Keystone Predator

Approximate time to complete: 2 — 4 hours

Background

What determines the structure of an ecological community? One popular method of addressing this question is to make a diagram showing which species eat which other species in that community. A diagram like this is called a *food web*, and from this outline of the community we can start asking more specific questions. Why are there a lot of individuals from one species in a community, while the population of another species is small? Do all species have equal importance to the community, or are some more important than others? Can we predict, just based on the food web, what will happen if one species is removed from the community, or do we need more information? These questions are not only interesting for a naturalist, they are also important in many practical situations, not the least of which is predicting what will happen to ecological communities as more and more species are driven to extinction by human activities.

In this lab we are going to explore these questions by the side of the ocean. If you go to the beach in most places on the west coast of the Americas, or in many other places along the world's oceans, you will find an area called the *rocky intertidal*, lots of rocks that are covered by algae, barnacles, mussels, clams, anemones, and all kinds of other interesting creatures. This habitat is a very good place to study how communities are structured, because it is interesting and complex, yet easily manipulated. The animals move around very slowly or not at all, making counting and observation relatively easy. You can also easily do experiments where you put species in or keep species out of some area of the intertidal, and observe what effects this has on the community. In this lab we'll try to figure out the structure of an intertidal community, using observation and species removals, and in the process we'll discover an important idea in ecology that came from studying the rocky intertidal.

Outline of This Lab

We're going to watch a small area a little way out from the beach in the intertidal area of the coast of Washington State. The rocks in this area contain nine species of plants and animals. There are three species of algae, very simple plant-like creatures that get energy through photosynthesis. *Porphyra* is a leafy green alga often served in Japanese restaurants. *Corralina* is a tougher alga that grows in segments. *Neorhodamela* grows in nifty whorls of tiny finger-like stalks. *Balanus* and *Mitella* are both barnacles, small animals with shells that are shaped like a volcano, with the bottom part cemented to a rock and the top part able to open to let food in and excrement out. *Mytilus* is a mussel, constructed similarly to the mussels and clams you might get in a seafood restaurant. Barnacles and mussels are stationary animals that eat by sticking feather-like extensions into the water and filtering out particles of food, a way of eating that is known as filter feeding.

The last three species are animals that move around and eat some of the other species. *Katherina tunicata* is a chiton, *Nucella* is a snail, and *Pisaster* is a starfish. All of these crawl around slowly through the intertidal, hanging onto the rocks so that they don't get washed away by the waves, and eating anything they consider food that lies in their path.

Among the stationary species, there is a relationship called a *competitive dominance hierarchy*. This means that some of those species can grow on top of others. For instance, a *Corralina* can start growing in an area currently occupied by *Porphyra* and eventually take over all the space that the *Porphyra* was growing in, but a *Porphyra* can't grow on top of a *Corralina*. We say that the *Corralina* is competitively dominant over *Porphyra*.

The goal of this lab is to understand whether the interactions between the different species help to determine which species you see in the intertidal and how abundant each species is. We'll start by trying to figure out which species are competitively dominant to others. Then we'll figure out who eats who, building this up into a diagram called a *food web*. Finally, we'll do some experiments in which we take out one species and see what happens to the rest of the community. From these observations and experiments, hopefully we'll be able to see how the intertidal community of species works, and figure out whether some species are more important than others in structuring this community.

Note: While this model is based on the community of species on the outer coast of Washington State, the model is only an approximation. The relationships between the species are reasonably accurate, but the strengths of these interactions, as well as the life history characteristics of the species, are fictional, largely because these numbers have not been measured by anybody. Despite the inaccuracies, this model behaves in a similar way to the real community when you do the experiments I suggest in this lab.

<Optional>

For those of you who are interested in exactly how the model is put together, here is a brief explanation. If you want more detail on anything described here, refer to the manual for EcoBeaker. All of the stationary species are modeled using a transition matrix. The way a transition matrix works is as follows. Let's say a certain patch of the intertidal is empty. Over the next year, there is a certain chance that this empty patch will be filled with *Porphyra*. There is also a chance that it will be filled with one of the other algal species, or with a barnacle or mussel. An empty square becoming filled with something is called a transition, and the chance of each transition happening is stored in the transition matrix. Of course, there's also a chance that an empty space will still be empty next year. In EcoBeaker, this is called the "No Change" transition.

