

POPULATION GROWTH: EXPERIMENTAL MODELS USING DUCKWEED (*Lemna* spp.)

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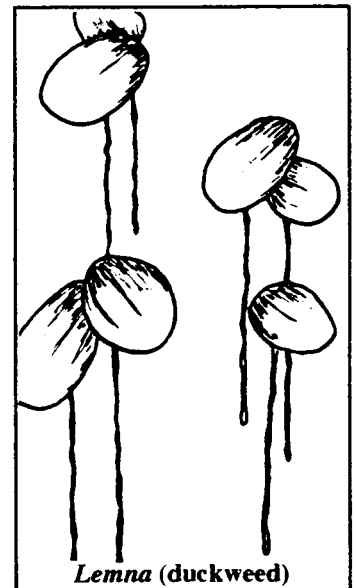
INTRODUCTION

It is easy to show that in the absence of environmental constraints, any population of organisms reproducing at their full potential would cover the surface of the earth in a relatively short time. At current rates of human population growth, for example, in another 2000 years the surface of the Earth would be expanding outward with new people at the speed of light.

It is clear that animal and plant populations are not growing in an uncontrolled explosive way. Limitations in resource availability define a maximum population size above which continued population growth is not possible. Resources that might be limiting for any given population might include sunlight, space for growth, nutrients, pollinators, refuges from harsh weather, or hiding places from predators. The availability of these resources will determine the carrying capacity, the maximum population size of that species the resources can sustain.

Resource availability and thus maximum population size can be influenced by the presence of other species. If two or more species share resources that are in limited supply, rates of population growth and

ESA
lab



maximum population size of each species may be depressed. We call this "resource competition." Light, space, and nutrients are examples of resources that might be the basis for competition.

LABORATORY OBJECTIVES

1. Understand the dynamics of exponential and logistic growth.
2. Investigate the effects of resource limitation on population growth.
3. Investigate the outcome of competition between two species of aquatic plants in the same and in different environments.
4. Determine relative growth rates.
5. Plot data to obtain population growth curves.
6. Determine carrying capacity under different environmental conditions.

conceptual

procedural

EXPERIMENT ONE

*reproduction
in duckweed*

Dynamics of population growth: exponential and logistic growth

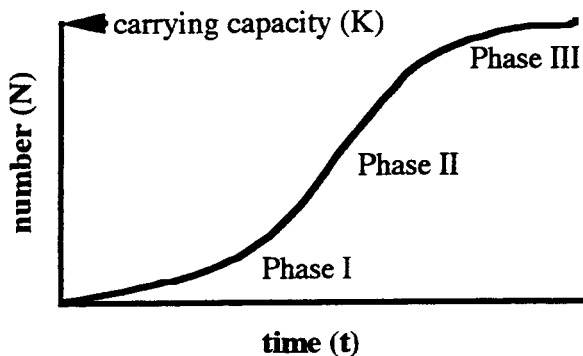
Few plants are suitable for studying **continuous population growth** because most plants have life cycles with discrete jumps in population size, their reproduction is seasonal and they respond to changes in population density by changing size and shape instead of population number (Harper, 1977). However, free-floating aquatic plants such as duckweeds (*Lemna* spp) or water ferns (*Azolla* and *Salvinia*) undergo continuous growth and therefore are excellent models for quantifying aspects of population growth (Clatworthy and Harper, 1962; Harper, 1977). These plants are stemless and have only one to four leaf-like structures called thalli (singular = thallus), if they are flowering plants, or fronds, if they are ferns. Roots from the thallus hang free in the water. Duckweeds can reproduce by flowering and setting seed (sexual reproduction) but seldom do. More commonly they reproduce asexually by producing a new thallus or frond directly from an old one. When a new thallus has grown large enough and has roots, it breaks loose from its parent plant and grows on its own as a separate plant. The growth of a population can be followed by counting thalli or measuring changes in biomass (dry weight).

If a pond or lab beaker is inoculated with one or two thalli and conditions are favorable, the plants commence exponential growth (Fig. 1, Phase I).

unimpeded growth

The growth rate of the population under these conditions is density independent; the population grows unimpeded by resource limitation or competition. We can estimate the intrinsic rate of growth (r - see the equations on following pages) by measuring the uninhibited growth of low density populations.

As thalli accumulate, the population becomes crowded and limited by the available resources. For a period, growth appears **constant** (Fig. 1, Phase II) as the width and thickness of the mat of floating plants **increases**. Eventually the beaker or pond fills with floating plants (Fig. 1, Phase III) and the population reaches a **steady state** (see the following equations). At this point, for every new thallus that appears, an existing one is shaded and dies, i.e., the population size is stable. The **logistic growth curve** (Fig. 1) illustrates all three Phases.



competitive growth

population stability

FIGURE 1.
logistic growth

MATERIALS

2 - 10 oz. plastic cups/student
(or any clear container: jar, beaker)
200 ml artificial pond water/cup
extra artificial pond water
(see notes to instructor)

forceps
light source
(grow lights, window,
greenhouse)

healthy *Lemna* plants

supplies

organisms

PROCEDURE

set-up

1. Fill two 10 oz. plastic cups with artificial pond water, 200 ml/cup. Mark the 200 ml water level on the cup so that you can refresh the culture solution to the same volume.

2. Place 2 healthy *Lemna* plants in one of the cups. Place 15 healthy *Lemna* plants in the second cup.

initial status

3. Because a plant can consist of one or more thalli, it is necessary that you now count the number of thalli in each cup. One thallus is any leaf unit that is over 1.5 mm. Record these data in the Day 0 column of Table 1.

