



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 back it up
- computational models are the way to synthesize 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.

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# 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

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 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.

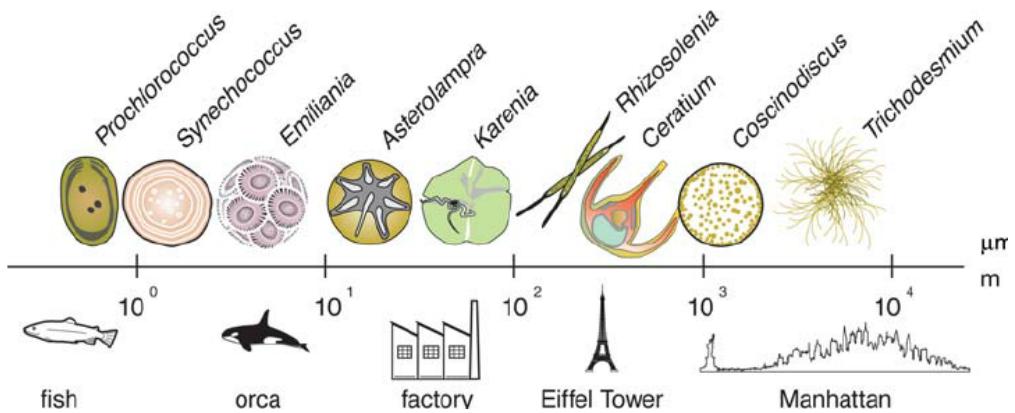


Figure 1.1: "A comparison of the size range (maximum linear dimension) of phytoplankton relative to macroscopic objects." from Finkel et al. (2010)

Wherever there are sufficient nutrients available within the euphotic zone, the depth where photosynthetically 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 ( 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<sub>2</sub> 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 (Engelen 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; Viole et al., 2007).

### 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.

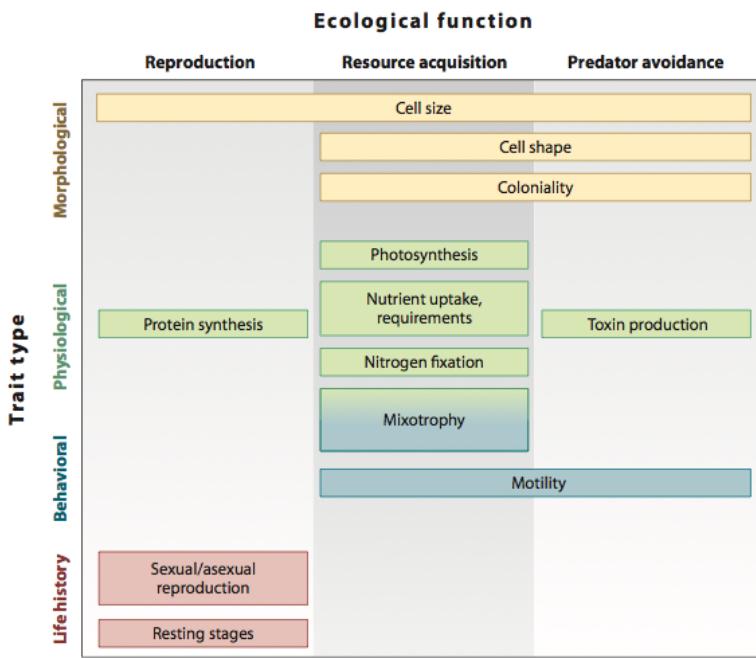


Figure 1.2: "A typology of phytoplankton functional traits" from Litchman & Klausmeier (2008)

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 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 into groups, 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 of such an approach is the work of Ramón Margalef. He 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 (XGregg 2003, Anderson 2005 and LeQuere 2005X). 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 silicifiers, 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 phytoplankton 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? It is important to keep in mind that PFTs 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 understand the full-scale implications.

Computational models of phytoplankton growth have been developed since the 1970s and have greatly increased in sophistication and complexity since then, co-evolving with the rise in computational resources. Ecosystem modelling started with simple box-model descriptions of a few trophic levels. These were the nutrient-phytoplankton-zooplankton (NPZ) and nutrient-phytoplankton-zooplankton-detritus (NPZD) models, which succeeded in reproducing the basic bloom dynamics observed in the temperate ocean (Evans 1988, Fasham et al. 1990). However, in their generalistic approach, these models unavoidably limit the characterization of a diverse phytoplankton community (Bruggeman 2009). To make up for this shortcoming, in the following two decades, these models were expanded to more complex plankton functional type (PFT) models (Le Quere et al. 2005).

For every group of species that fulfill a distinct ecosystem function, a new set of parameters was added, complicating the model structure and massively prolonging calculations. This somewhat intuitive approach of having every functional group represented in a model, however, did create 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 (Shimoda et al. 2016 ). Trait-based modeling, on the other side, tries to circumvent the problem of biodiversity (i.e. complexity) in natural systems with a radically different approach. The interactions of phytoplankton with their environment are based on multiple traits which characterize generalized physiological properties like nutrient affinities or motility. Ideally, these traits can be directly measured and are independent of species and therefore they can be directly related to the properties of the organisms function within the ecosystem, such as nutrient affinity for example deally, these traits can be directly measured and are independent of species and therefore they can be directly related to the properties of the organisms function within the ecosystem, such as nutrient affinity for example (Litchman and Klausmeier 2008).

