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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. Currently, I have developed my own model based on PhytoSFDM and plan to collaborate with Andrew Barton to extend this model with a treatment of phytoplankton diversity inspired by the DARWIN model. This will lead to a second collaborative project, which consists of coupling this model to a global circulation model (GCM) to study global patterns of diversity and how they might be affected in the future. To this end, I intend to join Andrew Barton and his group as a visiting scholar to the Scripps Institution of Oceanography in San Diego for one year, starting in September of 2019.

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Chapter 1

General Introduction XXX

1.1 Trait-based ecology

Understanding the structure and functioning of ecological communities is crucial if we are to unravel the effects of an ever-changing environment on terrestrial and marine ecosystems. In former times, ecologist relied on a species-based approach to explain the response of ecological communities and ecosystems to the variability of the environment. Since recently, investigating the variation of functional traits and their linkages to environmental gradients is emerging as a complementary, powerful approach (McGill et al., 2006; Violle et al., 2007).

Traits are described as: "a well-defined, quantifiable properties of organisms, usually measured at the individual level and used comparatively across species" (McGill et al., 2006). If traits influence the fitness of organisms by affecting growth, reproduction, or survival, then they are called functional traits (Violle et al., 2007). An organism may be characterized by several different traits, which tend to fall into three main categories: morphological, physiological, and behavioural traits. Under the scope of the energy allocation principle, the organisms divide the uptaked resources among different traits to maximize their fitness (Perrin & Sibly, 1993). The cost of investing in one trait over the other is defined as a trade-off. Thus, a trade-off is a negative relationship between two traits where an increase in one is associated with a decrease in the other (Tilman, 2000).

A trait-based perspective in ecology promotes generality and predictability, thus

closing the gap between developments in empirical and theoretical ecology. The focus of the trait-based modelling approach proposed in this thesis allows one to study ecological communities as single adaptive systems by focusing on macroscopic properties such as total biomass, mean trait value and trait variance. This leads to an understanding of processes such as species succession (Bruggeman, 2009) or species variations and compositions (Ackerly & Cornwell, 2007; Messier et al., 2010) in complex communities, processes that would otherwise be untreatable given the daunting high number of species typically comprising an ecological community or ecosystem.

The species-based approach is the classical perspective in which the role of each individual organism is considered in a community or ecosystem. In this approach, the studies of higher hierarchical ecological entities (i.e. populations, communities, ecosystems) are based on the understanding of the organism and species variations and on their responses to the changes in the environment. Many important processes are studied with this perspective, including competition, predation, and biodiversity (Begon et al., 2006).

To compare the trait-based approach with the species-based approach, we can consider a simple thought experiment. Let us imagine a hypothetical phytoplankton community on a temperate region of the world, this community is composed of n number of species and with a range of cell size from 0.2 to 200 μm. Different species with specific cell sizes will dominate the community at different times, depending on the environmental conditions. The community is subjected to temporal variations in light and nutrients, thus leading to continuous shifts in species composition (i.e. shifts in the dominant cell size). In this thought experiment, a species-based ecologist would study the shifts in species composition by considering the individual responses of the species to those temporal environmental changes. A trait-based ecologist, instead, would investigate the changes in the mean size values and size variance to the different environmental conditions. These features highlight the complementary of the two approaches, an aspect that has important implications when developing complex adaptive models for ecological systems.

1.2   Phytoplankton trait-based community ecology

Phytoplankton organisms are of global importance because of the key role they play in aquatic food webs and in the biogeochemical cycles of major nutrients (i.e. nitrogen, phosphorus and carbon). The study of phytoplankton community structure, also promoted by the work of Falkowski (1998), 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.

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. (Margalef, 1978) 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.

Phytoplankton can be characterised by many morphological, physiological, behavioural and life history traits and trade-offs (Litchman & Klausmeier, 2008; Litchman et al., 2010). Key functional traits are generally associated with energy and resource allocation, edibility or predation avoidance, and reproductive strategies (Figure 1.1). However, among all the possibilities, the morphological trait $cell\ size$ is the most structuring property of phytoplankton communities (Litchman & Klausmeier, 2008; Finkel et al., 2009; Litchman et al., 2010), influencing many different ecological functions, processes and performances in these organisms.

1.2.1   Cell size as a major trait for characterising phytoplankton community structure

The cell size has a major influence on many physiological and ecological processes, including growth, photosynthesis, nutrient acquisition, sinking rates, grazing, population abundance, and diversity (Finkel et al., 2009). Phytoplankton cell size varies across a wide range, from picoplankton (<2 μm) to macroplankton (200 to <2000 μm). Many
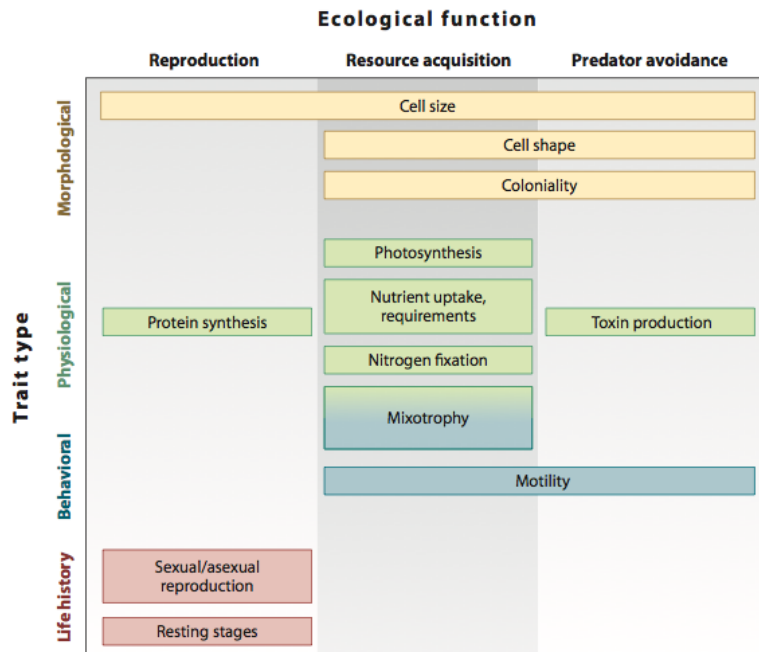
Figure 1.1: Phytoplankton functional traits. Taken from Litchman & Klausmeier (2008)

of the processes related to size can be described using a simple power law function: $Size \propto aV^b$, where V is the cell volume or biomass and a and b coefficients related to the specific species. This simple function has been proposed as a kind of universal law in biology (Platt & Silvert, 1981). Phytoplankton growth and intracellular concentrations of nutrients and carbon, for example, have been found to be negatively related to cell size (Tang, 1995), suggesting that larger cells grow slower than smaller cells.