4. Place the cups under fluorescent lights for a period of two weeks, check them periodically and refill the cups to the 200 ml line.

data collection

5. Count the number of thalli in each cup on Day 7 and Day 14. Record these data in the appropriate columns of Table 1.

TABLE 1.
dynamics of
population growth

Starting number of plants	Number of thalli (N)			Relative growth rate (λ)	
	Day 0	Day 7	Day 14	$\frac{N \text{ day 7}}{N \text{ day 0}}$	$\frac{N \text{ day 14}}{N \text{ day 7}}$
2					
15					

EXPT. 1 -PART A. population growth curves

DATA ANALYSIS

Using class data, graph the average (mean) number of thalli (N) as a function of time for the cultures that started with two plants and the cultures that started with 15 plants.

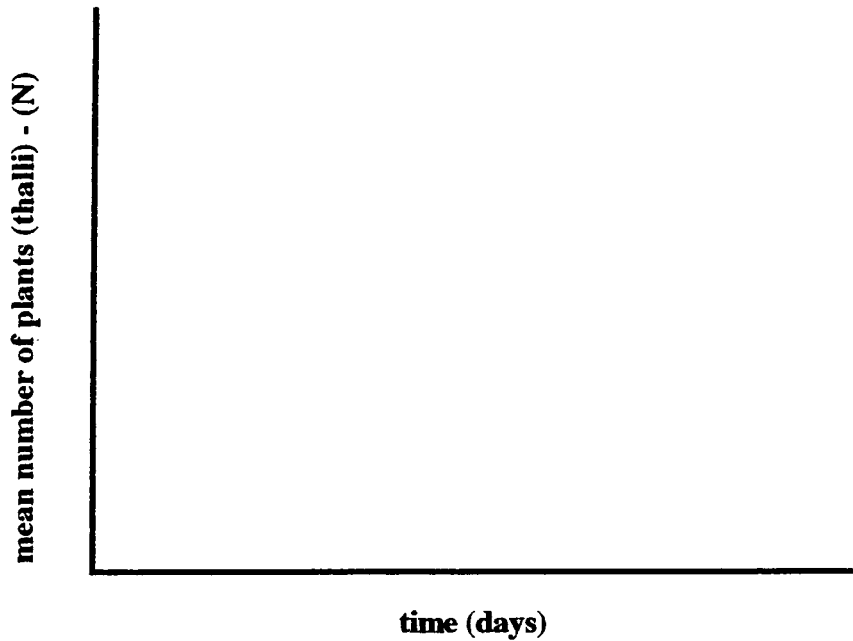


FIGURE 2.
population
growth curves
(class data)

Do the two lines on the graph differ or are they the same? What might account for this?

question

EQUATIONS: Pertinent to Data Analysis Parts B and C

1. The three equations shown below describe the exponential or geometric growth of populations

$$dN/dt = rN$$

$$N(t) = N(0) e^{rt}$$

$$\log N(t) = \log N(0) + rt$$

where N is the number of individuals in the population, r is the intrinsic rate of natural increase, e is the base of the natural logarithm, and t is time.

*exponential or
 geometric
 growth*

logistic growth

2. The factor by which a population increases in one unit of time (e^r) is the exponential or geometric growth rate of the population (λ). Therefore,

$$N(t+1) = e^r N(t) = \lambda N(t)$$

3. The following equation describes logistic growth of populations (Fig. 1)

$$dN/dt = rN(1 - N/K)$$

where K is the carrying capacity of the environment for that species.

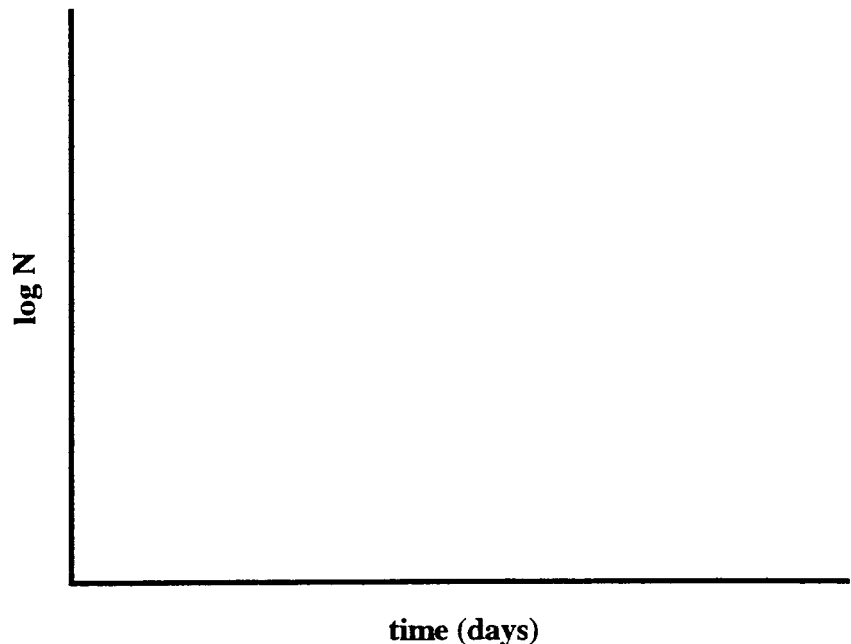
EXPT 1. -PART B.
estimating
geometric growth

DATA ANALYSIS (continued)

Method A: Plot $\log N$ as a function of t for the cultures that started with two plants. The slope of a line drawn through the mean $\log N$ at Day 0, Day 7, and Day 14 would approximate r . Make the same graph and calculations for the cultures that started with 15 plants.

