A model system approach to biological climate forcing the example of *Emiliania huxleyi* *

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Abstract

Biological climate forcing is important, but the huge diversity of organisms severely complicates a system's approach to global climate dynamics. The Global Emiliania Modelling Initiative (GEM) provides the strategy and infrastructure which is needed to overcome this problem, at least in so far as the pelagic ocean biota is concerned. GEM conducts an in-depth experimental and modelling study of a single representative organism, the calcifying alga *Emiliania huxleyi*, relating the cellular organisation of this phytoplankter to its ecology and to the fate of its products ($Ca\,CO_3$, organic carbon, and DMS). To make the resulting models more generally applicable, little additional experimentation and minor alterations in model structure are required. Here, we address the central problem of GEM – to establish a model of the *E. huxleyi* cell, defining how environmental factors affect the production of the climatically relevant products. An interactive experimental and modelling approach has been chosen, using chemostat cultures under carefully controlled conditions (nutrients, light and temperature). Molecular genetical analysis should provide an in-depth understanding of metabolic key processes.

1 Introduction

Three major mechanisms are distinguished by which the marine pelagic biota may influence the global climate system: (1) the drawdown of CO_2 from the upper mixed water layer and the atmosphere to intermediate and deep waters by the formation, export and remineralisation of particulate organic carbon (the organic carbon pump); (2) the production, downward transport and partial dissolution of calcium carbonate (the carbonate pump); and (3) large-scale albedo effects mainly owing to the formation of highly reflective clouds following gaseous emissions of dimethyl sulphide (DMS) from algal blooms. The

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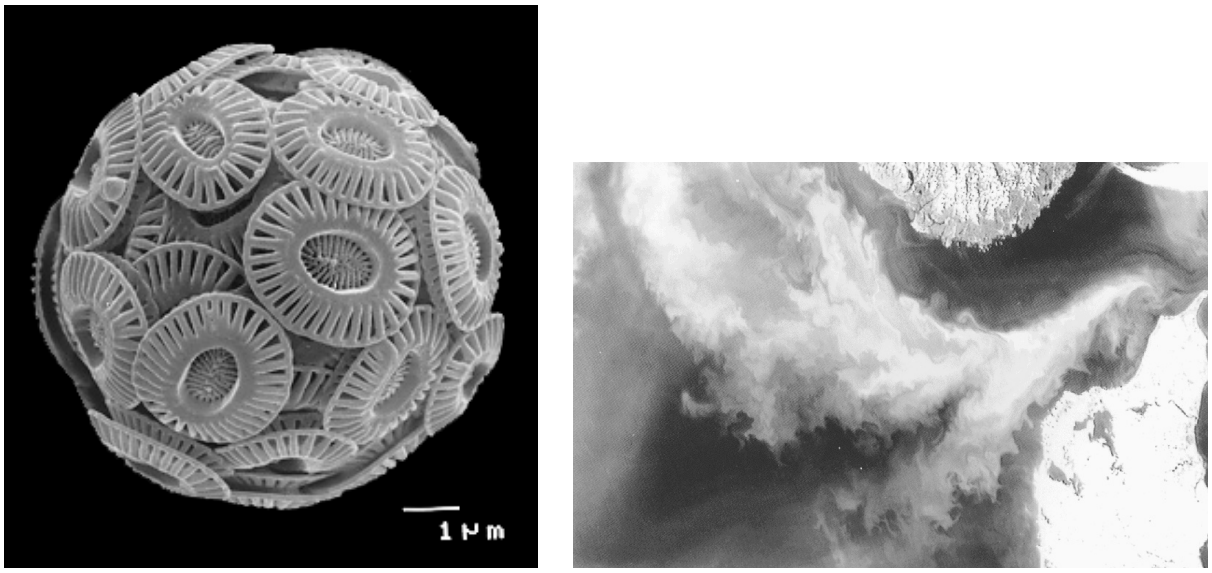

Figure 1: The coccolithophore *Emiliania huxleyi* is extremely abundant in the oceans, as illustrated by a satellite image of the Skagerrak (photo by Steve Groom/Patric Holligan). The calcium carbonate coccoliths are clearly visible in the left photograph. The alga is of importance to climate forcing by the production of calcium carbonate (which sediments), organic matter (export from surface to deep layers) and dimethyl sulphide (conversion to atmospheric sulphuric acid, where it affects the albedo).

