



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

Author:
Benjamin POST

Dissertation Committee:
Prof. Dr. Agostino MERICO
Prof Dr. Marc-Thorsten HÜTT
Dr. Esteban ACEVEDO-TREJOS
Prof Dr. Andrew D. BARTON

August 12, 2019

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.

Contents

1 General Introduction	2
1.1 The ocean, phytoplankton and why it matters	2
1.2 Characterizing phytoplankton	4
1.2.1 Functional types and traits	5
1.3 Modeling phytoplankton communities	6
1.4 The Cariaco basin & the CARIACO time series	8
1.5 Aims of the proposed PhD project	9
2 Understanding phytoplankton community shifts in the eastern Cariaco basin	11
2.1 Regime Shift in CARIACO data	11
2.2 Methods	12
2.2.1 Model physics in a tropical coastal setting	12
2.3 Preliminary Results	12
2.4 How to complete this project	13
3 PhytoMFTM - a flexible object-oriented PFT model	14
3.1 Python ecosystem model package development	14
3.2 Methods	15
3.2.1 Object-oriented structure	15
3.2.2 Model formulation and usage	15
3.3 How to complete this project	15
4 Further work	16
4.1 Where to go from here	16
4.1.1 BDEF	16
4.1.2 Method	16
4.2 Relevance	16
4.3 Time table	18
Bibliography	19

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 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. 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

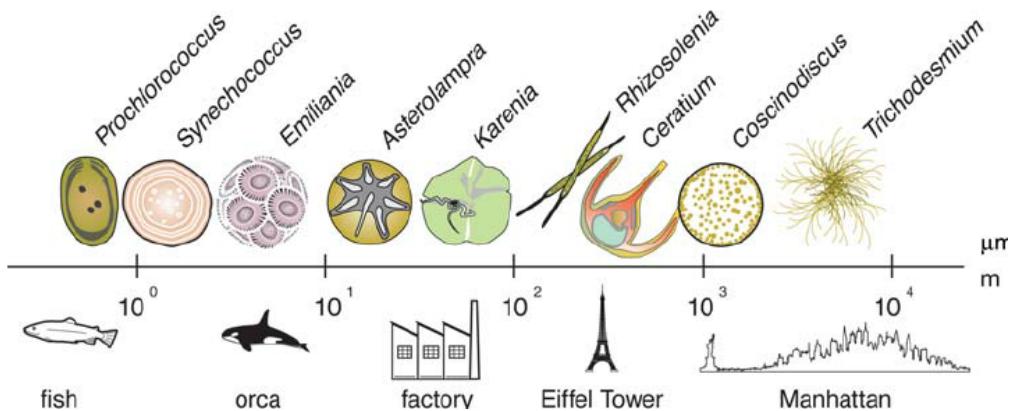


Figure 1.1: "A comparison of the size range (maximum linear dimension) of phytoplankton relative to macroscopic objects." from Finkel et al. (2010)

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 CO₂ 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

Given the relevance of phytoplankton to the global

How did Researchers start dealing with Phytoplankton?

Two approaches to isolate strains, or take bulk properties

Obviously bulk properties also have to be taken from specific depth

so this adds the problem of the complexity of the physical environment that is the ocean, with enormous volume, turbulence mixing, diffusion and absorbance

I want to look at phytoplankton diversity, particularly from a functional type point of view. Quantify diversity as it relates to ecosystem function (as production for example).

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.

"Moreover, major taxonomic groups of eukaryotic phytoplankton can be classified into distinct functional groups (Iglesias-Rodriguez et al. 2002a) with unique biogeographical signatures. Here, we combine the trait-based approach with the taxonomic sLASH phylogenetic information by broadly sampling relevant traits across major taxonomic groups of marine phytoplankton to gain new insights into the effects of evolutionary history on the physiological trait distributions and community structure. An important aspect of a trait-based approach to "community ecology" is the trade-offs between traits (Tilman 1990; Grover 1991; Bohannan et al. 2002). When competition for multiple resources is considered, species are thought to have trade-offs in their competitive ability for one vs. another nutrient (Tilman 1982) or for nutrient vs. light (Huisman & Weissing 1994; Leibold 1997; Klausmeier & Litchman 2001). Under non-equilibrium conditions, a trade-off between competitive ability and maxi-

mum growth rate may Litchman, E., Klausmeier, C. A., Schofield, O. M., & Falkowski, P. G. (2007). The role of functional traits and trade-offs in structuring phytoplankton communities: Scaling from cellular to ecosystem level. *Ecology Letters*, 10(12), 1170–1181. [https:doi.org10.1111j.1461-0248.2007.01117.x](https://doi.org/10.1111/j.1461-0248.2007.01117.x)

"Functional types can be composed of a large number of species with very different trait values, so the representation of a type by an average trait value may not be appropriate." (Irwin and Finkel 2018) XXX

"Phytoplankton can be characterised by many morphological, physiological, behavioural and life history traits and trade-offs (??).

"Studies on the phytoplankton community composition and their response to the environmental gradients are not novel. Ramón Margalef was probably one of the first ecologist to give an important momentum to the topic. (?) used observations of key traits, such as nutrient utilization and sinking rates, to support his well known concept called "Margalef's mandala". His classification of phytoplankton functional types (PFTs) at different nutrient and turbulent environmental conditions represents an excellent first example of how the trait-based notion can be applied to better understand phytoplankton community ecology, therefore setting up the stage for further developments in the field.

