ANTHROPOGENIC CHANGE VS NATURAL VARIABILITY: LESSONS LEARNED FROM THE CONTINUOUS PLANKTON RECORDER

by
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ABSTRACT

The Continuous Plankton Recorder (CPR) surveys have sampled plankton in the North Atlantic using ships-of-opportunity since 1958. The resulting unique, methodologically-consistent, multi-decadal datasets can distinguish between anthropogenic and natural variability. I show an example of a plankton group that may be driven by anthropogenic effects, another one that is likely due to natural variability and discuss changes in the North Atlantic plankton community structure in the context of multiple stressors.

As anthropogenic CO_2 emissions acidify the oceans, calcifiers such as coccolithophores are expected to be detrimentally affected. Our first study shows that CPR coccolithophore occurrence increased basin-wide from ~2 to over 20% from 1965-2010. Using Random Forest models to examine >20 possible environmental drivers, I found that CO_2 and the Atlantic Multidecadal Oscillation (AMO) were the best predictors. Since coccolithophore photosynthesis is strongly carbon-limited, increasing CO_2 and temperature may be accelerating its growth rate.

It is generally assumed that the distribution of the marine nitrogen fixer *Trichodesmium*, is restricted to warm, (sub) tropical oligotrophic waters. However, the second study demonstrates that Trichodesmium are widely distributed in "cold" North Atlantic waters. *Trichodesmium* presence near the British Isles increased approximately five-fold during the 1980s-1990s. Using NCEP reanalysis wind and pressure anomalies, and the Sahel precipitation anomaly, I propose that this can be explained by an increase in the Saharan dust source, coupled with wind and pressure anomalies that opened a pathway for iron-rich dust transport. As *Trichodesmium* can grow in temperatures below 20^{o} C, the N_2 fixation capability of *Trichodesmium* strains from extra-tropical regions must be reevaluated. This has important implications for the global Nitrogen budget.

The third study expands the first study to examine nine plankton groups, testing the hypothesis of a plankton phase shift in the North Atlantic. Results show a shift from large to small phytoplankton groups, changes in phenology, an increase in calcifiers and evidence of bottom-up and top-down effects. However, the change was not abrupt and the different timings and sensitivities to forcings across plankton groups suggest multiple drivers. No single parameter explained all the observed changes, although CO_2, AMO and diatoms were important predictors.

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1 INTRODUCTION

Marine productivity, fishery yields, air-sea carbon dioxide exchange and carbon export to the deep ocean are all controlled by the structure and function of planktonic communities (Karl et al. 2001). Although the standing stock of marine phytoplankton is less than 1% of the total global plant carbon, these short-lived microscopic organisms are responsible for mediating biogeochemical cycles and half of the planet's primary productivity (Falkowski et al. 2004). But there is also a tight and relatively fast coupling between environmental change and plankton dynamics. Marine phytoplankton may respond to anthropogenic CO_2 release and global warming by altering their physiology (Riebesell et al. 2000, Hutchins et al. 2007), relative abundance (Tortell 2000, Hare et al. 2007, Feng et al. 2009, Rose et al. 2009) and/or biogeography (Boyd & Doney 2002). The distribution and abundance of phytoplankton is the result of the non-linear combination of environmental parameters and their response can amplify the effect of subtle changes in the environment (Hays et al. 2005). Given this non-linear response, phytoplankton may be more sensitive indicators of climate change than the environmental parameters themselves (Hays et al. 2005). Therefore, understanding how climate change is affecting marine plankton is one of today's key issues.

Given the over 20,000 extant phytoplankton species; one pragmatic way to reduce this complexity is to group phytoplankton either in terms of Phytoplankton Functional Types (PFT) or size classes. Examples of widely used PFTs include: diatoms, dinoflagellates, coccolithophores, diazotrophs, silicoflagellates and chlorophytes. The term PFT often refers to the role or effects that each group exerts on biogeochemical processes irrespective of phylogeny (Nair et al. 2008).

This classification is a useful approach for community ecology, as well as biogeochemical studies. For example, marine ecologists place diatoms at the base of the copepod-fish food web, so that high diatom productivity will lead to healthy productive fisheries. By contrast dinoflagellates are thought of less nutritious, unpalatable and typically precursors of gelatinous organisms (McQuatters-Gollop et al. 2007a). Since fisheries are highly dependent on diatoms, much research has been done regarding this group. Diatoms have been reported as decreasing in the North Atlantic both in situ (Leterme et al. 2005) and in predictive models (Bopp et al. 2005), while jellyfish frequency and abundance of outbreaks may be increasing regionally and globally (Purcell et al. 2007, Brodeur et al. 2008, Licandro et al. 2010, Condon et al. 2012, Condon et al. 2013). It is projected that a consequence of global warming would be a warmer, fresher North Atlantic with stronger vertical stratification and decreased nutrient supply (Sarmiento et al. 2004, Barton et al. 2016a). These conditions would be expected to be detrimental for large phytoplankton, but could be beneficial to other groups such as smaller phytoplankton (Bopp et al. 2005) like coccolithophores, which exhibit smaller and slower metabolic demands and could lead to a strong reorganization of the ocean ecosystems. A clear example of such shifts can be seen in the Black Sea, where overfishing, stratification and changes in the balance of nutrient influx have led to a coccolithophore dominance and a decline in commercial fisheries (Cokacar et al. 2001, Daskalov 2002, Oguz et al. 2003, Cokacar et al. 2004, McQuatters-Gollop et al. 2008, Oguz & Velikova 2010).

Coccolithophores are also unicellular algae that are surrounded by microscopic calcite plates called liths or coccoliths. Although coccolithophores are not the dominant PFT, they can have a number of important impacts on the Earth System. Coccolithophores have attracted renewed attention because they are the primary calcifying photosynthetic algae on Earth and have a double role in both the biological pump of carbon from the atmosphere to the to the deep sea, and constituting a major source of biogenic calcium carbonate. Coccoliths constitute the major source of particulate inorganic carbon (PIC) in the ocean and serve as ballast for aggregates (Francois et al. 2002), thus impacting the carbon export to the deep sea (Armstrong et al. 2002). Calcium carbonate is responsible for 50-75% of the biogenic carbon deposition on the sea floor (Gordon et al. 2001, Dunne et al. 2007) and the range of annual calcite production has been estimated to vary between 0.5-1.4 Gt PIC/year (Feely et al. 2004, Dunne et al. 2007). In the long term carbon is buried in marine sediments but in the short term the formation of calcium carbonate plates releases carbon dioxide (Gordon & Balch 1999). The conspicuous sedimentary records from the Cretaceous (ca. 100Mya) reveal that coccolithophores were very abundant in the past, including periods with high atmospheric carbon dioxide. Furthermore, coccolithophores also have an impact in the marine sulfur cycle as important producers of dimethylsulfoniopropionate (DMSP), precursor of dimehylsulphide (DMS), which is a precursor of cloud formation (Matrai & Keller 1993, Matrai et al. 2007) and a potential feedback mechanism in regulating Earth's climate, as suggested by the CLAW hypothesis (Charlson et al. 1987). Despite their micron-size, coccolithophore blooms can last about a month and reach up to 995, 000 km^2 (Raitsos et al. 2006), becoming an important pulse in the ecosystem that is visible from space.

Diazotrophs (Nitrogen fixers) are another key phytoplankton group. By balancing the atmosphere-biosphere N reservoirs, diazotrophs play a crucial role in the global N budget. Within these, *Trichodesmium* is the most iconic marine diazotroph, thought to be responsible for half of the global nitrogen fixation in the ocean (Karl et al. 2002, N. et al. 2004). Although typically found in warm, tropical and subtropical oligotrophic waters, there has been much debate on what limits *Trichodesmium* distribution. Depending on the region, there are arguments for iron (Kustka et al. 2003a, Kustka et al. 2003b, Schlosser et al. 2014, Weber & Deutsch 2014), nitrates (Tyrrell 1999), phosphates (Sañudo-Wilhelmy et al. 2001, Tovar-Sanchez et al. 2006, Chen et al. 2011b), or even dissolved oxygen (Staal et al. 2003, Staal et al. 2007, Stal 2009, Luo et al. 2014) being the key limiting factor. A number of recent studies suggest that the projected ocean acidification, global warming and stratification will affect *Trichodesmium* directly -by affecting growth rates and Nitrogen fixation (Barcelos e Ramos et al. 2007, Hutchins et al. 2007, Levitan et al. 2007, Kranz et al. 2010, Levitan et al. 2010, Hutchins et al. 2015)- and indirectly -by expanding tropical oligotrophic regions (Polovina et al. 2008, Ward et al. 2013, Dutkiewicz et al. 2014). However temperature limitation and extra-tropical distributions are rarely discussed. Establishing an accurate global distribution of *Trichodesmium* is crucial to estimate the global nitrogen budget now and under future projections of climate change.

There is an ongoing debate on whether the North Atlantic oceanic productivity is decreasing given that some studies suggest that chlorophyll biomass has not changed or is increasing (Sarmiento et al. 2004, Antoine et al. 2005, Raitsos et al. 2005, Beaugrand 2009, McQuatters-Gollop et al. 2011). Part of the problem resides in the erroneous understanding that satellite-derived chlorophyll a concentration translates directly into carbon biomass (Behrenfeld et al. 2005) and the fact that chlorophyll a trends cannot be attributed to a single PFT. Although we need to analyze trends in terms of PFTs, it is difficult to precisely identify individual PFTs with current algorithms and sensors.

In order to study ecological impacts of climate change in variability, it is necessary to move beyond looking at annual mean chlorophyll and biomass during the satellite era. Changes in phenology associated with global warming have already been observed in the North Atlantic

(Edwards & Richardson 2004). The so-called “match-mismatch” hypothesis (Cushing 1990) suggests that synchronizing the timing of the phytoplankton bloom with the presence of grazers is more important than the magnitude of the bloom itself. Additionally, longer time series are required. According to (Henson et al. 2010), 40 years is the threshold to distinguish anthropogenic climate change from natural variability in the variability of chlorophyll a. In order to study community phase shifts a similar multivariate multi-decadal study is required. We cannot understand spatio-temporal distribution patterns of organisms without addressing interactions with other groups and competition for resources; it is equally important to represent both the biotic and abiotic components and bottom-up as well as top-down effects.

The goal of this thesis is to use available long-term datasets to evaluate whether there have been changes in the North Atlantic plankton communities and whether these can be attributed to natural variability or anthropogenic drivers. To do this I will use the Continuous Plankton Recorder survey, which is the longest and most extensive plankton dataset in the World Ocean, to evaluate long-term changes in some of the main plankton groups of the North Atlantic basin over the last 50 years. This general goal will be addressed within the next three chapters:

- **Chapter 2** focuses on long-term trends in North Atlantic coccolithophores and evaluates the role of CO_2 for this calcifying group.

- **Chapter 3** assesses *Trichodesmium* interannual variability, focusing on the area around the British Isles and the potential role of episodic events of iron fertilization from dust.

- **Chapter 4** evaluates the sensitivity and long-term change of nine plankton groups recorded by the CPR, discussing the idea of a regime shift in North Atlantic planktonic communities and its potential drivers.

2 MULTIDECADAL INCREASE IN NORTH ATLANTIC COCCOLITHOPHORES AND THE POTENTIAL ROLE OF RISING CO_2.

2.1 Abstract:

As anthropogenic CO_2 emissions acidify the oceans, calcifiers are expected to be negatively affected (Orr et al. 2005). However, using data from the Continuous Plankton Recorder we show that coccolithophore occurrence in the North Atlantic increased from ~2 to over 20% from 1965 through 2010. We used Random Forest models to examine >20 possible environmental drivers of this change, finding that CO_2 and the Atlantic Multidecadal Oscillation were the best predictors. Since coccolithophore photosynthesis is strongly carbon-limited (Rost et al. 2003), we hypothesize that higher CO_2 levels might be encouraging growth. A compilation of 41 independent laboratory studies supports our hypothesis. Our study shows a long-term basin-scale increase in coccolithophores and suggests that increasing CO_2 and temperature have accelerated the growth of a phytoplankton group that is important for carbon cycling.

2.2 Introduction

Coccolithophores, the main calcifying phytoplankton, are unicellular algae surrounded by calcite plates called coccoliths. Coccoliths are a major source of oceanic particulate inorganic carbon (PIC) and serve as ballast for sinking aggregates (Francois et al. 2002), thus accelerating carbon export (Armstrong et al. 2002). Given increasing partial pressures of atmospheric CO_2

(pCO$_2$), global warming, and ocean acidification, it is expected that coccolithophores will be affected, producing concomitant impacts on ocean carbon fluxes, dimethyl sulfide fluxes (Matrai et al. 2007), carbonate geochemistry (Rost & Riebesell 2004), and phytoplankton community structure (Rost & Riebesell 2004). Current evidence regarding how increased pCO$_2$ will affect coccolithophores is contradictory (Iglesias-Rodriguez et al. 2008, Riebesell et al. 2009, Beaufort et al. 2011, Smith et al. 2012). Most laboratory manipulations study how coccolithophores respond to the increased pCO$_2$ levels predicted for the end of the century rather than to the CO$_2$ changes observed in the last five decades.

Here we report changes in the occurrence of coccolithophores in the North Atlantic during the last 45 years, and use Random Forest (RF) statistical models to evaluate the importance of various environmental drivers for these changes.

2.3 Materials and Methods

In order to represent both top-down and bottom-up effects that could affect coccolithophore occurrence, we used a large number of predictors:

1. Biological Data: The Sir Alister Hardy Foundation for Ocean Science (SAHFOS) provided in situ plankton data from 1965-2010. SAHFOS has been collecting data from the North Atlantic and the North Sea on biogeography and ecology of plankton (phytoplankton and zooplankton) since 1931. This is the largest and most extensive on-going time series of plankton distribution in the world (Richardson et al. 2006). The instrument used for these surveys is the Continuous Plankton Recorder (CPR), which is a sub-surface sampling instrument towed by ships of opportunity on commercial routes. The CPR filters plankton on a band of silk that moves progressively with the inflow of water. The mesh size is 270µm. The filtering silk and a covering silk are rolled up together into a storage compartment containing borax-buffered 4%

formaldehyde for preservation (Reid et al. 2003). Silk movement is proportional to the ship's speed so that 10cm of silk correspond to 10 nautical miles of towing and ~3m^3 of water filtered (Reid et al. 2003) at a depth of ~7 m. Once the cruise is completed, each roll is examined under a microscope for cell counts (Reid et al. 2003). We selected for this study 6 phytoplankton groups (coccolithophores, diatoms, dinoflagellates, cyanobacteria (=*Trichodesmium*), chlorophytes, silicoflagellates) and two zooplankton groups (copepods and tintinnids). Each observation corresponds to cell counts per sample (10 cm of silk or 3m^3 of water). Coccolithophore presence was not regularly recorded until 1965. Coccolithophores, silicoflagellates and tintinnids were not counted until 1993. Before this time, only presence or absence was recorded for these groups. Therefore, we used probability of presence of these groups (= frequency of occurrence/number of samples in a 1 degree by 1 degree area and month) as proxy for abundance between 1965-2010 (Fig. S1).

2. Physical parameters: We selected for this study sea-level pressure (P), wind stress (W), zonal (U) and meridional (V) components of the surface wind, sea surface temperature (SST), total cloudiness fraction (C). These environmental variables were extracted for 1x1 degree cells in the North Atlantic between 1965-2010 from the International Comprehensive Ocean-Atmosphere Data set (ICOADS, http://icoads.noaa.gov/). These are all averages of historical in situ measurements from different sources (buoys, ships, etc.).

3. Nutrients: we used in situ monthly climatologically gridded 1-degree products on nitrate, silicate and phosphate concentrations from the World Ocean Data 2009 inventory (https://www.nodc.noaa.gov/OC5/WOA09/pr_woa09.html).

4. CO$_2$: Assuming that the monthly records of atmospheric CO$_2$ from Mauna Loa observatory (http://scrippsco2.ucsd.edu/data/in_situ_co2/monthly_mlo.csv) are representative of global long-

term *p*CO_2 trends, we used these records as an estimate of global *p*CO_2. Secondly, we used the Takahashi et al. climatology (Takahashi et al. 2009) to extract matching estimates of monthly dCO_2 at 4x5 degree resolution (http://www.ldeo.columbia.edu/res/pi/CO2/carbondioxide/pages/air_sea_flux_2000.html). This climatology is based on millions of in situ measurements of oceanic *p*CO_2 (usually from underway ships), extrapolated to a global grid. It should be noted that the spatial resolution is coarser than that of the other spatially resolved parameters. In the absence of collocated CPR and CO_2 measurements, we can only estimate local in situ *p*CO_2. By adding together the two previous parameters (global atmospheric pCO_2 and ocean climatological gridded d*p*CO_2) we produced a composite that attempts to supply the missing local in situ *p*CO_2.

5. Climate Modes: We evaluated the impact of four climate variables: the North Atlantic Oscillation (NAO), Arctic Oscillation (AO), El Niño Southern Oscillation (ENSO), and Atlantic Multidecadal Oscillation (AMO). NAO and AO indices were obtained from the National Weather Service Climate Prediction Center, National Oceanic and Atmospheric Administration (http://www.cpc.ncep.noaa.gov/). The Multivariate ENSO Index (MEI), which is the index utilized for ENSO, and the de-trended AMO time series were obtained from the Earth System Research Laboratory at NOAA (http://www.esrl.noaa.gov/psd).

6. Statistics: All statistical analyses were performed in R version 2.15.2. We tested twelve statistical models that can circumvent the irregular sampling issues and allow for inclusion of all available CPR data. Our dataset included 24 variables and 81,340 observations. The models evaluated were: a Classification and Regression Tree model (CART), a Bagged CART, a Generalized Linear Model (GLM), a Generalized Additive Model (GAM), a Random Forest Model (RF), four different single layer Artificial Neural Network (ANN, with 10, 20, 30 and 50

nodes, respectively), Multivariate Adaptive Regression Spline (MARS), Bayesian Additive Regression Trees (BART) and a Null (mean-only) model. Prior to building the models, the dataset was standardized to ensure that all the variables have the same weight in the analyses. Moreover, to ensure that variables are independent, correlation and co-linearity were tested. Pearson correlations were relatively high for some variables (e.g. NAO-AO, among nutrients, nutrients and SST, among CO_2 parameters, see correlation matrix), which is expected. The Variance Inflation Factors (VIF) were less than 7 for nutrients and less than 5 for the rest of the variables, which are below the accepted threshold of 10 for multicolinearity.

We performed a 50-fold cross validation test to evaluate the performance of the 12 models, with 90% of the data used for training, and 10% for evaluation. The models were compared via t-tests of mean absolute error (MAE), mean square error (MSE), and Root Mean Square Error (RMSE) results. We applied Bonferroni corrections to ensure that p-values were not due to random effects. Our analysis showed that the Random Forest is the most competent for our data set, consistently exhibiting the lowest MSE, RMSE and MAE of all models.

The Random Forest algorithm (implemented in the "randomForest" package in R) randomly selects bootstrap samples of observations, randomly selects a subset of a third of the variables to use for that sample, and either builds a regression or classification tree for each bootstrap sample with the selected subset of variables, hence the name "random forest". Trees are built by recursive binary partitioning of observations into subsets that are increasingly similar within a subset and different across subsets, as in a hierarchical decision tree. Basing each tree in the forest on a different, randomly selected, subset of predictor variables helps to ensure low correlation between the predictions of the different trees. Each tree is itself, asymptotically unbiased. The ensemble of trees then is approximately unbiased and has substantially reduced variability in predictions relative to a single-tree model. At each node in a single tree, the variables used to develop that tree are tested for the split in the data that achieves the greatest reduction in error. Random forest uses this ensemble of trees to make predictions based on the average response (regression) or majority vote (classification) to a given set of parameters. A portion of the observations is excluded from the tree building process (i.e. out-of-bag or OOB data) for each individual tree to be used as an independent estimate of the prediction accuracy. Random forests build a user-defined number of regression or classification trees; we used 1000 regression trees. Variable importance was used to identify ecologically important variables. Variable importance is integrated in the tree-building process. In the model-fitting process, variable importance can be measured by evaluating the increase in node purity on trees that exclude that variable. We used the percent increase in Mean Squared Error (MSE), which reflects the error in out-of-sample prediction caused by the exclusion of a given variable and replacement by random noise. These variable importance metrics (MSE and node purity) provide information about the relative contribution of each variable to the model's fit or predictive accuracy. Partial dependence plots are generated by averaging out the values for all the variables except the one of interest, isolating its marginal effect on the response variable. In general, the response variable (Y) depends on all the covariates (X_i). Letting X_a be the covariate of interest and X_b, X_c be the rest of variables:

$$Y = f(X) = f(X_a, X_b, X_c)$$

We then define the average or partial dependence plot of Y on X_a as:

$\bar{f}(X_a) = \frac{1}{N}\sum_{i=1}^{N} f(X_a, x_{ib}, x_{ic})$, where x_b, x_c are the values of X_b and X_c in the training data.

7. Limitations: One obvious limitation of this study is the different temporal and spatial scales compared. This study links growth rate processes at the micron and daily scale to environmental processes that take place on a monthly, decadal or even global scale. Being a retrospective study there is a trade-off between using available data and optimal data. In this study there is a substantial amount of available biological and physical data, but there are also gaps in space and time, and only climatological information for certain parameters. Some parameters were used as proxies for processes for which we do not have long term information such as irradiance, nutrient concentrations or stratification. Therefore we tried to be as inclusive and holistic as possible and, at the same time, limit the analyses to in situ data to avoid adding noise from interpolation or modeling algorithms. We only analyzed complete records, i.e., that hold information on all variables, so that the study would not be biased by any single parameter. Biological data had to be spatially and temporally aggregated to match parameters on monthly 1-degree grids.

A particular concern is that the local and climatological CO_2 parameters are on a coarser spatial scale (4 x 5 degree). However, previous analyses of underway pCO_2 variability in the North Atlantic (e.g. Appendix D of the 1998 LSCOP report (http://www.pmel.noaa.gov/pubs/PDF/bend2454/Appendix_D.pdf) indicate it to be small on this scale away from upwelling and deep convection regions (5-10ppmv), and much smaller than the annual cycle or large-scale spatial variability. Moreover, re-gridding the data to a 4x5 degree box did not change the relative importance of carbon dioxide predictors.

The purpose of this study was to show recent increases in coccolithophore occurrences in the North Atlantic and, secondarily, present a potential driving mechanism that is supported by a compilation of independent experiments. Given the underestimation of coccolithophore natural abundances derived from the mesh size of the CPR, our results cannot be taken as quantitatively exact but should instead be used to stimulate further research.

2.4 Results and Discussion

The in situ Continuous Plankton Recorder (CPR) surveys were developed to sample plankton in the North Atlantic using ships-of-opportunity. The surveys have followed the same methodology since 1946 (Richardson et al. 2006). Sample preservation methods (using Borax-buffered formalin) and analysis have remained unchanged since 1958 (Hays et al. 1995), producing a unique, consistent, multi-decadal dataset. While the CPR filtering system was designed to sample larger microplankton, coccolithophores are trapped, particularly in the intersection of the silk fibers (Hays et al. 1995). It is not possible to accurately quantify organisms that are smaller than the mesh-size, but we can use the dataset to estimate the probability of coccolithophore occurrence. While our sampling underestimates natural abundances, this probability is a proxy for changes in coccolithophore abundance (Figure 2.1). We calculated the annual probability of coccolithophore occurrence as the fraction of samples per year containing coccolithophores. The CPR data shows an increase in occurrence of coccolithophores across the North Atlantic from ~1% of samples in the 1960s to over 20% of samples with coccolithophores in the 2000s (Figure 2.2A-F,

Figure 2.3). Regional abundances of coccolithophores in the 2000s are at least ten times higher than those observed at the beginning of the data record. Our observations are supported by a shift in the opal: carbonate ratio in sediment traps in the Atlantic from the 1990s (Antia et al. 2001), satellite evidence of global poleward expansion of *Emiliania huxleyi* (Winter et al. 2013), and recurring blooms in areas where coccolithophores were previously absent or sparse (Smyth et al. 2004, Cubillos et al. 2007, Hovland et al. 2013, Winter et al. 2013).

To evaluate possible top-down and bottom-up drivers for the increase in coccolithophore occurrence in the North Atlantic, we investigated factors that could affect coccolithophore growth rates and biogeography. Temperature, nutrient availability, light levels, competition, and predation are critical on a local scale. In turn, these may be affected by large-scale processes such as climate modes, global warming, and increases in CO_2. The CPR sampling survey is irregular in time and space, making classic time series analysis inappropriate for this dataset. Additionally, the effects of different environmental forcings on phytoplankton groups are non-linear and inter-dependent. After evaluating a suite of statistical methods, we selected Random Forest (RF) models (Breiman 2001), an increasingly popular method in ecology that characterizes structure in high dimensional data while making no distributional assumptions about the response variable or predictors. RF has the advantage of allowing for non-linearities, geographically and temporally discontinuous data, and the ability to model complex interactions among predictor variables without overfitting the data.

Our RF model predicted the probability of coccolithophore occurrence, defined as the percentage of samples containing coccolithophores in a 1-by-1-degree area each month, as a function of over 20 biological and physical predictors. Since the CPR dataset is already complex and discontinuous, we only used in situ measurements of biological and physical parameters without interpolating data. The complete dataset included 81,340 observations from 1965-2010. The importance of each variable in predicting coccolithophore occurrence is ranked in a variable importance plot. Importance is measured as the percent increase of Mean Squared Error (MSE) in the prediction due to that variable. Partial dependence plots graphically represent the marginal effect of each variable on the response variable. Here we discuss the top predictors and how these could have driven the observed increase in coccolithophore occurrence.

The evaluation of CO_2 as a driver for observed increases in coccolithophore occurrence required special attention. While $p$$CO_2$ and CPR data were not collected simultaneously, there is information about spatial and long-term CO_2 variability. We created three random forests, each with a different predictor for $p$$CO_2$: 1) *global pCO₂* estimated from Mauna Loa that varies only in time ("Global_$p$$CO_2$" variable in the RF_GLOBAL model), 2) *climatological ΔpCO₂* from Takahashi et al. (Takahashi et al. 2009) that has no interannual variability ("delta_$p$$CO_2$" variable in the RF_CLIM model), and 3) *local pCO₂* estimated as the sum of the Mauna Loa and Takahashi dataset varying in time and space ("Local_$p$$CO_2$" variable in the RF_LOCAL model). Local $p$$CO_2$ in the North Atlantic can be lower than the global $p$$CO_2$ by 100 ppm in certain months (section 6.1.1, Figure 2.4).

Local and global $p$$CO_2$ were the best predictors of coccolithophore occurrence in our RF models (Figure 2.5A, B). In the RF_GLOBAL analysis, the partial dependence plot shows low coccolithophore occurrence (3-5%) at $p$$CO_2$ ranges between 320-360 ppm. This corresponds to atmospheric CO_2 observed at Mauna Loa from 1960 to ~1996. The increase in coccolithophore probability accelerated at $p\mathrm{CO_2} > 370$ ppm (~1997), reaching 22% at 400 ppm. In the RF_LOCAL model (Figure 2.5B, E, Figure 2.6), the partial dependence plot shows a three-fold range, with the largest coccolithophore probabilities corresponding to the highest CO_2 values. Maximum probabilities of finding coccolithophores coincided at global and local CO_2 levels above 360ppm (Figure 2.5D, E). As discussed below, such dependence falls within the envelope of laboratory responses of coccolithophore growth rates to increased CO_2.

Within RF_CLIM, the climatological "delta_$p$$CO_2$" variable is not a strong predictor (Figure 2.5C, F). Instead, the Atlantic Multidecadal Oscillation (AMO) becomes the top predictor in this model and other climate modes (AO=Arctic Oscillation, MEI=Multivariate

ENSO Index) rise in their ranking relative to RF_LOCAL and RF_GLOBAL, reflecting the importance of interannual variability. Recent studies have linked the AMO with phytoplankton (Edwards et al. 2013) and coccolithophore variability (Hovland et al. 2013). The AMO index tracks temperature anomalies in the North Atlantic and its positive trend in recent decades could mask global warming or enhance CO_2 effects (Figure 2.7). AMO ranked 13th in the RF_GLOBAL model, second in RF_LOCAL and first in the RF_CLIM analyses (Figure 2.5A-C, respectively). We propose two explanations: either AMO has a true effect on coccolithophore abundance, or in the absence of "global CO_2" or "local CO_2", AMO is the only other variable with a similar long-term trend in the last two decades (Figure 2.7). The highest coccolithophore probabilities are found during the recent positive AMO phases (Figure 2.5G). If the coccolithophore increase were due to positive AMO, their occurrence should have been high during previous positive phases i.e. 1960's (Figure 2.7). Unfortunately, the scarce information prior to 1965 limits our ability to draw strong conclusions, but based on the variability explained and the ranking in partial dependence plots (Figure 2.5A-G), we propose that AMO could be an important secondary driver. AMO has been related to changes in the Meridional Overturning Circulation that would alter nutrient supply (Gnanadesikan et al. 2014a). Positive AMO periods are associated with greater upward transport of nutrients in convective regions, but lower upward transport elsewhere. If AMO were the only mechanism responsible for the coccolithophore increase, it would be expected to produce opposite effects in the northwestern and eastern regions. Instead, all regions show increasing trends.

2.5 Conclusions

We hypothesize that synergistic effects due to CO_2, AMO, and global warming differentially accelerated coccolithophore growth rates, driving recent increases in their occurrence. Compared to other phytoplankton groups, coccolithophore photosynthesis is severely carbon-limited (Rost et al. 2003) and sedimentary records show a predominance of coccolithophores during interglacial (McIntyre & Be 1967) and high CO_2 periods (Hannisdal et al. 2012). Many studies agree that coccolithophores respond to an increase in CO_2 by decreasing PIC and increasing POC but there is disagreement with respect to the effects on growth rates (see section 6.1.2). We assembled a compendium of published growth rates as a function of CO_2 (41 laboratory experiments from 16 independent publications, Figure 2.8, Figure 2.9, see section 6.1.2). Results show a quasi-hyperbolic increase in coccolithophore growth rates with pCO_2, with scatter partly produced by differences in experimental treatments: temperature, species, strain, nutrients, and irradiance. Our local pCO_2 estimates between 1965-2010 (blue box in Figure 2.8) correspond to the ranges in pCO_2 where, based on Figure 2.8, we would expect changes in coccolithophore growth rates. This compilation reconciles previous contradictory conclusions on the effects of CO_2 on coccolithophore growth rates (see section 6.1.2), buttressing our hypothesis that CO_2 enhances coccolithophore growth. Additional RF partial dependence plots of other top-down and bottom-up processes (grazing, nutrients, temperature, etc.) are discussed in section 6.1.3 (Figure 2.10).

In order to project future coccolithophore abundances under elevated CO_2 levels we need to reassess the baseline. Our results show that today's numbers are an order of magnitude greater than those in the 1960's and will likely continue to increase before growth rates stabilize at ~500 ppm. This is critical for understanding changes in the export ratio, biological pump, and alkalinity pump. Our compilation suggests that the changes seen in the North Atlantic may represent a global trend. Contrary to the generalized assumption of negative effects of ocean acidification on calcifiers, coccolithophores may be capable of adapting to a high-CO_2 world

(Lohbeck et al. 2012) especially given evidence of highly calcified coccolithophores in areas with seasonally high pCO_2 or low pH (Beaufort et al. 2011, Smith et al. 2012). Coccolithophores show outstanding competitive abilities under the stratified, warm, nutrient-depleted conditions projected for the future ocean (Rost & Riebesell 2004). Nevertheless, with increasing pCO_2, we might expect changes in community composition and a decrease in calcification, leading to changes in rain ratio, export efficiency, and trophic effects higher in the marine food web.

