MATH3070 Assignment 3

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Question 1

We begin by running the simulation in one cell over a 100 year duration with the default values. The default PPMR plot is shown in Figure 2, the default timeseries biomass and growth plot in Figure 1, and the default biomass spectrum in Figure 3.
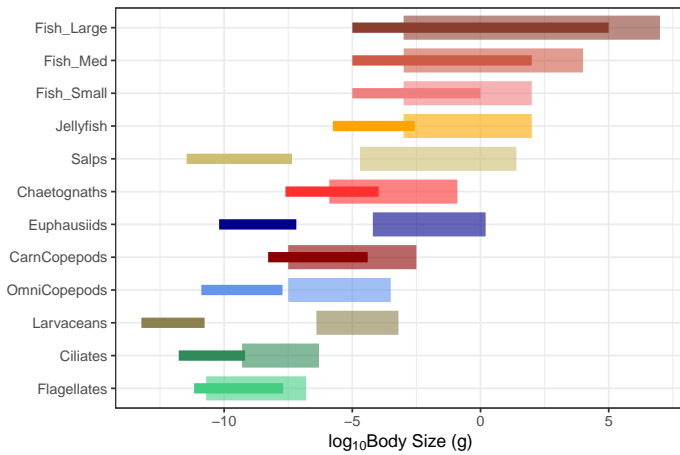

Figure 2. The predator-prey mass relationship in the default case shows the valid prey mass range (solid bars) for a given predator mass range (translucent bars) for each predator type (*y*-axis).
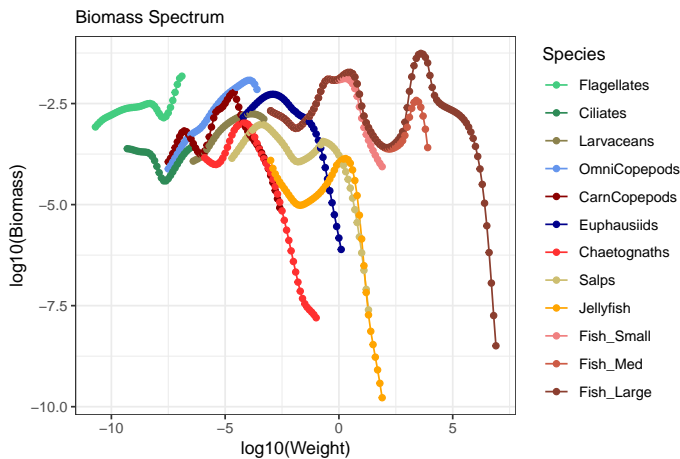

Figure 3. The biomass spectrum (at a single time) effectively shows the total energy storage in mass across a species type given an individual's weight.

Figure 2 shows the difference in mass (as a proxy of size)

ranges of each of our 'species' of interest. We see relatively diverse predatory-prey mass ratios (difference in solid and translucent bars) in the zooplankton species (the bottom 9 species), and a constant lower bound for all 3 fish species (the top 3 bars) where larger fish are *able* to consume larger prey.

From Figure 3, we see that for any given species, the population tends to cluster around a certain weight class as shown by peaks in the biomass spectrum. We also see that the peak biomass is roughly constant across weight classes, which indicates that there are generally smaller populations in higher weight species. This makes sense intuitively, as we expect the more massive predators to eat the less massive prey, and hence we need more low-mass individuals to compose a sufficient diet for high mass species (accounting for energy loss across trophic levels).

Finally, in Figure 1 we see the behaviour of the species' biomass and growth in the single cell system over time. We see extremely stable growth in the species which feed on the lowest trophic levels (flat lines in the growth rate), and only relatively stable growth for the other species. Consequently, those species that have a more stable growth tend to have a more stable (flat) biomass curve. The default system appears to initialise out of an equilibrium (given by the steep decline in some species' biomass at $t \sim 0$), which eventually leads to the instabilities later on, particularly with the jellyfish and carnivorous copepods.