1.2.1 Functional types and traits

"Ecology has traditionally focused on species diversity as a way of characterizing the health of an ecosystem. In recent years, however, the focus has increasingly shifted towards trait diversity both within and across species" - from Functional Diversity Book

We have incredibly diverse Phytoplankton, and want to analyze traits and model -*i* need to simplify somehow =*i* Functional Types

so I want to talk about: that phytoplankton can be divided in functional groups talk about the Work that Finkel and Irwin have done! question whether it makes sense to use functional types instead of species, . . . 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)

XXXX

XXXX

XXXX

1.3 Modeling phytoplankton communities

Going into the details is necessary to understand the whole picture

One tool of integration are mathematical models

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 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.

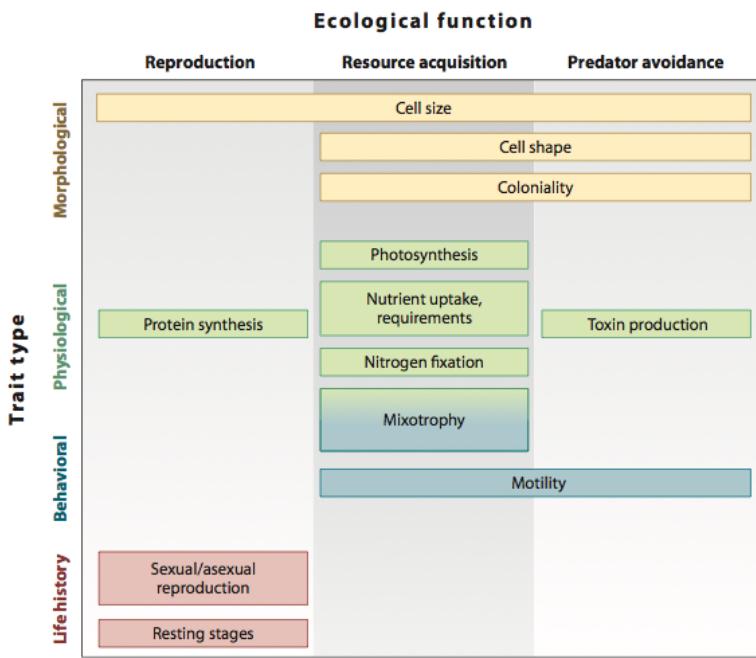


Figure 1.2: Phytoplankton functional traits. Taken from ?

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.

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,

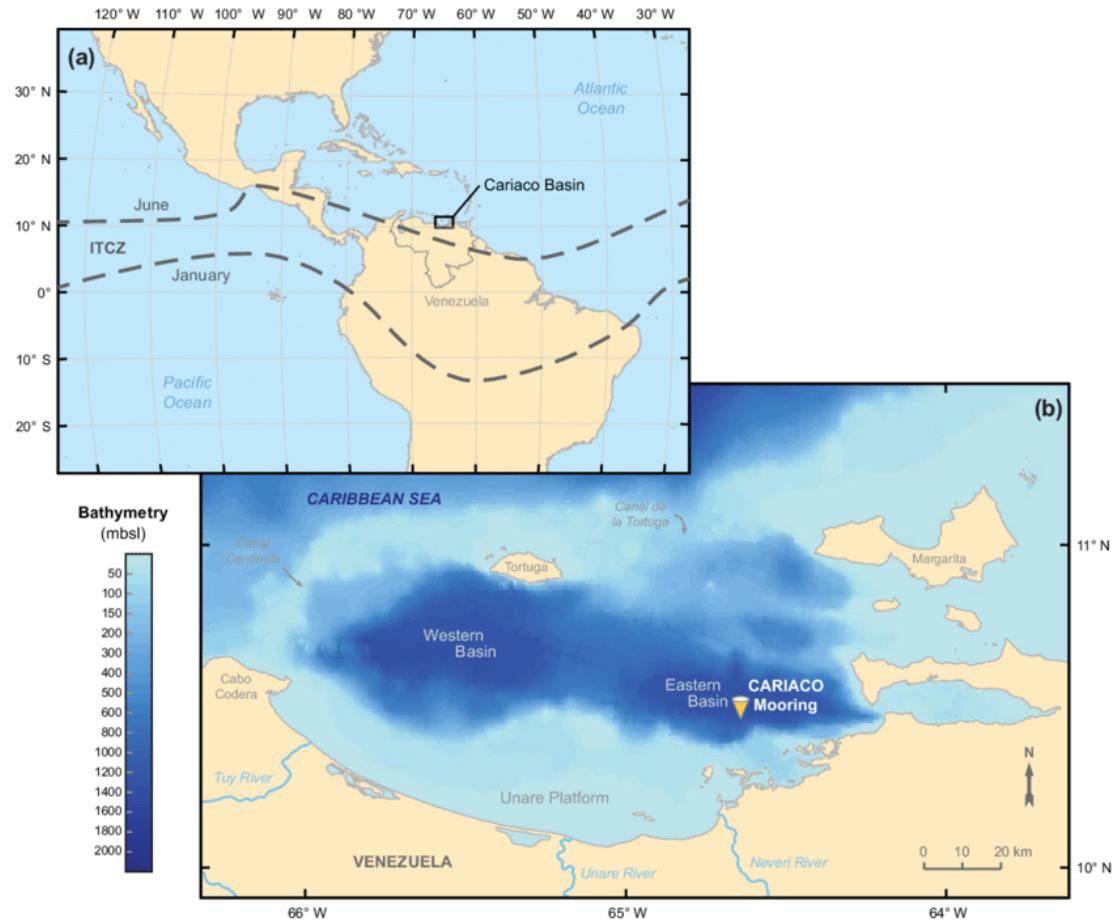


Figure 1.3: "Study area. A. Location of the Cariaco Basin off the Venezuelan coast in the southern Caribbean Sea, with January and June positions of the Intertropical Convergence Zone (ITCZ). B. Location of the CARIACO station in the eastern sub-basin, general bathymetry and local rivers emptying in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

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)

FUNCTIONAL TYPES STRUCTURE –*i* explain linkage between Pigment Data that I use and functional diversity measurements (XMoreno et al. 2012X) take this from Pinckney et al. 2015... 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

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.

