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Environmental selection for small cell size in phytoplankton

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1 Summary

We describe a new trait-based model for cellular resource allocation that we use to investigate the relative importance of different drivers for small cell size in phytoplankton. Using the model, we show that increased investment in nonscalable structural components with decreasing cell size leads to a trade-off between cell size, nutrient and light affinity, and growth rate. Within the most extreme nutrient-limited, stratified environments, resource competition theory then predicts a trend toward larger minimum cell size with increasing depth. We demonstrate that this explains observed trends using a marine ecosystem model that represents selection and adaptation of a diverse community defined by traits for cell size and subcellular resource allocation.

2 Motivation

• Phytoplankton cell size is often viewed as a "master trait", influencing the competitive ability of phytoplankton in different environments, the trophic structure of marine food webs, and various biogeochemical cycles (Litchman & Klausmeier, 2007).

• Size-dependent trade-offs in phytoplankton are reflected in the overall allometric scaling of organism growth rate (Figure 1). However, there remains considerable uncertainty regarding the relative importance of different traits and their relationship to cell size.

• Here we explore the hypothesis that an apparent reduction in growth rate for the smallest cells reflects the necessary allocation of resources to nonscalable structural components (Raven, 1994), using a trait-based model of subcellular resource allocation.

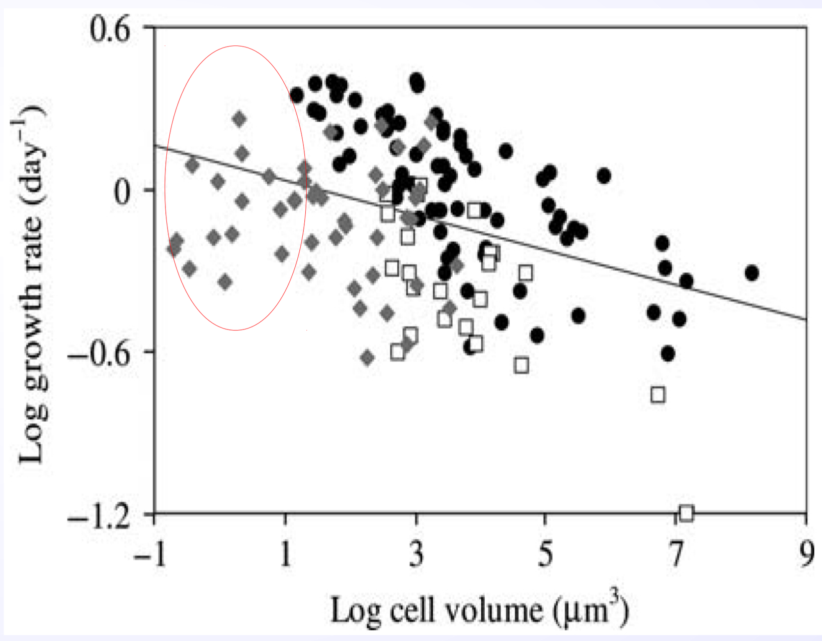

Figure 1 Size dependence of temperature-corrected growth rate for various taxonomic groups. From Finkel *et al.,* (2010).

