



SCIENTISTS IN CHARGE

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TITLE OF THE PROJECT

«Predicting plankton ecosystem response to 21st century climate change in a Global Ocean Model with Microbial Adaptation (GOMMA)»

SUMMARY

Marine microbes and among them planktonic primary producers are key players for the ecosystem functioning of the Earth oceans. Microbial plankton mediate the cycling of elemental nutrients, they are the basis of the food web that leads to fish production harvested by human societies, and they regulate the atmospheric climate by fixing carbon dioxide. The fate of microbial plankton communities under expected future climate change conditions is thus an area of great interest for both researchers and policy makers. Most of our current predictions of the ocean state in the future rely on computer simulations with numerical models that simulate the dynamics of microbial plankton. These models include most of the major **ecological** processes that affect the microbial communities in the sea, such as the uptake of nutrients, the harvesting of solar irradiance, the effect of temperature on the physiological rates, and the predation losses due to higher trophic level zooplankton. Some of the most state-of-the-art global ecosystem models of microbial plankton can also simulate many different ecotypes competing simultaneously. However, all these global models neglect the **evolutionary** dynamics of microbial populations which are known to allow them to adapt to changing environmental conditions. That is, the current generation of global ocean models of microbial plankton are missing a really critical key ingredient as is the **adaptive evolution** of the microbial ecotypes they are simulating. The physiological traits of these ecotypes in the real ocean are not constant as current models assume, but they can mutate in time at decadal scales. Therefore the current projections of microbial biogeography and ocean state in the future climate may be biased due to this lack of adaptation mechanisms of the simulated microbes. Global ocean ecosystem models should include the **ecology & evolution** (eco-evo) of microbial plankton to accurately simulate the expected changes in the patterns of diversity, community assembly and ecosystem functioning (i.e. productivity, stability) under future global warming conditions [1]. The GOMMA project will for the first time 1) include eco-evo dynamics into a model of microbial plankton in continuous-trait space at the global ocean scale; 2) simulate several evolving populations with the eco-evo model, each of them with adaptive capacity along a three-dimensional fitness landscape (nutrients, temperature, irradiance); 3) simulate the eco-evolutionary trajectories of microbial plankton to the future (2000 - 2100) using scenarios of climate change (IPCC Representative Concentration Pathways: RCP 2.6 – RCP 8.5 emission scenarios). Ecological indicators of ecosystem functioning such as primary production, biological carbon pump, community trait diversity, and food web structure, will be computed, analysed and compared to simulations using the same model without eco-evo dynamics. The overarching goal is to **evaluate the potential of adaptive evolution** to impact the response of marine ecosystems to current and future environmental changes.

Box 1 | Theoretical background

Lets assume a phytoplankton community, where each individual belongs to a phenotype defined by the values of N different functional traits ($\mathbf{x} = x_1, x_2, \dots, x_N$). The abundance of each phytoplankton phenotype is controlled by its reproduction rate by nutrient uptake $u(\mathbf{x})$ and its death rate by grazing mortality $g(\mathbf{x})$. The net growth rate $a = (u - g)$ provides a measure of «ecological fitness» because it determines what phenotypes grow fastest and become the most abundant if given enough time, and what phenotypes decline. In a discrete model, all individuals are divided into a finite number of phenotypes, and the state variables are the abundances of these phenotypes. This is the classical approach in phytoplankton modeling. By contrast, in the continuous approach we will use in GOMMA, the traits are assumed to follow a multivariate normal distribution, and the model state variables are the moments of the trait distribution up to the second order: total phytoplankton biomass (P), mean trait values (\bar{x}_i), trait variances (V_i) and covariances between traits (C_{ij}). These state variables are also called aggregate properties, because they characterize the whole community, not any particular individual or phenotype. The changes in the aggregate properties are described by the equations of adaptive dynamics, derived by making a Taylor expansion of the reproduction and net growth rates around the mean trait values [2]. The growth of the population depends on the net growth rate of the fittest species, with correction terms accounting for the presence of other, generally less fit, phenotypes:

$$\frac{\partial P}{\partial t} = P \left(a + \frac{1}{2} \sum_{i=1}^N V_i \frac{\partial^2 a}{\partial x_i^2} + \sum_{i=1}^{N-1} \sum_{j=i+1}^N C_{ij} \frac{\partial^2 a}{\partial x_i \partial x_j} \right)$$

$$a = (u(\mathbf{x}) - g(\mathbf{x})) = \text{uptake} - \text{grazing}$$

The mean trait values (\bar{x}_i) move toward the phenotype yielding the largest net growth rate. When trait i covary with trait j ($C_{ij} \neq 0$), the optimization of each trait interferes with the other. An extra term is added for each covariance:

$$\frac{\partial \bar{x}_i}{\partial t} = V_i \frac{\partial a}{\partial x_i} + \sum_{j \neq i} C_{ij} \frac{\partial a}{\partial x_j}$$