In a similar way, *Porphyra* that is growing in an area this year may be displaced by one of the other algal species next year. So *Porphyra* also has a transition matrix that gives the chance that a *Porphyra* this year will be replaced by each of the other species, stay *Porphyra*, or die (transition to Empty).

I have used the transition matrix to specify the relationships between all the stationary species in the model. Species that are better at settling into empty space have higher transition probabilities in the transition matrix of Empty. If species B can out compete species A, then the transition matrix of species A will have a non zero probability for becoming B. The higher the probability, the better B is at outcompeting A. Note that in this model, I made the competitive dominance hierarchy one-way. If B can grow on top of and outcompete A, then A has no chance of outcompeting B. The entry in B's transition matrix for probability of going to A is 0.

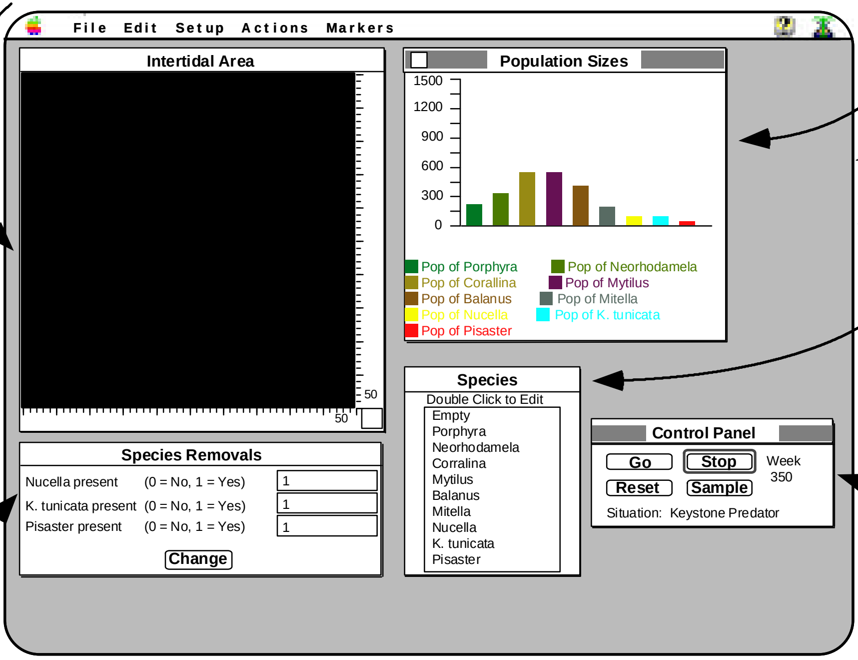
The moving predatory species are all modeled with a set of rules called "Predator". See the manual for a description of this procedure.

The Lab

1. Run EcoBeaker (click twice quickly on its icon).

2. Open the situation "Keystone Predator" (use the 'Open' command in the File menu).

After the situation loads, you should see several windows laid out on the screen as follows:



Species Removals

Nucella present (0 = No, 1 = Yes) 1

K. tunicata present (0 = No, 1 = Yes) 1

Pisaster present (0 = No, 1 = Yes) 1

Species list:

Empty
Porphyra
Neorhodamela
Corralina
Mytilus
Balanus
Mitella
Nucella
K. tunicata
Pisaster

Week 350

Situation: Keystone Predator

A view from above of the area of the intertidal where we'll be working

A graph showing the number of each species currently in the Intertidal Area

A list of the species in the model, showing each of their colors

The window you'll use to remove species from the model

The control panel used to control running and stopping the model

The big window in the upper left is a view of the Intertidal Area we'll be working in, showing the positions of all the creatures. Each creature has a different color that identifies what species it belongs to, and the key to these colors is given in the window labeled “Species”. The Species window has a list of all the different species in the model, with each name colored according to the color of that species in the Intertidal Area.

To the right of the Intertidal Area is a graph entitled “Population Sizes” showing how many of each species are within the area. Below the Intertidal Area is another window labeled “Species Removals”, which we'll use later to remove species from the model. Finally, in the lower right-hand corner there the called Control Panel window, which has the controls for running the model.