3 Resource allocation and traits

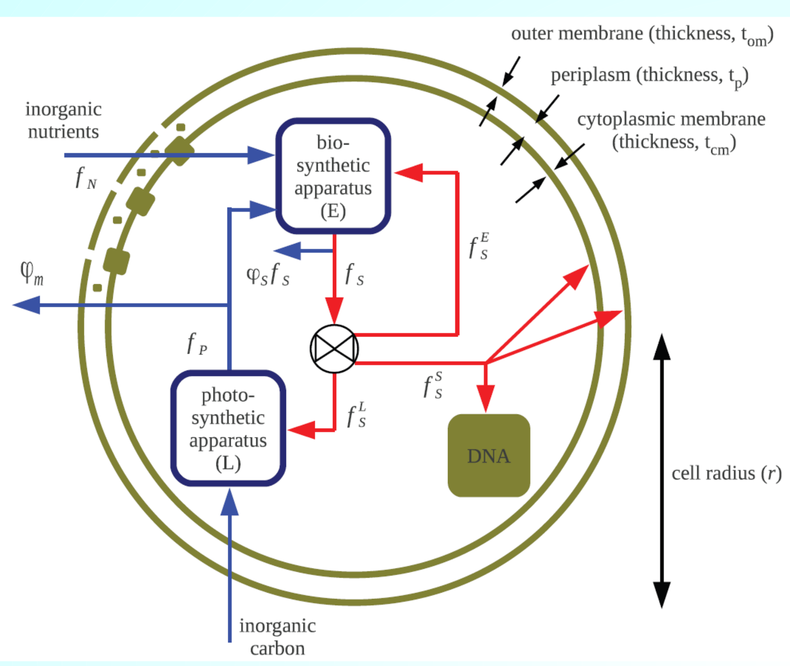

Figure 2 Model schematic.

Subcellular resource allocation within physiological constraints

• Allocation strategies (c.f. Shuter, 1979) and organism cell size are included as genetically defined quantities.

• Organismal traits (e.g. light or nutrient affinity) and trade-offs are determined by the adopted resource allocation strategy (Tilman, 1990) and basic physiological constraints.

Resource competition and optimal phytoplankton cell size

• Predicted growth rates for optimally allocating cells under high and low light conditions are shown in Figures 3A and 3B respectively.

• The predicted optimal cell size and corresponding equilibrium nutrient concentration follow from resource competition theory.

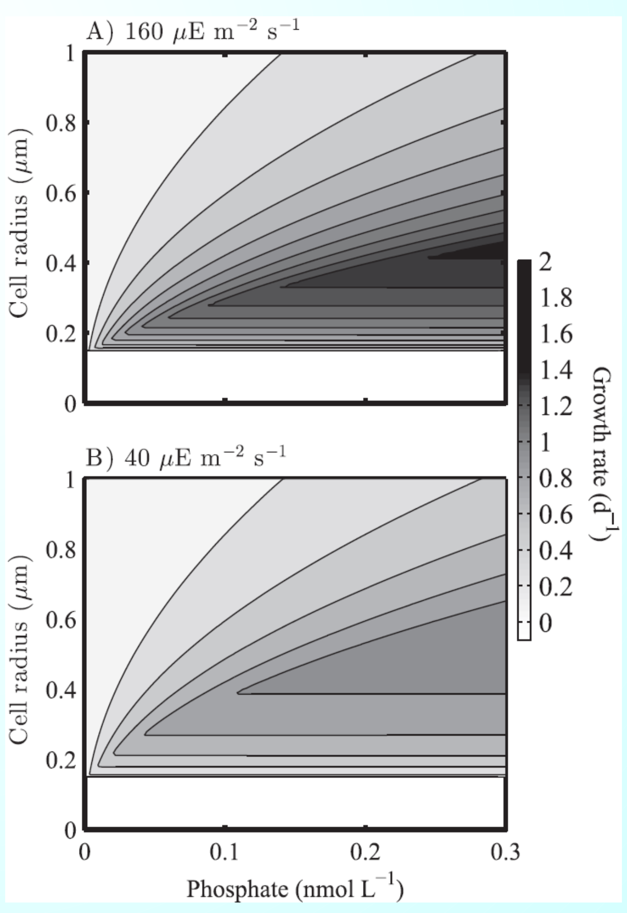

Figure 3 Predicted growth rates for optimally allocating cells.

4 Environmental selection in a model ocean

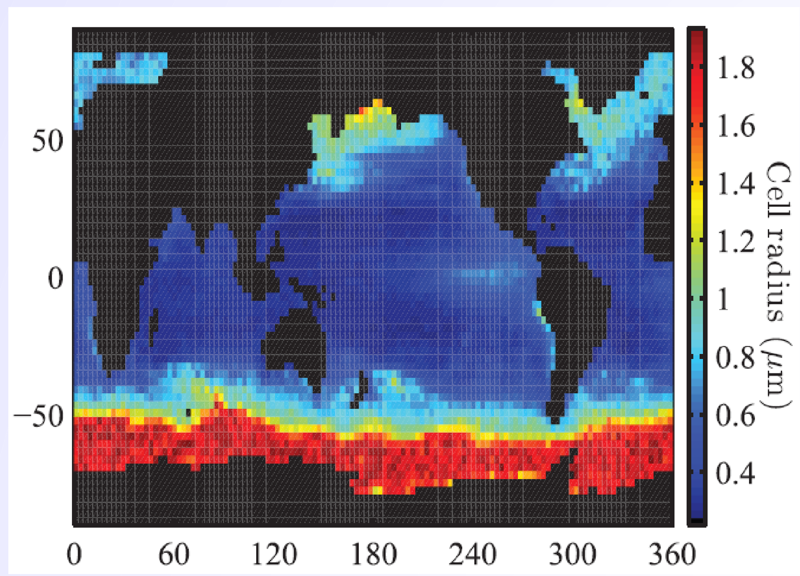

Figure 4 Annual mean population cell size.

