PART II: POPULATION GROWTH FOR TWO OR MORE SPECIES -COMPETITION

In the previous section, we didn't explicitly include the effects of other species on the population we were modeling. The effects of other species were indirectly accounted for in constants such as K or carrying capacity. We will explore species interactions by focusing on two species that are either competing or acting as predator and prey. Obviously the environment is frequently more complex than two species competing for resources or eating each other, but let's start simple. We'll get to multispecies interactions at the end of this exercise.

Competition occurs when two species *negatively* affect each other by decreasing each other's population growth rates or population numbers. This is a very broad definition that encompasses many different kinds of competition. In this exercise, two species will compete for the same resource, which is an example of **exploitation competition** (populations negatively effect each other through consumption of a shared resource)

Competition can occur within species or between species. **Intraspecific competition** is competition between individuals of the *same species* ("intra" means within) and **interspecific competition** is competition between individuals of *different* species ("inter" means between). We've already looked at a model dealing with intraspecific competition: the Logistic model from the previous section (the per capita population growth rate decreases with increasing population size – competition between individuals of the same population for some limiting resource).

What happens when two organisms need and have access to the same limited resource, such as nutrients? There are several possible outcomes:

1) Both will survive and divide up the nutrients (**coexistence**)

2) One will survive and drive the other away or drive the other to extinction (**competitive exclusion**)

3) Both will use up all the nutrients and go extinct.

The principle of **competitive exclusion** is summed up as: "complete competitors cannot coexist" (Hardin 1960). In order for species to **coexist**, they must use resources differently.

Can we predict the outcomes of competitive interactions? Further, can we predict the outcome when the limiting resource changes? This competition exercise will consist of two parts – first, we'll look at the Lotka-Volterra Competition model by looking at the effect of changing parameter values on the outcome of competition; second, we'll look at a case study from Riegman et al. 1992 in which the algal species we worked with in the previous section (*Phaeocystis* spp.) compete with other phytoplankton species for resources.

Section 1: Lotka-Volterra Competition Model and its predictions

LOTKA-VOLTERRA COMPETITION MODEL:

Competition can be examined mathematically as an extension of the logistic growth with the Lotka-Volterra Competition model. This model assumes that competing organisms will grow logistically but the growth of one organism will adversely affect growth of the other because both species require the same resource.

First let's imagine two species, Species 1 (N_1) and Species 2 (N_2) growing logistically independently (not affecting each other) – this model only includes intraspecific competition:

$$Species\ 1\text{:}\ \frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1}\right)$$

$$Species\ 2\text{:} \frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2}{K_2}\right)$$

Let's build on the Logistic Growth model by incorporating competition: now Species 1 (N_1) and Species 2 (N_2) compete for the same resource and each species' growth is reduced by the growth of the other species. The most general form of this model assumes that growth is depressed by some function (*f*) of the other species' population size. This model now includes both intraspecific and interspecific competition:

$$Species\ 1\text{:}\ \frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - f(N_2)}{K_1}\right)$$

$$Species\ 2\text{:} \frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - f(N_1)}{K_2})\right)$$

Note that in the absence of Species 2 ($N_2 = 0$), the equation describing population growth rate of Species 1 becomes logistic growth and the same is true for Species 2 in the absence of Species 1.

There are a variety of complex relationships we could insert into *f* to describe the effect of a competing species on growth rate, but the simplest formula assumes that the other species reduces a species' growth rate by a constant factor:

$$Species\ 1: \frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$$

$$Species\ 2: \frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right)$$

COMPETITION COEFFICIENTS (α AND β)

Competition coefficients describe the effect of one species on the other – α is the measure of the effect of species 2 on the growth of species 1 and β is the measure of the effect of species 1 on the growth of species 2.

If $\alpha = 1$, then each individual of species 2 has the same effect on the growth rate as species 1 (interspecific competition is as strong as intraspecific competition). Each new individual of species 2 reduces the growth of species 1 at the same rate as each new individual of species 1.

If $\alpha = 8$, then each individual of species 2 decreases the growth of species 1 by the same amount as adding 8 individuals of species 1 – interspecific competition (species 1 versus species 2) > intraspecific competition (species 1 vs species 1).

