



Leibniz Centre for Tropical Marine Research

Jacobs University Bremen

PhD Proposal

Understanding phytoplankton community shifts in the eastern Cariaco basin, Venezuela

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ABSTRACT

"Totally need to rewrite this:" At an unprecedented rate our oceans are changing and so are the organisms within it. 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	2
1.2.1	Functional types vs. traits	3
1.2.2	The relationship between diversity and ecosystem function . . .	3
1.3	Modeling phytoplankton communities	3
1.4	The Cariaco basin & the CARIACO time series	4
1.5	Aims of the proposed PhD project	4
2	Understanding phytoplankton community shifts in the eastern Cari-	
	aco basin	6
2.1	Regime Shift in CARIACO data	6
2.2	Methods	6
2.2.1	Model physics in a tropical coastal setting	6
2.3	Preliminary Results	7
2.4	How to complete this project	7
3	PhytoMFTM - a flexible object-oriented phytoplankton functional-	
	type ecosystem model	8
3.1	Regime Shift in CARIACO data	8
3.2	Methods	8
3.2.1	Model physics in a tropical coastal setting	8
3.3	Preliminary Results	9
3.4	How to complete this project	9
4	Further work	10
4.1	Size-based model	10
4.1.1	Background	10
4.1.2	Method	12
4.1.3	Relevance	13
4.2	Multi-trait size-based model	14

4.3	Paleo-reconstruction of planktonic communities	15
4.4	Time table	18
Bibliography		19

1. General Introduction

1.1 The ocean, phytoplankton and why it matters

"Phytoplankton is important. Phytoplankton is diverse. 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).

"it is amazing how little we actually know about phytoplankton globally and the effects that it has on biogeochemical cycles, and how it is affected by global change for example "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)

1.2 Characterizing phytoplankton

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

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 vs. traits

XXXX

XXXX

1.2.2 The relationship between diversity and ecosystem function

XXXX

1.3 Modeling phytoplankton communities

Going into the details is necessary to understand the whole picture

One tool of integration are mathematical models

"The study of phytoplankton community structure, also promoted by the work of ?, is therefore very relevant in marine ecology and is especially important for understanding how phytoplankton will respond to a changing climate and with which consequences.

XXX

XXX

XXX

XXX.

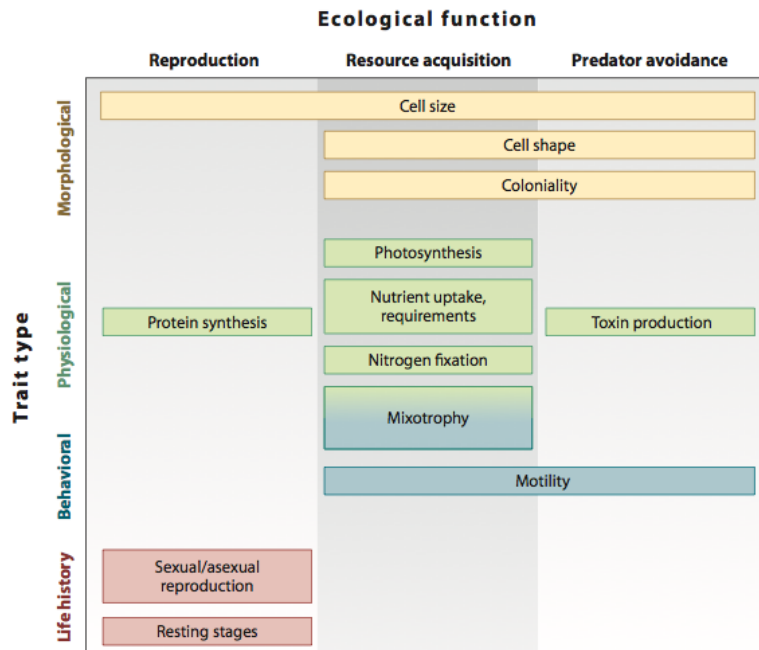


Figure 1.1: Phytoplankton functional traits. Taken from ?

XXX

XXX

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

1.4 The Cariaco basin & the CARIACO time series

XXXX

XXXX

XXX

THEN TALK ABOUT THE COLLAB/DATASHARE 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)

bb

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

2.2 Methods

XXX

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.