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

XXXXXXX

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

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
2011		Literature review		AMT data mining		Manuscript writing		Ph.D. proposal	Manuscript writing	Develop size-based model		
2012	Develop size-based model		Sensitivity analysis		Manuscript writing		Develop a coupled phytoplankton and zooplankton size-based model					
2013	Sensitivity analysis		Manuscript writing		Develop phytoplankton size-based evolutionary model			Sensitivity analysis	Manuscript writing			
2014	Manuscript writing	Ph.D. defense										

Bibliography

- Boyce DG, Lewis M, Worm B (2012) Integrating global chlorophyll data from 1890 to 2010. *Limnology and Oceanography: Methods* 10(11):840–852
- Bringué M, Pospelova V, Tappa EJ, Thunell RC (2019) Dinoflagellate cyst production in the Cariaco Basin: A 12.5-year-long sediment trap study. *Progress in Oceanography* 171:175–211
- Chavez FP, Messié M, Pennington JT (2010) Marine Primary Production in Relation to Climate Variability and Change. *Annual Review of Marine Science* 3(1):227–260
- Eppley RW, Peterson BJ (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282(5740):677
- Falkowski PG, Katz ME, Knoll AH, Quigg A, Raven JA, Schofield O, Taylor FJ (2004) The evolution of modern eukaryotic phytoplankton. *Science* 305(5682):354–360
- Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science* 281(5374):237–240
- Finkel ZV, Beardall J, Flynn KJ, Quigg A, Rees TAV, Raven JA (2010) Phytoplankton in a changing world: Cell size and elemental stoichiometry. *Journal of Plankton Research* 32(1):119–137
- Honjo S, Manganini SJ, Krishfield RA, Francois R (2008) Particulate organic carbon fluxes to the ocean interior and factors controlling the biological pump: A synthesis of global sediment trap programs since 1983. *Progress in Oceanography* 76(3):217–285
- Muller-Karger FE, Varela R, Thunell R, Luerssen R, Hu C, Walsh JJ (2005) The importance of continental margins in the global carbon cycle. *Geophysical Research Letters* 32(1):1–4
- Redfield AC (1958) The biological control of chemical factors in the environment. *American scientist* 46(3):230A–221

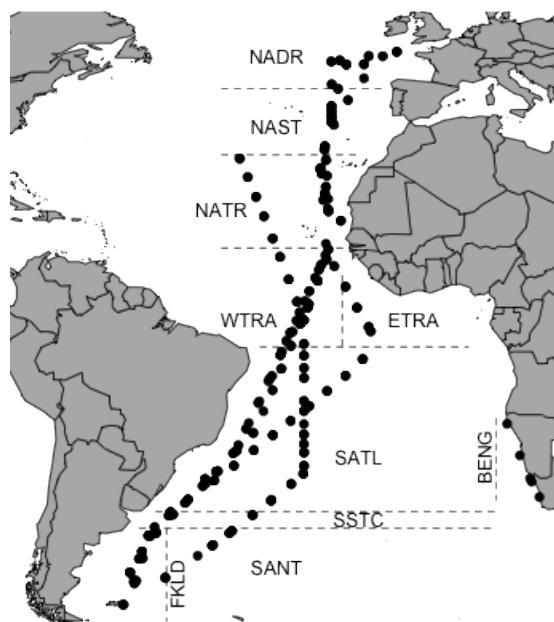


Figure 4.1: The AMT subset of 410 samples used in this study. The dashed lines represent the simplified limits of the Longhurst (2006) ecological provinces.

Stock CA, John JG, Rykaczewski RR, Asch RG, Cheung WWL, Dunne JP, Friedland KD, Lam VWY, Sarmiento JL, Watson RA (2017) Reconciling fisheries catch and ocean productivity. *Proceedings of the National Academy of Sciences* 114(8):E1441–E1449

Walsh JJ, Dieterle DA, Müller-Karger FE, Bohrer R, Bissett WP, Varela RJ, Aparicio R, Díaz R, Thunell R, Taylor GT, Scranton MI, Fanning KA, Peltzer ET (2002) Simulation of carbon-nitrogen cycling during spring upwelling in the Cariaco Basin. *Journal of Geophysical Research: Oceans* 104(C4):7807–7825

Yool A, Fasham MJR (2001) An examination of the “continental shelf pump” in an open ocean general circulation model. *Global Biogeochemical Cycles* 15(4):831–844

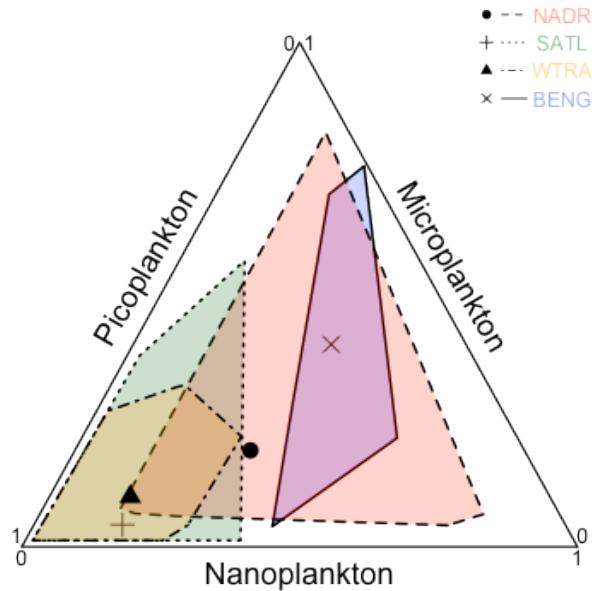


Figure 4.2: Phytoplankton community size structure of four ecological provinces in the Atlantic Ocean. The contours correspond to the convex hull of the size-fraction distribution of each province. The symbols indicate the corresponding mean values.