In a similar fashion one can determine the trade-off between size and metabolic processes. Results of studies focusing on this functional relation suggest that respiration rates increase with cell size (Laws, 1975; López-Urrutia et al., 2006) while photosynthetic rates, light absorption and pigment concentration decrease with cell size (Ciotti et al., 2002; Finkel et al., 2004). This evidence indicates that under light-limited conditions smaller cells are more efficient using the little energy available, probably due to a stronger package effect on larger cells. In this context the package effect is define as: "shading" effect of increased concentration of phytosynthetic pigments which leads to a reduction in the light absorption efficiency (Marañón, 2009). However, this effect is "masked" under natural conditions due to the assemblage of many species comprising

a community. Some species (especially larger ones) posses specific strategies that help them maintaining higher metabolic rates under adverse conditions (Marañón, 2009).

Nutrient uptake decreases with decreasing cell size. But the advective transport of nutrients is enhanced by turbulence, sinking, and swimming, all aspects that increase the flux of nutrients from the cell diffusive boundary layer thus favouring larger cell organisms over smaller cell organisms (Kiorboe, 1993). However, small phytoplankton could also benefit from the smaller surface to area ratios, which provides them with a competitive advantage under low nutrient conditions.

Sinking velocity is also associated with size. This dynamics can be described by Stoke's law, predicting that sinking velocity increases with cell size (Reynolds, 2006). Larger organisms such as diatoms, however, can regulate buoyancy by changing their density (Reynolds, 2006).

Other characteristics of higher hierarchical levels can also be described using an allometric relationship of size such as the population density, interspecific interactions and diversity. The abundance of certain population ($Num.cells/L$) can then be described as a function of input and output of nutrients, based on the Droop model (Droop, 1977), to scale up to species abundance (Irwin et al., 2006). Theoretical and empirical observations suggest that the popultaion abundance decreases with cell size (Irwin et al., 2006; Cermeño et al., 2008).

Interspecific interactions, such as grazing, are also often size-specific. Larger grazers feed on larger phytoplankton with a predator to prey size ratio of 1:10 (Kiorboe, 1993). This interaction has the potential to regulate the trade-off between size-related nutrient uptake and predation avoidance (Thingstad et al., 2005; Naselli-Flores et al., 2007).

The diversity of a community ($Num.species/L$) could be represented with a skewed log-normal distribution of the cell diameter, a mean cell diameter and a standard deviation on log scale (Irwin et al., 2006). In this functional relation, the highest diversity occurs at values smaller than the median (Irwin et al., 2006; Cermeño & Figueiras, 2008; Finkel et al., 2009). Although, phytoplankton are widely distributed they do not show any large-scale diversity pattern across latitudinal scales and productivity gradients. The involved mechanisms for such a lack of pattern could include: the high dispersal capabilities, the high patch connectivity, the chaotic biological interactions, the short generation times and the high frequency of environmental reset

(e.i. the rapid change of species composition due to changes in the environment) (Cermeño et al., 2008). Thus, the governing process over phytoplankton diversity in large scales appears to be non-equilibrium dynamics as suggested by Hutchinson(1961) in his plankton paradox tenet.

1.3   Trait-based models of phytoplankton communities

Early developments in plankton models were based on Lotka-Volterra predator-prey dynamics (Fleming, 1939). As advances in computational capabilities increased, models started to become more complex, up to a point where now the typical nutrient-phytoplankton-zooplankton-detritus (NPZD) models are resolved for various PFTs and then coupled to three-dimensional ocean circulation models. However, the increased number of PFTs in such models came with the cost of increased uncertainties, as reflected in increased number of free parameters the models had to contain. The challenge today is thus to be able to develop models that incorporate all the essential organisms and the relevant processes, but on the same time that are manageable with a reasonable computing power and with as less degrees of freedom as possible. (Anderson, 2010).

In conclusion, the trait-based perspective, with its capability of describing a phytoplankton community as a single adaptive entity through just a few macroscopic properties (total biomass, mean trait, and trait variance), appears today to offer a simple and reliable framework which best suits modelling implementations. The species-based approach requires a more detailed knowledge of all the single species comprising an ecological community and leads to models with too many degrees of freedom. Even if computing and technical capabilities today may appear sufficient for several ecological applications, the complexity of natural interactions and the incredible number of organisms, each with specific strategic repertoires, would still set an important limit to the species-by-species modelling of phytoplankton communities.

Since trait-based modelling approaches are based on first principles, such as energy allocation theories (Kooijman, 2009), they lead to a mechanistic description of traits dynamics and, as mentioned above, to a reduce model complexity by considering the two most structuring traits subject to a well defined trade-off (Merico et al., 2009; Follows & Dutkiewicz, 2011).

For phytoplankton communities, cell size appears to be the most suitable trait for this approach in particular when it is considered in relation to traits such as energy and nutrient allocation and susceptibility of being grazed (edibility) (Litchman & Klausmeier, 2008; Follows & Dutkiewicz, 2011; Merico et al., 2009). Trait-based models (Bruggeman & Kooijman, 2007; Merico et al., 2009) have been so far quite successful at describing the community dynamics of phytoplankton. Some models specify a top-down control by including a detail representation of grazers. Advances in this field could include a trait-based definition of the zooplankton community, in analogy with the phytoplankton community. Further developments in modelling the phytoplankton community size-structure will help us to understand mechanisms that drive natural variation under changing environmental conditions.

1.4   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:

- Collect the appropriate dataset and available observations for developing a trait-based characterization of phytoplankton communities in contrasting regions of the Atlantic Ocean by using advanced statistical analyses.

- Implement a size-based model to understand the factors shaping the phytoplankton community structure in contrasting regions of the Atlantic and explore how communities re-organise under different environmental change scenarios.

- Extend the proposed size-based model to incorporate a trait-based mechanistic description also for the zooplankton community and investigate the co-adaptation of these two different guilds under a changing environment.

- If time allows, set up the model for long-term evolutionary studies in order to understand the factors that shapes phytoplankton size evolution through geological times.

Chapter 2

A trait-based characterization of phytoplankton communities in contrasting environmental regions of the Atlantic Ocean

Manuscript to be submitted to Marine Ecology Progress Series

2.1 Introduction

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. One of the approaches adopted in this important quest is based on observations of key characteristics of organisms, populations or communities. These key characteristics are also called traits (McGill et al., 2006; Violle et al., 2007). Trait-based ecology aims at developing an understanding and a better predictability of natural communities by linking traits that influence organism performance and fitness to prevailing environmental conditions (McGill et al., 2006).