Do the slopes of these two lines differ? If so, how?

FIGURE 3.
geometric growth
(class data)



Method B: Geometric growth between one unit of time and the next can be described by this equation:

$$N_{t+1} = \lambda N_t$$

If $N_{\text{day } 7} = \lambda N_{\text{day } 0}$, then $\lambda = N_{\text{day } 7} / N_{\text{day } 0}$. Calculate λ for all the cultures that started with two plants and for the cultures that started with 15 plants. What is the highest λ recorded for the class?

calculations

DATA ANALYSIS (continued)

As the population of *Lemna* in your cup grows, the rate of growth will slow down. When the population reaches the carrying capacity of the cup, the growth rate of the population will be 0 ($dN/dt = 0$). There are two ways to estimate K for this experimental set-up. First, if you knew the area of the water surface and you knew the area of one thallus, you could estimate the number of plants it would take to cover the surface (K). Second, if you plot the geometric growth rate (λ , calculated in Part B above) for each cup, as a function of population size ($N[t]$), Fig. 4), you should have a linear plot where the y intercept (where $N = 0$) would approximate r and when $\lambda = 1$, $n = K$ (Fig. 4). Use the available graph to plot your data.

EXPT. 1 - PART C. estimating K

FIGURE 4.
using geometric
growth rate
to estimate K

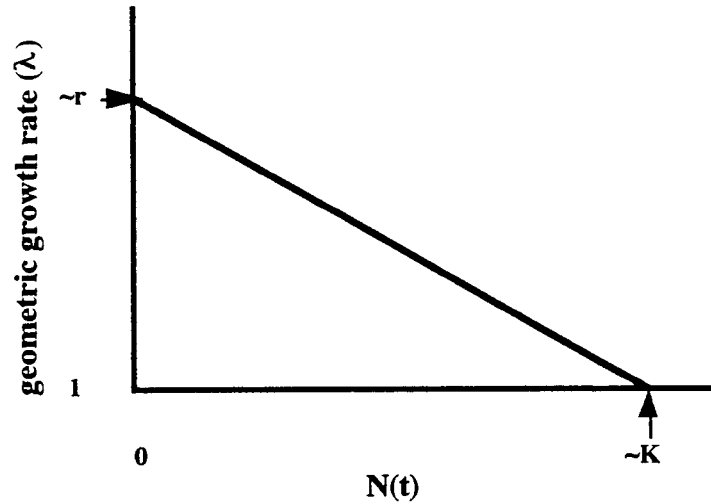
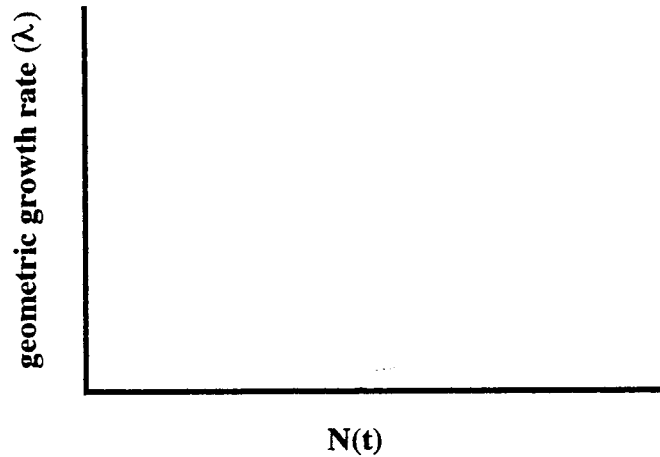


FIGURE 5.
using geometric
growth rate
to estimate K
(class data)



EXPERIMENT TWO

Resource limitation and population growth

The **intrinsic rate of increase** of a population represents the maximum rate of population growth that population can achieve under conditions of abundant resources and no competition. If resources are not limiting, populations of plants and animals can show explosive growth. Fortunately, under natural conditions, at least one resource is usually limiting and population growth falls below the intrinsic rate.

We can explore what conditions result in maximum population growth of *Lemna* by manipulating the resources that limit growth. Resources that might be limiting for *Lemna* in our culture situation might be nutrients, light, and space.

MATERIALS

The materials needed for this experiment will be determined by individual experimental designs.

PROCEDURE

Design an experiment to test the effect that varying the amount of one particular resource has on the population growth of *Lemna*. You can manipulate specific nutrients, such as phosphate, light levels, or surface area of the culture. For each set up, start with 15 plants and count the number of thalli on Day 7 and Day 14. Ideally, each experimental condition should be replicated at least 4 times, if space permits. Will you need a control? Use Table II to record your data.

NUTRIENTS: Steinberg (1946, as cited by Clatworthy and Harper, 1962) studied the nutrient requirements of *Lemna* and developed an ideal culture solution:

KH_2PO_4	100 mg/l	$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	0.18 mg/l
KNO_3	350 mg/l	$\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$	0.18 mg/l
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	100 mg/l	HBO_3	0.12 mg/l
$\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	295 mg/l	$(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$	0.037 mg/l
$\text{FeCl}_3 \cdot 6\text{H}_2\text{O}$	0.76 mg/l		

The pH of the culture solution is adjusted to 5.2-5.3 by the addition of dilute HCl or KOH.

Any one of these nutrients could be manipulated by adding various serial dilutions of a stock solution of the nutrient to artificial pond water. The maximum concentration of any nutrient should not exceed 10X that recommended by Steinberg.