If $\alpha = 0.5$, then each individual of species 2 decreases the growth of species 1 by the same amount as adding half an individual of species 1 (eek! You can also think of this as 2 individuals of species 2 would have to be added to have the same effect as adding 1 individual of species 1) – interspecific competition (species 1 versus species 2) < intraspecific competition (species 1 vs species 1).

In summary, α indicates the magnitude of the relative importance *per individual* of intraspecific and interspecific competition:

If $\alpha > 1$	Interspecific > intraspecific
If $\alpha < 1$	Interspecific < intraspecific
$\alpha = 0$	No interspecific competition, only intraspecific (Logistic growth)

* α is the per capita effect of species 2 on the growth of species 1 measured relative to the effect of species 1 on its own population growth.

The same reasoning applies for β as the effect of species 2 on species 1 – β is the per capita effect of species 1 on the population growth rate of species 2 relative to the effect of species 2 on its own population growth rate. α and β do not need to have the same value and frequently they don't – an increase of one individual of species 2 may have a significant effect on species 1, while an increase of one individual of species 1 may only have a small effect of species 2. Remember also that both species have separate carrying capacities (K_1 and K_2) – as we'll see in the next section, these parameters are critical in predicting the outcome of competition.

EXPLORING THE LOTKA-VOLTERRA COMPETITION MODEL:

We are going to start by changing the values of competition coefficients to see how that changes competitive outcomes between two species. Click on "Competition model" on the top menu. The sliders on the left side of the screen will change the values of the competition coefficients α and β – the growth rates (r_1 and r_2) are fixed (cannot change). To start, we won't change the carrying capacities (K_1 and K_2) either (until question 30) so the parameters for each species are:

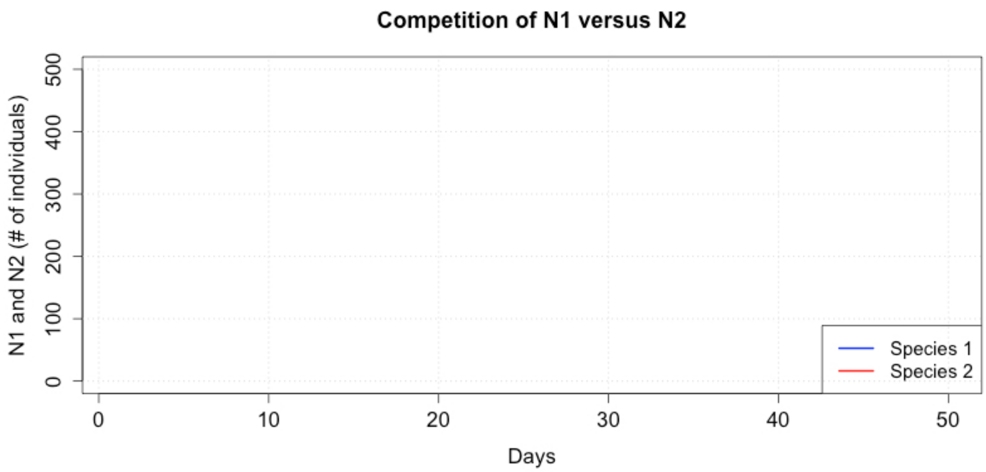
<u>Species 1:</u> $r_1 = 1$ day^{-1} $K_1 = 500$ individuals

<u>Species 2:</u> $r_2 = 1$ day^{-1} $K_2 = 300$ individuals

Exercise 2: Ecology by Computer

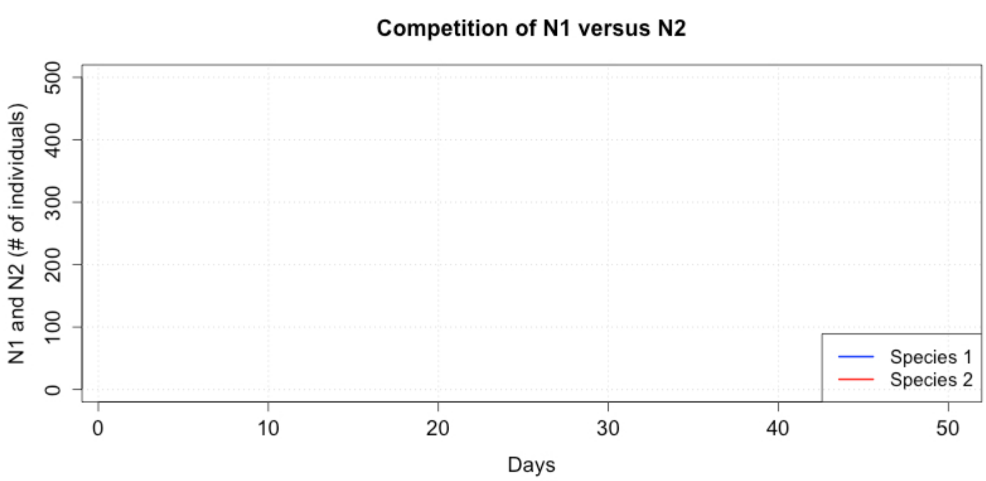
Questions:

[1] Set the competition coefficients α and $\beta = 0$. Sketch the graph you observe:



[2] In Q19, what is the effect of Species 1 on Species 2 and vice versa with these values for α and β? How would you describe the growth of each species?

[3] Set the competition coefficients α and $\beta = 1$. Which species "wins" (outcompetes the other)? Sketch the graph:



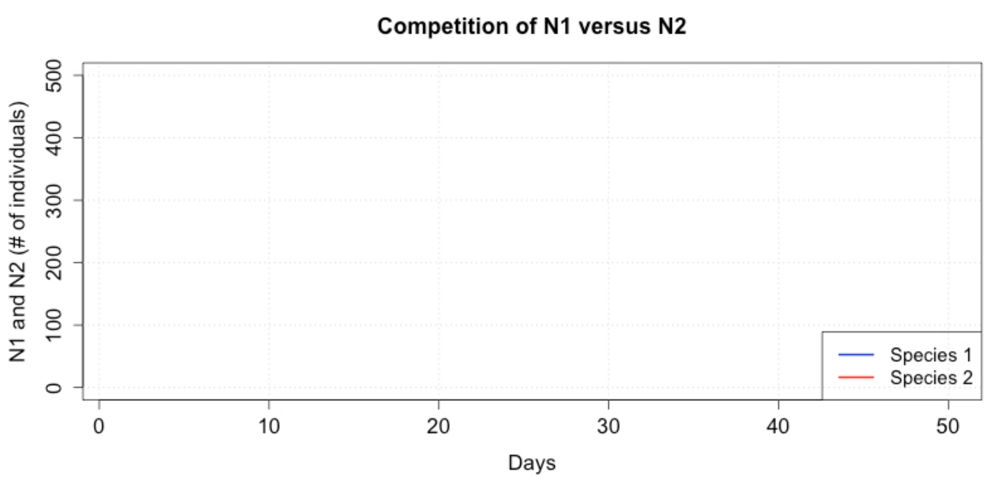
Exercise 2: Ecology by Computer

[4] Change the values of α and β such that the superior competitor switches (so if Species 1 outcompeted Species 2 in the previous section, change α and β such that Species 2 now wins). What value(s) of α and β change the superior competitor?

α:_______________

β:_______________

[5] Now set the competition coefficients α and $\beta = 0.25$. What happens? Sketch the graph:



[6] How does the outcome in Q23 differ from when α and $\beta = 1$?

[7] For these competition coefficient values (α and $\beta = 0.25$), which is stronger – interspecific competition or intraspecific competition?

[8] When α and $\beta = 0.25$ (Q23), are individuals of species 1 limited more by members of its own species or by individuals of species 2?

[9] What do you think this means in terms of how Species 1 and 2 utilize the shared resource? Do you think Species 1 and 2 use the resource the same way or in different ways? (Hint: remember the definition of **competitive exclusion**)

> Set the competition coefficients α and β= 1. (Q28-29)

[10] What is the *relative* effect of Species 1 on Species 2 and vice versa when the competition coefficients equal 1?

[11] What do you think this means in terms of how Species 1 and 2 utilize the shared resource? Do you think Species 1 and 2 use it the same way or in different ways?

> Keep α and β = 1 – let's see what happens when you change the values of the carrying capacities (K_1 and K_2). (Q30-32)

[12] Increase the carrying capacity of species 1 (K_1). Does this change the superior competitor?

[13] Change K_1 back to 500 individuals. Decrease the carrying capacity of species 2 (K_2)? Does this change the superior competitor?

[14] Set $K_1 = 500$ and $K_2 = 300$ individuals. Can you change K_1 and/or K_2 such that superior competitor switches? What values of K_1 and K_2 switch the superior competitor?