2.6 Figures

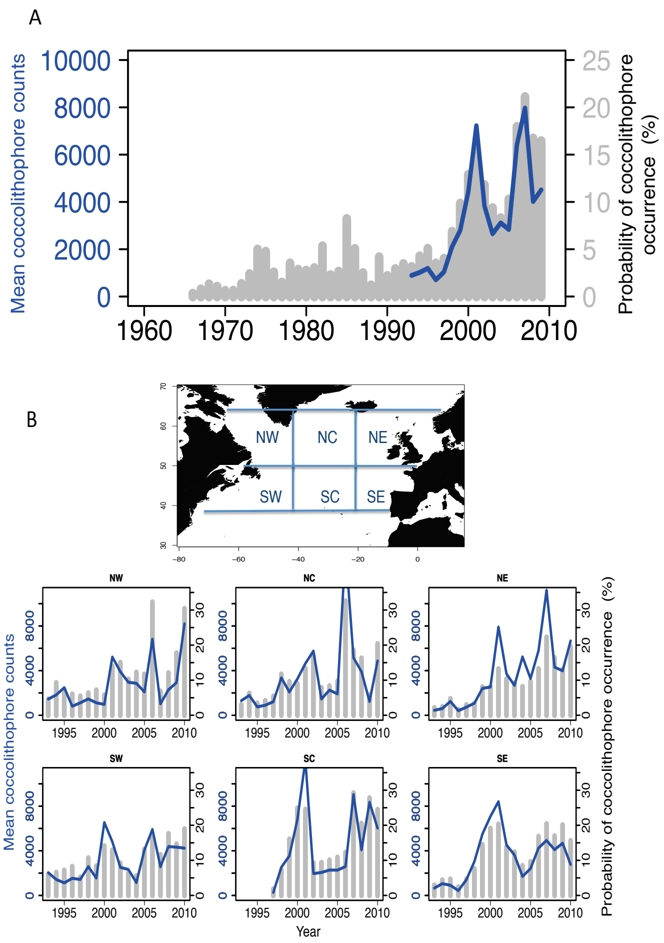


Figure 2.1. Coccolithophore probability of occurrence as a proxy for abundance. Since CPR analysts systematically counted coccolithophores after 1993, we used this quantitative data to evaluate whether the probability of occurrence (blue line) could be used as a proxy for abundance (grey bars). The blue line shows the average probability of coccolithophore presence in raw data (=sum of samples with coccolithophore records per year /total number of samples per year x100) and the grey bar chart shows the average coccolithophore counts in raw data (=mean coccolithophore counts per year). Our results show good agreement both at (A) the basin level and the (B) regional level: north-west (NW), north-central (NC), north-east (NE), south-west (SW), south-central (SC), south-east (SE).

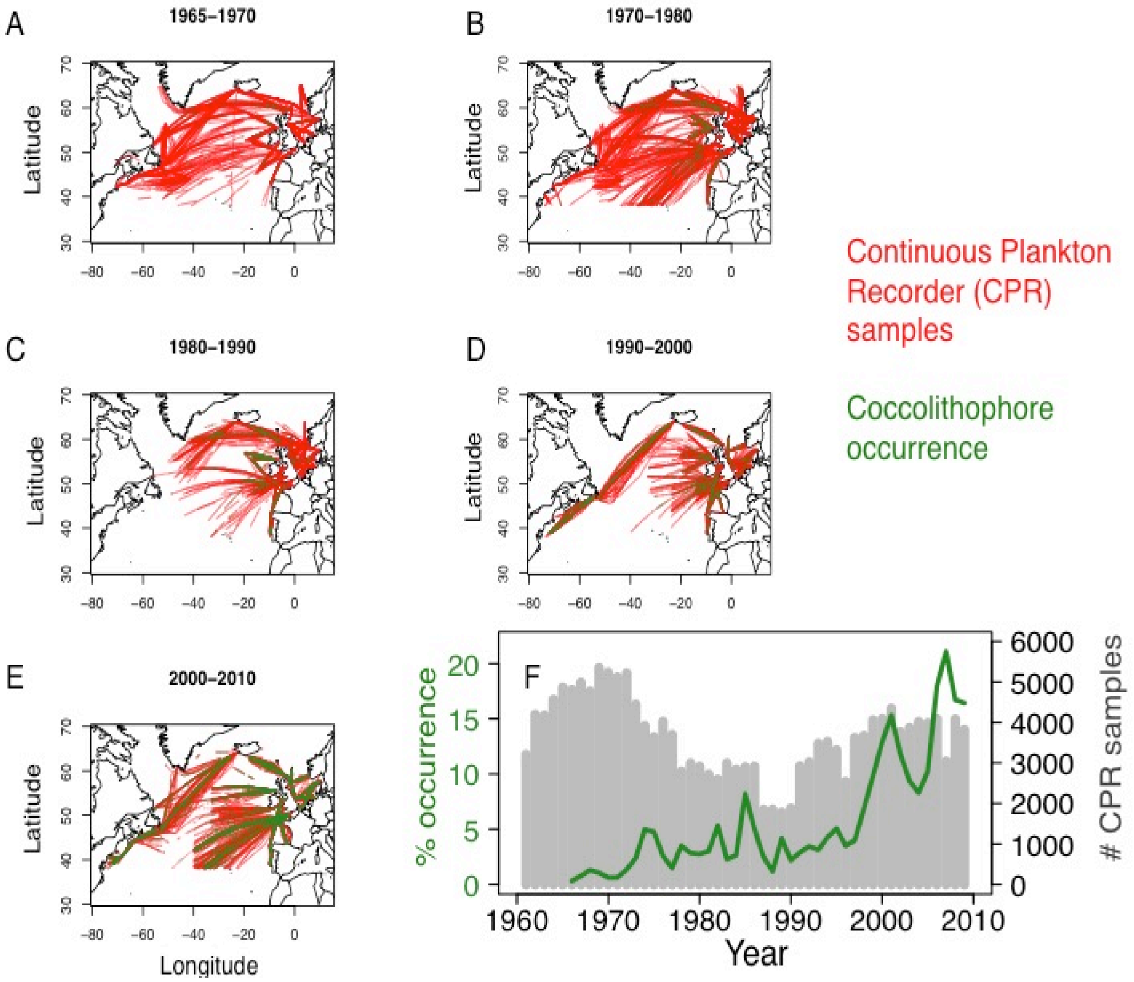


Figure 2.2. Distribution of CPR samples (red) and coccolithophore observations (green) per decade: (A) 1960s, (B) 1970s, (C) 1980s, (D) 1990s, (E) 2000s, (F) comparison of annual sampling effort (total number of samples per year in the North Atlantic) vs. average probability of coccolithophore occurrence in raw data (=sum of samples with coccolithophore records per year /total number of samples per year x 100). Each sample corresponds to observations found in 10cm of CPR silk (or ~3m^3 of water).

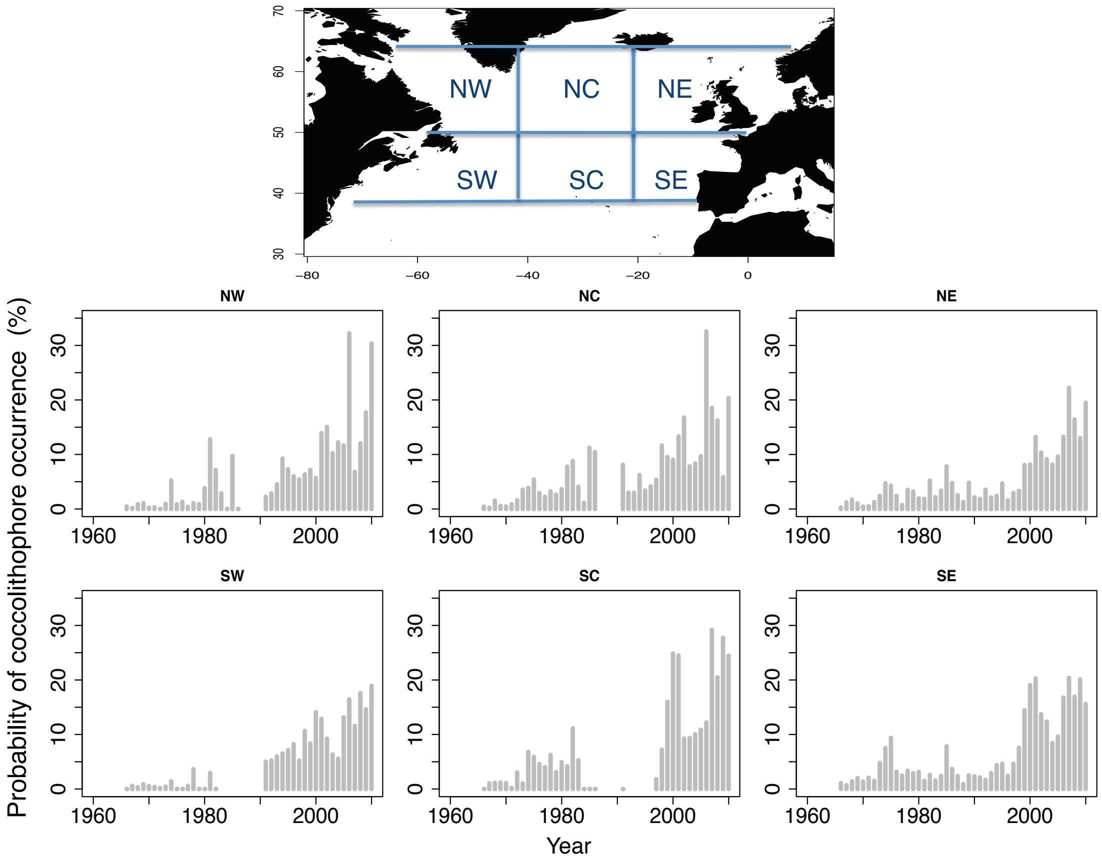
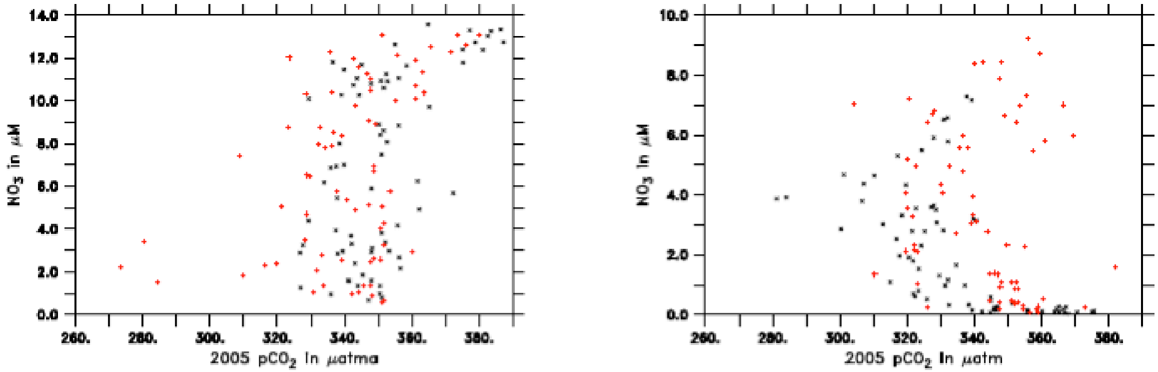
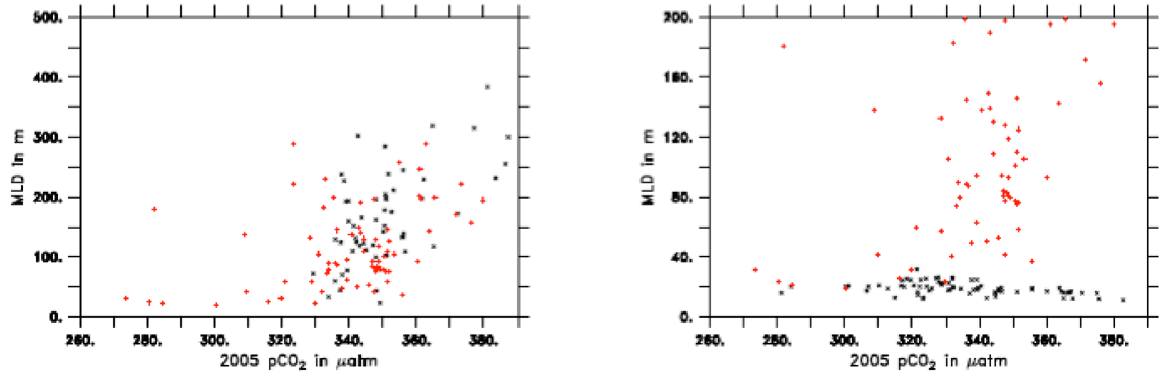


Figure 2.3. Interannual variability per region. North-west (NW), north-central (NC), north-east (NE), south-west (SW), south-central (SC), south-east (SE). All regions show increasing trends of differing slopes and starting times, they also show gaps in certain years and these differ among regions. Western and central regions (NW, NC, SC) show the greatest mean annual probabilities of finding coccolithophores



(A) DJF, MAM pCO$_2$ vs NO$_3$ (B) JJA, SON pCO$_2$ vs NO$_3$



(C) DJF, MAM pCO$_2$ vs MLD (D) JJA, SON pCO$_2$ vs MLD

Figure 2.4. Seasonal CO$_2$, nutrients and mixed layer depth. Local pCO$_2$ for the nominal year of 2005 from Takahashi (15) vs. climatological nitrate (NO$_3$, from World Ocean Atlas) and climatological mixed layer depth (MLD) for the North Atlantic region between 40-65N. Winter (December-February=DJF, black points), Spring (March-May =MAM, red points), Summer (June-August =JJA, black points), Fall (September-November=SON, red points). Local pCO$_2$ in the North Atlantic can be significantly lower than the global pCO$_2$ (by ~100 ppm in certain months).

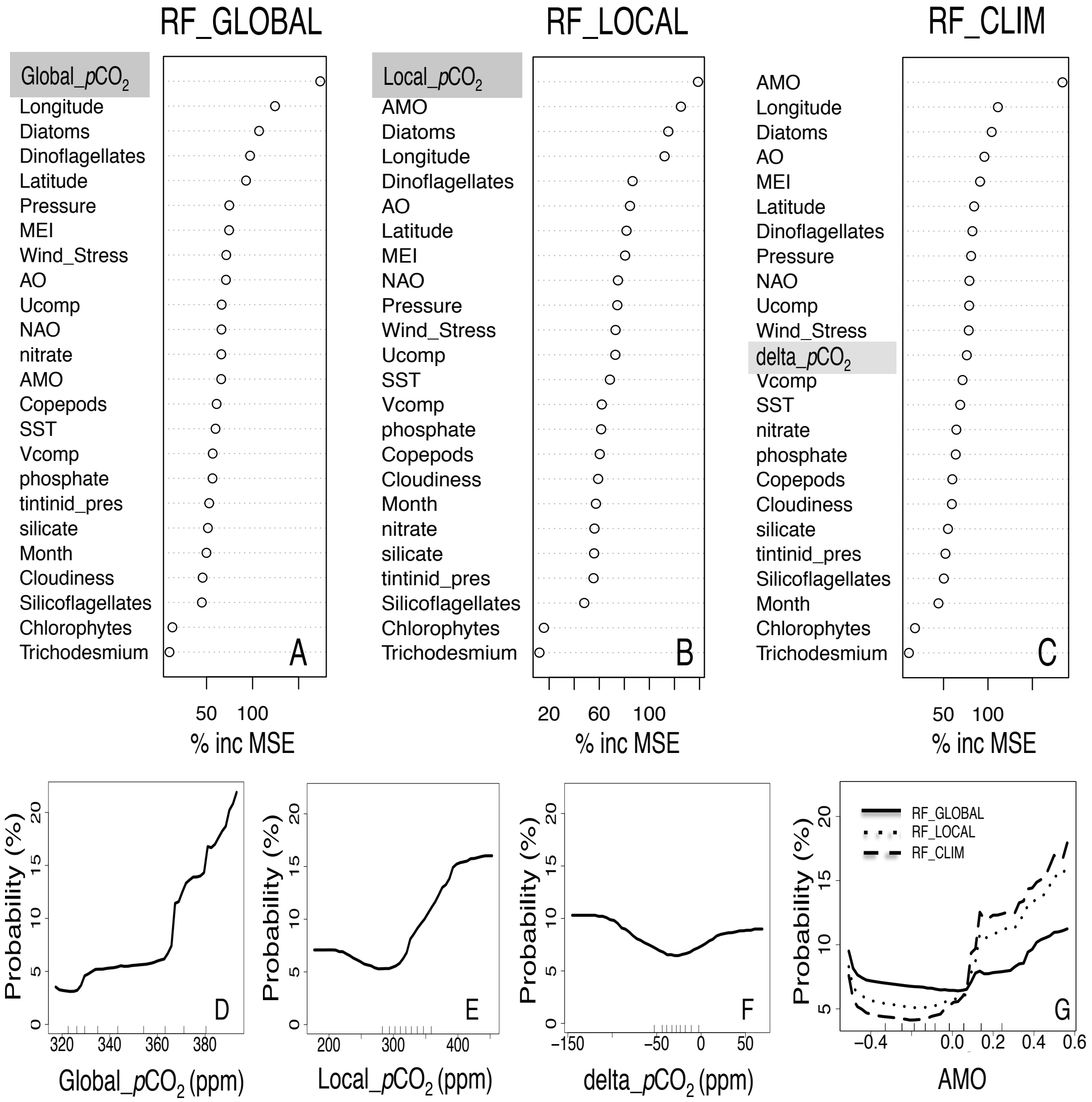
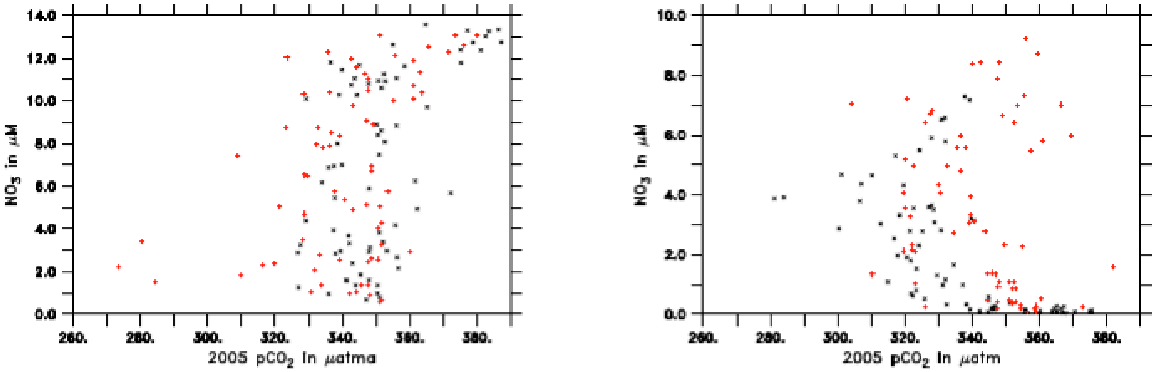
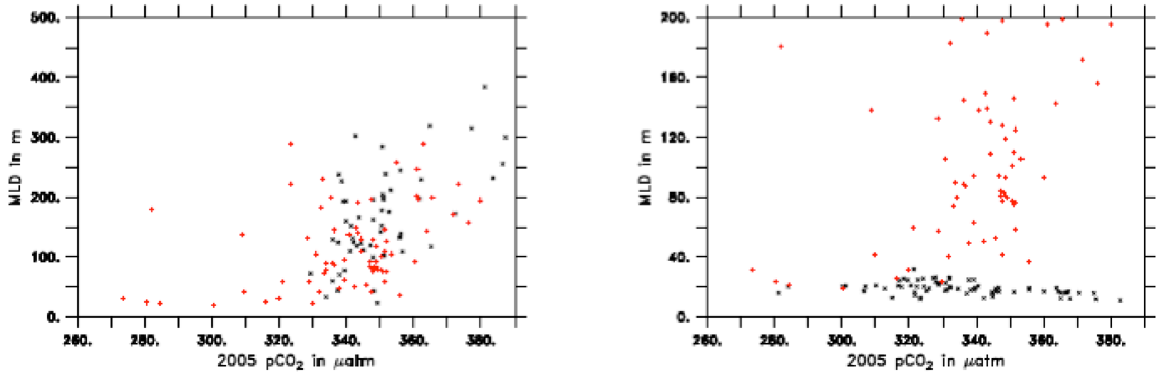


Figure 2.5. Random Forest analyses: (A-C) Variable importance plots for RF_GLOBAL, RF_LOCAL, and RF_CLIM models, respectively. A large increase in percent mean squared error (% inc MSE) means a variable is a better predictor of coccolithophore occurrence). Boxes highlight the ranking of CO_2 parameters within each model. (D-F) Partial dependence plots for CO_2 parameters in RF_GLOBAL, RF_LOCAL, and RF_CLIM models, respectively. (G) Partial dependence plot for Atlantic Multidecadal Oscillation (AMO) based on the probability of coccolithophore occurrence in each of the random forest models. This is the marginal effect of

the predictor on coccolithophore probability. Global_pCO_2= atmospheric pCO_2 based on Mauna Loa records, delta_pCO_2=climatological ΔpCO_2 (Takahashi et al. 2009), local_pCO_2=estimate of local pCO_2 based on the sum of spatial and long-term trends. MEI=Multivariate ENSO Index, U and Vcomp= zonal and meridional wind components, SST=sea-surface-temperature, tintinnid_pres= tintinnid occurrence.



(A) DJF, MAM pCO_2 vs NO_3 (B) JJA, SON pCO_2 vs NO_3



(C) DJF, MAM pCO_2 vs MLD (D) JJA, SON pCO_2 vs MLD

Figure 2.6. Local pCO_2 regional partial dependence plots. Based on the regions presented in Figure 2.1 and Figure 2.2, we built regional RF models to produce partial dependence plots for local_pCO_2, see below. These show how each region experienced different ranges of local CO_2 and different sizes of response in coccolithophore probability of occurrence. All regions show an increase in coccolithophore probability of occurrence between 300-400 ppm. The largest response was found in the Southwestern region (SW), where local CO_2 can reach 450 ppm and coccolithophore probability rose to 25%.

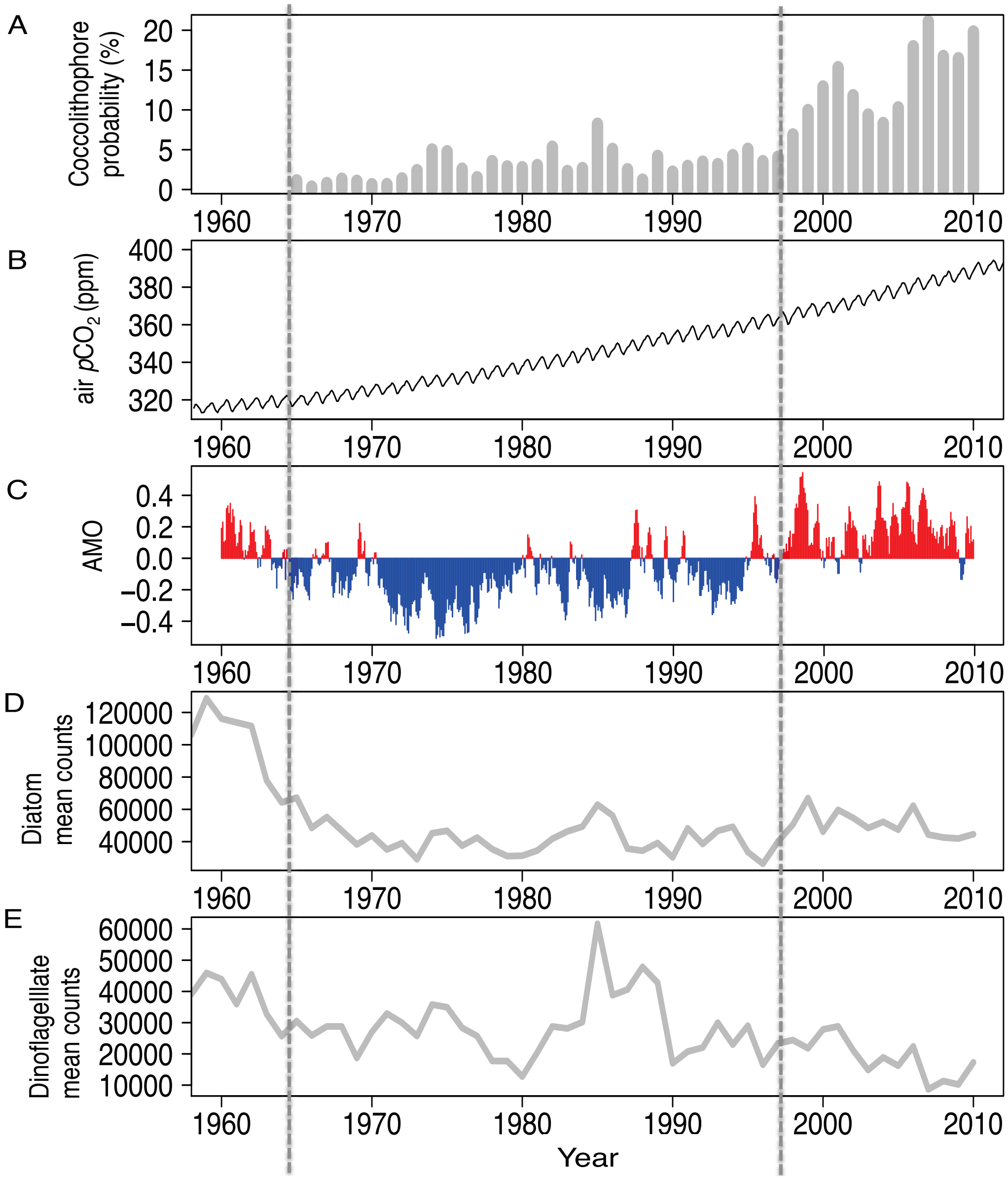


Figure 2.7. Long-term trends of: (A) annual basin-averaged coccolithophore probability in CPR samples (=sum of samples with coccolithophore records per year /total number of samples per year), (B) global atmospheric CO_2 measured from Mauna Loa, C) Atlantic Multidecadal Oscillation (AMO), (D-E) annual mean basin-averaged diatom and dinoflagellate counts in CPR samples per year. Vertical lines marking years 1965, 1997 are included for reference.

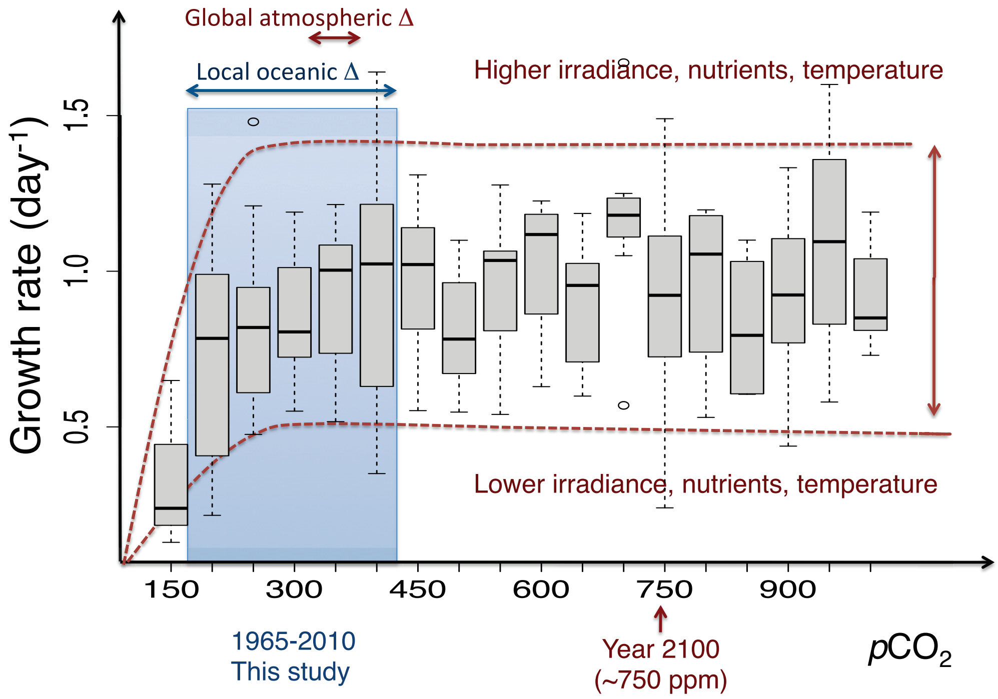


Figure 2.8. Relationship between CO_2 and coccolithophore growth rates based on 41 experiments from 16 publications and 4 species (see Table 2-1). Results are binned in 50ppm intervals, with minimum, quartiles, median, and maximum per interval used to construct box-and-whisker plots. Discontinuous lines represent schematic boundaries of this relationship depending on irradiance, nutrient, and temperature levels. Blue box = range of local oceanic pCO2 values observed across the North Atlantic during this time period, red arrow = global atmospheric equivalent.

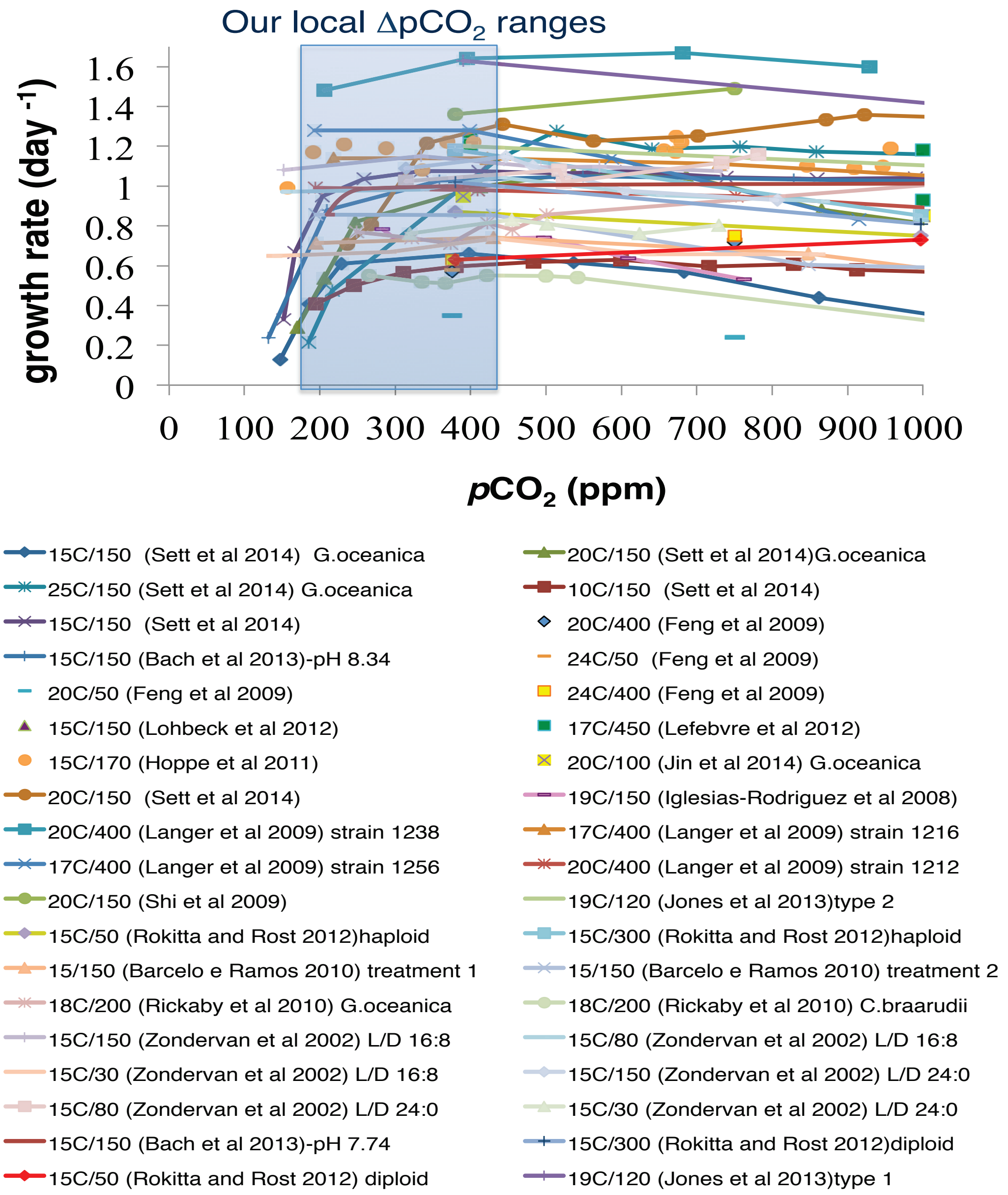


Figure 2.9. Relationship between CO_2 and coccolithophore growth rates. A compilation of published laboratory results found in 41 experiments from 16 publications. For each study, authors and experimental treatment details (temperature (in °C), light (in µmol m^{-2} s^{-1}) regimes, and species when it is not *E. huxleyi*) are noted in the legend. See Table 2-1 and discussion in section 6.1.2.

