x column. The eggs produced per surviving individual at each age (m_x), or **individual fecundity**, is measured as F_x divided by a_x. The number eggs produced per original individual at each age (l_xm_x) is

an important value to consider in population studies. By summing $l_x m_x$ across all ages, the **basic reproductive rate** (R_0) can be obtained in units of individuals $\cdot$ individual^{-1} $\cdot$ generation^{-1}. [If only females are considered, then R_0 is in individuals $\cdot$ female^{-1} $\cdot$ generation^{-1} units.] One can think of R_0 as the population's replacement rate: a R_0 of 1.0 means the population is just replacing itself each generation, $R_0 < 1.0$ indicates the population is declining, and $R_0 > 1.0$ shows the population is increasing.

TABLE 12. Cohort life table from a hypothetical caddisfly population.

Stage x	Number living at each stage a_x	Proportion of orgininal cohort surving to each stage l_x	Proportion of original cohort dying during each stage d_x	Mortality rate q_x	Eggs prduced at each stage F_x	Eggs produced per surviving individual at each stage m_x	Eggs produced per original individual in each stage $l_x m_x$
Eggs (0)	44,000	1	0.784	0.784	-	-	-
Instar I (1)	9513	0.216	0.136	0.629	-	-	-
Instar II (2)	3529	0.080	0.014	0.172	-	-	-
Instar III (3)	2922	0.066	0.010	0.158	-	-	-
Instar IV (4)	2461	0.056	0.004	0.065	-	-	-
Instar V (5)	2300	0.052	0.001	0.022	-	-	-
Pupa e(6)	2250	0.051	0.001	0.028	-	-	-
Adults (7)	2187	0.050	-	-	45,617	20.858	1.037

For the caddisflies used in this hypothetical example, R_0 is simple to calculate ($R_0 = 1.037$). Often, however, an investigator isn't able to make an accurate count of individuals in the early stages, making it difficult to construct a complete table. In these cases, investigators employ extrapolation techniques to estimate a_0 and l_0.

Static (Vertical) Life Table Based on Living Individuals

Most organisms have more complex life histories than found in the above example, and while it is possible to follow a single cohort from birth to death, it often too costly or time-consuming do so. Another, less accurate, method is the **static**, or vertical, **life table**. Rather than following a single cohort, the static table compares population size from different cohorts, across the entire range of ages, at a single point in time. Static tables make two important assumptions: 1) the population has a stable age structure—that is, the proportion of individuals in each age class does not change from generation to generation, and 2) the population size is, or nearly, stationary.

Static (Vertical) Life Table Based on Mortality Records

Static life tables can also be made from knowing, or estimating, age at death for individuals from a population. This can be a useful technique for secretive large mammals (e.g., moose) from temperate regions where it is difficult to sample the living members. Because the highest mortality of large herbivores occurs during the winter, an early spring survey of carcasses from starvation and predator kills can yield useful information in constructing a life table. Keep in mind, however, all static tables suffer from the same two assumptions stated above.

Because we keep good birth and death records on humans, static life tables can also be used to answer questions concerning our populations. For instance, we know that females today have a larger mean life expectancy than men. But, was this

true for our population 100 years ago? We can use data collected from cemetary grave markers to constuct a static life table and reveal interesting features of human populations from past generations. The following data were collected from a random sample of 30 females and 30 males off grave markers located in an Ann Arbor cemetary:

TABLE 13. Male and female age at death frequencies from a random sample of 60 Ann Arbor grave markers of individuals born prior to 1870. (From G. Belovsky, unpubl.).

Age at death	Females	Males
0–5	1	2
6–10	0	0
11–15	1	0
16–20	2	1
21–25	1	1
26–30	0	2
31–35	0	0
36–40	1	2
41–45	1	0
46–50	2	1
51–55	1	0
56–60	2	3
61–65	0	4
66–70	0	4
71–75	1	3
76–80	6	1
81–85	4	1
86–90	7	3
91–95	0	0
96–100	0	2

Population Features That Can Be Calculated from Life Tables:

