UC Riverside UCR Honors Capstones 2017-2018

Title

Assessing the Dynamics of a Generalist Predator/Prey Model Across Different Spatial Configurations

Permalink https://escholarship.org/uc/item/6dz3301t

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Publication Date

2018-04-01

By

A capstone project submitted for Graduation with University Honors

University Honors University of California, Riverside

APPROVED

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Dr. Richard Cardullo, Howard H Hays Chair and Faculty Director, University Honors Interim Vice Provost, Undergraduate Education Abstract

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INTRODUCTION

One of the major human impacts in ecosystems is habitat fragmentation. Ecological communities are being fragmented into smaller patches by the allocation of land to agricultural and urban development (Didham 2010). Spatial structure can promote heterogeneity by dividing communities into patches loosely connected by the dispersal of organisms (Fig. 1). Under these conditions, a large population of organisms is divided into a group of smaller populations, forming a metapopulation. Local extinction events can occur in individual habitat patches, but recolonization from populated patches results in long term species persistence across the metapopulation. Thus, spatial heterogeneity can prevent species from going extinct, buffering against the effects of habitat loss on community structure (Gonzalez & Chaneton 2002).



Fig 1. Landscapes with (A) high and (B) low degrees of connectivity. A connected structure generally has higher levels of functions than a fragmented one (Federal Interagency Stream Restoration Working Group).

One of the many ways to study the effects of habitat fragmentation is through protist microcosms. Microcosm experiments using protists are widely used to investigate general concepts in population biology, community ecology, and evolutionary biology (Altermatt et al., 2015). Microcosms are not intended to mimic the behavior of any particular natural system but rather complement studies of natural systems by allowing experiments that would be difficult or impossible to conduct in the field (Fox, 2007). A typical protist microcosm contains bacteria as the primary producers and different species of protists as the consumers. The relationships among the protists in microcosms have been well studied and the trophic interactions between protists have been determined (Warren et al., 2003, Fig. 2). Protists are useful model organisms because they possess rapid generation times, are large enough to count under standard magnification, and at the same time they are small enough to grow and manipulate in large numbers (Holyoak and Lawler, 2005).



Fig 2. An example of feeding relationships in an experimental microcosm. Bacteria are the basal food resource in this and many other similar microcosms. Figure reproduced from Warren et al. 2003.

Most microcosm studies of habitat fragmentation have focused on predator/prey interactions, and these have focused on the selective feeding of flagellates and ciliates that tend to be specialist predators.

However, amoebae are much less studied despite the fact that they also constitute an important component of freshwater ecosystems (Xinyao et al., 2006). Amoebas are generalist predators and are affected by interactions with other species, as they sustain a high abundance in interacting communities and are less successful in non-interacting ones where there is only a single species as a food source (Holt et al., 2002). Due to their difference in foraging strategies compared to a specialist predator, studying the interactions of a generalist predator/prey system is an interesting matter of study. Studies suggest a generalist diet allows these organisms to maintain high abundances (Petchey, 2000). However, more studies are needed. Here, we examine the effect of different spatial configurations on a predator/prey system using a generalist predator. Unlike specialist predators, generalists are expected to be over-represented in fragmented habitats and have longer persistence times, meaning that understanding their dynamics is important. In microcosm studies, amoeba act as predators to bacteria and to other protist species, like *Paramecium*.



Fig 3. Paramecium caudatum (400X).



Fig 4. Amoeba proteus (400X).

The objective of this project is to parameterize key population interaction terms of a predator/prey system using *Amoeba proteus* (predator, Fig.4) and *Paramecium caudatum* (prey, Fig. 3). These parameters will be used in future research projects to predict the effects of spatial configuration on the persistence time of both predator and prey.

METHODS

Medium preparation

The medium was prepared by mixing 1400 ml deionized water with 1 Protozoan Pellet (Carolina Biological Supply Company, Burlington, NC) and 0.14 g reptile vitamins. After sterilization in an autoclave, the medium was inoculated with three bacteria species (*Bacillus subtilis, Bacillus cereus*, and *Serratia marcescens*) previously subcultured in laboratory.