LIGHT: Depending on your situation you could vary light levels by growing the *Lemna* cultures closer to a light source (a difference of six inches from a light source can be significant for *Lemna* growth), adding lights, changing photoperiod, or shading cultures with translucent material (e.g., plastic screening used in cross-stitch comes with various size holes at craft stores). You can use a light meter (hand-held or on a camera) to estimate actual or relative light levels.

*write the
experimental
protocol*

vary nutrients

vary light

EXPERIMENT TWO DATA SHEET

_____ name

Species of aquatic plant: _____

Description of environmental manipulations:

Experimental Hypothesis:

TABLE 2.
Resource limitation
and population
growth

Resource level	Number of thalli (N)			Relative growth rate (λ)	
	Day 0	Day 7	Day 14	$\frac{N \text{ day 7}}{N \text{ day 0}}$	$\frac{N \text{ day 14}}{N \text{ day 7}}$

FIGURE 6.
geometric
growth
(class data)

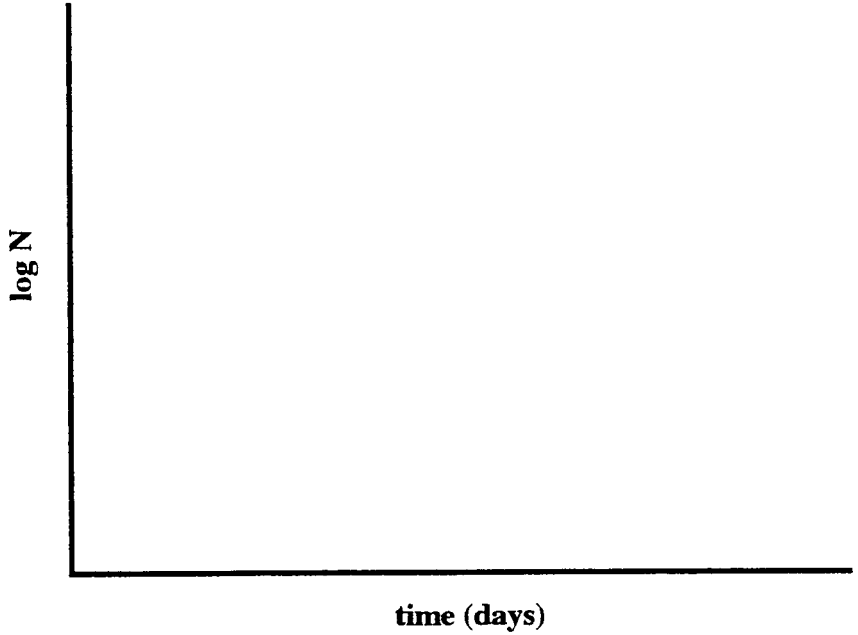
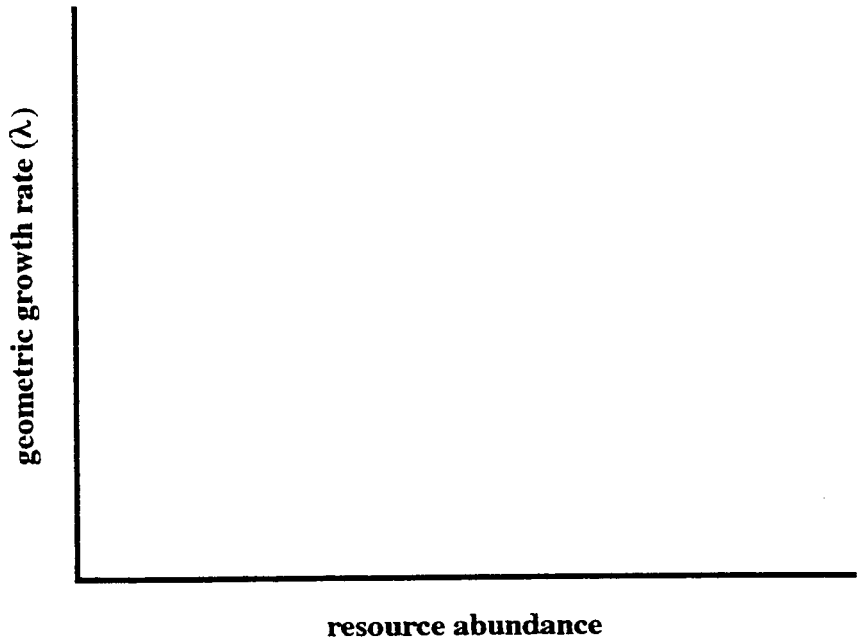


FIGURE 7.
geometric
growth
as a function of
resource
abundance
(class data)



Population growth and resource competition in *Lemna minor* and *Spirodela polyrhiza*.

If two or more species share resources that are in limited supply, the rates of population growth and maximum population size may be depressed. This is interspecific **resource competition**. Light, space and nutrients are resources that might be the basis for resource competition in floating aquatic plants.

We will study the population growth and competition of two species of floating aquatic plants, *Lemna minor* and *Spirodela polyrhiza*. There are many species of free-floating aquatic plants that could be used in this experiment (water meal, duckweeds, water ferns [see local keys to aquatic plants]). In the northeastern United States there are natural, mixed populations of *Lemna minor* and *Spirodela polyrhiza* and this is a good combination for experimentation. In other regions different species might be preferred.

Lemna minor is a species with small, round to ovate thalli or leaves (2-5 mm). It possesses a single long root. Thalli are commonly found in groups of 2 to 4. *Spirodela polyrhiza* has round thalli that are larger (3-8 mm). The thallus is concave and purplish underneath. It has numerous roots that are conspicuously shorter than the single root of *Lemna minor*. Small *Spirodela* plants can be distinguished from *Lemna* by the multiple venation of its thallus.