Phytoplankton communities are ideal systems for the application of a trait-based approach. They are relatively simple and have well defined ecological niches, which are

determined by physical and environmental conditions, by resource allocation strategies, and by inter-specific relationships (Litchman et al., 2007). Phytoplankton organisms have various well-understood morphological, physiological, behavioural, and life history traits. Among a number of potentially relevant traits, cell size is probably the one that can best characterize phytoplankton communities, because many ecophysiological processes such as nutrient and light acquisition and resistance to grazing are significantly correlated with cell size (Litchman & Klausmeier, 2008; Litchman et al., 2010). A variety of these traits are frequently measured *in vivo* and *in situ* due to the global importance of phytoplankton as a primary producer with a significant influence on the marine food-webs and on the biogeochemical cycles of major nutrients(Falkowski, 1998).

Since 1995 two scientific cruises of the Atlantic Meridional Transect (AMT) Programme have crossed the Atlantic Ocean from Plymouth (UK) to South America or South Africa almost every spring and autumn. The information collected during these cruises includes data on size-fractionated chlorophyll-a, on the concentrations of nitrate, nitrite, phosphate and silicate, on temperature, and on zooplankton abundances. The spatial extent of the transects, that cross a range of ecosystems from sub-polar to tropical and from euphotic shelf seas and upwelling systems to oligotrophic mid-ocean gyres, and the richness of the variables observed, make the dataset important for studying the size compositions of phytoplankton communities and the processes shaping them at an ocean basin scale. Previous analyses have focused on a description of the occurrences of the different size fractions (Marañón et al., 2001), but did not consider the direct influence of environmental conditions on the community structure. A more comprehensive analysis that includes the most recent observations and integrates the relevant environmental data with the available phytoplankton community size fractions is to our knowledge still lacking. The work we present here therefore intends to investigate the mechanisms determining the phytoplankton community structure in regions of contrasting environmental conditions (i.e. regions with different nutrient, temperature, and grazing regimes).

We broaden previous analyses by considering a larger and most up-to-date selection of data than any previous study. More specifically, we integrate phytoplankton size-fractions with temperature, various nutrient concentrations, and zooplankton abundances in a first attempt to disentangle the relative contribution of bottom-up and
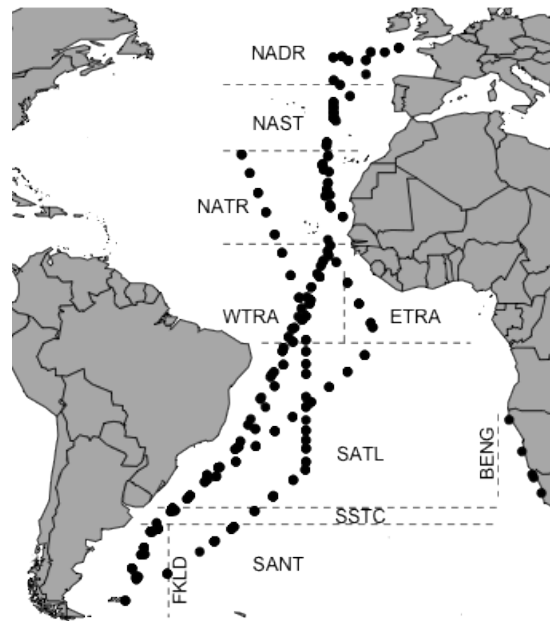
Figure 2.1: The AMT subset of 410 samples used in this study. The dashed lines represent the simplified limits of the Longhurst (2006) ecological provinces.

top-down processes in shaping the size structure of the phytoplankton community.

The first step in our analysis is to spatially separate the selected AMT dataset according to the well-established ecological classification of the world ocean by Longhurst (2006). In a second step, we classify the phytoplankton communities by using only the corresponding nutrients and temperature data and compare the results with the classification of Longhurst (2006). In a last step, we relate the environmental differences to the cell size compositions in order to highlight the emergent patterns of community structures at the ocean basin scale.

2.2 Methods

We collected a number of observed variables from the AMT Programme (www.amt-uk.org). The resulting dataset comprised size fractionated chlorophyll-a (phytoplankton size fractions hereafter), nitrate+nitrite, phosphate and silicate concentrations, temperature, and zooplankton abundance (considered as a qualitative indication of grazing pressure). We restricted our selection to the mixed layer depth, defined as the

depth at which a variation of 0.5 °C in temperature and of 0.125 in density is observed with respect to the surface value (i.e. the value at 5-10 m depth). The resulting dataset included 410 samples from a total of 9 AMT cruises (from AMT2 to AMT6, AMT10, AMT11, AMT13, and AMT14). These cruises took place in April-May or September-October of 1996 (AMT2 and AMT3), 1997 (AMT4 and AMT5), 1998 (AMT6), 2000 (AMT10 -AMT11), and 2003 (AMT13 and AMT14).

During most of the cruises the phytoplankton size fractions were in the range of 0.2-2 μm (picoplankton), 2 -20 μm (nanoplankton), and >20 μm (microplankon), although AMT13 and AMT14 measured four size classes (0.2-2, 2-5 5-10, >10 μm). For consistency, we considered the 2-5 and 5-10 μm size classes as part of the nanoplankton and the >10 μm class as part of the microplankton. The three size fractions were then normalized according to the proportion of each size fraction to the total chlorophyll-a concentration.

The selected dataset covered temperate, subtropical and tropical regions of the Atlantic Ocean (Figure 2.1). Following Longhurst's (2006) classification, ten ecological provinces were sampled by the AMT cruises: four temperate provinces, comprising of the North Atlantic Drift (NADR; 24 samples), the South Subtropical Convergence (SSTC, n=21), the Subantartic Water Ring (SANT, n=14), and the Falkland Island (FKLD; 52 samples); two subtropical provinces, comprising of the North Atlantic Subtropical Gyral (NAST; 37 samples) and the South Atlantic Subtropical Gyral (SATL, 129 samples); three tropical provinces, the North Atlantic Tropical Gyral (NATR, 51 samples), the Eastern Tropical Atlantic (ETRA, 13 samples) and the Western Tropical Atlantic (WTRA, 64 samples); and one upwelling region, the Benguela province (BENG, 5 samples). With this dataset the phytoplankton community size composition was analyzed by means of a linear mixed effect model (LME) to test if the community size-structure differs among ecological provinces. The ecological provinces were classified into regions, defined as: temperate (NADR, FKLD, SSTC, SANT), tropical (NATR, WTRA, ETRA), subtropical (SATL, NAST) and upwelling (BENG). The model was fitted to the data using the size fractions and the regions as fixed factors, and the ecological provinces as randomly varying factors.

