Leibniz Centre for Tropical Marine Research

Jacobs University Bremen

PhD Proposal

Modeling diverse phytoplankton communities in the eastern Cariaco basin, Venezuela

prop need broader title here for PhD Project

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Abstract

At an unprecedented rate our oceans are changing and so are the organisms within it.

- Global Change / Phytoplankton - it's important

- phytoplankton is a complex and diverse community, in a complex ecosystem, trait-based vs functional type

- CARIACO is a setting where both of these things are obviously happening/true and I have the data to backitup

- computational models are the way to synthesisze and test hypotheses about these complex systems

- I have built a modeling framework to test functional type hypothesis, first study looking at bulk biomass changes

- the modelling framework itself is interesting and publishable

- now going to San Diego to work with Andrew Barton on expand upon first study and look at more detailed BDEF and other such stuff

- goal is to improve understanding of ocean ecosystem and how it might be affected by global changes

"Totally need to rewrite this:

We are struggling to find ways to characterize and quantify the organisms and their interactions in ways that can be effectively utilized in computational models to predict future scenarios. Phytoplankton are an integral part of modeling the biogeochemical interactions taking place in the ocean. One of the key questions is how to accurately describe the interactions and effects on the ecosystem of the remarkably diverse planktonic community. The field of marine biogeochemical modeling has seen great advances in the last 20 years, in particular the "trait-based" approach promises ecologically meaningful descriptions of biodiversity by moving away from treating species explicitly, but instead looking at the way organisms interact with the environment (i.e. their traits). Two such models form the basis for my doctoral studies: The PhytoSFDM model, developed by my supervisor Esteban Acevedo-Trejos, and the DARWIN model, a framework developed at MIT and used extensively by Andrew Barton.

Contents

1. General Introduction

1.1 The ocean, phytoplankton and why it matters

The complexity of the ocean and its vast ecosystems has fascinated scientists to this day and most likely will continue to do so far into the future. Myriad life forms are embedded in a matrix so far removed from our mostly dry existence on top the earth's crust. In the ocean, life moves in dilution, and the equivalents of forests and grasslands are hard to spot unless the concentration of tiny phytoplankton is so large, that deep blue turns into a milky green.

The term phytoplankton refers to microscopic marine photosynthetic organisms. These microorganisms form the basis of the oceanic food web and are primary producers of planetary scale, contributing roughly half of the oxygen in our atmosphere through photosynthesis (Field et al., 1998). Phytoplankton consists of mostly single-celled organisms, prokaryotes and eukaryotes from a highly diverse evolutionary background (Falkowski et al., 2004). This large genetic diversity is accompanied by a remarkable range of survival strategies, biogeochemical roles, shapes and sizes within the polyphyletic phytoplankton (see Figure 1.1 for a size comparison). The emergence of such a large range of organisms and the mechanisms sustaining their persistence has been one of the key topics in phytoplankton ecology over the last 50 years. Hutchinson's paradox.X(REF here)X

——— also explain MLD in the following paragraph ———

The distribution of phytoplankton is driven by the complex physical forces that govern ocean currents and the chemistry of the bodies of water the move. The key

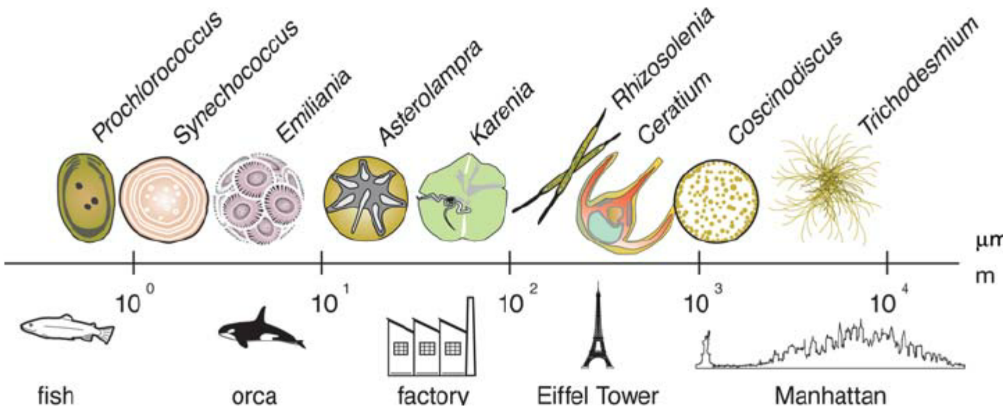

Figure 1.1: "A comparison of the size range (maximum linear dimension) of phytoplankton relative to macroscopic objects." from Finkel et al. (2010)

components are macronutrients (e.g. nitrogen & phosphorus) and micronutrients (e.g. iron & cobalt) welling up from the deeper ocean or flushed in from continental sources. Wherever there are sufficient nutrients available within the euphotic zone, the depth where photosyntheticaly available radiation (PAR) is 1% of the surface value, planktonic life begins to thrive. Ecosystems along continental margins provide a particularly productive habitat, with only 10% of total ocean surface area covered by continental margins, but 10-15% of marine primary production and more than 40% of carbon export to the seabed occurring along coastal lines (Yool & Fasham, 2001; Muller-Karger et al., 2005).

Phytoplankton growth indirectly feeds a considerable part of earth's population through fisheries (Stock et al., 2017) and even shapes the elemental composition of oceanic water itself (Redfield, 1958). The biomass produced is mostly consumed by higher trophic levels and either assimilated or excreted. Another large portion experiences natural mortality and viral lysis. Microbial degradation drives remineralization within the euphotic zone, which fuels regenerated production (Eppley & Peterson, 1979) [Perhaps put quotation about Microbial Loop here!]. A small fraction sinks out of the photic layer as fecal or detrital matter to the deeper ocean and an even smaller fraction reaches the sea floor as sediment (roughly 1 %) and remains there over geological times (Honjo et al., 2008). This process has been termed the biological carbon pump. Carbon sequestered this way is removed from the ocean-atmosphere system for potentially millions of years. Given the projected rise of atmospheric CO_2 levels, it is of grave importance to understand how changes in the phytoplankton community at the surface, driven by anthropogenic stressors and climate change, will affect the carbon burial potential of oceanic ecosystems. Studies have both reported a global declining trend in marine primary production (Boyce et al., 2012) and increasing trends in long-term ocean time series (Chavez et al., 2010). In order to answer questions of how phytoplankton will respond to a changing climate it is necessary to look the diverse phytoplankton community in greater detail.

1.2 Characterizing phytoplankton

From the early days of oceanographic research, scientists have been interested in the microscopic organisms that were floating in samples of sea water. These communities contain many species each and in total there are tens of thousands of species of phytoplankton that inhabit the surface ocean (De Vargas et al., 2015). All phytoplankton species use chlorophyll or bacteriochlorophyll to harvest light as the energy source to fix organic carbon, but there is wide variation in virtually all their other properties (Litchman & Klausmeier, 2008). In addition to the complex community composition, there are many factors affecting measurements of their bulk properties in the ocean, such as the viral and bacterial community and the influence of diverse grazers, all within the complex three-dimensional physical environment that is the ocean. Where earlier phytoplankton ecologists focused on identifying individual species, decoding their phylogeny or growing them in controlled lab cultures, recent research is trying to integrate the insights gained from these approaches and quantify the diversity on higher levels of organization in relation to other properties of the ecosystem. The focus has shifted towards trait diversity both within and across species and within and across phytoplankton groups. In order to scientifically describe this perplexing diversity the concepts of trait-based ecology and functional types have been developed (Tilman, 2001; McGill et al., 2006; Violle et al., 2007).