A simple example of a trait-based description of phytoplankton succession is scaling the maximal nutrient acquisition rate and the respective affinity with cell size. A trade-off would emerge between different size classes, allowing for a modeled succession along gradients of nutrient depletion. One example of a very similar approach is the PhytoSFDM model developed by Acevedo-Trejos and colleagues (Acevedo-Trejos et al. 2013, Acevedo-Trejos et al. 2015). In their approach, the trait-based modelling of phytoplankton is even further simplified, by describing an entire community as a size-distribution with a mean value and a variance, instead of modeling all the different size classes explicitly. This moment-based structure further simplifies the mathematical basis of the model, and leads to much faster processing times and less uncertainty in parameter estimation.

"quite a few publications using models go too far in their extrapolations, whilst the general discussion still strongly revolves around meaningful model structures.. but no consensus is anywhere to be seen! "need to identify the basic uncertainties and see if there is a way to discuss them scientifically "Michaelis Menten kinetics are really outdated.. and i suppose using them in a trait-based modelling approach is questionable just the same "plankton ecosystems are typically highly aggregated, a single variable gives the response of an incredibly diverse assemblage of phytoplankton species (P. Franks, 2009)

XXX

XXX

XXX

XXX.

XXX

XXX

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

## 1.4 The Cariaco basin & the CARIACO time series

A coastal tropical ecosystem

"continental margins constitute only about 10% of the total ocean surface area, these regions are responsible for about 10–15% of the global marine primary production and greater than 40% of seabed carbon sequestration (Yool and Fasham, 2001; Muller-Karger et al., 2005). "The Cariaco Basin, located off the coast of Venezuela, has been the site of high frequency water column sampling for marine biogeochemical and ecological observations since 1995. The observations were collected as part of the Cariaco Ocean Time-Series Program (Muller-Karger et al., 2001; Thunell et al., 2007).

XXXX

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.

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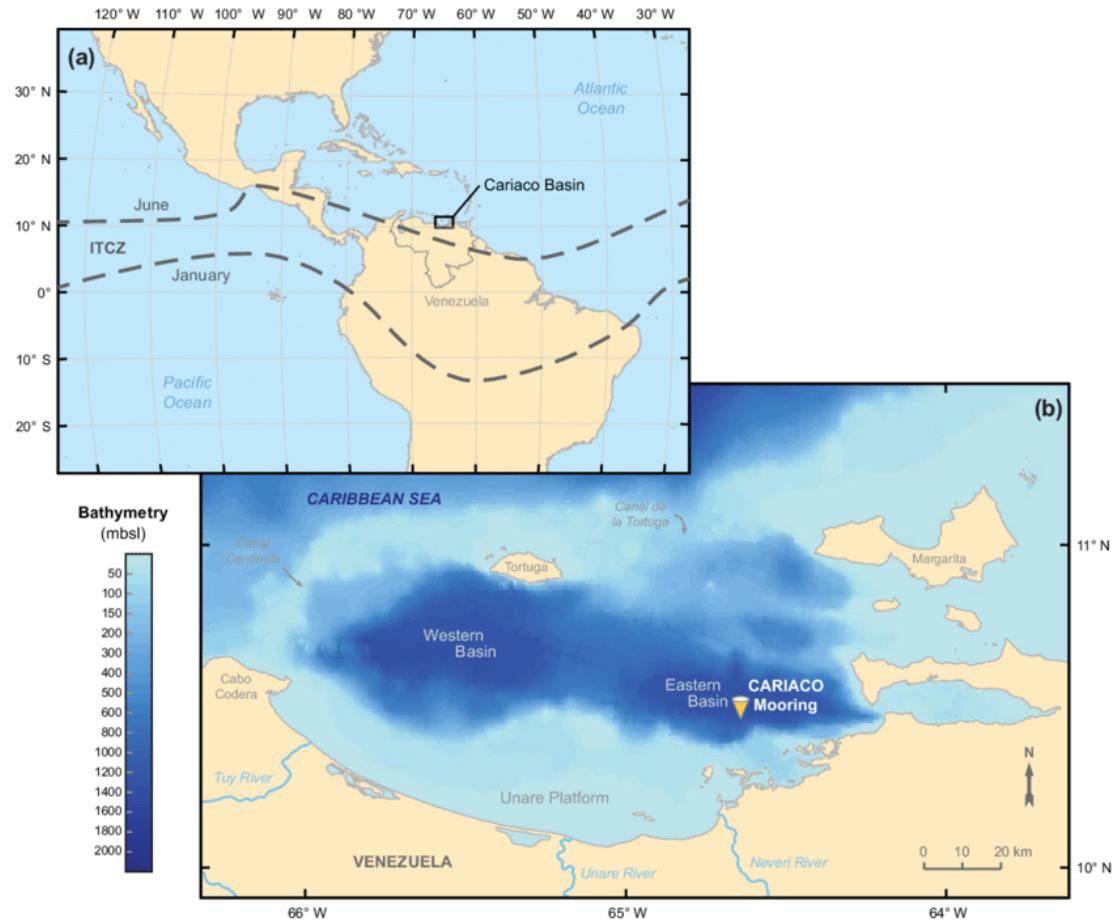


Figure 1.3: "Study area. A. Location of the Cariaco Basin off the Venezuelan coast in the southern Caribbean Sea, with January and June positions of the Intertropical Convergence Zone (ITCZ). B. Location of the CARIACO station in the eastern sub-basin, general bathymetry and local rivers emptying in the basin (bathymetric data from GEBCO\_08 Grid)" from Bringué et al. (2019)

XXX

THEN TALK ABOUT THE COLLABoRDATA SHARE 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"

## **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 somewhere)  
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

don't 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 research (and funding) has been most well developed. Fasham NPZD type slab 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 N<sub>0</sub> and Si<sub>0</sub> (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).

kkkkkkkkkkkkkkkkkkkkkkkk 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.. XXXXXXXX

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

teach PhD Students from the ground up to code their own models in Python, as of yet there is a lack of coherent resources. 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 they 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

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.

