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COMPETITION IN A SIMPLE POND: A 3D AGENT BASED MODEL APPROACH

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BY EMIL MONTANO

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DR. ISTVAN KARSAI, CHAIR

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Abstract

If two species are competing for a limited resource, the species that uses the resource more efficiently will eventually eliminate the other. This is known as the principle of competitive exclusion developed by Georgy Gause. To determine the effect of this competition, a simple three-dimensional model of a pond is created in which two species compete for a single source of energy (algae). The model is based solely on the conservation of the energy that flows through an ecosystem where primary production is the only source of energy. The first scenario tested is of two competing species with identical life histories; therefore it is predicted that one of the species will randomly become extinct. Another experiment demonstrates how the speed of extinction is dependent upon the energy input (external factors) of the environment. Results show a higher rate of life cycles and smaller fluctuation of population between life cycles in a higher energy input environment and slower but higher fluctuating life cycles in a low energy input environment. The introduction of a predator to the system shows that an additional level of hierarchy can have a short term stabilizing effect in populations of competing species with identical life histories. Predators cannot be too efficient due to the risk of prey depletion leading to predator extinction occurs. Stratification of the two competing populations was then added to further stabilize the populations causing coexistence within the simulation. Slight differences in life histories can create large differences in survival. The simulations include changing speed, size, and energy input. When referring to the different life histories model, one species with certain parameters competing with another species with different parameters may be more successful under a certain environmental condition and less successful under other conditions.

Introduction

Modeling of interactions between species in an environment has been studied for a long time. The Lotka-Volterra predator-prey model was proposed in 1910 (Lotka, 1910). The equation was first used to study chemical equations and was then used to study predator-prey interactions in 1925. The Lotka-Volterra model is the simplest model used to predict predator-prey cycles. The model, however, is limited in many ways because it only takes into consideration a small number of parameters. When using this model, the population change of one species depends on the current population, the reproduction rate, and the interactions with other species (Figure 1). The “x” and “y” term represent the number of prey and predators, respectively. “A”, “B”, “C”, and D represent parameters describing the interaction of the two species. The model ignores variations among individuals of the same species, does not take into consideration carrying capacities, and is always perfectly mixed within the environment. With the use of computers a new method for studying species interactions has emerged. The new modeling method is known as Agent-Based Modeling (ABM). This method is very dynamic as it takes into consideration population values and the threshold for reproduction at discrete times. Agent-Based Modeling Systems (ABMS) also have the potential to study population with non-uniform mixing because the space within the model is represented explicitly.

$$\frac{dx}{dt} = Ax - Bxy$$

$$\frac{dy}{dt} = -Cy + Dxy$$

Figure 1: Lotka-Volterra Equations

ABMS is a new approach being used widely in the study of specie interactions. It may have many real life applications in a multitude of fields. Applications range from modeling agent performance in supply chains, the trends in the stock market, predicting where epidemics will spread, or the threat and spread of bio-warfare (Marcal and North, 2006). The term “agent” can be defined in a couple of ways. Many ecologists think that an agent is any type of independent component that can perform a range of basic decision rules to a more complex artificial intelligence, while others believe that a component's behavior must be adaptive and make independent decisions. Modeling systems have been developed due to an increasingly complex world where modeling is the best way to stay organized and keep track of multiple parameters. The exponential growth in technology has made it possible to handle the type of software needed to run ABMS (Macal and North, 2006).

Many agent based programs of varying complexity have been created for a wide range of uses. StarLogo TNG is the programming system used for these experiments (Education, 2011). StarLogo TNG can recreate a specific real-life environment using blocks rather than text-based commands (Klopfer, 2007). Many modeling systems require either text-based commands or actual computer programming and contain limited visual projection. StarLogo TNG is a very user-friendly system that has a three-dimensional visual projection with "sliders" used to effectively change variables without having to alter any of the programming (Klopfer, 2007). This allows researchers, and the public with limited ABMS experience, to more deeply understand the biology of the system without having to worry about the detailed programming that many programs require.

The use of agent based modeling to predict a future outcome in a real-world situation is a fairly new and innovative technique. Prior to this technology, scientists relied on their scientific methods such as observation or experimentation. The problem with those techniques is that a hypothesis (that may have dire consequences) cannot be tested before it is implemented. This is especially important to conservation biologists who, in some cases, hold the fate of a species in no more than a hypothesis. Scientists do not know the outcome of changing the environment in hopes of saving an endangered species. Scientists would be forced to make predictions based entirely on experience of similar, but not identical, scenarios. This ‘blind’ method of conservation, while having success in some cases, can have major negative catastrophic effects. For example, the introduction of mongoose to Hawaii led to the extinction of multiple bird species (Baldwin et al., 1952). Using modeling systems allow scientists to test possible hypothesis until one works consistently.

The ‘blind’ method had detrimental consequences in Hawaii with the introduction of the Indian Mongoose. Rats were introduced to Hawaii on explorer ships and they had been feeding on the eggs of ground nesting native birds. Researchers hypothesized that if the Indian Mongoose was introduced to the environment, they would eat the rats and end the attack on the bird eggs. Once introduced, the Mongoose did not hunt the rats, but rather joined the rats in eating the bird’s eggs, a much easier meal to obtain. If agent based modeling was available at the time, a simulation of all environmental factors such as the number of ground nesting birds or the number of rats could have been created to identify how many Mongoose should have been introduced if at all. The introduction of the mongoose could have been tested on this system to see the ideal number needed to eradicate the rats without killing the birds, or they would find that the mongoose would target the birds due to the ease of the target (Baldwin et al, 1952). This would have been recognized in the model when all species parameters were implemented.

Successful models that altered the way that we think about conservation biology have already been created. Karsai and Kampis produced an agent based modeling system that was used to study how habitat fragmentation and the connection of those habitats affected the survival of animals in a simple model. Habitat fragmentation/stratification is becoming more prevalent as roads are built through previously undisturbed environments. In the experiment, a prey-predator interaction was constructed under a highly fragmented ecosystem, with tiny passages that allowed both species to cross between previously fragmented segments. The results clearly show that even small passageways between fragments yielded a much more stable prey-predator population cycle with more diversity throughout the ecosystem. The model can now be adapted to a specific situation in order to determine how many passageways are needed for a health ecosystem to thrive (Karsai and Kampis, 2011).

My research aims to study competition between species with identical life histories to support the competitive exclusion principle, proposed by Georgy Gause before the modeling systems were available. The affect of competition between species with different life histories in a simple aquatic environment is also studied to see how a slight change in the environment can favor one species over another. This is later used in evaluating species survival probabilities in varying aquatic environments.

In addition to studying species with identical life histories or slightly altered life histories, the effect that a predator has on the stability of an aquatic environment in which two prey species are competing for resources is also studied. A predator acts as a negative feedback control that stabilizes prey populations (Friman et al., 2008). A successful hunter consumes prey when prey is plentiful, but does not drive the population to local extinction. When healthy prey/predator life cycles are studied regular cycles are observed (Friman et al., 2008). A predator that is too effective may overexploit its resources, and regular population cycles of both predator and prey may be disrupted. In these predators, the negative feedback ability is too large and will drive the prey source to extinction, which eventually leads to the extinction of the predator.

Oswald J. Schmitz hypothesized that the addition of an adequate predator displaying equal favoritism in prey choice will consume larger amounts of one species when that species has a larger population size than the other, thus regulating and stabilizing the population of both species. Many real-world consumers use multiple resources depending on the distribution, quality, and abundance of the resource (Schmitz, 1995). The addition of the right predator may have an effect on the amount of time two similar species can coexist.

A final measure in the attempts to increase the rate of stabilization is to stratify the two competing species in the presence of a predator to demonstrate each species finds a particular niche within an environment, they become better suited for long-term coexistence.

Materials and Methods

To investigate the problems described, the StarLogo TNG modeling system is used to create a simple three-dimensional agent based environment. StarLogo TNG is a modeling system developed by Mitchel Resnick, Eric Klopfer, Daniel Wendel, and others at the MIT Media Lab and the MIT Teacher Education Program in Massachusetts. It is an extension of the Logo programming language, a dialect of Lisp. (a network of computer languages) designed for education. Microsoft Office Excel 2007 was used to store and analyze all gathered data. The computer used to run the program for is an Intel(R) Core(TM) 2 Duo CPU at 2.00 GHz 2.00 GHz with 3.00 GB memory (RAM) and a 32-bit Operating System.