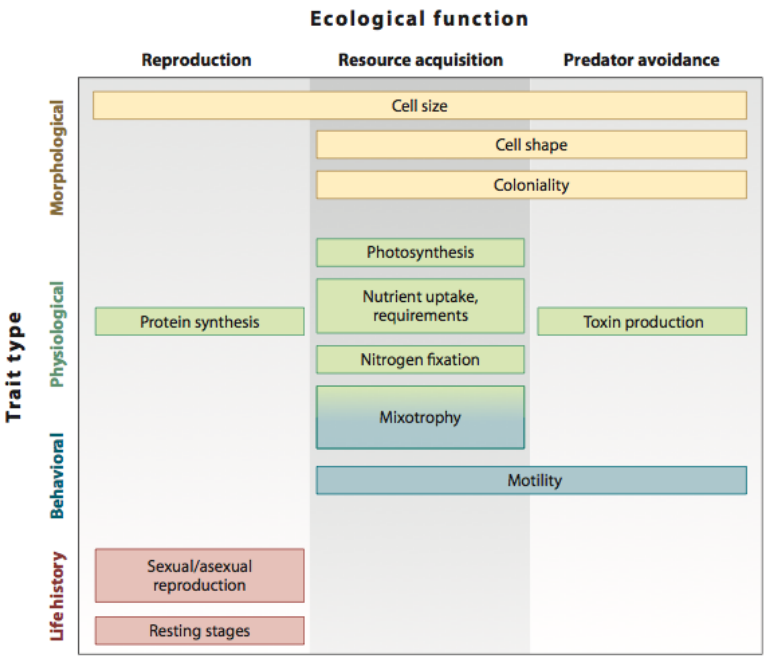

Figure 1.2: "A typology of phytoplankton functional traits" from Litchman & Klausmeier (2008)

1.2.1 Functional types and traits

In the following I will try to clarify the complementary terms of phytoplankton traits, functional traits, and functional types.

The trait-based approach to phytoplankton ecology has been growing in popularity. Part of the fascination evoked by this term stems from its origin in evolutionarily theory. Over the last three decades, it has been adopted by ecologists trying to understand communities and ecosystems. In this new context, the concept of traits has been stretched far beyond its original meaning, which can lead to some confusion surrounding the scope of trait-based methods (Violle et al., 2007). In the simplest definition, a trait is a surrogate of organismal performance. In the ecological context this has been expanded to surrogates for the performance of populations, communities and entire ecosystems. This can include ecophysiological traits, life-history traits, demographic traits or response and effect traits of ecosystems (see Figure 1.2 for a selection of phytoplankton traits). Theoretically, any property of an organism or ecosystem could be defined as a trait, but ideally a trait should be functional. Functional traits are defined by Violle et al. (2007) as "morpho-, physio- or phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival". An important facet of the trait-based approach is to describe organismal function via trade-offs between traits. For example when competing for multiple nutrients, phytoplankton species are thought to be constrained by trade-offs in their competitive ability for one over another resource (Tilman, 1990).

Phytoplankton are extremely diverse and the trait based approach lends itself to generalizations, as traits and ecological trade-offs can be defined and explored irrespective of species or taxa boundaries (McGill et al., 2006). However, depending on the study and hypotheses to be tested, it can be very helpful to structure the diversity of organisms into distinct groups. Major taxonomic groups of phytoplankton can be classified based on their ecological or biogeochemical roles within the ecosystem (Iglesias-Rodríguez et al., 2002; Flynn et al., 2015). The concept of functional groups is not in contrast to a trait-based ecology of phytoplankton, but can be complementary to it. By broadly sampling relevant traits across phytoplankton groups and species, functional types can be defined by functional traits and trade-offs and therefore extend the trait-based approach by another level of organization (Litchman et al., 2007). An early example is the work of Ramón Margalef. Margalef used observations of important traits, such as sinking rates and nutrient utilization to build the concept called "Margalef's mandala" to organize phytoplankton functional types (PFTs) on a spectrum of nutrient availability versus turbulence (Margalef, 1978).

The terms functional group and functional type are used interchangeably, with functional groups more often referring to the grouping of species and the functional type describing the group as a whole, often as implemented in computational models. In fact, the simplification of the phytoplankton community into functional types has been widely used for the design and interpretation of computational models that try to recreate or make predictions about the biogeochemical cycling, biogeographic distribution, productivity and other ecosystem functions of phytoplankton (Gregg et al., 2003; Le Quéré et al., 2005). Biogeochemically defined functional types are most often used, as these functional traits can usually be well defined within an ecosystem model. Typical examples of such functional groups are silicifers, which broadly correspond the phylogenetic group of diatoms, and calcifiers, which are usually represented by coccolithophores. Such functional types are always simplifications of the natural pyhtoplankton diversity. Silicoflagellates create silicified skeletons like diatoms, but are often not explicitly included because they rarely dominate modern phytoplankton assemblages. The choice of which functional groups to include in a model can also be driven by biogeography or analytical considerations concerning the measurement instrumentation used for a particular study (Irwin & Finkel, 2017).

————Perhaps small paragraph about functional diversity here?———— In biodiversity research, the trait-based approach has been readily adopted. It used to be that species diversity (i.e. the number of species) was the most important metric, but now it is functional diversity, which can be described by the variance in the value of a functional trait of the community or ecosystem.

It is important to keep in mind that functional types are often composed of many species with a possibly large variance in trait values. Recent research is trying to understand the effects of diversity within functional types and within species (Violle et al., 2012, 2017; Des Roches et al., 2018).

1.3 Modeling phytoplankton communities

Given the complexity of the ocean ecosystem, it is necessary to aggregate our knowledge of the many smaller parts into comprehensive ecological models in order to test mechanistic hypotheses and investigate their full-scale implications.

Computational models of phytoplankton growth have been developed since the 1940s and have greatly increased in sophistication and complexity since then, co-evolving with the rise in computational resources (Gentleman, 2002). Phytoplankton modelling started with formulations based on the Lotka-Volterra equations of predator-prey dynamics (Fleming, 1939). From these relatively simple descriptions models evolved to describe the oceanic physical environment and the ecosystem it contains including multiple trophic levels. Originally developed by John Steele with a model ocean split in two layers, the nutrient-phytoplankton-zooplankton (NPZ) and nutrient-phytoplankton-zooplankton-detritus (NPZD) models succeeded in reproducing the typical annual bloom dynamics observed in the temperate ocean (Steele, 1958; Evans, 1988; Fasham et al., 1990). Further developments have been in more exact physiological descriptions of phytoplankton based in cellular metabolism and energy allocation (Geider et al., 1997) and both simple and more complicated ecosystem formulations driven by local and global 3D circulation models (Lacroix et al., 2007; Hirata et al., 2013).

However, in their simplified approach, these models unavoidably limit the characterization of a diverse phytoplankton community (Bruggeman, 2009). These plankton ecosystem models are typically highly aggregated, such that a single variable determines the response of a diverse assemblage of phytoplankton species (Franks, 2009). Implementing a meaningful treatment of biodiversity in ecological models is a key challenge in the field of phytoplankton modeling (Queirós et al., 2015). The most apparent way of implementing this within the framework of established NPZD models is to include multiple equations and state variables for different phytoplankton functional types (Le Quéré et al., 2005). For every group that fulfills a distinct ecosystem function, a new set of parameters has to be added, which complicates the model structure and increases computational costs. This somewhat intuitive approach, however, does lead to problems. First and foremost, this is the lack and inherent uncertainty of data from field and culture experiments to constrain functional types. This again leads to the difficulty of validating the model output in light of insufficient information, leading multiple authors to criticize the PFT modeling approach as attempting to "run before we can walk" particularly when used for extrapolating into the future (Anderson, 2005; Shimoda & Arhonditsis, 2016).

The current scientific discussion can seem intimidating to an early career scientist, as both the most obvious future directions of ecosystem model design as exemplified by PFT models, as well as the very foundation of traditional NPZD models has come under scrutiny. Nowhere is this more apparent as with the formulation of nutrient uptake dynamics, which is traditionally defined by Monod kinetics that are based on the equations for Michealis-Menten enzyme kinetics. (Monod reference here)

ALSO: current modeling paradigms are discussed quite critically in the literature, in particular the Monod kinetics and also the lack of any adaptive mechanisms in these model (Smith et al., 2014) A bit earlier, but similar direction: (Flynn, 2010) and more recent, but focused on Monod: (Hellweger, 2017)

However, there are also examples of modeling approaches that show a way forward. To name an alternative to the modeling paradigm discussed so far, there is individual based modeling (IBM). In IBM the phytoplankton are explicitly represented as individual agents, allowing for a diverse and spatially interactive phytoplankton community (Hellweger & Bucci, 2009). The computational cost and structural complexity of this approach however does not yet lend itself well to studies of large-scale or even global ecosystems.