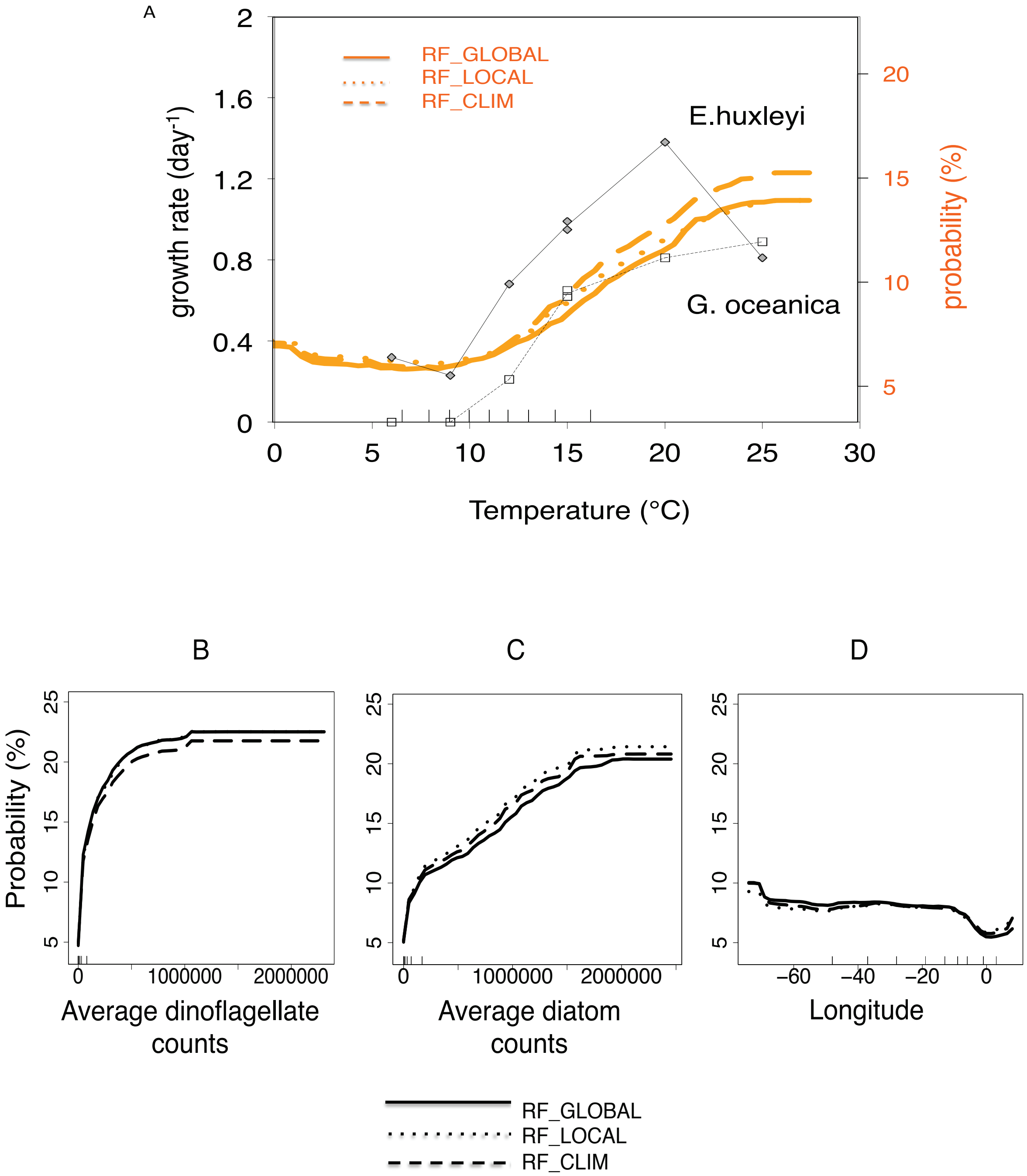


Figure 2.10. Additional Random Forest partial dependence plots. Each panel shows the probability of coccolithophore occurrence according to a given variable for each of the random forest models (see legend). (A) Sea-surface-temperature (SST) dependence. The left y-axis corresponds to the effect of temperature on laboratory growth rates of two dominant bloom-forming coccolithophore species: Gephyrocapsa oceanica and Emiliania huxleyi, based on

Buitenhuis et al., 2008 (18). Secondary y-axis (right) corresponds to the partial dependence plot for SST, showing an increase in coccolithophore probability with increasing temperature and an inflection point at 8-10oC. The different orange lines show the result for each Random Forest model (RF_GLOBAL, RF_LOCAL, RF_CLIM). (B-D) Partial dependence plot for the probability of occurrence of coccolithophores versus: (B) abundance of dinoflagellates, (C) abundance of diatoms, and (D) longitude.

Table 2-1. Details of studies compared.

	study	species	CO_2 ranges (ppm)	temp (^oC)	irradiance (mmol photons m^{-2} s^{-1})	specific treatment
1	Bach et al 2013	*Emiliania huxleyi*	131-1239	15	150	pH 8.34
2	Bach et al 2013	*Emiliania huxleyi*	209-3617	15	150	pH 7.74
3	Barcelo e Ramos 2010	*Emiliania huxleyi*	195-1486	15	150	counts at 0, 24h
4	Barcelo e Ramos 2010	*Emiliania huxleyi*	195-1486	15	150	counts at 2, 26hr
5	Feng et al 2009	*Emiliania huxleyi*	375, 750	20	50	low light, low temp
6	Feng et al 2009	*Emiliania huxleyi*	375, 750	24	50	low light, high temp
7	Feng et al 2009	*Emiliania huxleyi*	375, 750	20	400	high light, low temp
8	Feng et al 2009	*Emiliania huxleyi*	375, 750	24	400	high light, high temp
9	Hoppe et al 2011	*Emiliania huxleyi*	157-1206	15	170	DIC vs. TA, open vs. close system
10	Iglesias-Rodriguez et al 2008	*Emiliania huxleyi*	282-762	19	150	CO2 gradient
11	Jin et al 2014	*Gephyrocapsa oceanica*	390, 1000	20	100	CO_2 gradient
12	Jones et al 2013	*Emiliania huxleyi*	390-1340	19	120	type 1
13	Jones et al 2013	*Emiliania huxleyi*	390-1340	19	120	type 2
14	Langer et al 2006	*Coccolithus pelagicus*	100-900	17	350	results not shown
15	Langer et al 2006	*Calcidiscus leptoporus*	100-900	20	350	results not shown
16	Langer et al 2009	*Emiliania huxleyi*	206-929	20	400	strain RCC1238
17	Langer et al 2009	*Emiliania huxleyi*	218-1201	17	400	strain RCC1216
18	Langer et al 2009	*Emiliania huxleyi*	193-915	17	400	strain RCC1256
19	Langer et al 2009	*Emiliania huxleyi*	194-1096	20	400	strain RCC1212
20	Lefebvre et al 2012	*Emiliania huxleyi*	400, 1000	17	450	NH_4+NO_3
21	Lefebvre et al 2012	*Emiliania huxleyi*	400, 1000	17	450	NO_3
22	Lohbeck et al 2012	*Emiliania huxleyi*	400, 1100, 2200	15	150	CO_2 gradient
23	Rickaby et al 2010	*Gephyrocapsa oceanica*	250-2000	18	200	nutrient replete, high omega

24	Rickaby et al 2010	*Coccolithus braarudii*	260-2000	18	200	nutrient replete, high omega
25	Rokitta and Rost 2012	*Emiliania huxleyi*	380, 997	15	50	diploid
26	Rokitta and Rost 2012	*Emiliania huxleyi*	380, 997	15	50	haploid
27	Rokitta and Rost 2012	*Emiliania huxleyi*	380, 997	15	300	diploid
28	Rokitta and Rost 2012	*Emiliania huxleyi*	380, 997	15	300	haploid
29	Sett et al 2014	*Emiliania huxleyi*	194-4127	10	150	low temp
30	Sett et al 2014	*Emiliania huxleyi*	151-5521	15	150	intermediate temp
31	Sett et al 2014	*Emiliania huxleyi*	236-6039	20	150	high temp
32	Sett et al 2014	*Gephyrocapsa oceanica*	148-2345	15	150	low temp
33	Sett et al 2014	*Gephyrocapsa oceanica*	170-2145	20	150	intermediate temp
34	Sett et al 2014	*Gephyrocapsa oceanica*	185-3504	25	150	high temp
35	Shi et al 2009	*Emiliania huxleyi*	380, 750	20	150	nutrient replete
36	Zondervan et al 2002	*Emiliania huxleyi*	152-865	15	150	nutrient replete, CO_2 gradient
37	Zondervan et al 2002	*Emiliania huxleyi*	152-865	15	80	nutrient replete, CO_2 gradient
38	Zondervan et al 2002	*Emiliania huxleyi*	152-865	15	30	nutrient replete, CO_2 gradient
39	Zondervan et al 2002	*Emiliania huxleyi*	152-865	15	150	continuous light
40	Zondervan et al 2002	*Emiliania huxleyi*	152-865	15	80	continuous light
41	Zondervan et al 2002	*Emiliania huxleyi*	152-865	15	30	continuous light

3 INTERDECADAL *TRICHODESMIUM* VARIABILITY IN COLD NORTH ATLANTIC WATERS

3.1 Abstract

Studies of the nitrogen cycle in the ocean assume that the distribution of the marine diazotroph, *Trichodesmium*, is restricted to warm, tropical and sub-tropical oligotrophic waters. Here we show evidence that *Trichodesmium* are widely distributed in the North Atlantic. We report an approximately five-fold increase during the 1980s and 1990s in *Trichodesmium* presence near the British Isles. We propose that this can be explained by an increase in the Saharan dust source starting in the 1980s, coupled with changes in North Atlantic winds that opened a pathway for dust transport. Our results show that *Trichodesmium* can grow in temperatures below 20° C, and challenge assumptions about their latitudinal distribution. Our results show a need to re-evaluate the N_2 fixation capability of *Trichodesmium* strains found in extra-tropical regions. The temperature limitation bias underestimates *Trichodesmium* distribution ranges, which has important implications for the global N budget.

3.2 Introduction

Diazotrophy is a crucial process balancing the atmosphere and biosphere nitrogen reservoirs. *Trichodesmium* is the most studied and perhaps most quantitatively significant marine diazotroph because it is responsible for half of the global marine N_2 fixation, 100-200 Tg N/year (Karl et al. 2002, Galloway et al. 2004). Extrapolations from direct measurements of *Trichodesmium* N_2 fixation rates in the Atlantic Ocean suggest that the new N input through diazotrophy is comparable to that of upwelled deep-water nitrate (Capone et al. 2005).

There are a number of barriers to quantifying the global role of *Trichodesmium* in the nitrogen cycle. One is the lack of comprehensive global long-term information on *Trichodesmium* distribution (Luo et al. 2012) and the scarcity of nitrogen fixation measurements outside of blooms (Needoba et al. 2007). Attempts to estimate global *Trichodesmium* distribution, either with in-situ observations (Luo et al. 2014), or through bio-optical models and satellite imagery (Borstad et al. 1992, Subramaniam et al. 1999, Subramaniam et al. 2002, Westberry et al. 2005, Westberry & Siegel 2006) may be hampered by the temperature limitation assumption, whereby it is assumed that *Trichodesmium* is mostly limited to tropical regions. For example, Westberry & Siegel (2006) produced the first global map of *Trichodesmium* occurrence, but deliberately limited it to latitudes between 45° N and 45° S, and used a sea surface temperature (SST) mask that excluded data from regions with SST $<23.5^{o}$ C.

Trichodesmium colonies have been reported in cold waters and high latitudes (Lipschultz & Owens 1996). However, with laboratory studies concluding that *Trichodesmium* is unable to fix N_2 under low temperature regimes (Breitbarth et al. 2007, Breitbarth et al. 2008), it was assumed that those high-latitude findings were anecdotal and derived from colonies drifting from warmer regions. Consequently, extrapolations of global nitrogen fixation rates have been exclusively based on *Trichodesmium* abundances in warm temperature ranges.

There are a number of reasons why *Trichodesmium* distribution is assumed to be restricted to tropical and subtropical latitudes. One view is that nitrate deficiency favors diazotrophs by limiting growth of faster-growing competitors (Tyrrell 1999). Other limiting factors include phosphorus availability (Sanudo-Wilhelmy et al. 2001, Tovar-Sanchez et al. 2006, Chen et al. 2011a) and, more recently, dissolved oxygen concentrations, as oxygen is a nitrogenase inhibitor (Staal et al. 2003, Staal et al. 2007, Stal 2009, Luo et al. 2014). Therefore, warm tropical and subtropical waters with low nitrate, some remnant phosphate, and lower oxygen would potentially be optimum locations for *Trichodesmium* growth.

Iron is a critical element for phytoplankton growth and is a controlling factor in *Trichodesmium* growth and nitrogen fixation in the Atlantic. This “iron-centric hypothesis” is mostly driven by observations of African dust iron enrichment in the tropical Atlantic (Weber & Deutsch 2014). Sources of iron in the surface ocean are limited to upwelling from the deep ocean, coastal runoff and aeolian deposition. In the North Atlantic, African dust plays an important role in iron supply. There is a considerable amount of work on Saharan dust and transport across the Atlantic but, to our knowledge, no previous study has looked at its effects on *Trichodesmium* population trends in colder latitudes.

Here we show that *Trichodesmium* is not limited to tropical and subtropical regions, discuss factors limiting *Trichodesmium* growth at high latitudes, and briefly propose implications for nitrogen fixation and carbon export. In order to show that *Trichodesmium* populations exist at higher latitudes, we will describe a case study in the North Atlantic based on in-situ phytoplankton observations from the Continuous Plankton Recorder (CPR) in relationship to African dust export events in the North Atlantic between 1960-2010. We hypothesize that large episodic increases in *Trichodesmium* abundances are related to African dust deposition. We then consider the implications of these results for high-latitude nitrogen fixation.

3.3 Methods

We used data from the Continuous Plankton Recorder (CPR) - a mechanical filtration system trawled by ships-of-opportunity that collects near surface plankton samples. The data record includes more than 200,000 samples and over 400 taxa. The survey started in the 1930’s, and a consistent methodology was established in 1958. Each sample consists of plankton filtered from ~ $3m^3$ of water that are analyzed and identified to the species level wherever possible at the Sir Alister Hardy Foundation for Ocean Sciences (SAHFOS). The CPR methodology does not record absolute abundances but has been demonstrated to successfully reflect relative changes in abundances (Richardson et al. 2006, Irwin et al. 2012, Barton et al. 2013), which is the goal of this study. Because some very high counts in certain samples might be driving regionally-averaged abundances, we focused on the probability of presence of *Trichodesmium* (fraction of samples in a given time period containing *Trichodesmium*) in CPR samples expressed as a percentage. CPR data are more abundant in the central and eastern side of the North Atlantic due to the location of SAHFOS in Plymouth, United Kingdom, and to the use of ships-of-opportunity. More information on the CPR and methods can be found at www.sahfos.ac.uk. Here we studied the *Trichodesmium* record from 1960-2010, and the area between 38^o N-65^o N in the North Atlantic. Due to the reasons stated above, we will discuss basin-scale results, but will focus on a smaller area in the Bay of Biscay (corresponding to 45-55^o N and 0-10^o W). To estimate interannual trends we averaged *Trichodesmium* trichome occurrence (fraction of samples in a given year containing *Trichodesmium*) for the Bay of Biscay and for the rest of the basin. As shown in Figure 3.1a, this region has no gaps in coverage over the entire time period (in contrast to other parts of the basin, Figure 3.2). The averaged abundance (Figure 3.1b) does show a large peak in 1988, but this is embedded within a longer time period of high occurrence (Figure 3.1c).

To examine seasonal variability, we also mapped *Trichodesmium* samples per month in the entire basin and calculated the mean *Trichodesmium* abundance and percent occurrence per year and month in the Bay of Biscay, as well as the abundance of diatoms and dinoflagellates for comparison.

To evaluate frequency distribution of *Trichodesmium* as a function of SST, we extracted matching in situ temperature measurements for each CPR sample from the International Comprehensive Ocean Atmosphere DataSet (ICOADS(Woodruff et al. 2011)); these are monthly 1-degree measurements.

We do not have a suitable time series for iron deposition over the North Atlantic, as levels of dust in this area are often below the detection limit for standard satellite products (Mahowald & Dufresne 2004). However, we can examine connections with physical variables from both direct observations and reanalysis. To investigate sources and transport mechanism of African dust we used the Sahel Precipitation Anomaly Index (Janowiak 1988), Barbados dust time series (1965-2008), and NCEP reanalysis data (http://www.esrl.noaa.gov/psd/data/reanalysis/reanalysis.shtml).

Collocated measurements of *Trichodesmium* and macronutrients are also lacking over this time period. We estimate the potential for changes in climate to force changes in nutrients using an ocean general circulation model with embedded biogeochemical cycling forced by atmospheric reanalysis (Gnanadesikan et al. 2011). The model we used is the ocean component of the GFDL CM2.1 model (Gnanadesikan et al. 2006), with the Tracers of Ocean Productivity with Allometric Zooplankton (TOPAZ) biogeochemical model (Dunne et al. 2010).

3.4 Results and discussion

3.4.1 When and where are trichomes found in the CPR Data?

A synoptic view of relative abundance of *Trichodesmium* in North Atlantic waters from 1960-2010 (Figure 3.3**Error! Reference source not found.**) shows that *Trichodesmium* are not limited to tropical and subtropical waters. In the North Atlantic, colonies are found year-round at latitudes 38°-65° N (Figure 3.4), which are the latitudinal limits of this study. We divided the dataset into four periods (1960-1967, 1971-1980, 1981-1997 and 2000-2009) based on both *Trichodesmium* abundance and Sahelian precipitation (explained in more detail below). The period from 1981-1999 shows the largest abundances both in the Gulf Stream and in the Bay of Biscay. An analysis of the Bay of Biscay (Figure 3.5) shows that blooms occur outside the traditional phytoplankton growing season, either early spring (March-April) or late fall (October-December) and that there is a generalized increase in the 1980s-1990's period. These trends are however decoupled from the patterns seen in diatoms and dinoflagellates.

It is often assumed that growth and N_2 fixation of *Trichodesmium* is limited to temperature ranges of 20-34 ^oC, with optimal temperatures being 24-30 ^oC depending on species and growth conditions (Breitbarth et al. 2007, Chappell & Webb 2010, Chappell et al. 2012). Thus, presence of *Trichodesmium* outside the tropics has been explained by ocean current drift transport. For example, (Lipschultz & Owens 1996) noted the presence of *Trichodesmium* in CPR data between 1958-1968, but assuming that temperatures were too cold for N_2 fixation and growth, explained their presence by drift related to the Gulf Stream. Isotherms of average temperature superimposed over all CPR *Trichodesmium* observations since 1960 show persistent presence of *Trichodesmium* in waters below 20^oC (**Error! Reference source not found.**). Additionally, the frequency distribution of *Trichodesmium* abundance vs. SST shows temperature ranges between $0\text{-}30^oC$ (Figure 3.6 a). For the Bay of Biscay, most samples were found between $8\text{-}18^oC$ and peak numbers corresponded to $\sim 13^oC$ (Figure 3.6 b). Our findings therefore challenge this temperature limitation assumption.

While some of the *Trichodesmium* findings in the western side of the basin could be related to drift, the CPR records show that *Trichodesmium* is present all across the basin, even in regions many hundreds of kilometers from the North Atlantic Current. Using an average geostrophic flow in the North Atlantic Current of 10 cm/sec, populations found around the British Isles and as far north as Scandinavia would have to have survived for more than a year. Drifting colonies are not likely to survive to such a long journey unless they continue to grow during that time. Moreover, such a pathway for *Trichodesmium* would not explain its annual phenology, with large increases over the course of a month and occurring at significant distances from the North Atlantic Current.

3.4.2 Possible reasons for inter-decadal variations in *Trichodesmium* concentrations

3.4.2.1 Iron and dust

Trichodesmium requires iron. In the open ocean this can be provided by atmospheric dust. Dust events in Europe were described by Homer and Virgil thousands of years ago (Stuntz & Free 1911). Several studies have documented the dust events over Europe during the last century (Stuut et al. 2009) and references therein). Back-trajectory models and satellite imagery (e.g. (Prospero et al. 1970, Prospero et al. 2002) have identified two main dust sources: the Bodele depression -former Lake Chad- and the sand seas (Stuut et al. 2009). Bodele is the major source of Saharan dust (Prospero et al. 2002) and most of it is carried west towards the Atlantic and Caribbean. However, (d'Almeida 1986) estimated that 12% of the total Saharan dust is exported North accounting for about 80-120 million tons per year. Analysis of the Total Ozone Mapping Spectrometer (TOMS) satellite data show dust penetrating the troposphere over the Mediterranean Sea between May and September (Middleton & Goudie 2001), most of which is deposited in southern European countries through wet deposition (Stuut et al. 2009). Occasionally, however, some of it is carried further north to the British Isles. Within the 20th century, dust falls near the British Isles were extremely infrequent until the late 1970's. Prior to 1977 there are only four reports of dust rain events: 1902, 1903, 1930 and 1968 (Burt 1991).

However, twenty events were reported for the 1980s, primarily in the fall (September-October-November) (Burt 1991) and, more recently, Saharan dust falls on Britain were reported in 2003, 2004, 2005 (Goudie & Middleton 2006). The typical trajectory for these dust events to Britain was through the Bay of Biscay in mid tropospheric winds (Goudie & Middleton 2001). This dust pathway corresponds with the region that sees much higher *Trichodesmium* abundance during the 1980s and 1990s.

One obvious reason why dust delivery to the Bay of Biscay may have increased is a change at the dust source. Three main areas: the Western Sahara, the Moroccan Atlas and central Algeria have been identified as sources of transport to the British Isles (Tullett 1978, Tullett 1980, Wheeler 1986). The Sahel Precipitation Anomaly Index is based on the longest record of high quality precipitation measurements in this area (starting in 1900) and it is often used as a proxy for Western Africa precipitation anomalies. This time-series shows a long-term drought starting in 1970 that could have increased atmospheric dust loading. By combining *Trichodesmium* abundance and precipitation data from the Sahel (Figure 3.7) we identify four periods: P1) wet and low *Trichodesmium* abundances, P2) dry and low *Trichodesmium* abundances, P3) dry and high *Trichodesmium* abundances, P4) variable precipitation and low *Trichodesmium* abundances. Variability in dust load at source is not enough to explain the increase in *Trichodesmium* in the Bay of Biscay, requiring further evaluation of transport mechanisms of African dust into the North Atlantic. The longest ongoing record of dust variability observations is that of Barbados (1965-present). This time-series shows a four fold increase in dustiness in the 1980’s with respect to the 1960’s and seasonal maxima during the summer months (Prospero 2015). However, in contrast to Barbados, the Bay of Biscay is not directly downstream from the Sahel/Sahara, and maxima in *Trichodesmium* do not occur in the summer. This means that dust availability could be modulated by changes in north-south transport that might not be reflected in the Barbados dataset. In order to examine whether dust transportation mechanisms changed, we used the NCEP reanalysis data. We focused on the fall months (October, November, December =OND) because that is when we observed greater *Trichodesmium* presence. The left panels on Figure 3.8 show individual composite plots of wind stress and geopotential height at 925-850 hPa for each of the four distinct periods (P1: 1960-1967, P2: 1971-1980, P3: 1981-1997, P4: 2000-2009) minus the average long-term mean (1960-2009). CPR *Trichodesmium* abundances are displayed on the right, showing increased abundances during period 3. The data show a shift towards southerly winds (>4m/s) (Figure 3.9) during the time when we observed an increase in *Trichodesmium* abundance. Frequency plots of daily meridional wind support the results shown by the monthly means, with the period of high *Trichodesmium* showing fewer days with southward winds and more days with strong northward winds. The monthly wind results highlight the opening of a pathway favorable for dust transport, whereas the daily probability distribution functions suggest that there are strong northward wind events that could be responsible for dust transport (and production). Our results suggest an episodic conduit for African dust via meridional winds in period 3 that would transport iron-rich dust to higher latitudes. Additionally, the data show a shift to northerly wind during period 2 (drought, low *Trichodesmium*) that blocked the transport of African dust to the North Atlantic. This suggests that changes in wind patterns either blocked or enhanced the northward transportation of iron-rich dust, providing a plausible mechanism for iron deposition that explains the large episodic increases in *Trichodesmium* population.

Given that we do not have direct evidence of these iron fertilization events and that the dust pathway is not currently represented in numerical earth system models, it is worth asking if there are alternative sources of iron supply that might show similar variability. For example, African dust is not the only possible source of iron to the North Atlantic. One possible source is Icelandic proglacial dust storms (Prospero et al. 2012). However the timing of these dust storms in spring and early summer, notably April to June (Prospero et al. 2012, Dagsson-Waldhauserova et al. 2014) does not support this hypothesis. Moreover, according to Dagsson-Waldhauserova, the 1960s and 2000s were the most active decades for proglacial dust storms, undermining the hypothesis that Icelandic dust events were the driver for *Trichodesmium* variability. One might also think that upwelling of iron would be a plausible source of variability. However, upwelling would be expected to bring other nutrients to the surface as well, benefiting other phytoplankton species. That *Trichodesmium* increases are decoupled from trends in other phytoplankton groups counted in the CPR data (Figure 4), suggests that variation in upwelled iron is not a probable factor. In addition, the prevailing wind directions in figure 7 would favor upwelling along the coast during P1 but not during P3, discarding the idea of an oceanic iron source. Another hypothesis would be anthropogenic atmospheric nitrogen deposition (Jickells et al. 2005, Duce et al. 2008, Kim et al. 2014), as described by Kim et al in Korea or iron from combustion sources (Luo et al. 2008) but, again, the timing of *Trichodesmium* blooms between 1980s-1990's and the decoupling from other phytoplankton groups suggest otherwise.

3.4.2.2 Macronutrients

Anomalies in macronutrients could have also potentially driven the increase in *Trichodesmium* abundances. In absence of other forms of nitrogen, *Trichodesmium* has the ability to fix dissolved N_2. Since this process requires large amounts of iron and energy, it is only cost-effective under nitrogen-limited conditions Thus, if bioavailable nitrogen were anomalously low at the end of the growing season throughout Period 3 but high at other periods of time, this could explain the *Trichodesmium* abundance time series. Because we cannot test this with in-situ data, we used GFDL CORE-forced simulations to hindcast nitrogen limitation in the North Atlantic between October and December 1960-2004. Nitrogen limitation in this code is defined using a Michaelis-Menten formulation for ammonia, which reduces the Michaelis-Menten limitation for nitrate following (Frost & Franzen 1992). The limitation factor for nitrogen *(N_{limit})* is then:

$$N_{limit} = \min\left(\frac{[NO_3]}{K_{NO3}+[NO_3]} * \left(1+\frac{[\mathrm{NH_4}]}{\mathrm{K_{NH4}}}\right) + \frac{[\mathrm{NH_4}]}{\mathrm{K_{NH4}}+[NH_4]}, 1\right) \quad \text{(Eq. 1)}$$

Where $[NO_3]$ and $[NH_4]$ the concentrations of nitrogen and ammonia, respectively and K_{NO3} and K_{NH4} are the associated half-saturation constants- set to 3.0 mM and 0.6 mM respectively for large phytoplankton (Knapp et al. 2012).

The average results for 1981-1997 suggest that the Bay of Biscay is a region where nitrogen limitation is stronger than the zonal average between October-December (blue region in Figure 9a) and that this limitation is more intense from 1981-1997 than from 1960-1980 (blue region in Fig. 9b). However, the model predicts that nitrogen limitation continued to be more intense during the period from 1998-2004 when *Trichodesmium* was less abundant. A full time series model-predicted nitrogen limitation over the Bay of Biscay region during October-December (Figure 3.10 D) reveals a number of abnormally intense nitrogen limitation periods over the time series, but these do not correspond in any straightforward way to the time series in Figure 3.7c. Assuming the model has some skill in predicting nutrients (in particular events driven by anomalously windy or cold periods) they do not support the idea that macronutrients alone can explain *Trichodesmium* abundance changes. However they suggest that *Trichodesmium* abundance could have responded to the combination of abnormally low nitrate and ammonia concentrations and enhanced iron input. If it is true that both nitrogen limitation and high iron were responsible for higher *Trichodesmium* abundance, this would also suggest that N_2 fixation was occurring during the 1980s-1990s time-period, since it is only by fixing nitrogen that *Trichodesmium* would gain competitive advantage.

3.5 Conclusions

Our results show that *Trichodesmium* is present in a temperate region in the North Atlantic with episodic population increases near the British Isles that could be explained by iron inputs from African dust. The first result challenges the widespread assumption that *Trichodesmium* are only found over a limited latitude range and that they require high temperatures. Although *Trichodesmium* is one of the best-studied diazotrophs, most experiments have been done on two warm water strains of *Trichodesmium erythraeum*- the Atlantic ISM101 and the Kuroshio NIBB1067 (LaRoche & Breitbarth 2005). It is known that *Trichodesmium* can survive at lower temperatures ($<20^{o}$C) and darkness (White et al. 2006, Breitbarth et al. 2007), which is essential for their vertical migration as individual colonies continue to actively fix at 75m depth in the subtropical North Pacific (Letelier & Karl 1998). This may explain presence in temperate and potentially in cooler waters (Bergman et al. 2013). Moreover, *Trichodesmium*-like cyanobacteria have been recently reported in Arctic waters (Diez et al. 2012), suggesting a possible cold-adapted strain or a closely related species. In view of our results, the capability of *Trichodesmium* to grow and fix N_2 in cold waters should be evaluated using strains from these regions.

We cannot prove that the *Trichodesmium* described here were fixing N_2. We only provide circumstantial evidence that blooms were occurring at times when iron deposition was potentially high, and the GFDL ocean reanalysis simulates low nitrogen levels. Resolving this question is important, as the whole-ocean nitrogen budget remains uncertain. Some studies suggest that fluxes of N to the ocean may only balance 1/3 of the fluxes of N out of the ocean (Codispoti et al. 2001, Codispoti 2007), while others suggest that it is in balance (Gruber & Sarmiento 1997, Gruber 2004, Deutsch et al. 2007). Differences between geochemical inference and direct extrapolations are partly responsible for this uncertainty. Since the initial estimates in 1997, global estimates keep rising (Karl et al. 2002) and the growing importance of recently discovered diazotrophic unicellular cyanobacteria and bacterioplankton (Zehr et al. 2001, Falcon et al. 2002, Falcon et al. 2004, Montoya et al. 2004) suggest that these numbers may keep increasing in the near future (Grosskopf et al. 2012). *Trichodesmium* nitrogen fixation in high latitudes could help to close the gap.

Fluctuations in dust observed far from source regions may be a combination of dust load at source, transport and depositional changes (Mahowald et al. 2005). These may be influenced by changes in gustiness, wind speeds or transport paths (Mahowald et al. 2005). We suggest that an increase in dust load was due to the sustained drought, and that temperature and pressure anomalies enhanced gustiness and opened a meridional pathway across the Bay of Biscay. We emphasize that the mechanism that opens this conduit is not well understood. We explored previously suggested drivers of dust transport such as NAO (Moulin et al. 1997, Chiapello et al. 2005), ENSO (Prospero & Lamb 2003), latitudinal shifts of Azores high (Riemer et al. 2006), and shifts in the position of the ITCZ (Doherty et al. 2012), but none of these seem to correlate with our *Trichodesmium* time-series. Identifying the exact mechanism that controls this dust pathway is important in order to model past events and predict future ones. At the moment, coupled dust-climate variability is not included in most Earth System Models. Our results suggest that it should be.

3.6 Future projections

The projected global warming, ocean acidification, increased stratification and shallower mixed levels will likely increase the NH_4+/NO_3-ratio in surface waters (Wyatt et al. 2010, Beman et al. 2011), favoring more N_2 fixation and thus more new production and carbon export. The increased CO_2 levels are also projected to irreversibly increase *Trichodesmium* N and C fixation rates (Barcelos e Ramos et al. 2007, Hutchins et al. 2007, Levitan et al. 2007, Kranz et al. 2009, Levitan et al. 2010), seemingly irreversibly (Hutchins et al. 2015). Hutchins et al (2007) projected that by year 2100 (750ppm) *Trichodesmium* Nitrogen fixation rates will increase by 35-65%, while CO_2 fixation will increase 15-128% relative to present day (~400ppm). This enhanced photosynthesis, growth and N_2 fixation would stimulate productivity in N-limited oligotrophic regions, providing a negative feedback to rising atmospheric CO_2 concentrations (Kranz et al. 2009).

However, such projections need to consider the large uncertainties in iron and dust projections. While observational studies suggest that global desert dust has doubled since preindustrial times (Mahowald et al. 2010) the human effect on desert dust emissions is unclear, ranging from a 10% reduction to a 60% increase (Mahowald & Luo 2003, Mahowald 2007, Mahowald et al. 2009). Some of the uncertainty is associated with the reduced number of long-term records of dust measurements and composition. Another source of uncertainty in our projections is due to new sources of atmospheric nutrients and changes in iron solubility. Iron solubility (often the fraction of Fe II versus Fe III) is used as a proxy for bioavailable iron but the process is not well understood (Mahowald et al. 2005). Solubility values vary widely in space and time from ~0.01-70% (Mahowald et al. 2009) and changes in iron solubility have impacts on ocean biogeochemistry (Krishnamurthy et al. 2009), but many models prescribe a single constant value for solubility. New anthropogenic sources of atmospheric nutrients (N, P, Fe) such as ship emissions (Wang et al. 2008), industrial combustion (Luo et al. 2008, Wang et al. 2015), and agriculture (Galloway et al. 2008) are also becoming increasingly important. An increasingly acid atmosphere from pollutants and industry will also increase iron solubility (and potentially bioavailability) during atmospheric transport. In contrast, ocean acidification decreases iron solubility in the ocean (Shi et al. 2010), further exacerbating iron limitation. Even if dust deposition were increasing, toxic amounts of additional dust components (e.g. copper) may counteract the fertilization effect of nutrient deposition (Paytan et al. 2009). As most global climate models (GCMs) use climatology to estimate iron deposition, episodic events such as the one described here will not be simulated, nor will the coupled effects of future changes.