We note the ambiguous impact of trait variance, a proxy for diversity, on phytoplankton communities. The biomass equations tells us that a highly diverse community contains many unfit phenotypes, reducing the net growth rate and primary production. However, variance is needed for a community to adapt to its environment, as shown by the mean trait equations. The equations of biomass and mean traits do not require the traits to be normally distributed and are not affected by mutations, because mutations are not a source of biomass and do not favor any particular direction of change. Trait variances tend to be reduced over time by competitive exclusion [3], and must be sustained by another mechanism. In GOMMA, trait diffusion will play this role by allowing phytoplankton to undergo small mutations at each generation [4]. In a continuous model, the diffusion of trait i is simply a source of variance proportional to the reproduction rate and to a constant mutation rate (ν_i). The full variance equation for trait i is then:

$$\begin{aligned} \frac{\partial V_i}{\partial t} = & V_i^2 \frac{\partial^2 a}{\partial x_i^2} + \sum_{j \neq i} 2C_{ij} V_i \frac{\partial^2 a}{\partial x_i \partial x_j} + \sum_{j \neq i} C_{ij}^2 \frac{\partial^2 a}{\partial x_j^2} \\ & + \sum_{\{j \neq k\}} \sum_{\neq i} 2C_{ij} C_{ik} \frac{\partial^2 a}{\partial x_j \partial x_k} + 2\nu_i \left(u + \frac{1}{2} \sum_{i=1}^N V_i \frac{\partial^2 u}{\partial x_i^2} + \sum_{i=1}^{N-1} \sum_{j=i+1}^N C_{ij} \frac{\partial^2 u}{\partial x_i \partial x_j} \right) \end{aligned}$$

If the mean traits are close enough to their optimal values, the second derivatives will be negative: they represent the loss of diversity due to competitive exclusion. The adaptive dynamics framework is then completed by the covariance equations:

$$\begin{aligned} \frac{\partial C_{ij}}{\partial t} = & V_i C_{ij} \frac{\partial^2 a}{\partial x_i^2} + V_j C_{ij} \frac{\partial^2 a}{\partial x_j^2} + (V_i V_j + C_{ij}^2) \frac{\partial^2 a}{\partial x_i \partial x_j} \\ & + \sum_{k \notin \{i, j\}} (C_{ij} C_{ik} + V_i C_{jk}) \frac{\partial^2 a}{\partial x_i \partial x_k} + \sum_{k \notin \{i, j\}} C_{ik} C_{jk} \frac{\partial^2 a}{\partial x_k^2} \\ & + \sum_{k \notin \{i, j\}} (C_{ij} C_{jk} + V_j C_{ik}) \frac{\partial^2 a}{\partial x_j \partial x_k} + \sum_{\{k \neq l\}} \sum_{\neq i \neq j} (C_{ik} C_{jl} + C_{il} C_{jk}) \frac{\partial^2 a}{\partial x_k \partial x_l} \end{aligned}$$

In this model, there is a single phytoplankton community and no notion of species. Hence, the adaptation described in the mean trait equations represents both ecological selection of the fittest species and adaptive evolution of each species to new environmental conditions. In order to assess the relative role of ecological selection and adaptive evolution, we will upgrade this framework and simulate several phytoplankton species competing with each other, each one described by its own aggregate properties. Mutations will allow species to change their phenotypes at each generation, but not to have offspring of a different species. Hence the trait dynamics of each species will represent its adaptive evolution, and the competition between species will represent ecological selection.

GENERAL OBJECTIVES

The main goal of **GOMMA** is to build a global ocean ecosystem model able to disentangle the effects of **ecological selection & adaptive evolution** [1] on the structure and function of marine plankton communities. Our **working hypothesis** is that allowing species to evolve will improve projected changes in phytoplankton biogeography, ecosystem functioning, biogeochemical cycles, and the biological carbon pump, when compared to the current generation models where ecological shifts in species composition are the only possible response because traits are not allowed to mutate by design. After initial validation at the **global ocean scale**, a formal comparison with a standard non-evolutionary model will be made to test this hypothesis and to quantify the error made when adaptive evolution is neglected. GOMMA is inter-disciplinary because it combines knowledge from different disciplines in order to move forward the field evolutionary ecology of marine plankton. More precisely, GOMMA combines plankton ecology with evolutionary biology by using theoretical techniques that come from the fields of physics and mathematics. Furthermore, this coupling of knowledge from multiple scientific disciplines is placed within the broader context of marine sciences, where the interplay of the five major scientific disciplines (biology, geology, chemistry, physics, and mathematics) is well established. Knowledge in physical oceanography, the biogeochemical cycles of the main nutrients and climate science will be necessary to build the model and analyse its outputs. The phytoplankton model we propose to develop will be coupled with a general circulation model (MITgcm) and climate change simulations will be used to force phytoplankton dynamics. In turn, improved estimates of phytoplankton community structure and of the biological carbon pump are expected to have relevance for future IPCC simulations of phytoplankton under climate change and for the management of marine resources.

