**Modelling marine plankton community response to increasing atmospheric CO2 levels**

The effects of anthropogenically-driven climate change throughout the twenty-first century will significantly affect oceanic primary productivity (Krumhardt et al., 2017). Altered atmospheric CO2 levels are expected to affect the ocean biogeochemical cycles in a manner which will directly impact plankton communities according to well-understood physiological responses. Metabolic rates in phytoplankton species are positively affected by rising temperature (Padfield et al., 2016), as are heterotrophic respiration rates (Regaudie-de-Gioux, Duarte, 2012). Importantly, higher temperatures increase phytoplankton photosynthetic carbon assimilation rates and nutrient uptake rates in particular (Trombetta et al., 2019), in addition to zooplankton grazing rates (Chen, Laws, 2017).

Primary productivity is expected to be impacted negatively by the effects of increased stratification in the tropics and subtropics, and positively by decreased mixed layer depth and increased sea surface temperature (SST) in the high latitudes (Boyd, Doney, 2002). Increased stratification is expected to exaggerate tropical oligotrophication due to depleted surface-layer nutrients resulting in nutrient limitation of phytoplankton in the surface layer (Mojica et al., 2014), limiting primary productivity. In high latitudes, decreased mixed layer depth provides more favourable light conditions for phytoplankton growth (Schofield et al., 2018) which acts in conjunction with positive effects of elevated temperatures on plankton biomass. At high latitudes, communities will benefit from increased iron and phosphate as a result of atmospheric processes (Compton et al., 2000, Deppeler, Davidson, 2017, Terhaar et al., 2021)

Associated community composition changes will therefore vary by region. In eutrophic high latitude waters, with increased SST, top-down regulation of phytoplankton by zooplankton increases; larger phytoplankton experience reduced grazing pressure (Acevedo-Trejos et al., 2015). This is exacerbated by a higher impact of temperature on heterotroph metabolism (Boscolo-Galazzo et al., 2018). In the tropics and subtropics, greater stratification will enforce bottom-up control (nutrient limitation) on phytoplankton populations, driving communities towards a lower cell size, as greater nutrient assimilation efficiency is required (Tsiola et al., 2016), and towards lower overall biomass (Gasol et al., 1997). In terms of overall global biomass, whilst there will be a regional variation in response to global warming, decreased overall primary productivity is the most likely outcome of future global warming trends (Behrenfeld et al., 2006)

The myriad of complex effects of increasing atmospheric CO2 necessitates the use of predictive models built on our current understanding of the processes involved in earth and ocean system dynamics. Such models are key in understanding expected changes in primary productivity and oceanic food web structure, which will carry consequences for our interactions with global ecosystems. Here, the ECOGEM package extension to the EcoGENIE Earth System Model is used to simulate alterations in plankton community dynamics in response to global warming effects predicted in the Earth System model, using Representative Concentration Scenario 8.5 for atmospheric CO2 projections. Surface inorganic nutrients pass through a complex plankton community; here updated environmental conditions as per EcoGENIE projections impact production and export. Altered community composition is modelled through responses of different phytoplankton zooplankton size groups with set ecophysiological parameters.

Decreased spatial and temporal resolution relative to other modern ecosystem models is a necessary feature of this model in extending large-scale annual predictions over a significant time period; this model is built to output broad regional predictions rather than representing intricate differences between smaller-scale locales. Some simplification of plankton community dynamics in regards to heterotrophic activity, and assumed instant remineralization of organic matter may also decrease predictive power. Further limitations of this model are found in the use of closed system nutrient cycling, and the authors note underrepresentation of nutrient cycling in some areas.

**Experimental setup**

Briefly, 8 phytoplankton size classes are introduced. The effects of water temperature, nutrient uptake, photosynthesis and zooplankton grazing pressure are regulated to different degrees according to size class. The 8 different zooplankton classes are also distinguished in respiration rate, temperature limitation and grazing rate. Top-down zooplankton control also differs according to food source availability. Organic matter in the water column results from imperfect assimilation by zooplankton, and phytoplankton and zooplankton mortality, and is remineralized instantly. The full alterations to the EcoGENIE model provided by the ECOGEM package are described by Ward et al. (2018).

The RCP 8.5 scenario utilized in this model (Fig. 1) is sourced from a series of greenhouse gas emission projections described by Moss et al. (2010). Out of these, the RCP 8.5 scenario represents the pathway with the highest relative greenhouse gas emissions scenario. The use of ‘worst-case scenario’ projections here is used because it should result in the most extreme and therefore most easily identifiable changes in plankton community composition.

**A**

**Chart

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***Figure 1*** *- Increasing atmospheric CO2* ***(A)*** *and global mean SST* ***(B)*** *from 1765-2010 (highlighted in grey) from 2010 to 2100.*

**Results**

Differences in SST are most pronounced at the equator and at high latitudes in the Pacific, and generally decrease with distance from the equator (Fig. 2); in the Arctic and Southern oceans the increase is far less pronounced.

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**Figure 2** – Global variation in relative increase between RCP 8.5 and Control predicted sea surface temperature.