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 4.5).

kkkkkkkkkkkkkkkkkkkkkkkkkk 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

XXXXXXXXX

XXXXXXXXX

X

XXX

3. PhytoMFTM - a flexible object-oriented phytoplankton functional-type ecosystem 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 graphics XXX

XXXX

3.2.2 Model formulation and usage

xXXX

explain how to run the model!

XXXX

XXXX

XXX

End Methods here

3.3 Preliminary Results

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 CARIACO time-series data

Phytoplankton organisms are significantly limited by nutrient diffusion and by sinking. These two crucial processes in water pose important constraints on phytoplankton morphological traits such as cell size. Cell size is therefore subject to an important selection pressure that tends to favour those shapes and sizes that allow phytoplankton access nutrient resources more efficiently while maintaining themselves in the surface waters to access light (?). Size plays also a major role in growth and metabolism (?). The importance of this trait has motivated the development of a number of size-based ecological models. For example, ? developed a 1D, size-based model of three major group of organisms (phytoplankton, protozoan and metazoan) that takes into account a certain number of size-classes. Each of these classes of organisms could be further subdivided into defined functional groups or species that can be mathematically represented with state variables. Baird and Suthers' (?) model is formulated independently of the number of size classes, this help to reduce the complexity in terms of number of state variables and free parameters. However, with increasing number of size classes the model becomes computationally more expensive without any apparent benefit in the understanding of the system dynamics and with a clear increase in model sensitivity. Although size-based, which is still an unusual practice in phytoplankton modelling, this approach follows the typical tendency of introducing extra complexity in models, beyond the simple nutrient-phytoplankton-zooplankton-detritus (NPZD) configurations, when more size classes are considered. This tendency, however, faces numerous difficulties, particularly because of the poorly understood ecology, the lack

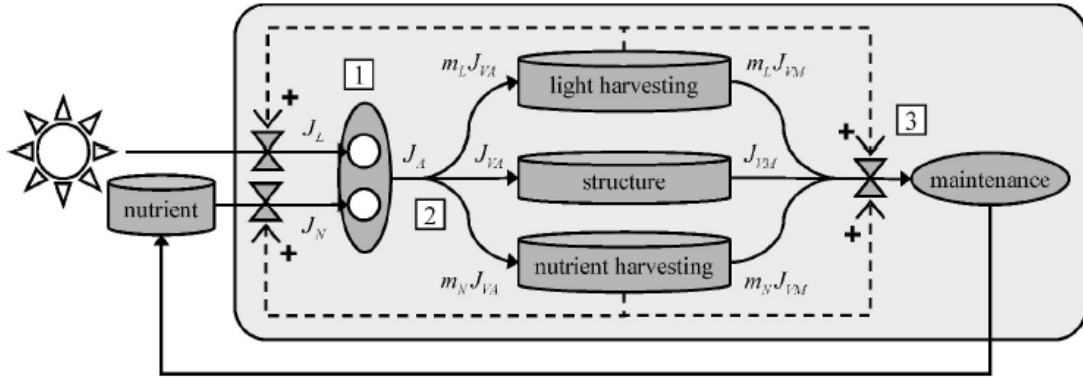


Figure 4.1: Bruggeman and Kooijman model scheme. Taken from ?

of data, the problems connected with aggregating diversity within functional groups into meaningful state variables and constants, and the higher sensitivity of outputs to the parameterizations in question (?).

Interesting alternatives to this modelling practice are obtained if principles of the Dynamic Energy Budget theory (DEB) of ? and trait-based approaches are considered into plankton models. DEB theory attempts to build a quantitative background in one of the most fundamental processes in biology, the individual metabolism. The key principles on which this theory is based are: the conservation of mass and energy, the general applicability to all possible species (its not species-specific), the structure of metabolic modules (reservoirs and structures), the consistency with empirical data, the simple model specification (Occam's razor) and the capacity of organisms to increase the control of their metabolism (strong, weak, structural acquisition and thermal homeostasis) (?).