In **Part A** of this experiment you will monitor the growth of lab populations of *Lemna minor* and *Spirodela polyrhiza* grown alone and in mixed cultures. By comparing the rate of population growth under these two conditions (mono- and mixed culture), you will be able to detect the effects, if any, of each species on the other. A variety of interactions are possible, from no interaction at all to mutually negative effects we call "competition." You can determine the magnitude of the competitive effect of *Spirodela* on *Lemna* ($\alpha_{Lemna-Spirodela}$) by contrasting the relative rate of growth of a population of *Lemna* grown in monoculture with the relative rate of growth of *Lemna* grown with *Spirodela*.

The outcome of species interactions can depend on the environmental conditions. Ponds in which *Lemna* and *Spirodela* naturally occur vary in both nutrient concentration and the availability of light. In **Part B** of this experiment, you will explore how the magnitude of interaction can vary by growing monocultures and mixed cultures under conditions of two nutrient concentrations and two levels of light intensity.

EXPERIMENT THREE

*duckweeds
in nature*

*duckweed
morphology*

*species
competition*

MATERIALS

10 oz clear containers (plastic, glass; 3 cups/student)	additional plastic cups
200 ml artificial pond water/cup (A)	healthy <i>Lemna</i> plants
200 ml low nutrient culture fluid/ cup (B)	healthy <i>Spirodela</i> plants
200 ml high nutrient culture fluid/cup (B)	low intensity light racks
extra artificial pond water	high intensity light racks
extra low and high nutrient culture fluid	forceps

EXPT. 3 - PART A

COMPETITION IN THE SAME ENVIRONMENT

PROCEDURE

set-up

1. Prepare 3 cups with 200 ml of artificial pond water. Mark the 200 ml level on the cups. Place 10 *Lemna* plants in one cup, 10 *Spirodela* plants in a second cup, and 5 plants of each species in a third cup. Mark each cup appropriately.

initial status

2. Because a plant can consist of one or more thalli, count the number of thalli in each cup. One thallus is any leaf unit that is over 1.5 mm. Record these data in the Day 0 column of Table 3.

3. Place the cups under fluorescent lights for a period of two weeks, check them periodically, and refill them to the 200 ml line.

data collection

4. Count the number of thalli of each species in each cup on Day 7 and on Day 14 and record these data in the appropriate columns of Table 3. Be careful when censusing the mixture cups in distinguish between the two species.

DATA ANALYSIS

plotting the data

1. Using combined class data, plot the mean log N (number of thalli) over time for *Lemna* in monoculture, *Lemna* only in mixed culture, *Spirodela* in monoculture, and *Spirodela* only in mixed culture. The slope of each line will be the relative growth rate (λ) of the populations of each species. When you use the combined class data, plot all points and

indicate the mean. This will enable you to see the variation. (Use a different symbol for each type of culture.)

type of culture	Number of thalli (N)			Relative growth rate (λ)	
	Day 0	Day 7	Day 14	$\frac{N \text{ day 7}}{N \text{ day 0}}$	$\frac{N \text{ day 14}}{N \text{ day 7}}$
<i>Lemna</i> in monoculture					
<i>Spirodela</i> in monoculture					
<i>Lemna</i> in mixed culture					
<i>Spirodela</i> in mixed culture					

TABLE 3.
population growth
and resource
competition in
Lemna and
Spirodela

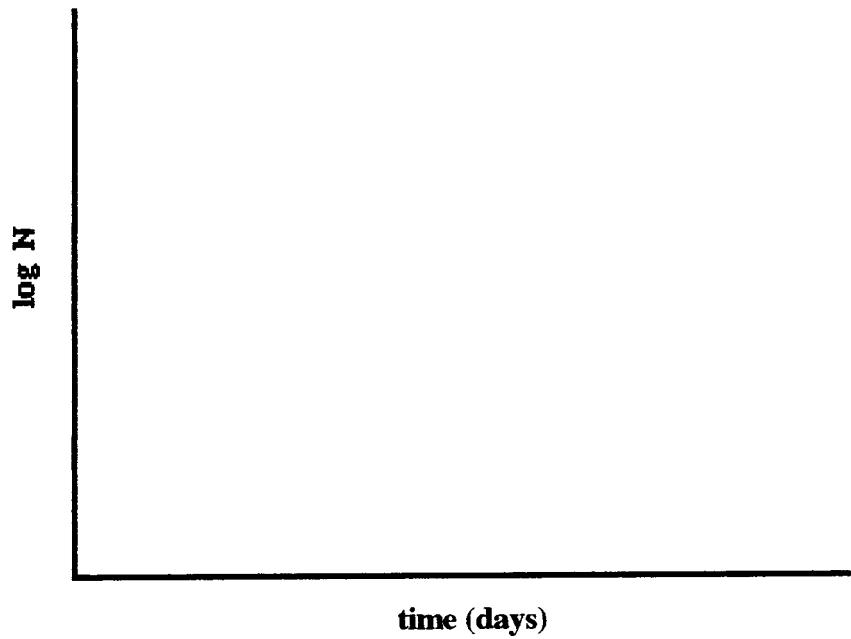


FIGURE 8.
competitive
growth
(class data)

DATA ANALYSIS CONT.

2. Estimate the competitive effect, $(\alpha_{ij}N_j)/K_i$, by subtracting the relative growth rate $(N(t+1)/N(t) = \lambda)$ of the monoculture from the relative growth rate of that species in mixed culture. How does this indicate competition?