We note that the default values for the zooplankton wet weight is 0.374 mass units (to my knowledge undefined in the ZooMS MATH3070 R file), and the fish wet weight is 1.197 mass units.
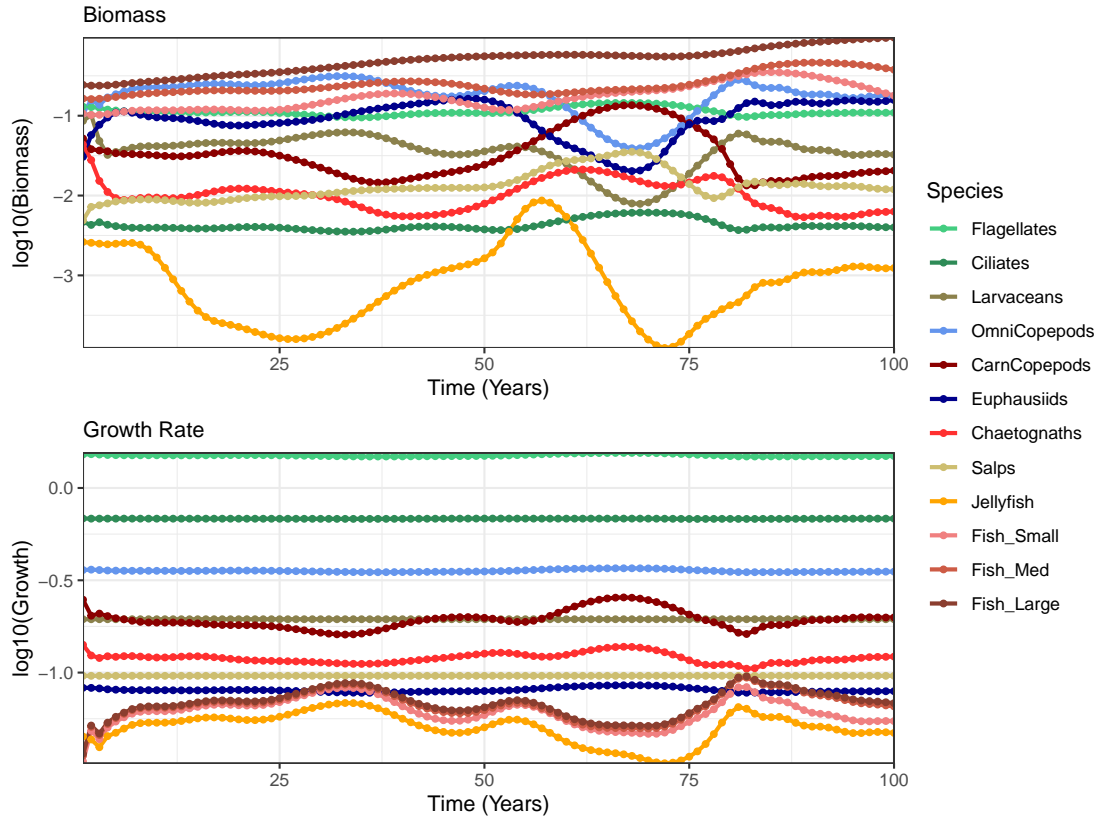
Figure 1. We show the species biomass and growth rate as a function of time in a 100 year simulation of a single cell in the ZooMS2 model. Each species has a characteristic (and not necessarily constant) growth rate which is reflected somewhat in the biomass plot, generally with some time lag.
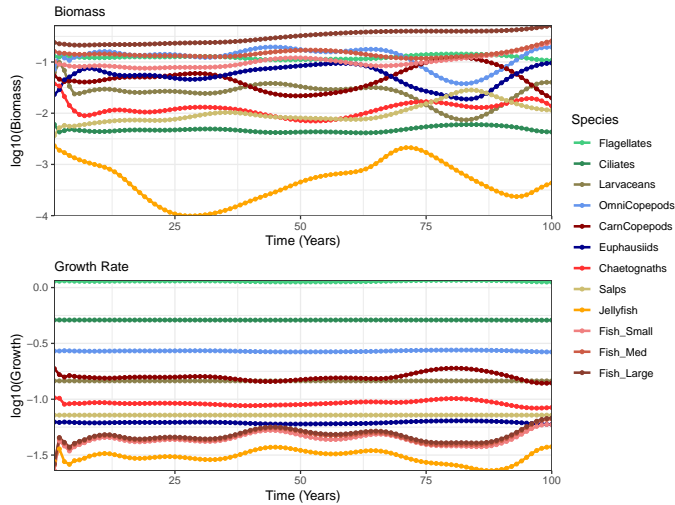
Question 2

Figure 4. The biomass and growth timeseries data across the 100 year duration, with a modified coefficient of search volume of $\gamma = 480 \text{ m}^3\text{g}^{-0.8}\text{yr}^{-1}$.
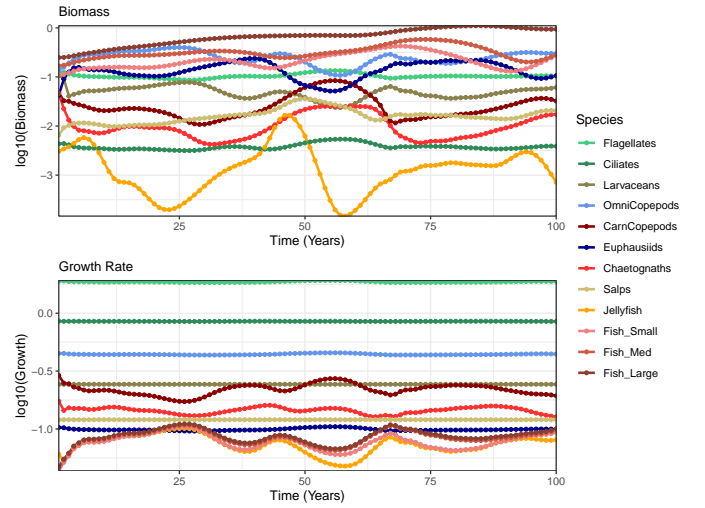