StarLogo TNG is a model development system for agent-based simulations, upon which individuals interact with the environment. Agents are controlled by programming the system to direct the agents in exactly what to do throughout the simulation. This model has an environment that goes from -50 to 50 in the X and Y direction and 0 to 75 in the Z direction. It is programmed to have a prey species (algae) and two competing predator species (paramecium and algae eater 2), and run entirely on the flow of energy through the system. The addition of a predator is present in later simulations, and works on the same energy flow premise. At the start of all the simulations, there are 1000 algae with a random energy from 1 to 10, and there are 200 of both competitor species with energy ranging from 1 to 20. When predators are present, there are 40 individuals at the start of each simulation with an energy level ranging from 1 to 400 (Fig 1). The initial individuals are dispersed randomly within the entire three-dimensional environment at the beginning of the simulations (Fig 2).

The only energy input throughout the simulations comes from primary production of the algae where a constant sunlight input in the system is assumed. Therefore, a constant energy increase into the alga bodies is implemented. Energy of the competitors is lost through movement (every agent moves a programmed distance each turn), and in some simulations, collisions with a non-food source (Table 1). Energy is gained through collision and results in the consumption of algae. Energy is conserved so that if a paramecium eats an alga with an energy level of eight it will gain eight energy units. Reproduction takes place when a species reaches or exceeds its maximum energy level (Fig 2), at which point the energy is conserved and split evenly between the mother and offspring. The conservation of energy assumes that the system does not include entropy, which simplifies the model enough to more easily study certain parameter changes in various species. Finally, death happens when any species reaches an energy level of zero.

Table 1: Baseline parameter levels for each species in the environment

Simulation Parameters				
	Algae	Paramecium	Algae Eater 2	Predator
Starting # of Individuals	1000	200	200	40
Size	1	2	2	4
Speed	1	2	2	4
Energy Change Per Step	+1	-1	-1	-4
Energy level of Reproduction	10	20	20	400

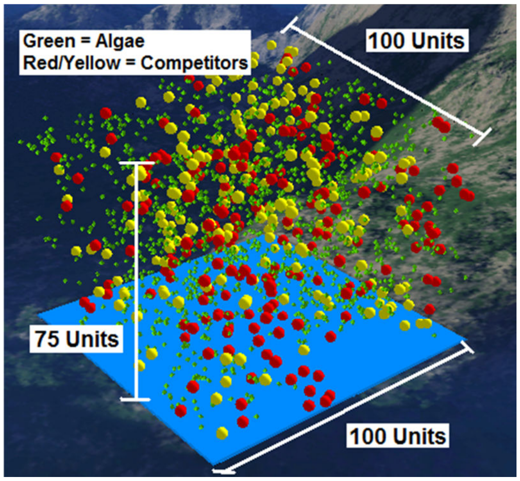


Figure 2: visual representation of the three dimensional aquatic environment during a simulation

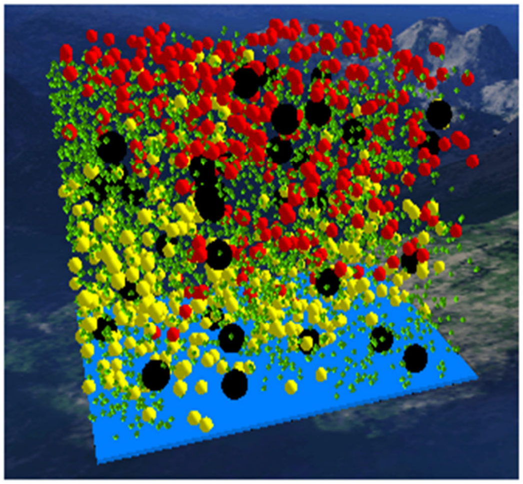


Figure 3: visual representation with the addition of a predator and stratification

*The term algae, paramecium, algae Eater 2, and predator are used as a ‘template’ for basic primary producers and primary/secondary consumers. These are used to make understanding the system easier and can be changed when specie-specific parameters are added to the program in a real world application.

StarLogo TNG uses stochasticity and therefore has the need to generate random numbers within a programmed range each time a movement is performed. Movement on a two- dimensional plane is easily programmed using the “forward,” and “right,” and “left” blocks which are similar to natural movement in found nature. The “right” and “left” blocks use this stochasticity to produce random and natural degrees of turns. The program generates a random number from 1 to 90 for both left and right turns. This means that a maximum left turn would be a 90 degree turn to the left, and a 1 degree turn to the right resulting in an overall 89 degree turn to the left. StarLogo TNG does not have the ability to directly program movement in the vertical direction. This problem was fixed by using stochasticity to generate random up

```
Paramecium
- Move Paramecium
left degs random 90
right degs random 90
forward steps 2
up steps random 8 - random 10
if test altitude < 1
   then set altitude 1
if test altitude > 75
   then set altitude 75
Paramecium
inc Paramecium Energy
Paramecium
Peracecium Step
```

Figure 5: Programming for agent movement in A three dimensional environment

and down movements. The programmed vertical movement was completed for algae using the following: “Up” random 3 – 2. For each primary producer a logical function was used so that in each time step an agent could move up one step (3-2), down one step (1-2), or remain that at its current altitude (2-2). The same methodology was used to program movement for the two primary consumer species and the predator, but at differing values (Table 1) to allow more movement per step. When stratification was used as a strategy for species longevity the movement in the X direction had to be altered. The movement for paramecium was set at “Up” random 8 – random 10, which makes the likelihood of a downward movement greater than in the upward direction (Fig 4). The opposite programming was done in for the Algae Eater 2: “Up” random 10 – random 8. By using this method of stratification, the degree to which each species is stratified can easily be changed by increasing or decreasing the 8.

The programming for parameters that are altered during different simulations are accompanied by “sliders”. A slider is a tool that allows you to change the value of some variable without having to manually change the value within the programming. Sliders were made for the energy change per step of all species and for the collision cost for each of the competing species. A number of different output methods are implemented as a means to view the results of the simulation. A graph of total Paramecium, Algae Eater 2, and Predator births in a simulation, and a graph of the population cycles of all species were implemented. All sliders and output graphs are on the same window as the three-dimensional environment separate from the window containing the programming.

Results

Identical Life Histories

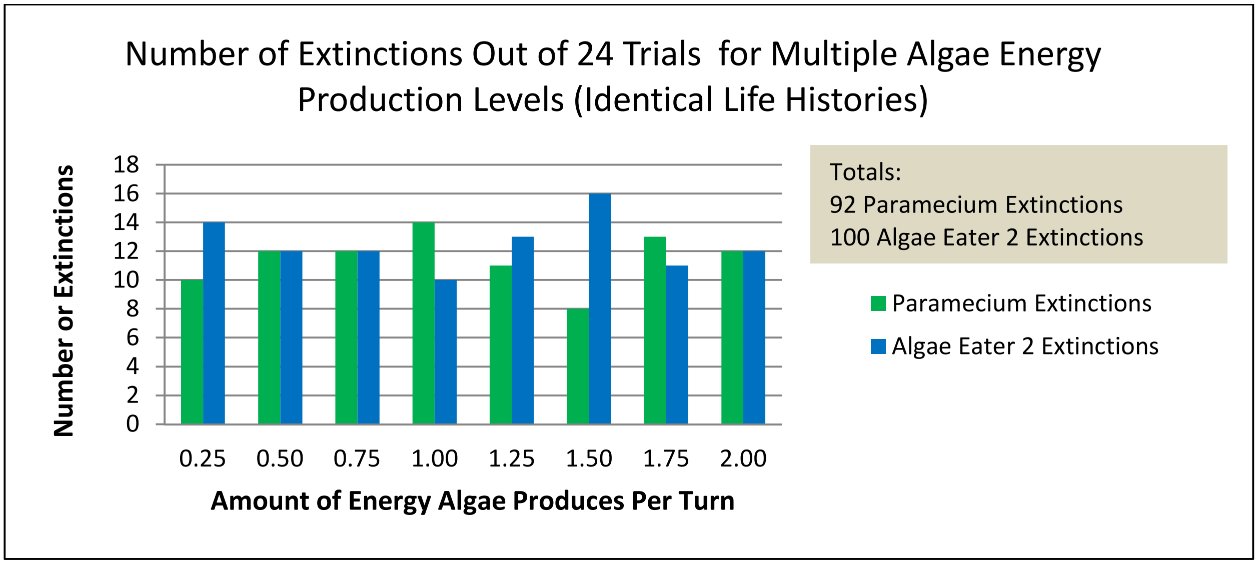


Figure 5: Amount of times each competing species goes extinct at each algae production level

Paramecium and algae eater 2 were programmed to have identical life histories, and thus should both become extinct at an equal probability. To test this, 24 parallel runs were conducted at each energy input level for a total of 192 runs. A Chi-Square Test was performed for each set of simulations. At energy input level of 1.50 where there was the largest disparity between extinctions Chi-Square (1, N=24) = 2.67, $p > 0.05$ but was not significantly different. A Chi-Squared test was also performed with the total simulations for all energy input levels: Chi-Square (1, N=192) = 0.33, $p > 0.05$. From this analysis it can be concluded that the life histories of each competing species are similar enough to equally outcompeting one another. The simulations are further analyzed to look at possible effects that a difference in energy input has throughout the simulation itself rather than just the outcome.