In 2007 ? developed a trait model based on DEB concepts to study phytoplankton diversity and succession. The model (4.1) captures the seasonal dynamics of the phytoplankton community structure and key process which influence diversity, such as migration. However, they had to face the problem of having to consider too many species (and therefore too many state variables and parameters) when tackling biodiversity studies. ?, however, elegantly resolved the problem by approximating the full model with a simpler one. Using a moment closure technique to estimate the few, most important macroscopic properties of the full, complex system, such as total biomass, mean trait value, and trait variance, as previously proposed by ??, Bruggeman and

Kooijman's(?) obtained a simpler model, which dynamics compared remarkably well with the one of the full model. It should be noted, however, that this method assumes a normal distribution of the trait possibly omitting interesting multimodal dynamics (?). Following studies refined this approach by providing a complete mechanistic framework for developing these kind of models and by confirming the quality of the approximation in capturing the essential physiological and ecological characteristics of the full model (?).

4.1.2 Method

The main focus of my PhD work is to develop a size-based model following the approaches of ?? in order to further explore the detailed mechanisms leading to the observed phytoplankton size structure distributions in regions of the Atlantic Ocean of contrasting environmental conditions. The guiding principle for defining the traits and the tradeoffs to be incorporated into my model will be based on the concept that organisms face trade-offs in their ability to allocate limited energy and resources to growth, reproduction and defence, which is central to most theories explaining the diversity of life on Earth (?). Based on available observations, I will therefore develop a trade-off between competitive ability for nutrient acquisition and resistance to grazing (4.2). I will then include a specific grazing pressure that relates to both phyto- and zooplankton mortalities.

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:

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

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

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

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

4.1.3 Relevance

The work proposed with this PhD project will be important for further developing trait-based models of planktonic communities. Previous studies have not been able to consistently address complex adaptive systems with a reduced amount of complexity. The ability to model a complex system as a single adaptive entity while retaining the most fundamental ecological processes shaping its dynamics is doubtlessly elegant and attractive.

As shown in chapter 2, different regions in the Atlantic Ocean have specific community patterns. With my model I will attempt to capture the observed community structures regions of the Atlantic Ocean with contrasting environmental conditions. To our knowledge no effort have been made yet to develop such a trait-based model in this region of the world. As typical of any modelling study, my work will provide also quantitative understanding of the relative contribution of the most important physiological and ecological processes shaping the phytoplankton community size structure.

of this process in regulating the phytoplankton community structure(??). Technically, I will mechanistically derive two trade-off functions, one for the phytoplankton as explained in the previous section, and the other for the zooplankton. The new trade-off function will be based on the size of the zooplankton and on the size of the predated phytoplankton. The type of model approximation used will be the once estimated from the moment closure, in analogy to the size-based model proposed in section 3.1.2.

With this multi-trait implementation we expect to reduce the parameterization and overall complexity of early models possibly leading to a significant advance in plankton ecosystems modeling by developing a more parsimonious mechanistic description.

4.3 Paleo-reconstruction of planktonic communities

Since Darwin times, ecologists have tried to understand the evolutionary processes that lead to the current patterns of biodiversity. ? was fascinated by the capacity of phytoplankton communities to produce such a large diversity from a limited range of resources from which they compete. In the history of life on Earth, phytoplankton emerged at around 2.5 billion years ago when cyanobacteria started to spread in the earth oceans, thus creating an enormous impact on the global environment. Later ~ 1.6 -1.8 billion years ago, unicellular eukaryotes arose when they started to "use" prokaryotic cells as their metabolic slaves. From that point on, different kinds of unicellular eukaryotes emerged, until three characteristic groups of phytoplankters originated from an ancestral red alga, and started to dominate earth's aquatic environments (Figure 4.3) (?). Since the Middle Triassic these well known groups, dinoflagellates, coccolithophores and diatoms, began to play an important role on the biogeochemistry of our planet and supported a wide range of life forms in more and more complex food webs (?).

?? develop a size-based evolutionary model, based on game theory, to determine the driving processes which could produce the different size distributions of diatoms. Their model results suggest the nitrogen to phosphorus stoichiometric ratio, the nutrient fluctuation, and the changes on mixed layer depth, as major mechanisms leading to the size differences in diatoms.