Another approach which lends itself very well to just such studies is to extend traditional NPZD models via moment-based estimation of aggregate properties (Merico et al., 2009). A specific implementation of this is the PhytoSFDM model developed by Acevedo-Trejos et al. (2016). Instead of modeling multiple size-classes of phytoplankton explicitly, the community is described not only by the biomass, but also by the mean size and size variance. Size is used as a master trait, with size variance being used as a proxy for functional diversity. Trade-offs related to nutrient uptake, grazing and sinking structure the phytoplankton community along the size spectrum as driven by the physical forcing. The model was used to investigate latitudinal diversity gradients in the Atlantic Ocean (Acevedo-Trejos et al., 2018). One point of criticism for this approach is that due to the mathematical structure the size distribution is fixed to the shape of a skewed log-normal distribution, not allowing for the emergence of other (e.g. multi-modal) distributions that could arise in natural phytoplankton communities (Urusla Gercke, Tony Klaus, Francesco paper on size dist in lakes). This lends the PhytoSFDM model (in it's current formulation) more to studies of large scale processes and biogeographic patterns rather than to local ecosystem modeling studies.

looking at aggregate properties, how complex model has to be, how simple it has to be, aggregate model can not capture all of the variability, model capturing all of variability (Hellweger, Science article, biogeographic patterns emerging - GLOBAL FIX ERROR BEFORE)

1. very complex -¿ IBM 2. DARWIN 3. aggregate with adaptive dynamics and PhytoSFDM, similarly to optimality based model I am for interemdiate levels of optimality

Tom Anderson "Running before we can walk"

ALSO: problem of looking at within FT diversity, look at the details of diversity -¿ including PFTs very complicated!

perhaps not cutting edge, but my method allows me to catpure variability wihtin functional groups!

don't rubbish other models/papers

A major advancement in the field of phytoplankton modeling was the DARWIN model developed at MIT (Follows et al., 2007). In the general framework of the DARWIN model, large numbers of phytoplankton types are initialized with equal biomass but with different parameters for the most important traits, namely those related to light harvesting, temperature dependence, and nutrient acquisition. These parameters are chosen stochastically from broad ranges of values, based on laboratory and field data, and constrained by simplified allometric functions describing ecological trade-offs. Different functional types are prescribed in the model via varying nutrient utilization traits (e.g. small phytoplankton that cannot assimilate nitrate as Prochlorococcus analogs). Over multi-annual runs this community self-assembles through ecological competition and physical changes produced by the simulated environment of a global circulation model (GCM). In the random initialization of phytoplankton types, the DARWIN model allows for the emergence and development of diverse phytoplankton communities. This approach of modeling biodiversity has been termed "selection-based" (Follows & Dutkiewicz, 2011). ——more attention to this review—— The model framework is continually modified and expanded, for example for exploring the effect of grazing formulations (Prowe et al., 2012), the biogeography of phytoplankton traits (Barton et al., 2013) and the influence of ocean acidification at a global scale (Dutkiewicz et al., 2015). A study of particular interest is the size-structured food-web model component developed by Ward et al. (2012), because the modeling approach combines the trait-based approach of scaling parameters allometrically along cell size with a PFT modeling approach. Each functional type is assigned a different allometry based on the size ranges and relationships taken from data. Together with the selection-based biodiversity representation that the DARWIN framework provides, this seems to be a promising direction for future models. The model has however only been applied and compared to data at a global scale and the code of this specific implementation is not publicly available.

PhytoFLEX -¿ Systems of infinite Diversity -¿ structure paragraph along axis of complexity?

ALWAYS NEED A GOOD BASIS IN DATA TO VALIDATE MODELS AND HYPOTHESES

1.4 The Cariaco Basin and the CARIACO time-series

At the beginning of my PhD I was tasked with the mission to find publicly available ocean time-series data that could be used as the basis for my modeling work. Initially the plan was to choose multiple locations, to compare results from model applications in contrasting environments. Not surprisingly the search did quickly yield results, among the most prominent: the Bermuda Atlantic Time-series Study (BATS) and the Hawaii Ocean Time-Series (HOTS). Quickly the issues of public ocean time-series data became apparent. Links often lead to defunct sites and servers were sporadically maintained. In particular for my application the problem was that the basic physical parameters and bulk properties such as total chlorophyll were readily available, but more specific phytoplankton functional type or taxonomy data was harder to find, if not missing. In particular the type of phytoplankton data that was available differed widely between the stations and would have not allowed for a straightforward comparison. It was only later in my search that I came across the CARIACO time series, an acronym for "CArbon Retention In A Colored Ocean", located in the Cariaco Basin off the coast of Venezuela. The data is available through the University of South Florida (USF) at http://imars.marine.usf.edu/cariaco and includes a wealth of data that was collected since 1995. Most importantly to my purposes, the data included both phytoplankton pigment measurements and taxonomic data of the phytoplankton community at monthly intervals. It was the first ocean time-series with such detailed public phytoplankton data and soon I decided to focus my work on this time-series.

In addition to the recent importance of the cariaco basin as the site of an important paleo-oceanographic time sereis, the Cariaco basin has served as a natureal laboratory for biogeochemists for over 50 years. This basin has been key in constructiong stoichiometric models of organic matter remineralization (Redfield et al 1963 and Richards 1975!), developing residence time and box models, and numerous other studies.

———perhaps what is above is not entirely needed –¿ maybe less colloquial, more why CARIACO is interesting! ——————

THE BASIN The CARIACO Ocean Time-Series program was established in 1995 off the coast of Venezuela (10° 30′ N, 64° 40′ W, see Figure 1.3). Located in the south-eastern Caribbean Sea, the Cariaco Basin is a 160 km long and 70 km wide tectonic depression, reaching up to 1400 m in depth. The two deeper parts of the basin are separated by a saddle of 900 m depth, with the time-series mooring located in the eastern part. The entire basin is bound to the west and north by a shallow ridge at 100 m depth, restricting the exchange of deep water with the Caribbean Sea. The restricted circulation and high productivity at the surface resulted in anoxic conditions below 250 m depth within the basin (Richards & Vaccaro, 1956). The hydrography at the surface is influenced by Guyana and North Equatorial currents that flow into the Caribbean Sea from a south-eastern direction, but this exchange is restricted to the two channels above the 100 m ridge. Observed and modeled horizontal surface water velocities within the basin are relatively weak, indicating a minimal influence of horizontal transport at the mooring site (Alvera-Azcárate et al., 2009).

SAMPLE COLLECTION The program was established as a joint-project of the Venezuelan Fondo Nacional de Cienca, Tecnología e Investigacíon (FONACIT) and the US National Science Foundation (NSF), with the particular interest in creating a time-series of surface ocean biogeochemistry that could be linked to satellite observations and the sedimentation accumulating in the anoxic basin. Since 1995 there were over 200 core cruises at mostly monthly intervals, in addition to sediment trap and microbial-biogeochemistry process cruises.

MEASURED DYNAMICS

LONG TERM TRENDS

Say that JPinckney loves me and how this is a promising data set, given the history, wealth of data, incl phytoplankton diversity data, and long term trends here.

XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX

SAMPLE COLLECTION

SEA SURFACE DYNAMICS

LONG TERM TRENDS

XXXX

XXXX

XXX

THEN TALK ABOUT THE COLLABorDATASHARE WITH JPINCKNEY AND CBENITEZNELSON, and how this allows an even deeper look at the biomass dynamics

1.5 Aims of the proposed PhD project

"The general goal of my Ph.D. project is to study the processes that structure the phytoplankton community in contrasting environmental regions of the Atlantic Ocean, using a trait-based modelling perspective. The specific aims during the course of the project are to:

- MANUSCRIPT 1 "Understanding Shifts in CARIACO"
- MANUSCRIPT 2 "technical paper" - Geoscientific Model development
- MANUSCRIPT 3 "BDEF in CARIACO"