Our findings indicate a need to review our assumptions about *Trichodesmium* biogeography and temperature limitation, improve our understanding about trajectories and fate of African dust, and to properly represent iron deposition in Earth System Models. Accurately defining the biogeography of such an important diazotroph is crucial for monitoring and projecting the consequences of a changing climate in ocean biogeochemical cycles.

3.7 **Figures**

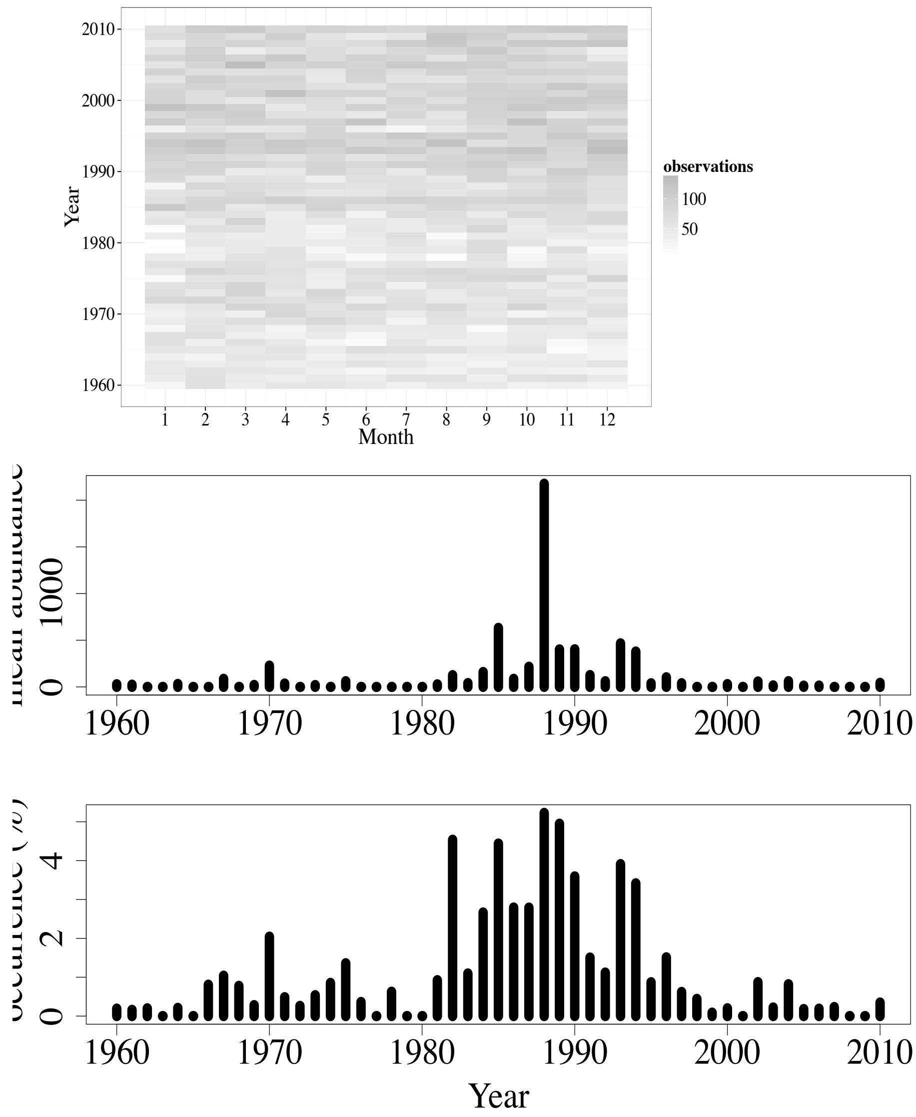


Figure 3.1. a) Total number of CPR samples per month in Bay of Biscay. b) Mean annual abundance and c) mean annual occurrence of *Trichodesmium* in the Bay of Biscay.

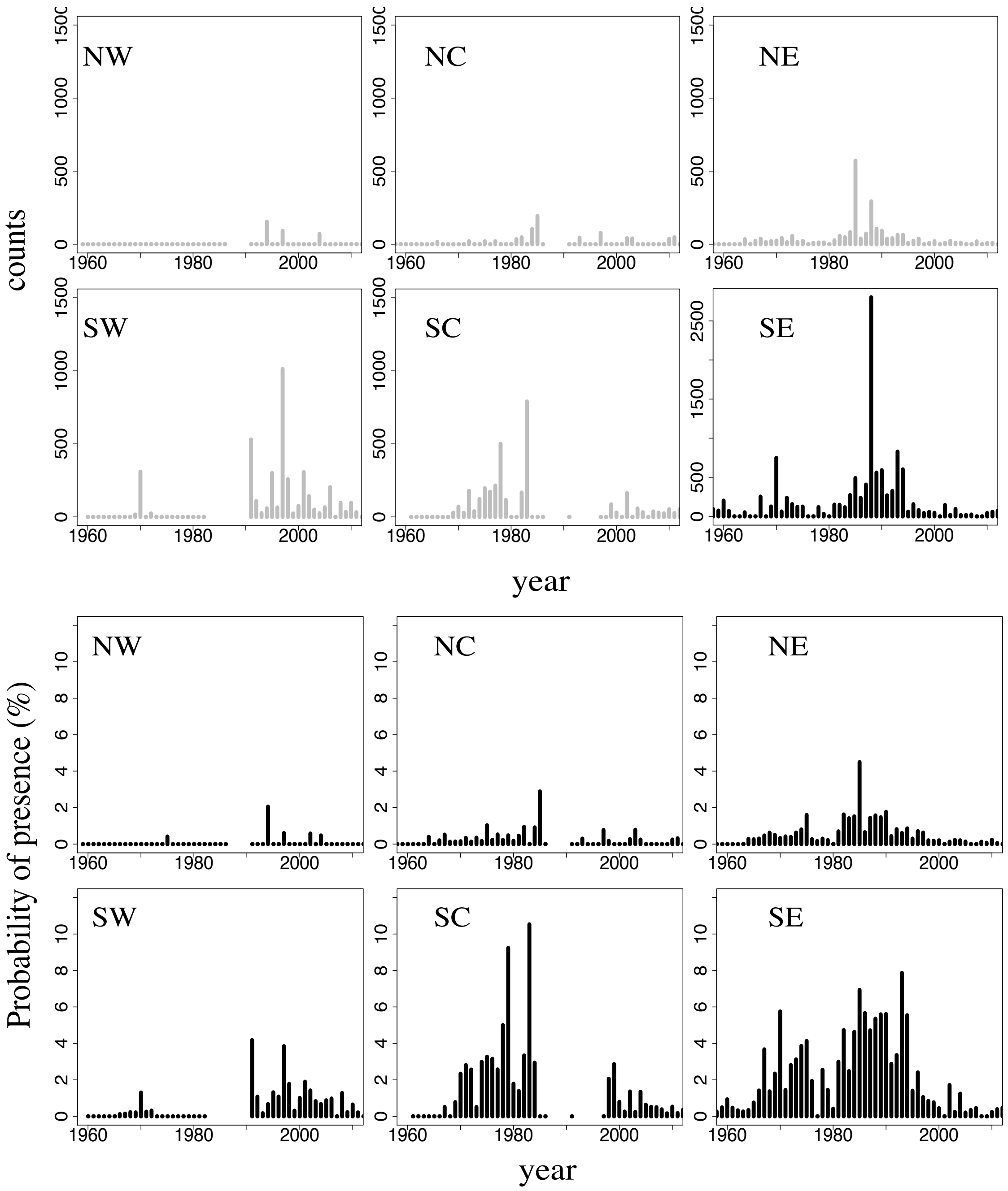


Figure 3.2. Regional *Trichodesmium* time-series per region: (NW) North-West, (NC) North-Central, (NE) North-East, (SW) South-West, (SC) South-Central, (SE) South-East. Top six panels correspond to the mean annual counts time-series, note the different y-axis for SE. Bottom six panels correspond to the mean annual probability of presence (%).

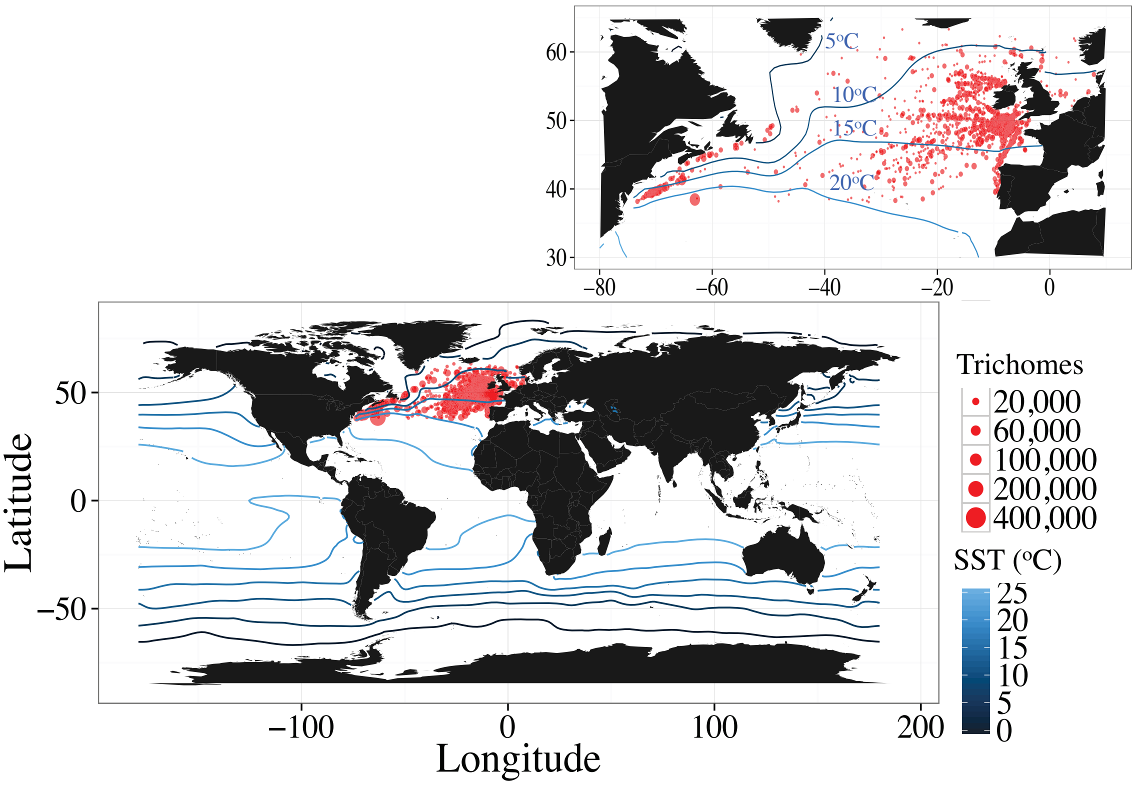


Figure 3.3. Distribution of all the CPR *Trichodesmium* observations from 1960-2010 (n=1610) and 5°C isotherms superimposed. Most samples were found at SST<20°C and as cold as 0°C. The area between Spain, France and the United Kingdom (here referred to as the Bay of Biscay) showed some of the largest concentrations.

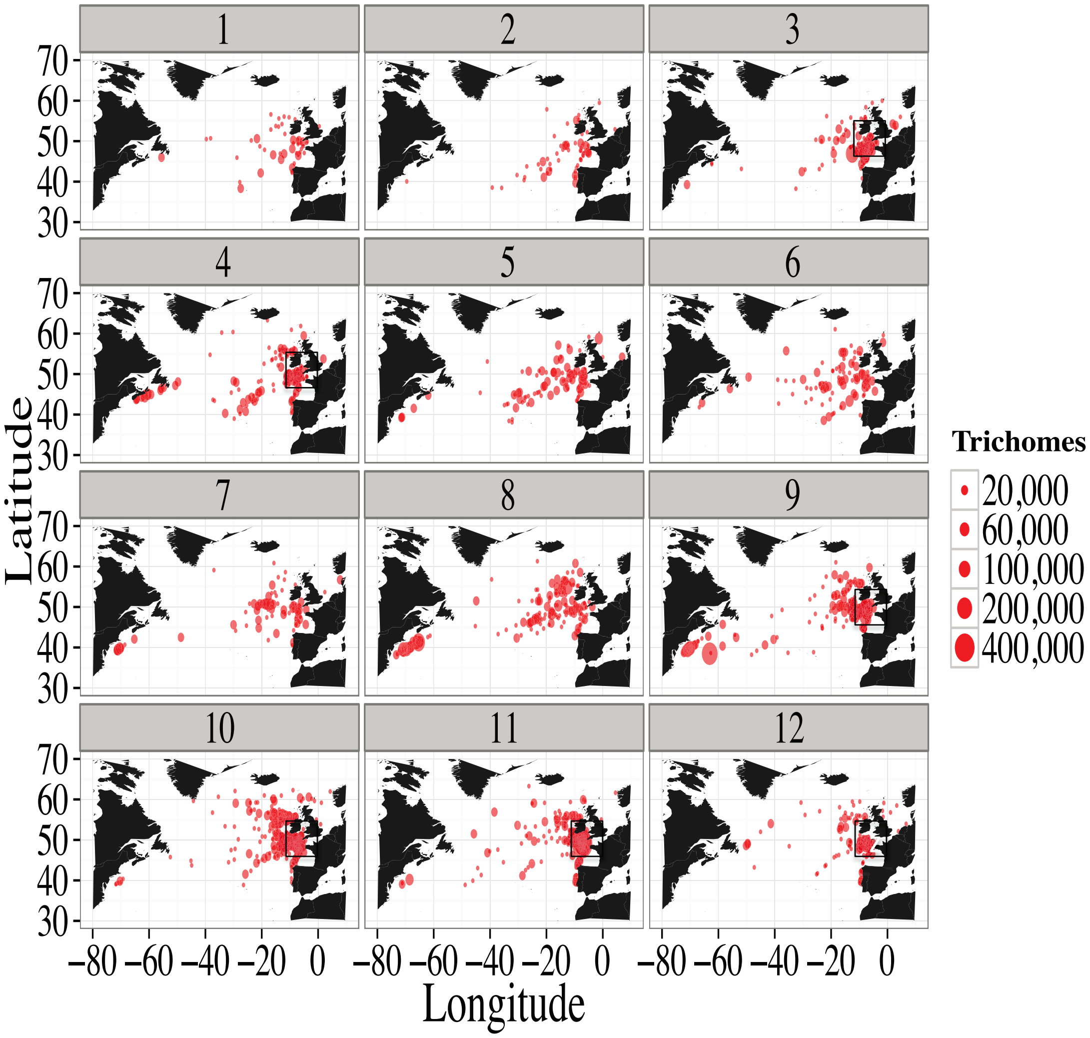


Figure 3.4. Monthly climatologies of 50 years of CPR *Trichodesmium* observations. *Trichodesmium* were found year round in CPR samples. In the Bay of Biscay (box), greatest numbers were found in March, April, September, October, and November. In the western side of the North Atlantic, greatest abundances were found in the summer months (July, August, September). Size of the marker is proportional to abundance.

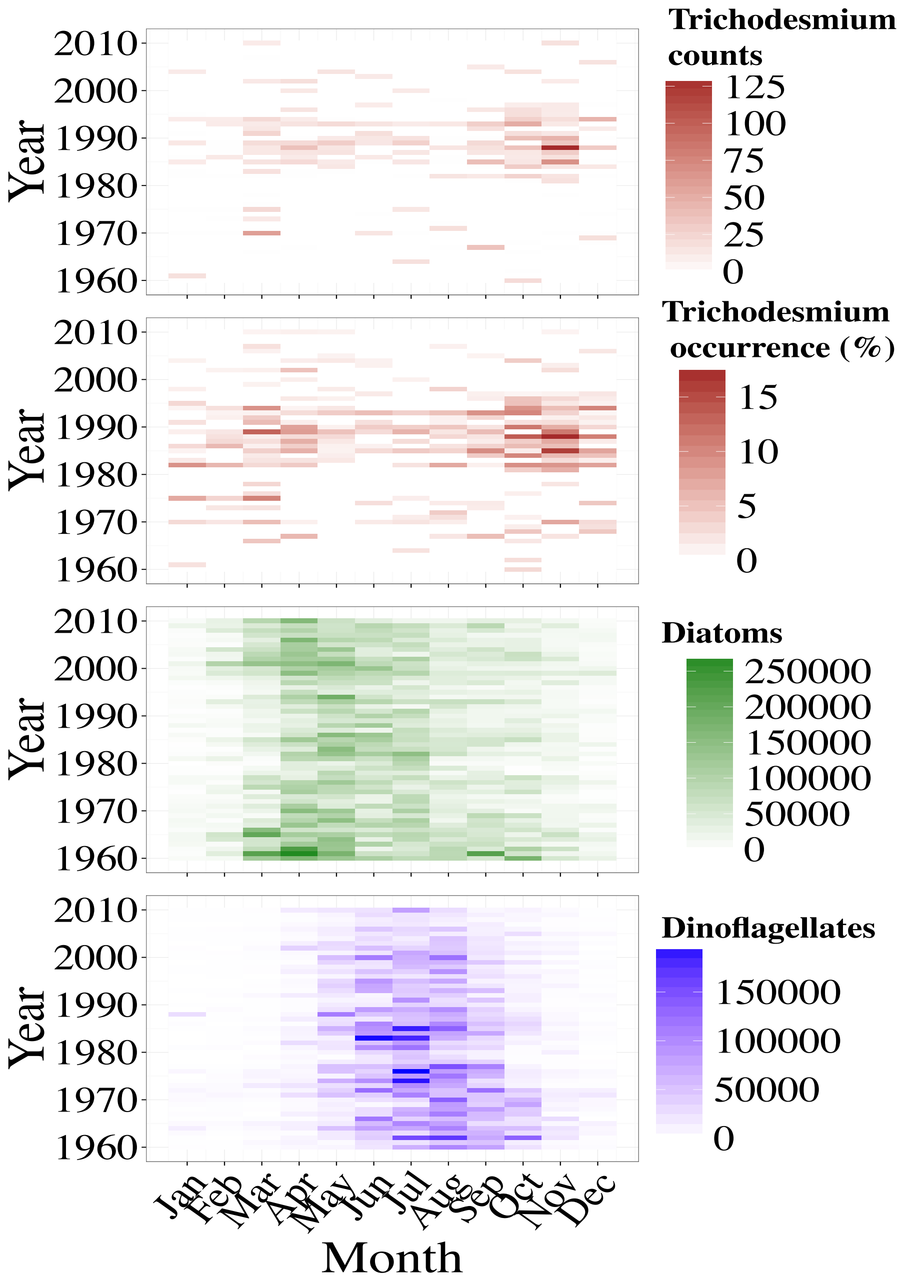


Figure 3.5: Monthly abundances of *Trichodesmium*, diatoms, and dinoflagellates and monthly *Trichodesmium* probability of presence (%) in the Bay of Biscay 1960-2010, showing that the increases in *Trichodesmium* abundances are not in phase with other phytoplankton species.

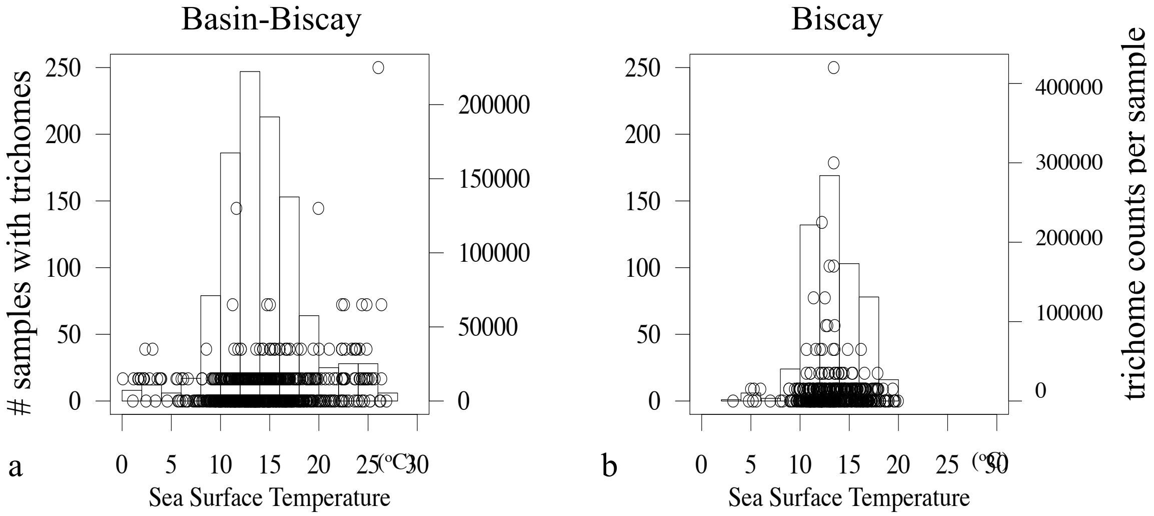


Figure 3.6. *Trichodesmium* observations as a function of Sea Surface Temperature (SST in ^{o}C): a) the entire North Atlantic basin excluding Bay of Biscay (n=1079), b) the Bay of Biscay (n=531). CPR *Trichodesmium* samples were matched up with the average ICOADS SST observations for the same month and 1-degree grid location. All samples ranged between 0-27^{o}C, with a maximum frequency at 13^{o}C. In the Bay of Biscay temperature ranged between 3-20^{o}C. Bar heights show the number of samples found within a temperature bin (left axis). Symbols show the estimated trichome count (right axis).

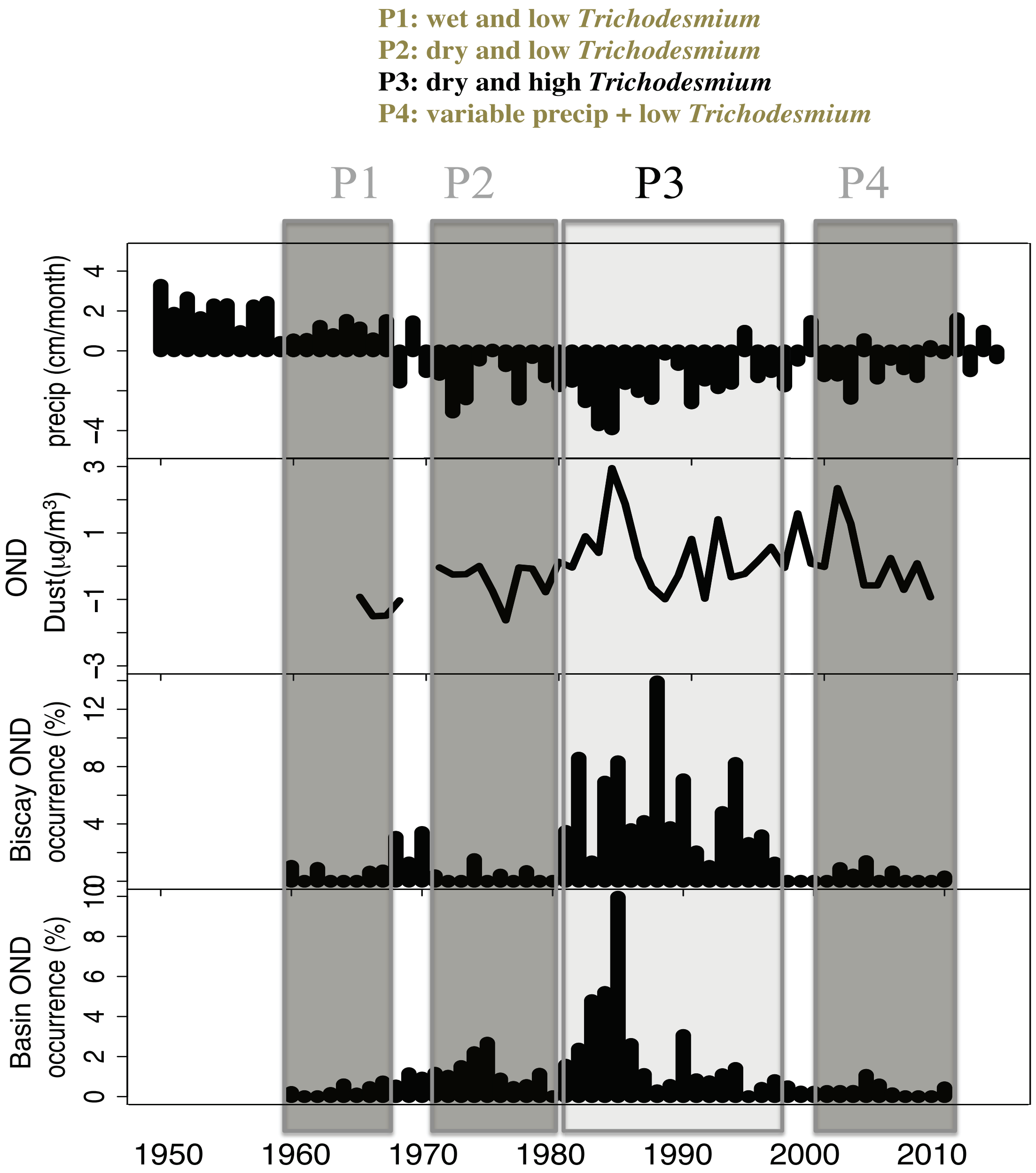


Figure 3.7. Time series of precipitation, dust and Trichodesmium records. a) Sahel Precipitation Anomaly index, b) normalized Barbados annual dust record only for October-December (1965-2008), c) Bay of Biscay *Trichodesmium* OND occurrence, d) North Atlantic basin *Trichodesmium* OND occurrence. Colored boxes show the delimitation of the 4 periods based on Sahel precipitation and *Trichodesmium* trends.

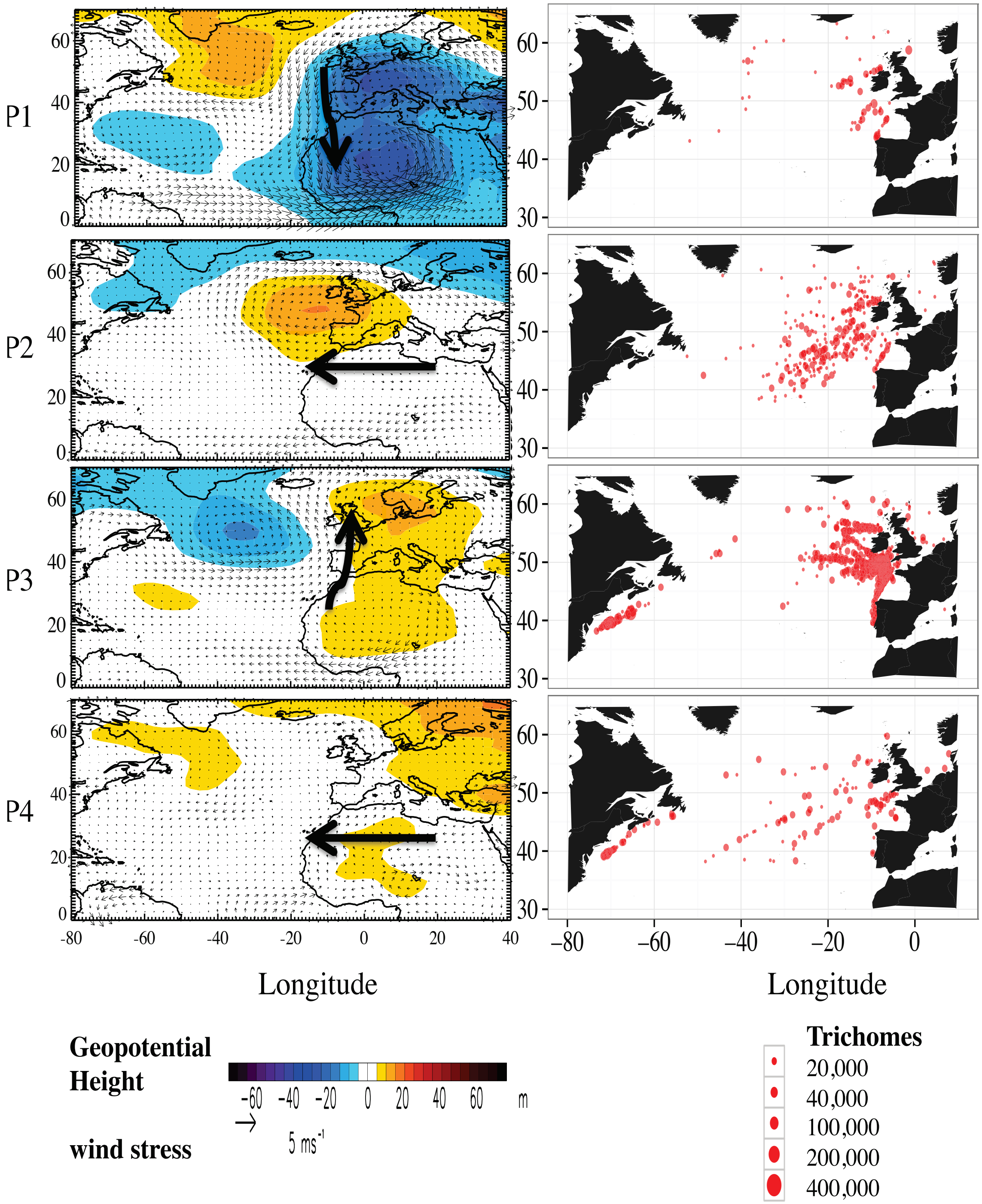


Figure 3.8. Wind and pressure anomalies per period and spatio-temporal distribution of CPR samples. Left panels: NCEP reanalysis Composite plots for total horizontal wind (arrows) and geopotential height (color bar) averaged over 925-850 hPa layer for October-December. Each panel corresponds to one of the time periods (in fig. 5) minus the long-term 50-year period

(1960-2010): P1 (1960-1967), P2 (1971-1980), P3 (1985-1997), P4 (2000-2009). Large arrows show the prevailing wind trends. Period 3 is the only one showing northward wind trends. Right panels: *Trichodesmium* counts (red dots) per period. Size of the dots is proportional to the number of trichome counts per sample. Each panel corresponds to one of the 4 periods: P1 (1960-1967), P2 (1971-1980), P3 (1981-1997), P4 (2000-2010). P3 shows the greatest *Trichodesmium* numbers and anomalous northward winds.