Following these approaches, I plan to adopt my trait-based modelling approach to study the changes in the phytoplankton community composition during the Cenozoic period. This approach will be based on the size-based model developed for the Atlantic

Ocean but obviously appropriately set up for targeting environmental changes operating on a geological time scale. The species diversity will be mechanistically captured in my model by the variance of the trait distribution, and the prevailing mean trait value at a specific time will give an indication of the characteristic group or species dominating the community. Due to the distinct morphological differences in the three functional groups, it is appropriate to use size as a key trait to disentangle the different mechanisms shaping phytoplankton diversity across the Cenozoic era.

4.4 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

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

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 4.9 and 4.10) 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 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 gen-

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

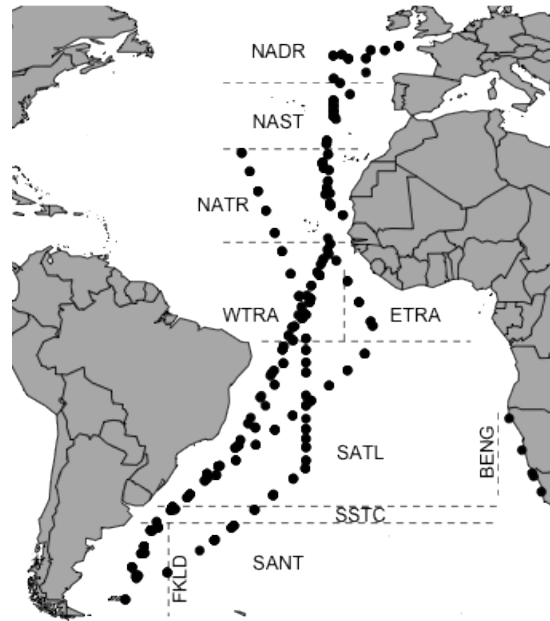


Figure 4.4: The AMT subset of 410 samples used in this study. The dashed lines represent the simplified limits of the Longhurst (2006) ecological provinces.

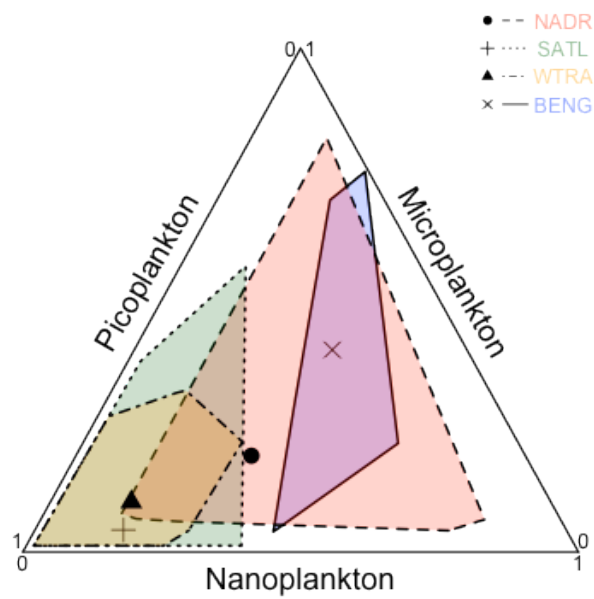


Figure 4.5: Phytoplankton community size structure of four ecological provinces in the Atlantic Ocean. The contours correspond to the convex hull of the size-fraction distribution of each province. The symbols indicate the corresponding mean values.