To measure the survivability of a species we measured the amount of time it takes for a primary consumer to become extinct. As the energy input in the system and hence the alga production is increased, the competing species are able to survive for longer periods of time. An independent samples t-test indicates a significant difference between the average time of extinction for energy input of 0.25 (M= 310.46; SD= 153.63) and energy input of 1.25 (M= 1239.25; SD= 962.07); t (46) = 4.67, $p < 0.0001$. This may be due to the fact that the increased energy input is stored in the alga, allowing the consumer, on average, to increase energy gains by feeding on the same amount of algae. This allows a consumer to survive longer without eating and leads to an increases coexistence time (Fig 6).

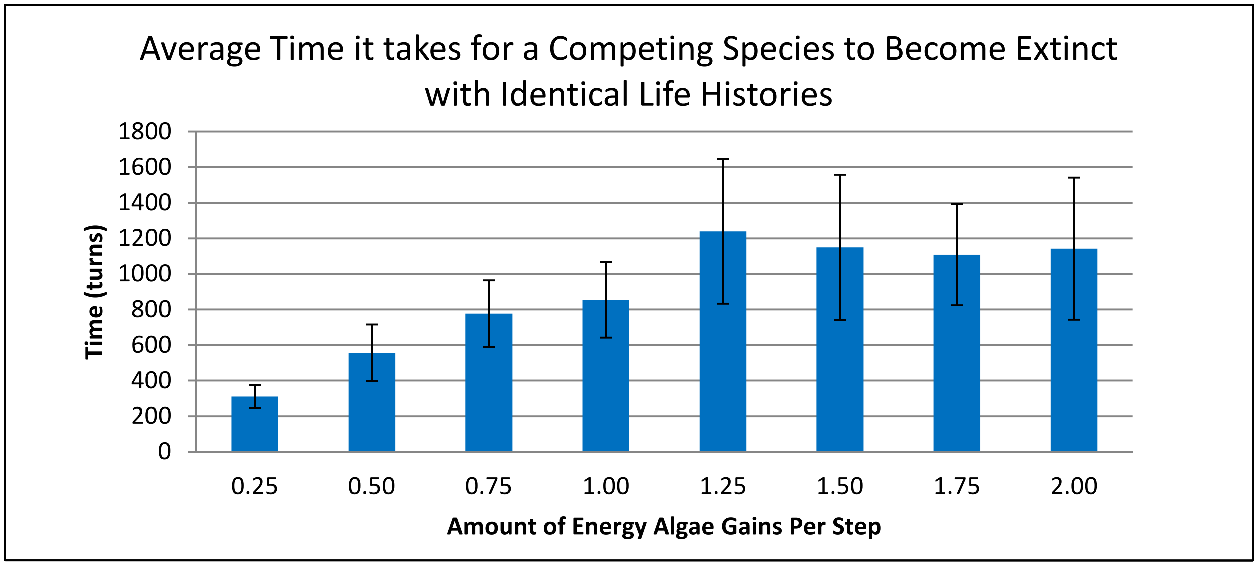
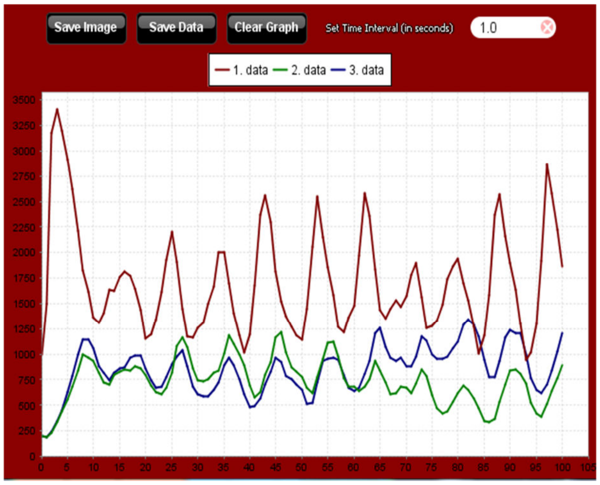


Figure 6: Time it takes for one competing species to become extinct based on the amount of energy available to an alga per turn with standard deviations

The statistically identical competitors vary in extinction time, but the dynamics during the simulation was also studied using the life cycles of all species in the environment to explain this difference.

Figure 7 (Top): Large prey-predator cycles due to a small input of energy to the system (0.25 per step)

Figure 8 (Bottom): Small stable prey-predator cycles due to a large input of energy to the system (2.00 per step)



When energy input levels to an environment are extremely low, population fluctuations are larger and slower because the transfer of energy occurs at a slower rate. Paramecium and algae eater 2 populations near extinction during each populations cycle, leading to an eventual extinction of a single population (Fig 7). Individual population sizes decrease an average of 25 individuals in each life population cycle. On the contrary, when large amounts of energy enter an ecosystem there is more transfer of energy leading to rapid and stable population cycles (Fig 8). There are four population cycles in the low energy system and eleven population cycles per one hundred time steps. Based on the number of life cycles the higher energy input system is more regulated due to the stimulation brought on by the high rate of energy input.

The effect of body size and cruising speed

After analyzing competition when each species functioned with identical life histories, alterations were made to see what affects speed and size had on the competitors. In this series of experiments, we altered size and speed for both paramecium and algae eater 2 (Table 2). The size differences are calculated in surface area to be exactly 25 percent different and indirectly proportional to the distance per turn. Take note that increased speed should be viewed as increased displacement because each agent can only feed at the endpoint of the movement. To stay consistent with the runs performed for the identical life history simulations, 24 runs were also performed at each of the energy input levels.

Table 2: Parameters for simulations with different life histories

Parameters for Competitors and Prey Different Life Histories			
	Algae (prey)	Paramecium	Algae Eater 2
Energy Per Step	Variable (0.25-2.00)	-1.00	-1.00
Collisions	(-)	-1.00	-1.00
Energy Eating	(-)	1.25	1.00
Distance Per Turn	1	1.5	2
Size	1	3	2

When competitors have identical life histories they always coexist longer than competitors with inversely proportional size and speed (Fig 6, 9). However, when the life histories are not identical, the duration that the competing species coexists decreases dramatically at extremely high energy input levels not seen when the species are identical.

The average time it took for a species to die out when the competitors had different life histories was low at both energy extremes and higher at a more moderate level. This high rate of extinction was due to the fact that a high energy input environment favors the large and slow competitor while a low energy input environment favors the small and fast competitor. When the input of energy to the system is low, there are large population cycles (Fig 7) leading to periods of time where the number of competitors and prey are low in density. This favors the faster competitor, who can better find the limited prey, and ultimately drives the larger competitor to extinction. The high energy input environment produces very stable population sizes and the prey source is never limited. The larger competitor has a higher probability of colliding, and thus consuming an alga. Its limited mobility does not play a factor due to the continuously high density of prey in the high energy input environment. This eventually leads to the extinction of the smaller competitor. The time it took for a species to become extinct was so much higher at a moderate level because it was a favorable environment for both species, while the time it took at an energy input extreme was much lower because one species had a major advantage over the other species and was able to take over quicker (Fig 10).