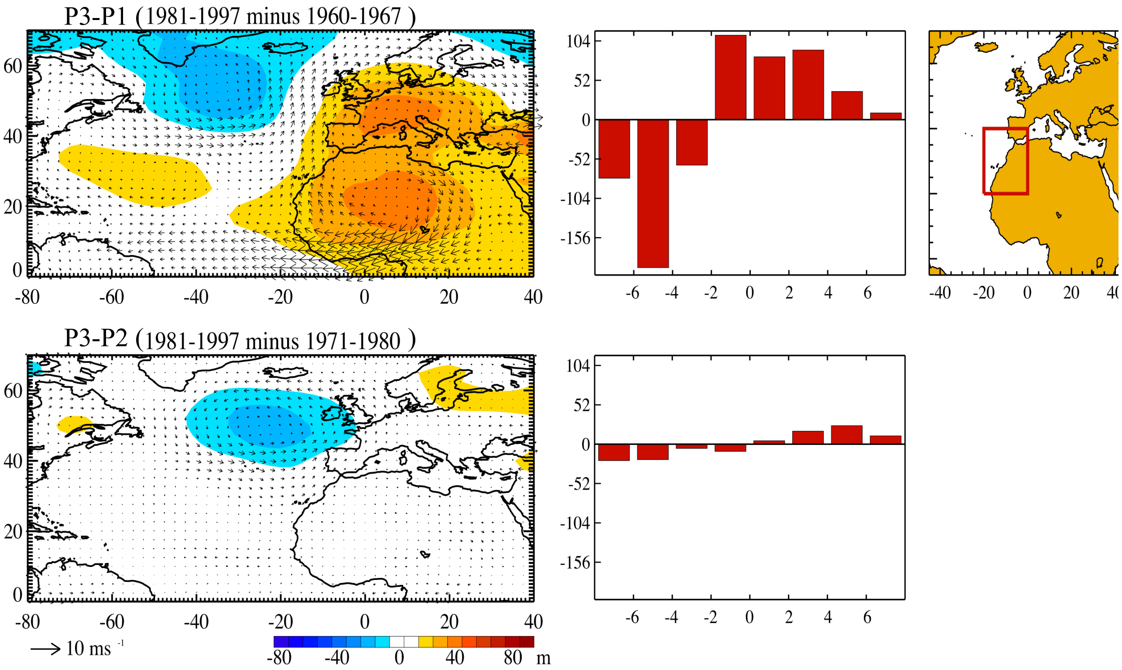
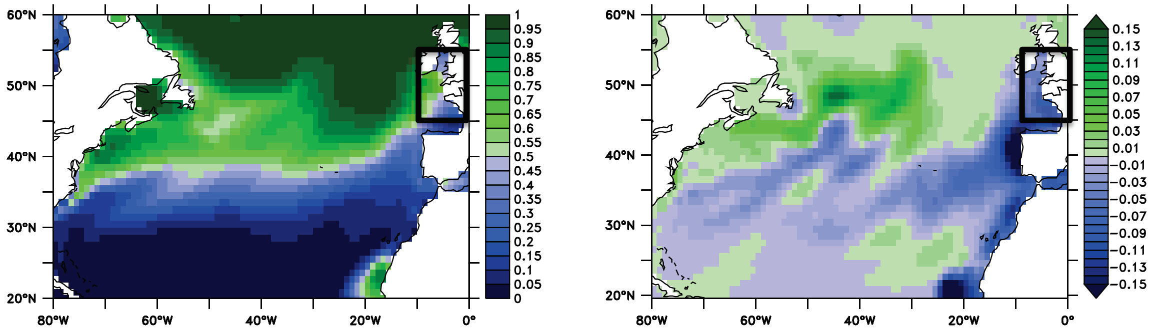
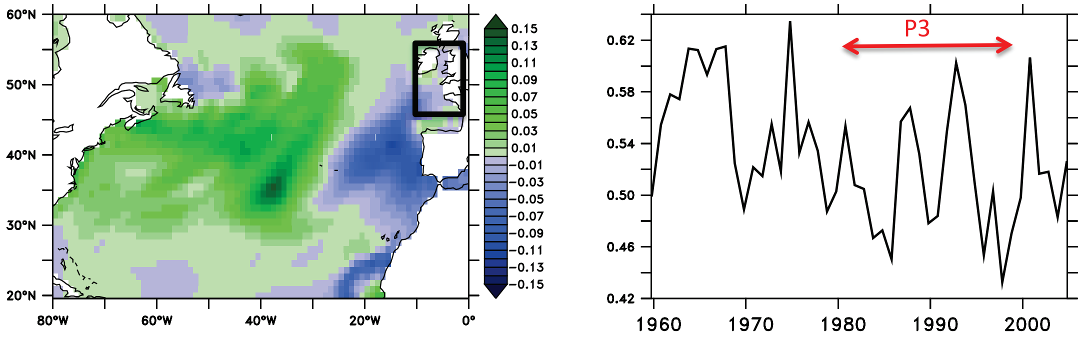


Figure 3.9. Difference in the frequencies of daily meridional wind between P3 and P1 (top panels) and between P3 and P2 (bottom panels) from October to December. Histograms show the frequency of days (y axis) per meridional wind stress value (x axis) averaged over the red box in m/s. Note that because the three time periods have different lengths, the two shorter ones are adjusted to the longest period (i.e., 1981-1997) by applying a scaling factor equal to the ratio of their lengths. The extreme meridional winds, which may be defined as winds with an absolute magnitude greater than 4 m/s, are primarily responsible for the dust transport from the Sahara/Sahel to our region of interest. This is particularly important as the mean meridional wind over this box retains a southward direction in all three periods, although its magnitude varies from -.94 to -1.39 to -2.46 for 1985-1997, 1971-1980, and 1960-1967 periods, respectively.



(A) OND N_{limit} 1981−1997

(B) ΔOND N_{limit} (1981−1997)−(1960−1980)



(C) ΔOND N_{limit} (1981−1997)−(1998−2004)

(D) Nitrogen limitation OND, 10W−0

Figure 3.10. N limitation in the GFDL CORE simulation reported in Gnanadesikan et al. (2011). Equation (1) was applied to the monthly mean nitrate and ammonia concentration at the surface and averaged over October, November, December (OND). (A) Mean limitation from 1984-1995. (B) Difference between 1984-1995 and 1960-1983. (C) Difference between 1984-1995 and 1996-2004. (D) Annual time series of OND nitrogen limitation averaged over the Bay of Biscay box. Blue=N limited.

4 PLANKTON CHANGES IN THE ANTHROPOCENE: CLIMATE CHANGE OR NATURAL VARIABILITY?

4.1 Abstract

Several studies have shown that North Atlantic plankton communities have experienced significant changes over the last century. Whether this is the result of natural oscillations, anthropogenic forcing or a combination of both is up for debate. Here, we applied the random forest methodology used in Rivero-Calle et al. (2015) to evaluate the sensitivity and long-term change of 9 plankton groups over the last 50 years. By combining all 6 phytoplankton (diatoms, dinoflagellates, coccolithophores, *Trichodesmium* sp., chlorophytes, silicoflagellates) and 3 zooplankton (copepods, foraminifera, tintinnids) groups measured by the Continuous Plankton Recorder along with environmental parameters, we create a holistic representation of the community and its environment. The goals were to: 1) test the hypothesis of a generalized plankton phase shift in the North Atlantic, 2) discuss the influence of potential anthropogenic and natural drivers. Results show a shift from large to small phytoplankton groups, an increase in calcifiers, changes in phenology and evidence of bottom-up as well as top-down effects. However, this shift is neither abrupt nor well synchronized. The different timings and sensitivities to forcings across plankton groups suggest multiple stressors at play. No single parameter can be assumed to be responsible for all the observed changes, but CO_2, AMO and diatoms are important predictors. A shift towards small phytoplankton groups may have consequences in primary productivity, rain ratio and carbon export. The relative proportion of phytoplankton groups (i.e. community composition) also affects several biogeochemical cycles.

Continuation of data-rich decadal time series is fundamental to understand past and future variability.

4.2 Introduction

Relatively small changes in environmental conditions can lead to large changes in ecosystem structure. In the ocean, phytoplankton community shifts can lead to drastic changes in higher trophic levels and thus severe impacts on important economic activities such as fisheries or recreational activities. A clear example of the scale of these economic impacts and drastic ecosystem changes is that of the Black Sea, where overfishing, stratification and changes in nutrient influx led to coccolithophore dominance and a decline in commercial fisheries (Cokacar et al. 2001, Daskalov 2002, Oguz et al. 2003, Cokacar et al. 2004, McQuatters-Gollop et al. 2008).

A regime shift can be defined as a sudden substantial change in the composition, state or primary productivity of an ecosystem at a regional level, which could reflect a major hydrographic change (Reid et al. 2001, Beaugrand 2004, McQuatters-Gollop et al. 2007b). Additionally, this change is generally synchronized across multiple ecological groups, particularly amongst the phytoplankton. One well-known example is that of the North Pacific phase shift in the 1970s (Hare & Mantua 2000, Karl et al. 2001) but other regime shifts have been described for the Mediterranean (Conversi et al. 2010), North west Atlantic (Greene et al. 2013), or the Northeast Atlantic and North Sea (Aebischer et al. 1990, Beaugrand & Reid 2003, Alheit et al. 2005, Hatun et al. 2009, Beaugrand & Reid 2012, Edwards et al. 2013).

The fishing industry has a long tradition and a strong socio-economic importance in the North Atlantic (Kurlansky 1998). Different studies have documented a decline in fisheries in the North Atlantic over the last decades (e.g.(Myers et al. 1996, Christensen et al. 2003, Drinkwater

2009), with overfishing generally being blamed. At the same time, other studies suggest a decrease in ocean primary productivity (Gregg et al. 2003, Behrenfeld et al. 2006, Boyce et al. 2010) and an expansion of areas of low productivity (Polovina et al. 2008). A few authors have even proposed that there has been a regime shift from large to small phytoplankton (Marinov et al. 2010, Moran et al. 2010). Moran et al. (2010) and Daufresne et al. (2009) suggested that global warming can change the phytoplankton size structure, benefiting small plankton groups. Ocean acidification has also been linked to an overall decline in nitrification rates, which could also produce a shift from large to small plankton groups (Beman et al. 2011). The purpose of this paper is to examine whether this paradigm of a regime shift is robust with the North Atlantic when multiple planktonic functional groups are considered. While several studies have documented regime shifts in the North Atlantic at different trophic levels (e.g. (Aebischer et al. 1990, Alheit et al. 2005, Beaugrand et al. 2008, Beaugrand 2009, Hinder et al. 2012a), this is the first study spanning phytoplankton community shifts beyond the two dominant groups (diatoms and dinoflagellates).

One difficulty in detecting regime shifts is that ocean ecosystems experience multiple stressors, sometimes simultaneously. These include anthropogenic ones such as increased atmospheric CO_2 levels, global warming and ocean acidification. But underlying these human forcings there is a considerable fraction of variability derived from natural drivers. Some of these are well known climate modes such as El Nino Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) but others such as the Atlantic Multidecadal Oscillation (AMO), have just begun to be understood and have much longer frequencies. These long-period forcings can mask or enhance anthropogenic effects and are difficult to distinguish from long-term drivers such as anthropogenic global warming. Moreover, interactions among all these stressors will likely have non-linear effects.

One way to approach the issue of multiple stressors is to use PCAs and EOFs but these methods cannot isolate and rank individual effects. Previous work by (Rivero-Calle et al. 2015) used random forests to distinguish carbon dioxide (CO_2) from temperature impacts in the Continuous Plankton Recorder (CPR) dataset. This analysis also showed the potential for ranking bottom-up versus top-down effects acting upon coccolithophore populations in the North Atlantic. Another promising result was the agreement of empirical relationships found between coccolithophore abundances and environmental parameters (e.g. temperature or $p\mathrm{CO}_2$) in the field and in laboratory controlled settings. In this paper, we extend the analysis applied in Rivero-Calle et al. (2015) to a larger set of plankton groups.

Despite limitations discussed below, the CPR survey is the largest and most complete on-going time series on plankton distribution in the World (Richardson et al. 2006). CPR methodology has been kept intact since the 1940's allowing for consistent, unique multi-decadal data sets that can potentially serve our purpose of distinguishing between anthropogenic and natural variability forcings. In this study, we applied the methodology used in Rivero-Calle et al. (2015) to evaluate the sensitivity and long-term change of 9 different plankton groups in the last 50 years. By combining all CPR phytoplankton groups (diatoms, dinoflagellates, coccolithophores, *Trichodesmium* sp., chlorophytes, silicoflagellates) and 3 zooplankton groups (copepods, foraminifera, tintinnids) this study recreates a more holistic representation of the planktonic community and its environment in order to: 1) test the hypothesis of a plankton phase shift in the North Atlantic, 2) discuss some potential anthropogenic and natural drivers.

We will first present the historical patterns found for 9 plankton groups (diatoms, dinoflagellates, coccolithophores, Trichodesmium sp., chlorophytes, silicoflagellates, foraminifera, copepods, tintinnids) and the phytoplankton color index (PCI) based on the CPR dataset from 1960-2010. We will then discuss plausible explanations for these trends combining statistical inference and ecological knowledge of bottom-up and top-down effects of environmental parameters on plankton groups.

4.3 Methods

a.) Sources of data

Plankton: Our estimates of plankton abundance were obtained from the Continuous Plankton Recorder survey (CPR). Started in 1931, the CPR survey is an ongoing operation thanks to the Sir Alister Hardy Foundation for Ocean Science. Ships of opportunity, many of which operate on well-established commercial routes, tow the instrument behind the vessel filtering plankton along the way (for more information visit www.sahfos.ac.uk). The inflow of water moves filtering and covering bands of silk, rolling them together into a storage compartment containing buffered formaldehyde for preservation (Reid et al. 2003). Silk movement is kept proportional to the ship's speed so that 4 inches of silk correspond to 10 nautical miles of towing and $3m^3$ of water filtered (Reid et al. 2003). Once the cruise is completed, each roll is returned to SAHFOS and examined under a microscope (Reid et al. 2003). The dataset generated spanned the North Atlantic basin and North Sea for the years 1960-2010 between 38-65 N. Although over 400 different species are recorded, some of these are only found rarely, requiring us to group different species into functional groups.

Our analysis considers six phytoplankton groups (diatoms, dinoflagellates, coccolithophores, *Trichodesmium* sp., chlorophytes, silicoflagellates) and three zooplankton groups (copepods, foraminifera, tintinnids). For diatoms, dinoflagellates, chlorophytes, and copepods, each sample corresponded to cell counts per group found in approximately 3m^3 of water filtered at about 7m deep at a given time, date and location. Certain groups (coccolithophores, foraminifera, silicoflagellates, tintinnids) were routinely recorded as present or absent but not counted until 1993. Coccolithophores and silicoflagellates were not regularly recorded until 1965 and they are not top predictors for other groups. Therefore, available data for coccolithophores and silicoflagellates prior to 1965 was only used when considered as covariates but not as response variables. That is, the random forest models for coccolithophores and silicoflagellates were built using only data from 1965-2010.

In this study the chlorophyte group represents the cumulative abundance of 4 genera of nanophytoplankton (*Hexasterias, Pachysphaera, Pterosperma, Halosphaera*). While these organisms are orders of magnitude smaller than the mesh size, their non-motile stage (phycoma) is considerably larger, getting trapped in the silk and easily identified under the microscope. The phycoma stage usually happens at the end of the growing season and may represent a hibernation strategy. As such, chlorophyte counts may not be representative of the abundance of this group throughout the growing season.

Within zooplankton, we selected 3 groups: copepods as large zooplankton with a key role in fisheries, tintinnids as representatives of small zooplankton that have been studied before (Hinder et al. 2012b), and foraminifera as calcified zooplankton for their potentially greater sensitivity to ocean acidification. These groups represent predators that will graze upon phytoplankton, respond to environmental cues, and may have different sensitivities to different stressors. We also consider the Phytoplankton Color Index (PCI), an index of the greenness of the sample that has been linked to changes in chlorophyll a and phytoplankton community changes (e.g.(Leterme et al. 2005, Raitsos et al. 2005, Leterme et al. 2006, McQuatters-Gollop et al. 2007b, Raitsos et al. 2013, Raitsos et al. 2014).

Rivero-Calle et al., 2015 showed that probability of occurrence within a 1x1 degree grid box can be used as a proxy for changes in coccolithophore abundance during the shorter time period over which abundance was estimated. Similarly, we applied the same methodology to other groups where only presence or absence had been recorded (coccolithophores, silicoflagellates, foraminifera and tintinnids) and also found good correspondence (Figure **4.1**). Consequently, for these groups we studied changes in frequency (probability) of occurrence instead of mean counts, enabling us to use the much longer time series.

Climate modes. We selected four climate indices that could have a possible impact over the North Atlantic: the North Atlantic Oscillation (NAO), Arctic Oscillation (AO), El Nino Southern Oscillation (ENSO), and Atlantic Multidecadal Oscillation (AMO). NAO and AO indices were obtained from http://www.cpc.ncep.noaa.gov). For the ENSO time series we used the Multivariate ENSO Index (MEI), and the AMO time series (http://www.esrl.noaa.gov/psd). In this study we used the monthly values of each index from 1960 to 2010.

In situ physical parameters. Six gridded in situ environmental variables were extracted for the North Atlantic between 1960-2010 from the International Comprehensive Ocean-Atmosphere Data set (ICOADS) (http://icoads.noaa.gov/): sea-level pressure (P), wind stress (W), zonal (Ucomp) and meridional (Vcomp) components of the surface wind, sea surface temperature (SST), total cloudiness fraction of the sky (Cloudiness). The resolution of ICOADS is of 1 degree and it corresponds to the monthly average of the integrated measurements (in situ, airborne, radar, etc.) for that area and time period.

Carbon dioxide (CO_2). We used the sum of global mean atmospheric pCO_2 from the Mauna Loa time-series and the gridded monthly climatologies of delta pCO_2 from Takahashi et al. to obtain an estimate of the local dissolved pCO_2 across the entire time period (see Rivero-Calle et al 2015 for more discussion of this approach). Note that this approach means that all interannual variation in surface pCO_2 is driven by the atmospheric concentration, not changes in ocean circulation.

Salinity and nutrients. Since historical data on nutrients and salinity are lacking or patchy we used monthly 1-degree climatologies from the World Ocean Atlas version 09 (WOA https://www.nodc.noaa.gov). Within our analysis, these variables are thus capable of helping to explain spatial patterns of occurrence or abundance, but not interannual trends.

Preprocessing: To match the resolution of the environmental variables and following the same methodology of Rivero-Calle et al (2015), CPR plankton data were aggregated into monthly estimates per 1-degree bins. For diatoms, dinoflagellates, *Trichodesmium*, copepods and chlorophytes, aggregation corresponded to average counts for those groups. For coccolithophores, foraminifera, silicoflagellates and tintinnids, aggregation gave us a probability of occurrence (sum of presences/number of observations). After matching up ICOADS, WOA, pCO_2, climate modes and CPR observations and eliminating samples with missing values, the dataset was composed of 79,872 complete observations and a total of 28 variables. The aggregation process reduced bias and autocorrelation effects associated with sampling along ship-tracks while increasing the variability explained by the model. Additionally, all variables had the same spatial and temporal resolution and the dataset reduction significantly decreased computing time. However, as a result of this aggregation, information on variables such as "day of the year" or "time of day" was lost.

b.) Statistical methodology

The dataset was standardized to ensure that all the variables had the same weight in the analyses. Correlation and collinearity were tested to ensure that variables were independent. Pearson correlations were relatively high for some variables (e.g. NAO-AO or latitude-SST, Table 2) but the Variance Inflation Factors (VIF) were less than 7. All statistical computations were carried out using the R Statistical Package 2.15.2 (R, 2012) on a two 12 core Xeon CPU X5670 (2.93GHz), 64gig RAM, eight 2TB hard drives.

Following the same methodology as in Rivero Calle et al., (2015) we used the package "randomForest" (Breiman 2001) to build the RF regression models (ntrees=1000), variable importance plots and partial dependence plots. Nine RF models were created, one for each plankton groups (coccolithophores, diatoms, dinoflagellates, chlorophytes, *Trichodesmium*, silicoflagellates, copepods, tintinnids, foraminifera). This was done by selecting one of the groups as the response variable and including the others with the rest of covariates. RF models were then used to provide insight into the processes, interactions and relations between variables and per group. In order to do this, variable importance plots were created, as well as partial dependence plots for the most important variables. Variable importance informs about the relative contribution of each variable to the model and partial dependence plots show the marginal effect of each covariate on the response variable.

c.) Potential issues with the data and analysis

One question that obviously arises when looking at trends is whether they could result from changes in analysis practice or analyst. This idea was already discussed in Rivero Calle et al with regard to the order-of-magnitude coccolithophore increase reported in that paper. It was argued that coccolithophores showed sharp increases at different times in different regions, making it unlikely that the increases were out a simple change in procedure or human error. Our present results support this conclusion, in that we also find different timing of changes for different plankton groups.

Secondly, it has been suggested in the past that a possible increase of other gelatinous forms of plankton may lead to clogging of the mesh altering the chances of plankton being captured. An increase in gelatinous organisms in the World and in the Atlantic in particular, is certainly a reality/concern (Attrill et al. 2007, Lynam et al. 2010). However, we agree with (Hinder et al. 2012b) in that this is highly unlikely to be the cause of these trends. (Barton et al. 2013) also discussed and discarded the importance of clogging.

4.4 Results

a) Basin-wide variability

When plankton indices are aggregated per year over the entire basin (Figure 4.2) differences in interannual variability and trends can be clearly appreciated. Large phytoplankton such as diatoms and dinoflagellates show a decreasing trend since 1960, whereas small phytoplankton like coccolithophores, silicoflagellates and chlorophytes show differing but overall increasing trends. This is not the case with *Trichodesmium*, which shows a single four-fold-peak increase in presence/average counts from the early 1980s to the late 1990s. Diatoms drastically dropped by more than half during the first decade as opposed to dinoflagellates, which also decreased by half but in a gradual way until the early 2000s, where this decline is enhanced. Coccolithophores started increasing their probability of occurrence after the first decade, and then exhibited two sharp increases, the first around year 2000 and the second around 2005. This suggests that the first decade marks the beginning of a decrease in the two dominant PFTs as well as the beginning of the rise in coccolithophores/small phytoplankton. However, the rise in chlorophytes is not apparent until the 1990s and silicoflagellates show steady numbers until late 1990s, when they practically doubled. The Phytoplankton Color Index (greenness of the sample) showed a phase shift in the mid 1980's from low PCI values to high PCI values. Turning to the zooplankton groups, copepods showed an overall decreasing trend since 1960, with a relatively high interval in the 1980s-1990s. The average annual numbers in the last 15 years are half of those at the beginning of the time-series. On the other hand, foraminifera and tintinnids showed increasing trends. Foraminifera have approximately tripled their numbers, whereas tintinnids have doubled since the 1960s, both groups have risen faster in the last two decades. Almost all plankton groups show a relative increase in the mid 1980s; this is more evident for dinoflagellates, *Trichodesmium* and all three zooplankton groups, particularly in the year 1985.

These interannual changes occur within a context of strong seasonal cycling. To investigate the role of seasonality and annual variability we plotted the basin-wide monthly mean counts (or mean percent presence) per plankton group per year (Figure 4.3). In general terms, we can see that some groups show a single peak in abundance, while others (e.g. diatoms, silicoflagellates) can have two. The CPR dataset shows the expected successional trends in the North Atlantic: the canonical spring diatom bloom in April-May followed by another one in the summer, the dinoflagellate bloom peaking in the summer months(McQuatters-Gollop et al. 2007a, Alvain et al. 2008), the summer and fall peaks for coccolithophores(Iida et al. 2002, Rost & Riebesell 2004) and summer increases in chlorophytes. On the other hand, *Trichodesmium* occasionally showed higher numbers early in the spring but primarily peaked late in the fall, whereas silicoflagellates showed two distinct blooms: one in the spring and another one in the fall. The PCI shows overall greater values in April and May. Zooplankton groups showed highest numbers between May and October.

Between 1960 and 2010 the general pattern of seasonal cycling is relatively stable, however, it is clearly modulated by the long-term trends discussed above. PCI, coccolithophores, chlorophytes, silicoflagellates, foraminifera and tintinnids showed an overall increasing tendency, especially in the last decade (2000-2010), where we have also found a possibly faster or relatively greater increase with respect to prior decades. In the last two decades, the timing of the peak of the diatom bloom seems to have shifted earlier, from May to April and we only seem to observe one peak in the spring as opposed to the two blooms seen in the 1960's. This could be due to nutrient availability limiting the second bloom or it could be due to a change in the composition of diatom species shifting from species that typically exhibit a bimodal phenology to those that have single blooms. Another overall feature is the lengthening of the growing season and an earlier onset. For example in the case of coccolithophores, the beginning of the growing season appears to have shifted from June to April, and in the last decade, coccolithophores were observed year round, with 20% probability as early as February and extending as late as November. This relatively earlier onset and later decay of blooms is also apparent in PCI, silicoflagellates, chlorophytes, foraminifera, and tintinnids. In contrast, dinoflagellates did not display significant changes in phenology on the group level but they did on species level. *Trichodesmium* showed again the decoupled decadal trends, while diatoms and copepods showed an overall decadal decrease in numbers.

Studying phenological changes requires defining the onset, duration and height of the growing season accurately, as well as additional analyses (in particular tracking inter-decadal changes in nutrient and light) that are beyond the scope of this study. Therefore phenology changes will not be discussed further here but will be addressed in a follow-up manuscript. Instead we will focus on drivers of change that are resolved by the dataset and which can be attacked using the Random Forest methodology, which proved fruitful in Rivero-Calle et al., (2015).

b.) Latitudinally and longitudinally resolved variability

One obvious question in looking at the basin-wide variability is whether it might be due to spatial shifts in the boundaries of ecosystems or whether basin trends are driven by regional changes. We used the partial dependence plots derived from our random forest models, to explore decadal latitudinal (Figure 4.6) and longitudinal (Figure 4.7) trends for each plankton group. In general terms, latitudinal patterns of each group were generally consistent throughout the five decades. Inter-decadal trends generally match the basin mean trends with most groups showing greater abundances north of 55°N. There are however some structural differences in dinoflagellates, silicoflagellates and copepods that may be indicative of greater relative sensitivity or stronger forcing at certain latitudes. For dinoflagellates there was greater variability at latitudes greater than 50°N, while for silicoflagellates it was at those smaller than 50°N. On the other hand, copepods showed a differential increase at latitudes greater than 55°N but only during the last decade. Once again, the overall probabilities for coccolithophores, foraminifera and tintinnids increased with each decade, especially in the last decade. This tendency to increase in the last two decades was also observed in chlorophytes, while it was only in the 1980s-1990s for *Trichodesmium*.

Similarly, when we investigated the variations in longitude we also observed inter-decadal trends that matched the long-term trends but there was also greater structure in the response. The smaller plankton groups (chlorophytes, coccolithophores, foraminifera, tintinnids) showed an accelerated increase during the last two decades. However, copepods, *Trichodesmium* and dinoflagellates showed a peak in the 1980's on the western side of the basin. With the exception of dinoflagellates and copepods, plankton numbers are relatively lower in the eastern ranges of the basin (east of 10°W), which is also where most previous CPR studies have focused. In fact, the decadal longitudinal trends show the sharp decrease in diatom abundance between 1960-1980 and the following slow recovery thereafter. The only case where diatom recovery reached the 1960's abundance values corresponds to the eastern North Atlantic (east from Greenwich), this is important to mention because results from the shelf have often been extrapolated to the rest of the basin.

c.) Full random forest analysis

In order to investigate the drivers of the long-term changes, we now turn to our full Random Forest analysis. We investigated the relative importance of 28 variables for each of the 9 plankton groups (Figure 4.5). The pseudo R^2 values for each model ranged between 30-45% except in two cases (*Trichodesmium* and chlorophytes), where these were less than 10%. This low percent of variability explained is one of the reasons why our recent manuscript (Rivero-Calle et al. Interdecadal Trichodesmium variability in cold North Atlantic Waters, manuscript subm.to GBC) did not use random forests to explain *Trichodesmium* interannual variability. For the other phytoplankton groups, despite the large number of observations (hundreds of thousands), the models capture at most half of the variability. However some variables were responsible for large percentages of the percent mean squared error when excluded (% MSE).

An important result that emerges from the variable importance plot is the heterogeneity of which predictors matter most. The top predictors across models include: diatoms, local CO_2, AMO, latitude, longitude, SST, Month, silicoflagellates, salinity and copepods. There are some commonalities. Diatom abundance was the single most important variable for silicoflagellates, copepods and dinoflagellates and it was also one of the top four parameters for all plankton groups except *Trichodesmium*.

Other predictors also show up in many groups. CO_2 was one of the top two predictors for coccolithophores, tintinnids, dinoflagellates and foraminifera, and one of the top four predictors for all plankton groups except chlorophytes and diatoms. AMO was the second predictor for coccolithophores, copepods and Trichodesmium and one of the top 7 for all except chlorophytes, and silicoflagellates.

However, there are some relationships that are specific to a few groups. Month was the first and second top predictor for diatoms and silicoflagellates, respectively, and the partial dependence plots agree with phenological observations described above. Silicoflagellates were the second most important predictor for diatoms and tintinnids. Copepods were a top predictor of chlorophytes but were not good predictors for any other phytoplankton or zooplankton group. Similarly, tintinnids were relatively important in predicting silicoflagellates but did not seem to be important for any other group. SST only ranked high (second position) for diatoms. Longitude was one of the top 3 predictors for zooplankton and *Trichodesmium*, whereas latitude was only relevant to *Trichodesmium* and dinoflagellates. Salinity has a secondary importance to diatoms, coccolithophores and silicoflagellates.

With the exception of CO_2, salinity and AMO, most physical parameters, nutrients and climate modes were not highly ranked as predictors for all groups except for *Trichodesmium* and chlorophytes. In the case of chlorophytes, climatological nitrate seems to be a relatively important variable, whereas for *Trichodesmium*, AMO and phosphates seem to be more relevant. While these two groups are also the ones with the lowest variability explained, so that our results should be taken with caution, the potential of RF as an exploratory method should also be noted since the relevance of AMO and phosphates can be easily explained in the case of *Trichodesmium* and nitrates and chlorophytes can also be easily linked. Climate modes are not ranked high in variable importance plots, except for AMO, which is clearly the most important climate mode for coccolithophores and copepods. In general, AMO is ranked higher than other regional climate modes (AO, NAO).

i, Local pCO_2

Our analyses showed that CO2 was one of the top two predictors for coccolithophores, tintinnids, dinoflagellates and foraminifera and one of the top four for all plankton groups except diatoms and chlorophytes. Partial dependence plots for that variable (Figure 4.8) showed that increased CO_2 levels had a positive feedback on coccolithophores, chlorophytes, tintinnids, foraminifera, whereas the effect is the opposite for dinoflagellates, diatoms and copepods. The percent MSE increase from excluding CO_2 as a covariate in the respective random forest is less than 80% for diatoms, dinoflagellates and copepods but it is greater than 140% for coccolithophores, tintinnids, silicoflagellates and foraminifera. It is unclear whether the CO_2 dependence seen in the random forest partial dependence plots are all due to physiological effects on carbon fixation rates or whether, as the only variable with a long-term trend, it may be reflecting this long-term trend. We will return to this point in the discussion.

ii. AMO

AMO was the second predictor for coccolithophores, *Trichodesmium* and copepods and one of the top 7 for all except chlorophytes, silicoflagellates. The comparison of the marginal dependence of AMO for each group (Figure 4.9) revealed that each group responds with different intensities, sign and to different phases. The positive AMO phase (warm phase) had a positive feedback on coccolithophores, chlorophytes, tintinnids and foraminifera, whereas the negative or cold AMO phase only had a positive feedback on *Trichodesmium*. The increase in MSE derived from excluding AMO in models is generally slightly lower than that of CO_2; greatest values correspond to silicoflagellates, foraminifera, tintinnids and coccolithophores (~100-140%), diatoms ~90%, dinoflagellates and copepods ~60%. A phase-dependent response is not very clear on most groups except perhaps coccolithophores and chlorophytes for the positive AMO phase and negative for Trichodesmium. Whether this response is truly due to AMO or a correlation with long-term trends is debatable.

iii. SST

In general, the partial dependence plots for sea-surface-temperature (SST, Figure 4.10) show larger abundances of all plankton groups with higher in situ temperatures. The exceptions to this were diatoms, which exhibited lower numbers with increasing temperatures and tintinnids, which did not show a clear trend. It should be noted however that fewer observations were made below 5°C or above 20°C. However, despite the general increasing trend with temperature, the inflection points and effect on MSE differed. We distinguished four inflection points: first one at ~5°C, where diatoms rapidly decline, while foraminifera and silicoflagellates start to increase, second one above 9-10°C, where dinoflagellates, coccolithophores and copepods tended to increase, then the 15°C threshold corresponded to chlorophytes maxima, and a fourth one at ~22°C, corresponding to the *Trichodesmium* threshold. Temperature variability has a doubling or tripling effect on the dominant groups (diatoms, dinoflagellates, coccolithophores) but is less than doubling for silicoflagellates, foraminifera, and copepods. On the other hand temperature seems to reveal a clear threshold for Trichodesmium and chlorophytes, which show a greater than six-fold increase with warm temperatures. This is in contrast with the low predictive accuracy of the *Trichodesmium* and chlorophyte models. In terms of MSE, excluding SST only produces a 20% increase in MSE for dinoflagellates, 50-60% for copepods and coccolithophores, ~80% for tintinnids, but it is ~100% for diatoms, silicoflagellates and foraminifera.

iv. Copepods

Copepods were the top predictor for chlorophytes but showed intermediate or low rankings for the rest of plankton groups. In terms of ranking in variable importance plots, copepods showed intermediate importance for diatoms and foraminifera but in terms of percent mean squared error, the account for ~100% for silicoflagellates and foraminifera and below 60% for diatoms, dinoflagellates, coccolithophores, tintinnids. However, all partial dependence plots were similar, showing an asymptotic increase as copepods increased (Figure 4.11).

v. Tintinnids

Tintinnid occurrence on the other hand appeared to be the third predictor for silicoflagellates and the eighth for foraminifera but very low ranking for any other plankton group. With the exception of foraminifera and silicoflagellates, the increase in MSE ranged between 15-50% for all groups. The partial dependence plots showed similar results for all groups, a linear relationship of increased plankton abundance with increased tintinnid occurrence (Figure 4.12).

vi. Diatoms

Diatoms were one of the top three predictors for all groups except Trichodesmium, for all other groups, excluding diatoms as predictors produces a MSE increase that varied between at least 70% and as much as 300% for silicoflagellates. The partial dependence plots showed asymptotic relationships with all groups, when diatom abundance is low, all groups show low numbers, as diatoms increase all groups increase (**Error! Reference source not found.**Figure 4.13). However, all the other groups reach a saturation threshold at ~1.5 million mean diatom counts.

4.5 Discussion

a. Plankton phase shift: less large, more small.