Figure 5. The biomass and growth timeseries data across the 100 year duration, with a modified coefficient of search volume of $\gamma = 800 \text{ m}^3\text{g}^{-0.8}\text{yr}^{-1}$.
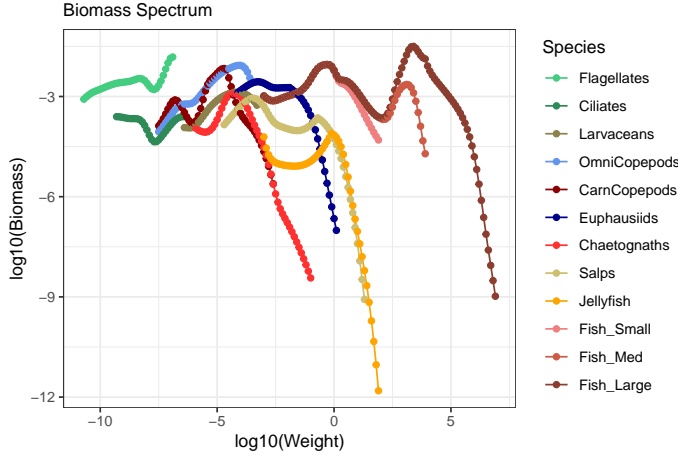
Figure 6. The biomass spectrum for all zookplankton and fish species, with a modified coefficient of search volume of $\gamma = 480$ m^{3}g$^{-0.8}$yr^{-1}.

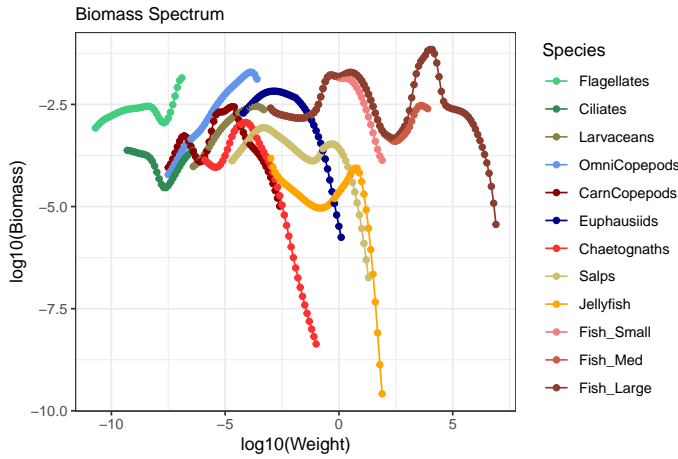**Figure 7.** The biomass spectrum for all zookplankton and fish species, with a modified coefficient of search volume of $\gamma = 800$ m^{3}g$^{-0.8}$yr^{-1}.

We ran the single-cell simulation again with non-default parameters, changing the coefficient of search volume, γ, from the default 640 m^{3}g$^{-0.8}$yr^{-1} to both 480 m^{3}g$^{-0.8}$yr^{-1} (Figures 4, 6) and 800 m^{3}g$^{-0.8}$yr^{-1} (Figures 5, 7). We see immediately that *all* timeseries biomass and growth curves are shifted downwards in the 480 case (relative to the default), while all growth and most biomass values are shifted up in the 800 case. This is reflected by the zooplankton and fish wet weight of 0.292 and 0.673 mass units respectively for the 480 case, and 0.477 and 1.565 mass units respectively in the 800 case. This makes sense, as a higher search efficiency naturally results in more food being found and more biomass being accumulated for each individual.

We see that the characteristic behaviour of the system is accelerated with a higher search volume (i.e. instability behaviour is shifted to lower time) while it is slowed with a lower search volume.

The biomass spectrum is largely similar in all cases even with a changing search coefficient. Notably, we see a strong decrease in the jellyfish spectrum 'tail' with a decreased search

coefficient, and a strong increase in the large fish 'tail' with increased search coefficient. We also note that the biomass spectrum peaks get somewhat smoothed out with a decreased search coefficient. This may be due to the reduced growth across species dampening the biomass changes (and hence clustering towards efficient weight classes).

Mathematically, the changes described in the search coefficient directly affect the growth rate of all species. For some species i, the growth rate is formulated in the McKendrick-von Foerster (MvF) model as

$$g_i(w,t) = V_i(w)\, D_{ij}(w,t)\, GE_{ij} \tag{1}$$

where $V_i(w)$ is the search rate for that predator group, expressed as

$$V_i(w) = \gamma w^\alpha \tag{2}$$

for an α search exponent, w predator weight, and γ coefficient of search rate. Naturally, a constant shift in the coefficient γ directly corresponds to a shift in the growth for that species. This explains the observed vertical shift in Figures 4 and 5 with respect to the default parameters.

Question 3

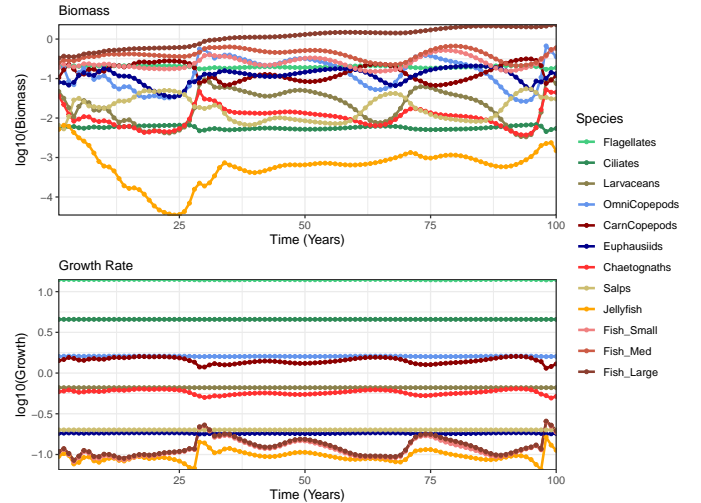Now we turn our sights to a shifting α, the search exponent in equation (2).