Predator and prey growth

Four 175 ml Nalgene bottles were filled each with 40 ml of medium. One wheat seed was added to each bottle. One ml of *Paramecium* stock was added to each bottle. These bottles were sampled for three times a week for 20 days. After this, 1 ml of *Amoeba* stock was added and the bottles were sampled for three times a week for 30 additional days.

Predator functional response

A stock culture of *Paramecium caudatum* was used to make dilutions of 10, 20, 30, 40, 50 and 100% and 1mL of each dilution was placed into the wells of 24-well plates, making a total of three replicates for each dilution. Twenty *Amoeba proteus* were added to one well of each concentration. The remaining wells of each concentration were controls that received no predators. After three hours, *Amoeba proteus* was censured in the entire 1 mL of predation treatments. Each well was sampled twice and *Paramecium* were counted in each sample.

Predator and prey colonization

Arrays were made by connecting two 175 ml Nalgene bottles with a tube of varying length. The different tube lengths were 7, 13.5, and 20 cm. Four replicates of each tube length

were assembled. 40 ml of medium and one wheat seed were added to all bottles. One ml of *Paramecium* stock was added to only one side of each array. All bottles in the arrays were sampled for three times a week for 20 days. After this, 1 ml of *Amoeba* stock was added to only one side of the arrays and the bottles were sampled for three times a week for 30 additional days.

Sampling

Sampling for all experiments consisted of extracting 10 drops of 20 μ L onto a preweighed petri dish. Then, the weight of the drops was recorded. The petri dishes were placed under the microscope and preys and predators were counted in every drop.

Data analyses

Prey growth

Counts of individuals were used to calculate the concentration (measured in individuals/mL) and abundance of individuals on each bottle for every sampling date. Analyses using Maximum Likelihood Estimation (MLE) on R were performed using an exponential growth model and a logistic growth model. These analyses were done in order to obtain parameters r (*per capita* growth rate) and K (carrying capacity).

Predator functional response

Counts of *Paramecium* were used to calculate the concentration before and after three hours. The consumption rate was calculated according to Holyoak et al., 2000:

$$\varepsilon_{b\subset d} = \frac{C_d - P_{b\subset d}}{3\hat{Y}_{b\subset d}}$$

Where:

 ε_{bd} = Consumption rate for each well (b) at concentration d (in units of prey per predator per hour).

 C_d = Mean of the final prey concentration for controls at each concentration, where d is the concentration.

 $P_{b \subset d}$ = Final prey density in well b at concentration d.

 $\hat{Y}_{b \subset d}$ = Geometric mean of the initial and final number of predators in well b with concentration d.

Analyses using Maximum Likelihood Estimation (MLE) in the software platform R (R Code Team) were performed to estimate the parameters of Holling's Type II equation:

$$P_c = \frac{a'NT}{1 + a'T_hN}$$

Where:

Pc=Prey consumed per predator

a'= attack rate

 T_h = handling time

T=total time

N=Prey density

These analyses were done in order to obtain parameters that quantify the strength of consumption of *Amoeba* on *Paramecium*.

Prey dispersal

Counts of individuals were used to calculate the concentration (measured in individuals/mL) and abundance of individuals on each set of bottles for every sampling date. Analyses using Maximum Likelihood Estimation (MLE) on R were performed to obtain dispersal rate parameters for each dispersal treatment.

RESULTS



Fig 5. Growth of *Paramecium caudatum* as a function of time (days). Results show mean density from 4 replicates \pm Standard Error.



Maximum Likelihood Estimation-Exponential Growth

Fig 6. *Per capita* growth rate of *Paramecium caudatum*. Model fitting was done following exponential growth. Blue triangles show growth rates obtained from experimental data and the red line indicates the estimated *per capita* growth rate from the model ± Standard Error, r= 0.217±0.011.

Fig. 5 shows the growth of *P. caudatum* over the course of the experiment (20 days). The MLE analysis originally included both exponential and logistic growth. However, fitting with the logistic model did not produce realistic parameters so the final graph depicts the *per capita* growth rate using exponential growth (Fig. 6). The value for the *per capita* growth rate obtained from MLE estimations was $r=0.217\pm0.011$.