3. What was the effect of the presence of a second species?

Mathematical theory pertinent to Experiment Three

When grown alone, the population growth curve for species i can be described by the logistic equation

$$dN_i/dt = r_i N_i [1 - N_i/K_i]$$

where N_i is the number of individuals in the population of species i , r_i is the intrinsic rate of natural increase of species i , and K_i is the carrying capacity of the environment for species i . As the population of species i grows, each new individual added to the population slows or reduces the rate of population growth.

When a second species, j , is introduced to the environment, each individual of species j may consume resources that could have gone to species i . Therefore, just as more individuals of species i slow the growth of population i (intraspecific competition), increasing the number of individuals of species j may slow the growth of species i (interspecific competition). The logistic equation for the population growth of species i can be modified to include the effect of species j on its growth:

*estimating
competition*

calculations

one species

two species

$$dN_i/dt = r_i N_i [1 - N_i/K_i - (\alpha_{ij} N_j)/K_i]$$

This is the Lotka-Volterra equation which models interspecific competition (Vandermeer, 1981; Ricklefs, 1990). The last term of the equation, $(\alpha_{ij} N_j)/K_i$, can loosely be interpreted as the number of individuals of population j it would take to equal an individual of population i in terms of the effect on the per capita rate of increase in population i .

COMPETITION IN DIFFERENT ENVIRONMENTS

PROCEDURE

1. In teams of students (assigned by your instructor), arrange a set of 12 cultures of aquatic plants as shown below (See Experiment II for suggestions on how to manipulate light and nutrients):

set-up

High light			Low light		
low nutrient	high nutrient		low nutrient	high nutrient	
L	S	M	L	S	M
L	S	M	L	S	M

Each team will prepare 6 plastic cups with 200 ml low nutrient culture fluid and 6 with 200 ml high nutrient culture fluid. Place 10 *Lemna* plants into 2 cups with low nutrient fluid and into 2 with high nutrient fluid, place 10 *Spirodela* plants into 2 cups with low nutrient fluid and into 2 with high fluid, and place 5 plants of each species into 2 cups with low nutrient fluid and into 2 with high nutrient fluid. Mark the 200 ml level on each cup and indicate its nutrient level, species content, and lighting regime. (Note that each combination of light and nutrient is replicated for *Lemna* alone, *Spirodela* alone, and for the mixed culture).

initial status

2. Because a plant can consist of one or more thalli, count the number of thalli in each cup. One thallus is any leaf unit that is over 1.5 mm. Record these data in the Day 0 column of Table IV.
3. Place the cups under the indicated levels of light for a period of two weeks, check them periodically and refill them to the 200 ml line with the **appropriate** culture fluid.

data collection

4. On Day 7 and on Day 14, count the individuals of each species in each cup and record these data in Table IV. Count each thallus that is greater than 1.5 mm as an individual; in most cases several thalli will be connected together.

record conditons

5. Make note of the specific nutrients and their concentrations in the low and high solutions and measure the light intensities used, if possible.

DATA ANALYSIS

*plotting
the data*

1. Using the combined class data, plot the mean log N (number of thalli) over time for *Lemna* in monoculture and *Lemna* only in mixed culture for the four environmental conditions. Plot the mean log N (number of thalli) over time for *Spirodela* in monoculture and *Spirodela* only in mixed culture. The slope of each line will be the relative growth rate (λ) of the population under those conditions. When you use the combined class data, plot all points and indicate the mean. Use a different symbol for each type of culture (i.e., *Lemna* in monoculture, *Lemna* in mixed culture). Space is available on the following pages for separate plots of each environmental combination.

*estimating
competition*

2. Estimate the competitive effect, $(\alpha_{ij} N_j)/K_i$, by subtracting the relative growth rate ($N(t+1)/N(t) = \lambda$) of the monoculture from the relative growth rate of that species in mixed culture. Do this for each combination of light and nutrient level.

calculations

EXPERIMENT THREE DATA SHEET

name _____

Conditions (circle) Light: low high

Nutrients: low high

Other comments regarding experimental conditions:

Experimental hypothesis(es).

type of culture	Number of thalli (N)			Relative growth rate (λ)	
	Day 0	Day 7	Day 14	$\frac{N \text{ day 7}}{N \text{ day 0}}$	$\frac{N \text{ day 14}}{N \text{ day 7}}$
<i>Lemna</i> monoculture					
<i>Spirodela</i> monoculture					
<i>Lemna</i> mixed culture					
<i>Spirodela</i> mixed culture					

TABLE 4.
population growth
and resource
competition in
Lemna and
Spirodela

FIGURE 9.
competitive
growth rates

high light intensity
- low nutrient level
(class data)

