EcoGEnIE: A practical course in global ocean ecosystem modelling

Lesson 3: Build it up, tear it down.

1. A fully size-structured global plankton ecosystem. We are now going to switch to a more diverse version of the size-structured ecosystem model. This configuration has 8 size classes of phytoplankton, and 8 size classes of zooplankton, as shown in Table 1.

Table 1: Plankton functional groups and sizes.					
j	PFT	Diameter (μm)	j	Functional Type	Diameter (μm)
1	Phytoplankton	0.2	9	Zooplankton	0.6
2	Phytoplankton	0.6	10	Zooplankton	1.9
3	Phytoplankton	1.9	11	Zooplankton	6.0
4	Phytoplankton	6.0	12	Zooplankton	19.0
5	Phytoplankton	19.0	13	Zooplankton	60.0
6	Phytoplankton	60.0	14	Zooplankton	190.0
7	Phytoplankton	190.0	15	Zooplankton	600.0
8	Phytoplankton	600.0	16	Zooplankton	1900.0

1.1. Save the *ecosystem configuration* file under a new name, replacing the existing plankton populations with the ones described in Table 1.

1.2. Update the *user-config* to point to the new *ecosystem configuration* file, and save again under a new name. (It is generally a good idea to make a note of the name and goal of each experiment as you set it up.)

1.3. Run the new model for at least 20 years (this will probably take about 10-15 minutes).

2. Ecosystem characteristics. We can now begin to look at the size and diversity metrics of the phytoplankton community in a meaningful way.

2.1. Look first at (1) the total carbon biomass, (2) the carbon uptake flux (i.e. primary production) and (3) the geometric mean size. Make sure in each case that you are looking at the last year of model output. You may also find it useful to adjust the colour scale, or to change to a logarithmic colour scale (e.g. try a logarithmic scale from 2 to 20 microns for the geometric mean size).

Looking at the maps, we can perhaps pick out three different "biomes" in terms of their community properties...

- 1. The low-latitude oligotrophic gyres are relatively unproductive, and support some of the lowest annual mean biomasses in the surface ocean. In these regions the mean phytoplankton size is very small.
- 2. Subpolar latitudes between 40° and 50° N or S are much more productive, and support very high annual mean biomass. These communities also have the highest mean sizes of any region.
- 3. The polar oceans are also highly productive (except perhaps the high Arctic), and support relatively high annual mean biomasses. These communities are made up (in the model, at least) of slightly smaller phytoplankton than we see in the subpolar regions.

2.2. What can we find out about the community structure in these regions? Open up some of the other metrics describing the community (standard deviation of size distribution, size fractionation, diversity, limiting factors). What can you find out about the community structure within each region, in terms of coexistence and exclusion?

- Does the community span a broad or narrow size range?
- How many size classes are coexisting in each biome?
- What is the smallest and largest size class in each biome?
- How much biomass is concentrated in each size fraction (picoplankton, nanoplankton and microplankton)?

Do the patterns that you see in the model fit in with what you have seen and heard during the lectures? What factors do you think are most important in terms of dictating the global distribution of each size class?

3. Ecosystem characteristics. To find out the answers to these questions, you are going to pull the model apart, and then put it back together. At each stage the aim is to bring in a different limiting factor, so that you can see its effect on the model behaviour.

3.1. The fundamental niche. The first step is to find out the impact of abiotic factors on the distribution of different phytoplankton sizes. In other words, we need to find out what the distribution of the phytoplankton would be in the absence of any ecological interactions, such as resource competition and predation. This is effectively their 'fundamental niche'.

The fundamental niche is fairly abstract, and not something that can be measured in the real world. In model world, however, we can get a useful estimate of the fundamental niche by making a few simple changes to the model.

3.1.1. First of all, you can remove all predation, simply by removing the zooplankton from the *ecosystem* configuration file. Once again, you will need to save a new and appropriately named *user-config* file.

3.1.2. Next, you also need to remove all competition for nutrients and light. This involves tweaking the model equations so that the phytoplankton are not nutrient limited, and do not attenuate light. To do this, all you need is to add the following line to the *user-config* file.

eg_fundamental = .TRUE.

3.1.3. If you now run the model (just 10 years should do in this case), you should have a community of eight phytoplankton size classes that are growing solely as a function of the incoming light and the temperature. This growth will be balanced balanced the basal (i.e. non-grazing) mortality. As there is no feedback between the ecosystem and the environment, populations that can survive will grow exponentially and without limit, potentially reaching astronomical abundance in very little time. Populations that cannot survive will rapidly decline to almost nothing.