XXXX

XXXX

XXXX

### 4.3 Time table

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

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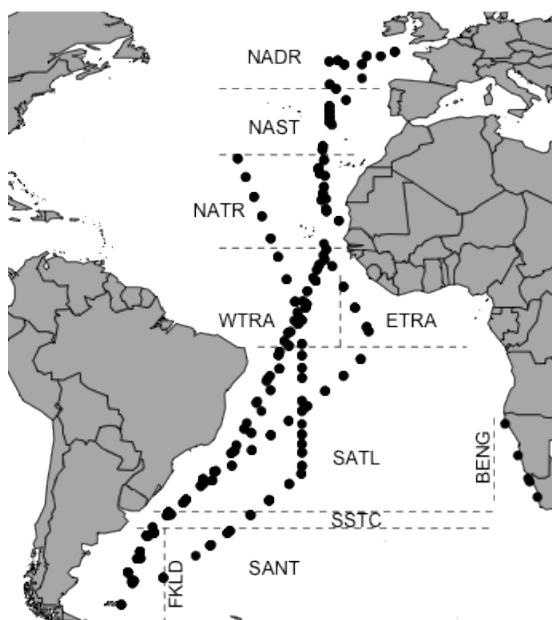


Figure 4.1: The AMT subset of 410 samples used in this study. The dashed lines represent the simplified limits of the Longhurst (2006) ecological provinces.

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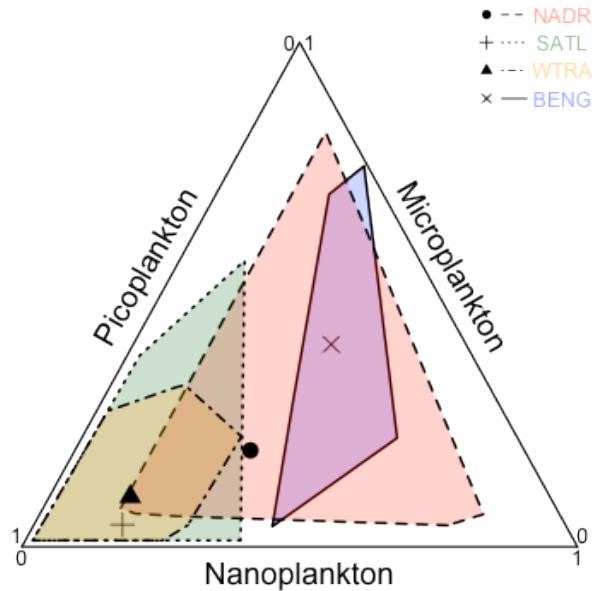


Figure 4.2: Phytoplankton community size structure of four ecological provinces in the Atlantic Ocean. The contours correspond to the convex hull of the size-fraction distribution of each province. The symbols indicate the corresponding mean values.

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

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

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

The approach of defining a trade-off that relates size to the competitive ability for nutrient acquisition and resistance to predation (?) 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

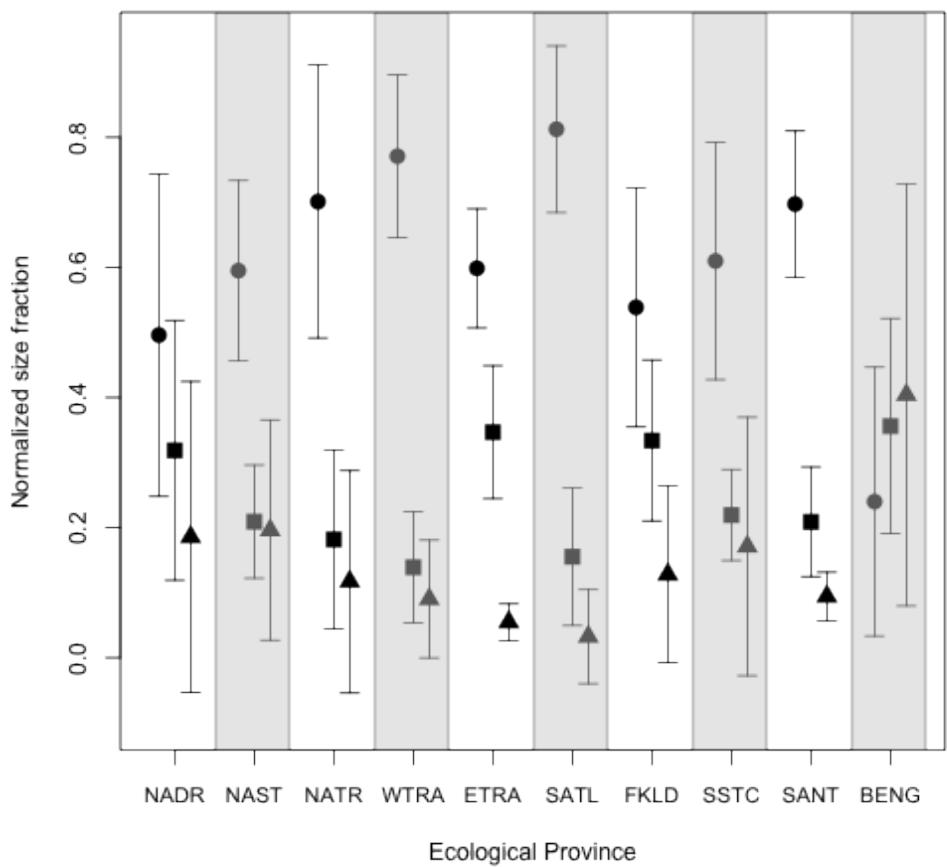


Figure 4.3: Relative mean abundances ( $\pm$ sd) of three phytoplankton size fractions of ten ecological provinces of the Atlantic Ocean. The symbols indicate the mean values of the normalized size fractions: picoplankton (●), nanoplankton(■) and microplankton (▲).