Besides R_0, the basic reproductive rate, several other population characteristics can be determined from life tables. Some of the most common features are the **cohort generation time** (T_c), **life expectancy** (e_x), and the **intrinsic growth rate** (r). Cohort generation time is quite easy to obtain from our first example, a semelparous annual life cycle (T_c = 1 year), but generation time is less obvious for more complex life cycles. Generation time can be defined as the average length of time between when an individual is born and the birth of its offspring. Therefore, it can be calculated by summing all the lengths of time to offspring production for the entire cohort divided by the total offspring produced by the survivors:

$$T_c = \frac{\sum x \cdot \langle l_x \cdot m_x \rangle}{\sum \langle l_x \cdot m_x \rangle}$$

Life expectency is a useful way of expressing the probability of living 'x' number of years beyond a given age. We usually encounter life expectency in newspaper articles comparing the mean length of life for individuals of various popula-

tions. However, this value is actually the life expectancy at birth. One can also calculate the mean length of life beyond any given age for the population. Life expectancy is a somewhat complicated calculation. Because l_x is only the proportion surviving to the beginning of a particular age class, we must first calculate the average proportion alive at that age (L_x) :

$$L_x = \frac{l_x + l_{x+1}}{2}$$

Next, the total number of living individuals at age 'x' and beyond (T_x) is:

$$T_x = L_x + L_{x+1} + \ldots + L_{x+n}$$

Finally, the average amount of time yet to be lived by members surviving to a particular age (e_x) is:

$$e_x = \frac{T_x}{l_x}$$

The following example shows life expectancy changes in a hypothetical population that experienced 50% mortality at each age:

TABLE 14. Life expectancy in a hypothetical population.

Age (years)	l_x	L_x	T_x	e_x (years)
0	1.0	0.75	1.375	1.375
1	0.5	0.375	0.625	1.25
2	0.25	0.1875	0.25	1.0
3	0.125	0.0625	0.0625	0.5
4	0.0	-	-	-

The basic reproduction rate (R_0) converts the initial population size to the new size one generation later as:

$$N_T = N_0 \cdot R_0$$

If R_0 remains constant from generation to generation, then we can also use it to predict population size several generations in the future. To predict population size at any future time, it is more convenient to use a parameter that already takes generation time into account. This term is 'r', the intrinsic rate of natural increase, and it can be calculated (or approximated for complex life cycles) by the following equation:

$$r \cong \frac{\ln R_0}{T_c}$$

The term, r, is used in mathematical models of population growth discussed later.

Survivorship Curves:

Plotting survivorship (l_x) against time often shows where mortality influences the population. There are three basic shapes of **survivorship curves**: Type I populations experience greatest mortality at older ages, Type II have a constant death rate per unit time, and Type III populations have mortality concentrated at the youngest ages. Many large mammals exhibit Type I curves, whereas some birds and most invertebrates have survivorships that resemble Type II and Type III curves, respectively.

FIGURE 4. Three basic types of survivorship curves.
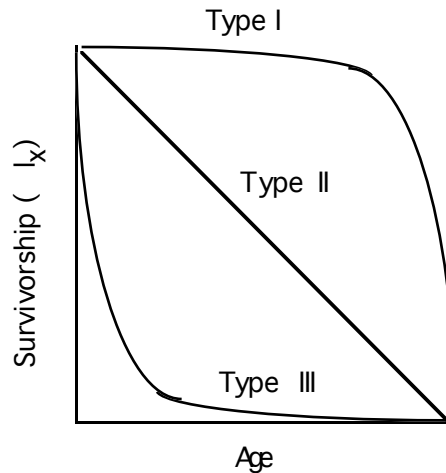
Mathematical Models:

While life tables are extremely valuable in studying populations, they require a large amount of effort to construct. Mathematical models are a more convenient method of studying the effects of various parameters on population size. Some of the first to propose such models were P. F. Verhulst in the mid-1800's study of human populations of France, and A. J. Lotka, V. Volterra, G. F. Gause, and Robert Pearl in the early 1900's. The aim of this lab exercise is to explore and manipulate some of the most basic models.

One way to catagorize these models is based on assumptions on the reproductive biology of organisms. Some organisms have **discrete breeding seasons**, while others, like humans and bacteria can reproduce **continuously** all year long. Another way to group them is according to assumptions based on **density independent** and **density dependent** population growth. Populations that grow independent of their density often show exponential increases in number until acted upon by a major outside force, such as floods or droughts. Populations that exhibit density dependent growth often begin with near exponential growth, but slow down as they approach the **carrying capacity** (K).

