**1.018/7.30J Ecology 1: The Earth System**
**Problem Set 3, Fall 2009**
**Assigned: Ses #16 Due: Ses #20** at the beginning of class.
Please turn in your assignments (hard copy) to the TAs.
You may work individually or in groups of up to three.

1. (8 points) On your first day as a UROP in the Chisholm Lab, you want to impress your new boss by setting up an experiment that combines two of her favorite things: chemostats and *Prochlorococcus*. You decide to make a phosphorous-limited system.

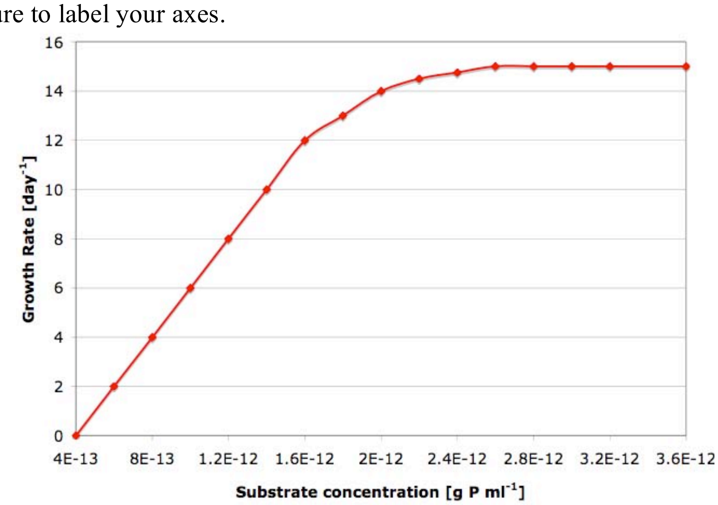
a. You find some standard media that is designed to obtain maximum growth rates. What would you expect the Redfield Ratio of this media to be? Is this acceptable for your experiment? Why or why not?
Generally, ecosystems require N and P at a ratio of 16:1, so you would expect maximum growth rates at N:P = 16:1. This is not acceptable for your experiment because a phosphorous-limited system is desired, so you would need to increase the N:P ratio of the media, i.e. N:P = 16:0.001.

b. You put $10^8$ *Prochlorococcus* cells into your culture vessel, turn on the chemostat, and allow it to reach steady state. The volume of your chemostat is 1000 ml, the flow rate is 500 ml $day^{-1}$, and you know $r_{max}$ for *Prochlorococcus* is 15 $day^{-1}$. What is the growth rate of *Prochlorococcus*? Why?
The growth rate must be equal to the dilution rate at steady state.
$D = f/V = 500 \text{ ml day}^{-1}/1000 \text{ ml} = 0.5 \text{ day}^{-1}$

c. What is the doubling time of this population?
Assume exponential growth.
Doubling time = $\ln(2)/r = \ln(2)/0.5 \text{ day}^{-1} = 1.39$ days

d. The average *Prochlorococcus* cell contains $10^{-15}$ g P $cell^{-1}$. You have set up your fresh culture media (the influent to your chemostat) so it has a concentration of $10^{-12}$ g P $ml^{-1}$. Approximate the cell concentration in the culture vessel at steady state.
Assume S = 0 because $S_i >> S$. Therefore, $N \sim S_i/Q = 10^{-12} \text{ g P ml}^{-1}/10^{-15} \text{ g P cell}^{-1} = 10^3 \text{ cell ml}^{-1}$

e. Sketch the relationship between the concentration of P in the culture vessel and growth rate at different steady states. Be sure to label your axes.