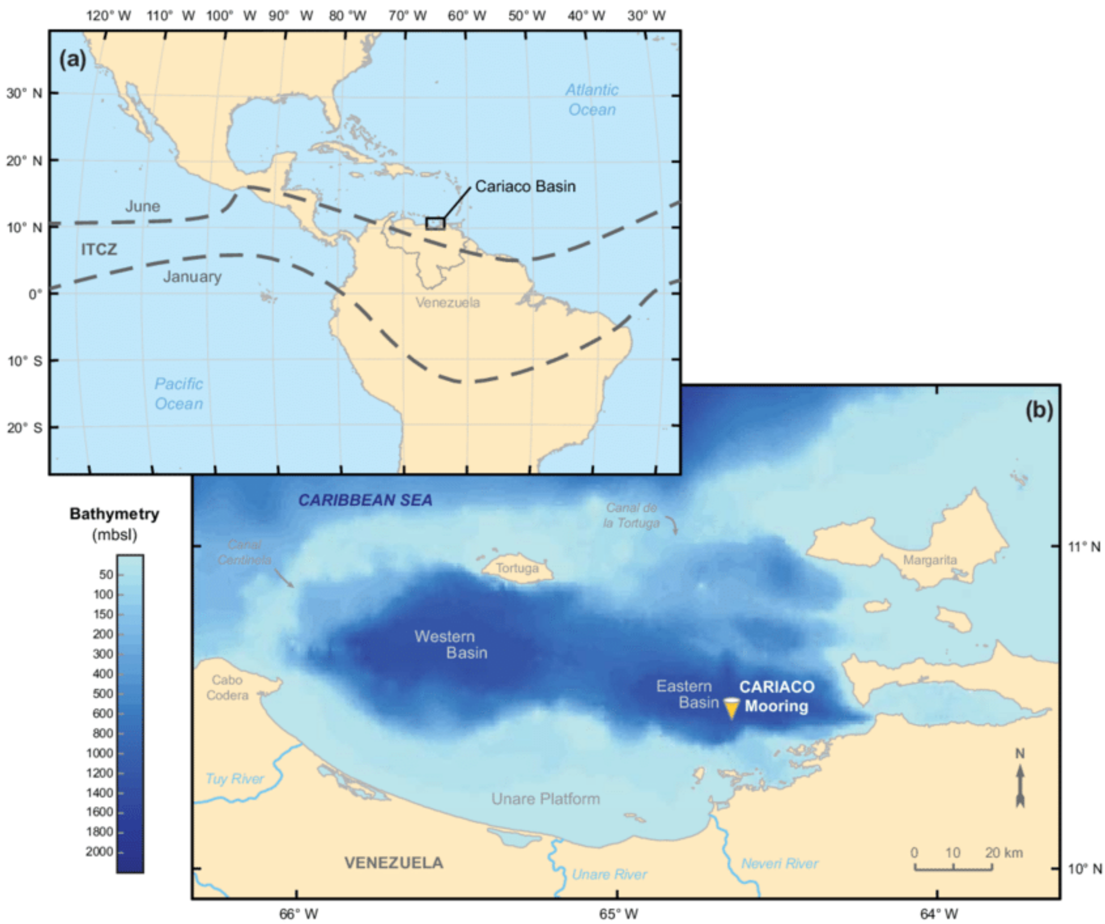

Figure 1.3: "Study area. A. Location of the Cariaco Basin off the Venezuelan coast in the southern Caribbean Sea, with January and June positions of the Intertropical Convergence Zone (ITCZ). B. Location of the CARIACO station in the eastern sub-basin, general bathymetry and local rivers emptying in the basin (bathymetric data from GEBCO_08 Grid)" from Bringué et al. (2019)

2. Understanding phytoplankton community shifts in the eastern Cariaco basin

2.1 Regime Shift in CARIACO data

General intro sentence" For decades ecologists have been trying to understand how the structure of phytoplankton communities is associated to the environmental conditions, with a particular focus on the causes and consequences of natural variation.

Something about identifying and modeling regime shifts

Talk about the data again

This will be a first! first proper ecological model apart from this Export Flux model only including diatoms (Walsh et al., 2002) Also talk about mutshinda et al studies!

FUNCTIONAL TYPES STRUCTURE –¿ explain linkage between Pigment Data that I use and functional diversity measurements (XMoreno et al. 2012X) take this from Pinckney et al. 2015... Thus, photopigment-based measures offer an efficient way to quantify community or functional diversity (X Moreno et al., 2012 X). (From Pinckney et al 2015)

Interesting thing is that there was this shift in the PhytoplanktonCommunity but apparently no real reduction in Export! (This is in Taylor and Pinckney somehwere) bb

LOOKING AT BIOMASS DYNAMICS, leading over from Intro where i mentioned JP CBN data at the end (ad-lib) XXX

EXPLAIN THE HYPOTHESES HERE; AND HOW THEY CAN BE TESteD

2.2 Methods

dont really go into depth here, just generally state how things are done, python, odeint, system of ODEs

COPY METHODS SECTION FROM PhytoSFDM in a way, but with the current model setup including the equations and allofthat!

SHOW MODEL SCHEMATICS!

XXXX

2.2.1 Model physics in a tropical coastal setting

xXXX

Most models built for temperate oceans, since that is where reasearch (and funding) has been most well developed. Fasham NPZD type slabe physics explain. Why won't this fit well in the Cariaco setting? - mostly due to shallow and comparatively invariable MLD, and nutrient fluxes don't correlate. Problem of nutrient forcing! If MLD driven, nutrients below MLD are highly variable, only below 100m do we get towards a relatively constant N0 and Si0 (can show plots here!)

Moved from slab physics of PhytoSFDM model (Acevedo-Trejos et al., 2016) which is based on Fasham (Evans & Parslow, 2003; Fasham et al., 1990) to a box model formulation adapted from Tyrrell (Tyrrell, 1999) The specific differences are (show equations):

HERE I CAN SHOW THE DIFFERENT MODEL RUNS, explain the difference for this box model needs to get running! This won't be so easy.. so plan ample time my friend!

XXXX

XXXX

XXX

End Methods here

2.3 Preliminary Results

SHOW PROPER RUN, With Biotic components fitting the base run comparatively well, try it!

XXXX (Figure 4.2).

$kkkkkkkkkkkkkkkkkkkkk$ here the results start, at least the text of it

°C°%°C°%°C°%°C°%

get it, get it

2.4 How to complete this project

XXXXXXXX

essentially just check model physics again, and then create nice runs, and then go and test the hypotheses, like so and so and so.. XXXXXXX

X

XXX

3. PhytoMFTM - a flexible object-oriented PFT model

3.1 Python ecosystem model package development

General intro sentence"

why would this be interesting to anyone else

movement towards open source programming languages

Open Source, Open Access, Open Science! comparability

!!!!cite a nice pushing for this publication here!!!!

teach PhD Students from the ground up to code their own models in Python, as of yet there is a lack of coherent ressources. Definitely cite the PhytoMFTM model and publication (**?**)

extensible framework bb

XXX

3.2 Methods

3.2.1 Object-oriented structure

Explain Code structure, with some nice graphicx XXX

XXXX

3.2.2 Model formulation and usage

xXXX

explain how to run the model!

XXXX

XXXX

XXX

End Methods here

3.3 How to complete this project

Just say that this model was the basis for the previous chapter work, and will be for the rest of my PhD, a toolkit for testing ideas with multiple functional types! go towards selection-based models, like DARWIN and how the allow to change the biodiversity explicitly, to test hypothesis

4. Further work

4.1 Where to go from here

4.1.1 BDEF

HERE I should cite the Tilman and Ptacnik Papers that Esteban recommended, talk about how Biodiversity influences ressource use efficiency

ALSO BDEF MODEL BY LOREAU: (Loreau, 1998)

And then say how the model I am building is actually very well equipped to deal with this kind of

XXXXX

4.1.2 Method

XXXX

4.2 Relevance

Again talk shortly about how biodiversity means ecosystem resilience (kinda) and how climate change and anthropogenic stressors will test, if not break the boundaries of the ecosystem resilience. We are still trying to understand the basic connections between the main organisms and functional types in the ocean. Such that we can only guess at what steady state lies behind the boundary, but perhaps we should better never find out.