K_1: ________________ **K_2:**________________

Change $\beta = 2$ (keep $\alpha = 1$). Set $K_1 = 500$ and $K_2 = 500$ individuals. (Q33-34)

[15] What happens to the 2 species? Who is the superior competitor? Why?

[16] Can you change K_1 and/or K_2 such that superior competitor switches? What values of K_1 and K_2 switch the superior competitor?

K_1: ________________ **K_2:**________________

You just discovered a few predictions of the Lotka-Volterra Competition model through this exercise. Let's go through them – circle the correct prediction:

1. Species are more likely to coexist if interspecific competition is (stronger / weaker) than intraspecific competition.

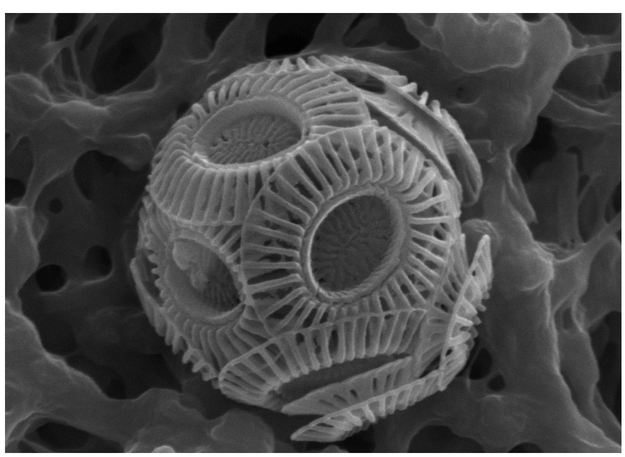
2. If species are similar in their resource use, the species with the (highest / smallest) carrying capacity will outcompete the other species.

3. Say Species 1 has a larger effect on the population growth rate of Species 2 than Species 2 on Species 1 ($\beta > \alpha$). The only way Species 2 can outcompete Species 1 is if the carrying capacity of Species 2 (K_2) is (much greater than / equal to / much less than) the carrying capacity of Species 1 (K_1).

Section 2: Using the Lotka-Volterra model to predict competition outcomes in nature

As we discussed in the Logistic Model exercise, harmful algal bloom (HAB) producing species may be partially driven by increased nutrient concentrations in the environment. This may be partially due to the fact that some HAB species are superior competitors for certain nutrients compared to other phytoplankton (algae) species. Algae of the genus *Phaeocystis* that we studied in the previous sections are particularly good competitors for nitrogen, such that they are able to out-compete other phytoplankton species and bloom to huge population sizes that can be toxic to marine organisms.

The competitive dynamics between *Phaeocystis* spp. and other phytoplankton species was studied in depth by researchers after they observed an increasing number of harmful *Phaeocystis* blooms in Dutch coastal waters[1]. Phytoplankton need nitrogen and phosphorus to grow (along with other nutrients which vary between algal species), and algal growth is frequently either limited by nitrogen or phosphorus, which is determined by the available nutrient concentration. The construction of a dam changed the flow of water to the Dutch coastline such that phosphorus discharge doubled (increase by 100%) and nitrogen discharge increased by 50%[1]. This caused a shift from P-limitation to N-limitation, which scientists hypothesized explained the sudden increase in the number of *Phaeocystis* harmful algal blooms. They tested this hypothesis by growing *Phaeocystis* and a competing phytoplankton species, *Emiliania huxleyi* (a coccolithophore), in cultures in the lab. They manipulated nutrient concentrations and observed which species outcompeted the other under P and N limitation. We are going to look at these data and test the hypothesis that *Phaeocystis* is a superior competitor to *E. huxleyi* under N limitation and the opposite is true under P limitation using the Lotka-Volterra model.



Emiliania huxleyi – an abundant coccolithophore (phytoplankton).

Source: Paul Matson http://www.paulmatson.org/

[1]Riegman, Roel, Anna AM Noordeloos, and Gerhard C. Cadée. "Phaeocystis blooms and eutrophication of the continental coastal zones of the North Sea."*Marine Biology* 112.3 (1992): 479-484.