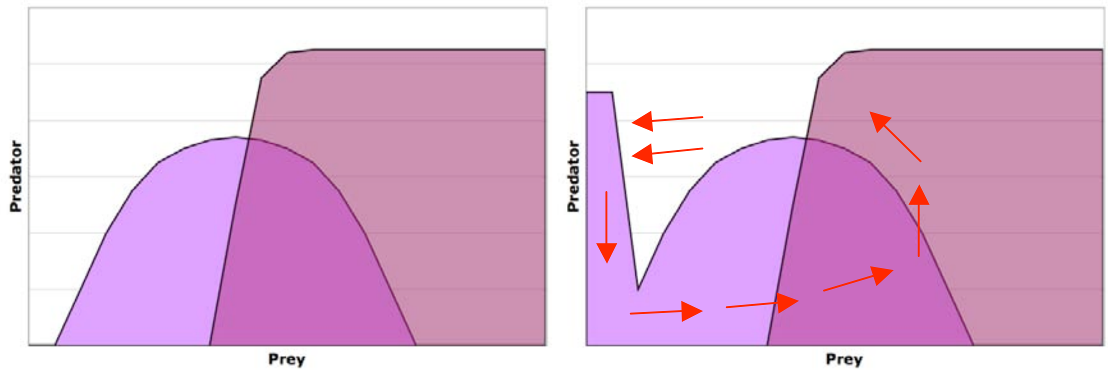

2. (6 points) On Prof. DeLong's recent trip to the Galapagos Islands he took some time to study the predation habits of carnivorous land iguanas. He noticed that the iguanas on Isabela Island eat a wide variety of food, while on Hood Island they eat just one or two kinds of prey.

a. Explain why these differences in diet selection exist using the concepts presented in your lecture notes and textbook. Describe the conditions under which you would expect to find an iguana eating many or few kinds of prey.

According to optimal foraging theory, the profitability of prey is the energy value per handling time ($T_h$). When $T_h$ is much greater than search time, $T_s$, each prey must have a high energy value to make the investment of handling time worthwhile, so iguanas should be specialists. When $T_s$ is much greater than $T_h$, then even though the prey energy value may be low, consuming prey is profitable. Under these conditions a predator should be a generalist.

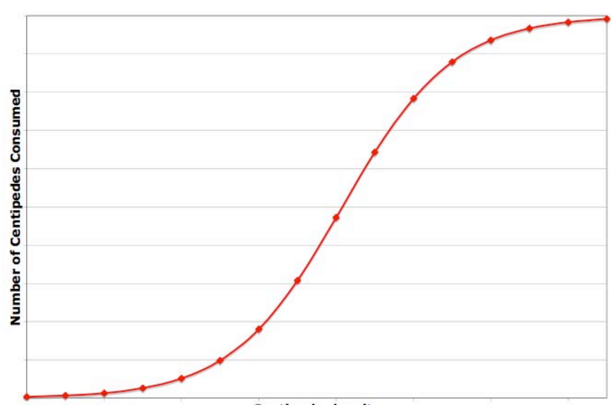
Differences in diet selection could also result from interspecific competition. If on Isabella Island iguanas are able to realize their entire fundamental niche, they will be able to eat a wide variety of food. If competition for food is high on Hood Island, iguanas will have a much smaller realized niche and only be able to successfully acquire a small range of prey species.

b. On Hood Island, he observed that the iguanas are very efficient at eating centipedes. However, the centipedes do not go extinct because they can maintain a small population in tiny holes that the iguanas can't enter. Which of the following graphs represents this situation? Explain your selection and sketch the outcome on the figure.




The graph on the right represents the case of prey refuges, where a portion of the prey population is able to escape predation, even at high predator densities. The intersection of the predator isocline at the peak of the prey isocline suggests a relatively efficient predator. As a result, both populations tend to oscillate in a stable manner.

c. On closer investigation, Prof. DeLong discovered that when the centipede population density is low, iguanas on this island eat almost exclusively beetles, while at moderate to high centipede population densities, the iguanas eat almost exclusively centipedes. Draw the predation response to centipede density. Be sure to label your axes. Identify and explain this type of functional response.




This is a Type III functional response. The attack rate is very low at low prey densities, and then increases as prey increases. At high prey densities, handling time limits predation. In this case, the predator exhibits prey switching.

2. (6 points) Briefly define and give an example of the following:

a. Character Displacement
A gradual evolutionary separation of two species in morphology or physiology as an outcome of competition for a resource. An example is Darwin's finches. Competition has selected for different beak sizes in birds coexisting in the same area, a form of niche differentiation.

b. Niche Overlap
Two or more species using a portion of the same resource, such as food. The amount of niche overlap is assumed to be proportional to the degree of competition for that resource. When fundamental niches overlap, some niche space is shared and some is exclusive, enabling the two species to coexist. Large niche overlap does not necessarily mean high competition. Competition occurs because of a shortage of resources. If there are abundant resources, then there may be extensive niche overlap between two species with little competition. An example is the coexistence of the grasshopper sparrow and the savannah sparrow. The grasshopper sparrow and the savannah sparrow have overlap in territory size and vegetation cover.

c. Competitive Exclusion Principle
Two competing species with identical ecological requirements cannot occupy the same area. If two competing species coexist in a stable environment, they do so as a result of differentiation of their realized niche. An example is Pyke's bumblebees, where bees that rely on the same size flower for food show negative correlations in abundance.

