PHYTOPLANKTON

Millennial-scale plankton regime shifts in the subtropical North Pacific Ocean

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Climate change is predicted to alter marine phytoplankton communities and affect productivity, biogeochemistry, and the efficacy of the biological pump. We reconstructed high-resolution records of changing plankton community composition in the North Pacific Ocean over the past millennium. Amino acid–specific $\delta^{13}C$ records preserved in long-lived deep-sea corals revealed three major plankton regimes corresponding to Northern Hemisphere climate periods. Non–dinitrogen-fixing cyanobacteria dominated during the Medieval Climate Anomaly (950–1250 Common Era) before giving way to a new regime in which eukaryotic microalgae contributed nearly half of all export production during the Little Ice Age (~1400–1850 Common Era). The third regime, unprecedented in the past millennium, began in the industrial era and is characterized by increasing production by dinitrogen-fixing cyanobacteria. This picoplankton community shift may provide a negative feedback to rising atmospheric carbon dioxide concentrations.

Gone is the paradigm of the oligotrophic subtropical gyres as vast oceanic deserts. In the recent instrumental record, a new picture has emerged of substantial dynamics in plankton community structure, biogeochemical cycling, and export production (*1*–*4*). Numerous lines of evidence suggest that shifts in phytoplankton community regimes are intimately connected to oceanographic conditions (*2*, *4*, *5*). For instance, the 1976 polarity reversal of the Pacific Decadal Oscillation caused a shoaling of the mixed layer and subsequent declines in available nutrients to the North Pacific Subtropical Gyre (NPSG); these conditions probably promoted the food-web regime shift from a eukaryotic to a prokaryotic, cyanobacteria-dominated system (*2*). Such changes are superimposed on secular shifts associated with the areal increase of subtropical gyres that has been ongoing for at least 25 years (*6*). In the face of increasing climate change, it is imperative to understand recent changes at the base of the NPSG food web in the context of longer-term trends. However, our understanding of how NPSG plankton communities have shifted on centennial time scales has been limited by a lack of available methods and paleoarchives of sufficient length and resolution.

Hawaiian gold corals (*Kulamanamana haumeaae*) are extraordinarily long-lived deep-sea organisms that record the biogeochemical signatures of recently exported production in their proteinaceous skeletons (*7*, *8*). We generated millennial-length records of bulk stable carbon isotopes ($\delta^{13}C_{bulk}$) from specimens of *K. haumeaae* collected from the top of the mesopelagic zone at two sites in the Hawaiian archipelago (Fig. 1). The $\delta^{13}C_{bulk}$ records showed remarkable congruence, characterized by a gradual increase of ~1.0 per mil (‰) from ~1000 to ~1850 CE, followed by a rapid decrease of –1.0‰ from ~1850 to the present, after correcting for the Suess effect (Fig. 2A) (*9*–*11*). These changes in $\delta^{13}C_{bulk}$ imply multicentennial-scale shifts in $\delta^{13}C$ values associated with primary production, which we hypothesize reflect major changes in plankton community structure over the past 1000 years.

Bulk $\delta^{13}C$ records integrate the combined influences of the $\delta^{13}C$ value of inorganic carbon utilized during carbon fixation, shifts in plankton community structure, trophic changes, and biochemical fractionation. To isolate plankton source signatures within this signal, we applied a powerful fingerprinting approach to the sampled deep-sea corals, based on the normalized $\delta^{13}C$ values of essential amino acids ($\delta^{13}C_{EAA}$) in primary producers (*11*). These $\delta^{13}C_{EAA}$ fingerprints reflect the substantial metabolic diversity in EAA synthesis pathways and associated isotope effects among evolutionarily distinct primary producers (*12*, *13*). We found diagnostic multivariate patterns in literature values of normalized $\delta^{13}C_{EAA}$ among four key source end-members relevant to the NPSG [eukaryotic microalgae, dinitrogen (N_2)–fixing and non–N_2-utilizing cyanobacteria, and heterotrophic bacteria] (fig. S2). Because animals cannot synthesize the carbon skeletons of EAAs (*14*), these $\delta^{13}C_{EAA}$ fingerprints are incorporated, virtually unmodified, into upper-trophic-level consumers, including gorgonin corals (*15*). Furthermore, $\delta^{13}C_{EAA}$ fingerprints are robust to the many factors affecting bulk $\delta^{13}C$ values, such as environmental and growth conditions (*13*, *16*).