We begin by considering how to describe the changes in planktonic ecosystems in the North Atlantic. Several studies have documented the phase shift in PCI values in the North

Atlantic. (McQuatters-Gollop et al. 2007b) argued that PCI changes in the North Sea were evidence of a regime shift, which they characterized as a “stepwise modification in the composition and productivity of an entire ecosystem at a regional scale, reflecting substantial hydrographic change”. It would be expected that such a change would be seen first in the plankton and, indeed, other studies have tried to relate this PCI change to a change in dominance from diatoms to dinoflagellates (e.g. (Leterme et al. 2005, Leterme et al. 2006, Hinder et al. 2012a). While this mechanism explained some of the PCI variability, it has proven to be insufficient and other studies have suggested investigating the role of small phytoplankton groups such as coccolithophores (Leterme et al. 2006, Llope et al. 2012, Barton et al. 2016a). Our study extended the time-series analysis to show an overall shift from large phytoplankton (diatoms and dinoflagellates) to small phytoplankton (coccolithophores, silicoflagellates and chlorophytes) in the last five decades. Additionally, we also found changes in the selected zooplankton model groups: copepods were reduced by half since the1960’s, while tintinnids doubled and foraminifera tripled in the last two decades. The first decade (1960s) appears to mark the beginning of a decrease in the two larger dominant phytoplankton groups and copepods, whereas the 1990s was the beginning of the rise in small plankton and foraminifera. Therefore, we cannot say that there is an abrupt change; the transition takes at least two decades, with changes in small plankton and foraminifera being particularly fast and conspicuous in the last decades. This alteration of the phytoplankton community is consistent with the previously observed regime shift towards high PCI values, however, the magnitude and exact timing of the change in abundance differs from one group to another, suggesting multiple forcing factors. It also challenges the definition of a regime shift, as it is not the typical well-orchestrated sudden change in the entire ecosystem.

Instead of a single regime shift associated with a single driver, our analysis of the rich CPR dataset reveals many ecological, climatic and trophic relationships. Since it is virtually impossible to tackle every single topic or all possible explanations for each plankton group, we decided to examine some of today's hot topics, considering whether these drivers could explain the long-term trends found and the so-called regime shift. We will discuss ocean acidification, global warming, trophic interactions, AMO and diatoms. The first three can be thought of as single drivers and cover both anthropogenic and bottom up vs. top-down effects. The latter two can be thought of as acting as a proxy for multiple drivers. For each driver we will ask three questions: 1. For which groups is it one of the top predictors of variability? 2. Does it explain the long-term trends in that group? 3. If it does explain the long-term trends, does the result make sense biologically?

b.) Comparing individual drivers of change

i.) Ocean acidification

The global increase in atmospheric CO_2 levels is leading to elevated ocean CO_2 concentrations and, consequently, ocean acidification and changes in $CaCO_3$ saturation state (Feely et al. 2004, Orr et al. 2005, Doney et al. 2009a, Doney et al. 2009b, Feely et al. 2009). The most immediate concern is the negative effect that decreased calcite and aragonite saturation levels and decreased pH may have on calcifying organisms such as corals, coccolithophores, foraminifera and pteropods. The general expectation is that calcifiers will be unable to fix $CaCO_3$ and dissolve (Riebesell et al. 2000, Feely et al. 2004). However, making such a generalization is problematic, as it depends on the group, species or even morphotype evaluated (Langer et al. 2006a, Langer et al. 2009a, Langer et al. 2011).

Our analyses showed that CO_2 is important for all plankton groups, in fact one of the top two predictors for several groups (coccolithophores, foraminifera, tintinnids and dinoflagellates). As a result, the percent MSE increase from excluding CO_2 was greater than 140% for coccolithophores, foraminifera, tintinnids and silicoflagellates. It was not surprising to find that CO_2 had a high predictive power for the two calcifiers (coccolithophores and foraminifera) but it was surprising that increasing CO_2 had a positive effect on foraminifera.

Based on laboratory experiments, it is known that coccolithophore carbon fixation rates are undersaturated at today's CO_2 levels (Rost et al. 2003, Rost & Riebesell 2004).Therefore an increase in CO_2 could explain higher growth rates and thus greater occurrences, as contended in Rivero-Calle et al (2015). Other studies have documented greater presence of coccolithophores in diverse places, such as Bermuda (Krumhardt et al. 2015), Barents Sea (Smyth et al. 2004), Bering Sea (Harada et al. 2012), and Southern Ocean (Cubillos et al. 2007) in the last decades. One question about all of these results is whether they reflect changes in speciation. Some species are perhaps more sensitive to CO_2 concentrations and energy allocation but coccolithophores species identification in CPR samples is currently not done. Most published studies focus on *Emiliania huxleyi* and *Gephyrocapsa oceanica*, which seem to be highly sensitive to low CO_2 levels (Bach et al. 2013, Sett et al. 2014) but capable of adapting to CO_2-enriched conditions (Lohbeck et al. 2012, Jin et al. 2013). While these are not the only species found in CPR samples they represent some of the most ubiquitous and cosmopolitan species and they are bloom-forming species, whose optimum biogeographical limits include the CPR study area. However, (Bolton et al. 2016) suggest that larger species of coccolithophores may be *more* sensitive to changes in pCO_2 than smaller species. Therefore it would not be unreasonable to think that CO_2 may have enhanced coccolithophore growth rates, resulting in greater abundances in the last decades.

The long-term dinoflagellate decline is supported by partial dependence plots and is consistent with the general idea that dinoflagellates do not benefit from increased CO_2 levels (Tortell 2000). It is possible however that the high ranking of the CO_2 parameter as an explanatory variable may be reflecting to the long-term decline of the group and not the result of a direct physiological response to CO_2. The relationship between higher CO_2 levels and dinoflagellates or foraminifera may also need to be explored at the species level. For example, the group defined as dinoflagellates include a wide range of sizes, trophic strategies and exoskeleton structure and composition, so that different species would be expected to respond differently to CO_2.

Similarly, the relationship between CO_2 and foraminifera should be explored at the species level because this zooplankton group includes mixotrophs and heterotrophs. Foraminifera in CPR data are not identified to species but it is possible that they include mixotrophic species that could benefit from higher CO_2 concentrations in a similar way to coccolithophores. Alternatively, heterotrophic foraminifera could be responding to the indirect effect of CO_2 on a greater abundance of their prey or decreased number of competitors or predators. Either way, there is a potential physiological or ecological explanation for the relationship found between CO_2 and foraminifera in our random forest results that deserves future attention.

However, the response of other plankton groups such as tintinnids or silicoflagellates to increasing CO_2 is virtually still unknown. Some recent studies have begun to investigate the response of tintinnids (Suffrian et al. 2008, Rose et al. 2009, Biswas et al. 2012) with mixed conclusions. Suffrian et al (2008) found no changes in the microzooplankton composition at different CO_2 levels during a phytoplankton bloom in Norwegian waters, while Rose et al. (2009) and Biswas et al. (2012) found alterations of the microzooplankton communities as a result of CO_2 or greenhouse conditions. In both cases they described increased tintinnid numbers, which were attributed to a change in the phytoplankton composition towards smaller groups such as coccolithophores or bacteria. These studies suggest an indirect effect of CO_2 in the microzooplankton composition due to changes in the phytoplankton species, alteration of trophic structure and grazing pressure rather than direct physiological effects on zooplankton. In our case, tintinnids may also be responding to increased abundance of small phytoplankton such as coccolithophores and silicoflagellates; in fact, silicoflagellates are the second predictor of tintinnids (more discussion in section iii). Since microzooplankton play a key role in energy transfer and marine trophic dynamics further research on these groups is necessary (Biswas et al. 2012).

Alteration of the phytoplankton community composition under elevated CO_2 levels have been described in experimental and mesocosm setups (e.g. (Hare et al. 2007, Feng et al. 2009, Biswas et al. 2012). To our knowledge there is not enough evidence of CO_2 effects on non-calcifiers such as silicoflagellates, chlorophytes, and more work needs to be done on planktonic foraminifera and microzooplankton. Therefore it is unclear whether the CO_2 dependence seen in the random forest partial dependence plots are all due to physiological effects or changes in the phytoplankton community composition. Whether these are direct or indirect effects of increased CO_2 levels, the tendencies found in partial dependence plots resemble the long-term trends of the groups and variable importance plots identified the most sensitive groups (coccolithophores, foraminifera, tintinnids and dinoflagellates), encouraging subsequent future studies.

ii. Global warming

Because temperature has long been recognized as one of the key parameters affecting biological rates, the effects of global warming have dominated much of the scientific discussion in the last two decades. Temperature is expected to have a direct physiological effect on ectotherms such as plankton, for example SST triggers gonad development and reproduction of many species (Edwards and Richardson in Beaugrand 2009). Changes in timing of critical life history events (e.g. developmental, reproduction) have been interpreted as responses of organisms to global warming (Beaugrand et al. 2008). For example, some calanoid copepod species are known to be very sensitive to temperature changes and some studies have linked global warming with the recent polar migration of cold-water copepod species (e.g. (Beaugrand et al. 2002). However, temperature in our statistical analysis is an umbrella factor; it may account for direct physiological effects, a global warming signal or seasonal temperature variability. Temperature changes may also reflect latitudinal or biogeographical shifts in ecosystem boundaries. Therefore temperature can also serve as a proxy for seasonality or even nutrient variability (e.g. related to seasonal upwelling, thermal stratification). As a result, attributing a temperature effect to the observed plankton changes is challenging.

In this study, SST was not a skillful predictor for any plankton group except diatoms (although they are a relatively high predictor for *Trichodesmium* the amount of variance explained is relatively small). The partial dependence plot shows that diatom abundance decreases by half as SST increases from 0-27°C. Long-term trends are consistent with the partial dependence plot trends in terms of the sign and magnitude of the 5-decade response. We note, however, that the mean global warming in the North Atlantic is <1°C, which although important, is considerably smaller than the SST increase necessary to produce the two-fold decline in diatoms. Based on our partial dependence plot results, there needs to be at least a 5°C warming to produce a response of such magnitude. Attributing this decline to temperature alone also conflicts with the fact that diatoms in the laboratory generally grow faster at warmer temperatures (e.g. (Suzuki & Takahashi 1995, Montagnes & Franklin 2001). The sharp threshold found in the partial dependence plot is consistent with temperature being a proxy for nutrients, suggesting that trends with warming temperatures increase stratification and reduce nutrient supply. Therefore we hypothesize that although global warming is important for plankton, temperature alone is unlikely to explain the diatom two-fold drop in mean abundance. Decadal changes in latitude-dependence also contradict the idea of a poleward migration, as the latitudinal pattern is similar across decades, with the entire population rising or falling in unison. Instead, trends in thermal stratification and nutrient supply (especially silicates and nitrates), which were not directly included in this analysis, might be able to explain these diatom trends

Although several studies have linked global warming with changes in the plankton community composition (Hare et al. 2007, Daufresne et al. 2009, Moran et al. 2010) and poleward movement of species (e.g. (Beaugrand et al. 2002), our study does not identify temperature as the key driver for most of the plankton groups studied. It is possible that the discrepancy is related to our focus on functional groups rather than species but it could also be that direct and indirect effects of CO_2 are better/stronger predictors than temperature. Additionally, warming and CO_2 may have additive effects manifesting at different times.

iii. Trophic interactions

Bottom-up drivers such as temperature and nutrients are often thought of as the main drivers of phytoplankton variability but top-down effects such as selective grazing could potentially explain the differing trends among plankton groups found. Our random forest models captured/found some evidence of trophic interactions. For example, diatoms are key prey for copepods, and were the top predictors of copepods in the RF model. A 50% decline in food supply could explain why copepods have decreased by half in the last five decades. However, copepods are not an important predictor of diatoms, making it unlikely that copepod variability was responsible for the diatom decline. If that were the case, we would expect a long-term increase in copepods as diatoms declined. Therefore, diatom trends can explain copepod trends but not vice versa.

The opposite relationship was found between copepods and chlorophytes. Copepods were one of the top predictors of chlorophytes, suggesting that grazing pressure is important for this phytoplankton group. However, copepods prey on a wide range of organisms and chlorophytes are not the main prey, therefore copepods may regulate chlorophytes populations but not the opposite. It is possible that the overall decline in copepods had a positive effect on chlorophytes' long-term trends by reducing grazing pressure. Nonetheless, the partial dependence plots for copepods suggest that copepods are abundant when any of the other groups are in high numbers. The asymptotic relationships found could be interpreted in terms of resource limitations. Copepods may continue to grow and increase their numbers beyond other phytoplankton or zooplankton groups that become saturated much earlier. A similar effect was found when diatoms were considered as the covariate and will be discussed in section v.

The trophic relationship between tintinnids and silicoflagellates also deserves further attention, as they appeared as top predictors of each other. Silicoflagellates were ranked as the second best predictor of tintinnids after CO_2. Tintinnids appeared as third best predictor of silicoflagellates after month and diatoms. These results suggest that silicoflagellates are an important source of food for tintinnids, which are perhaps their key predators. Based on this premise it makes sense that they both increased in the last decades. It also suggests that phenology, perhaps related to nutrient supply (i.e. silica), exerts an important regulatory effect on silicoflagellates. Moreover, it is worth investigating whether the increase in tinntinids was in part due to an increase in food supply. A shift from large phytoplankton to small phytoplankton or a long term decrease in diatoms might leverage competition pressure for silicoflagellates and would explain the high ranking of CO_2 and diatoms for tintinnids. While this would explain the long-term results it does not explain the partial dependence plots, whereby silicoflagellates are high when diatoms are also high.

Tintinnids are not important predictors for any other group suggesting that they are not important competitors nor predators for the groups selected. On the other hand, a strong relationship was found between copepods and diatoms. One possibility is that size structures the trophic relationships between predators and prey (phytoplankton and zooplankton), as has been suggested in (Dunne et al. 2005). Even though these generalizations may not be true for all species, such allometric relationships can be useful to parameterize plankton groups in Earth System Models.

In conclusion, our random forest models show some trophic relationships that may be of relevance in shaping North Atlantic plankton communities. Changes in grazing pressure as well as changes in the food supply can explain some of the long-term trends found but not all. We have identified some interactions that need to be studied further at the species level or be empirically tested through experiments, which are clearly beyond the scope of this work.

iv. AMO

Because climate indices represent the synchronous interaction of many environmental parameters they would be expected to serve as potentially good predictors. Several CPR studies have attributed changes in phytoplankton distributions to regional climate modes such as NAO (Greene & Pershing 2000, Conversi et al. 2001, Barton et al. 2003, Attrill et al. 2007, Henson et al. 2012), but except for Rivero-Calle et al., (2015) no previous CPR study has evaluated 4 climate modes simultaneously. Recent studies have attributed ecosystem shifts (Edwards et al. 2013) and coccolithophore variability to AMO (Hovland et al. 2013). The phytoplankton color index, zooplankton, sardine and herring fisheries seem to correlate well with AMO variability (Edwards et al. 2013) and a strong correlation between SST, AMO and calcifying organisms has been suggested (Beaugrand et al. 2012). In our analysis AMO appears repeatedly as a top predictor. AO seemed to have a secondary importance for all groups except diatoms and copepods, where the NAO seemed to be the second most important climate mode after AMO. However, none of the climate modes considered were found to explain as much variability as AMO, nor appeared as top predictors. Therefore, we will focus on the AMO because this was one of the single best predictor across plankton groups capable of partially explaining the long-term trends. In addition, our analysis will complement previous studies focusing on other single climate modes.

Both observational and modeling studies have related the dynamics of the AMO oscillation with changes in the strength of the meridional overturning circulation (Delworth & Mann 2000, Knight et al. 2006). According to (Lozier et al. 2010), the North Atlantic subtropical region has become more saline and warmer, while the subpolar region has become fresher and cooler. This caused a decrease in the meridional density gradient in the last 50 years, which is directly related to the strength of the Meridional Overturning Circulation (MOC) and thus has implications for heat transport, convection and consequently nutrient availability (Lozier et al. 2010). Global warming is expected to warm the Atlantic as a whole but to decrease overturning and convection (Barton et al. 2016b), whereas higher AMO is associated with stronger overturning, which results in more convection and nutrient supply during winter months (Gnanadesikan et al. 2014b). We would therefore expect to find greater abundances of all groups during positive AMO phases. Although this can be seen in chlorophytes, coccolithophores, foraminifera and perhaps diatoms and tintinnids, it does not apply to dinoflagellates or silicoflagellates. However, in Earth System Model simulations, some regions are more correlated to AMO than overturning and depending on the location there are competing impacts between nutrients and light (Gnanadesikan et al. 2014b). This suggests that our analysis may need to be repeated at a regional scale in a future study.

We conclude that the MOC is an important mechanism in shaping the North Atlantic phytoplankton community structure in the long-term and that the AMO should be the climate mode prioritized in further studies. Current available phytoplankton data records are not long enough to unequivocally prove a possible oscillatory pattern, so that modeling studies such as (Gnanadesikan et al. 2014b) are a valuable approach.

v. Diatoms

One of the most important variables for all groups was the abundance of diatoms, the dominant group in North Atlantic waters. This may suggest that diatoms play a central role in shaping the North Atlantic plankton communities, a master variable. However, partial dependence results do not match the long-term trends, which show that diatoms declined since 1960 while coccolithophores, foraminifera, silicoflagellates and tintinnids all increased. Partial dependence plots show that the abundance of all groups rise when diatoms rise, following an asymptotic curve that is consistent with the idea of a “rising tide lifts all phytoplankton” (Barber & Hiscock 2006). This hypothesis states that when there is a favorable onset of optimal light and nutrients, both diatom and non-diatom taxa increase. However, since diatoms have faster growth rates, the relative abundance of diatoms is greater. Thus although a bloom is seen as a succession event, the entire assemblage grows, including grazers. The positive parallel trends observed in partial dependence plots suggest that the interaction between diatoms and other organisms is not that of competition and exclusion, but may be representing a proxy for light availability and nutrient replete conditions that favor all groups. We therefore contend that diatom abundance may be representing a proxy for a combination of parameters that are not well represented with the suite of variables examined here (e.g. nutrients, salinity, mixed layer depth, etc.) which vary spatially and seasonally and thus characterize optimum growth conditions. However when we consider long-term trends, other parameters may be detrimentally affecting diatoms and dinoflagellates, while enhancing growth of background non-dominant phytoplankton groups such as coccolithophores, silicoflagellates or chlorophytes. It is unclear whether this is permanent or a transitory phase in between the two-states.

c.) Caveats

The fact that all the groups behave differently suggests that trends are not due to either changes in methodology or a single forcing acting equally upon all groups. Although the results for some of the smaller phytoplankton should be taken with caution, the fact that the CPR methodology has remained unchanged since 1958 provides confidence in the overall relative trends and its suitability for a long-term study. It is acknowledged that for coccolithophores, silicoflagellates, tintinnids and foraminifera we studied changes in frequency of occurrences as opposed to mean counts, and that the chlorophytes group represents the cumulative abundance of 4 genera. Despite potential issues derived from CPR sampling, our results agree with other independent studies.

One potential caveat of this study is that we are discussing basin trends along with responses found on the 1-degree monthly scale. Time series here correspond to the average basin-wide trends. Due to the uneven sampling per year and region, these time series may differ regionally. Preliminary results found that regional trends are similar to basin-wide trends for at least diatoms, dinoflagellates and coccolithophores (results not shown), however, we have yet to examine regional random forest analyses in detail. The next step would be to repeat the analysis per Longhurst region, taking into account the sampling effort.

4.6 Conclusions

One of the main outcomes of this study is that the main drivers responsible for the interannual variability appear to be different across groups. There is not a single obvious mechanism that can explain the long-term trends for all the groups. Finding that the abundances of other plankton groups were better predictors than physico-chemical parameters or climate modes was a rather unexpected result. Most studies do not have the luxury of exploring so many drivers simultaneously within a community and often focus on the biological response of one group to a particular physico-chemical driver. This highlights the importance of the ecological perspective and studying the ecosystem as a community rather than isolated cause-and-effect relationships. It also suggests that interactions among groups (e.g. competition, predation) should not be ignored when evaluating hydrodynamic drivers (e.g. Tintinnids and CO_2).

The results of this study may reconcile the idea of a decrease in ocean productivity and an increase in biomass (as shown by phytoplankton color index). It also potentially contradicts Cabré et al. (2014), which shows that Earth System Models tend to project future higher primary productivity and biomass at high latitudes and a decrease in low latitudes. This has implications on fisheries management and reevaluation of current Earth System Models as well as climate models. If such a phase shift is happening and small phytoplankton are expected to increase, it is in our best interest to understand the dynamics of these background non-dominant groups.

It is also often assumed that, in the presence of climatic changes in the environment, the first mechanism for plankton is “to modify their phenology or life cycle in a way that their critical developmental phases are tuned with the seasonal variability”(Beaugrand 2009). Phenology changes have important implications in terms of the so-called “mismatch hypothesis” (Cushing 1990), there are several records of such changes in the North Atlantic. CPR data and

RF analyses capture natural variability in phytoplankton groups and show typical seasonal cycles that agree with standard paradigms. However, despite the observed phenological differences among groups, the overall importance of the variable month is unexpectedly low except for diatoms. That month strongly predicts diatoms is consistent with the importance of the spring diatom blooms in the North Atlantic and may be related to the pulse of nutrients and shoaling of the mixed layer depth in the spring (Sverdrup 1953, Behrenfeld 2010)). Changes in the timing of this event may have important consequences for the rest of the plankton community. Further exploration of the importance of this issue is left to future work repeating this analysis on a regional scale.

Finally, local conditions appear to be better predictors than climate modes. Contrary to general expectations, SST was not found to be the key parameter (except in the case of diatoms). Instead carbon dioxide, diatoms or predators were found to be good predictors across plankton groups. Although some links were found between climate modes and plankton patterns, none of them are enough to completely explain the trends seen. Some of the dominant groups show a strong AMO influence that should be explored further. However, the CPR time series (1960-2010) is not long enough yet to distinguish between AMO and global warming signals. Continuation of data-rich decadal time series such as CPR and ICOADS are fundamental to understand past and future variability. Combination with modeling studies may enable identification of early warning signals that can prevent/anticipate ecological changes of regional or even global socio-economic relevance.

4.7 Figures:

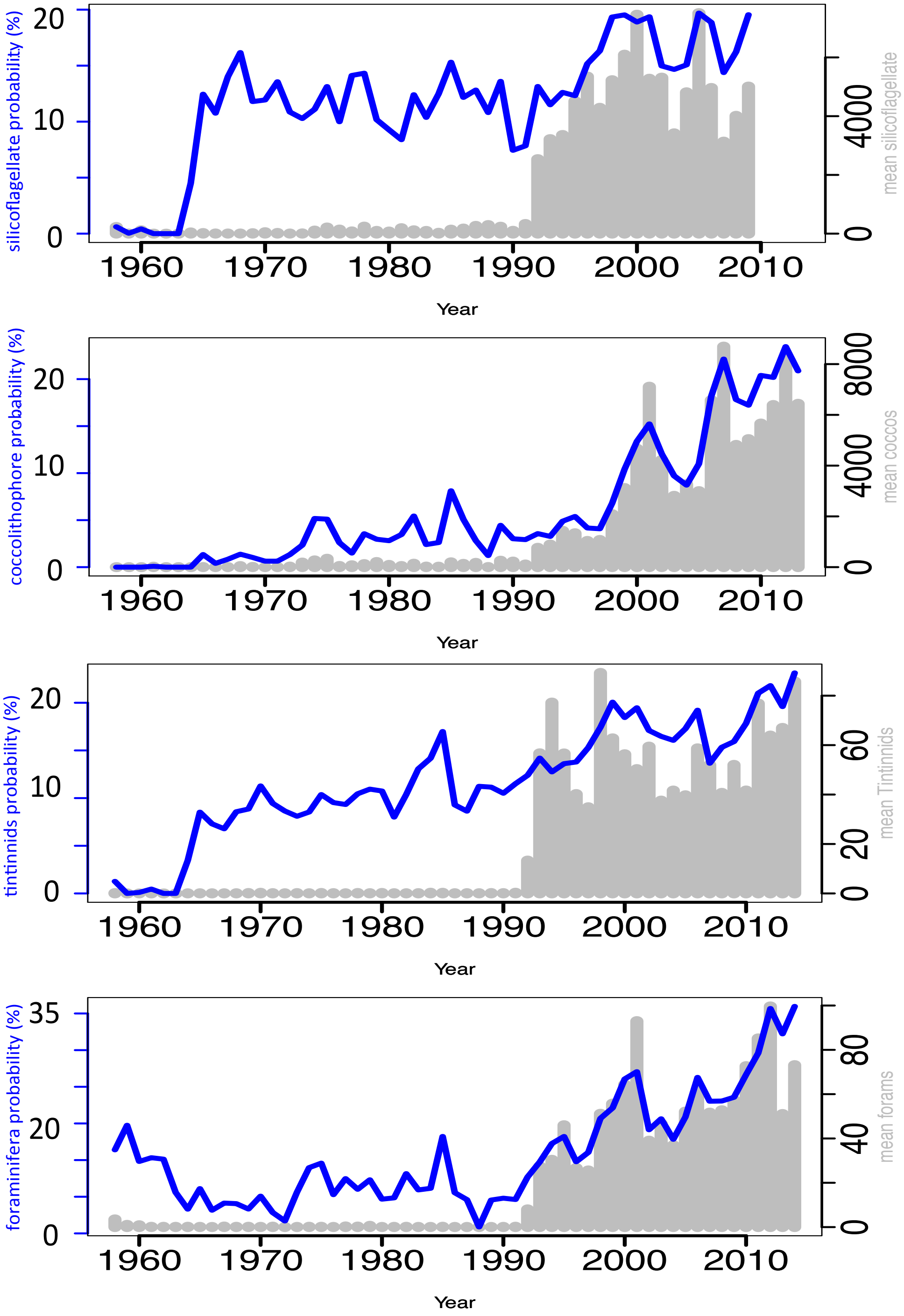


Figure 4.1 Probability vs. abundance: A) silicoflagellates, B) coccolithophores, C) tintinnids, D) foraminifera.

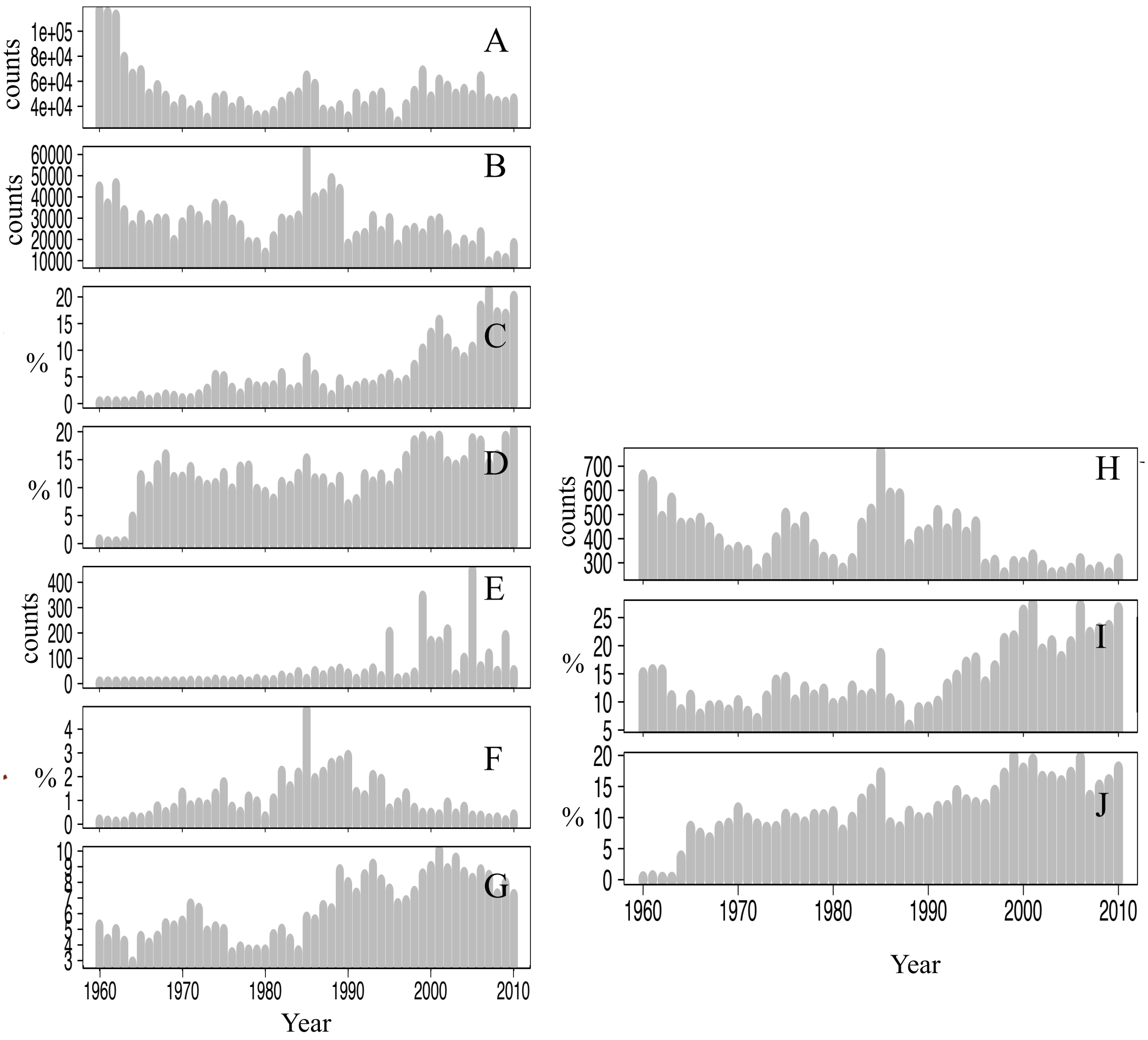


Figure 4.2 Basin-scale long-term trends: A) diatoms mean counts, B) dinoflagellates mean counts, C) coccolithophore mean occurrence, D) silicoflagellates mean occurrence, E) chlorophytes mean counts, F) Trichodesmium mean occurrence, G) mean Phytoplankton Colour Index, H) copepod mean counts, I) foraminifera mean occurrence, J) tintinnids mean occurrence.

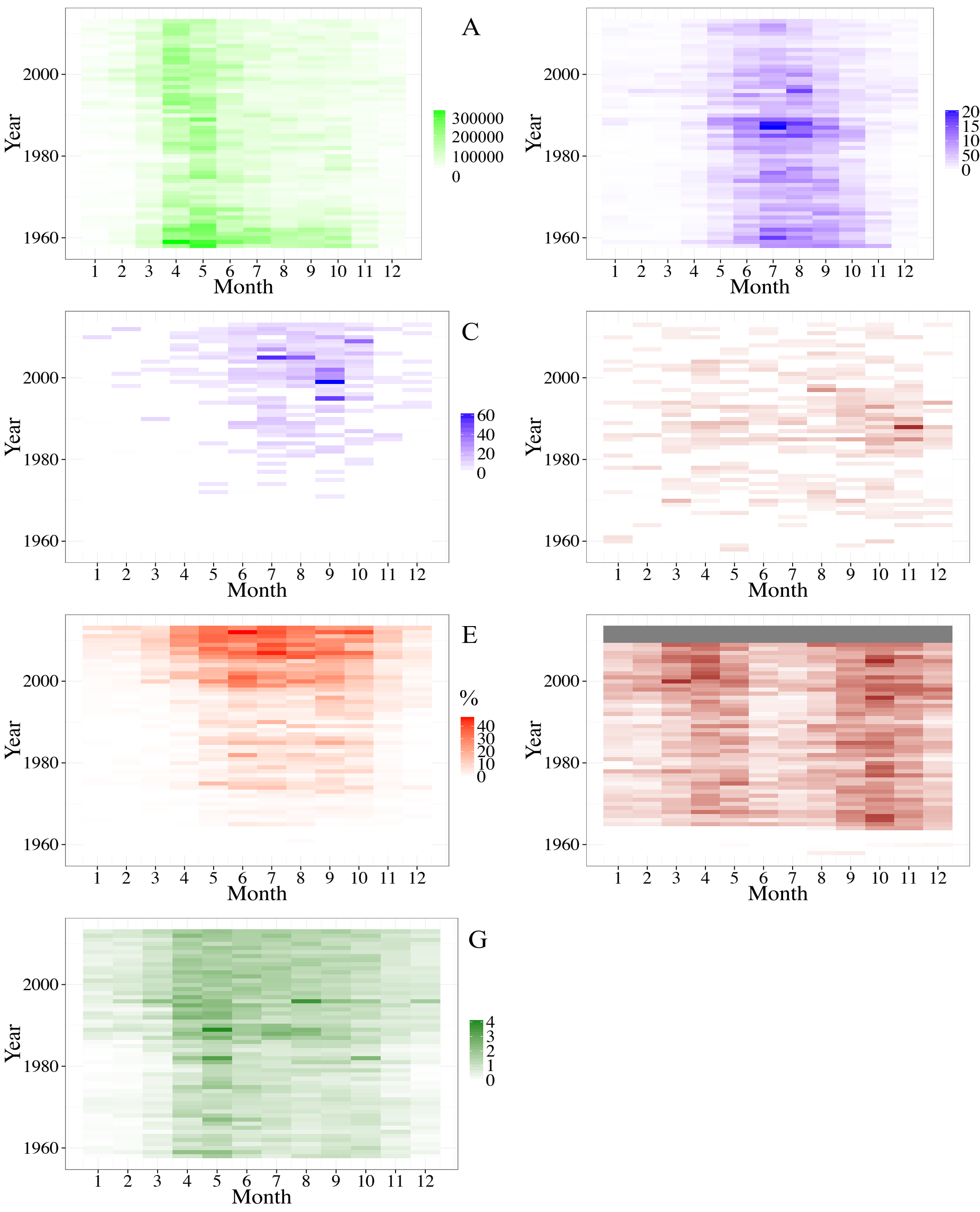


Figure 4.3. Monthly variability per phytoplankton group and PCI: A) diatoms mean counts, B) dinoflagellates mean counts, C) chlorophytes mean counts, D) Trichodesmium mean counts, E) coccolithophore occurrence, F) silicoflagellate occurrence, G) Phytoplankton Colour Index.