Figure 8. The biomass and growth timeseries data across the 100 year duration, with a modified search exponent of $\alpha = 0.7$.
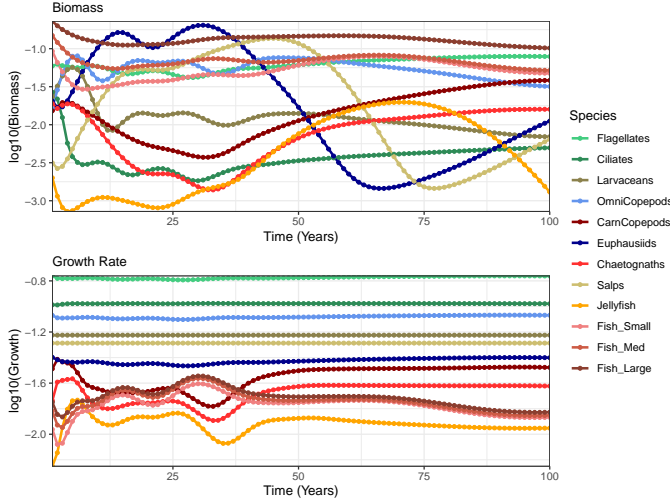
Figure 9. The biomass and growth timeseries data across the 100 year duration, with a modified search exponent of $\alpha = 0.9$.
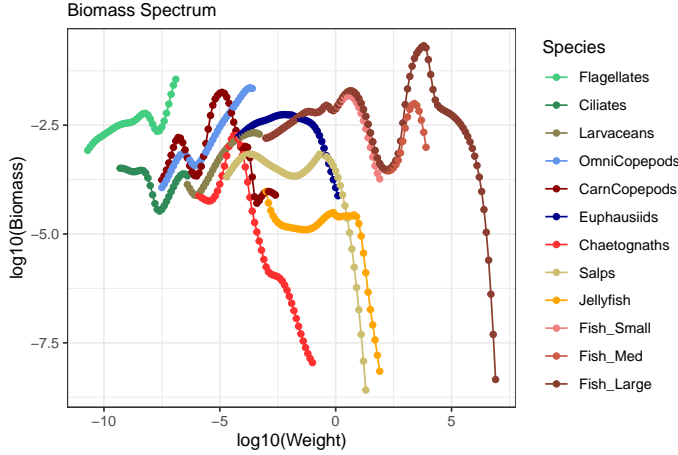

Figure 10. The biomass spectrum for all zookplankton and fish species, with a modified search exponent of $\alpha = 0.7$.
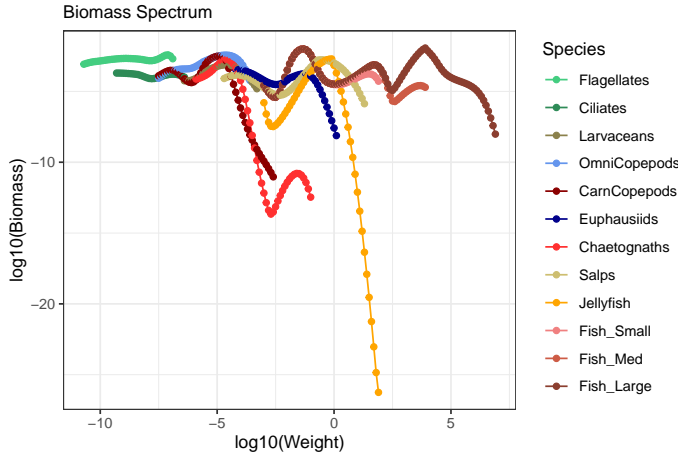

Figure 11. The biomass spectrum for all zookplankton and fish species, with a modified search exponent of $\alpha = 0.9$.

Since all individual zooplankton weights are $w < 1$ gram, we note that a smaller exponent actually corresponds to a more gradual change in search rate (eq. 2) with mass, with the contrapositive being true also. That is, a smaller exponent means that there is a smaller disparity in search efficiency between different weight class species. This results in a larger, more consistent growth rate in all species while their mass is less than 1g, which we see in our timeseries growth rate plots.

We see in Figures 8 and 9 (in comparison to the default) that the biomass and growth appear more and less stable in time respectively. In the $\alpha = 0.7$ case instabilities are sharper but are lesser in magnitude change. We see extreme change in the biomass timeseries in the $\alpha = 0.9$ case, although the growth rate appears to stabilise nearer to $t \sim 100$ years; a longer duration simulation would be needed to determine if this is truly approaching an equilibrium state.