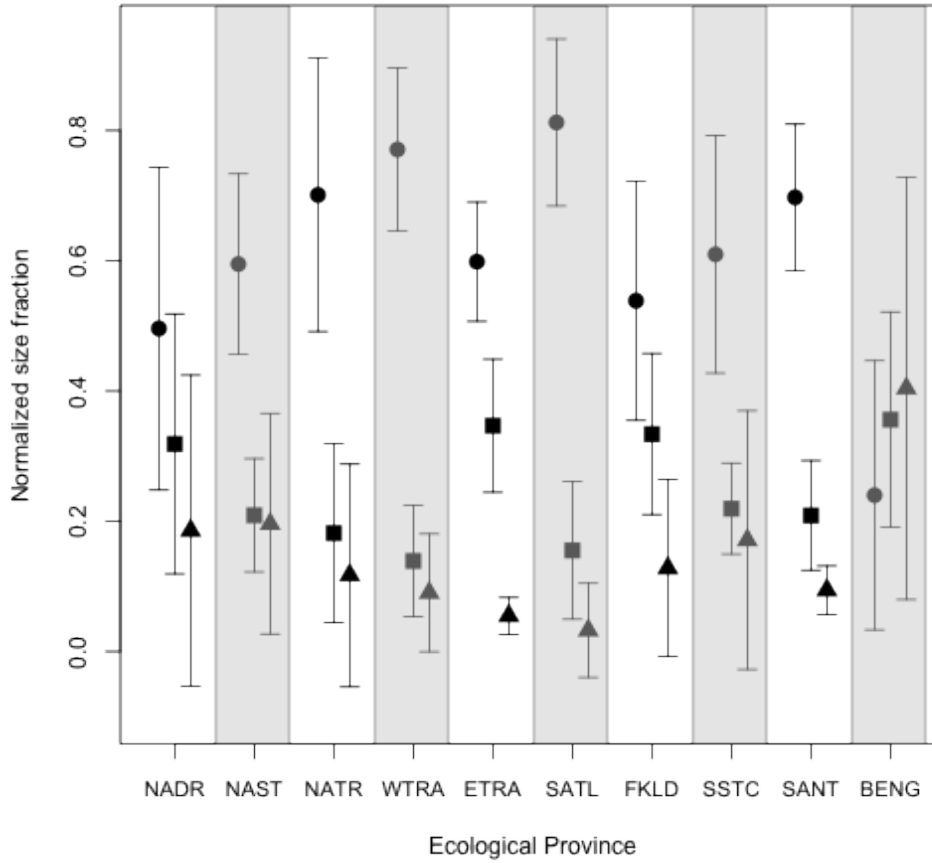


Figure 4.6: Relative mean abundances (\pm sd) of three phytoplankton size fractions of ten ecological provinces of the Atlantic Ocean. The symbols indicate the mean values of the normalized size fractions: picoplankton (●), nanoplankton(■) and microplankton (▲).

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

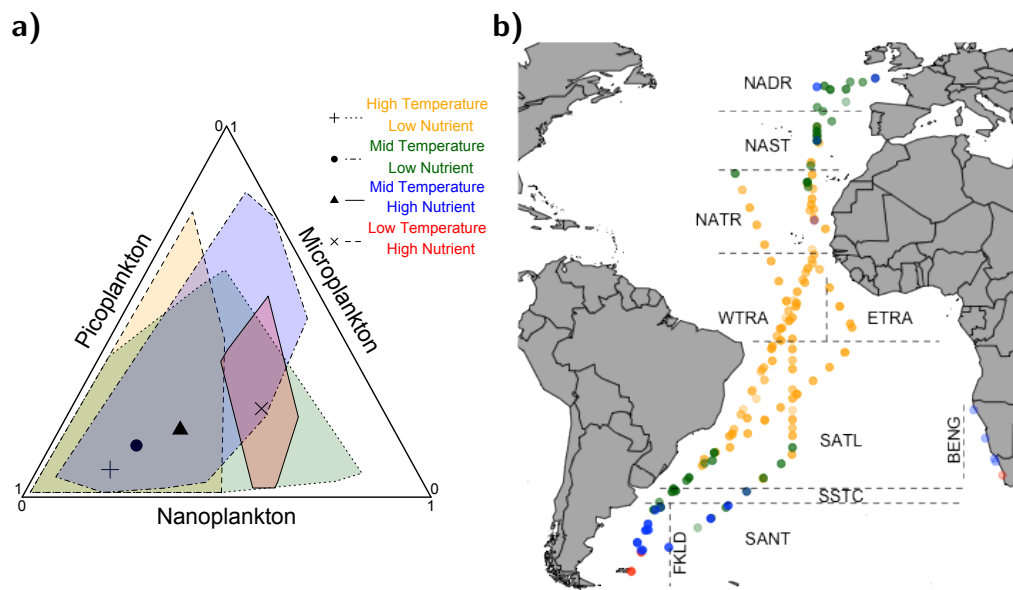


Figure 4.7: Caption comes here my friend"""""""" .

eral "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.