Polar regions also present different changes in predicted mixed layer depth (Fig. 3). At high latitudes, a decrease in mixed layer depth is observed. Unlike sea surface temperature however, predicted mixed layer depth is more and more similar closer to the equator, where it is unchanged.

Graphical user interface

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**Figure 3** – Global variation in relative increase between Control and RCP 8.5 predicted sea surface temperature.

Ocean surface nutrient predictions also differ in polar waters (Fig. 3). Control surface phosphate predictions are equivalent at the equator, and at high and low latitudes higher than in the RCP 8.5 scenario (Fig 3A). Dissolved surface iron shows almost the opposite pattern; it is higher in the RCP 8.5 scenario predictions outside the polar regions, and lower closer to the equator (Fig 3B).

**A**

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**Figure 4** – Variation in Control and RCP 8.5 predicted average latitudinal surface phosphate **(A)** and iron **(B)** concentrations in 2100.

Particulate Organic Carbon (POC) export flux is decreased in the RCP 8.5 scenario model predictions compared to the control scenario at most latitudes (Fig. 5). The opposite is true however for Southern Ocean waters. These trends are mostly reflected in total plankton carbon biomass (Fig. 6). Here though, the Antarctic predictions are no different from other latitudes; predictions are globally lower than in the control scenario. Likewise, chlorophyll biomass is lower globally (Fig. 7).

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**Figure 5** – Variation in Control and RCP 8.5 predicted average latitudinal POC export in 2100.

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**Figure 6** – Variation in Control and RCP 8.5 predicted average latitudinal carbon biomass in 2100.

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**Figure 7** – Variation in Control and RCP 8.5 predicted average latitudinal chlorophyll biomass in 2100.

These biomass differences are not reflective of uniform responses in plankton communities. RCP 8.5 Picophytoplankton chlorophyll biomass is greater at high and low latitudes, whereas Nanophytoplankton chlorophyll biomass is lower globally. On the other hand, microphytoplankton chlorophyll biomass is higher in Antarctic waters, and consistently lower above.

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**Figure 8** – Global variation in relative decrease between control and RCP predicted 8.5 picophytoplankton **(A),** nanophytoplankton**(B)** and microphytoplankton biomass.

Associated changes in geometric plankton cell size reflects mostly the trends in microphytoplankton chlorophyll biomass. RCP 8.5 scenario mean cell size is higher in the Southern Ocean, and generally lower above this region, though at the very high latitudes in the Arctic ocean it is greater again (Fig. 9A). The standard deviation of cell diameter in the Southern Ocean is markedly larger than at the tropics, being larger in Antarctic waters and equal at the equator (Fig. 9B). There is however also a greater difference in the north Atlantic and Mediterranean.

**A**

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**Figure 9** – Global variation in relative increase between RCP 8.5 and Control predicted mean cell diameter **(A)** and standard deviation of cell size **(B)**.

**Discussion**

Evidence for an altered high latitude plankton community composition in the RCP 8.5 scenario is seen in biomass and POC export flux trends. Globally, plankton carbon and chlorophyll biomass is decreased. POC export flux however is increased in the Southern ocean and decreased elsewhere. Total biomass decrease when coupled with an increased Southern Ocean export flux clearly marks significant plankton community composition changes, not simply lower overall plankton populations. Consistent with this, higher cell diameter and standard deviation is predicted in the southern high latitudes, which is reflective of an increase in the local relative biomass of larger size classes. Drivers of community composition change are less pronounced in the northern high latitudes, as cell diameter is equal or lower than in the control scenario; nevertheless different standard deviation indicates some community composition shift. In the low latitudes, a clear overall change in phytoplankton community structure is manifested in a shift towards the smaller size classes, reflected in a relative decreased geometric mean of cell diameter. This decrease is particularly pronounced at the equator. Standard deviation is essentially unchanged however.

Differing high latitude predicted community structure can be explained firstly through increased zooplankton grazing pressure on phytoplankton. This grazing pressure occurs due to increased SST, allowing an accompanying higher growth rate and therefore increased overall zooplankton biomass. Resultant higher grazing pressure causes an increase in population in larger phytoplankton classes, as the smaller classes are more affected by grazing pressure. Here, imperfect assimilation of phytoplankton biomass by zooplankton grazers bears increased POC export flux in the Southern Ocean. This is not replicated in the northern high latitudes however. This may be due to smaller relative zooplankton populations. This assumption is supported by the fact that lower carbon biomass, but similar chlorophyll biomass is predicted in these regions in comparison to the southern high latitudes.

Predicted SST differences in the high latitudes are more extreme, often surpassing 2C. However, this temperature increase in the equatorial regions does not translate to an increase in plankton biomass. Increased temperature-dependent metabolic processes are thus offset by other factors. Low cell size and standard deviation indicates that the top-down control of phytoplankton by zooplankton grazing seen in the high latitudes is in contrast with clear bottom-up control of phytoplankton in the low latitudes, likely with increased grazing refuge.