A change in search exponent gives especially large changes in the biomass spectra for copepods in particular. We see that those copepods who have weight classes below and above that 1g characteristic value are subject to an especially steep decline for $w > 1$g when α is increased to 0.9. This is, once again, due to that increase in disparity for growth rate changes with respect to weight class; very few copepods grow to a large weight class (on account of their reduced growth rate once reaching it) and so they have a correspondingly low biomass for that large weight class.

With a search exponent of $\alpha = 0.7$, our zooplankton and fish have wet weights of 0.555 and 2.447 mass units respectively. In the $\alpha = 0.9$ case, they are 0.136 and 0.265 mass units respectively. In comparison to the default case, we clearly see a large shift in the total biomass with respect to search exponent where the lower exponent allows lower mass individuals to more efficiently search their surroundings and find food. Hence, the model output seems to be significantly more sensitive to the α value than the γ value.

Question 5

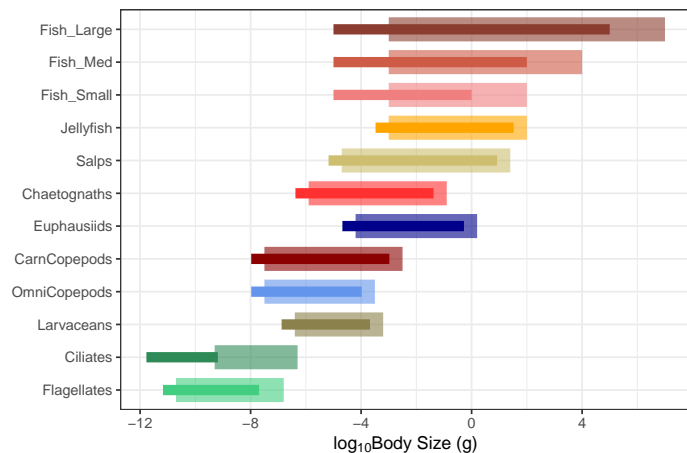Now, we set the predator-prey mass ratio (PPMR) to 3 for all zooplankton groups.

Figure 12. The predator-prey mass relationships for the modified case of a flat PPMR = 3 for all zooplankton species.
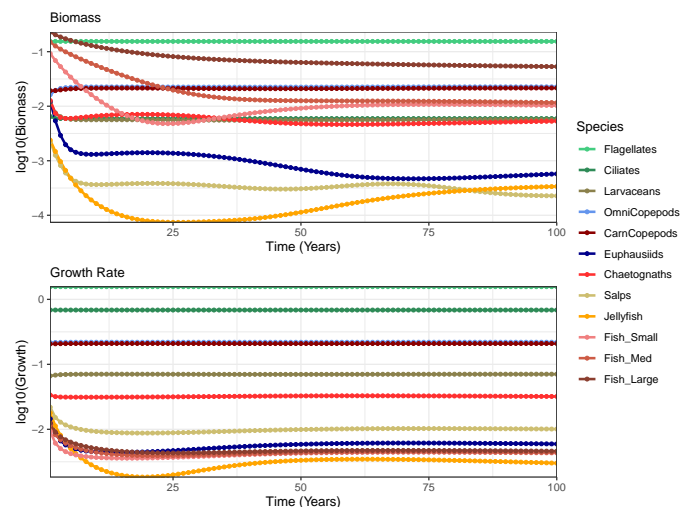
Figure 12 shows, in contrast to the default in Figure 2, that predators now only predate on prey very similar in size as expected. We see a universal drop in the growth rate across all species (apart from the Flagellates and Ciliates whose PPMR wasn't changed) as a result of the *forced* inefficiency in energy transport from the additional trophic levels in the food chain. The biomass spectrum is consequently shifted down for all affected species for this same reason. The result is a wet weight of 0.055 mass units for zooplankton, and 0.080 mass units for fish.

Finally, we see the system settle into an equilibrium (at least in growth rate) quite quickly compared to the other parameter combinations discussed in this assignment. This may be due to each predator only predating on prey immediately to the lower size class, rather than some predators competing with others across a range of size classes and hence reduces the complexity in the n predator to prey dynamics.

Question 6

We now set the PPMR to 10^6 for all zooplankton groups.

Figure 15. The predator-prey mass relationships for the modified case of a flat PPMR = 10^6 for all zooplankton species.