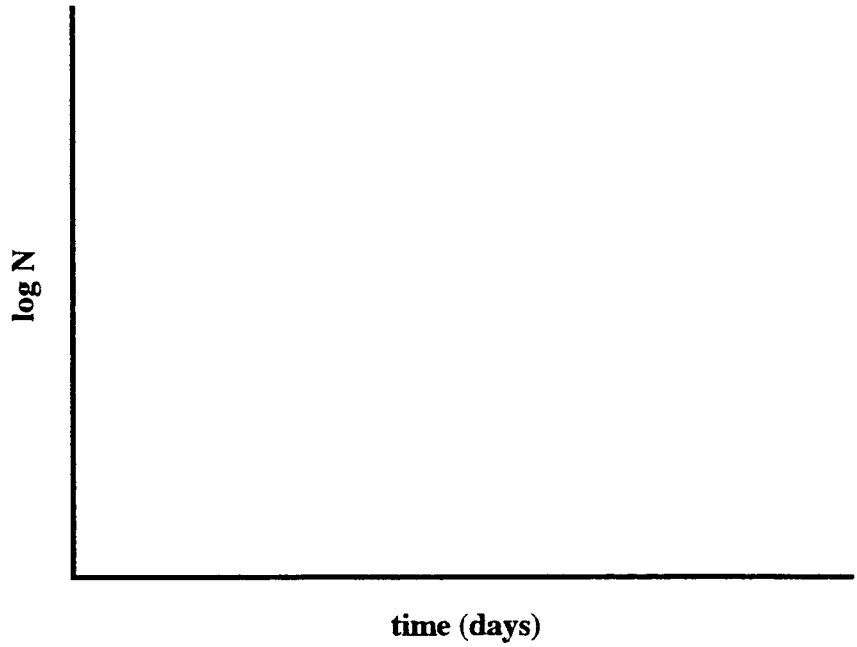
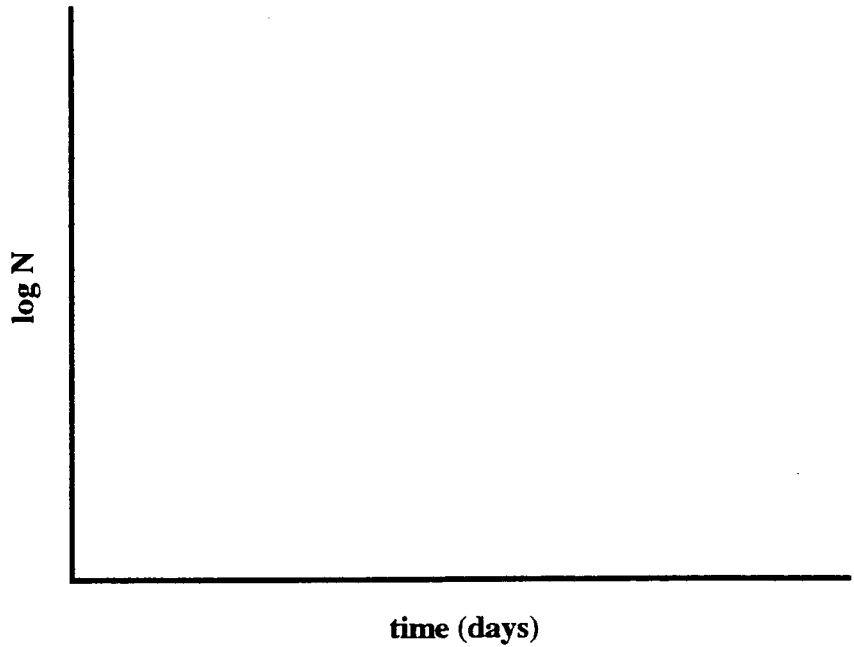


FIGURE 10.
competitive
growth rates

high light intensity
- high nutrient level
(class data)



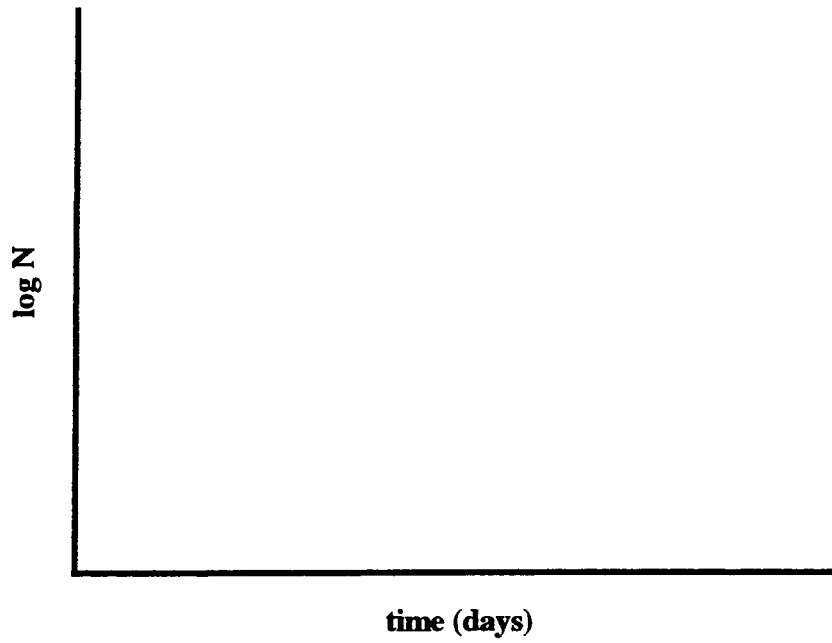


FIGURE 11.
competitive
growth rates

low light intensity
- low nutrient level
(class data)