We utilized a cluster analysis based on the k-means algorithm (a statistical method that partitions n observations into k clusters in which each observation belongs to the cluster with the nearest mean) to alternatively classify the data with respect to
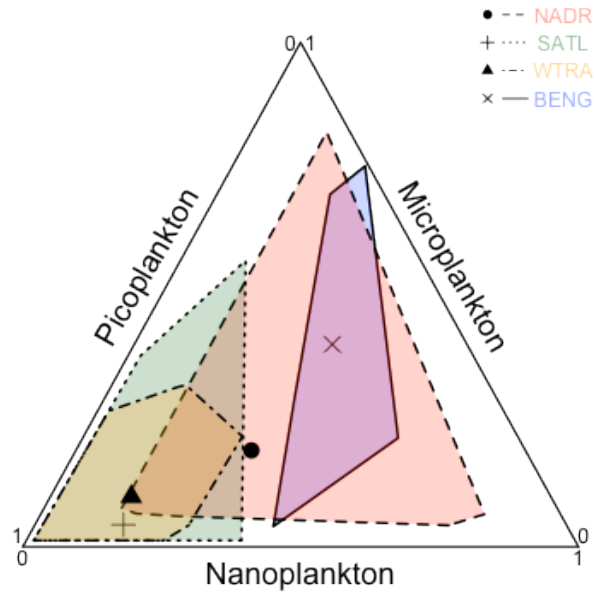
Figure 2.2: Phytoplankton community size structure of four ecological provinces in the Atlantic Ocean. The contours correspond to the convex hull of the size-fraction distribution of each province. The symbols indicate the corresponding mean values.

the prevailing environmental conditions. The environmental variables considered were nitrate+nitrite, phosphate and silicate concentrations, and temperature.

We also applied a principal component analysis (PCA) to the environmental variables and the normalized size fractions to assess the effect of a specific environmental gradient to changes in the phytoplankton size fractions. We quantified the linear relationships between the environmental data and the size-structure information.

In addition, we quantified the relation of the three size fractions to the grazer abundance relatively to AMT3 and AMT5, because zooplankton data were only available for these two cruises. These analyses were carried out using R v2.12.2 (The R Foundation for Statistical Computing, 2011).

2.3   Results

The size-structure of the phytoplankton communities is highly variable in different ecological provinces of the Atlantic Ocean (Figure 2.2). When the mean size-fraction of only four selected provinces are compared, an increasing trend towards bigger phyto-
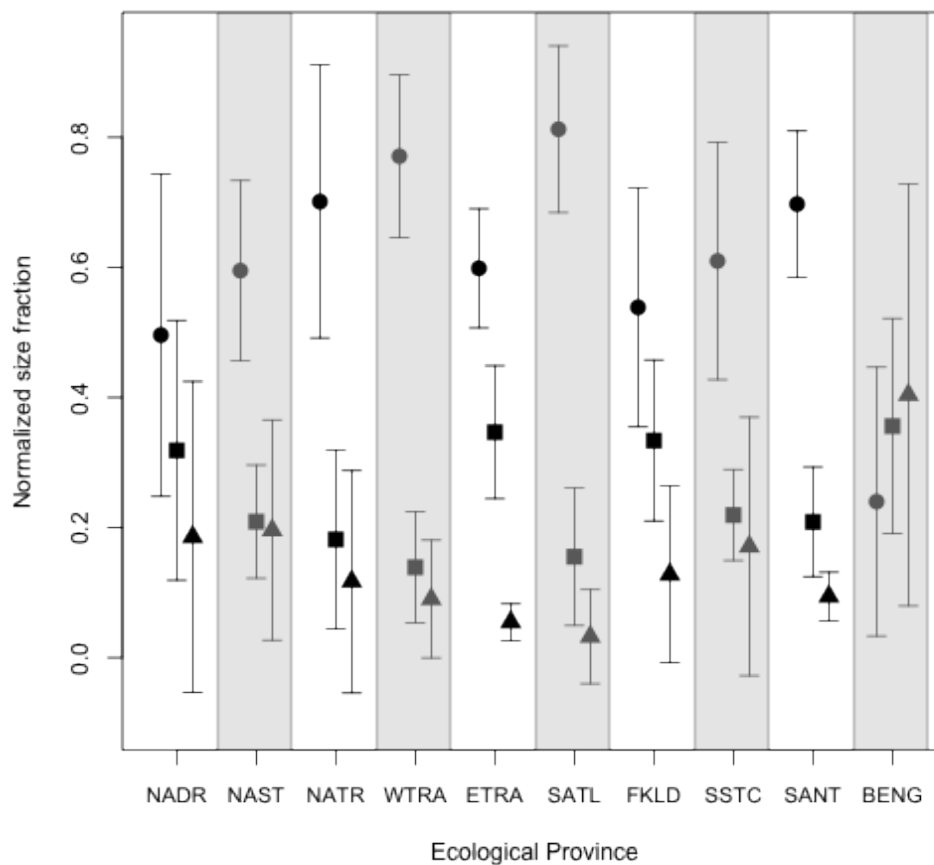
Figure 2.3: Relative mean abundances (±sd) of three phytoplankton size fractions of ten ecological provinces of the Atlantic Ocean. The symbols indicate the mean values of the normalized size fractions: picoplankton (●), nanoplankton(■) and microplankton (▲).
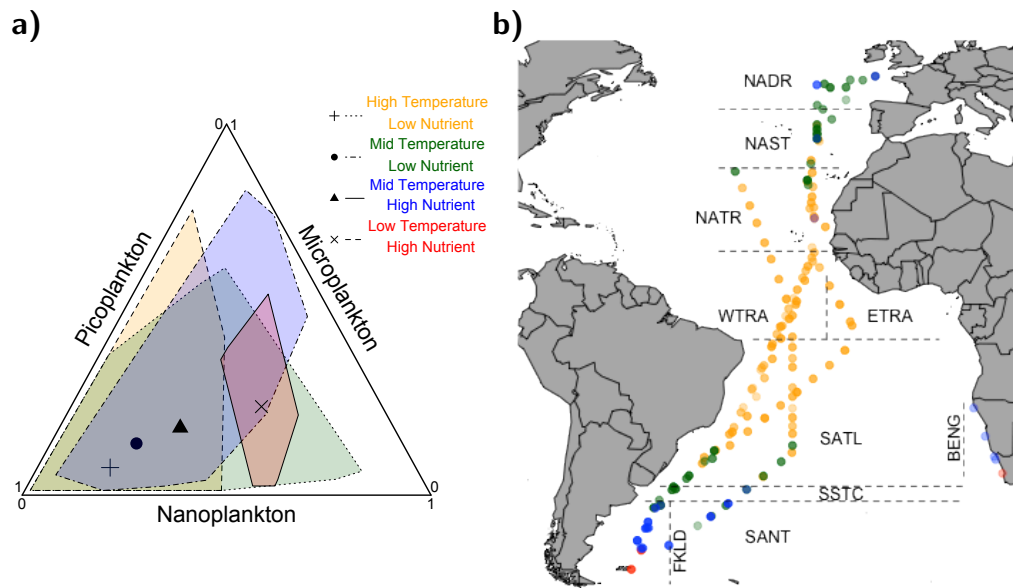
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Figure 2.4: Phytoplankton community size structure and environmental conditions. a) Distributions of size-classes clustered according to water temperature and nutrient concentration with contours corresponding to the convex hull of the size-fraction distribution of each cluster; symbols denoting the mean values of the size fractions. b) Geographical distribution of the clusters compared to Longhurst provinces. The colour coding reflects the cluster classification.