4. Run the simulation (click on the ‘Go’ button in the Control Panel).

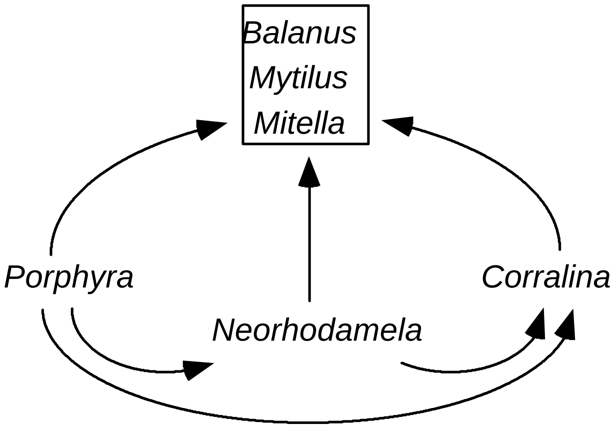
In the intertidal window you will see *K. tunicata*, *Nucella*, and *Pisasters* start running around, eating. As they eat, they leave behind bare rock (colored black), which will quickly get settled into by one of the stationary species. Some of the stationary species will also settle on top of other stationary species and outcompete them. In the graph, you will see that the number of each species in this area goes up and down over time.

5. Spend a few moments watching all this action and getting a feel for what's happening.

6. If you are having trouble distinguishing between some of the species in the model because the colors are too similar, try this. Stop the model (push the 'Stop' button on the Control Panel). Then move your mouse so that it's pointing to the creature you want to identify. Click and hold down the mouse button. A small window will pop up at the bottom of the screen, telling you the species name of that creature, along with some other information that we'll use below. When you're done, start the model running again ('Go').

We are going to do some simple experiments in this system to try to determine the importance of the different species in the model. We'll concentrate on the three species that can move around, *Nucella*, *K. tunicata*, and *Pisaster*. Before we start these experiments, we should try to figure out exactly what each of the moving species eats. We should also figure out the competitive dominance hierarchy of all the other species.

To help you figure out the competitive dominance hierarchy, I am going to give you part of it in a diagram and then let you finish it:



The arrows in this diagram point from poorer to better competitors. For instance, the arrow pointing from *Porphyra* towards *Neorhodamela* shows that if *Porphyra* is growing in some area, *Neorhodamela* can come along and take over that area. Similarly, *Corralina* can take over space from either *Porphyra* or *Neorhodamela*, as indicated by the arrows pointing from the other two algae species to *Corralina*. However, neither of the other two algal species can take over space occupied by *Corralina*, so *Corralina* is the most competitively dominant algae among these three.

As shown by the arrows, any of the filter-feeding species can take over space occupied by any of the algal species. I haven't given you the competitive dominance hierarchy between the filter feeders themselves, though, and this is what you will figure out next.

7. To figure out the competitive dominance hierarchy among the two barnacles and the mussel, we need to do some observations. Find a square containing *Mitella*. Watch that square until something else replaces the *Mitella*. You now know that whatever replaced the *Mitella* is competitively dominant to it. Find several other squares containing *Mitella* and repeat the process until you are fairly sure you have seen everything that is likely to competitively displace *Mitella*. Note that a *Mitella* getting eaten and then a new species moving into the empty square doesn't count towards competitive dominance. When you are done, make a new diagram like the competitive dominance hierarchy shown above, and add arrows into it showing the new competitive relationships you just discovered.

Now you know the species that are dominant over *Mitella*. In this model (and for the most part in the real intertidal) the competitive dominance hierarchy is one way — *Mitella* will not be able to grow on top of one of the species that you just found was dominant to it. So in building up the hierarchy, if you see some species displacing *Mitella*, then you can be pretty sure that *Mitella* will never displace that other species.

If you are having trouble seeing your square change colors because the model is running too fast, then you can slow the model down as follows. Find the Setup menu, and select ‘Other...’. A big dialog box will appear. Look near the bottom of this dialog box for an item that says “Timesteps / sec”. This is the number of weeks the model will run for every second of computer time. Currently, it should be set to 60 (the maximum — though your computer is probably not fast enough to run models that quickly). You can lower this number to slow the model down. For instance, if you set it to 1, then only one week will pass each second you run the model. When you have set it the way you want, click the ‘OK’ button at the bottom of the dialog box. Later, when you want the model to run quickly again, repeat the procedure and set “Timesteps / sec” back to 60. You can also make the squares larger by making the window bigger. Click in the lower right-hand corner of the window, hold down the mouse button, and move the mouse to expand the window.