3. (5 points) Read the Byers 2000 paper, "Competition Between Two Estuarine Snails: Implications for Invasions of Exotic Species".

a. Identify and explain the type of competition described in this paper.
Exploitative competition occurs when one competitor has the superior capability to gather resources, as opposed to directly interfering with the other organism. The paper explains that exploitative competition has two main components, the consumer's per capita consumption rate ($\alpha$) and its conversion efficiency ($\varepsilon$). Usually these two components are combined into one equation that is density dependent, but in this paper they examine how each component differs between the two snail species.

b. Write the Lotka-Volterra competition equation for *Cerithidea californica* in general terms.

$$\frac{dN_{C.californica}}{dt} = r_{C.californica} N_{C.californica} \left( \frac{K_{C.californica} - N_{C.californica} - \alpha N_{B.attramentaria}}{K_{C.californica}} \right)$$

c. What is the invasion criteria described in the Byers paper? Define each variable. Explain which variable is the focus of this paper and why.
$m_1/\alpha_1\varepsilon_1 > m_2/\alpha_2\varepsilon_2$

Species two will win if it has a lower death rate ($m_2$), a higher conversion efficiency ($\varepsilon_2$), or a higher per capita consumption rate ($\alpha_2$). This paper examines the conversion efficiency because even though both snails had the same impact on food resources, the introduced/invasive species in this experiment was much better at converting resources, thus surviving and dominating over the native species.

4. (9 points) Read the opinion piece by Olivia Judson entitled "Humpty Dumpty and the Ghosts". Write an opinion (~400 words) about how the concepts that you have learned in class relate and contribute to the existence of Humpty Dumpty communities and Ghosts. Use specific examples from your readings and lecture notes to support your arguments. If you use any outside sources, please cite them.
A few examples of concepts in class that could be related to the Judson article are described below:

**Humpty Dumpty Communities**

Keystone Species, Predator-Prey Models – Keystone species have a large influence on the structure and stability of an ecosystem. If these species are eliminated, the ecosystem is fundamentally changed and "broken" without any possibility for repair. Usually the keystone species is a predator. Once removed, the organisms that it suppresses through predation explode in population and outcompete other species. An example of this is in California kelp forests, where sea otters are crucial to keeping sea urchins in check. When the sea otter population is reduced (by hunting, habitat degradation, etc.), urchins multiply and consume the kelp forest. This removes habitat for organisms that live in the kelp forest and thus the ecosystem turns into an urchin barren. If one were to reintroduce kelp, urchins would consume it immediately. If you try to reintroduce sea otters, they have no habitat (they also live in the kelp).

Fundamental vs. Realized Niches – When one species is removed from an ecosystem, other species on the same trophic level (that they compete with) may expand their realized niches. These species now have the potential to evolve with the ecosystem and completely occupy/expand their fundamental niche, making it hard for the old species to move back in. This could potentially occur if one species of Darwin's finch were removed from the Galapagos or a particular species was overfished.

**Ghosts**

Invasive Species – When a new species is introduced to a system, it may push another species to extinction; however, the introduced species may go extinct shortly afterward. In the Byers paper there is a parasite that leaves the invasive species of snails, *B. attramentaria,* essentially castrated and unable to reproduce. If this parasite were to wipe out *B. attramentaria* after it outcompetes the native population, the ecosystem is fundamentally changed with neither snail present. Examples of exotic species introduced to systems in lecture tended to show that the invasive species became established and altered the system without becoming ghosts, which supports the Judson's assertion that ghosts are relatively rare.

Nutrient Loading – Adding unnatural amounts of phosphate, nitrogen, or other nutrient (such as iron) can create abnormally large populations of organisms (e.g. phytoplankton, zooplankton, etc.). However, nutrient loading may be cyclic or short-lived, such that the large populations created by the loading disappear, even though their presence may have significantly altered the food web through competition with other organisms and utilization of nutrients.

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