climatic effects of these mechanisms vary geographically and through time, as they depend on the abundance of the participating organisms. Many species of algae, protozoa, bacteria, viruses and animals interact with the physico-chemical environment and with each other, and it is from all these interactions that the climatic effects emerge. In view of these complexities, the crucial question is: Can we formulate general rules that adequately describe these interactions and that at the same time are simple enough to be useful for climate modeling? The Global Emiliania Modelling Initiative (GEM) addresses this problem. We are convinced that at all levels of organization, biological systems obey a limited set of fundamental rules. GEM is an attempt to track down some of these rules and to implement them in models of biosphere-climate interactions.

1.1 GEM - a system's approach

The concept underlying the Global Emiliania Modelling Initiative (GEM) is clear and attractive: a single dominant organism, the coccolithophore alga *Emiliania huxleyi*, is selected as an exemplary model system, much as the bacterium *Escherichia coli* became a key to the biochemistry of all living organisms. Climate forcing by *E. huxleyi* is studied in depth in an interactive modelling and experimental investigation and the acquired understanding of this system then serves as a key to investigate the wider implications of biological climate forcing. *E. huxleyi* is a major component of virtually all open marine plankton worldwide, and forms very large blooms, particularly at mid latitudes (see Figure 1). All three climate forcing functions are coupled, and its history can be reconstructed from the archive at the floor of the deep sea. Major assets of the GEM strategy are the

following: (1) it offers a key to the problem of biological diversity, as in-depth information on *E. huxleyi* may be extended to include a wide range of other organisms; (2) it highlights the highly non-linear character of the biological intervention in the climate system; (3) it allows the intimate coupling of the three forcing functions to be modeled; (4) it optimally exploits the excellent accessibility of *E. huxleyi* for laboratory and field research; and (5) the integration of biological and stratigraphic studies permits quantification of carbonate fluxes to the ocean floor as well as extensive model validation by comparing biological responses to diverse climate regimes.

1.2 Objectives

The objectives of the research are (1) to develop a dynamic model of the physiology of *E. huxleyi* as far as climatically relevant products are concerned; (2) to generate a solid data base on the steady state performance under various nutrient, light and temperature levels; (3) to evaluate the model implications for a canonical ecosystem; and (4) to obtain insight in the applicability of our results to other calcifying organisms. Expected results are: (1) a model succinctly describing the relationships between environmental circumstances, cellular characteristics, and the production of new biomass, DMSP (a precursor of DMS) and $CaCO_3$; (2) precise experimental data on the dependence of cellular characteristics on environmental circumstances; (3) estimates for the rate of carbonate production. The application of molecular techniques to cellular processes in *E. huxleyi* will lead to a much more detailed picture of the physiological key-processes. The result to be expected from the experiments described below is the isolation of genes encoding key-enzymes in cellular processes such as calcification, photosynthesis, cell-division and nutrient metabolism. These genes will be used as molecular markers to determine how cellular processes are intertwined and how environmental changes, as e.g. changes in light intensity and nutrient concentration, influence these processes. These molecular markers will be used to determine cellular activities and responses in the natural environment. Furthermore we hope to isolate (novel) genes involved in the calcification process which will provide insights in this process which until now is regarded as a black box.

2 Dynamic Energy Budget theory

The Dynamic Energy Budget (DEB) model consists of a set of simple, mechanistically inspired, rules for the uptake and use of substrates (food) by an individual organism (see Figure 2). It specifies the key processes of feeding, assimilation, development, maintenance, growth, reproduction (or division) and ageing quantitatively, and is meant to apply to all organisms on earth. These processes can by specified realistically for animals, feeding on other animals, with only one internal reserve and structural body mass as state variables, while cumulated damage is required as third state variable to specify the aging process. Organisms that can be limited in their growth by several types of nutrients (and/or light), such as algae, require more types of reserves. Plants, which use different organs for the uptake of different nutrients and light, also require more types of structural biomass. These extensions with respect to the simpler model for animals, follow naturally from the set of simple rules, and specify all energy and mass fluxes simultaneously, on the basis of the principle of homeostasis. These fluxes include dissipating heat, water, oxygen and