A subset of the deep-sea coral samples spanning the entire 1000-year record was analyzed for $\delta^{13}C_{EAA}$ at ~20-year resolution (table S1). $\delta^{13}C_{EAA}$ values were strongly correlated with $\delta^{13}C_{bulk}$ (fig. S1), indicating that trends in $\delta^{13}C_{bulk}$ can be attributed to changes in source carbon at the base of the food web (*15*). For example, the $\delta^{13}C_{EAA}$ of

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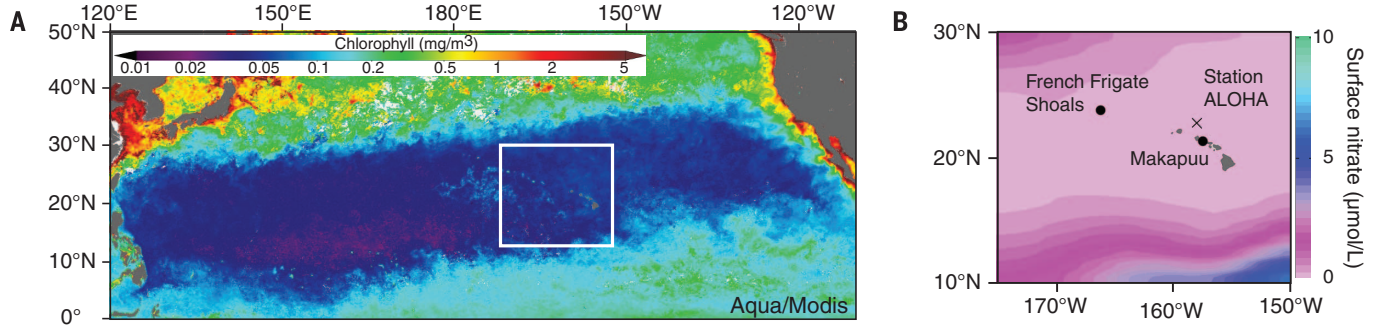

Fig. 1. NPSG productivity distribution, with sample locations. (**A**) Spatial extent of the oligotrophic NPSG, determined from spring 2012 chlorophyll a concentrations measured remotely by NASA's Aqua/MODIS (Moderate Resolution Imaging Spectroradiometer). The white box indicates the area shown in (B). [Image courtesy of NASA Goddard's Ocean Biology Processing Group] (**B**) *K. haumeaae* sampling locations at Makapuu and French Frigate Shoals relative to the oceanographic station ALOHA (indicated by the X), overlain on ocean surface nitrate concentrations (National Oceanographic Data Center, 2013; https://www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl?parameter=n).

phenylalanine (Fig. 2B) mirrored that of $\delta^{13}C_{bulk}$ (Fig. 2A); however, the magnitude of change was 10 times larger than in $\delta^{13}C_{bulk}$. This suggests that isotopic contributions from other macromolecules had a strong muting effect on $\delta^{13}C_{bulk}$ values, and thus $\delta^{13}C_{EAA}$ is likely a more sensitive record of changes in primary producer $\delta^{13}C$ than $\delta^{13}C_{bulk}$ is (*15*). Our results indicate that variability in $\delta^{13}C$ values of exported production was much larger than would be inferred from coral $\delta^{13}C_{bulk}$ records alone, and strongly suggest broad changes in the sources of exported primary production through time.

To reconstruct past shifts in the relative contributions of major phytoplankton groups to export production in the NPSG, we applied a Bayesian stable isotope–mixing model to published source end-member $\delta^{13}C_{EAA}$ fingerprints (*11*) and the $\delta^{13}C_{EAA}$ records of *K. haumeaae*, normalized to their respective means (fig. S2 and table S2). Over the entire 1000-year record, photoautotrophic carbon dominated the corals' sinking particulate organic matter (POM) food source (mean, 87 ± 6%), with a relatively small heterotrophic bacterial contribution (13 ± 6%) (Fig. 3). Likewise, prokaryotic cyanobacterial sources dominated photoautrophic carbon (63 ± 14%), with a moderate mean contribution from eukaryotic microalgae (24 ± 10%) (Fig. 3). On centennial time scales, however, relative contributions from photoautotrophic end-members shifted dramatically. For example, between 1000 and 1850 CE, cyanobacteria decreased from 80 to 50% of total exported production, offset by an equivalent increase in eukaryotic microalgae up to a peak contribution of ~45% in the early 1800s. Although previous studies have noted enhanced diatom abundances in the NPSG associated with mesoscale oceanographic features (*17*), such a sustained high level of eukaryotic microalgal production has never been observed in the modern instrumental record. The most conservative explanation of our data is that the changes in the phylogenetic identity of sources contributing to export production reflect changes in the relative community composition of surface plankton through time. An alternate, albeit highly unlikely, hypothesis is that surface plankton community composition has remained relatively constant through time, and instead the degree of decoupling between surface and export production has undergone dramatic changes as a function of climate shifts (*11*).