Figure 13. The biomass and growth timeseries data across the 100 year duration, with a modified PPMR of 3 for all zooplankton species.
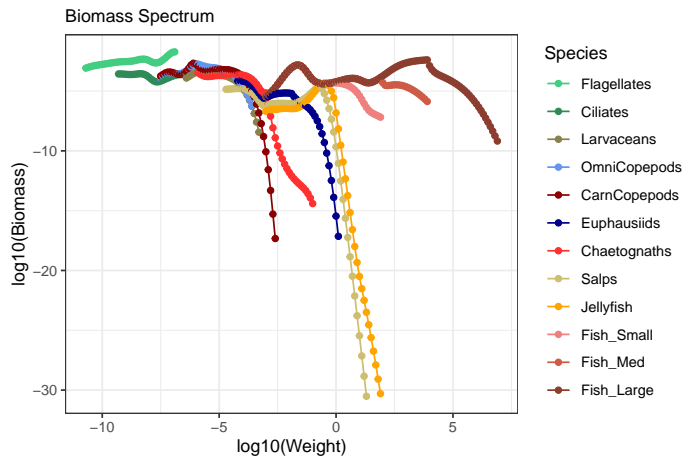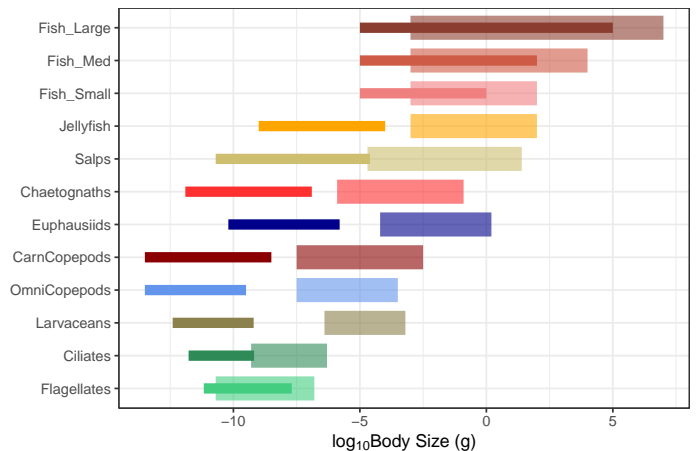

Figure 14. The biomass spectrum for all zookplankton and fish species, with a modified PPMR of 3 for all zooplankton species.
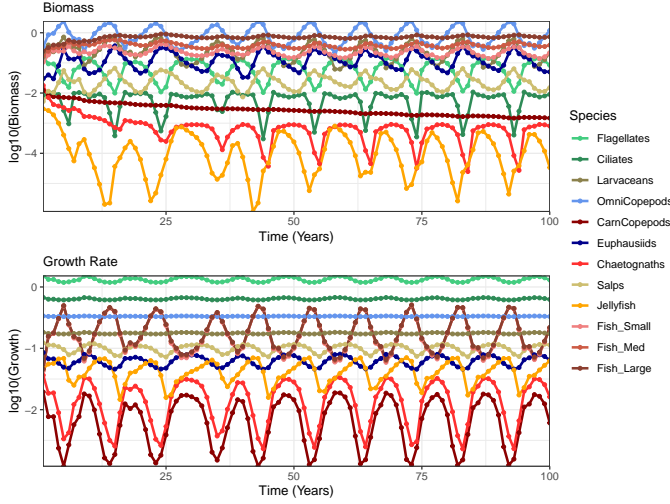
Figure 16. The biomass and growth timeseries data across the 100 year duration, with a modified PPMR of 10^6 for all zooplankton species.
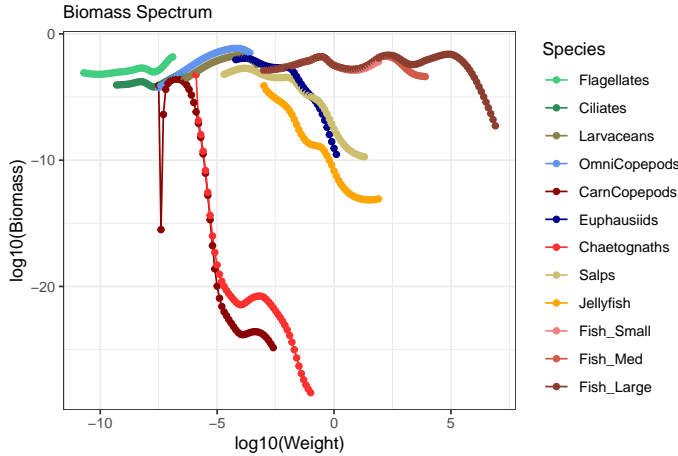

Figure 17. The biomass spectrum for all zookplankton and fish species, with a modified PPMR of 10^6 for all zooplankton species.

On setting the PPMR for zooplankton to such a high value, we clearly and immediately see quasiperiodic variation in the biomass and growth rates in the affected species. On viewing Figure 15, we see now that zooplankton are all more or less predating on similar size-class prey (and not each other). Hence, they will often collectively predate the prey to low numbers, growing to unsustainable populations (biomass) in the process and then subsequently die off. Since the predators now have a low population, the prey may now quickly repopulate (increase in biomass), and the cycle continues. We can identify the key prey and predator species by identifying lags in the oscillations of Figure 16; clear and prominent examples are omnivorous copepods/larvaceans and flagellates, euphausiids/salps and ciliates, etc. Interestingly, we see that the strictly carnivorous zooplankton suffer in this scenario, as given by their steep biomass curves in Figure 17. Similarly, we see a strong decrease in their timeseries growth rate. This is due to the increased competition from other,

omnivorous zooplankton who are now taking advantage of a rich prey ecosystem in a lower trophic level. As fish (of all sizes) prey on these carnivorous zooplankton in particular, we see oscillatory behaviour in the fish biomass and growth over time as a direct result of the zooplankton oscillation.