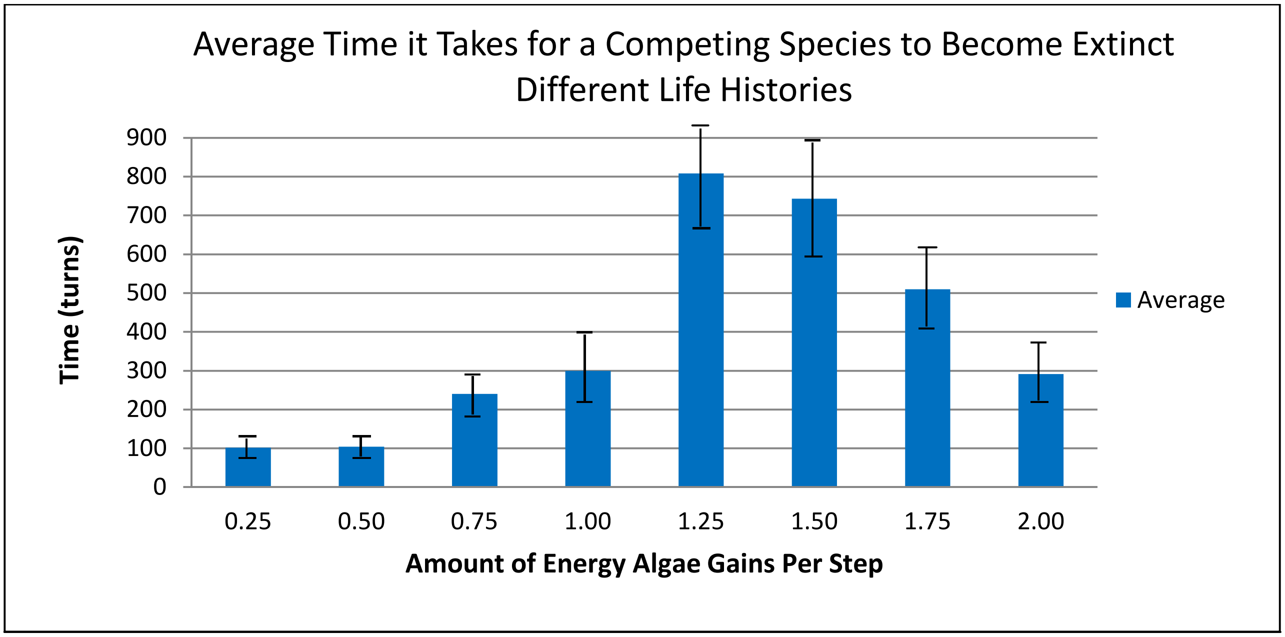


Figure 9: Time it takes for one competing species to become extinct based on the amount of energy an alga produces per turn (different life histories). Standard deviations are calculated at a 95 percent confidence interval.

To study which species had an advantage at each extreme the extinction probabilities of each competing species was analyzed. The algae eater 2, who was smaller and faster, is better suited for a low energy environment (Fig 10). It was demonstrated that when energy input is low the population cycles are very extreme, which lead to periodic low levels of food sources. This is adventitious to a faster species that can better find and exploit these small clusters of algae when the population cycle is at its low point. At high energy environments paramecium, which are larger and slower, have a distinct advantage. This occurs because in this type of environment algae are readily available due to very stable population cycles and a larger species has a greater chance of finding (colliding with) a food source. In this type of environment, there is no need to be fast because the food source is in high density throughout the environment.

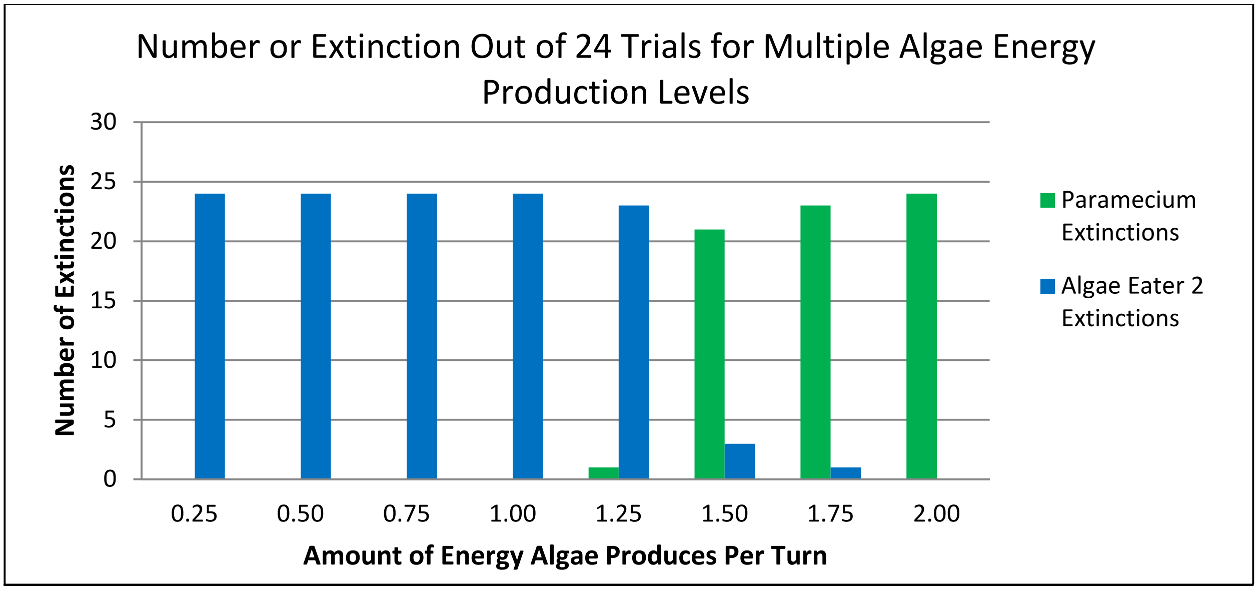


Figure 10: Amount of times each competing species goes extinct at each algae production level. Standard parameters are used except for the speed and size of the competitors. Paramecium had a size of 3 and a speed of 1.5, and the Algae Eater 2 had a size of 2 and a speed of 2.

After testing just one size and speed level among varying energy input levels, varying size and speed combinations are tested at a single energy input level. An energy input level of 1.0 is chosen, and the size and speed of the paramecium are initially set at the standard size of 2. The size and speed of the algae eater 2 is set up at 10% intervals in surface area ranging from -50% to +50% of the paramecium's size. The speed of the algae eater 2 is also set to be proportional to its surface area (Fig 11). This is not indicative of what is normal in nature, but is vital for establishing a baseline. This baseline data is compared to the data gathered when the two parameters are set indirectly proportional to one another in order to see whether speed or size plays a larger role in the survivorship of the population.

When the size and speed of the algae eater 2 are both 10% larger than the paramecium, they survive every time. When the parameters are set at 10% smaller than the paramecium, they become extinct each time (Fig 11). The combination of a larger surface area and a faster speed contribute to a better life history resulting in the survival of the population.

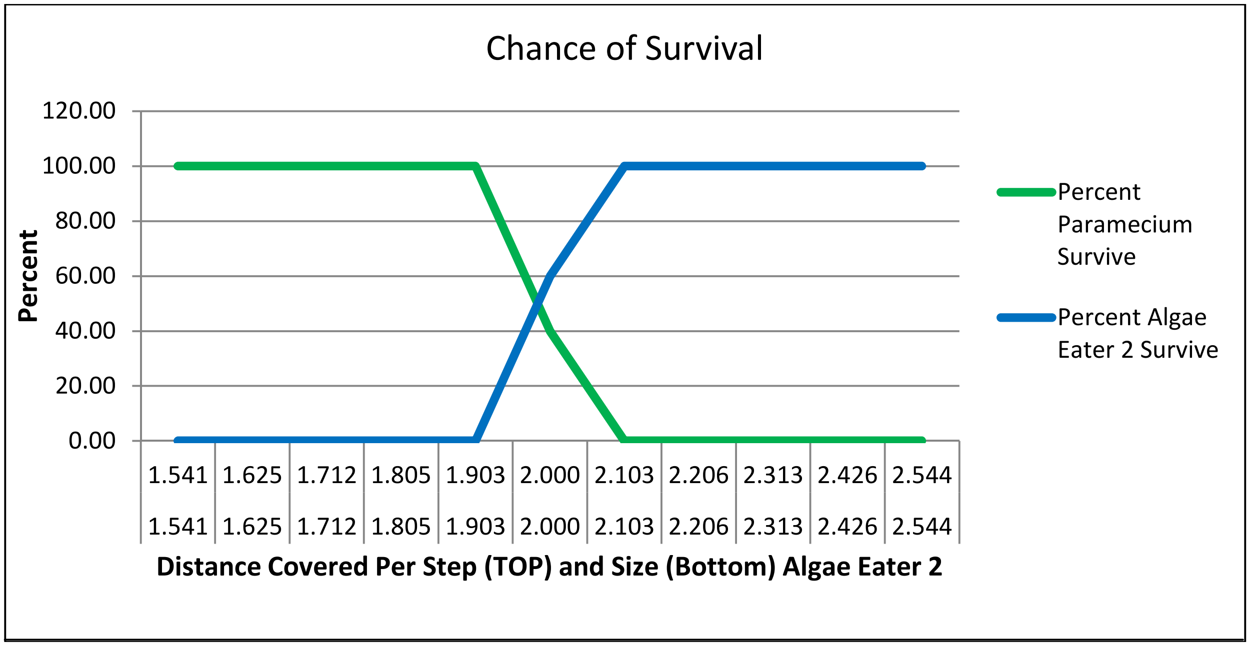


Figure 11: Percent survival of competing species whose speed and surface area are directly proportional

The two parameters altered in the algae eater 2 are now altered indirectly proportional to one another to see which parameter has a larger effect on the ability to survive. The size is more determinant than speed in survival chances (Fig 12). When the size is increased by 10% and the speed decreased by 10% the chance of survival is 65% compared to the 100% chance of survival when both the size and speed were increased by 10%. Due to the fact that this number is not 100%, speed does have some effect on survival, but because the percent is larger than 50% size is a more effective factor in increasing survivorship. When the size is further increased to 40% and speed decreased by 40% the chance of survival is 100%. The decrease in speed has the same effect as if the speed were the same as the competing species when the size is 40%, larger and does not have an effect on the populations' survival chances.