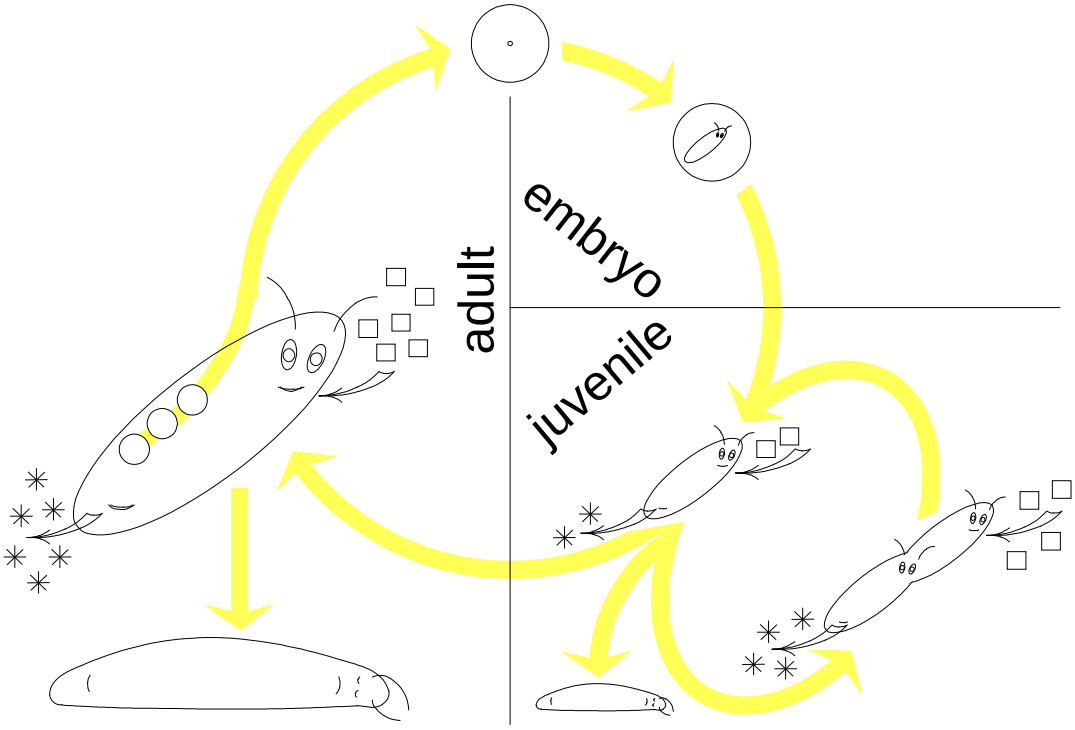

Figure 2: Dynamic Energy Budget theory aims to quantify the energetics of individuals as it changes during life history. The key processes are feeding, digestion, storage, maintenance, growth, development, reproduction and aging. The theory amounts to a set of simple rules, and a wealth of consequences for physiological organization and population dynamics. Although some of the far reaching consequences turn out to be rather complex, the theory is simple, with only one parameter per key process. Intra- and inter-specific body size scaling relationships form the core of the theory and include dividing organisms, such as microbes, by conceiving them as juveniles.

carbon dioxide (among others). The theory, therefore, provides a fundamental basis for the coupling between energy and mass fluxes in organisms.

Since the DEB model relates substrate uptake to surface area and maintenance to volume of structural biomass, changes in shape are important in the specification of the key processes. The DEB model reduces to a very simple structure for 1D-isomorphs: organisms for which surface area is proportional to volume. It can be shown that organisms that divide into two parts at a fixed investment into maturation, such as microorganisms, behave approximately as 1D-isomorphs, irrespective of their actual changes in shape during growth. Several popular models for the growth of microorganisms turn out to be special cases of the DEB-model. The distinction between the individual and population level disappears for 1D-isomorphs, and physiologically structured population models reduce to unstructured ones, which can be represented as a simple set of ode's. This does not hold for organisms with big ratios between adult and neonate size.