The zooplankton biomass spectrum appears to be shifted up and flattened significantly (with respect to the default) for the lower mass, omnivorous species. This is reflected in their wet weight of 1.409 mass units, while the fish stayed relatively similar to the default with 1.324 mass units of wet weight.

Question 7

The previous two questions show that a change in PPMR across the board results in significant changes in the system behaviour over time. A low PPMR tends to suit the growth of carnivorous zooplankton on account of the reduced competition from their omnivorous counterparts, and forced predation on more like-size species. A large PPMR means that all (or at least most) zooplankton species are all feeding on the same prey and so the interspecies competition gives rise to oscillatory instabilities. On comparison with the default case, we can conclude that lower PPMRs yield higher stability in the system and higher yields instability.

In direct correlation with the instability, we suppose that these carnivorous zooplankton tend not to live as long (due to the greatly fluctuating availability of food) and so they tend to not grow as large. This gives the steep size spectrum that we see in Figure 17 in comparison to Figure 14.

All of the qualitative statements made before are supported on analysing the behaviour of the prey density term, D_{ij}, in equation (1),

$$D_{ij}(w,t) = \int_{w_p}^{w} \phi_i(w,w') \ N_j(w',t) \ w' \ dw' \qquad (3)$$

where ϕ_i describes the probability of predator species i eating some prey of species j. Since many predator preferences in the 10^6 PPMR case are now clustered around a very few number of prey species, the number of prey N_j quickly dwindles for some constant probability ϕ_i (summed across all predators). The result is a correspondingly lower density of that prey, which means a lower growth rate for all those predators and an unsustainable population subsequently lowers. A lower PPMR means that fewer predators prefer some individual prey species, and so N_j can stay relatively large for a constant ϕ_i. The result is a more gradual transfer of energy across trophic levels which avoids the instability associated with a high PPMR.

In the low PPMR case, we see a tendency for a low biomass in fish of all size classes due to their high trophic level and the inefficiencies in energy transport across levels. With a high PPMR, the fish have a lower trophic level (as their prey does) and so they have more access to energy. This is reflected in the comparison of their wet weights between PPMR changes,

where a more efficient energy transport results in a larger total biomass.

Question 10

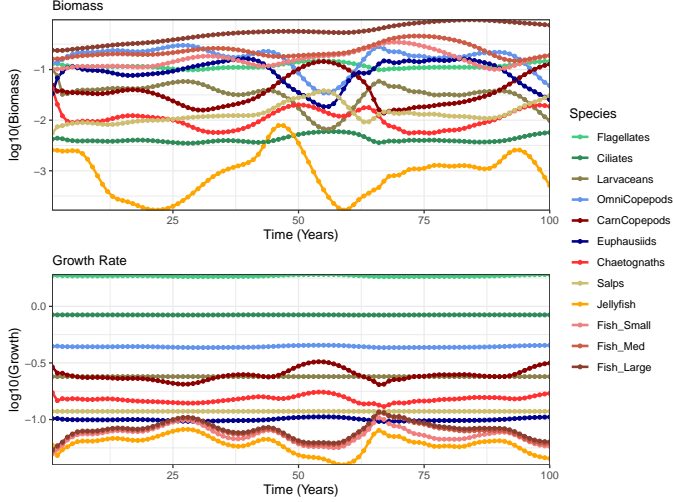We now increase the average temperature in the single cell simulation by 3°C.

Figure 18. The biomass and growth timeseries data across the 100 year duration, with a modified temperature of 3°C above the global mean (i.e. 18°C).
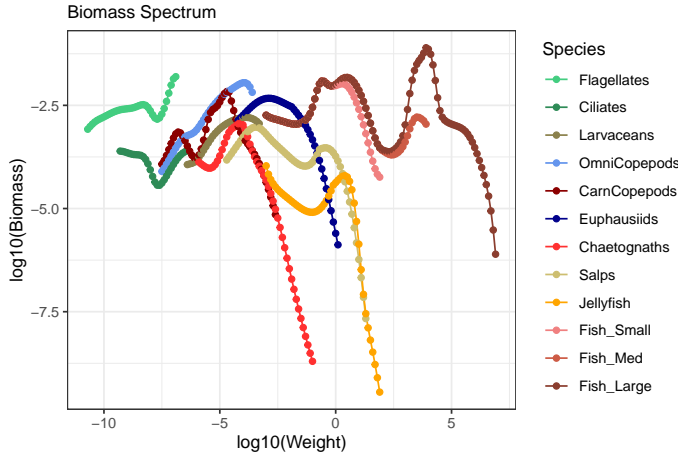

Figure 19. The biomass spectrum for all zookplankton and fish species, with a modified temperature of 3°C above the global mean (i.e. 18°C).