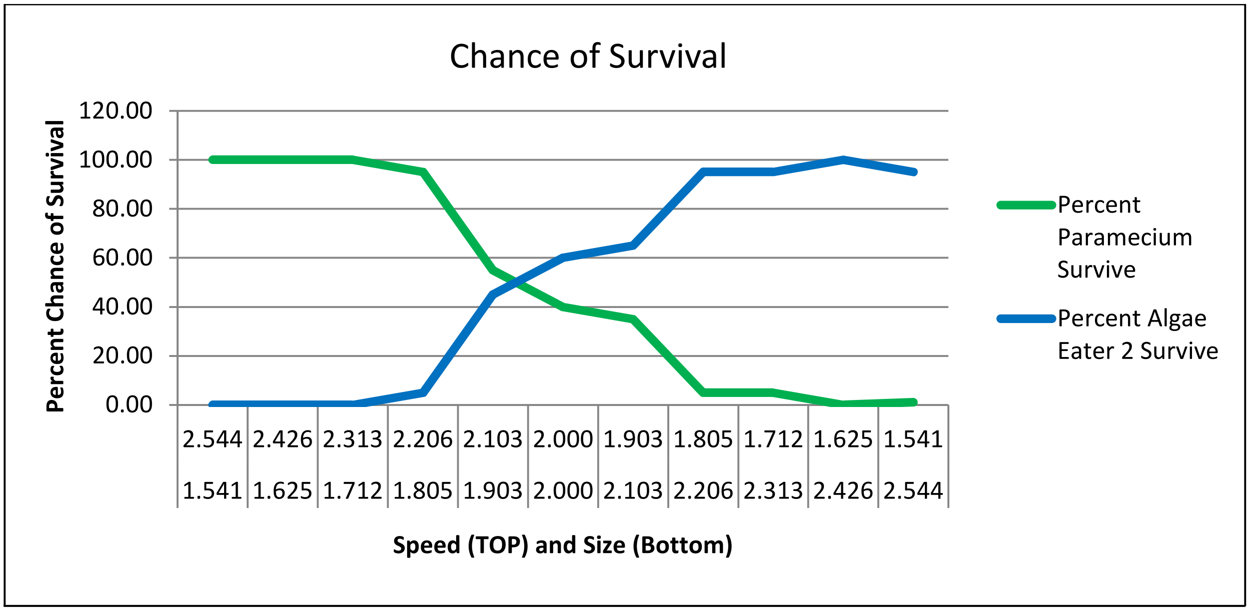


Figure 12: Percent survival of competing species whose speed and surface area are directly proportional

Changing surface area and energy for movement

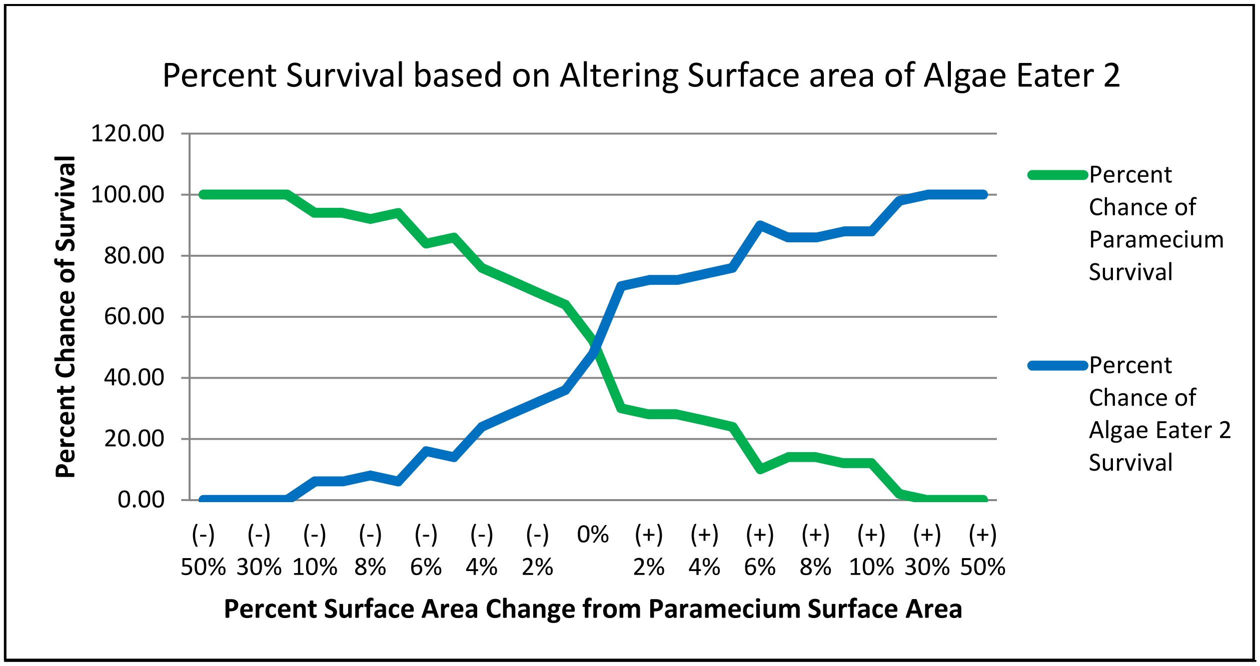


Figure 13: Chance of survival when the surface area of Algae Eater 2 is altered from the surface area of the Paramecium

Now that it has been established that size (surface area) alterations have a much larger effect than does speed on the ability to survive, size differences are studied alone. It is logical that the competing species with a larger surface area will drive its competing species to extinction more than half of the time. However, it is necessary to establish a baseline before changing a new variable (speed used above) to account for the increase in surface area. The paramecium size was set at 2 throughout the experiments and the size of the algae eater 2 was set at intervals ranging from -50% to +50% (Fig 13). The algae eater 2 outlived the paramecium more than 50% of the time when it was larger (+10% or more), and less than 50% when it was smaller (-10% or more). When the algae eater 2 was 20% larger, it always outcompeted the paramecium, and when it was 20% smaller it was always outcompeted by the paramecium. In addition to analyzing extinction probabilities, simulations dynamics were also studied.

A more specific range of surface area differences in competing species is studied to show how increases in surface area favor the larger species, but has a different effect in population dynamics (Fig 14). As the surface area difference between the two species increases, so does the time it takes for extinction to occur. An independent samples t-test indicates a significant difference between the average time of extinction between when algae eater 2 is 3% smaller than the paramecium (M= 180.72; SD= 122.37) and when algae eater 2 is 9% smaller than the paramecium (Mean= 120.48; Std. Dev. = 82.89); t = 2.88, N= 20), $p < 0.005$. When one species is 3% larger, it takes 60.24 time steps longer for a species to become extinct than if it were 9% larger, because at a surface area difference of 3% competing species have more similar life histories increasing competition.