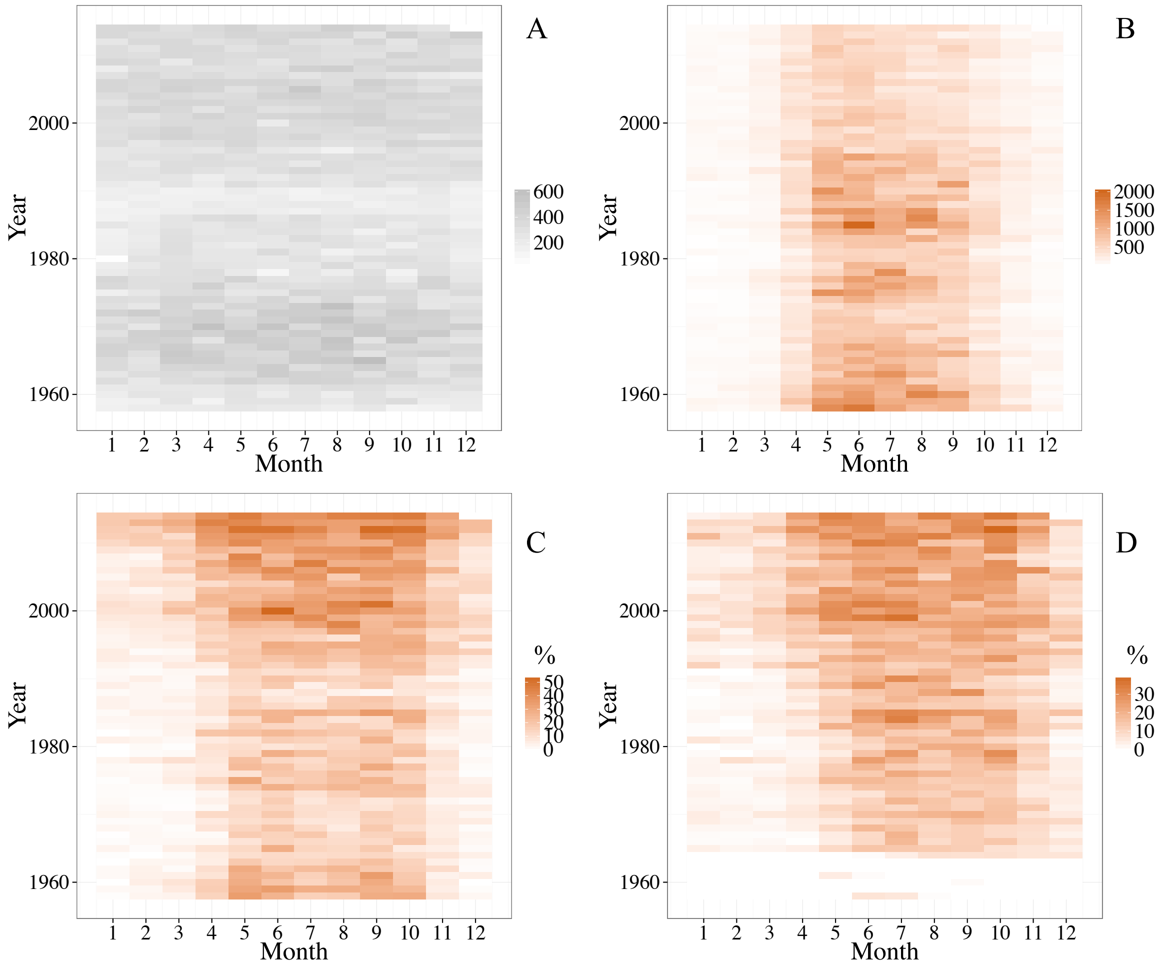


Figure 4.4. Monthly number of samples and variability per zooplankton group. A) number of samples, B) copepod mean counts, C) foraminifera occurrence, D) tintinnids occurrence.

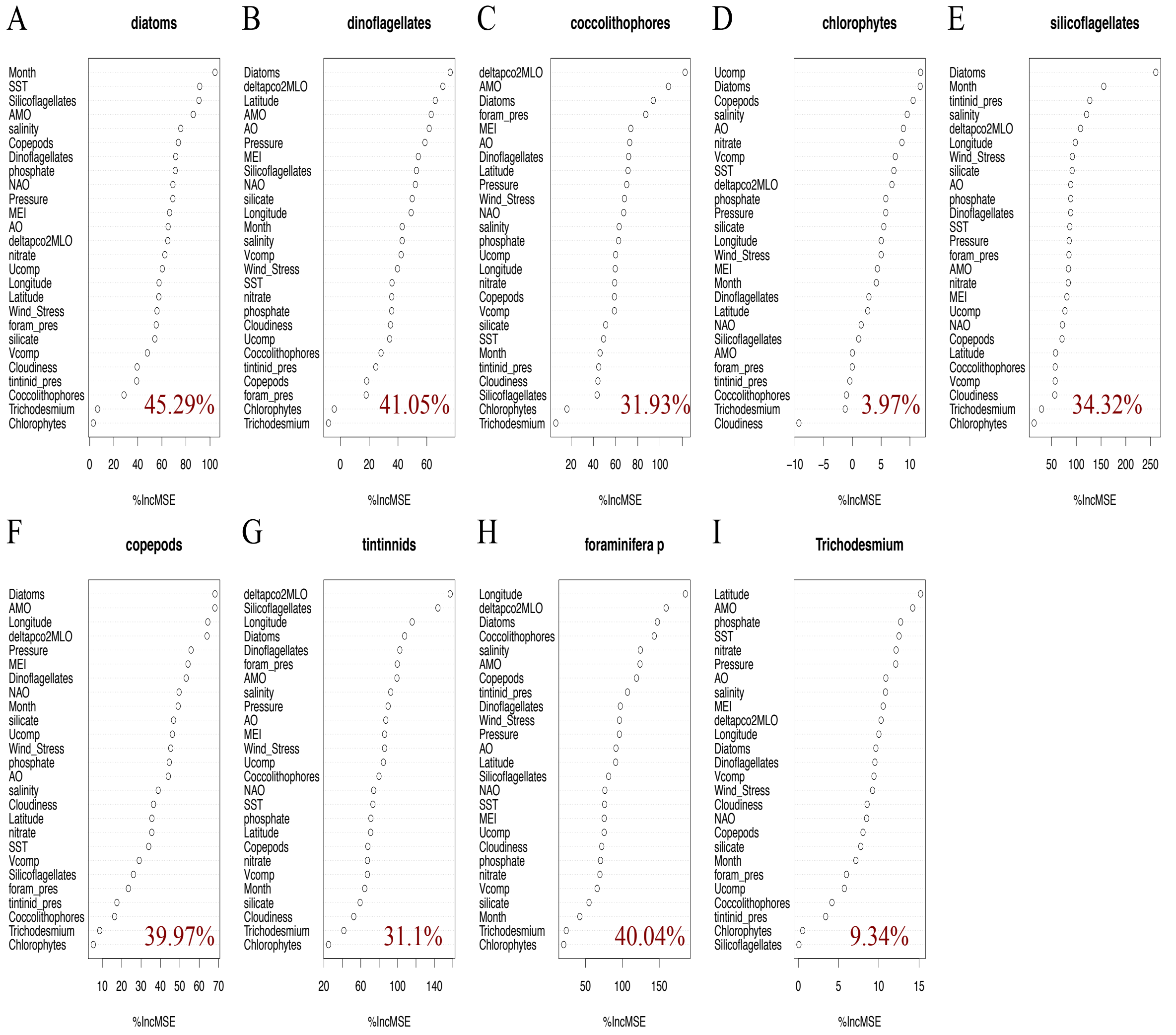


Figure 4.5. Variable importance plot for each group: A) diatoms, B) dinoflagellates, C) coccolithophores, D) chlorophytes, E) silicoflagellates, F) copepods, G) tintinnids, H) foraminifera, I) *Trichodesmium*

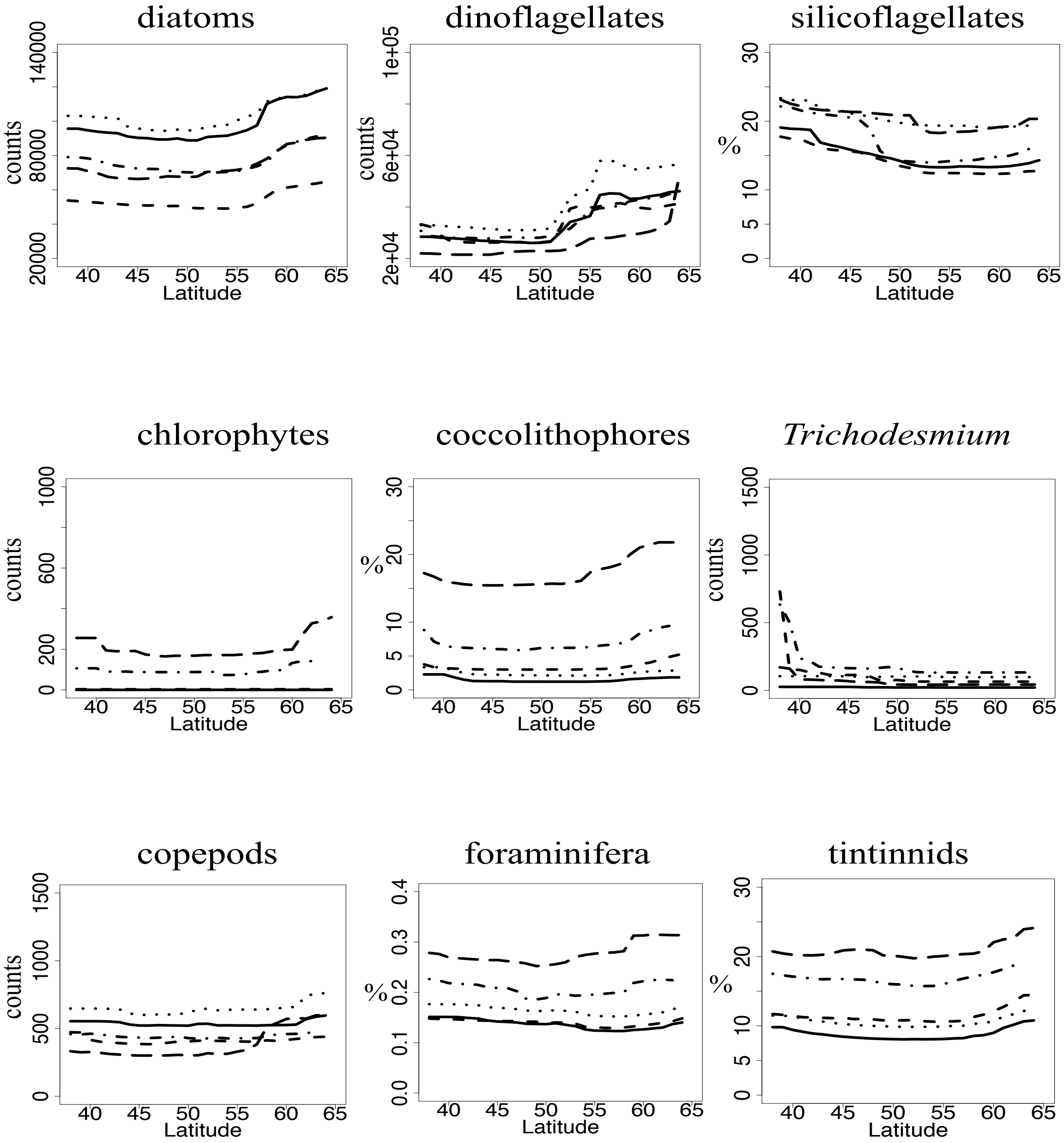


Figure 4.6. Decadal latitudinal and longitudinal variability based on partial dependence plots: A) diatoms mean counts, B) dinoflagellates mean counts, C) silicoflagellates mean occurrence, D) chlorophytes mean counts, E) coccolithophore mean occurrence, F) *Trichodesmium* mean counts, G) copepod mean counts, I) foraminifera mean occurrence, J) tintinnids mean occurrence.

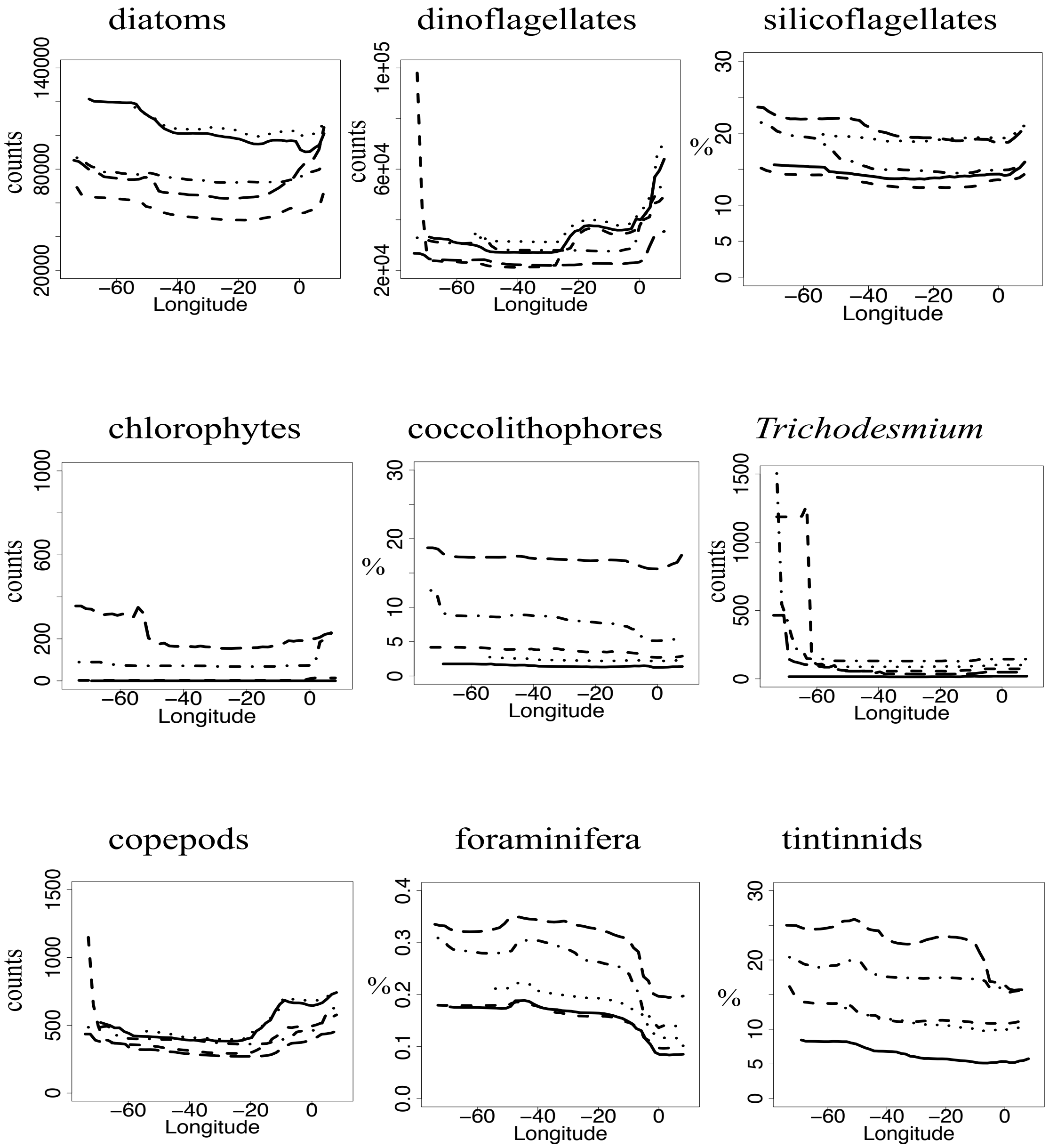


Figure 4.7. Decadal latitudinal and longitudinal variability based on partial dependence plots: A) diatoms mean counts, B) dinoflagellates mean counts, C) silicoflagellates mean occurrence, D) chlorophytes mean counts, E) coccolithophore mean occurrence, F) Trichodesmium mean counts, G) copepod mean counts, I) foraminifera mean occurrence, J) tintinnids mean occurrence.

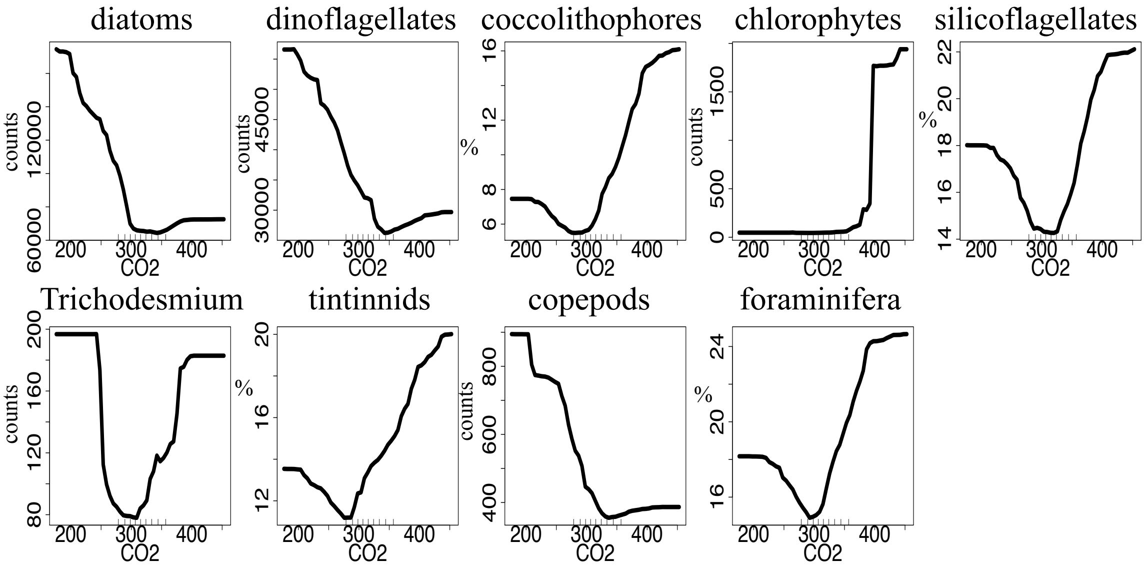


Figure 4.8. $p\mathrm{CO}_2$ partial dependence plots

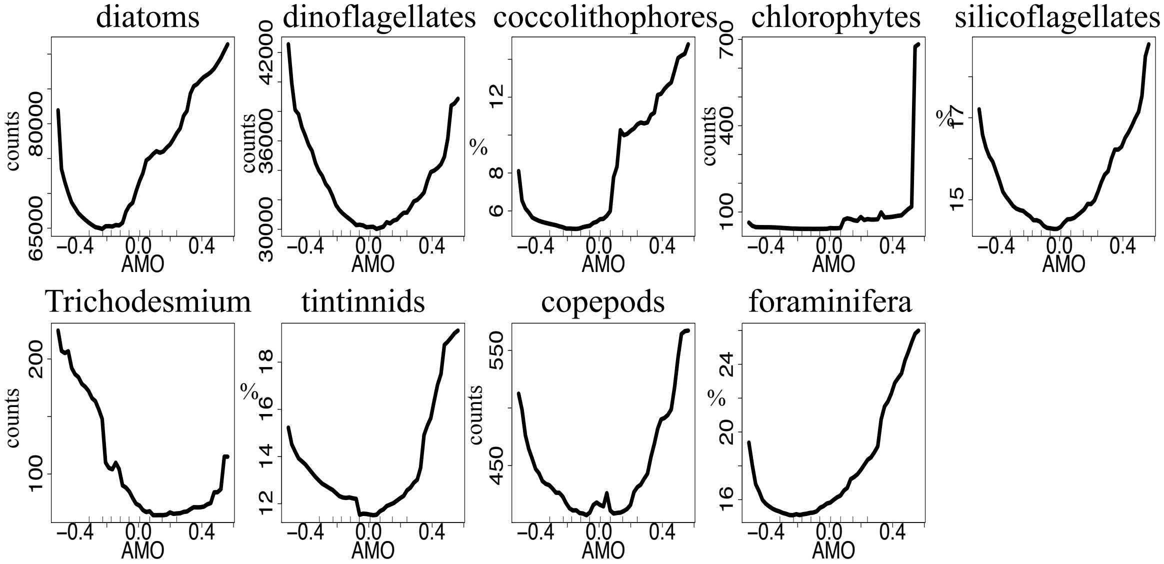


Figure 4.9. AMO partial dependence plots

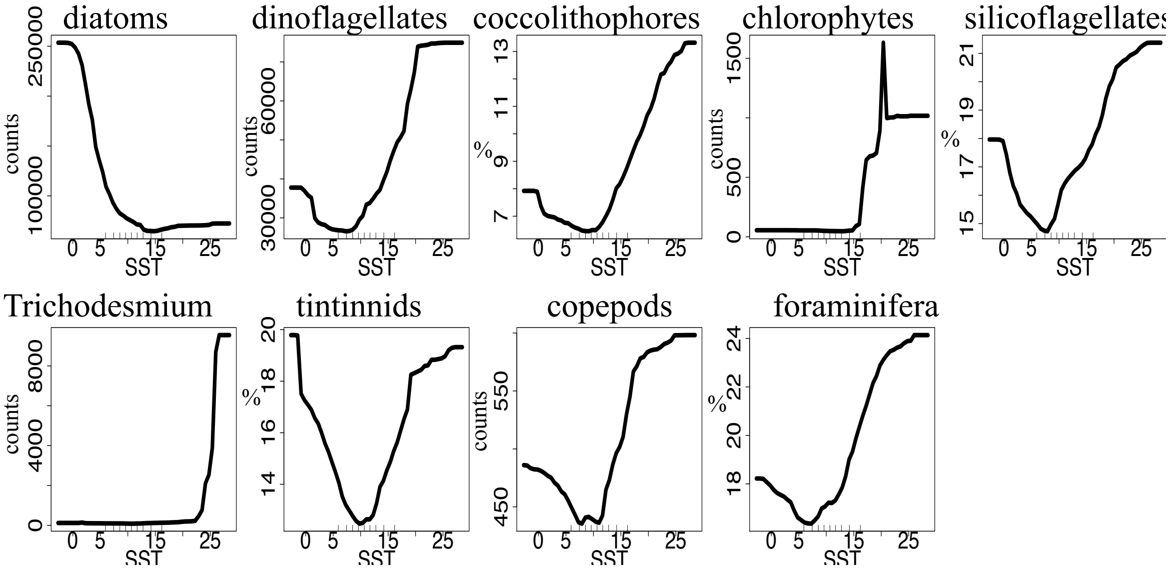


Figure 4.10. SST partial dependence plots

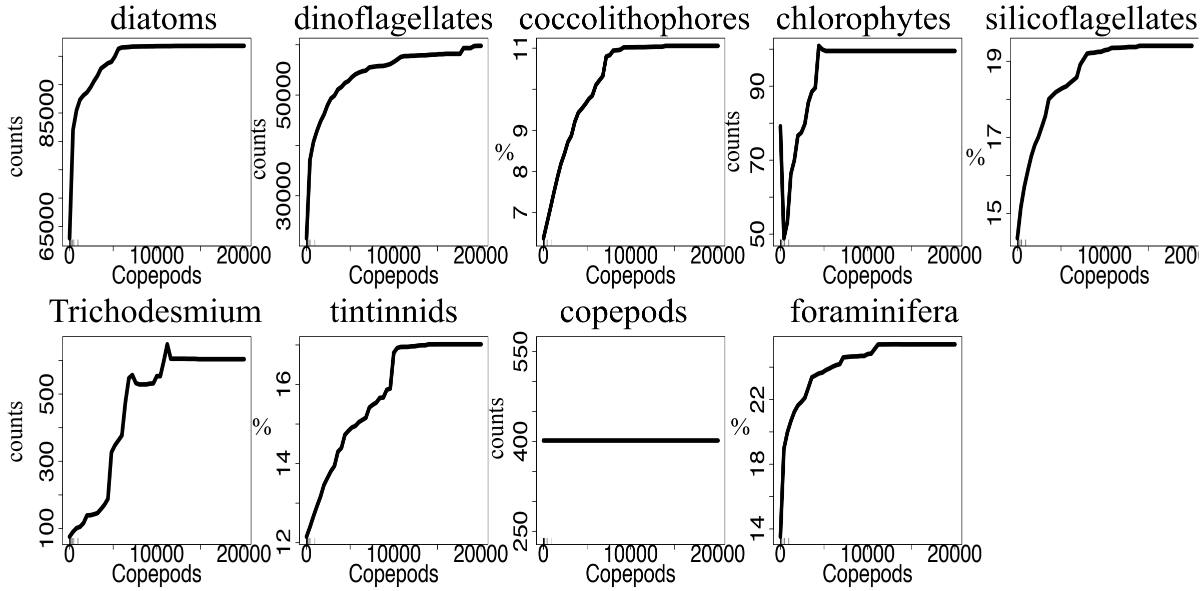


Figure 4.11. Copepods partial dependence plots

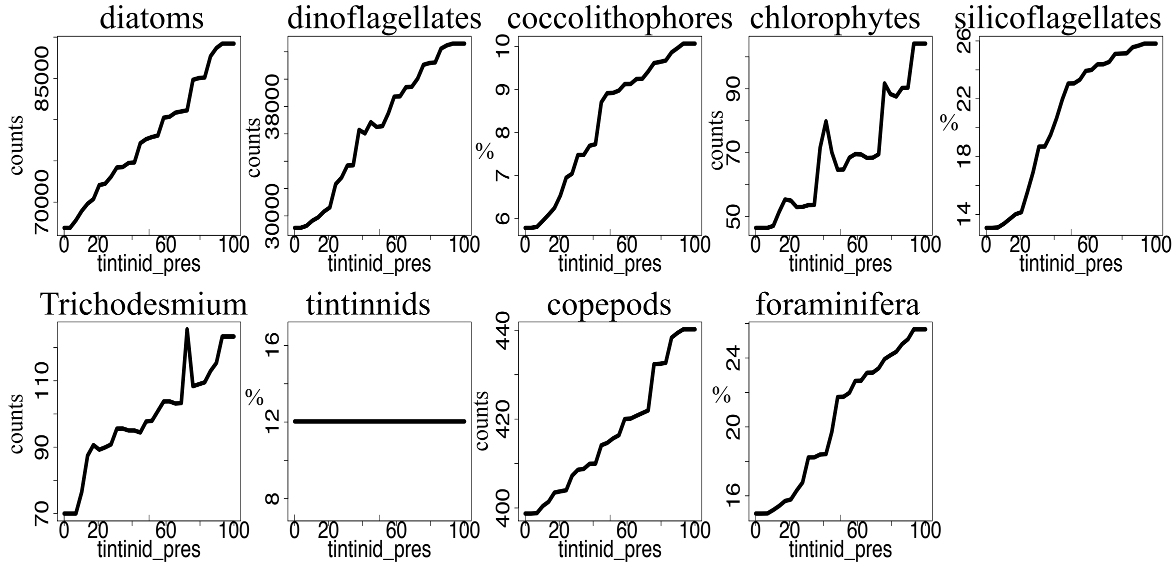


Figure 4.12. Tintinnids partial dependence plots

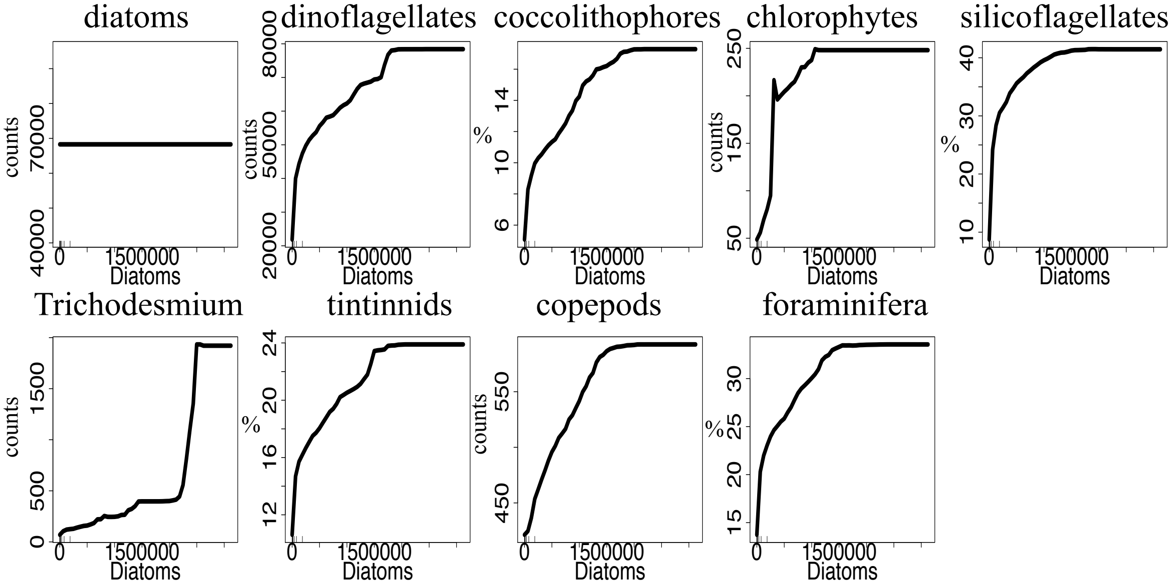


Figure 4.13. Diatoms partial dependence plots

5 GENERAL CONCLUSIONS

This study documents interdecadal changes in North Atlantic planktonic organisms that are key for biogeochemical cycling and primary productivity. I found an order of magnitude increase in an important calcifying group in recent decades and an episodic five-fold increase in one of the most significant marine nitrifiers, while the overall plankton communities experienced a profound reorganization towards smaller groups. I showed examples of changes driven by both anthropogenic and natural variability, including CO_2, AMO, dust events, as well as trophic interactions involving both bottom-up and top-down processes.

One of the highlights of this work is the spatial and temporal range of the analysis. This work was only possible thanks to the early development of a low-maintenance sampling device, the crew aboard ships of opportunity, international collaboration and continuation of sampling and analysis efforts for more than five decades. Such a long time series is crucial for understanding long periodicity climate modes such as AMO and to be able to identify climate change effects. This unusually long and extraordinarily extensive time series enabled exploring inter and intrannual variability changes for the entire North Atlantic basin. Moreover this field data complemented laboratory experiments and mesocosm studies necessary for scaling up processes.

One of the strengths of the CPR dataset is the potential to be used from species-level to group level or even trophic level. Our goal for this study was to identify changes at the functional group level but resolving whether these large-scale changes were driven by certain species and subsequently identifying the key players would be the logical next step. Future work should also compare our North Atlantic basin results with other CPR sister surveys (Australia and Pacific). While these span shorter time periods, they may corroborate or contradict my findings; for example, the hypothesis that coccolithophores are increasing globally due to increased atmospheric CO_2 levels or the shift towards smaller phytoplankton groups.

But despite the spatio-temporal resolution of the dataset, CPR surveys are discontinuous and heterogeneous. The gaps in space and time and accounting for multiple non-linear effects were clearly a challenge here and in any future studies. Here, I circumvented the problem by using a suite of powerful advanced statistical models that are able to isolate individual effects and handle incomplete datasets. More specifically, random forests have proven to be useful for ecological exploratory purposes because they do not require an underlying distribution assumption, nor much tuning. Despite the ability to reflect physiological and ecological relationships, none of the RF models showed strong predictive power, as they only capture half of the natural variability. While this low predictability is not desirable, it is nevertheless within the accepted ranges for natural biological systems. Some of the reasons for this low performance include spatial and temporal variability and heterogeneity that was lost when aggregating data into one-degree bins or missing parameters such as in situ nutrients, light, mixed layer depth, etc., which are known to affect phytoplankton distributions.

Nevertheless the findings described in this dissertation are of great value to the fields of plankton ecology and biogeochemistry because they either challenge general assumptions, support previous hypotheses or present new ideas. These findings are important in scaling up processes and bridging laboratory experiments to global processes.