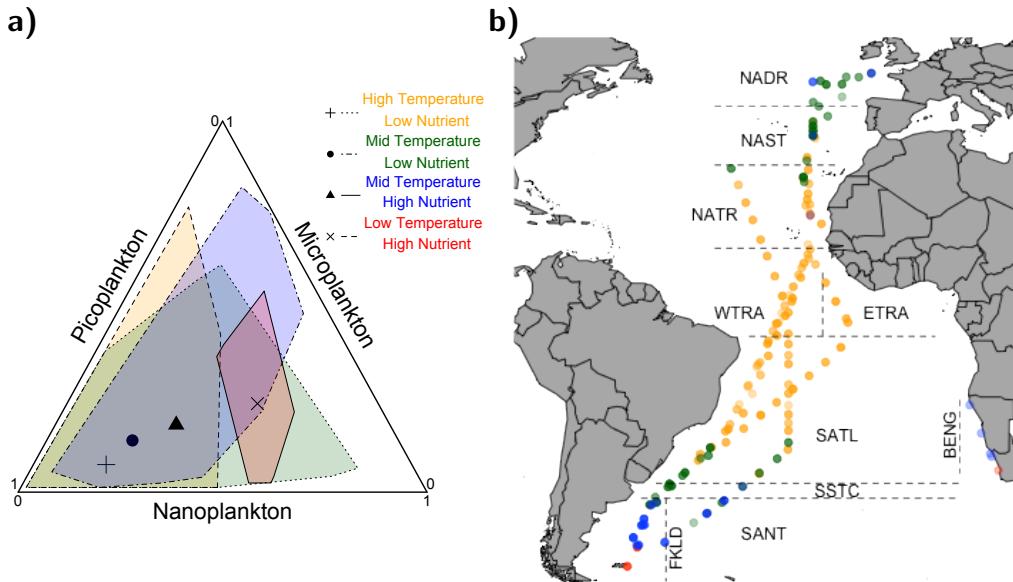


Figure 4.4: Caption comes here my friend"""""""".

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	$\text{NO}_2^- + \text{NO}_3^-$	$\text{PO}_4^{3-}$	$\text{SiO}_4^{2-}$	Temperature
HTLN	$0.150 \pm 0.575$	$0.064 \pm 0.078$	$1.097 \pm 0.575$	$25.299 \pm 2.000$
MTLN	$0.556 \pm 1.102$	$0.112 \pm 0.141$	$0.816 \pm 0.617$	$17.894 \pm 2.191$
MTHN	$9.027 \pm 3.593$	$0.799 \pm 0.373$	$2.423 \pm 1.375$	$11.925 \pm 2.797$
LTHN	$30.324 \pm 4.549$	$1.336 \pm 0.208$	$4.590 \pm 1.926$	$6.810 \pm 3.435$

will be tested against and constrained by the AMT observations on environmental data and community size structures in the Atlantic Ocean (chapter 2).

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  $\text{NO}_3^- + \text{NO}_2^-$  and temperature on all three size fractions. Pico- and nanoplankton size fractions, however, appeared more sensitive to changes in  $\text{PO}_4^{3-}$ ,  $\text{SiO}_4^{2-}$  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

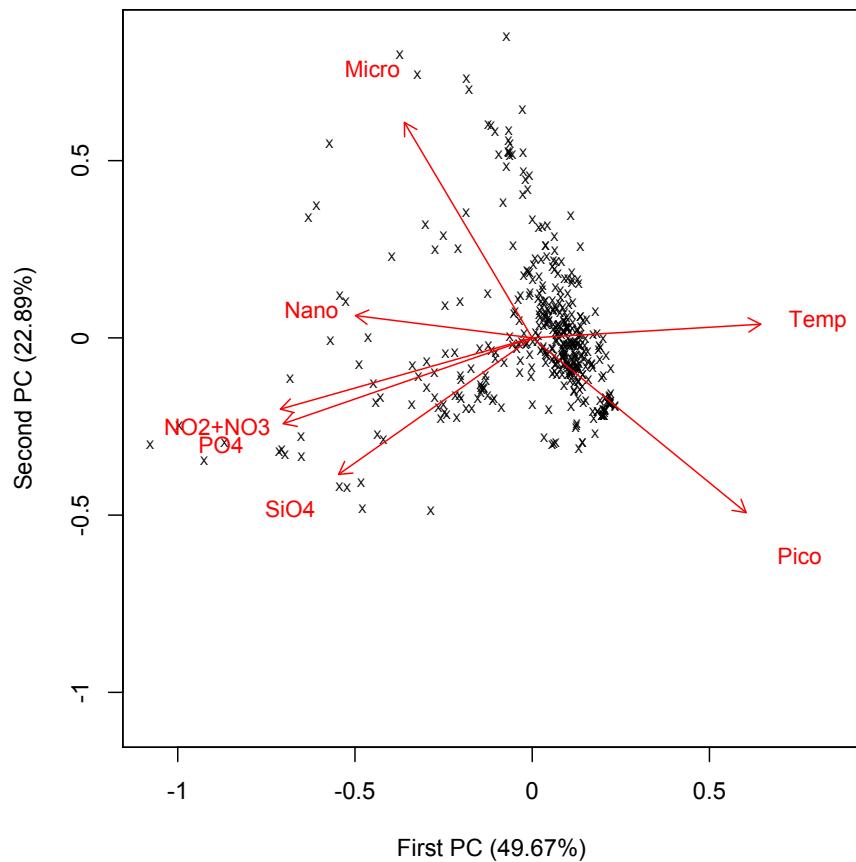


Figure 4.5: Principal Component Analysis of environmental parameters and normalized phytoplankton size fractions.