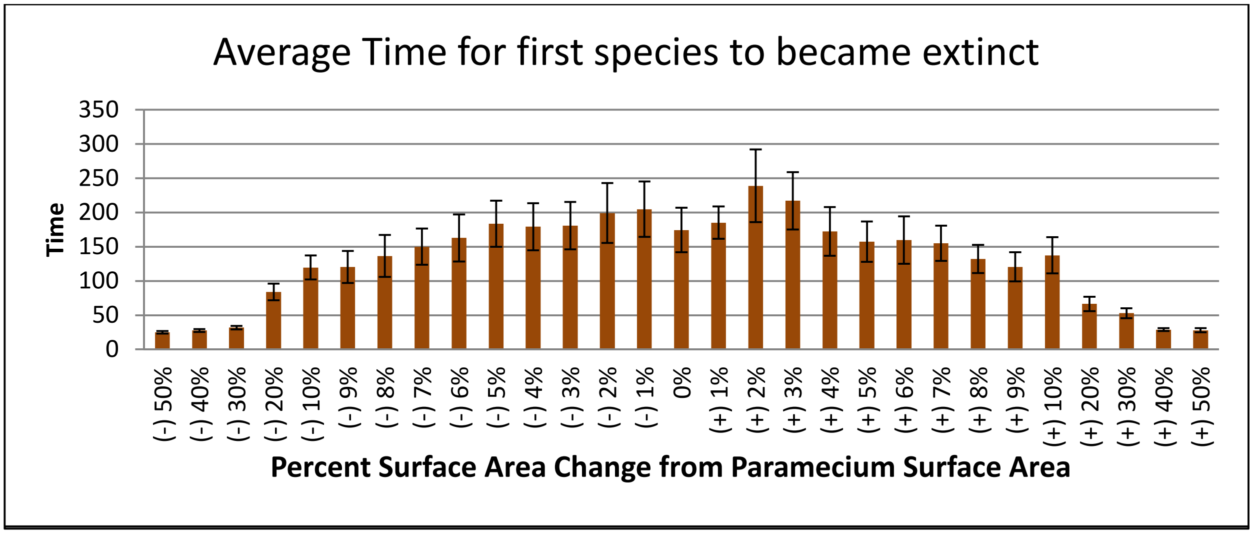


Figure 14: Time (steps) it takes for one species to become extinct at altered Algae Eater 2 surface areas. Standard deviations are calculated at a 95 percent confidence interval.

To compensate for a disadvantageous decrease in surface area, a decrease in energy cost is programmed. The decrease in energy loss comes from the smaller amount of energy needed to sustain a smaller body. Surface area decreases in paramecium were set at 5%, 10%, 20%, and 30% in both surface area and energy loss. Two different aspects of the simulations were studied. First, the time it took for one species to become extinct at various surface area and energy cost levels (Table 3), and second, the extinction percentage of paramecium for each level (Table 4).

Table 3: Average extinction times for changes in surface area and energy loss parameters

Time To Extinction		Surface Area Decrease (Paramecium)			
		5%	**10%**	**20%**	**30%**
Energy Loss Decrease Per Turn (Paramecium)	**5%**	178.60	232.00	99.20	36.00
	10%	107.60	120.20	233.40	44.00
	20%	47.00	51.40	77.80	92.00
	30%	30.40	29.20	286.88	321.60

Table 4: Average Paramecium survival probabilities for changes in surface area and energy loss

Percent of Time Paramecium Surviving (10 Runs)		Surface Area Decrease (Paramecium)			
		5%	**10%**	**20%**	**30%**
Percent Less Energy Loss Per Turn (Paramecium)	**5%**	90%	80%	10%	0%
	10%	100%	100%	40%	0%
	20%	100%	100%	100%	0%
	30%	100%	100%	100%	90%

When the paramecium surface area decrease is less than or equal to that of the decrease in energy loss, with the exception of 30% decrease in surface area, the paramecium will survive 100% of the time (orange) (Fig 15). On the contrary, when the surface area decrease is more than that of the decrease in energy loss, the paramecium will always go extinct (blue). The green portion of the graph indicates where competition between species was the most even. The competition leads to approximately equal rates of extinction. At these levels coexistence is not feasible for longer than about 200 time steps because they are competing for the exact same resources in the exact same environment.

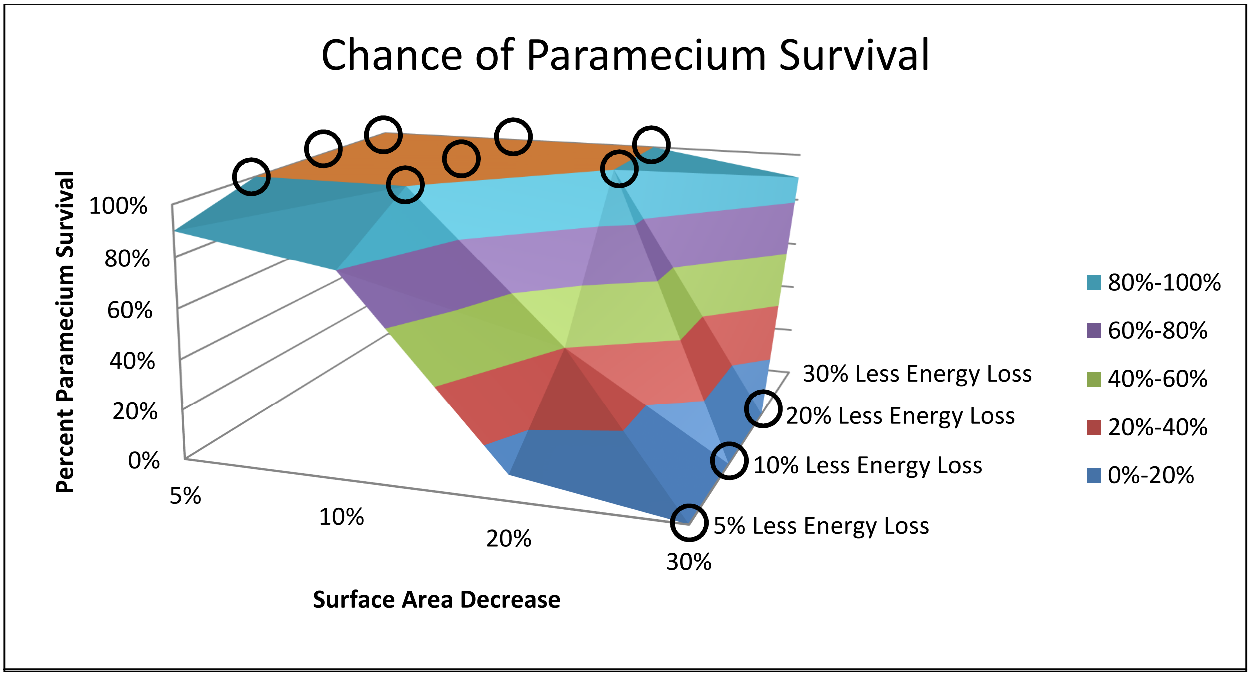


Figure 15: Visual representation of survival probabilities

Addition of Predator to the competitive system

In an attempt to study ways in which coexistence between competing species can be prolonged a predator was added. We hypothesized that this will increase the stability of the system. The addition of a trophic level in nature creates a negative feedback loop. If the population of one species increases, the non-biased predator will consume a larger number of that species because they are more readily available. This, in essence, helps keep one species from out-competing the other through natural positive feedback. The independent variable is the amount of energy that a predator loses per step.

Twenty runs were conducted at each energy level. At each energy level the competing species are statistically becoming extinct at equal probability (fig 16). An interesting aspect of this experiment is the probability at which the predator becomes extinct. The predators are most effective with an energy level of -4.0 per turn. It may be logical to think that they would survive best when they lose the least amount of energy (-1.0). However, at this level the predator is too good of a hunter and overexploits its prey. This leads, in 80% of the simulations, to the extinction of both competitors resulting in the eventual extinction of the predator. At higher levels of energy loss, the predators are not able to find food fast enough to fulfill their energy needs resulting in extinction. These predators, under the parameters of the program, survive best at an energy level loss of 4.0 (Fig 16).

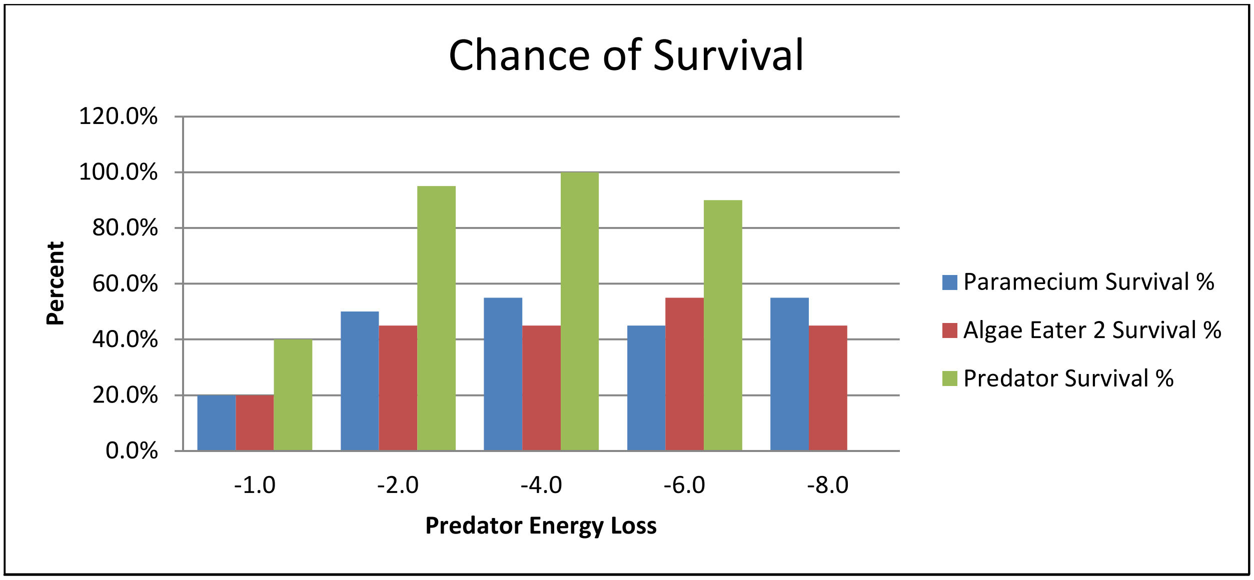


Figure 16: The chance of survival for each species throughout a 1000 time step simulation