The set of rules that specify the DEB-model imply the existence of a maximum body size for each species of organism, and classifies all its parameters into two categories: intensive parameters that do not depend on maximum body size, and extensive parameters that can be shown to be proportional to volumetric length. The rules, therefore, imply trends in parameter values, when species with different maximum body sizes are compared. These trends turn out to be realistic for many physiological and life history quantities that can

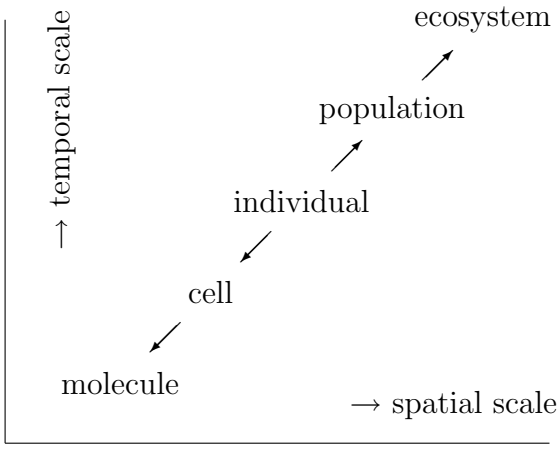

Figure 3: The DEB theory specifies a model for the individual, which is used to model populations in terms of individuals and ecosystems in terms of populations. We simplify while increasing the level of integration, and incorporate new processes that typically operate at that level of organisation. The model for the individual serves as a constraint for modelling sub-organismal processes that specify details of the (physiological) behaviour of the individual, such as regulation processes. This approach implies a link between scales in space and time, which excludes rapid processes at large spatial scales and slow processes at small spatial scales.

be written as functions of parameter values, such as respiration rate, life span, maximum reproduction rate, etc. This property is of great help to reduce the number of parameters in the application of the DEB-model to specify the dynamics of food webs, for instance.

The DEB-model is simple enough to obtain some analytical results for populations in steady state, while some popular software packages can be used successfully to analyse the population dynamics in simple environments, such as the chemostat. It appears to be possible to obtain at least some of the rules on which the DEB-model is based from more detailed models on molecular kinetics. The DEB-model seems, therefore, useful in linking physiological processes to population dynamics (see Figure 3).

3 Algal eco-physiology modelling

The DEB theory can be used to quantify the eco-physiology of algae, but a number of processes requires some additional modules, which we here indicate briefly.

The ratio of chlorophyll *a* per cell and carbon per cell is a key variable in many models for phytoplankton growth. Models based on this ratio bypass the individual cell as a model entity. This approach clearly has its advantages, but has it drawbacks, too. For instance, both chlorophyll *a* and carbon per cell vary with growth conditions, but such variations are outside the scope of a model that deals only with the chlorophyll *a* to carbon ratio. Our aim is to predict the chlorophyll *a* to carbon ratio from a cell-based model. This approach may provide different insights than models that bypass the individual cell.

To deal with light-limited as well as nutrient-limited growth, we formulated a model that characterises a phytoplankton cell by three variables: permanent volume, with a fixed C:N ratio, and two transient nutrient pools, for carbon and nitrogen. These nutrients are mobilized from the pools to form permanent biomass. If the demand for carbon limits the growth rate, growth is said to be light-limited, otherwise it is nitrogen-limited. In nitrogen-limited phytoplankton, the rate of chlorophyll production is taken proportional to the nitrogen pool size. The cellular chlorophyll concentration decreases through dilution by growth. In light-limited growth, the chlorophyll production rate varies with light intensity. The model structure outlined here leads to descriptions of the chlorophyll *a* to carbon ratio in both light- and nitrogen-limited phytoplankton. The model predictions were in line with