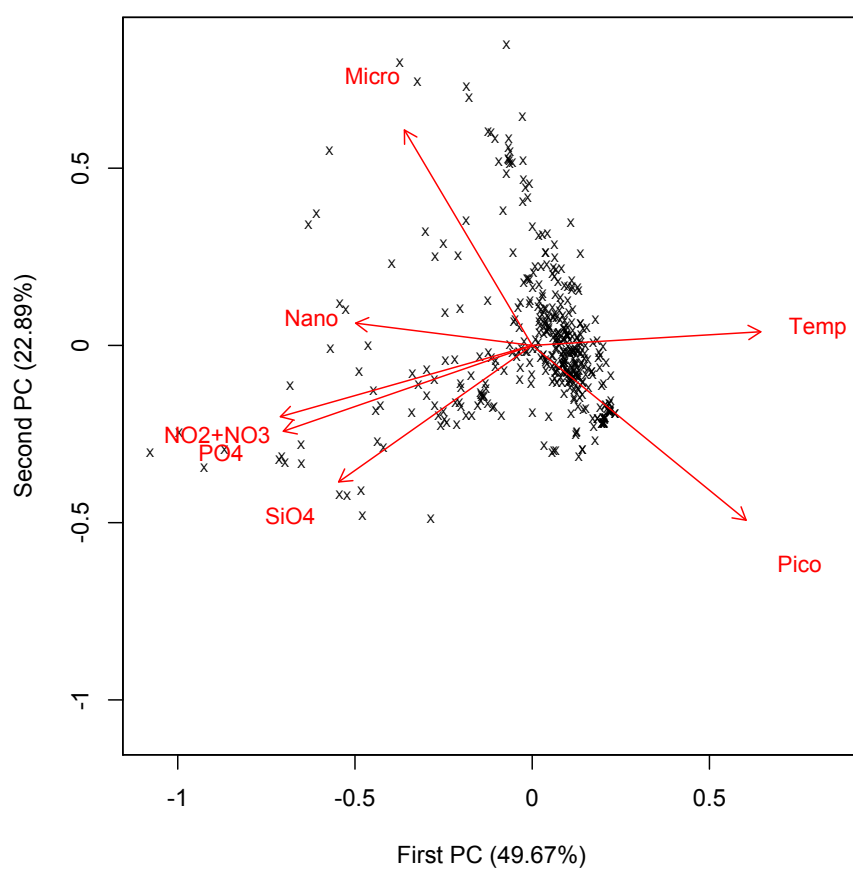


Figure 4.8: Principal Component Analysis of environmental parameters and normalized phytoplankton size fractions.