plankton sizes can be observed from the warmer provinces of the tropics and subtropics to the colder provinces of, for example, the Benguela upwelling. In tropical and subtropical waters (such as WTRA and SATL), picoplankton is the most common size class, with only a few occurrences of nano- and microplankton. In contrast, temperate provinces such as NADR are characterised by a more heterogeneous distribution of size classes and the upwelling province is dominated mainly by pico- and microplankton. Provinces located in the temperate regions have a larger cell size variability, as indicated by the larger standard deviation there than in the provinces located in the tropical regions (Figure 2.3). These differences are rather significant for the picoplankton (LME/anova, df=3, F=6.6315, p=0.0247) and the microplankton (LME/anova, df=3, F=5.5189,p=0.0368) size fractions, while they are less significant for the nanoplankton (LME/anova, df=3, F=2.03341, p=0.2108) size fractions.

The k-means clustering analyses of temperature, nitrate+nitrite, phosphate, and silicate concentrations reveals that regions between 30° North and South share similar

Table 2.1: Mean values of environmental parameters for the different clusters: High temperature - Low nutrients (HTLN), Mid temperature - Low nutrients (MTLN), Mid temperature - High nutrients (MTHN and Low temperature - High nutrients (LTHN).

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

environmental characteristics of high temperatures and low nutrient concentrations (HTLN, yellow dots in Figure 2.4b, cf. Table 2.1). Observations from temperate provinces are clearly separated from HTLN data. They are categorized into three clusters: Mid temperature - Low nutrients, Mid temperature - High nutrients and Low temperature - High nutrients (respectively green, blue and red dots in Figure 2.4b, cf. Table 2.1). In summary, we obtained a new classification of the data into four regions, which explains 87.3% of the variance. The mean size of phytoplankton in the four clusters indicates an increasing trend from the high-temperature, low-nutrient region towards the low-temperature, high-nutrient regions (Figure 2.4a). The PCA on all data shows highest loadings for temperature (positive loading) and nitrate+nitrite concentration (negative loading) with respect to the first principal component (Figure 2.5). Furthermore, the relative occurrence of picoplankton is positively correlated with temperature, while nutrient concentrations are positively correlated with occurrences of nano- and microplankton (Figure 2.5).

The results of the regression analyses of all data show that phytoplankton size composition varies with the environmental conditions irrespective of temporal changes (see Figure 2.6 and Table 2.2). A shift from a picoplankton dominated community towards a nano- and microplankton dominated community occurs with increasing nutrient concentrations (see Figure 2.6a, 2.6b and 2.6c). By contrast, the relative abundance of picoplankton increases from about 40% to about 80% with a temperature increase from 4.8-9°C to 25-29°C, whereas the fractions of nano- and microplankton decreases by about 50%.

When restricting the regression analysis to the only two cruises that also sampled zooplankton (AMT3 and AMT5), we observe an increase in copepod abundance in association to a decline in the relative occurrence of picoplankton from 70% to less

Table 2.2: 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

than 40% and an increase of the relative occurrence of nanoplankton from 20% to 60%. The microplankton size fraction is, however, not affected by changes in the zooplankton abundance (Figure 2.7).