Exercise 2: Ecology by Computer

For the Lotka-Volterra model, *Phaeocystis* will act as species 1 and *E. huxleyi* as species 2:

$$Phaeocystis\ (N_P):\frac{dN_P}{dt}=r_P N_P\left(\frac{K_P-N_P-\alpha N_E}{K_P}\right)$$

$$E.huxleyi\ (N_E):\frac{dN_E}{dt}=r_E N_E\left(\frac{K_E-N_E-\beta N_P}{K_E}\right)$$

We'll start by looking at the data for how the species interact under phosphorus limitation and then we'll see what happens when the limiting nutrient changes to nitrogen. We know the values of the growth rates and carrying capacities of the two species in the two environments.

A *Phaeocystis* bloom storms a castle off the coast of France.

Source: *https://en.wikipedia.org/wiki/Coccolithophore#/media/File:PhaeocystisFortd%27Ambleteuse8.jpg*

Questions:

[17] We will assume that the growth rates of the two species do not change depending on the limiting nutrient (r_P and r_E are the same under P and N limitation). However, the carrying capacities for each species *are* different depending on the limiting nutrient – why? Think back on the definition of carrying capacity (Hint: we talked about this during the logistic model exercise).

Exercise 2: Ecology by Computer

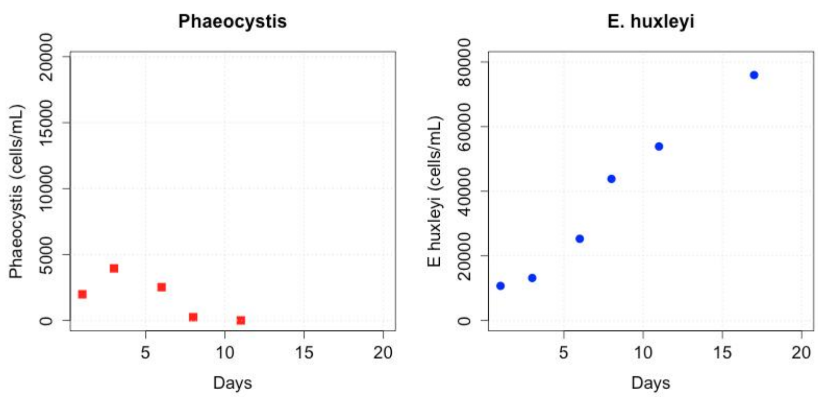
[18] Click on "HAB vs E. hux – P limitation" to get started on the exercise. On this figure, the lines reflect the Lotka-Volterra model predictions and the circles and squares represent the data from competition experiments conducted by Riegman et al. (1992). In P-limited culture, which species outcompetes which (look at the data points) – circle one:

Phaeocystis outcompetes *E. huxleyi*

E. huxleyi outcompetes *Phaeocystis*

The parameter values r_P, r_E, K_P and K_E are given. We know that *Phaeocystis* has a large negative effect on *E. huxleyi* in competition, so β (the measure of the effect of *E. huxleyi* on *Phaeocystis*) = 8. (Q37-Q40)

[19] What happens with α = 0? Sketch the graph:



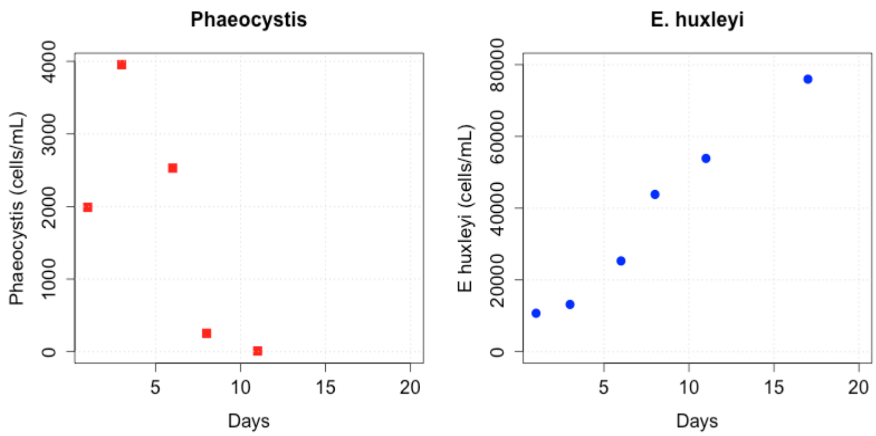
[20] Why? Describe the competition between *Phaeocystis* and *E. huxleyi* if α = 0.