XXXXX

XXXX

XXXX

4.3 Time table

<table>
<tr><th></th><th>Jan</th><th>Feb</th><th>Mar</th><th>Apr</th><th>May</th><th>Jun</th><th>Jul</th><th>Aug</th><th>Sep</th><th>Oct</th><th>Nov</th><th>Dec</th></tr>
<tr><th>2011</th><td></td><td colspan="2">Literature review</td><td colspan="3">AMT data mining</td><td colspan="2">Manuscript writing</td><td>Ph.D. proposal</td><td>Manuscript writing</td><td colspan="2">Develop size-based model</td></tr>
<tr><th>2012</th><td colspan="2">Develop size-based model</td><td colspan="2">Sensitivity analysis</td><td colspan="3">Manuscript writing</td><td colspan="5">Develop a coupled phytoplankton and zooplankton size-based model</td></tr>
<tr><th>2013</th><td colspan="2">Sensitivity analysis</td><td colspan="3">Manuscript writing</td><td colspan="3">Develop phytoplankton size-based evolutionary model</td><td colspan="2">Sensitivity analysis</td><td colspan="2">Manuscript writing</td></tr>
<tr><th>2014</th><td>Manuscript writing</td><td>Ph.D. defense</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
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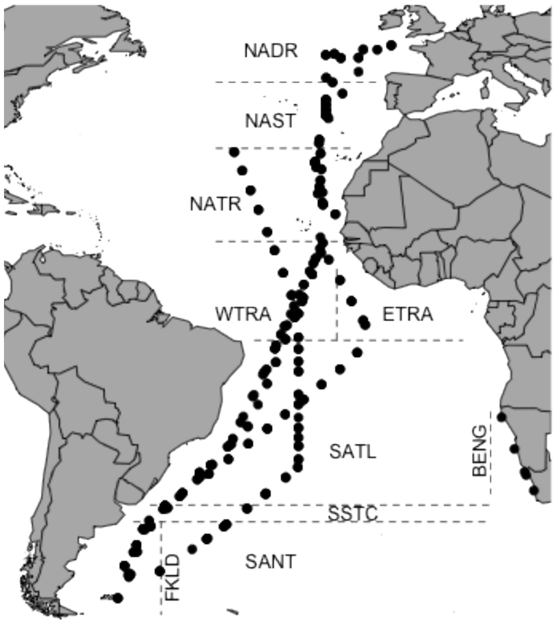


Figure 4.1: The AMT subset of 410 samples used in this study. The dashed lines represent the simplified limits of the Longhurst (2006) ecological provinces.

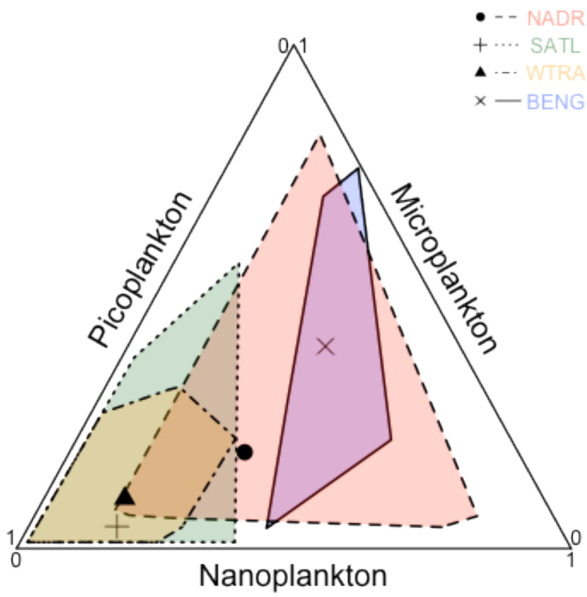


Figure 4.2: Phytoplankton community size structure of four ecological provinces in the Atlantic Ocean. The contours correspond to the convex hull of the size-fraction distribution of each province. The symbols indicate the corresponding mean values.

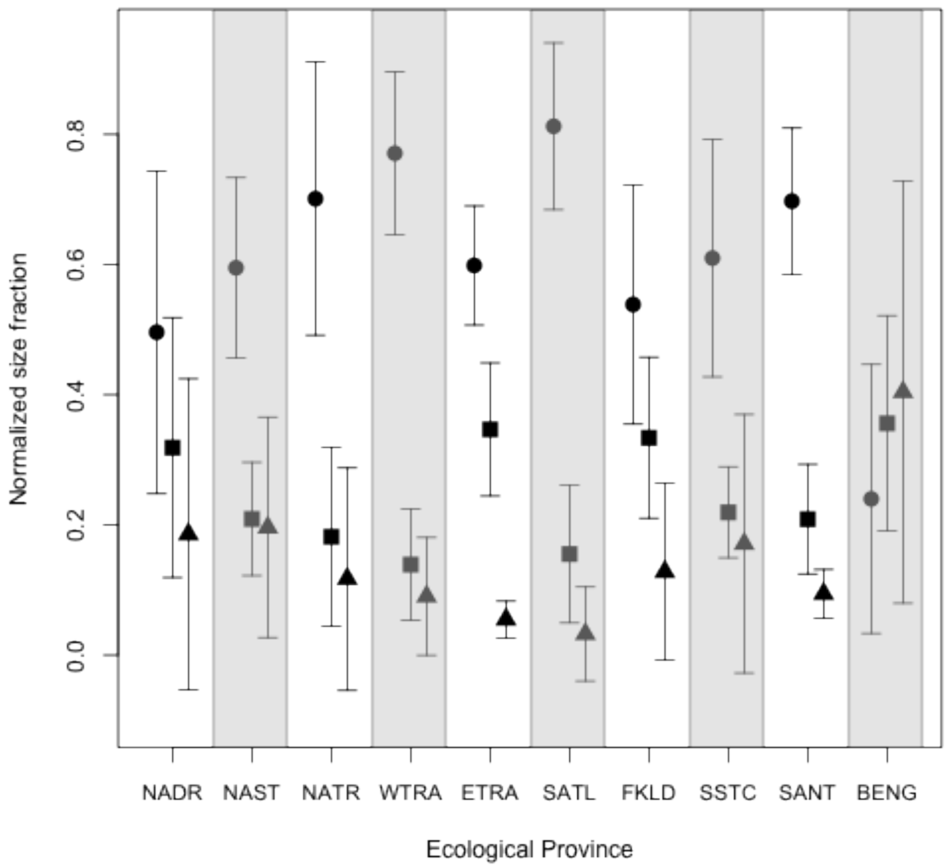


Figure 4.3: Relative mean abundances (±sd) of three phytoplankton size fractions of ten ecological provinces of the Atlantic Ocean. The symbols indicate the mean values of the normalized size fractions: picoplankton (●), nanoplankton(■) and microplankton (▲).

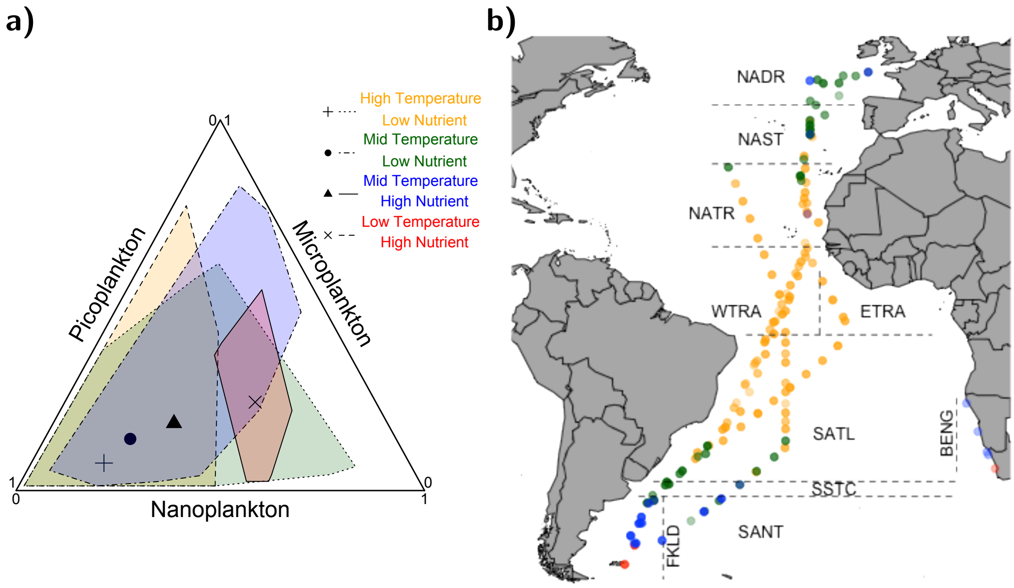


Figure 4.4: Caption comes here my friend"""""""".

$$\frac{dP}{dt} = \left[r(\bar{s}) + \frac{1}{2} v \frac{\partial^2 r(\bar{s})}{\partial s^2} \right] P$$

$$\frac{d\bar{s}}{dt} = v \frac{\partial r(\bar{s})}{\partial s}$$

$$\frac{dv}{dt} = v^2 \frac{\partial^2 r(\bar{s})}{\partial s^2}$$

The approach of defining a trade-off that relates size to the competitive ability for nutrient acquisition and resistance to predation (Merico et al., 2009) leads to mechanistically capture bottom-up (nutrient availability and acquisition capabilities) versus top-down (avoid grazing) processes, major shaping forces of a phytoplankton community. The model will be tested against and constrained by the AMT observations on environmental data and community size structures in the Atlantic Ocean (chapter 2).