2.4 Discussion

We analyzed cruise data from different regions of the Atlantic Ocean covering mainly two seasons (late spring/early summer and autumn) in the period 1996 to 2003. Our results showed, consistently with the geographical classification of Longhurst (2006) (Figures 2.2 and 2.3), patterns of phytoplankton size distributions characterized by the dominance of picoplankton in oligotrophic (SATL) and tropical (e.g. WTRA) waters and by the dominance of larger size classes in nutrient-rich waters (BENG). These patterns are also consistent with the works of Marañón et al. (2000, 2001); Poulton et al. (2006); Moreno-Ostos et al. (2011); Huete-Ortega et al. (2011). Our new classification method, based on the prevailing environmental conditions (Figure 2.4) and independent from spatial and temporal information, maximizes differences of the environmental properties among clusters of data and generates patterns of phytoplankton size distributions similar to the ones obtained by the Longhurst's classification, which uses a richer and spatially informed dataset. The value of our approach is therefore in the fact that it leads to results consistent with the present day understanding of phytoplankton biogeography and ecology of the Atlantic without requiring information on the geographical and temporal origin of the data. Our finding also proves the generality and robustness of the trait-based approach and confirms the sensitivity of phytoplankton cell size to environmental conditions and possibly (because of the
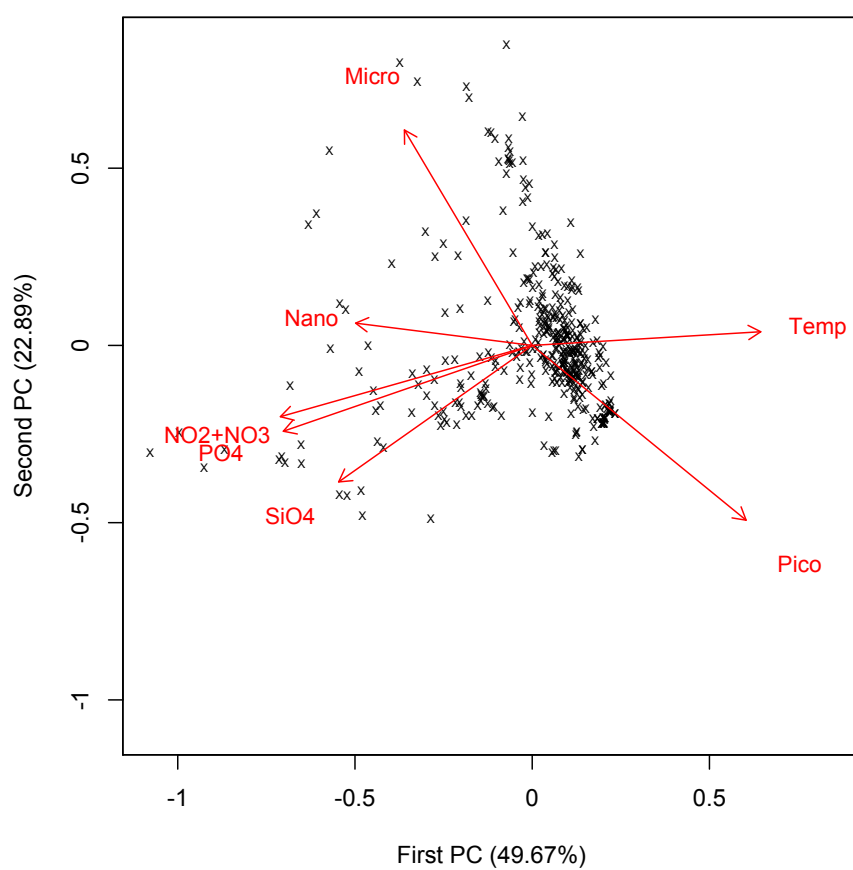
Figure 2.5: Principal Component Analysis of environmental parameters and normalized phytoplankton size fractions.
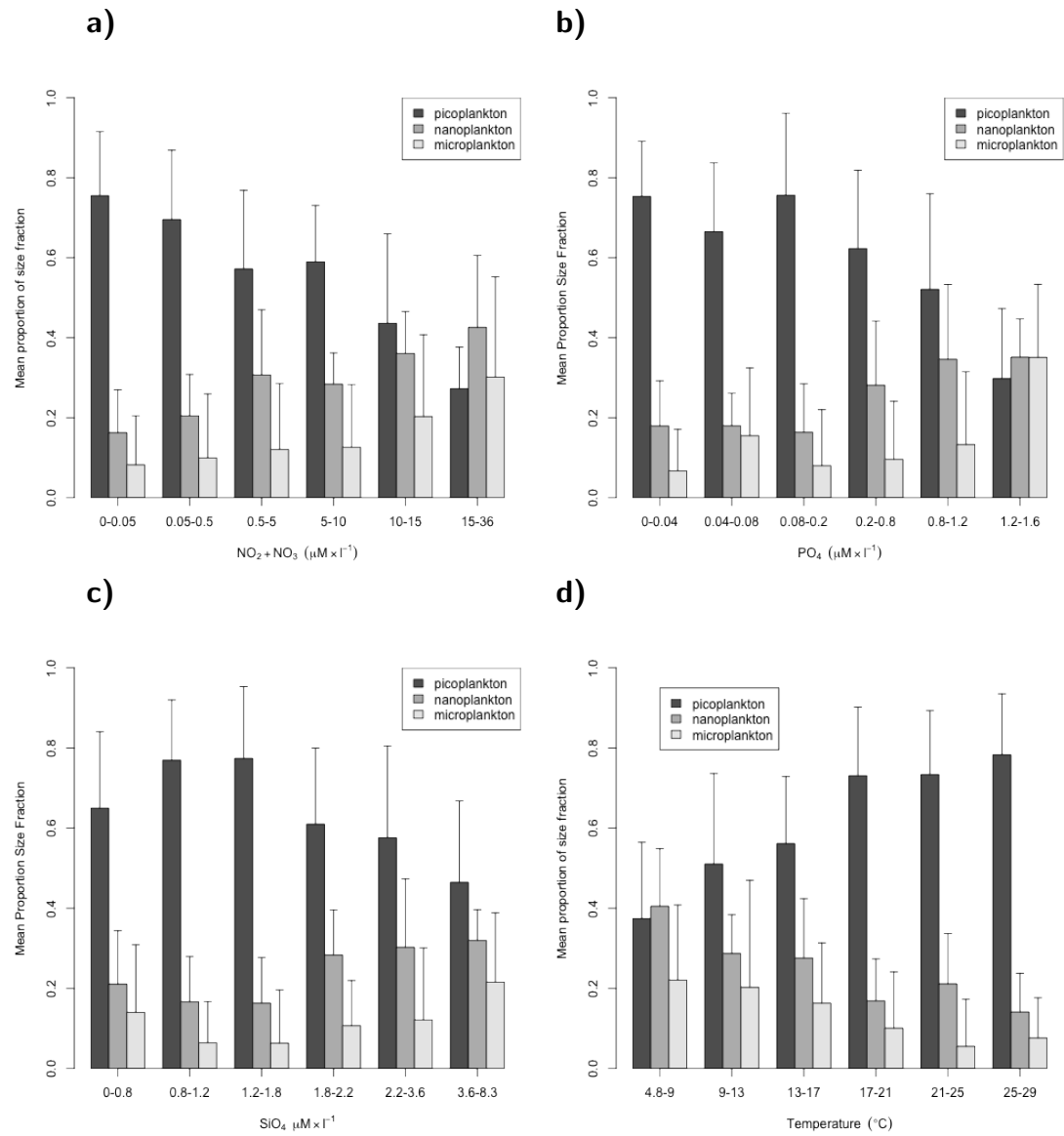
Figure 2.6: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with concentrations of nitrate+nitrite (a), phosphate (b), and silicate (c) and with temperature (d). The bars represent mean values and the error bars indicate the standard deviation.
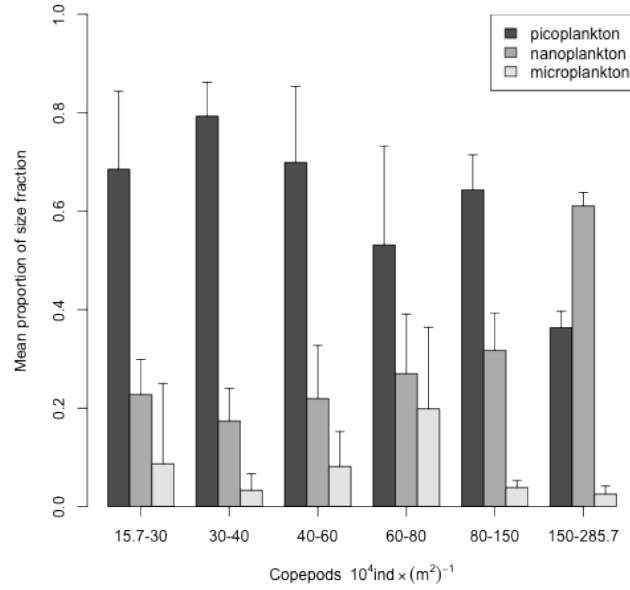
Figure 2.7: Relative composition of picoplankton, nanoplankton and microplankton size fractions changing with copepod abundance. The bars represent mean values and the error bars indicate the standard deviation.

paucity of zooplankton data) to grazing pressure. In fact, the phytoplankton size compositions resulted to be strongly associated with prevailing environmental conditions (Figures 2.6 and 2.7). Furthermore, the consistency of our results with similar previous studies of the Atlantic Ocean that used either less AMT data than our study (Marañón et al., 2000, 2001; Poulton et al., 2006) or data from sources different than the AMT cruises (Moreno-Ostos et al., 2011; Huete-Ortega et al., 2011) suggests that the different phytoplankton size structures observed are robust features of the Atlantic Ocean.