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

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

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

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

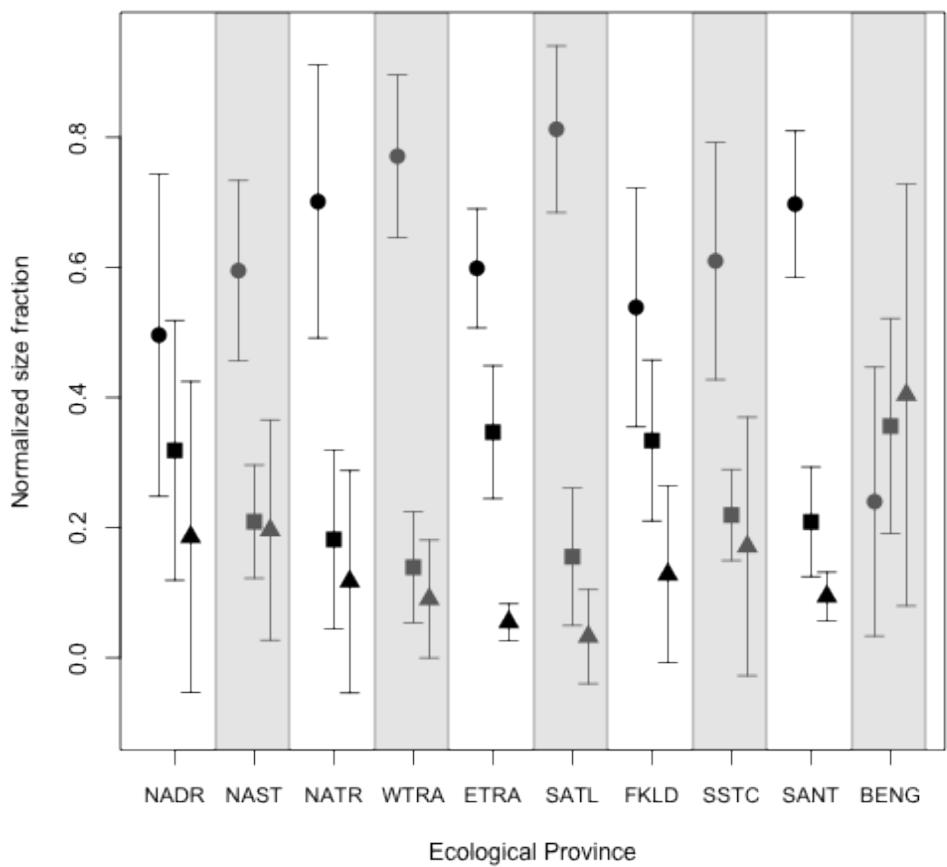


Figure 4.3: Relative mean abundances (\pm sd) of three phytoplankton size fractions of ten ecological provinces of the Atlantic Ocean. The symbols indicate the mean values of the normalized size fractions: picoplankton (●), nanoplankton(■) and microplankton (▲).

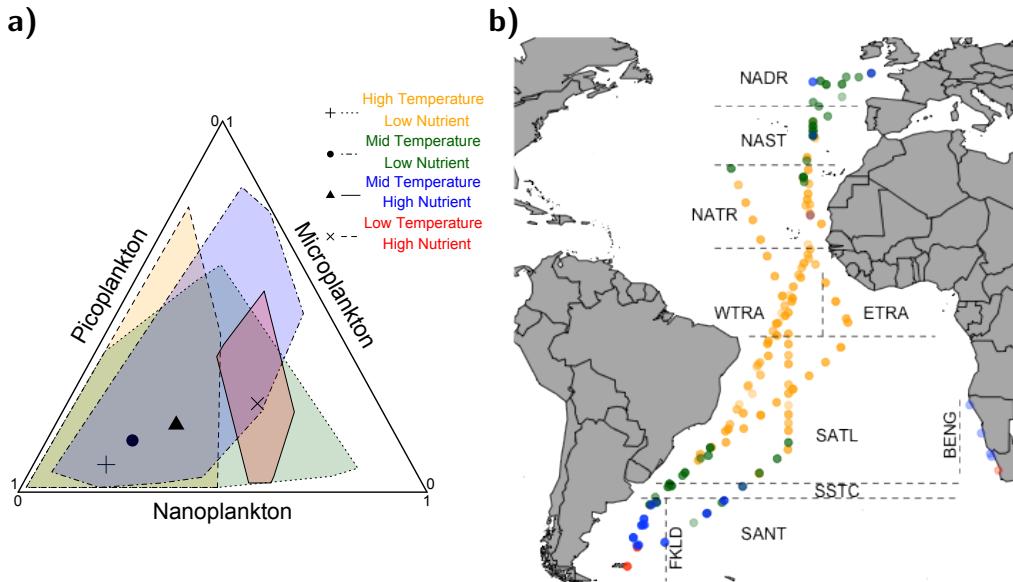


Figure 4.4: Caption comes here my friend"""""""".