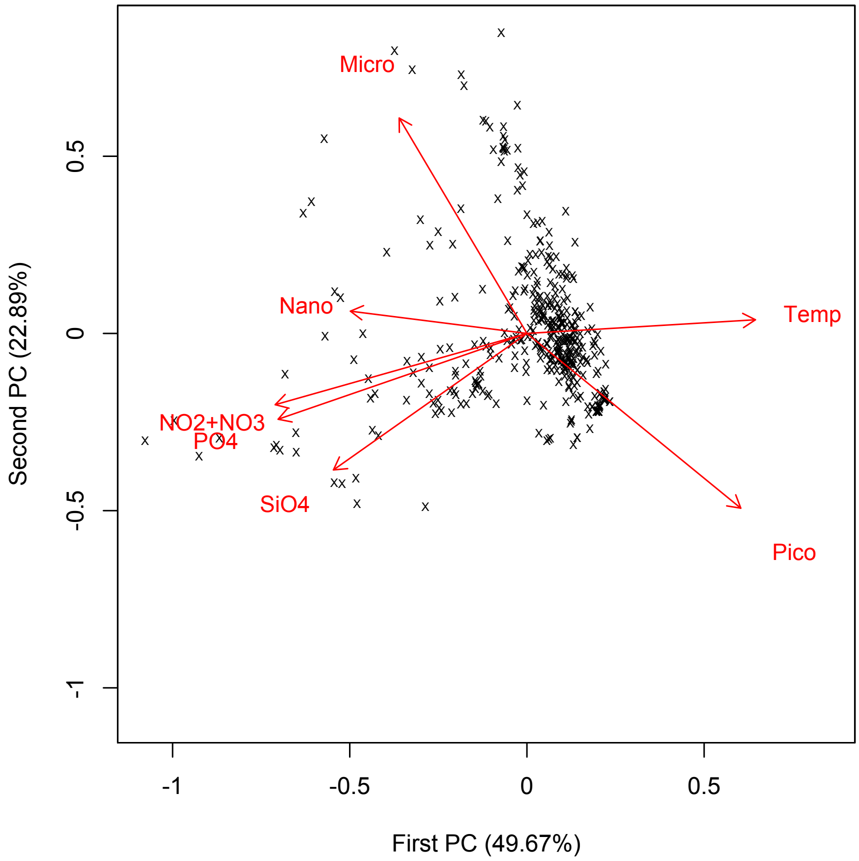


Figure 4.5: Principal Component Analysis of environmental parameters and normalized phytoplankton size fractions.

Table 4.1: Mean values of environmental parameters for the different clusters: High temperature - Low nutrients (HTLN), Mid temperature - Low nutrients (MTLN), Mid temperature - High nutrients (MTHN and Low temperature - High nutrients (LTHN).

cluster	$NO_2^- + NO_3^-$	PO_4^{3-}	SiO_4^{2-}	Temperature
HTLN	0.150±0.575	0.064±0.078	1.097±0.575	25.299±2.000
MTLN	0.556±1.102	0.112±0.141	0.816±0.617	17.894±2.191
MTHN	9.027±3.593	0.799±0.373	2.423±1.375	11.925±2.797
LTHN	30.324±4.549	1.336±0.208	4.590±1.926	6.810±3.435

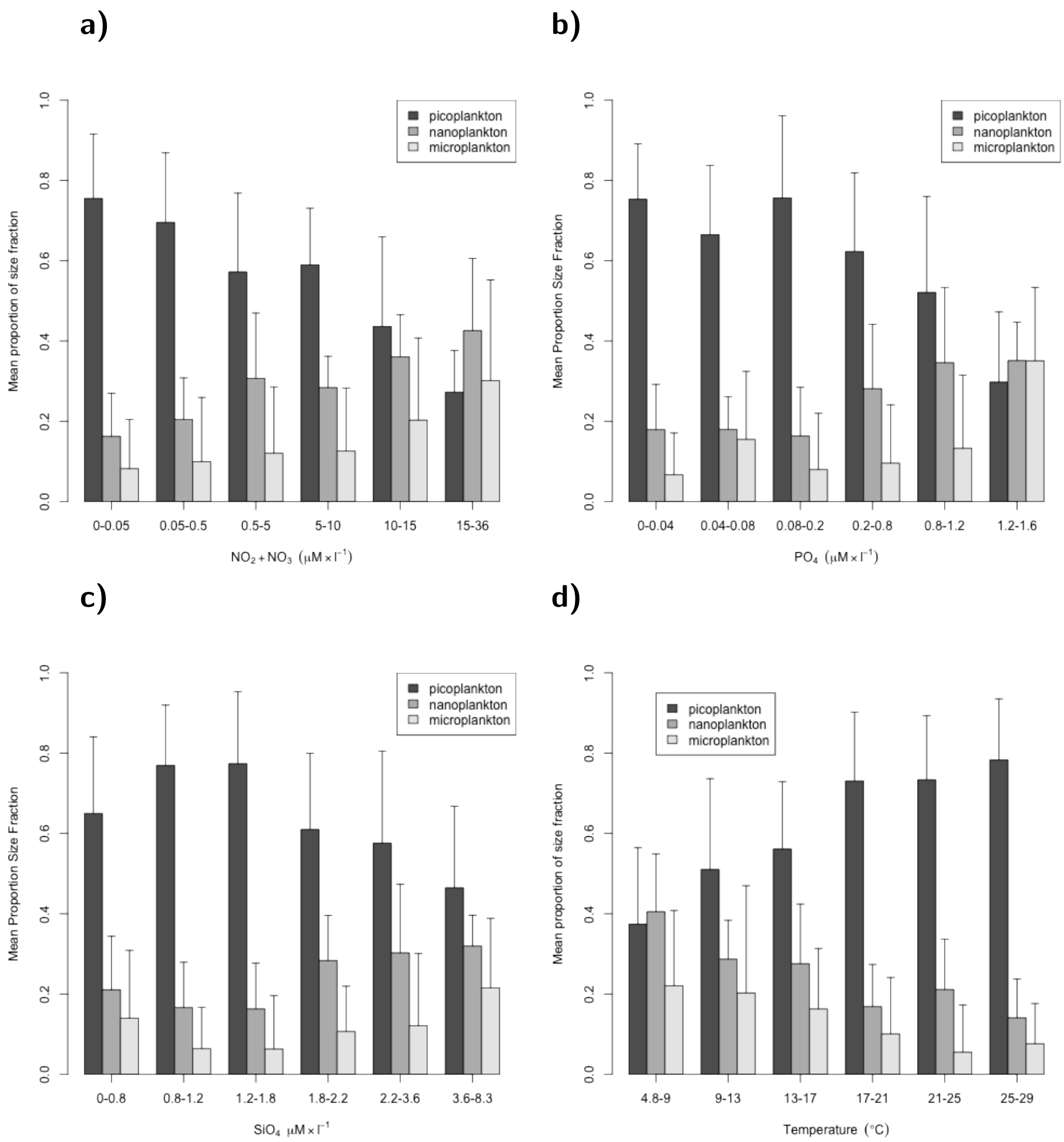


Figure 4.6: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with concentrations of nitrate+nitrite (a), phosphate (b), and silicate (c) and with temperature (d). The bars represent mean values and the error bars indicate the standard deviation.

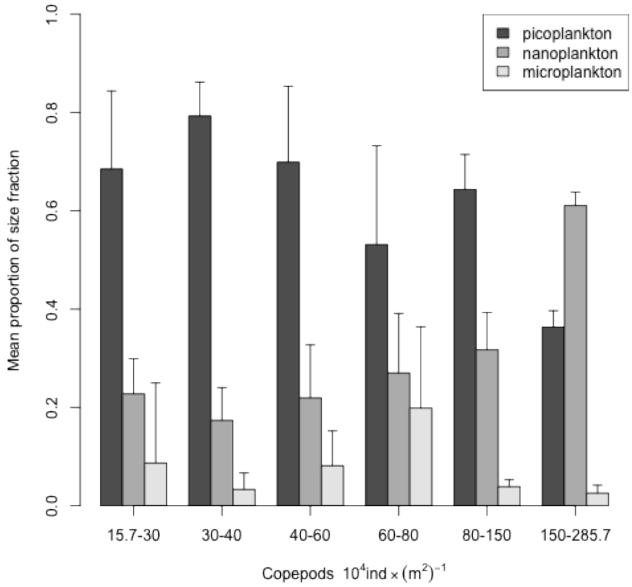


Figure 4.7: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with copepod abundance. The bars represent mean values and the error bars indicate the standard deviation.