8. Repeat step 7 for the other barnacle species, *Balanus* , and the mussel, *Mytilus*. Draw new arrows in your competitive dominance diagram for new competitive relationships you discover.

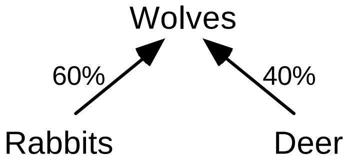
Next we want to find out what each of the predator species eat. One trick that ecologists use to find out what creatures have been eating is to look at what’s in their guts or in their excrement. If you eat something, it’ll hang around in your stomach for a little while, and then whatever parts of it you didn’t digest will come out the other end. The partially digested food in the gut is called the gut contents. Normally, when people look at gut contents they have to kill the animal and cut it open. (Can you believe people actually do this as a job?) Within EcoBeaker I have devised a kinder and gentler method for finding gut contents, and we’ll use that to figure out what each of the predatory species is eating.

9. Stop the model (push the ‘Stop’ button on the Control Panel). Then find a creature for whom you want to know the gut contents. Move the mouse so that the pointer is on top of this creature and press down and hold the mouse button. A window will pop up on the screen telling you the species name of this creature and some other information. Among the other information is something labeled “Gut Contents”, with a number next to it. This number tells you what’s in this creature’s gut. Note that this will only work for the moving species, not for the stationary ones. The algae don’t have guts, and the barnacles and mussels have gut contents that are just too mushy to distinguish anything.

When you get the mushy contents out of an animals gut, its not obvious what that mush came from. You have to interpret it a little. In EcoBeaker, the interpretation is easy. Take the number that you got for Gut Contents, look over at the Species window, and count down from the top until you get to your number. The number 1 means that your creature recently ate a *Porphyra*, the number 5 means it recently ate a *Balanus* and so on. 0 means it hasn't eaten anything recently, and its gut is empty.

10. Look at the gut contents of the *K. tunicata*, *Nucella*, and *Pisaster* in our area of the intertidal. As you're gathering the information, write down not only which species are eating which other species, but also the importance of each prey species to each predator. For instance, record what percentage of *Pisasters* have recently eaten a *Neorhodamela*, what percentage recently ate a *Balanus*, and so on.

11. Make a little picture showing which species eat which other species. You can do this similar to how you drew the competitive dominance hierarchy. Write down all the species on a piece of paper, and then draw arrows from each species to the other species that eat it. Next to each arrow, write down the relative importance of that prey to that predator (from the percentages you calculated above of predators that recently ate that prey instead of other prey). A simple example of this type of diagram (for illustration only, and not at all related to this model) might look like:



This picture shows that 60% of the diet of these wolves is rabbits and the other 40% is deer.

12. You may want to run the model for a while longer ('Go'), then stop it again ('Stop') and repeat step 11. This repetition will tell you how constant the percentages you found are, and how much the food that each species eats changes over time.

This diagram you have just drawn, known as a *food web*, is a common type of information for ecologists to gather about the system they are working in. Unless you are a real artist, your food-web drawing probably looks like a real mess, which is what most real-life food webs look like. This makes it a bit hard to do anything with them, although many people have tried.

The next step in this lab is for you to try using your food web to make some guesses about how this community functions. What we're going to do is remove each of the three predatory species in turn and look at what effect its removal has on the whole community. Before we do that, however, you should make some notes on what the community is like now, and then try to predict what effect the removals will have.

13. Take some notes on the community as it is now. This is the baseline; you'll compare the results of your experiments to this. Look at the Population Sizes graph and write down which species are most abundant and which are least abundant. Look at the Intertidal Area and make some notes about what the distribution of species looks like there. You may also want to make notes on how much all of this has been changing as you were running the model (or you could run the model for a little longer and watch how stable it is).

<Optional> For those of you who are interested in being more quantitative in this laboratory, there are several statistics within EcoBeaker that you can use to measure aspects of species richness. For a more quantitative approach, look in the manual to figure out how to set up a statistics window (it's in the Graphs section), and use Simpson's or Shannon's diversity indices, and other statistics that you think might be appropriate.