• Spatial patterns in phytoplankton cell size obtained by nesting the trait-based model of subcellular resource allocation in an evolutionary individual-based marine ecosystem model, coupled to the MIT OGCM (Clark *et al*., 2013) are shown in Figure 4.

• Smaller cells dominate in stable low-latitude oligotrophic environments, where competition for resources results in the competitive exclusion of larger cells.

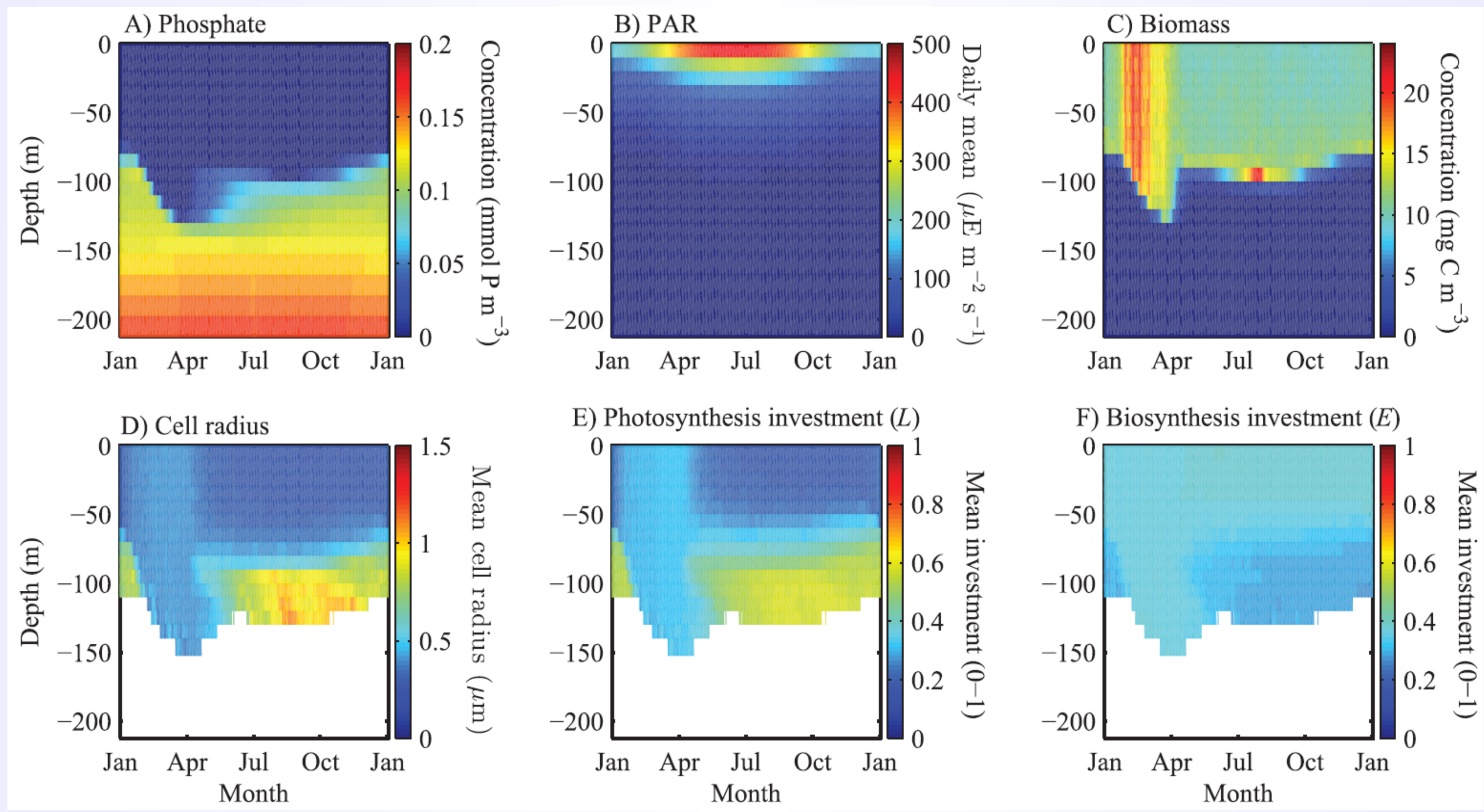

Figure 5 Seasonal dynamics at BATS.