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	$\text{NO}_2^- + \text{NO}_3^-$	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

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 (??). 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 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

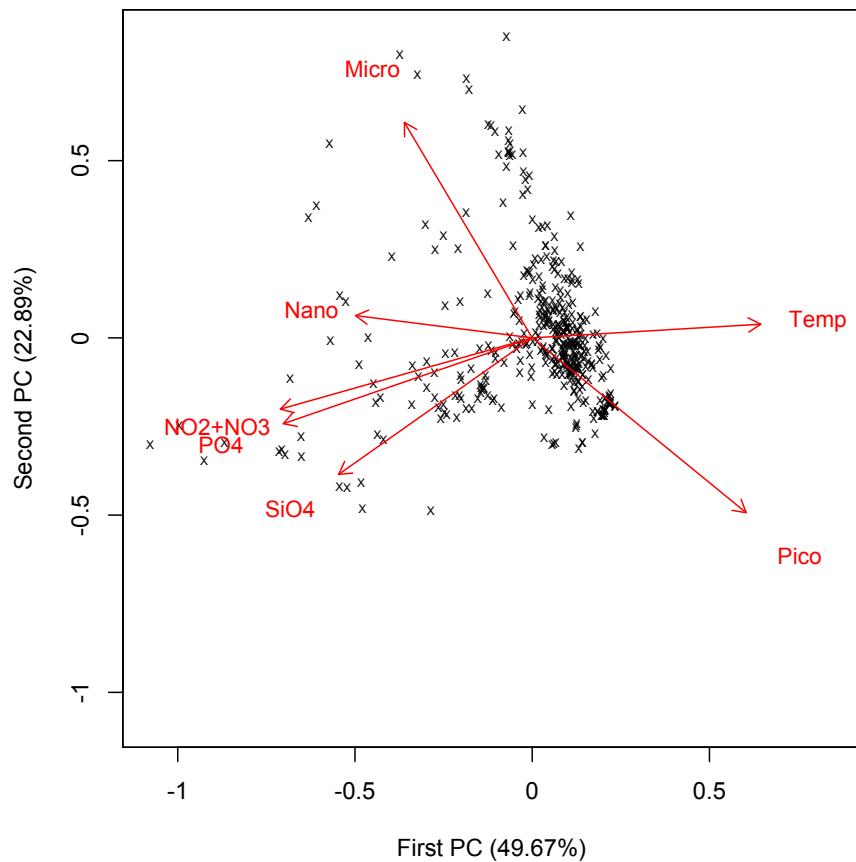


Figure 4.5: Principal Component Analysis of environmental parameters and normalized phytoplankton size fractions.

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

	Picoplankton			Nanoplankton			Microplankton		
	slope	p-value	r 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

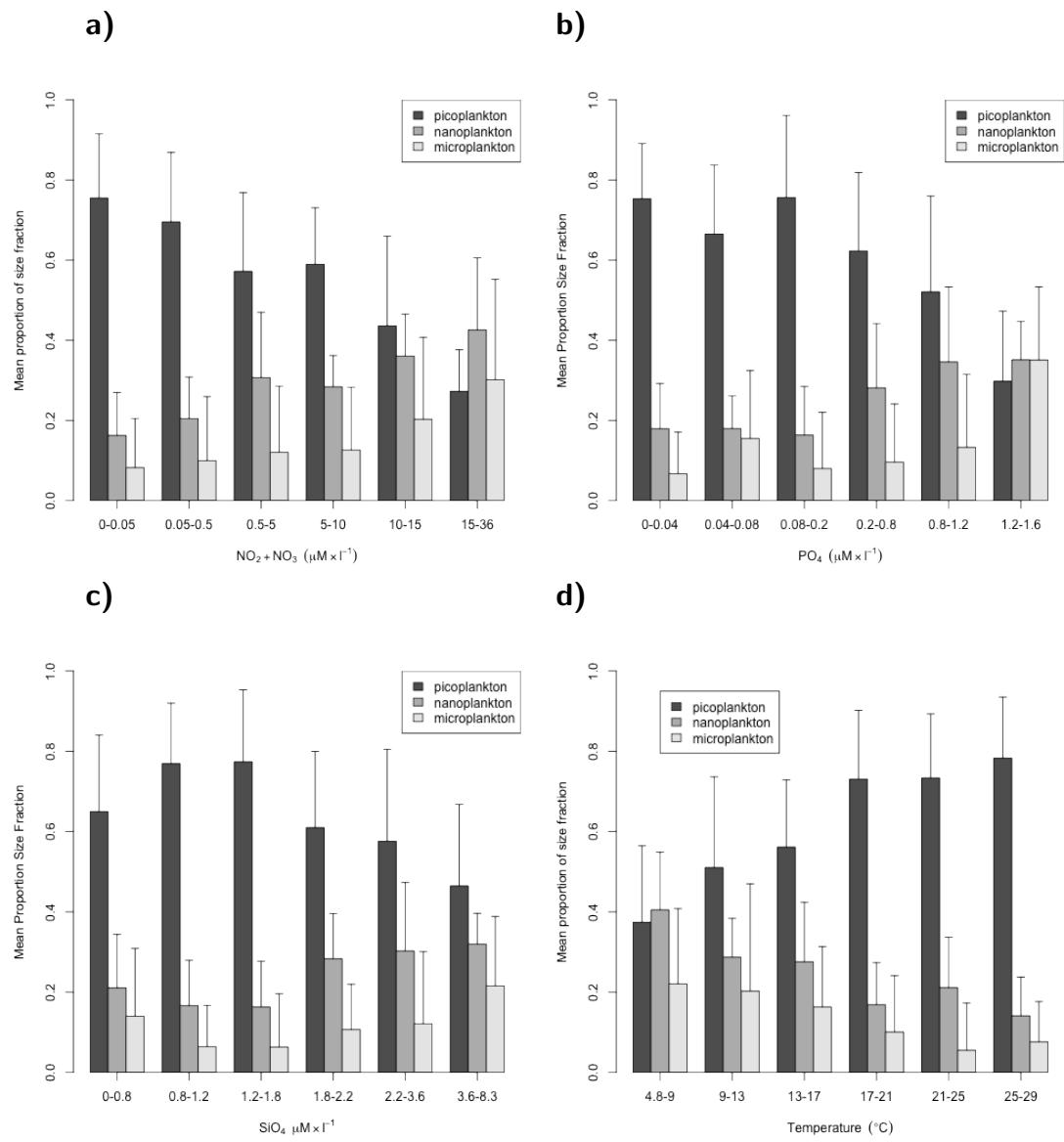


Figure 4.6: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with concentrations of nitrate+nitrite (a), phosphate (b), and silicate (c) and with temperature (d). The bars represent mean values and the error bars indicate the standard deviation.