Predator Functional Response





Fig. 7 shows the results from the predator functional response experiments. Fitting was done following Holling's Type II equation and the MLE estimates obtained for attack rate and handling time were 0.012 ± 0.013 , 0.606 ± 0.289 , respectively.

Prey Dispersal



Fig 8. Density of Paramecium caudatum A) Before adding predators and B) After adding predators for 2-patch arrays with three different distances between patches (7, 13.5, and 20 cm). Results show the mean density obtained from 4 replicates ± Standard Error. Legend: Blue: Side A, Red: Side B.

Fig. 8 shows the population curves for *P. caudatum* for each dispersal treatment. Since these experiments were performed using a 2-patch system, the blue lines represent the side where organisms where added and red lines represent the other side of the array. The three top graphs show the population densities before adding *A. proteus* monitored over the course of 20 days. The three graphs below are the same population curves after the addition of predators, and these populations were followed for 30 days. The MLE estimates of dispersal rate were 0.123 ± 0.028 , 0.089 ± 0.011 , and 0.258 ± 0.067 , respectively.

DISCUSSION

We have obtained several parameters for the final model. Most of these parameters involve the dynamics of the prey, *P. caudatum*. Additionally, we have obtained information about the nature of *Paramecium* growth and its relationship with the predator, *A. proteus*.

The estimations for the growth of *P. caudatum* were tested using exponential and logistic growth. Ultimately, the per capita growth rate for *P. caudatum* was obtained following an exponential model, since the experiments were performed over a short period of time and the growth curve did not show a plateau (Fig. 5), meaning that by the time the experiment ended, the *Paramecium* population was still in exponential phase. Further experiments that monitor *Paramecium* populations for longer times are needed in order to obtain better parameters for the model such as growth rate and carrying capacity. Fig. 6 shows the per capita growth rate of *Paramecium* as a function of density. The data points show that at lower *Paramecium* densities the growth rate is higher and at high densities the growth rate is lower, which confirms dynamics that would follow the logistic model.

For the functional response experiment, we observe that as the prey density increases, the consumption rate increases as well, reaching a saturation point (Fig. 7). This follows Holling's Type II functional response curve, which was expected. However, we see a lot of variability in the data. Additional replicates are needed in order to obtain more data points to make our MLE analyses more accurate.

Figure 8 shows the density of *Paramecium* populations as a function of time. Here, we see that before adding predators, all the populations show a growing trend. However, once predators are added, the population curves show cycling and almost extinction in some arrays.

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This confirms that there is an effect of *A. proteus* on the dynamics of *Paramecium*. Due to the generalist nature of the predator, we would expect the bacterial populations in the arrays to show cycling. However, for these experiments we did not analyze bacterial data. Additional experiments that take into account both *Paramecium* and bacteria will provide a better picture of the effect of *Amoeba* on its prey.

Further work will include analyses for the predator population dynamics, growth, extinction, and patch colonization. Once the model is parameterized we will choose spatial configurations based on previous studies (Holyoak, 2000) that used a specialist predator, such as *Didinium* (Fig. 9). The computer model will make predictions about predator and prey persistence in these configurations based on the parameters obtained. At the same time, physical arrays of these configurations will be built and cultured in laboratory settings, in which predator and prey will be counted using the same sampling techniques mentioned above. Finally, the model predictions will be compared with the experimental microcosms and we will determine the accuracy of our estimations. For the evaluation of the system over different spatial configurations, we expect longer predator persistence times and greater variability among spatial configurations due to the generalist diet of our predator.

In summary, protist microcosm experiments represent an inexpensive and straightforward approach to understand the effects spatial configurations in predator/prey persistence. Furthermore, this project will also contribute to aid in the studies of population dynamics of natural protist communities that are currently being isolated and cultured in laboratory settings.

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Fig 9. Example of spatial configurations used in a *Didinium/Colpidium* model. Bars show mean predator persistence time. Image extracted from Holyoak et al., 2000.

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