For example, temperature has long been identified as a key parameter for plankton physiology and distribution; it has been used to constrain both remote sensing algorithms and modeling parameterizations. My analysis however does not find temperature as the top predictor for any plankton groups except diatoms. This work challenges the assumption that temperature limits *Trichodesmium* distribution at higher latitudes of the North Atlantic. *Trichodesmium* culture experiments often only focus on one or two strains from a few species of warm water origin. I suggest that the difficulty associated with maintaining a wide range of species or strains in laboratory cultures may have limited the experiments to a few predominantly warm-water strains that may not be representative of those in our study. In order to prove this hypothesis, I propose that additional strains or species from cold-water origin should be collected and cultured in the laboratory. Moreover, the lower numbers in extratropical waters and the resemblance of the 1960s CPR *Trichodesmium* distribution to the gulf stream current may have been misleading, suggesting that their presence in cold waters was due to drift. My work not only shows that *Trichodesmium* is not restricted to warm oligotrophic waters but instead suggest that aeolian iron input may have dictated interannual trends. This result reinforces the need for a dynamic dust component in ESMs and further work on dust production and deposition. Future work should also look for evidence of the *Trichodesmium* increase in the 1980s-1990s in the Bay of Biscay in sediments or isotopes, other time series (e.g. the Western English Channel time series) as well as in satellite imagery. Additionally iron enrichment and nitrogen fixation experiments in situ or with strains from the Bay of Biscay are crucial to test these hypotheses.

Another fundamental finding is the role of rising CO_2, levels for plankton. On one hand, CO_2 appeared to be an important predictor for most plankton groups but we also found that some of these relationships may not be directly mediated through physiology but due to a change in the community composition. On the other hand we showed that CO_2 plays an important role in coccolithophore growth rates and could explain the increasing trends in occurrence over the last decades. Our results suggest that including CO_2 in parameterizations of certain plankton growth rates will improve projections.

Due to the implications for global biogeochemical cycles, many ocean acidification experiments on plankton have focused on coccolithophores and *Trichodesmium*, but this study highlights the need to explore CO_2 effects on non-dominant groups. My analyses showed a long term increase in secondary groups such as silicoflagellates, planktonic foraminifera, chlorophytes, some of which may be related to temperature, nutrients, light variability or lower predator pressure but some of which may be, as my models suggest, related to ocean acidification. Another important outcome of this work is the realization that ocean acidification can affect different organisms and different processes depending on whether we focus on changes in CO_2 concentrations, pH, carbonate or bicarbonates. This has implications for experimental design (for example, whether acidification is simulated by adding acid rather than bubbling CO_2).

Among the intriguing results from the study of multiple phytoplankton groups are the functional relationships between tintinnids, diatoms and copepods and the other functional groups. Tintinnids seem to be an index of overall growth, while diatoms and copepods continue to grow after other organisms have saturated. Such relationships are consistent with allometric theories of grazing proposed in Dunne et al. (2005) and may represent interesting constraints for models.

In conclusion, this thesis gives another perspective to changes in North Atlantic marine plankton communities in the last fifty years. Different plankton groups show different sensitivities and magnitudes of response to anthropogenic and natural variability processes. Some of these can be explained, others require future work: additional parameters, experiments or longer time series. Regardless, there is a not a well-synchronized abrupt regime shift, as previously contended. The consequences of such an alteration of the oceanic plankton structure remain to be seen.

6 REFERENCES

6.1 APPENDICES

6.1.1 Challenges in relating climatological *p*CO_2 to coccolithophore occurrence

One question that emerges from the results of the Random Forests is why the relationship with *p*CO_2 over time is so different from the relationship with *p*CO_2 over space. In particular, why is the relationship with climatological *p*CO_2 so weak, and why does the partial dependence plot (Figure 2.5 F) show high coccolithophore probabilities under climatological low d*p*CO_2? Part of the answer is that *p*CO_2 is only one of a number of possible limiting factors and changes in *p*CO_2 over the course of a season may be correlated with some of those factors. In Figure 2.4 A-D, *p*CO_2 for a nominal year of 2005 from Takahashi (*15*) is plotted against climatological nitrate from the World Ocean Atlas (http://www.nodc.noaa.gov/OC5/woa09/) and mixed layer depth (http://dods.ipsl.jussieu.fr/cgi-bin/nph-dods/ocmip/phase5/DATA/gridded/de_Boyer_Montegut/mld_DR003.nc) for the North Atlantic region between 40-65N. In the wintertime, (December-February=DJF, black points, Figure 2.4 A, C), the highest values of *p*CO_2 are associated with high nutrients, but also with deep mixed layers, implying light limitation. A similar picture holds during the spring (March-May =MAM, red points, Figure 2.4 A, C). During the summer (June-August =JJA, black points, Figure 2.4 B, D), the highest values of *p*CO_2 are associated with shallow mixed layers, so that light limitation would be expected to be weak, but also with very low nitrate concentrations. By contrast, the lowest values of *p*CO_2 during the summertime are associated with much higher nutrients and relatively abundant light. Phosphate (not shown) shows a similar relationship. In the fall, (September-November=SON, red points Figure 2.4B,D) there are a few points with high $p\mathrm{CO_2}$ and high nutrients, but these are also associated with deep mixed layers. For this reason, extracting carbon limitation from modern datasets will be difficult. Note as well that the seasonal atmospheric $p\mathrm{CO_2}$ variability is smaller than the seasonal oceanic $p\mathrm{CO_2}$ variability. For example, in this specific case of year 2005, according to Mauna Loa records, the intra-annual atmospheric $p\mathrm{CO_2}$ varied between 376-382 ppm (~6ppm). In the panels below we show that the local $p\mathrm{CO_2}$ in the North Atlantic can be significantly lower than the global $p\mathrm{CO_2}$ (by ~100 ppm in certain months).

6.1.2 Growth rates and $\mathrm{CO_2}$.

In order to evaluate whether the increases in coccolithophore concentrations are consistent with laboratory results, we examined the relationship between $\mathrm{CO_2}$ and growth rate based on 41 experiments from 16 published studies (Zondervan et al. 2002, Langer et al. 2006b, Feng et al. 2008, Iglesias-Rodriguez et al. 2008, Feng et al. 2009, Langer et al. 2009b, Shi et al. 2009, Ramos et al. 2010, Rickaby et al. 2010, Hoppe et al. 2011, Lefebvre et al. 2012, Lohbeck et al. 2012, Rokitta & Rost 2012, Bach et al. 2013, Jin et al. 2013, Jones et al. 2013, Sett et al. 2014). Since the focus of most of these studies is PIC and POC production rates under future ocean acidification conditions, only few of them considered $\mathrm{CO_2}$ levels below 400ppm or explored a wide range of values. In those cases where $\mathrm{CO_2}$ was measured as a concentration, we converted it to a partial pressure (in ppm) based on:

$Pressure = K_H * concentration$

Where K_H is Henry's law coefficient, which is a function of the temperature and the gas. For example, for CO_2 at 298K, K_H=29.41 L atm mol^{-1}.

As mentioned earlier, the scatter is partly produced by differences in experimental treatments (temperature, species, strain, irradiance, nutrients, number of generations, etc.) but the general trend is clear. Growth rates increase between 200-400ppm but above 400-450 ppm the general tendency is for growth to stabilize. Although species-specific, temperature seems to modulate the sensitivity of growth, photosynthesis and calcification rates to increases in pCO_2 (Buitenhuis et al. 2008, Sett et al. 2014). Low light levels under high CO_2 concentrations can severely limit growth rates (Feng et al. 2009). But if light is not limiting (and coccolithophores show a notable lack of photoinhibition), POC production rates increase, growth rates accelerate, and some energy can be invested in PIC production, partially offsetting the negative impact of high CO_2 on calcification (Rokitta & Rost 2012). Furthermore, nutrients may override the negative impact of low CO_2 levels on coccolithophore growth rates. Under low CO_2 and high ammonia concentrations, coccolithophore growth rates increase and are comparable to those under high CO_2 levels, independent of ammonia to nitrate ratio (Lefebvre et al. 2012).

Only 5 studies showed little or no differences in growth rates between 200 and 400ppm (Zondervan et al. 2002, Langer et al. 2006b, Ramos et al. 2010, Rickaby et al. 2010, Hoppe et al. 2011). One other experiment showed weak dependence for some strains of *E. huxleyi* (strains 1256, 1216, 1212) (Langer et al. 2009b). We suggest that aside from species-specific responses, extreme treatments under high light, high temperatures and nutrient replete conditions may have overridden the CO_2 limitation by upregulation of CO_2 concentrating mechanisms (CCMs), masking the expected effect on growth rates. Similarly, some growth rates (Feng et al. 2009) were low considering the high temperature and irradiance treatments but this could be the result of the nutrient deplete and/or a mesocosm setup where coccolithophores compete with other phytoplankton groups. In other cases ((Shi et al. 2009, Jones et al. 2013) and strain 1238 (Langer et al. 2009b)), results agree with the overall trend but show high growth rates that could also be attributed to nutrient-replete, high light and high temperature conditions. We should emphasize that these nutrient-replete, high light and high temperature conditions are considered extreme conditions because, along with increased CO_2 and temperatures, future projections include an increase in stratification and a **decrease** in nutrients. Stratification will shoal the mixed layer depth and increase irradiance levels in the mixed layer but it will also decrease the upwelling of nutrients, negatively impacting diatoms (one of the strongest competitors) while potentially favoring coccolithophores both directly and indirectly by reducing competition with other groups.

In light of the results derived from this compilation and the CPR analyses, we suggest that the "greenhouse conditions" of high $CO_{2,}$ increased stratification and higher SST-accelerated growth rates in the last 50 years and this translated into a greater number of coccolithophore observations in CPR samples. A recent study using ship-board continuous cultures from the North Atlantic proves that these conditions favor a differential increase in coccolithophore growth rates and higher relative abundances with respect to other phytoplankton groups (Feng et al. 2009), buttressing our hypothesis. A CO_2 enrichment effect differentially favors coccolithophores, whose outstanding low affinity for CO_2 (Rost et al. 2003) and extremely high half-saturation coefficient for CO_2 are unique and several-fold higher than diatom species *(Rost et al. 2003)*. Changes in growth rates are most noticeable below 500ppm, where cells need to invest energy in carbon concentrating mechanisms. At higher CO_2 levels, more energy can be diverted into biosynthesis, PIC, POC and growth until the decrease in carbonate ions will become excessive and will lead to a reduction or inhibition of calcification. Based on these studies, growth rates will likely remain maximal for several decades, while calcification will ultimately decline.

Another important outcome from this study is the difference between global atmospheric trends and the local oceanic pCO_2 variability and how this is not addressed in laboratory setups. Laboratory experiments focus on global atmospheric CO_2 levels (~320-390ppm in this study) and these seem to produce a small change in growth rates in Figure 2.8 (~0.2), but we have also shown here that these atmospheric increases translate into a much greater local oceanic pCO_2 variability (170-420 ppm). Therefore we show both variabilities in Figure 2.8. Local dissolved pCO_2 is the one that phytoplankton will truly experience and it can be significantly lower than the global atmospheric pCO_2 (by ~100 ppm in certain months in the North Atlantic), the response in growth rate within this oceanic pCO_2 range is now of importance (from ~0.2-1.2 day^{-1}). We note that no one point in the ocean will have seen this entire range of pCO_2 levels over the past 50 years. As is clear from Figure 2.4 and Figure 2.6, some locations where pCO_2 lies well below the atmospheric average will experience the lower part of the range. Others, which are far better equilibrated with the atmosphere, will experience the upper part. Our argument is that given a linear scaling between growth rate and abundance, our results are broadly consistent with the partial dependence seen in RF_LOCAL. It is by no means obvious, however that the scaling should be linear. Observations of changes in diatom concentration during iron fertilization experiments, for example, show that a doubling of growth rate can lead to an 8-fold increase in biomass. If differences in sensitivities or response to CO_2 are also associated with certain coccolithophore strains or species, one can easily scale the pCO_2 partial dependence in RF_LOCAL to fit within the envelope of growth rates.

We would like to emphasize that this compilation does not intend to be exhaustive but rather to support a possible underlying mechanism for the coccolithophore increase found in the past decades. In fact, four conclusions arise from it: 1) further studies on the effect of CO_2 enrichment on species other than *E. huxleyi* are clearly needed, 2) consensus on experimental treatment conditions is essential to make studies comparable, 3) the difference between global atmospheric CO_2 variability and local oceanic CO_2 concentrations needs to be considered, and 4) more realistic approaches such as nutrient-depleted, community-based or mesocosm experiments are essential to upscale laboratory studies to natural populations. These next steps will allow for predictions of coccolithophore populations in the future.

6.1.3 Alternative mechanisms

In this section we show additional results that explain why we discarded alternative mechanisms for the increase in the probability of coccolithophore occurrence in the last 5 decades:

Sea Surface Temperature (SST): The partial dependence plot for SST (Figure 2.10A) showed a minimum occurrence of coccolithophores at ~8°C and tripling at ~25°C. The curve is consistent with laboratory growth rates for both *Emiliania huxleyi* and *Gephyrocapsa oceanica* and with the known temperature-dependency of coccolithophore growth rates in the laboratory (Eppley 1972, Buitenhuis et al. 2008) and natural populations (McIntyre & Be 1967). However, in situ SST is not ranked as one of the top predictors (Figure 2.5 A to C) and the variability explained is much lower than that of AMO or CO_2. Part of the reason is that the increasing trend in local SST is relatively small across the 50-year time-period (of order 1°C at most points, which Figure 2.10 A would suggest could result in a change of, at most, 2%) and comparatively smaller than the increase in CO_2. According to our results, temperature alone cannot explain the large changes in coccolithophore occurrence.

Interactions with other phytoplankton groups: Our results show that unlike other phytoplankton groups, diatoms and dinoflagellates are relatively good predictors of coccolithophore occurrence (Figure 2.5 A to C. Partial dependence plots for co-located diatoms and dinoflagellate abundances (Figure 2.10B, C) showed that there is a greater probability of finding coccolithophores at a certain place and time when these groups are abundant. We suggest that abundance of collocated diatoms and dinoflagellates represent a combination of optimal light, nutrient, and temperature conditions for phytoplankton growth, in general. However, the relationship found in the partial dependence plots at the local monthly 1-degree level disagrees with basin-scale long-term behavior, where the increasing occurrence of coccolithophores contrasts with the overall declines in the abundance of diatoms and dinoflagellates (Figure 2.7 D, E (Hinder et al. 2012a)). The contradiction is not fundamental and could be explained by these groups capturing annual and spatial variability in the partial dependence plots but not the long-term trend. However, long-term declines in diatoms and dinoflagellates could reduce either the concentration of zooplankton that also graze on coccolithophores (something we evaluate below) or reduce competition with coccolithophores for nutrients. Evaluating the last hypothesis is complicated by the fact that there are other possible competitors not collected by the CPR (e.g. nano and picoplankton).

Zooplankton: Another possible cause for coccolithophore increase is a decrease in the grazing pressure. Exact predators of coccolithophores are unknown but since coccoliths have been found in tintinnid lorica (Henjes & Assmy 2008), copepod guts and fecal pellets (Honjo & Roman 1978, Harris 1994, Milliman et al. 1999), we considered these groups. Our results (Figure 2.5 A to C) show that none of these groups rank high in variable importance plots, suggesting that a reduction in grazing pressure is not driving the increase in coccolithophore occurrence.

Nutrients: We hypothesized that the increase in coccolithophore occurrence could also be driven by either: (1) an increase in nutrients, in which case we would expect large phytoplankton to increase as well (perhaps more than the nanophytoplankton), or (2) a decrease that leveraged competition with these microphytoplankton. Given the lack of information on long-term nutrient trends, this hypothesis could not be fully tested (see methods). However, our RF analyses do not rank nutrients among the top predictors. As noted above, if instead of comparing the RF in situ results, we examine the basin-wide time series, CPR data show a long-term decline for both diatoms and dinoflagellates

(Hinder et al. 2012a) (Figure 2.7 D , E) that would undermine the first hypothesis, while the low variable importance for copepods and tintinnids undermines the second.

Longitude was ranked as an important predictor in all the models. This may reflect previous work on coccolithophore biogeographical regions (McIntyre & Be 1967), which shows a contrast across the North Atlantic Current. The partial dependence plot (Figure 2.10 D) shows lower probabilities in the eastern side of the basin, which is consistent with our regional time-series (Figure 2.3) and with the previous biogeographical results. However, the small overall range of variability in coccolithophore probability explained by longitude suggests that shifts in biome boundaries cannot explain the long-term trend.

Other: Other alternatives include: changes in growth-limiting micronutrients (e.g. zinc, iron), or alteration of collection efficiency due to more Transparent Exopolymer Particles (TEP). We do not have the observational data to test such hypotheses, but note that these alternatives would also be expected to increase the abundance of other phytoplankton groups.

In conclusion, we have discussed several bottom-up and top-down mechanisms for the coccolithophore trends based on RF analyses. Some of these could not be fully tested due to lack of long-term observations or further information on the ecology of coccolithophores. However, none of them explain why coccolithophore occurrence increased by an order of magnitude, while microphytoplankton simultaneously declined.

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7 CURRICULUM VITAE

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EDUCATION

PhD. Biological Oceanography, Johns Hopkins University. Baltimore, MD. January 2016
  Dissertation: Anthropogenic change versus natural variability: lessons learned from the Continuous Plankton Recorder
  Advisors: Dr. Anand Gnanadesikan & Dr. Carlos del Castillo

M.S. Biological Oceanography. University of Puerto Rico, Mayaguez. Puerto Rico. 2010
  Thesis: Ecological Aspects of Sponges in Mesophotic Coral Ecosystems.
  Advisor: Dr. Roy Armstrong

B.S. Biology. Complutense University of Madrid, Spain. 2005. Major in Zoology.
  Thesis: Sponge Population Census along the Southeastern Coast of the Sinai Peninsula.

Erasmus Program. Environmental Marine Sciences Dept. University of Genoa, Italy. 2002-2003

International Scientific Baccalaureate, Madrid (Spain). Graduated with honors in 1999

ADDITIONAL TRAINING AND WORKSHOPS

2015: Data Carpentry workshop. Baltimore. June 25-26.

2014: Ecological Dissertations in the Aquatic Sciences. University of Hawaii. October 19-25.

2011: - Ocean Optics: Calibration and Validation. University of Maine. July 11-29.
  - Remote Sensing for Biological Oceanographers. Cornell University. June 3-17.

2008: Light and photosynthesis in coral reefs. Universidad Nacional Autonoma de Mexico. 2007: Taxonomy & Ecology of Sponges. Smithsonian Tropical Research Institute, Panama. 2005: Geographic Information Systems. Universidad Politécnica de Madrid. 2 weeks.

EMPLOYMENT

2010-2015	Graduate Research Assistant, Johns Hopkins Applied Physics Laboratory. Advisor: Dr. del Castillo
2015	Graduate Teaching Assistant. Johns Hopkins. Advisors: Dr. Waugh and Dr. Zaitchik
2006-2010	Graduate Research Assistant, University of Puerto Rico. Advisor: Dr. Armstrong
2005	Research Assistant, Ecology Department Universidad Complutense de Madrid.

TEACHING EXPERIENCE

Guest lecture on “Remote Sensing applications for Biological Oceanography” as part of the course “Remote Sensing of the Environment” taught by Dr. del Castillo and Dr. Zaitchik. Johns Hopkins University. November 19, 2014

Graduate Teaching Assistant. “Climate Change: Science and Policy” taught by Dr. Waugh and Dr. Zaitchik. Johns Hopkins University. Spring semester 2015.

ADDITIONAL EXPERIENCE IN RESEARCH OR CONSERVATIONAL PROJECTS

Hyperspectral airborne remote sensing of coral reefs in southwestern Puerto Rico using NASA AVIRIS. Center for Subsurface Sensing Imaging Systems (CenSSIS), Department of Marine Sciences, UPR. Supervisors: Dr. Goodman, Dr. Guild, and Dr. Armstrong.

Irradiance data processing and monitoring, NOAA Integrated Coral Observing Network Coral Reef Early Warning System (ICON/CREWS) La Parguera, Puerto Rico. 2010. Dr. Armstrong

Center for Subsurface Sensing Imaging Systems (CenSSIS) SeaBED Autonomous Underwater Vehicle imagery analysis. Department of Marine Sciences, UPR. 2006-2010. Supervisor: Dr. Armstrong.

Environmental Volunteering in the National Marine Park of Cabrera Island. SEO/Birdlife and National Spanish Parks. 27th September- 4th October 2004. Supervisor: Ana Íñigo

Human impact and habituation behavior of blackbird (*Turdus merula*) populations in Madrid. Natural Sciences National Museum. May-October 2004. Supervisor: Dr. Rodríguez Prieto.

Loggerhead Sea Turtle (*Caretta caretta*) conservation project at Zakynthos National Marine Park. Archelon (The Sea Turtle Protection Society of Greece). September 2003. Supervisor: Kostis Grimanis

Sponge Population Census along the Southeastern Coast of the Sinai Peninsula. Dipartimento per lo studio del Territorio e delle sue Risorse. University of Genova, Italy. July 2003. Supervisor: Dr. Pronzato, Dr. Milanese

Environmental Volunteering. Asociación de Naturalistas del Sureste español (A.N.S.E.). Murcia, Spain. August 2002

Whale and Dolphin Conservation and Research Volunteer Project. Proyecto Ambiental Tenerife. 17-30 July 2001. Supervisor: Edward Bentham

Interactions between Killer Whales and Traditional Fishing Methods in the Strait of Gibraltar, Spain. Sociedad Oceánica de Cetáceos (SOC).10-16 May 2000. Supervisor: Mario Morcillo

AWARDS, SCHOLARSHIPS AND FELLOWSHIPS

2013	Associated External Researcher Fund, Sir Alister Hardy Foundation for Ocean Science.
2012	- Ocean Optics Meeting Student Travel Award from The Oceanography Society. - EPS and GH Williams Fund for summer fieldwork
2011-2014	Johns Hopkins Applied Physics Laboratory Fellowship
2011	American Society of Limnology and Oceanography (ASLO) Student Travel Award.
2008	- ICRS Field trip scholarship. Gulf Stream Natural Gas. July 2008 - José Trias Monge Travel Award, University of Puerto Rico
2007-2010	Sea Grant Travel Awards (2007, 2008, 2009, 2010)
2006-2010	Center for Subsurface Sensing Imaging Systems (CenSSIS). Research Assistantship
2005-2006	University of Puerto Rico and Complutense University graduate scholarship.
2005	Research assistantship at the Department of Ecology, Complutense University.
2002-2003	European Erasmus Student Exchange Scholarship University of Genoa, Italy.
1999	Beca del Estado por Méritos Académicos, (Spain) Graduated from high school with Honors, thus earning scholarship to underwrite the first year of university.

PUBLICATIONS

Rivero-Calle S, Gnanadesikan A, Del Castillo CE, Balch WB, Guikema S. Multidecadal increase in North Atlantic coccolithophores and the potential role of rising CO_2. Science, 2015: 350 (6267), 1533-1537.Published online 26 November 2015 [DOI:10.1126/science.aaa8026]

Co-authors in alphabetical order: R. Appeldoorn, R. Armstrong, D. Ballantine, C. Caldow, Christopher F.G. Jeffrey, **S. Rivero-Calle**, H. Ruiz, E. Weil, AGRRA, CARICOMP and NOAA Biogeography Branch. GCRMN Caribbean report: Status and Trends of Caribbean Coral Reefs: 1970-2012. Puerto Rico Chapter. Editors: J Jackson, M. Donovan, K. Cramer, V. Lam. 2014 http://cmsdata.iucn.org/downloads/caribbean_coral_reefs___status_report_1970_2012.pdf

Co-authors in alphabetical order: A. Arellano, N. Briggs, F. Cao, A. Chase, H. Chen, A Dave, C. Goyens, F. Henderikx, C. Kearney, M. Kheireddine S. Mishra, A. Neeley, M. Omand, L. Powers, A. Reisinger, **S. Rivero-Calle**, B. Russell, B. Seegers, R.

Vandermeulen, W. Zhu. Technical document on Measurement, Processing, and Analysis Techniques for Optical Oceanography Data. University of Maine. 2011.

Rivero Calle, S. Ecological Aspects of Sponges in Mesophotic Coral Ecosystems. M.Sc. dissertation, University of Puerto Rico, Mayaguez (Puerto Rico), 2010. http://bio-optics.uprm.edu/docs/thesis_riverocalle.pdf

Armstrong RA, Singh HA, **Rivero S**, Gilbes F. Monitoring Coral Reefs in Optically-Deep Waters. Proceedings of the11th International Coral Reef Symposium. 2008. Vol. 1; 593-597.

Rivero-Calle S. Armstrong RA, Soto-Santiago FJ. Biological and physical characteristics of a mesophotic coral reef: Black Jack reef, Vieques, Puerto Rico. Proceedings of the 11th International Coral Reef Symposium. 2008. Vol. 1: 567-571.

MANUSCRIPTS SUBMITTED OR IN PREPARATION

Rivero-Calle S, Del Castillo CE, Gnanadesikan A, Dezfuli A., Zaitchik B. Johns. D. (**under review**). Interdecadal *Trichodesmium* variability in cold North Atlantic waters. Global Biogeochemical Cycles.

Asch R, Pilcher D, **Rivero-Calle S**, Holding J. **(in preparation**). Demystifying models: Answers to Ten Common Questions that Ecologists Have about Earth System Models.

Coble A., Kremer C., Asch R., **Rivero-Calle S**., Strock K., Holding J., Finiguerra M. (**in preparation**). Climate is variable, but is our science?

Malinverno E., **Rivero-Calle S**., Dimiza M., Triantaphyllou M.V. (**in preparation**) Coccolithophore contribution to sea surface PIC along a latitudinal transect in the West-Pacific sector of the Southern Ocean under non-bloom conditions.

Corman J, **Rivero-Calle S**, Fields L, Heffner L, Smyth A. (**in preparation**). Multiple stressors: eutrophication and acidification in calcifiers.

Rivero-Calle S, Gnanadesikan A, Del Castillo CE. (**in preparation**). Plankton changes in the Anthropocene: climate change or natural variability?

Rivero-Calle S, Gnanadesikan A, Del Castillo CE. (**in preparation**). Early warning signals and tipping points in the North Atlantic phytoplankton regime shift.

INVITED TALKS AND SEMINARS

Rivero-Calle S, Del Castillo CE, Gnanadesikan A, Dezfuli A., Zaitchik B. Johns. D. Interdecadal *Trichodesmium* variability in cold North Atlantic waters. Global

Modeling and Assimilation Office, NASA Goddard Space Flight Center, Greenbelt, MD. December 2015.

Rivero-Calle, S., Gnanadesikan A, Del Castillo CE, Balch WB, Guikema S. Multidecadal increase in North Atlantic coccolithophores and the potential role of rising CO_2. OneNOAA Science Seminars. Spring 2016.

Rivero-Calle S, Gnanadesikan A, Del Castillo CE, Balch WB, Guikema S. Multidecadal increase in North Atlantic coccolithophore presence driven by CO_2 and warming. Ocean Ecology Lab, NASA Goddard Space Flight Center, Greenbelt, MD. June 2015.

PRESENTATIONS

Rivero-Calle S., Del Castillo C.E., Gnanadesikan A., Dezfuli A., Zaitchik B. Multiyear *Trichodesmium* increase in the North Atlantic at higher latitudes (38-65N) in the 1980's. Ecological Society of America. Baltimore, August 2015. Oral

Rivero-Calle, S., Del Castillo C.E., Gnanadesikan A., Dezfuli A., Zaitchik B. Dust deposition and *Trichodesmium* increase in temperate North Atlantic from 1980-1990s. Ocean Carbon and Biogeochemistry (OCB) Workshop, Woods Hole, MA. July 2015. Poster

Malinverno E., **Rivero-Calle S**., Dimiza M., Triantaphyllou M.V. Coccolithophore contribution to sea surface PIC along a latitudinal transect in the W-Pacific sector of the Southern Ocean under non-bloom conditions. International Nannoplankton Association Meeting, Philippines, March 2015. Poster

Rivero-Calle, S. Regime Shifts in Aquatic Ecosystems. ECO-DAS. Hawaii. October, 2014. Oral

Rivero-Calle, S, C.E. Del Castillo, A. Gnanadesikan, W.B. Balch, S. Guikema. Have coccolithophore abundances increased in the North Atlantic over the last 50 years? Evidence from the Continuous Plankton Recorder. International Nannoplankton Association Meeting, Crete, Greece. October, 2014. Oral

Rivero-Calle, S, A. Gnanadesikan, C.E. Del Castillo, W.B. Balch, S. Guikema. Why do CPR coccolithophores seem to be increasing in the North Atlantic in the last 50 years? Is the North Atlantic becoming the next Black Sea? Ocean Sciences Meeting, Honolulu, Hawaii. February, 2014. Oral

Rivero Calle, S. and Del Castillo, C. Climate Change and Long-Term Trends of Coccolithophores in the North Atlantic (1960's-present). Ocean Optics Meeting. October 8-12, 2012. Glasgow, UK. Poster.

Goyens, C.; **Rivero-Calle, S.;** Boss E. Ocean Optics Course 2011: Calibration and Validation for Ocean Color Remote Sensing. NASA Carbon Cycle & Ecosystems Workshop. Arlington, VA. October 2011. Poster.

Rivero-Calle, S.; Goyens, C.; Seegers, B.; Freitas, F. H.; Cao, F.; Mischra , S.;

Vandermeulen, R. Closure in Calibration and Validation of Ocean Color Remote Sensing: Ocean Optics Summer Course 2011. Ocean Sciences Meeting, Salt Lake City, Utah. February, 2012. Poster.

Rivero-Calle, S.; Goyens, C.; Dave, A.; Chase, A.; Omand, M.; Seegers, B.; Vandermeulen, R. Ocean Optics Summer Course: Building a community of Optical Oceanographers. Ocean Sciences Meeting, Salt Lake City, Utah. February, 2012. Poster.

Rivero-Calle S. and R.A. Armstrong. Ecological Aspects of Sponges in Mesophotic Ecosystems. ASLO Meeting San Juan, PR. February, 2011. Oral

Rivero-Calle S. and R.A. Armstrong Ecological Aspects of Sponges in Mesophotic Coral Ecosystems. 8th World Sponge Conference. Girona, Spain. September 20-24, 2010. Poster.

Rivero-Calle S. and R.A. Armstrong. Diversity and Abundance of Sponges at the Mesophotic Reef of Bajo de Sico, Puerto Rico. 34th Scientific Meeting of the Association of Marine Laboratories of the Caribbean (AMLC). Dominica. May, 2009. Oral

Rivero-Calle S. and R.A. Armstrong. Patterns of Vertical Zonation in Mesophotic Reef Communities of Southwestern Puerto Rico and Vieques Island. 11th International Coral Reef Symposium (ICRS). Fort Lauderdale, Florida. July 2008. Oral.

Rivero S. and R.A. Armstrong. Characterization of Shallow and Deep Reef Communities of Vieques Island using the Seabed AUV. Caribbean Coral Reef Investigator (CCRI) Meeting San Juan, Puerto Rico. December 2008. Oral.

Rivero S. and R.A. Armstrong. Characterizing The Deep Zooxanthellate Coral Reefs of Puerto Rico with the Seabed Autonomous Underwater Vehicle. 33rd Scientific Meeting of the Association of Marine Laboratories of the Caribbean (AMLC). St Thomas. June, 2007. Poster.

Zayas-Santiago, C.; **Rivero-Calle, S**.; Armstrong, R.A.; and Gilbes-Santaella, F. Spectral Libraries of Submerged Biotopes for Benthic Mapping in Southwestern Puerto Rico (2007). SeaBED Presentations. Paper 4. http://hdl.handle.net/2047/d10009267 . Poster

OTHER

Driver’s license: July 2000.
SSI Open Water Diver: June 2003. PADI Advanced Diver 2006, Nitrox Certified 2006.
Emergency First Response (EFR), First Aid and CPR 2009, Rescue Diver 2010.
U.S. Coast Guard Auxiliary Boating Skills and Seamanship Course, 2005.

INFORMATION TECHNOLOGY

R, MATLAB, IDL, ferret, python, UNIX / Bash scripting.
SeaDAS, ArcView, ENVI, ERDAS

LANGUAGES SPOKEN

Spanish, English, Italian, French, Japanese.

PROFESSIONAL COLLABORATORS

Roy Armstrong, University of Puerto Rico
Barney Balch, Bigelow Laboratory for Ocean Sciences
Seth Guikema, University of Michigan
Rebecca Asch, Princeton University
Darren Pilcher, Pacific Marine Environmental Laboratory
Johnna Holding, Institut Mediterrani d'Estudis Avançats (IMEDEA), Spain
Jessica Corman, University of Wisconsin-Madison
Ashley Coble, University of New Hampshire
Ashley Smyth, Virginia Institute of Marine Science
Leanna Heffner, Louisiana State University
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Johnna Holding, Mediterranean Institute for Advanced Studies (IMEDEA)
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David Johns, Sir Alister Hardy for Ocean Science (SAHFOS), UK
Elisa Malinverno, Milano University
Maria Triantaphyllou, University of Athens

PROFESSIONAL AFFILIATIONS

Association for the Sciences of Limnology and Oceanography (ASLO)
The Oceanography Society (TOS)
International Nannoplankton Association (INA)
Ecological Society of America (ESA)
Earth Science Women Network (ESWN)