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

	Picoplankton			Nanoplankton			Microplankton		
	slope	p-value	r <sup>2</sup>	slope	p-value	r <sup>2</sup>	slope	p-value	r <sup>2</sup>
NO <sub>2</sub> <sup>-</sup> + NO <sub>3</sub> <sup>-</sup>	-0.090	0.002	0.908	0.050	0.001	0.921	0.040	0.010	0.792
PO <sub>4</sub> <sup>3-</sup>	-0.0812	0.021	0.711	0.042	0.012	0.777	0.039	0.125	0.354
SiO <sub>4</sub> <sup>2-</sup>	-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

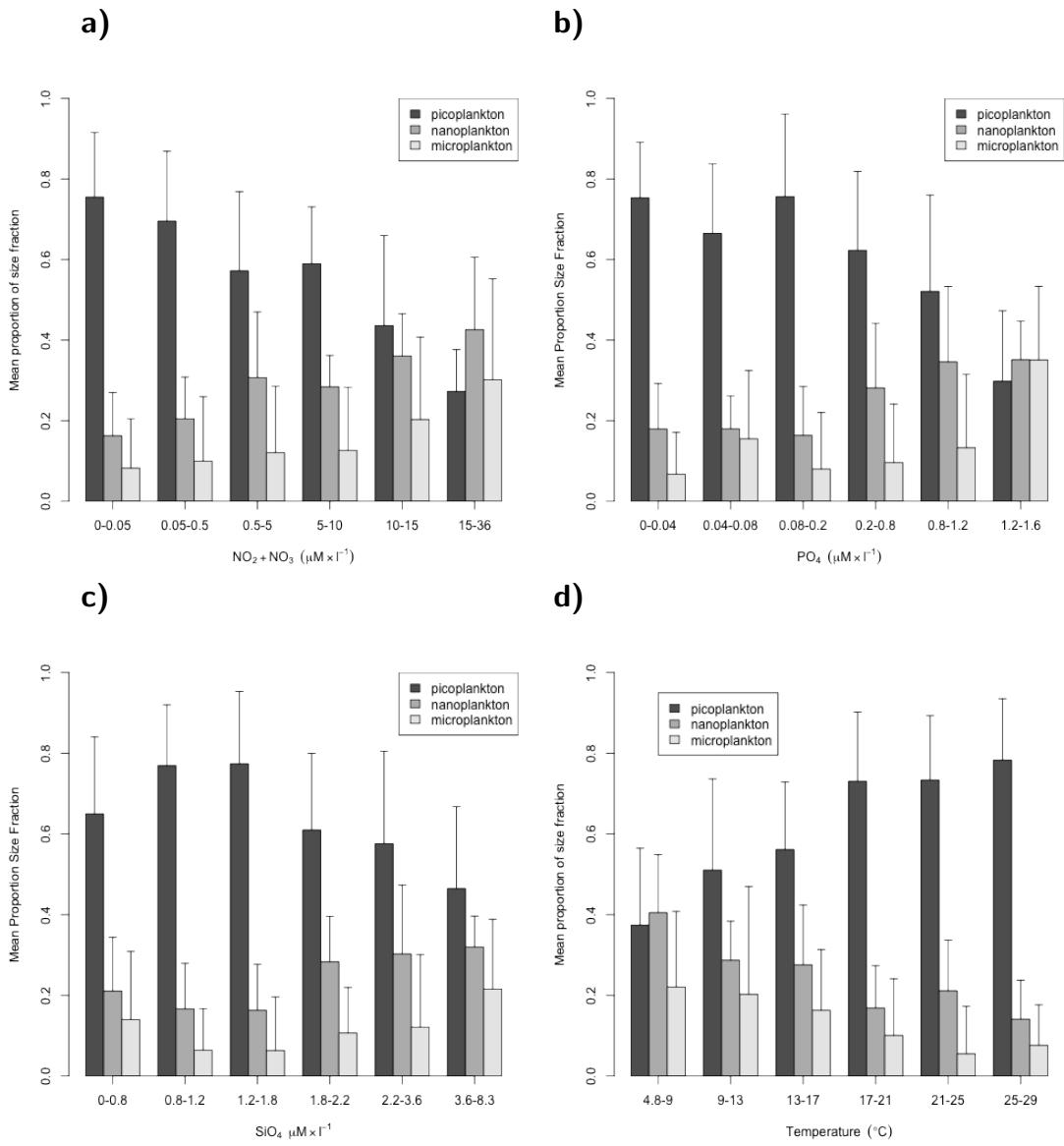


Figure 4.6: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with concentrations of nitrate+nitrite (a), phosphate (b), and silicate (c) and with temperature (d). The bars represent mean values and the error bars indicate the standard deviation.