To further study the effectiveness of the predators, a count of all predator births were followed during each 1000 time step simulation. The average number of predator births at energy level of -6.0 is more than double that of the next highest energy level (Fig 17). At this energy level, the predators seem to thrive the best, however 10% of the time the energy loss it too great to overcome and they become extinct. 90% of the time predators survive at the energy level -6.0, and are the most successful hunters, but the hunters at energy level -4.0 are more consistent long-term hunters that always survive.

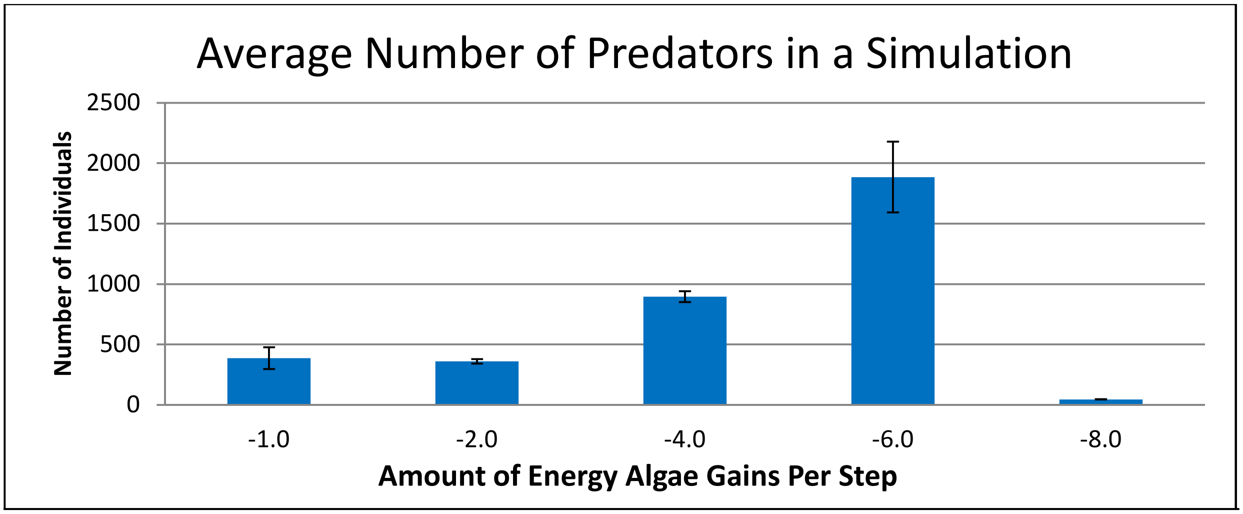


Figure 17: Number of predators throughout a simulation of 1000 time steps at each energy loss level. Standard deviations are calculated at a 95 percent confidence interval.

The addition of a predator as a way to increase the amount of time the competing species can coexist had the opposite effect. For a small period of time the predator was able to act as a negative feedback agent for a population that outnumbers its competition, but shortly thereafter the predator hunts a prey population to extinction. The average amount of time it took for one species to become extinct in the presence of a predator with energy level of -6.0 per turn was 269.77. The average extinction time for competing species with identical life histories lacking the presence of a predator was 854.67.

Stratifying the two species with identical life histories

Another method in which competing species tend to coexist is by occupying separate niches. In this experiment we kept the presence of the predator and added an elevation preference as the only source of life history difference between the competing alga consuming species. Three levels of preference were used in the experiment. The most extreme stratification has the paramecium preferring moving an average of 1.5 steps up per turn, and the algae eater 2 moving an average of 1.5 steps down per turn. The other two levels used are at 0.5 and 1.0 steps in each competitor's respective direction. Each competing species still has a chance to move in the opposite direction, because movement is generated through a number generator, but lower percentages which produces a natural overlapping of niches. Twenty runs were conducted at each of the three levels of stratification: extreme (1.5), moderate (1.0), and slight (0.5). The predator energy loss was set at -4.0 throughout the experiment because the pervious experiment determined that at this energy level the predator is effective and stable over long periods of time.

Table 5: Level of stratification for both competitors and average time of extinction of one competing species

Stratification Level	Average Number of steps in Respective Direction	Average Time to First Extinction
(Extreme)	1.5 steps	548.57
(Moderate)	1.0 steps	3075.89
(Slight)	0.5 steps	934.68
(Neutral)	0.0 steps	211.60

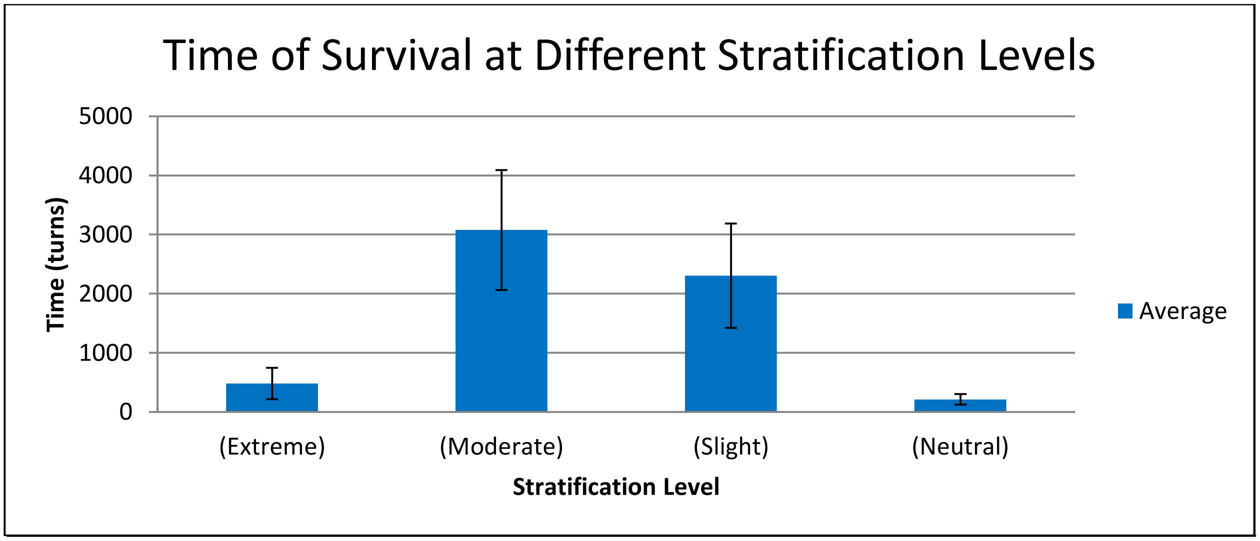


Figure 18: Time it takes for one competing species to become extinct at different levels of stratification. Standard deviations are calculated at a 95 percent confidence interval.

The two competing species were able to coexist at all three stratified conditions longer than they were able to when there was no stratification (Fig 18). At extreme stratification levels survivorship was more than double as long as no stratification was present. At extreme stratification levels, the paramecium were confined to the surface of the environment, and the algae eater 2 was confined to the bottom of the environment (Fig 19). This allowed for very little utilization of the middle levels of the environment leading to an extreme decrease in consumption of alga in these areas. Competing species were very high in concentration because they were confined to such niche altitudes, which lead to death due to a lack of consumption. At slight levels of stratification the competing species coexisted on average longer than when the level of stratification was extreme. The competing species were able to utilize the entire environment, but were too alike in

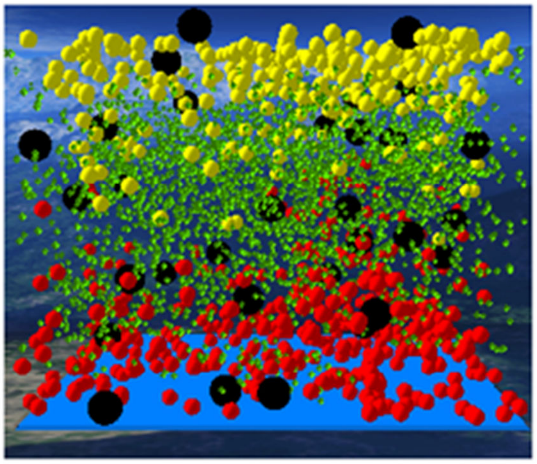


Figure 19: visual representation of competing species with extreme stratification (average 1.5 steps per turn in their respective direction)

life histories to have the ability to truly coexist. A more moderate level of stratification was implemented to find a medium between the extreme and slight stratification.