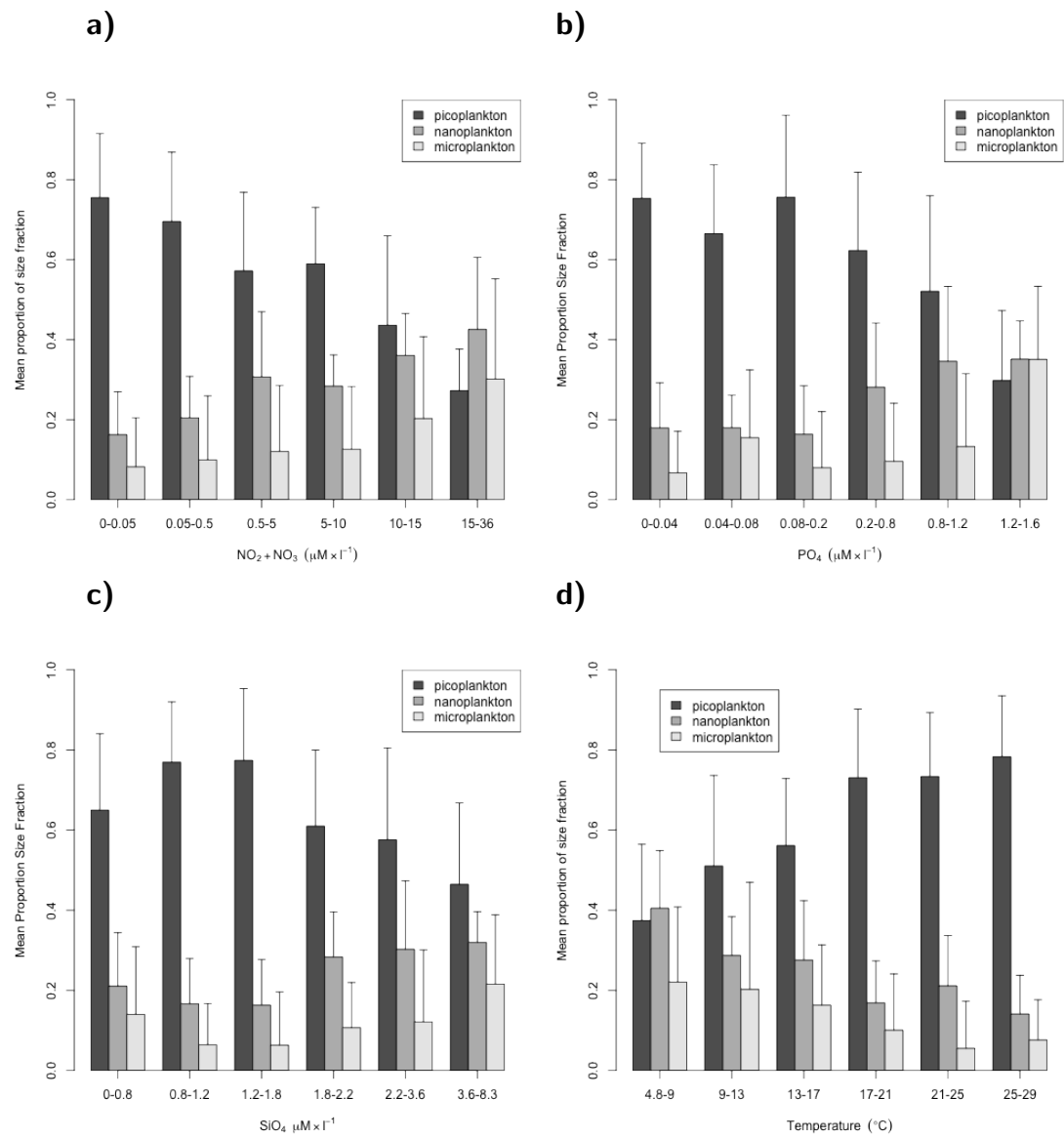


Figure 4.9: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with concentrations of nitrate+nitrite (a), phosphate (b), and silicate (c) and with temperature (d). The bars represent mean values and the error bars indicate the standard deviation.

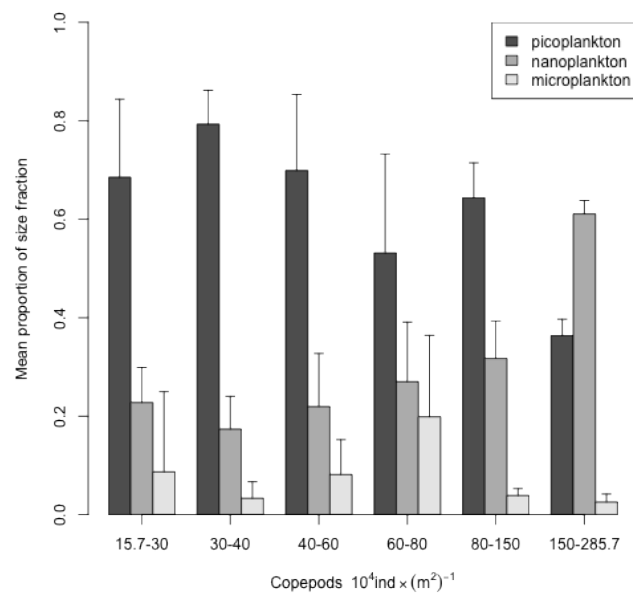


Figure 4.10: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with copepod abundance. The bars represent mean values and the error bars indicate the standard deviation.