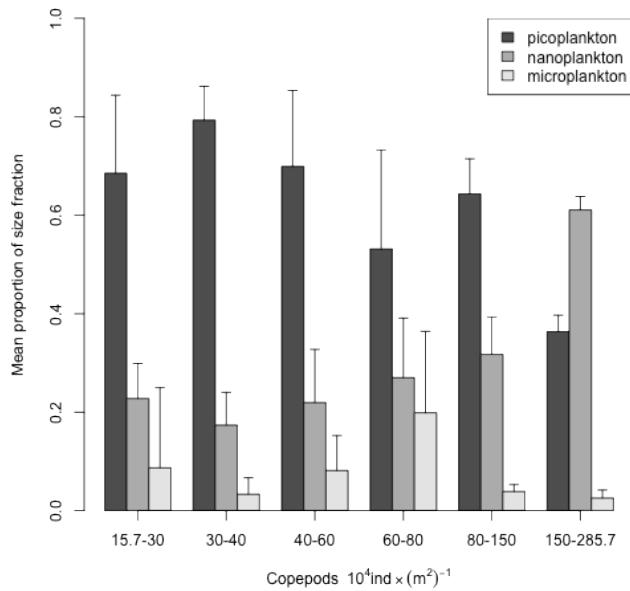


Figure 4.7: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with copepod abundance. The bars represent mean values and the error bars indicate the standard deviation.

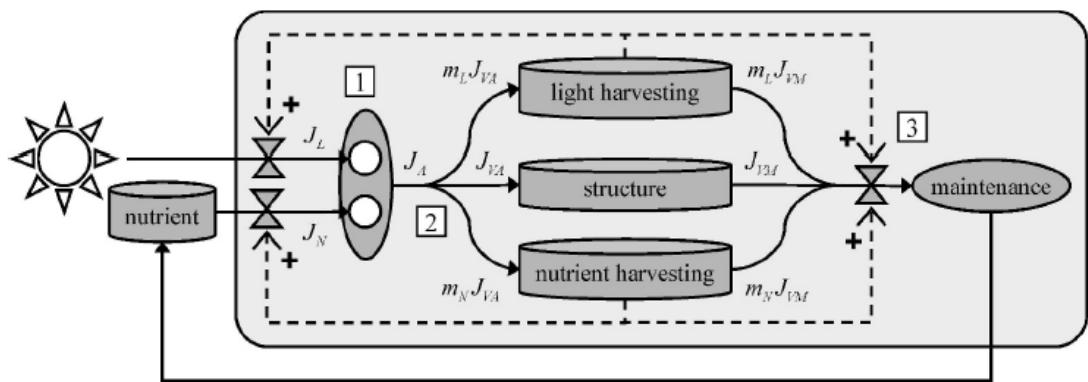


Figure 4.8: Bruggeman and Kooijman model scheme. Taken from ?

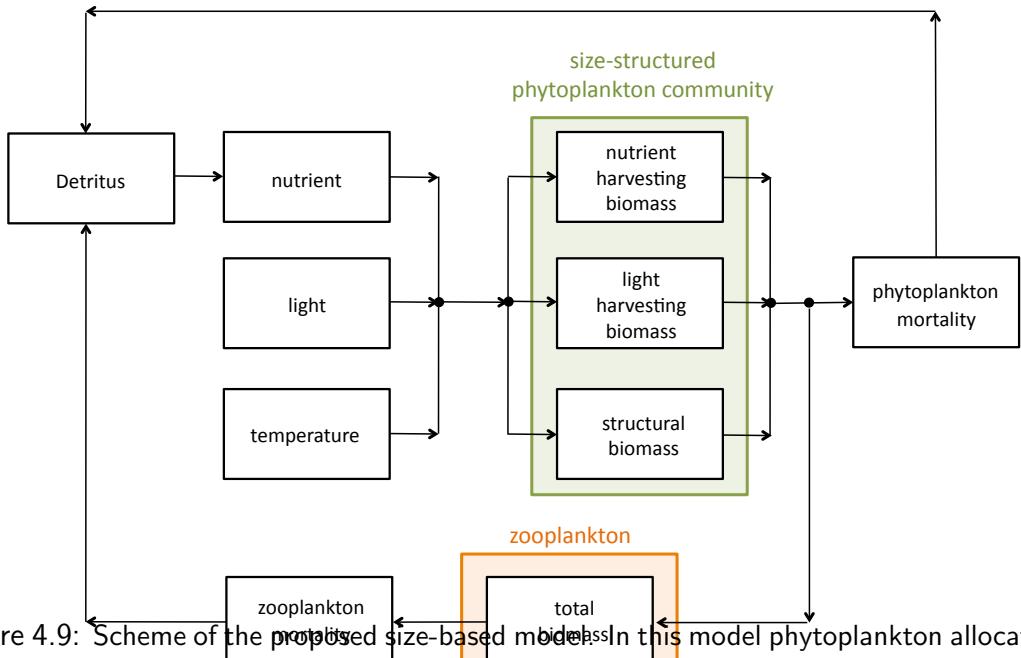


Figure 4.9: Scheme of the proposed size-based model. In this model phytoplankton allocates energy (or biomass) to different pools such as nutrient and light harvesting biomasses and generic structural biomass. A certain fraction of the phytoplankton biomass flows into the zooplankton biomass and a remaining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

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 ?. The phytoplankton total biomass ( $P$ ), the mean trait ( $\bar{s}$ ), and the trait variance ( $v$ ) will be formulated as follows:

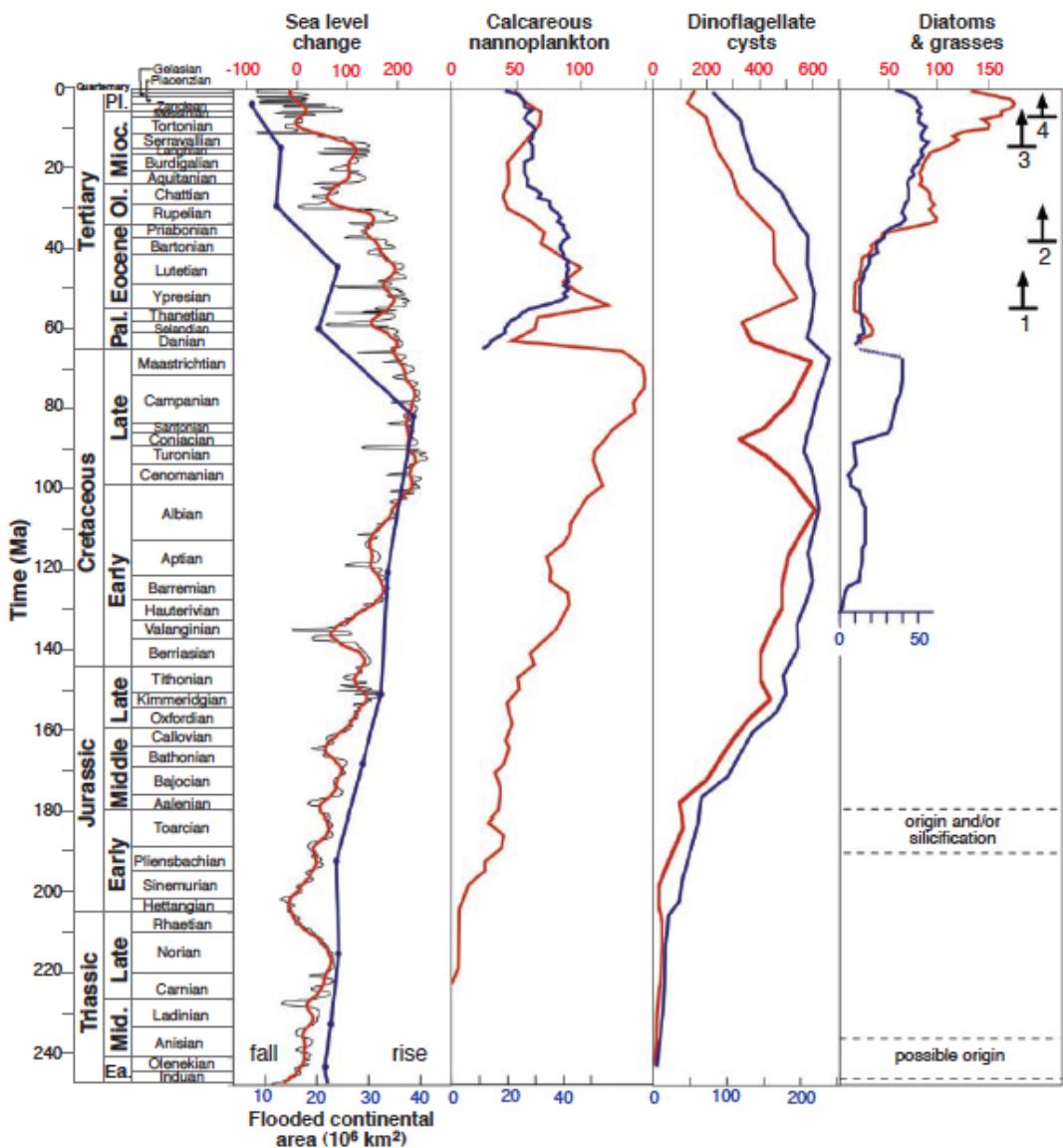


Figure 4.10: Comparison of major phytoplankton groups with sea-level change. The red line accounts for species diversities from published studies. The blue line accounts for the genus diversity compiled from public databases by the authors. Taken from Falkowski et al. (2004).