The results we obtained with the clustering technique (Figure 2.4) revealed that the areas between $30°$ N and $30°$ S are characterized by nutrient and temperature regimes that give picoplankton a competitive advantage over larger phytoplankton. In contrast, a wider range of phytoplankton size classes distinguishes colder waters with high nutrient concentrations.

Smaller phytoplankton cell sizes have a competitive advantage over larger phytoplankton under low nutrient, low light and low grazing pressure (Litchman & Klausmeier, 2008; Litchman et al., 2010). From our regression analyses (Figures 2.6 and 2.7)

we inferred a strong control of $NO_3^- + NO_2^-$ and temperature on all three size fractions. Pico- and nanoplankton size fractions, however, appeared more sensitive to changes in PO_4^{3-}, SiO_4^{2-} and copepod abundance. We propose that these effects are caused by a trade-off between resource acquisition and predation pressure, although with the caveat represented by the paucity of the zooplankton data and by the qualitative value we attribute to zooplankton abundance as an indication of grazing pressure. There are a number of important physiological and ecological processes that strongly depend on phytoplankton cell size (Kiorboe, 1993; Cermeño & Figueiras, 2008; Finkel et al., 2009), 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" (Finkel et al., 2009). 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.

Our size-based analyses therefore substantiate remarkable properties of the variation of a key trait at an ocean basin scale. Moreover, these findings are corroborating Baas Becking's tenet "everything is everywhere, but the environment selects" (Baas Becking, 1934) over a large-scale environmental gradient. Here we evidenced how the partitioning of resources along our selected trait, phytoplankton size, is a strong feature at an ocean basin scale. These observations lend weight to arguments supporting the niche partitioning theory rather than the unified neutral theory of biodiversity. The importance of the finding that the prevailing environmental condition is the major driver of the phytoplankton community structure in the Atlantic Ocean need to be further investigated using the trait-based modelling approach of Bruggeman & Kooijman (2007); Merico et al. (2009). This modelling tool will help to disentangle the relative contributions of the top-down vs. bottom-up processes in shaping the phytoplankton community structure, a research direction also promoted very recently by Follows & Dutkiewicz (2011).

2.5   Acknowledgements

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Chapter 3

Further work

3.1 Size-based model

3.1.1 Background

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 (Litchman & Klausmeier, 2008). Size plays also a major role in growth and metabolism (Finkel et al., 2009). The importance of this trait has motivated the development of a number of size-based ecological models. For example, Baird & Suthers (2007) 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' (2007) 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
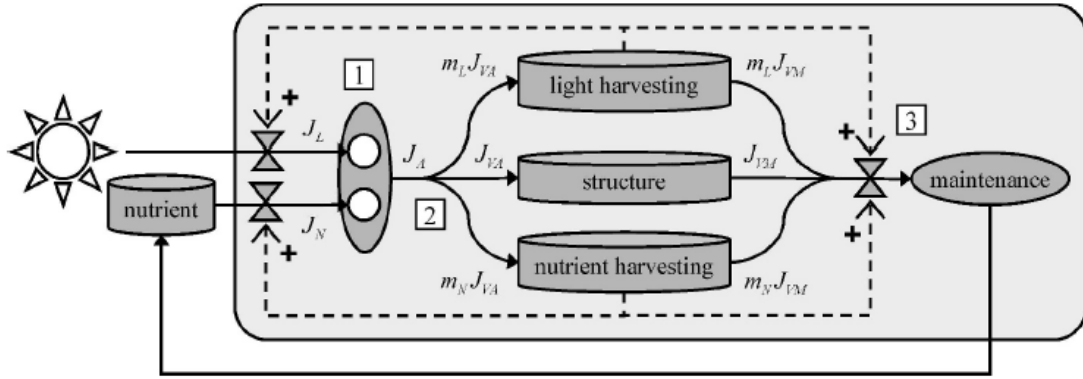
Figure 3.1: Bruggeman and Kooijman model scheme. Taken from Bruggeman & Kooijman (2007)

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 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 (Anderson, 2005).

Interesting alternatives to this modelling practice are obtained if principles of the Dynamic Energy Budget theory (DEB) of Kooijman (2009) 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) (Sousa et al., 2010).

In 2007 Bruggeman & Kooijman (2007) developed a trait model based on DEB concepts to study phytoplankton diversity and succession. The model (3.1) 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

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of having to consider too many species (and therefore too many state variables and parameters) when tackling biodiversity studies. Bruggeman & Kooijman (2007), 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 Wirtz & Eckhardt (1996); Norberg et al. (2001), Bruggeman and Kooijman's(2007) 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 (Bruggeman & Kooijman, 2007). 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 (Merico et al., 2009).

3.1.2   Method

The main focus of my PhD work is to develop a size-based model following the approaches of Bruggeman & Kooijman (2007); Merico et al. (2009) 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 (Tilman, 2000). Based on available observations, I will therefore develop a trade-off between competitive ability for nutrient acquisition and resistance to grazing (3.2). 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 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:

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

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

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

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

3.1.3 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
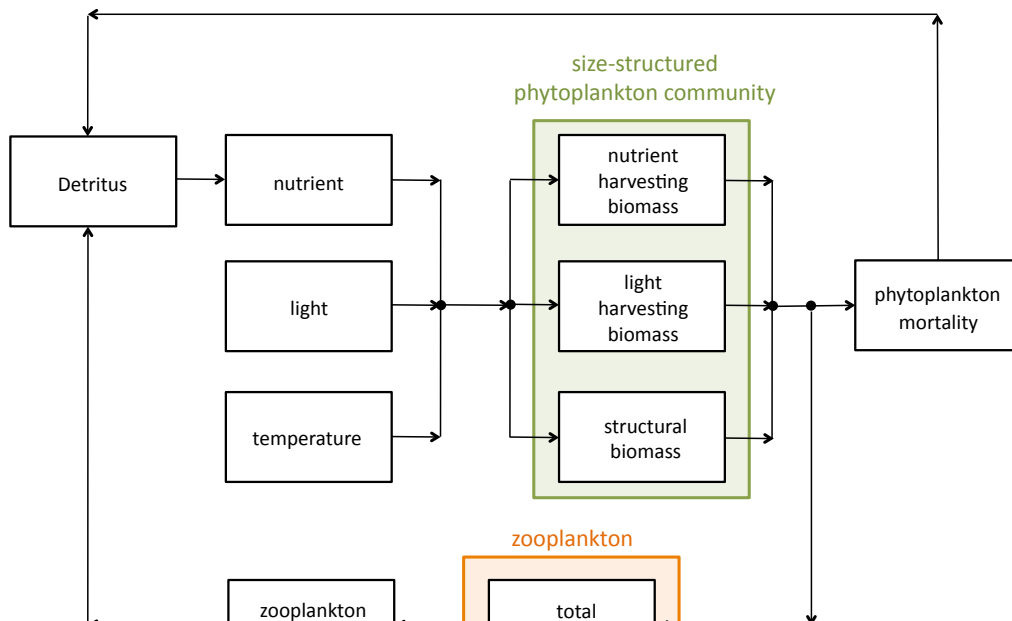
Figure 3.2: Scheme of the proposed size-based model. In this model phytoplankton allocates energy (or biomass) to different pools such as nutrient and light harvesting biomasses and generic structural biomass. A certain fraction of the phytoplankton biomass flows into the zooplankton biomass and a remaining fraction is remineralized into the nutrient pool

and ecological processes shaping the phytoplankton community size structure.