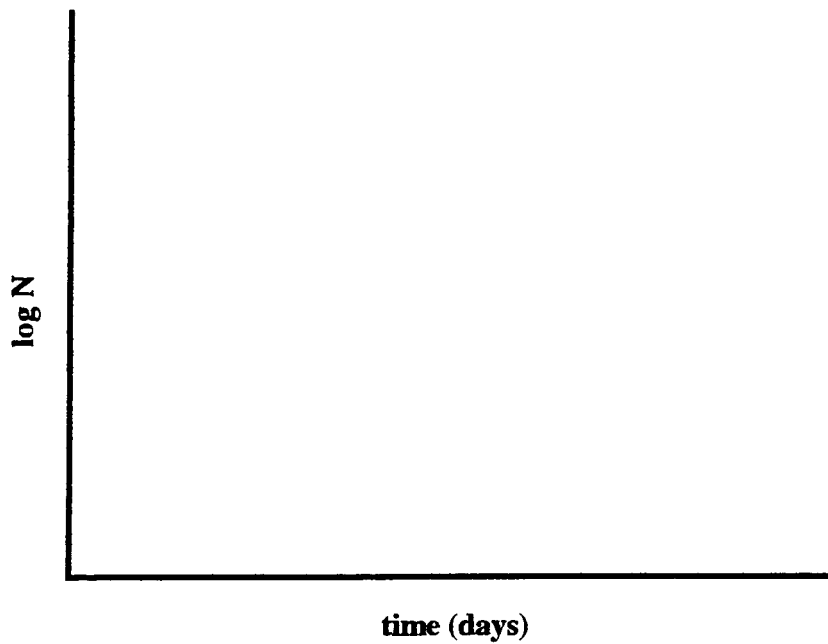


FIGURE 12.
competitive
growth rates

low light intensity
- high nutrient level
(class data)

questions

1. Summarize your findings. How did the plants do under the various growing conditions?
2. Was the effect of the presence of a second species on population growth positive, negative or neutral?
3. Was the magnitude or direction of the effect the same in each environmental circumstance? Was it the same for each species?
4. Was one species competitively superior under the experimental growing conditions? Based on the results of this experiment, if the two species were growing together in a pond or lake, which species would you predict would eventually become dominant?
5. Compare your results with those of Clatworthy and Harper (1962, also cited in Harper, 1977).

REFERENCES

- Clatworthy, J.N. and J.L. Harper. 1962. The comparative biology of closely related species living in the same area. V. Inter- and intraspecific interference with cultures of *Lemna* spp. and *Salvinia natans*. *Journal of Experimental Biology* 13: 307-324.
- Harper, J.L. 1977. *Population Biology of Plants*. Academic Press, NY.
- Ricklefs, R.E. 1990. *Ecology*. W.H. Freeman and Co., NY.
- Vandermeer, J. 1981. *Elementary Mathematical Ecology*. John Wiley and Sons, NY.

NOTES TO INSTRUCTORS

1. *Lemna* and other species of floating aquatic plants can be collected locally in the summer and fall or purchased from Biological Supply Companies.
2. *Lemna* can be grown in sterilized artificial pond water using the following recipe (from Pat Brown, Biology Department, Siena College)

pond water

Artificial Pond Water (for 20L carboy)

Solution A: 1.04g NaCl
2.35g $\text{CaCl}_2 \cdot (\text{H}_2\text{O})_2$
0.15g KCl

First, dilute the salts in 500 ml distilled H_2O .
Second, add solution A to 15 L of distilled H_2O ,
then make solution B.

Solution B: 0.34g NaHCO_3

First, dilute the salt in 500 ml distilled H_2O .
Second, add solution B to container of solution A
and fill with distilled H_2O to the 20L mark.

The final concentration of the salts in this solution is
1.3 mM NaCl, 0.8 mM CaCl_2 , 0.1 mM KCl, and 0.2
mM NaHCO_3 .

It is a good idea to autoclave the artificial pond water
to reduce contamination of the cultures with algae or
other microorganisms that might be present in the water.
Sterilized tap water is also a suitable growth medium
although one has no control over mineral or nutrient
content.

recipe

3. The experiments may run 4 weeks, or longer. There is a chance the cultures may crash at some point due to algal contamination, evaporation, or neglect. Students can usually investigate and discuss the causes of population crashes.
4. *Lemna* plants contain 1-4 thalli per plant. Therefore, 2 plants will not

duration of experiments

thallus vs. plant #

equal 2 thalli. Students will have to count the number of thalli at day 0 after adding 2 or 15 plants to their cups. One could start the cultures with exactly 2 or 15 thalli, if you want all students to start with the same N (number of thalli).

counting

Counting the cultures on Day 7 and Day 14 takes about 15 minutes when each student is monitoring two cultures.

5. Checking the cultures at "regular" intervals depends upon the circumstances in your lab (i.e., student access to the lab, potential frequency of student visits to lab). If low humidity is a problem and cultures readily evaporate the instructor may have to assist with the watering regime.

replicates

6. The number of replicates depends on the number of students and the space available to grow the cultures. If each student can only do one set of cultures per experiment, there will be at least as many replicates as there are students in the class. With large enrollment classes, students may need to work in teams resulting in less replication. However, if class data are pooled and there are several lab sections there still will be ample data for analysis.

EXPERIMENTS TO TEACH ECOLOGY FEEDBACK FORM

POPULATION GROWTH: Experimental Models Using Duckweed

Please complete this form after you have used this experiment and mail it to the address given on the reverse side of this page.

1. Was the introduction clear and informative? What changes would you suggest?
2. Was the list of materials complete? Would you suggest any additions or modifications?
3. Was the procedure easy to follow? What changes would you suggest?
4. Were the illustrations and data charts adequate? What others would you include?

5. Were the instructor's notes complete? If you noted any omissions, what were they?

6. What level of students used the experiment? Was it suitable for this level? If not, what changes would you suggest?

7. Did the experiments work? Please explain any problems you had when using these experiments?

8. On a scale of 1-10, with 10 as outstanding and 1 as terrible, how would you rate this experiment? Would you recommend this experiment to others?

9. Was it helpful for this laboratory exercise to have been written for the student rather than as an instructor's guide?

Please mail the completed form to: Dr. Jane M. Beiswenger
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