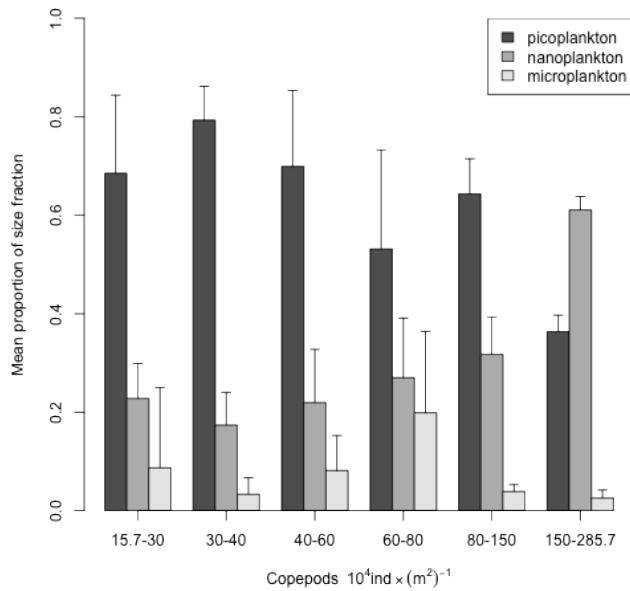


Figure 4.7: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with copepod abundance. The bars represent mean values and the error bars indicate the standard deviation.

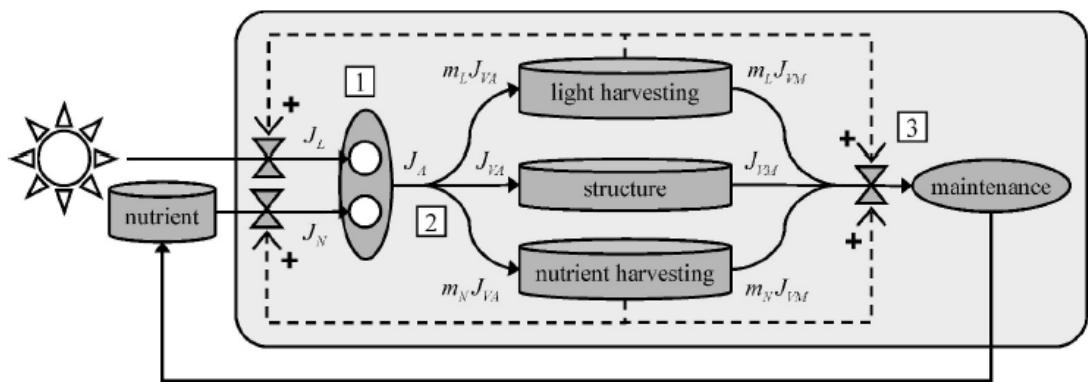


Figure 4.8: Bruggeman and Kooijman model scheme. Taken from ?

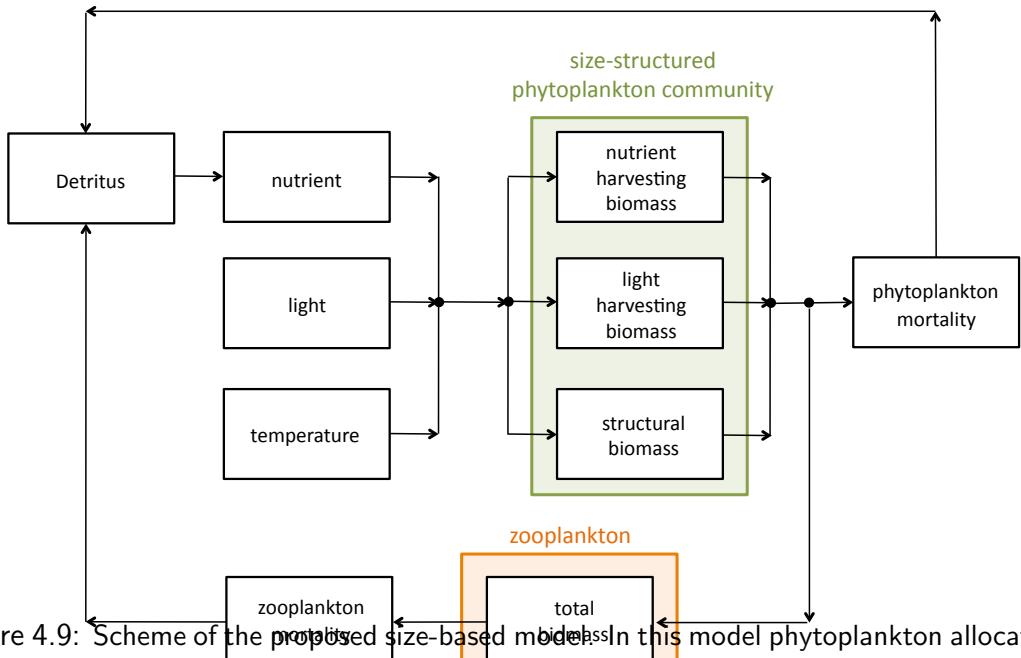


Figure 4.9: Scheme of the proposed size-based model. In this model phytoplankton allocates energy (or biomass) to different pools such as nutrient and light harvesting biomasses and generic structural biomass. A certain fraction of the phytoplankton biomass flows into the zooplankton biomass and a remaining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