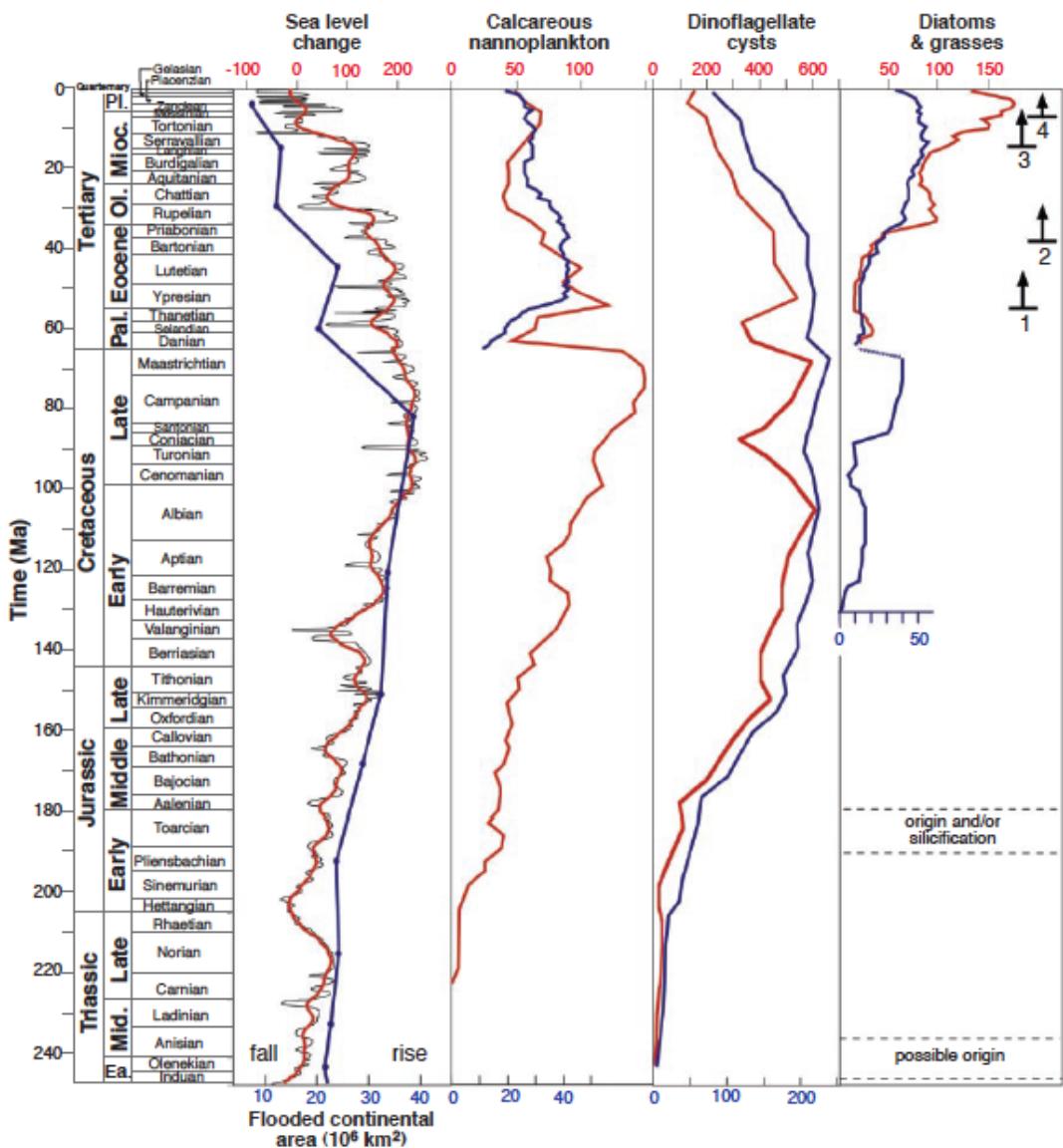


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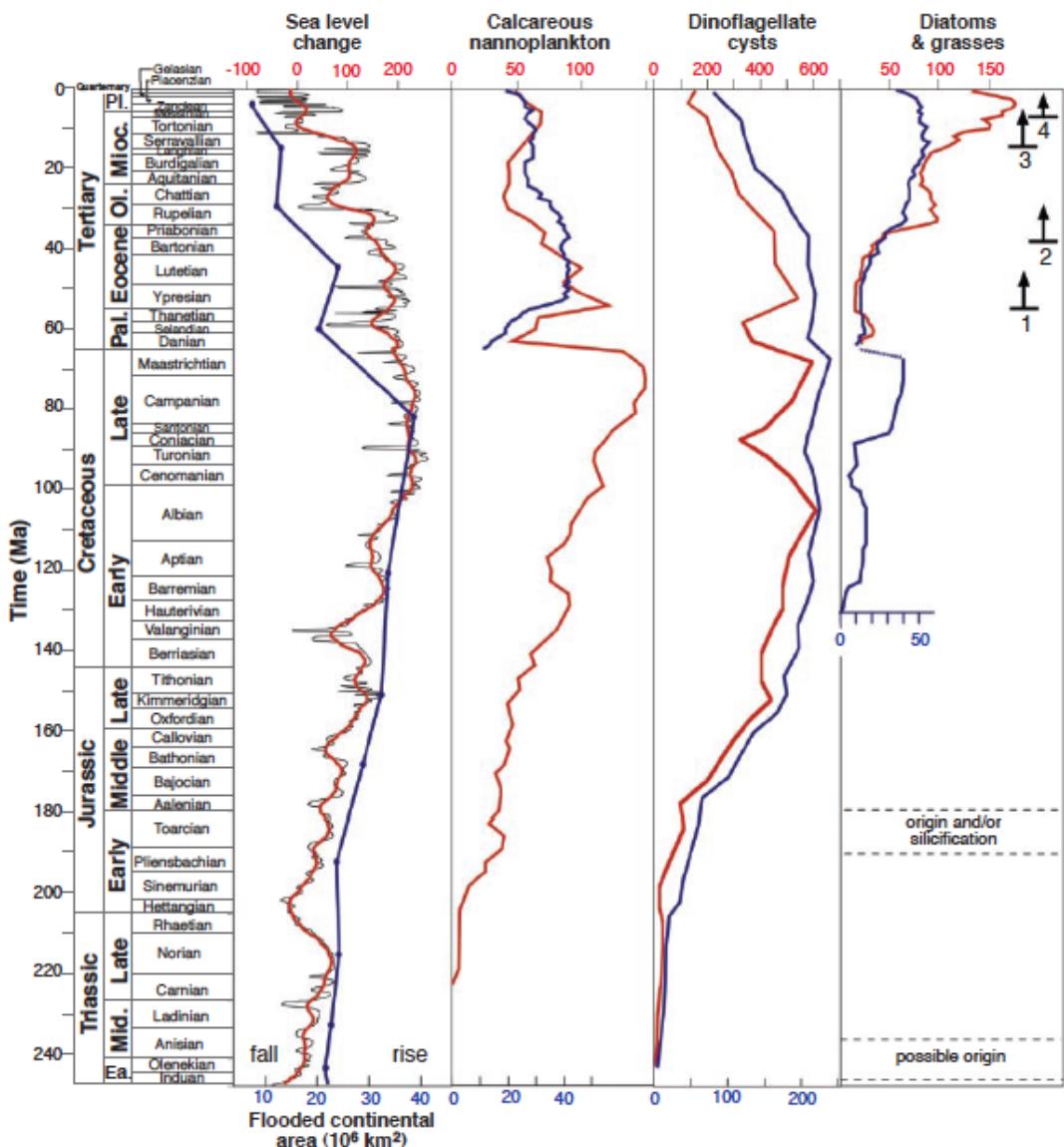


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