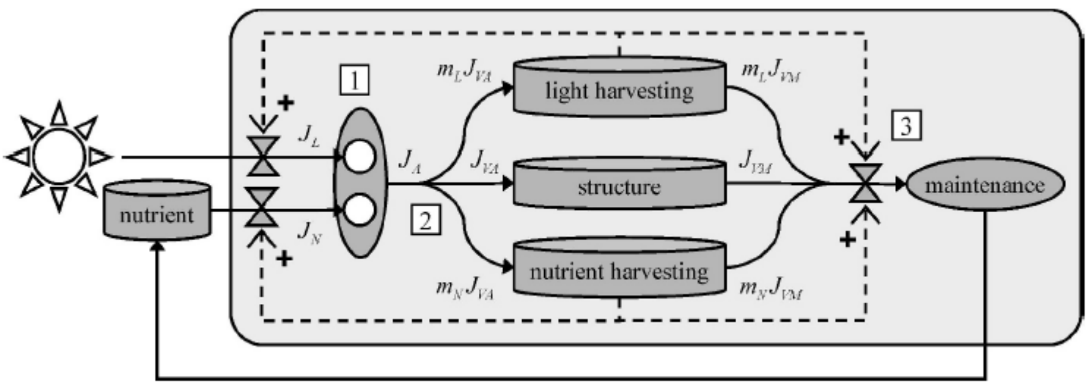


Figure 4.8: Bruggeman and Kooijman model scheme. Taken from **?**

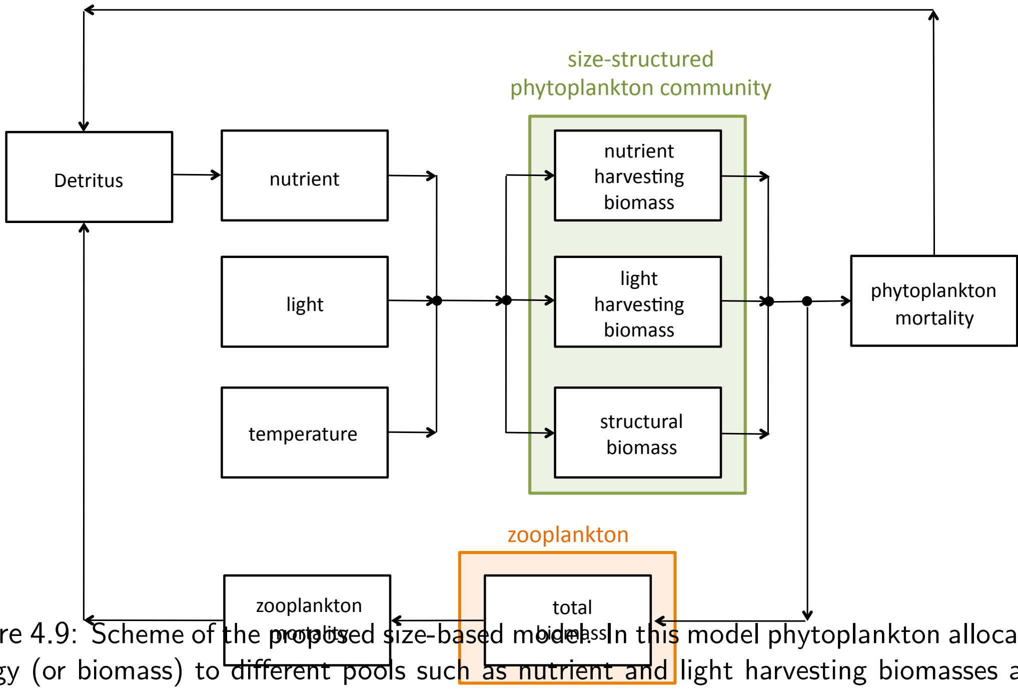


Figure 4.9: Scheme of the proposed size-based model. In this model phytoplankton allocates energy (or biomass) to different pools such as nutrient and light harvesting biomasses and generic structural biomass. A certain fraction of the phytoplankton biomass flows into the zooplankton biomass and a remaining fraction is remineralized into the nutrient pool

Table 4.2: Summary statistics for linear fittings of the three size fractions to each environmental variable.

	Picoplankton			Nanoplankton			Microplankton		
	slope	p-value	r^2	slope	p-value	r^2	slope	p-value	r^2
$NO_2^- + NO_3^-$	-0.090	0.002	0.908	0.050	0.001	0.921	0.040	0.010	0.792
PO_4^{3-}	-0.0812	0.021	0.711	0.042	0.012	0.777	0.039	0.125	0.354
SiO_4^{2-}	-0.047	0.085	0.455	0.030	0.044	0.597	0.016	0.247	0.142
Temperature	0.082	0.001	0.914	-0.047	0.008	0.812	-0.035	0.003	0.885
Copepods	-0.063	0.064	0.520	0.068	0.051	0.567	-0.004	0.788	-0.222

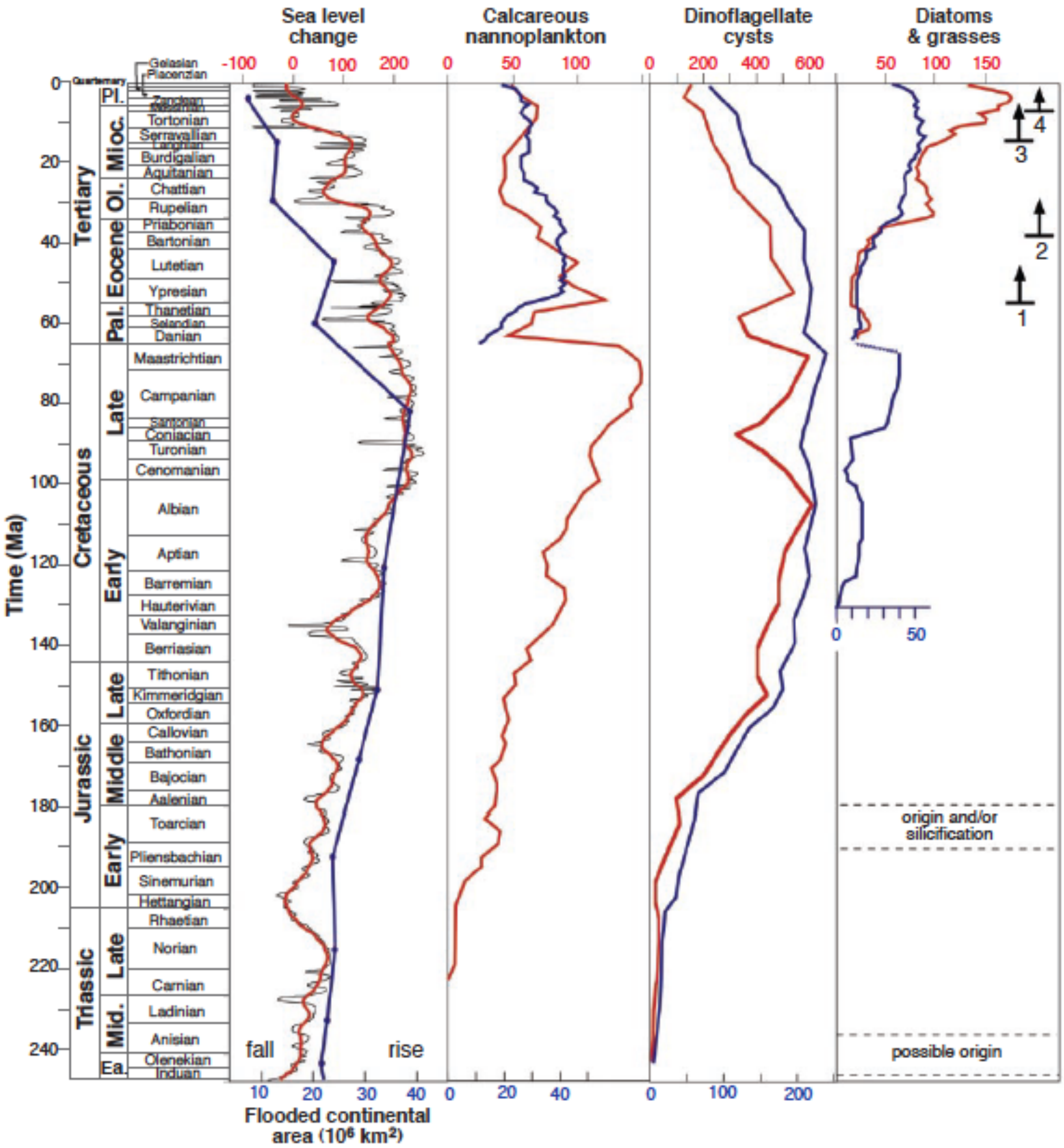
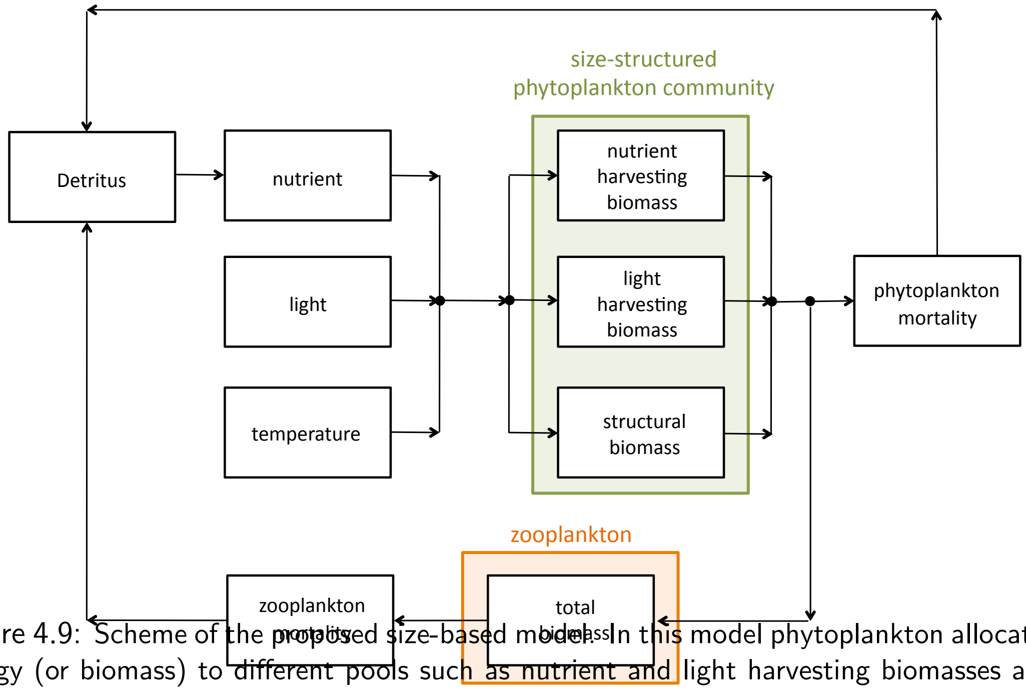