14. Now, for each of the three species that we'll try removing (*K. tunicata*, *Nucella*, and *Pisaster*), make a prediction about what's going to happen to the rest of the community after that species is gone. You can predict what will happen to population sizes of each species, what will happen to the distribution of species in the intertidal, or any other characteristic that you think is interesting. If you have quantitative predictions, that's even better. Write these predictions down.

Let's start by taking out *K. tunicata*, the chiton.

15. Find the window at the bottom of the screen labeled Species Removals, and look the item called "K. tunicata present". Change the 1 in this box to a 0. Then click on the 'Change' button at the bottom of the Species Removals window.

What you've just done is to remove every *K. tunicata* individual that enters the Intertidal Area as soon as it enters. This is like hiring a research assistant to stand over this little area of beach and watch for *K. tunicata*, and every time she sees one come in, to pick it up and throw it back out. In order to save time, I am not going to explain what we just did in modeling terms, but if you're interested, you can figure it out by reading about transition matrices in the manual.

16. Now watch for a while longer as the model runs along. What changes do you see? Was your prediction right? Try to be a little quantitative — the population of this species went up around 10%, that one seems to have dropped in half, and so on — and write down these observations. Make sure to watch for a while before continuing to the next step so that the community has time to come to an equilibrium, where the population sizes are more or less stable. A good length of time to wait is perhaps 100 weeks. The Control Panel shows how many weeks have gone by.

17. When you are pretty sure that the community has come to its new equilibrium, and you have taken as many notes on this experiment as you want, it's time to add *K. tunicata* back in. Go to the Species Removals window and change the 0 for "K. tunicata present" back to a 1. Click on the 'Change' button. Then run the model for a while longer, until the original equilibrium is reestablished.

18. Now let's try removing *Nucella*. The procedure for removing *Nucella* is the same. Change the 1 for "Nucella present" to a 0, and click on the 'Change' button.

19. Again, let the model run for a while until a new equilibrium is reached. What is this equilibrium like? How different is it from the control situation, and from the situation when *K. tunicata* was removed? How close was your prediction? Try to be a little bit quantitative, and make notes about what you see.

20. When you've figured out what happens upon removing *Nucella*, then put it back in. Wait for a while till the original equilibrium is reestablished.

21. Finally, let's try removing *Pisaster*. This change uses the same technique as the other two. Find "Pisaster present" in the Species Removals window and change the 1 to a 0. Then click on the 'Change' button.

22. Run the model for a while longer. What's happening now? How is this different from when *Pisaster* was in the model? How is it different from removing one of the other two species?

More Things to Try

If you want to play around more, you could try removing some of the other species in the model, and seeing what happens then. This is a little more complicated since I haven't set it up for you, but its not too bad. Find the species you want to remove in the Species window. Double-click on its name (move the mouse to point at its name and click twice quickly). A complicated-looking dialog box will appear. Look in the right side of the dialog box for the set of numbers called the "Transition Matrix". Write down all these numbers. Then change them all to 0 except the one labeled "Empty", which you should change to 1. Then click on the 'OK' button. That species will now be removed. When you want to put it back in, go back to its transition matrix and type in all the numbers exactly as they were before.

You might also want to try removing two species at once. For instance, you might try removing both *Pisaster* and *Mytilus*.

Perhaps more interesting than doing more removals is to try to figure out when you do and don't get keystone predator behavior (see description below). Try to guess one change that you could make in the transition matrix of one of the species that would make the phenomena of keystone predation disappear. Then try it.

Notes and Comments

As you saw in this lab, not all species are equal in an ecosystem. Removing one of the species in the model had a much larger effect on the community than removing either of the other two. This species is called a *keystone species* for this ecosystem, because it, more than any of the other species, determines the structure of the community. This species is the keystone even though it is usually the least, or second-to-least common species when you are running the model. Note that the keystone species in this model is a predator at the top of the food chain. This position is typical of many keystone species, and these *top predators* are often also the most vulnerable to natural or man-made disasters. As you saw in this lab, if the population of these predators is reduced, that change can have large consequences in the ecosystem, much larger than you might guess from the size of the predator population alone.

References

Paine, R. T. 1966. Food web complexity and species diversity. *The American Naturalist* **100**: 65–75.