Before we begin examining these models, two terms, '**r**' and '**K**', must be defined. The intrinsic rate of natural increase, 'r', is the average rate of increase per individual and is the mathematical equivalent of 'average number of births per individual per unit time minus the average deaths per individual per unit time'. The concept of 'r' frequently becomes clear to students only after they plot equations using the term. When conditions are ideal, population increase is said to be at the biotic potential or maximum increase per individual (r_{max}). Carrying capacity (K) is the maximum number of individuals a particular habitat can sustain. Any reproduction above the carrying capacity will result in an equivalent amount of mortality. For natural populations, the carrying capacity of a habitat is often, but not restricted to, the amount and quality of food it produces.

Density Independent Model for Organisms with Discrete Breeding Seasons:

This model can have slightly different forms, but in general, if we know the population size at a particular time (N_t), the generation time (T) in years, and the intrinsic reproductive rate (r), then the population size one generation later (N_{t+T}) can be calculated by the following difference equation:
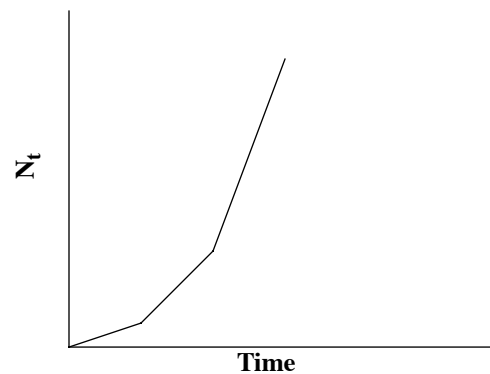
$$N_{t+T} - N_t = T \cdot r \cdot N_t$$

or this can be rewritten as:

$$N_{t+T} = N_t + (T \cdot r \cdot N_t)$$

N_t plotted against time shows how the population changes each generation under density independent conditions.

FIGURE 5. **Exponential increase of a population with discrete breeding seasons.**

Density Dependent Model for Populations with Discrete Breeding Seasons:

Density dependent growth takes into account how close the population is to the carryng capacity. A **difference equation** rearranged to solve for population size after one generation (N_{t+T}) for the density dependent condition can be written as:

$$N_{t+T} = N_t + \left[T \cdot r \cdot N_t \cdot \left(\frac{K - N_t}{K} \right) \right]$$

As N_t approaches K, the expression (K–N_t/K) approaches 0 and N_{t+T} comes closer to N_t; and at K, N_{t+T} equals N_t. If for some reason N_t exceeds K, then (K–N_t/K) is negative and N_{t+T} becomes less than N_t until the population returns to K. There are four possible outcomes of this discrete model based on the relationship between 'r' and 'K': 1) if 0 < rT<1, then the population will not overshoot K, 2) if 1<rT<2, then it will first overshoot K but afterwards have dampened **oscillations** around K, 3) if 2<rT<2.7, then the population will have **stable cycles** above and below K, and 4) if rT>2.7, then chaos results.

Plotting Nt versus time shows the effect of 'r' and 'T' on density dependent populations.

FIGURE 6. **Logistic increase for density dependent populations with discrete breeding seasons.**
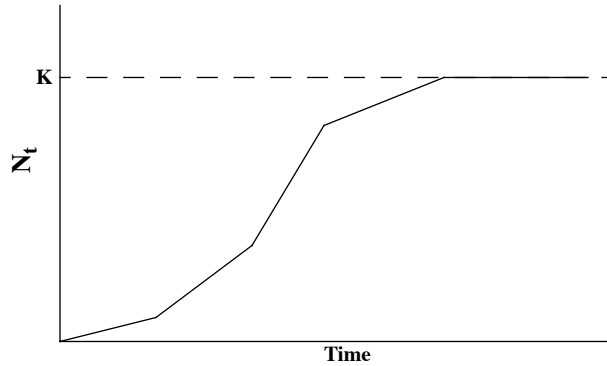
Density Independent Model for Continuously Breeding Populations:

Population increase for continuously breeding organisms can be described by the following equation:

$$N_t = N_0 \cdot e^{r \cdot t}$$

where 'N$_0$' is the initial population size, 'e' is 2.71828 (the base of natural logarithms), 'r' is the intrinsic growth rate, and 't' is time. Usually this equation is written in its continuous differential form:
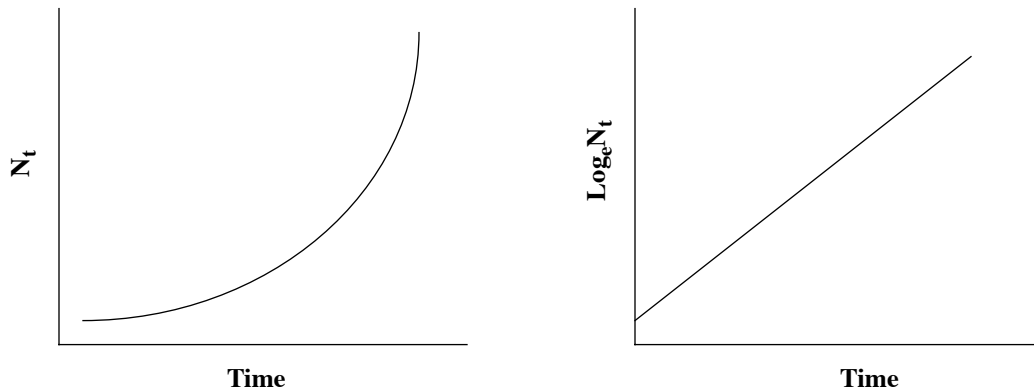
$$\frac{dN}{dt} = r \cdot N$$

Note if we divide both sides of the above equation by N, we get the per capita rate of increase, which is the definition of 'r':

$$\frac{dN}{dt} \cdot \frac{1}{N} = r$$

Plotting Nt versus time shows exponential increase. The relationship can be linearized by plotting log$_e$N versus time.

FIGURE 7. **Normal and log$_e$ plots of population size versus time.**

Populations increasing at 'r_{max}' would be increasing at the fastest possible rate for that species, hence reaching their biotic potential.

Density Dependent Growth for Populations with Continuous Breeding:

The continuous model for density dependent population growth, first proposed by Verhulst in 1845, looks very similar to that of the discrete model discused earlier. Written in its continuous differential form, the model is:

$$\frac{dN}{dt} = r_{max} \cdot N \cdot \left(\frac{K-N}{K}\right)$$

This relationship can be solved for population size at time 't' by the following equation:

$$N_t = \frac{K}{1 + e^{-(r_{max} \cdot t)}}$$

As with the discrete model, population size follows the logistic pattern of first increasing slowly, then rapidly, and then slowing assymptotically to the carrying capacity. The difference with the continuous model, however, is that it always tracks 'K' perfectly—that is, it never overshoots 'K'.

FIGURE 8. **Plot of logistic population increase of the continuous density dependent model.**
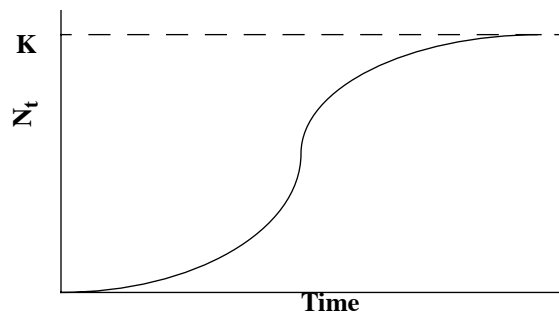
Sometimes it is useful to examine how the per capita rate of increase ($dN/dt \cdot 1/N$) changes as the population increases towards 'K'. This can be plotted as follows:

FIGURE 9. **Plot of per capita rate of increase as a function of population size for the logistic equation.**
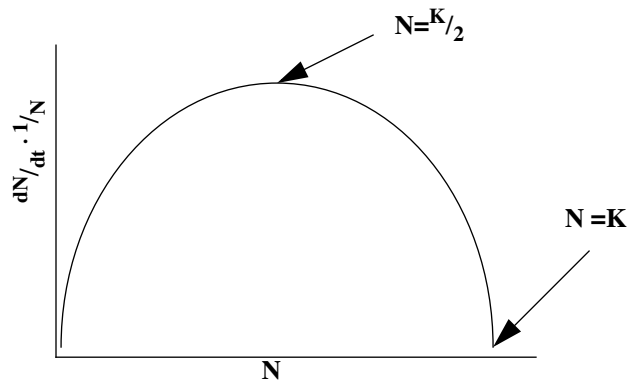
One problem with this model is that natural populations are rarely perfect 'K' trackers. The model can be improved by adding a time lag before the population can sense where it is with respect to 'K'. This might be analagous to a mouse population where the decision to mate is determined before gestation (i.e., the gestation period is the lag time). The addition of a time lag is given in the following equation:

$$\frac{dN}{dt} = r_{max} \cdot N_t \cdot \left(\frac{K - N_{t-L}}{K} \right)$$

where 'L' is the **time lag**. There three possible outcomes of the time-lag model based on the relationship between 'r_{max}' and 'L': 1) if $0<rL<\pi/2$, then N will overshoot K followed by dampening oscillations around K; 2) if $\pi/2<rL<2$, then N will exhibit stable cycles above and below K; and 3) if $2 \leq rL$, then N will exhibit divergent oscillations about K until the population becomes extinct.

Acknowledgements

References:

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Exercises:

1. Complete the following static life table based on age at death data (prior to 1870) collected from an Ann Arbor cemetary:

TABLE 15. **Life table worksheet for Ann Arbor cemetary data from individuals born prior to 1870 .**

Mean age x	Females							Males	
	a_x	l_x	d_x	q_x	m_x	$l_x m_x$	$x \cdot l_x m_x$	a_x	l_x
0	30				0			30	
2.5	29				0			28	
7.5	29				0			28	
12.5	28				0.015			28	
17.5	26				0.300			27	
22.5	25				0.610			26	
27.5	25				0.450			24	
32.5	25				0.315			24	
37.5	24				0.150			22	
42.5	23				0.060			22	
47.5	21				0.005			22	
52.5	20				0			21	
57.5	18				0			21	
62.5	18				0			18	
67.5	18				0			14	
72.5	17				0			10	
77.5	11				0			7	
82.5	7				0			6	
87.5	0				0			5	
92.5	0				0			2	

2. What is the cohort generation time based on female data? Calculate R_0 and the approximate r. What do these values tell about this population? Is there a difference in life expectency at birth between males and females from this data set? Show your calculations.

3. On the same graph (use graph paper or a computer generated plot), plot male and female survivorship curves. What type of survivorship do they demonstrate? Where is the mortality rate the highest for each sex?

4. Computers in the Holmes Hall Mac Lab (Rm. C1) and the one in the Biology Lab (Rm. C2) should have Mathcad© installed. Obtain a copy of worksheet entitled "population bio" and open it with Mathcad©. Once the document is opened, simply follow the directions on the worksheet. Manipulate the "r", "K", "L", and "T" variables of the discrete and continuous models of density independent and density dependent population growth to see how these variables affect the models. Print out graphs showing:

- density independent population growth using 2 different "r" values (e.g., 0.4 and 0.8) for both the continuous and discrete models.

- density dependent population growth while keeping "r" constant and manipulating "K" in the continuous model.

- dampened oscillations, stable cycles, and divergent oscillations by adjusting the time lag ("L") and "r" in the density dependent model for continuous breeding with a time lag.

- dampened oscillations, stable cycles, and chaos by adjusting the generation time ("T") and "r" in the density dependent model for dicreete breeding seasons.

   Be sure to give all the variable settings with each graph.

5. Suppose a team of fisheries biologists set out to estimate the density of Brook Trout in the East Branch of the AuSable River. At a randomly selected starting point, they electrofished a 1000-m section of the stream (its mean width was 5 m). The captured fish were measured, recorded, fin clipped, then released. Two days later, they resampled the same reach and recorded the number of marked and unmarked fish in each of 4 size classes. Here are their data:

TABLE 16. Capture-recapture data from the East Branch AuSable River.

Size (cm)	Number individuals Day 1	Number of individuals Day 2	
		Unmarked	Marked
< 10	73	64	22
10–20	35	28	13
20–30	20	22	18
> 30	6	4	2
Total	134	118	55

Using these data, estimate the density (number/hectare) of each size class plus the overall density. [Note: 1 hectare = 10,000 m^2.]