Figure 4.10: Comparison of major phytoplankton groups with sea-level change. The red line accounts for species diversities from published studies. The blue line accounts for the genus diversity compiled from public databases by the authors. Taken from Falkowski et al. (2004).

Smaller phytoplankton cell sizes have a competitive advantage over larger phytoplankton under low nutrient, low light and low grazing pressure (Litchman & Klausmeier, 2008; **?**). From our regression analyses (Figures 4.6 and 4.7) we inferred a strong control of NO_3^-+NO_2^- and temperature on all three size fractions. Pico- and nanoplankton size fractions, however, appeared more sensitive to changes in PO_4^{3-}, SiO_4^{2-} and copepod abundance. We propose that these effects are caused by a trade-off between resource acquisition and predation pressure, although with the caveat represented by the paucity of the zooplankton data and by the qualitative value we attribute to zooplankton abundance as an indication of grazing pressure. There are a number of important physiological and ecological processes that strongly depend on phytoplankton cell size (**???**), including metabolic rates, maximum nutrient uptake rate, nutrient diffusion, light absorption, sinking velocity, trophic interactions and even diversity within taxa, which is often a log-normal distribution of body size. Our results are therefore consistent with this general "size rule" (**?**). To our knowledge it is the first time that this feature is observed in data extending across an entire ocean basin and irrespective of temporal changes.

The resulting, full size-based model will be approximated with a simpler model of aggregate macroscopic properties using the moment closure approximation proposed by **??** and further refined by **?**Merico et al. (2009). The phytoplankton total biomass (P), the mean trait ($\bar{s}$), and the trait variance (v) will be formulated as follows:



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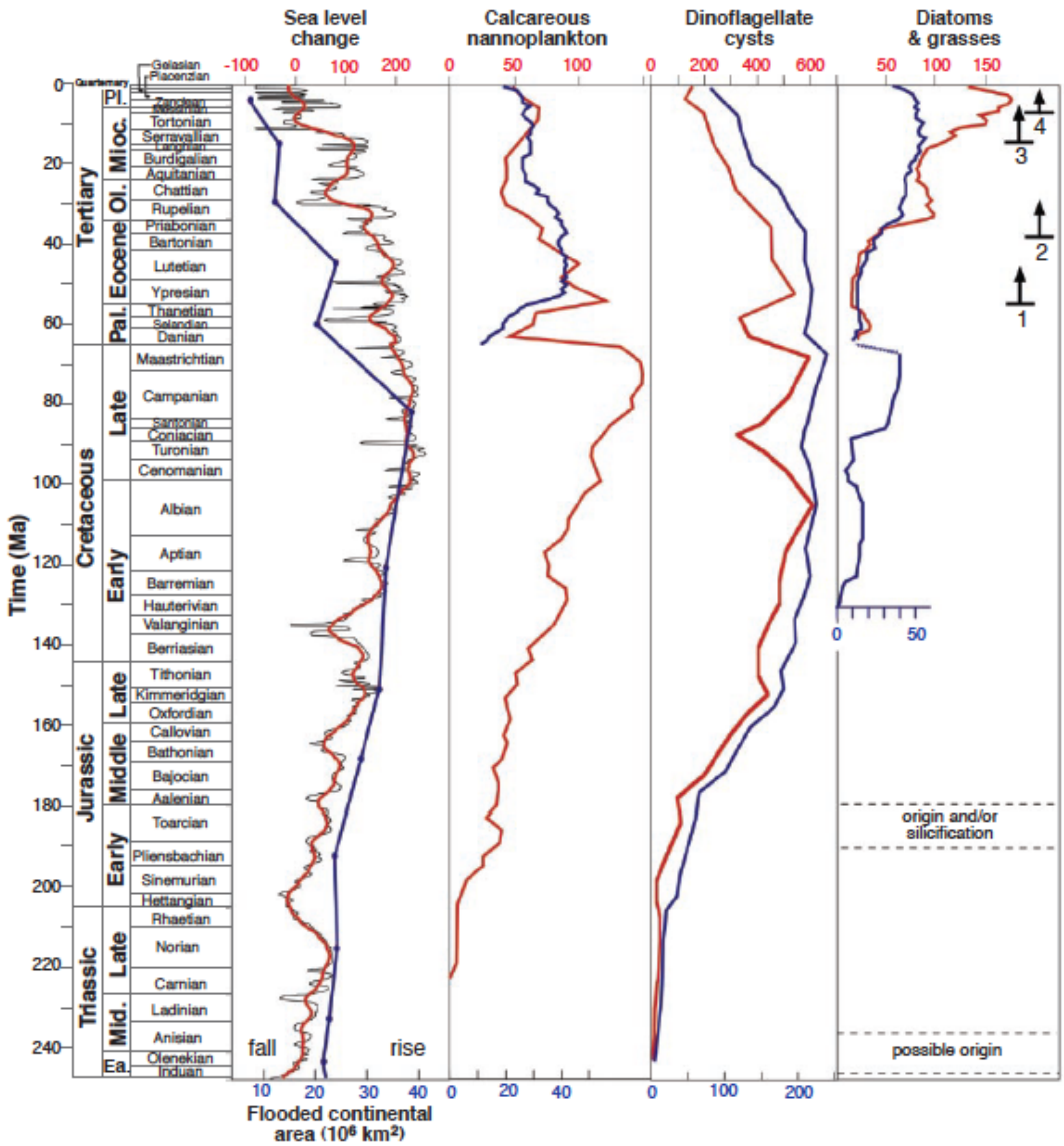
SiO_4^{2-}	-0.047	0.085	0.455	0.030	0.044	0.597	0.016	0.247	0.142
Temperature	0.082	0.001	0.914	-0.047	0.008	0.812	-0.035	0.003	0.885
Copepods	-0.063	0.064	0.520	0.068	0.051	0.567	-0.004	0.788	-0.222



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