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:

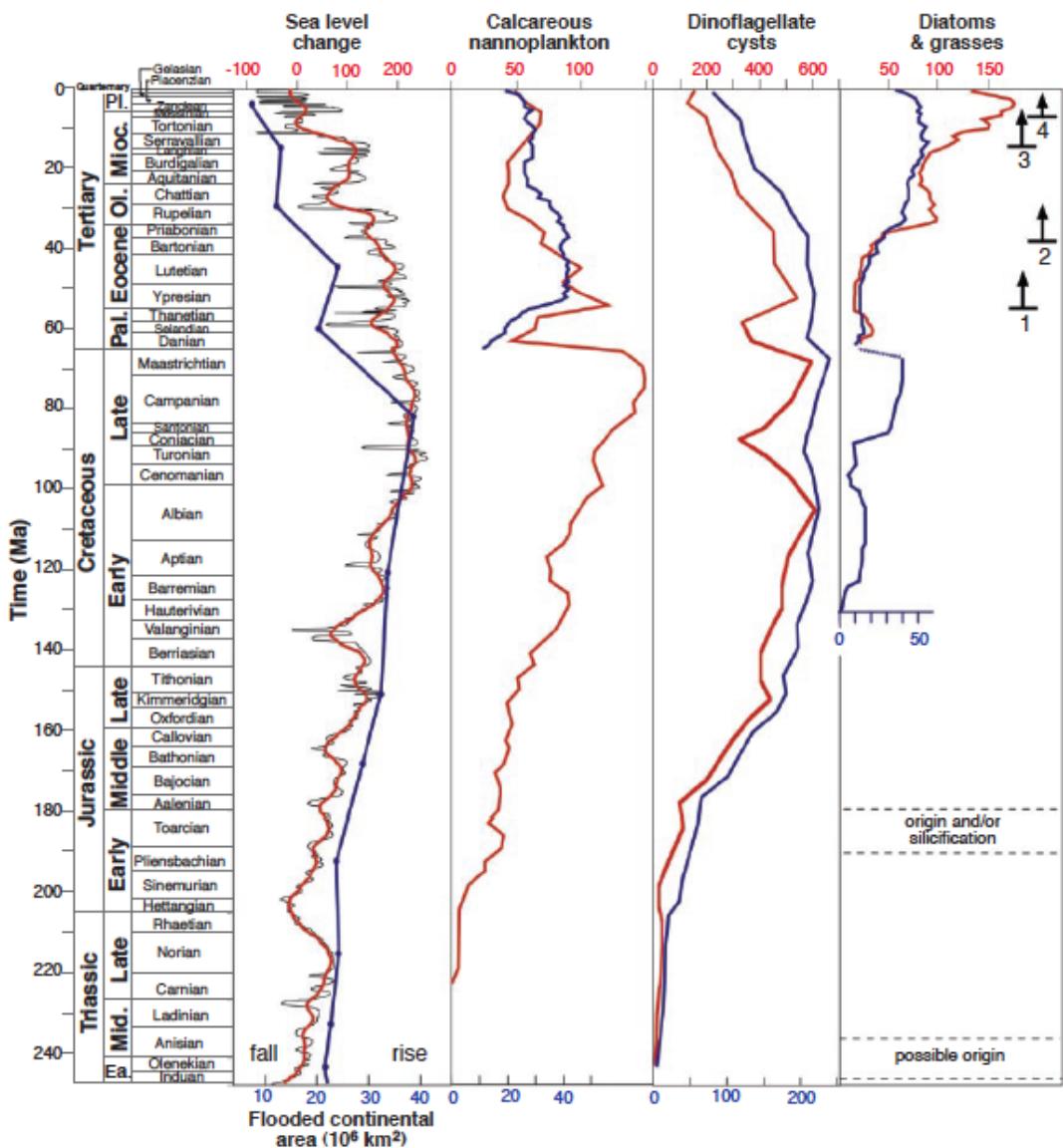


Figure 4.10: Comparison of major phytoplankton groups with sea-level change. The red line accounts for species diversities from published studies. The blue line accounts for the genus diversity compiled from public databases by the authors. Taken from Falkowski et al. (2004).