• Seasonal dynamics in a 1-D environment representative of the oligotrophic Bermuda Atlantic Time Series (BATS) site in the Sargasso Sea are shown in Figure 5. Increases in (pico) phytoplankton cell size in the deep chlorophyll maximum are in qualitative agreement with observations for *Prochlorococcus* at BATS (DuRand *et al.,* 2001).

• As the water column stratifies coming into the summer, larger cells are competitively excluded (Figure 6).

• However, the observed prevalence of larger picoeukaryotes is not reproduced, possibly reflecting the absence of phagotrophy in the model (Hartmann *et al.*, 2012).

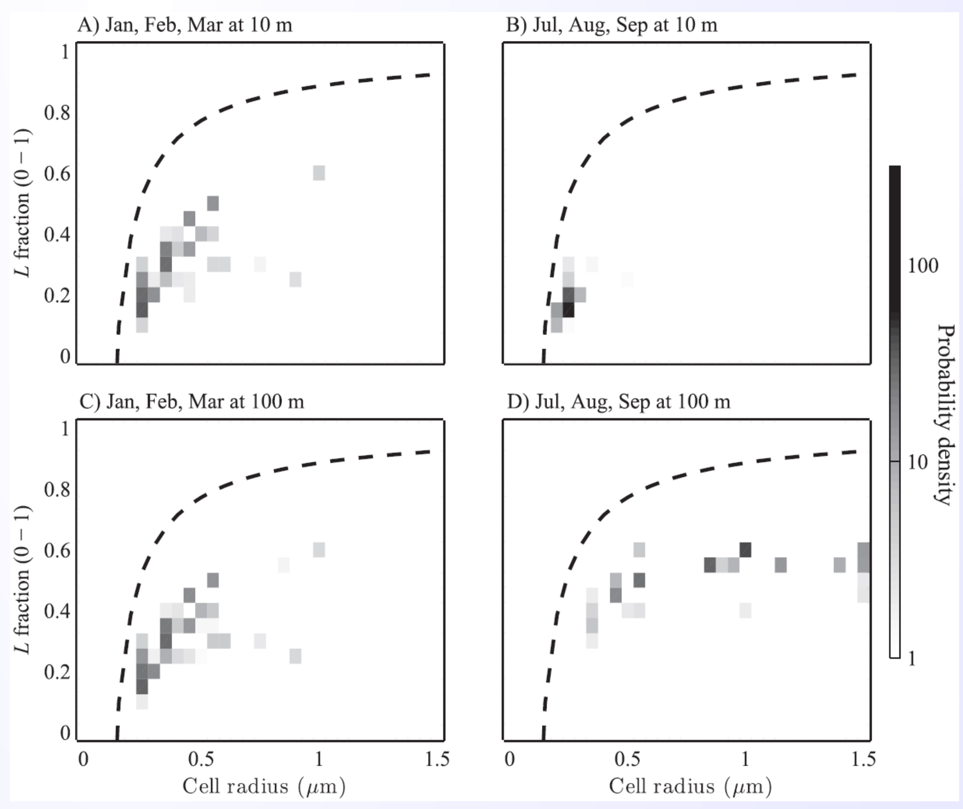

Figure 6 Time integrated agent biomasses during the spring bloom, and during the summer for two depth slices: one at 10m, and one at 100m.

5 Conclusions

• The model indicates that the necessary increased allocation of resources to non-scalable structural components in small cells results in a trade-off between growth rate, light and nutrient affinity, and cell size, which is consistent with observed trends in picophytoplankton cell size in oligotrophic environments.

• Our approach has also been extended to look at trends in organism stoichiometry (Toseland *et* al., In press; Daines *et al.*, In review).

References
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