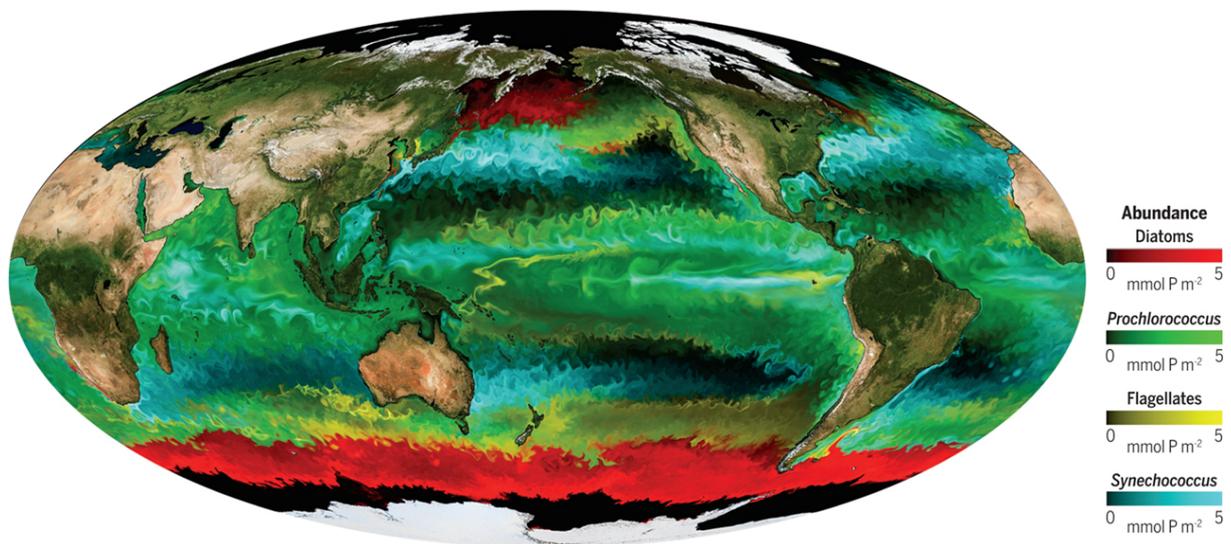


Figure 1: The most dominant types of phytoplankton in the world's oceans simulated by the MIT-Darwin model [5]

SPECIFIC OBJECTIVES

- **Objective 1:** The first specific objective is to couple the SPEAD 1.0 eco-evo model [1] of marine phytoplankton for one population with adaptive evolution along a three-dimensional fitness landscape currently being developed by our group to the MIT general circulation model (MIT-gcm), in order to obtain global ocean simulations. This will be the first time that a global ocean model includes microbial adaptive evolution. The results will be validated for primary production, phytoplankton biomass, and trait diversity, using the in-situ observations from the MAREDAT database [6]. The trait diversity estimated by the eco-evo model will also be compared to the observed species richness [7], which is another indicator of biodiversity. The effect of phytoplankton trait-diversity on marine ecosystem functioning (i.e. productivity, stability) will be evaluated. The open-source code and user guide will be made publicly available using a software repository (GitHub).
- **Objective 2:** The second objective is to include several populations in the global ocean model obtained during the first specific objective, each of them with adaptive evolution along a three-dimensional fitness landscape. Evolutionary indicators such as the proportion of extinction under environmental changes and the relative contribution of ecological selection and adaptive evolution in the community changes will be estimated. The conditions and mechanisms leading to either evolutionary branching or evolutionary convergence of species will be determined. If successful, this approach will lead to a global ocean model of phytoplankton where evolutionary branching and extinction can be resolved and where each species would find the value of its own functional traits and fill its own ecological niche without them being imposed by the modeler.
- **Objective 3:** The third specific objective is to run the eco-evolutionary phytoplankton model at the global scale under scenarios of future climate change (IPCC Representative Concentration Pathways: RCP 2.6 – RCP 8.5 "business as usual" emission scenarios). Ecological indicators of ecosystem functioning such as primary production, biological carbon pump, community trait diversity, and food web structure, will be computed and analysed. The results will be compared to that of a model without adaptive evolution. The goal is to evaluate the potential of adaptive evolution to modify the current projections of carbon (CO₂) sequestration by the oceans under climate change scenarios.

INTERNATIONAL COLLABORATIONS

- **Massachusetts Institute of Technology (MIT)**, Department of Earth Atmospheric and Planetary Sciences (EAPS) @ Cambridge, MA, USA. Principal Research Scientist Dr. Stephanie Dutkiewicz will be collaborating with the project by providing technical support with the Darwin ecosystem model and hosting the PIs and other participants of the project during short-term research stays in the course of the project [8].
- **Japan Agency for Marine-Earth Science and Technology (JAMSTEC)**, Yokohama Institute for Earth Sciences (YES) @ Yokohama City, Japan. Senior Scientist Dr. Lan Smith will be collaborating with the project by providing technical support with the Adaptive Dynamics mathematical framework and hosting the PIs and other participants of the project during short-term research stays in the course of the project [9].
- **Michigan State University (MSU)**, Kellogg Biological Station (KBS) @ Hickory Corners, MI, USA. Professor Christopher Klausmeier will be collaborating with the project by providing complementary skills on the theoretical aspects regarding moment closure approximations to trait-based models and plankton community dynamics and hosting the PIs and other participants of the project during short-term research stays in the course of the project [10].

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