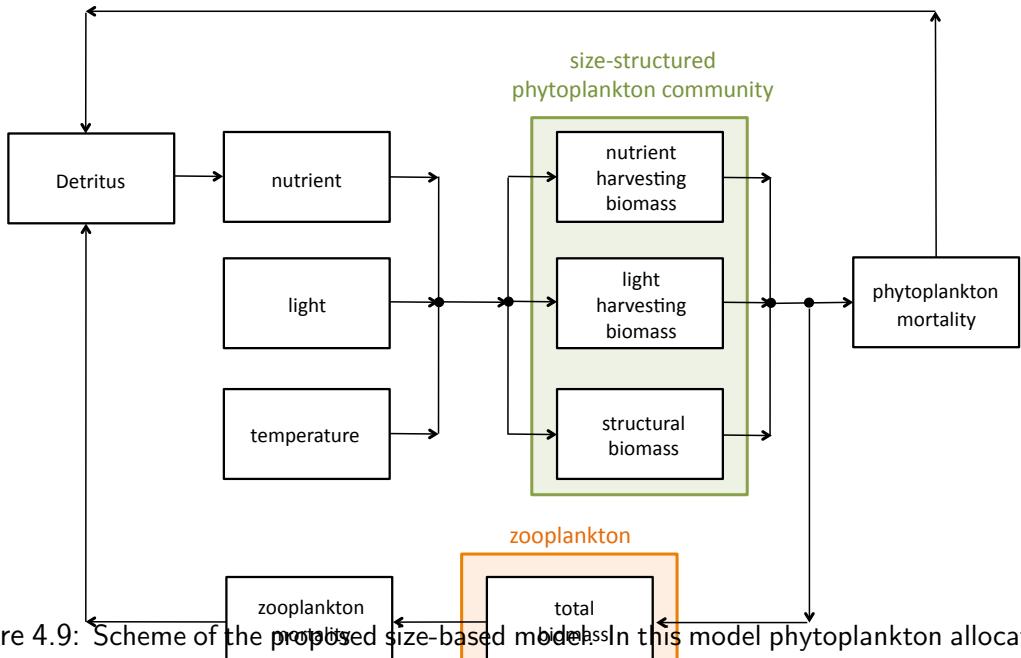


Figure 4.9: Scheme of the proposed size-based model. In this model phytoplankton allocates energy (or biomass) to different pools such as nutrient and light harvesting biomasses and generic structural biomass. A certain fraction of the phytoplankton biomass flows into the zooplankton biomass and a remaining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

by Wirtz & Eckhardt (1996); Norberg et al. (2001) and further refined by Bruggeman & Kooijman (2007); Merico et al. (2009). The phytoplankton total biomass (P), the mean trait (\bar{s}), and the trait variance (v) will be formulated as follows:

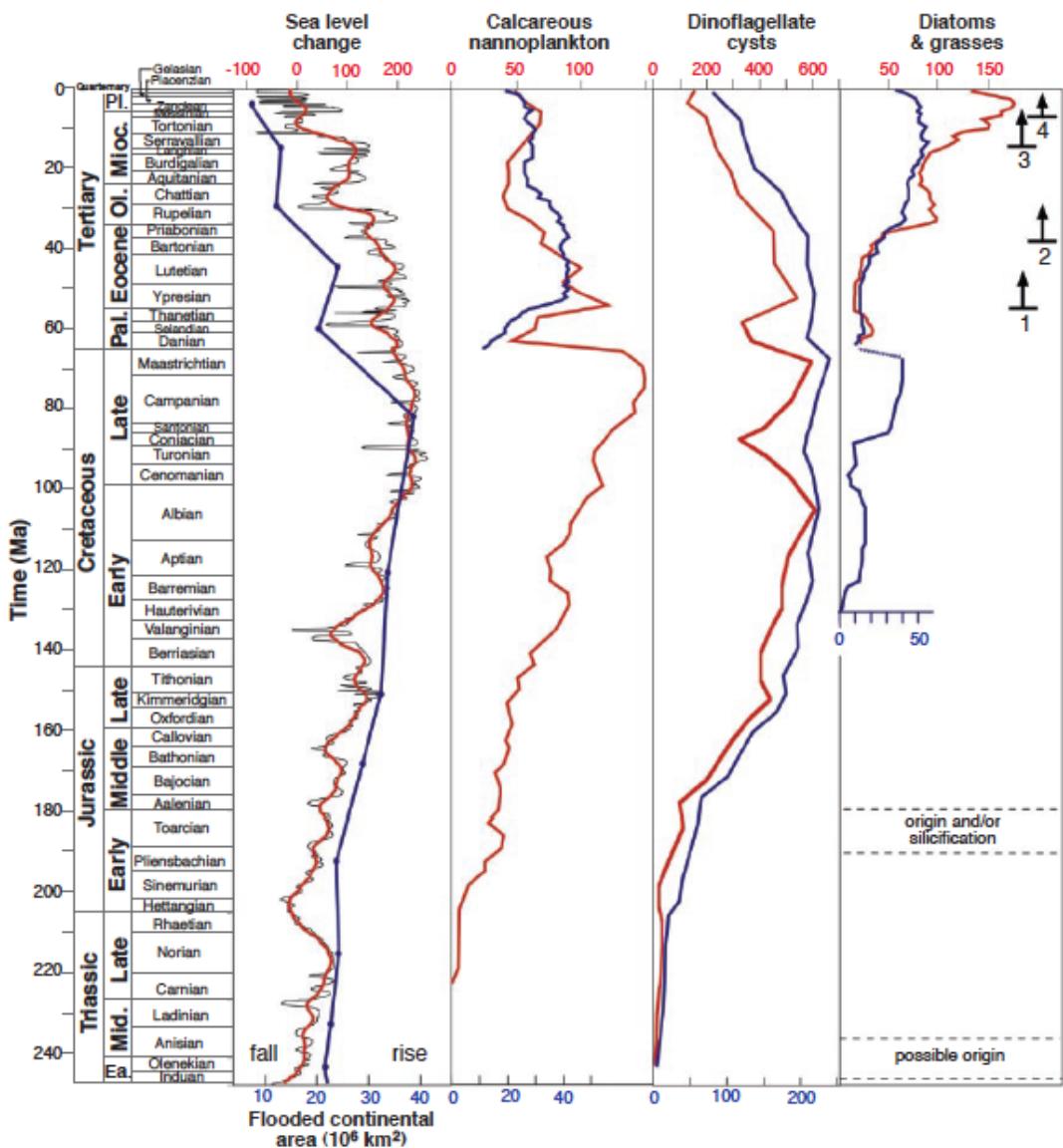


Figure 4.10: Comparison of major phytoplankton groups with sea-level change. The red line accounts for species diversities from published studies. The blue line accounts for the genus diversity compiled from public databases by the authors. Taken from Falkowski et al. (2004).