To emulate behavioural changes in tropical vs arctic (as two disparate examples) species, the ZooMS model modifies equation (2) to include a unitless temperature multiplier, ω,

$$V_i(w) = \omega \gamma w^\alpha \tag{4}$$

where higher temperatures correspond (nonlinearly) with a higher parameter value according to the Q_{10} equation,

$$\omega = Q_{10}^{\left(\frac{T - T_{\text{ref}}}{10}\right)} \tag{5}$$

for some simulation temperature T and reference temperature unique to each species. Here, the reference temperature describes the optimal conditions for a species i to search their environment for food. With a wet weight for zooplankton of 0.366 mass units and 1.246 mass units for fish, we see effectively the same trends in the biomass spectrum and timeseries data for a larger search coefficient but without the associated increase in biomass magnitude. That is, a temperature increase largely emulates the behaviour of the $\gamma \sim 800$ simulation where the behaviour of the system is accelerated compared to the default case. On looking at equation (4) we see that a temperature increase is mathematically the same as a search coefficient increase for an individual species, where the inconsistency between this temperature case and the $\gamma = 800$ case lies in the different species having different optimal temperatures for searching; some species adapt better to the temperature (euphausiids, large fish) while some do worse (namely chaetognaths) as given by their biomass spectrum tails.

Of course, this simple single cell simulation is analysing the *mean* temperature behaviour in the oceans. Increasing this cell's temperature by 3°C effectively just shifts (what would be) the cell's true position from a medium latitude towards the equator. In this sense, we still expect some stable behaviour from the system and this is exactly what we see.
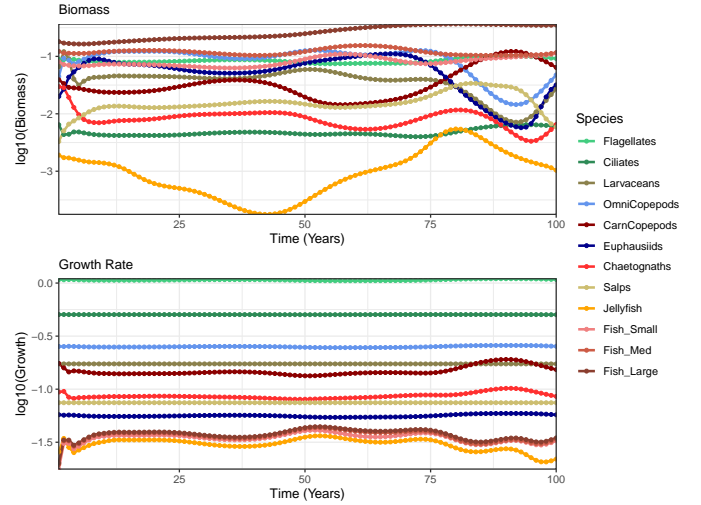
Question 11

Figure 20. The biomass and growth timeseries data across the 100 year duration, with a modified chlorophyll-α 25% below the default (i.e. 0.15).
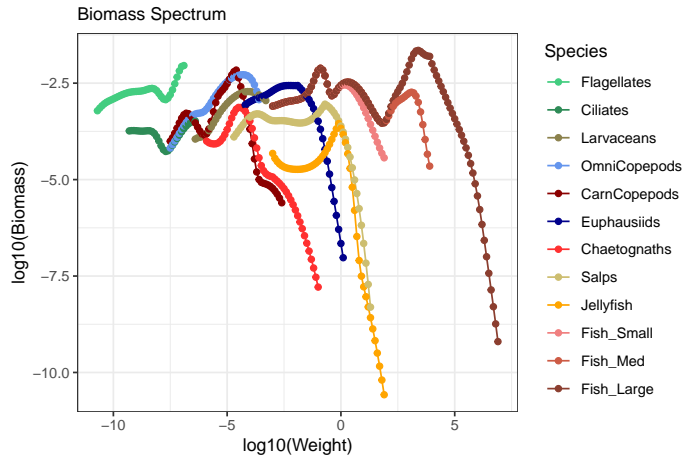
Figure 21. The biomass spectrum for all zookplankton and fish species, with a modified chlorophyll-α 25% below the default (i.e. 0.15).

On decreasing the chlorophyll-α concentration, we see that the high-weight tail of the biomass spectrum is most affected in species that eat the lowest-mass prey. That is, the ciliates, larvaceans, and omnivorous copepods have their high-weight individual biomass significantly reduced. As these species form a bulk of the biomass in the lower trophic levels, all subsequent species are affected. Hence the search efficiency is reduced for higher-weight prey, effectively emulating a reduction in the γ parameter and lower wet weights of 0.250 mass units for zooplankton and 0.553 mass units for fish. The growth rates and total biomasses are hence reduced across all species, and we see that carnivorous species (chaetognaths, carnivorous copepods) biomass spectra are impacted in particular.

The actual direct result of a decrease in chlorophyll-α is a shift in the proportion of phytoplankton size classes (Lecture 4 slides, page 20). Where the chlorophyll-α decreases, phytoplankton are increasingly (in proportion) smaller in size (micro vs pico prefixes) and so it effectively increases the trophic levels of all zooplankton automatically and decreases the energy transport efficiency. Hence the biomass and growth rate of all species is reduced.

With all of this in mind, based on an very simplified model, we posit that climate change affecting the chlorophyll-α results in more significant changes relevant for the future fisheries compared to warming, on account of the reduction in overall biomass. Perhaps for a global simulation (instead of a single cell), we might see some more significant changes in biomass as warming shifts specific ecosystems away from the equator and the dissolution of existing ant/arctic ecosystems.