The regions in which each plankton shows positive growth defines its fundamental niche. This is a function of abiotic conditions only, and is the absolute limit of its geographical range. Look at the carbon biomass distribution in each size class (set the data range in each case from 0 to 1 mmol C m-3)

- How and why does the fundamental niche vary with size?
- Could the limits of the fundamental niche explain some of the patterns seen in the full model?

3.2. Resource competition. The next step is asses the impact of resource competition. We are first going to do this in the absence of any zooplankton grazing.

3.2.1. All you need to do at this stage is to re-enable nutrient and light competition. To do this, simply delete 'eg_fundamental = .TRUE.' from the *user-config* file, and save under a new name. Leave the *ecosystem configuration* file as it is.

3.2.2. You should have a community of eight phytoplankton size classes that are competing for nutrients and light, again as a function of temperature. This is a much more realistic simulation, as feedbacks between the ecosystem and the environment serve to limit the size of the phytoplankton populations.

Examine the model to find out:

- What size classes are able to persist when resource competition is enabled?
- Why are different size classes more or less abundant in different areas?
- How does the distribution of each size class compare to the fundamental niche?
- What are the reasons for any differences?

Phytoplankton biogeography at this stage begins to approximate the realised niche, which defines the range of conditions that support a population in the presence of ecological interactions. Note that at this stage, however, we have ignored the effects of any predator-prey interactions, as the zooplankton grazers are still missing.

3.3. Resource competition + **one generalist zooplankton** The previous simulation is clearly unrealistic (although, hopefully, informative). You are now going to add back in just a single zooplankton class, that grazes equally on all plankton (including itself).

3.3.1. Add a 100 micron zooplankton into the *ecosystem configuration* file, and save under a new name. Also update the *user-config* file to reflect the change, and save under a similar name.

3.3.2. You need to modify the model so that the zooplankton eats all prey with equal preference. This can be done by adding the following lines to the *ecosystem configuration* file.

eg_ns = 1 eg_pp_sig_a = 1.0e99

Note: For afficionados, the first parameter disables prey-switching (i.e. predators no longer preferentially attack the most abundant prey). The second parameter increases the width of the grazing kernel (i.e. predators can attack a range of prey across a huge size range with equal preference).

3.3.3. The addition of zooplankton to the model community should give a more accurate approximation of the realised niche.

- Does the addition of a single zooplankton grazer enable more or less coexistence?
- What factors might be responsible for any shifts in biogeography?

3.4. Resource competition + **one "switching" zooplankton** You began with a full food-web containing 8 phytoplankton and 8 zooplankton size classes. The diversity of zooplankton clearly has an effect on the phytoplankton community that is not seen in the previous experiment. This effect can be imitated with just one generalist zooplankton if we instruct it to graze preferentially on the most successful prey.

Re-enable this "prey switching' effect by changing the following control parameter to a '2' ...

eg_ns = 2

Compare this simulation to the first experiment (8 phytoplankton and 8 zooplankton) to see how the inclusion of prey switching increases coexistence through the 'kill-the-winner' mechanism.

- How does nutrient limitation change with phytoplankton size, and how might zooplankton be affecting this?
- Look at the C:P biomass ratio in the community as a whole, and compare to your estimates from the NPZD model (Lesson 1).
- How does the C:P ratio vary with size? How does having a diverse community affect the coupling of carbon and limiting nutrients?

4. Questions to answer

- What sets the fundamental niche, and how does it change with size?
- How is the fundamental niche modified by resource competition?
- What species are favoured in terms of nutrient competition?
- How is the outcome of competition affected by...
 - Abiotic conditions?
 - Increased mortality (through generalist grazing)?
 - Density-dependent mortality (through specialist grazing)?

• Do these experiments tell you all you need to know? What other modifications can you think of making?

5. Mixotrophy Try adding some mixotrophs to the phytoplankton and zooplankton already present in the community. These will have exactly half the nutrient uptake traits of phytoplankton of a similar size, and half the prey capture traits of zooplankton if a similar size.

- How does this effect the mean and standard deviation of cell size? (Size and diversity metrics will be calculated for phytoplankton and mixotrophs together)
- How does mixotrophy effect the C:P ratio of organic matter?
- How does the realised niches of mixotrophs compare to the fundamental niches of phytoplankton?