A key aspect with our approach is that under any given environmental condition, typical community size-structures will emerge consistently to the Bass Becking's principle that "Everything is everywhere, but the environment selects" (Baas Becking, 1934). More generally, I expect that this work will provide the possibility to test different ecological hypothesis proposed for explaining biodiversity, including the niche and the neutral hypotheses (Hubbell, 2001; McGill, 2003).

3.2 Multi-trait size-based model

A recent review on the current developments of plankton models by Follows & Dutkiewicz (2011) stress that most of the trait-based models elaborated so far have been only focusing on photoautotroph. It appears reasonable to start extend trait-based formulations also to other groups such as zooplankton, as in our proposed size-based model (3.2). I will therefore extend my model to include a dynamic selection of the prey based on the size of predator.

I believe that the allometric scaling of predator-prey interactions in planktonic systems is a key aspect for further advances in trait-based models due to the importance of this process in regulating the phytoplankton community structure(Agrawal, 2001; Litchman & Klausmeier, 2008). 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.

3.3   Paleo-reconstruction of planktonic communities

Since Darwin times, ecologist have tried to understand the evolutionary processes that lead to the current patterns of biodiversity. Hutchinson (1961) was fascinated by the capacity of phytoplankton communities to produce such a large diversity from a limited range of resources fro 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 $\sim$ 1.6-1.8 billion years ago, unicelular eukaryotes raised when they started to "use" prokaryotic cells as their metabolic slaves. From that point on, different kind of unicellular eukaryotes emerged, until three characteristic groups of phytoplankters originated from an ancestral red alga, and started to dominate earths aquatic environments (Figure 3.3) (Falkowski et al., 2004). Since the Middle Triassic these well know 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 (Falkowski, 1998).

Jiang et al. (2005); Litchman et al. (2009) develop a size-based evolutionary model, based on game theory, to determine the driving processes which could produce the difference size distributions of diatoms. Their model results suggest the nitrogen to phosporus stoichiometric ratio, the nutrient fluctuation, and the changes on mixed
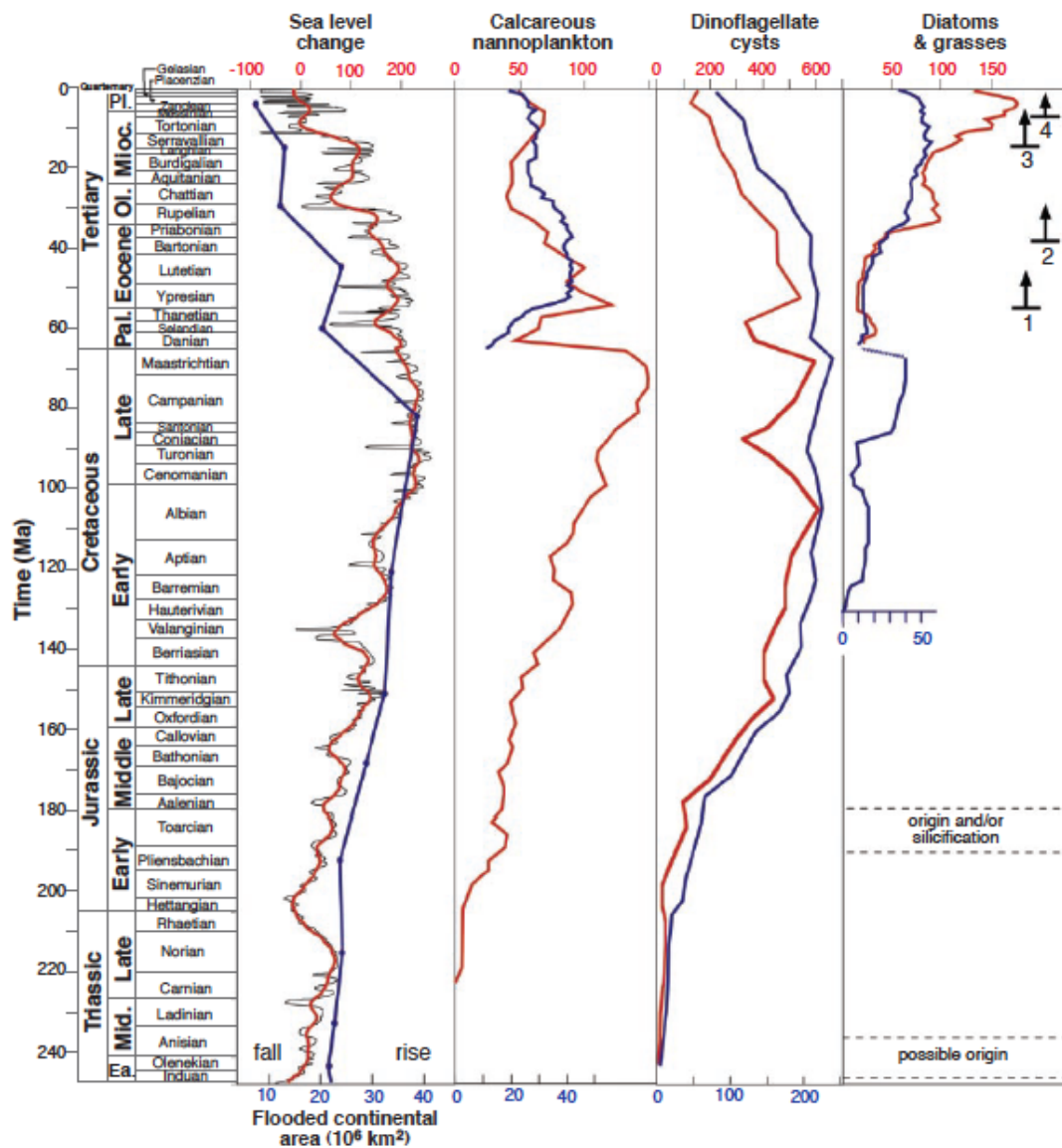
Figure 3.3: Comparison of major phytoplankton groups with sea-level change. The red line accounts for species diversities from published studies. The blue line accounts for the genus diversity compiled from public databases by the authors. Taken from Falkowski et al. (2004).

layer depth, as major mechanisms leading 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 prevaling 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.

3.4 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										

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