At moderate levels of stratification, there was an extreme increase in coexistence. The average time two competing species could coexist was 3075.89 time steps, which was slightly more than the slight stratification level which was 2304.3 time steps (Fig 18). At the moderate levels of stratification, the competing species' environments are different enough to prevent one from driving the other to extinction, and have enough overlap to prevent their prey from not being properly utilized.

Discussion

Our model was able to demonstrate the principle of competitive exclusion in a variety of energy input environments. As long as the life histories of the two competing species, regardless of environmental parameters, are identical, extinction of one species always occurs. The number of times one competing species becomes extinct is equal to the number of times the other species becomes extinct at each energy input level. When looking exclusively at the extinction rates of paramecium and algae eater 2 at various energy input levels, there appears to be no difference at each energy input level. When the average time it takes for a competing species to become extinct was calculated, differences between energy input levels become evident (Fig 6). The amount of time it took for a species to become extinct increased as the energy input to the system increased until the energy input level reached 1.25 where the extinction times leveled off. The reason for small coexistence times in low energy input levels was explained looking at the population cycles of each species (Fig 7 and 8). Population cycles were more extreme in low energy input levels, which increased the likelihood of extinction at the low point of the population cycle. The stabilizing effect of a high energy input environment decreased the likelihood of extinction among the competing species leading to higher periods of coexistence.

It is evident that the system dynamics in simulations of varying energy input were much different. We wanted to change the competitor's life histories to see which parameters were more advantageous at the varying energy input levels. We found the smaller and faster species thrive better in a low energy environment because these individuals can more easily find food when the food source densities were small. In a high energy environment, we found that larger and slower species thrived better because these individuals had a larger chance of colliding with an alga and did not need to actively seek alga because the prey population density was relatively high and stable. At intermediate energy environments, the competing species were able to coexist longer because they both had different variables that were advantageous at these energy level environments (Fig 9).

We were interested in determining which parameter played a larger role in survivorship, speed or size. To do this we set the paramecium size and speed at 2 and inversely altered the size and speed of the algae eater 2 by 10%. When the size of the algae eater 2 was 20% larger and 20% slower than the paramecium, the algae eater 2 out-competed the paramecium (Fig 12). When the size of the algae was 20% smaller and 20% faster than the paramecium, the algae eater 2 was not able to out-compete the paramecium even though it was 20% faster. This indicates that the size of a competing species has more of an effect on survivorship than does speed.

We then decided to alter the size of one competing species, leaving all other parameters identical, to study the time of coexistence between the two species. The coexistence times of the competing species were higher when the size of the competing species is more similar (Fig. 14). This provides more evidence that the level of competition increases when the two competing species have more similar life histories. It is obvious that if the only difference between competing species is size, the larger species will out-compete the smaller species. To compensate for a decrease in size, a decrease in energy consumption was added. It was determined that an identical percent change in both the decrease in size and energy consumption neutralize each other making it identical in survivorship to a species that was not altered at all.

Each of the experiments performed regardless of the parameters resulted in the relatively rapid extinction of one competing species. The addition of a third trophic level in an attempt to increase coexistence using negative feedback. The competing species with the largest population is hunted at a higher rate until population sizes stabilize (Friman et al., 2008). Hunting the more readily available prey is in many instances instinctual because the survivorship of a consumer increases if they choose the resource “prey” that is either more widely distributed, of higher quality, or in higher abundance (Schmitz, 1995). A predator’s main goal is to minimize energy loss and maximize energy gains.

The predator was programmed to lose a certain amount of energy per step, which represented the effectiveness of the predator. The less energy a predator lost the more effective it was as a hunter. When the predator was very ineffective at hunting, it could not sustain itself and quickly became extinct which prevented the two competing species from having the benefit of the negative feedback system. When the predator was too effective at hunting, it overexploited its resources and drove one of the species to extinction (Fig 17). Average hunters did, however, show some short term stabilizing effects due to the natural negative feedback survivorship mechanism but did not result in an increase in coexistence time. The coexistence time in the presence of a predator was lower than that coexistence time in the absence of a predator.

Utilizing geographical changes in life histories in the form of stratification was successfully used to increase coexistence of two competing species. Stratification has been previously shown to allow very similar organisms to live in similar geographical locations without a level of competition that leads to extinction. Rhodomonas minuta and Rhodomonas lens are two closely related planktonic flagellate species that have slowly changed physiologically to thrive at increasingly differing depths (Sommer, 1982). This allows each species to fill a specific habitat niche and prosper without the threat of competition from the other species. Different degrees of stratification were used in these experiments. It was observed that extreme stratification isolated one species at the surface, and the other at the bottom of the environment preventing them from the exploiting their prey in a large portion in the middle section of the environment, driving them to extinction due to starvation. Slight levels of stratification act too much like simulations where there was no stratification leading to similar coexistence times. Moderate levels of stratification, however, provided a good mixture of the two extremes. The competing species were not isolated to the point where they were not utilizing all of the available prey, but stratified enough in their geographical niches that they could successfully coexist for extended periods of time, and in some cases, indefinitely.

Future Direction

The programmed modeling system used to study competition between competing species was complex enough to study the general concepts of competition. There is much more that can be studied with the current complexity of the program, but there are also some vital possible additions that would allow us to draw more complex results based on a more realistic environment in the future.

The first and most important addition to the program is to vary the amount of photosynthesis that takes place at different depths in the environment. Light intensity decreases with water depth and plays a major role in the amount of photosynthesis the algae can perform. The more sunlight that an alga is exposed to, the more photosynthesis it can carry out.

There are two possible ways to incorporate this decrease of photosynthesis at increased depths to the environment in an agent based approach. One way is to create a new "invisible" agent that represents light. The agents of this species will start at the surface of the environment, and fall at a consistent rate while losing energy as they do. When algae collide with the "invisible" agents, they will increase their own energy by the energy level of that specific "invisible" agent. This energy increase represents the amount of photosynthesis performed by the algae. A second way to incorporate variable photosynthesis is to simply decrease the amount of energy an algae gains depending on its current depth. To do this, the depth of each alga will be identified after each turn, and a programmed increase in energy will be added to each algae. The current model is most similar to this second method because it uniformly increases the algae energy in every turn, but does so independently of depth.

A possible downfall in creating a new virtual species is that an algae near the surface may not always collide with an "invisible" agent and, thus, not perform photosynthesis while another algae that at the same depth may collide and perform photosynthesis. Light intensity is uniform at a certain depth, so two algae at the same depth should perform equal amounts of photosynthesis. A benefit to this method, however, is that programming the energy decrease as the agent falls would be very specific: decrease energy by X amount each time the "invisible" agent moves. The programming for energy increase of algae using the second method would have to categorize the depth of each alga into zones. For example, if an alga is between a depth of 10 and 15, the algae increase their energy by X amount. This prevents the second method from being quite as specific as the first method, but this method assures that each algae does perform some degree of photosynthesis in each turn.

Whether the first or second method of photosynthetic stratification is used, the program should also take into consideration changes that occur within a twenty-four hour day. Photosynthesis does not occur at all during the night and even throughout the day the intensity of sunlight changes.

The addition of differences in photosynthesis at varying depths and varying times throughout the day helps make the model both more realistic and more valuable to scientists that who may use the model to study aquatic environments. Pollution is one of the main contributors to a loss of aquatic biodiversity (Moyle, 1992). Many types of pollution alter water clarity and thus alter the amount of photosynthesis that primary producers can perform. Scientists studying the effects varying levels of water clarity caused by pollution can easily study how an entire ecosystem changes by simply altering the rate of dynamic photosynthesis.

The value of this model is that many alterations and additions can be made to specifically recreate the parameters of the real-life situation being studied. Beyond the immediate needed changes to allow for dynamic photosynthesis, the future direction of the model lies in the problems it is used to solve.

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