Exercise 2: Ecology by Computer

[21] What value of α causes that the model predictions (the lines) to match the data points (the blue circles [*E. huxleyi*] and red squares [*Phaeocystis*])? Changing the value of α has an effect on both species, so make sure the α value you chose gives the best fit to *both* sets of data (for both species).

α: ____________________

[22] Sketch the fit of the model (the lines) at this α value:



Now click on "HAB vs E. hux – N limitation". These data are from the same study, but this time the two species were grown under nitrogen limitation. Remember the growth rates for the 2 species (r_P and r_E) haven't changed and we're going to assume that the values for α and β don't change moving from phosphorus to nitrogen limitation. (Q41-Q42)

[23] In N-limited culture, which species outcompetes which (look at the data points) – circle one:

Phaeocystis outcompetes *E. huxleyi*

E. huxleyi outcompetes *Phaeocystis*

[24] So the superior competitor has changed moving from phosphorus to nitrogen limitation. We've said that the values α and β have not changed from phosphorus to nitrogen limitation – how is it possible that the superior competitor has changed? (Hint: what parameters *have* changed?)

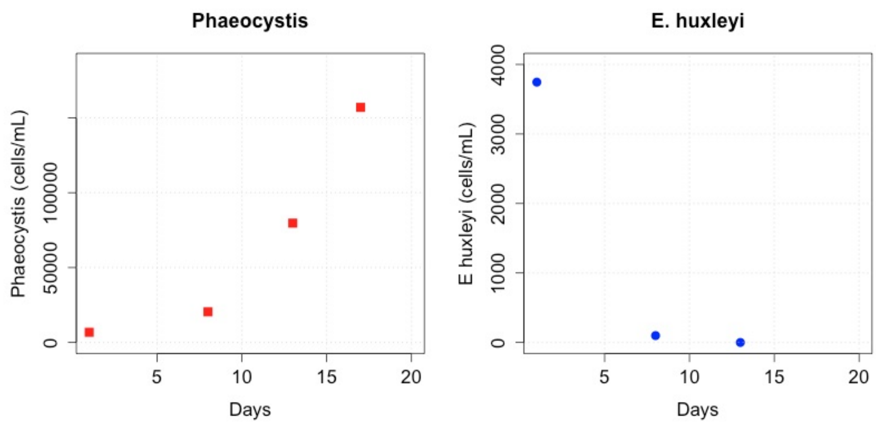
Exercise 2: Ecology by Computer

> Let's confirm the prediction you made in the previous question. Start by entering the value for α that fit the previous data set best (value in question 39) and keep $\beta = 8$. You also know that the carrying capacity for *E. huxleyi* (K_E) = $5*10^4$ cells/mL (it is set to this value – you don't need to change it). (Q43-45)

[25] What value of K_P (the carrying capacity of *Phaeocystis*) causes that the model predictions (the lines) to match the data points?

K_P: ________________

[26] Sketch the graph:



[27] Do the parameter values (the values of K_E and K_P) in Q43-44 match your explanation (in Q42) as to why the superior competitor switches when the system shifts from P to N limitation?

Exercise 2: Ecology by Computer

To summarize:

[28] In **P-limited** culture, which species outcompetes which (look at the data points) – circle one?

Phaeocystis outcompetes *E. huxleyi*

E. huxleyi outcompetes *Phaeocystis*

[29] What are the parameter values for the Lotka-Volterra competition model for *Phaeocystis* and *E. huxleyi* under **P limitation** (fill in the missing value)

Phaeocystis: $r_P = 0.32$ day^{-1}, $K_P = 2e4$ cells/mL, α = ________

E. huxleyi $r_E = 0.27$ day^{-1}, $K_E = 8e4$ cells/mL, $\beta = 8$

[30] In **N-limited** culture, which species outcompetes which (look at the data points) – circle one?

Phaeocystis outcompetes *E. huxleyi*

E. huxleyi outcompetes *Phaeocystis*

[31] What are the parameter values for the Lotka-Volterra competition model for *Phaeocystis* and *E. huxleyi* under **N limitation** (fill in the missing values)

Phaeocystis: $r_P = 0.32$ day^{-1}, K_P = ______ cells/mL, α = ______

E. huxleyi $r_E = 0.27$ day^{-1}, $K_E = 5e4$ cells/mL, $\beta = 8$