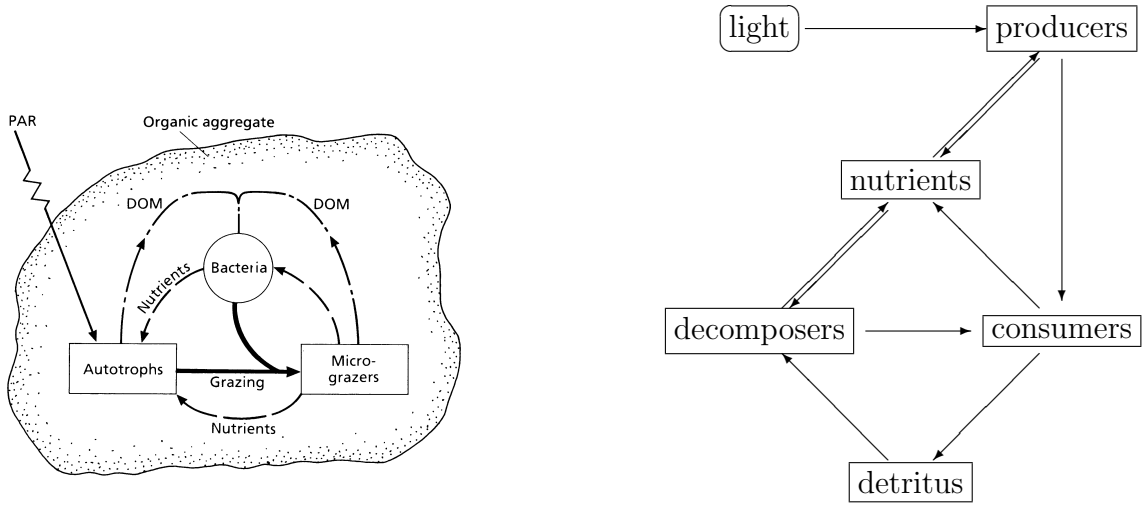

Figure 4: The left diagram shows mass transfer in a microbial pelagic floc, as presented by Mann and Lazier [5]. It one realization of a canonical community (right diagram), which consists of three components: producers that gain energy from light and take up nutrients to produce biomass, consumers that feed on producers and decomposers that recycle nutrients from producers and consumers. The community is rather closed for nutrients, but requires a constant supply of energy. Influx and efflux of nutrients largely determine the long term behaviour of the community.

data from steady-state chemostat (nitrogen-limited growth) and turbidostat (light-limited growth).

In the aquatic sciences, many mathematical descriptions for the photosynthesis–irradiance relationship, or PI-curve, are in vogue. Few of them are based on mechanistic models. None of these properly deals with the dark reactions of photosynthesis. Remarkably so, as PI-curves are ubiquitously used in studies on phytoplankton, and the dark reactions have been known for nearly a century. To remedy this situation, we propose a model for the PI-curve that explicitly accounts for the dark reactions of photosynthesis. These may be either substrate-limited or enzyme-limited. For increasingly enzyme-limited dark reactions, the PI-curve gradually changes from the rectangular hyperbola for completely substrate-limited dark reactions, to the Blackman curve for completely enzyme-limited dark reactions. The model accounts for the impacts of photoacclimation on both the number and the size of photosynthetic units. It also accounts for variation in the absorption cross-section in response to changes in chlorophyll content of the cells. A satisfactory description of data regarding the PI-curves of phytoplankton grown at different irradiances, presupposes that photoacclimation also affects the maximum rate at which the dark reactions proceed.

4 Canonical community

Figure 4 illustrates the structure of an idealized, simple, three-component ecosystem. Producers use light and nutrients to produce organic matter, which is transformed by consumers, while decomposers release nutrients from the organic matrix. The system is "open"

to energy flow, but closed to inputs or removal of elemental matter. The structure, which might represent a closed bottle containing daphnids, algae and bacteria, is found in many ecosystems; for example, it is very similar to the one used for material turnover in microbial flocs in sea-water plankton systems [5]. It can, therefore, be regarded as a canonical community.

The canonical community can be used to analyze how light affects mass turnover, which is a first step to understand production processes in the pelagic environment on the basis of sound mass and energy balance equations. This is essential to quantify the carbon and sulphur flux, and to evaluate the role of primary production on a global scale.

5 Outlook

Theory and data acquisition within the project developed more or less in parallel, so far. We plan to use the data to test model predictions, and estimate parameter values, during the second half of the project. The molecular work aims to test a number of assumptions qualitatively, by checking which genes are involved on the calcification process, and when they are active. We aim to modify the molecular techniques such that they can also be used in the field.

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