Some simplification of community dynamics here, namely the uniform treatment of the response of heterotrophic behaviour and photosynthesis to increased temperature may result in an underestimation of grazing pressure (Ward et al., 2018), as heterotroph metabolism in fact increases at a greater pace (Boscolo-Galazzo et al., 2018). As grazing pressure shapes phytoplankton community structure and biomass, as well as POC export flux, there is some degree of underrepresentation of relative changes in these in the high latitudes. This underrepresentation is unlikely in the tropics on the other hand; different treatment of heterotrophs would not impact low latitude predictions as these are too limited by nutrients. Overall though, the model’s prediction of enhanced zooplankton grazing in eutrophic waters with global warming is consistent with current understanding of plankton community dynamics (O’Connor et al., 2009, Chen et al., 2012).Indeed, this trend has been observed in real world shifts by zooplankton communities towards the poles since pre-industrial times (Jonkers et al., 2019). These trends observed in the model output as such are likely predictive of future real-world changes.

High iron and phosphate nutrient flux occurs in the high latitudes in both scenarios. In response, increased cell diameter and standard deviation relative to the tropics are predicted, reflecting different plankton community structure. Decreased high latitude surface nutrient levels however are predicted by the RCP scenario relative to the control. As such, in isolation, nutrient availability would predict greater total biomass, cell size and standard deviation in the control; lower surface nutrients in the RCP 8.5 scenario should result in smaller phytoplankton populations as smaller phytoplankton classes are more efficient in nutrient uptake. This is only observed in the high latitudes. This indicates that a combination of increased zooplankton grazing and slightly higher nutrient limitation explains why Southern Ocean biomass is lower, yet mean cell size and standard deviation is higher. Significantly lower phosphate flux in northern relative to southern high latitudes though indicates nutrient limitation is the important differentiating factor in decreased mean cell size in these regions. Lower phosphate and iron levels compared to the control scenario indicate nutrient limitations on cell size in phytoplankton as greater nutrient stress results in a greater competitive advantage for smaller plankton capable of higher nutrient uptake and assimilation efficiency.

The model predicts relative decreased mixed layer depth at high latitudes in the RCP 8.5 scenario, though not at the equator. This would drive elevated photosynthetic, heterotrophic respiration and universal planktonic growth rates due to irradiance and higher temperature. This would as such represent a driver towards greater total chlorophyll and carbon plankton biomass. In combination with greater nutrient availability, in particular elevated surface iron, this may explain abnormal differences observed in North Atlantic plankton community composition in comparison to close-by high latitude regions. Like these regions, high standard deviation and decreased mean cell size is seen, but carbon biomass sees a sharp decrease in this region compared to nearby latitudes, whereas chlorophyll biomass does not. This is the case for both the RCP 8.5 and control scenarios, and in fact more pronounced changes, along these lines as a result of global warming are predicted in the north Atlantic (Barton et al., 2016). The model predicts a sharp increase in mixed layer depth in this region may here result in a plankton community which is not highly nutrient-limited, but is limited by decreased temperature and irradiation. The effect of these limitations may be a decreased phytoplankton cell size as a response to a higher need for photosynthetic efficiency, acting in concert with temperature pressure on zooplankton populations. Zooplankton populations in this case may be decreased, but still large enough to exert influence on phytoplankton cell size standard deviation.

As noted by the authors, surface phosphate in several regions is underestimated by the model, largely due to an underestimation of upwelling. In the northern high latitudes, this may translate to exaggerated prediction of phosphate limitation. With a decrease in this limitation, the northern high latitudes in the RCP 8.5 scenario may follow trends seen in the Southern Ocean, with increased zooplankton biomass, phytoplankton cell size and standard deviation, and POC export flux. Lower total plankton biomass relative to the control would still be expected, as this underestimation also limits control populations.

Another limitation of this model is it’s use of a fixed oceanic phosphate inventory, assuming remineralization of all organic phosphorus with no additional input. Therefore this model does not account for the fact that atmospheric CO2 is projected to drive both an increase in oceanic phosphate levels through enhanced weathering and a decrease due to organic carbon burial (Baroni et al., 2020). There are also further model limitations in nutrient cycling configuration. Changes in iron inventory through atmospheric iron deposition are included in the model, however the full complexity of processes involved in the iron cycle, which is affected for example by vegetation cover (Baroni et al., 2020) is not included. The fixed inventory of iron is also in opposition to projected increase in iron inputs (Maher et al., 2010)

Decreased global surface phosphate, with lower phosphate flux due to increased stratification between 2010 and 2100 is in line with projections by other models. (Fu et al., 2016, Moore et al., 2018). Though surface iron level predictions by EcoGENIE may be simplified, these other models likewise predict increased iron flux through to 2100AD. Phosphate limitation appears to be a very important factor in determining future plankton community composition. EcoGENIE may in this regard be more limited than other models in areas where it underestimates phosphate upwelling.

Overall, large-scale changes in phytoplankton and zooplankton community structure resulting from elevated projected increased atmospheric CO2 levels are seen, in line with other models and current understanding of plankton community dynamics. In some areas, predictive power in comparison with other models is limited in nutrient flux. However, the model clearly provides clear general predictions of the responses of global plankton communities to increasing atmospheric CO2 through the twenty-first century which provide us with a basis for understanding how oceanic primary productivity will change over the next 80 years.

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