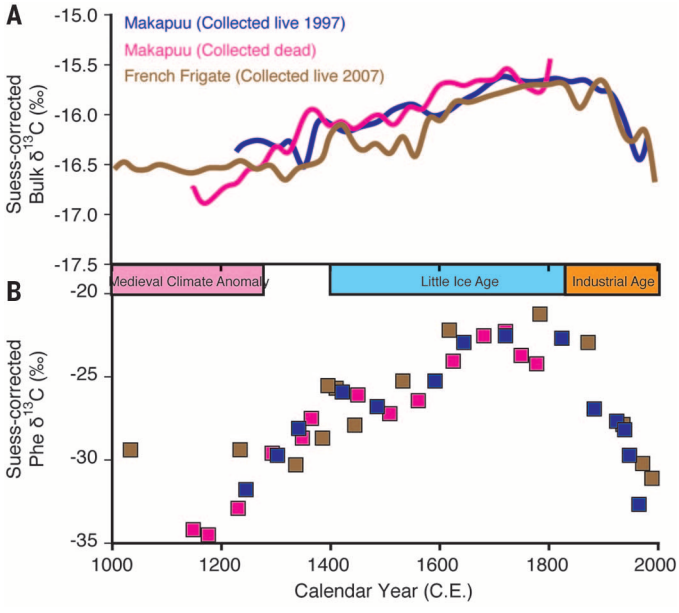

Fig. 2. 1000-year bulk and essential amino acid $\delta^{13}C$ records from deep-sea corals in the NPSG. *K. haumeaae*–derived records of (**A**) $\delta^{13}C_{bulk}$ (solid lines show the 20-year average; analytical error, 0.05‰) and (**B**) $\delta^{13}C_{Phe}$ (Phe, phenylalanine; squares; analytical error, 0.2‰) from Makapuu live coral (purple), Makapuu fossil coral (magenta), and French Frigate Shoals live coral (brown). All records have been corrected for the oceanic Suess effect since 1860 (*10*, *11*). Well-known Northern Hemisphere climate phenomena are overlaid for reference (*18*).

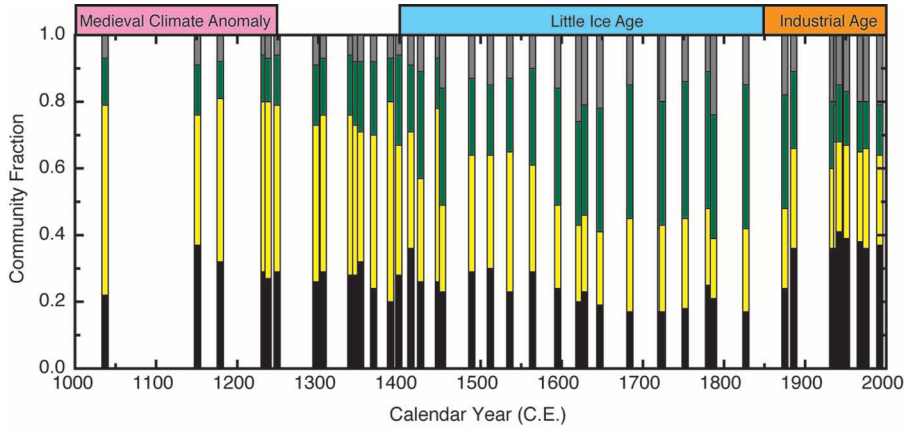

Fig. 3. Millennial record of relative carbon contributions from different primary producers recorded in deep-sea corals. Shown are the relative contributions of carbon from N_2-fixing cyanobacteria (black), non–N_2-utilizing cyanobacteria (yellow), eukaryotic microalgae (green), and heterotrophic bacteria (gray), recorded in deep-sea corals over the past 1000 years. Corals were collected at 450 m depth in the Hawaiian archipelago in the NPSG. Relative contributions are based on a compound-specific Bayesian stable isotope–mixing model of normalized phytoplankton end-member and coral $\delta^{13}C_{EAA}$ values.

To better constrain the patterns of changing plankton community composition, we applied a hierarchical cluster analysis to the normalized $\delta^{13}C_{EAA}$ data (*11*). This approach identified three distinct plankton community regimes that corresponded temporally to well-known Northern Hemisphere climate phenomena (Fig. 4). The first regime corresponded to the Medieval Climate Anomaly [MCA; 950–1250 CE (*18*)], with $\delta^{13}C_{EAA}$ fingerprints indicative of export production dominated by nitrate (NO_3^-)–utilizing cyanobacteria. There is general consensus that the putative MCA in the northern mid-latitudes was similar to the climate of the mid-20th century (*18*, *19*), implying relatively warm sea surface temperatures, weak winds, shallow mixed-layer depths, and resultant nutrient limitation, all favoring a microbial loop–dominated community (*2*). The second regime corresponded to the Little Ice Age [LIA; 1400–1850 CE (*18*)]. In this regime, the plankton assemblage contributing to export production transitioned from a cyanobacteria-dominated community to one far more strongly influenced by eukaryotic microalgae (Fig. 3). This shift probably reflects a transition in the LIA to cooler sea surface temperatures, a reduction in stratification, an increase in mixed-layer depth, and an inferred increase in the supply of inorganic nitrate from depth (*4*, *20*).

The third and current regime began at the end of the LIA and at the onset of the modern industrial age (~1850 CE) (Fig. 4). This regime is distinguished by a transition back to a cyanobacteria-dominated system. However, unlike the MCA period, the current regime is characterized by a biogeochemically distinct group of cyanobacteria, the N_2-fixing diazotrophs. Historically, the availability of inorganic nitrogen (N) and/or phosphorus (P) was thought to limit plankton production in the NPSG (*21*). Since ~1850 CE, however, sea surface temperatures have increased, accompanied by a likely decrease in the trade winds concomitant with gyre expansion, as a result of Northern Hemisphere warming. The resulting increase in stratification and decrease in nutrient availability may have selected for a N_2-fixing cyanobacterial community, as observed in the instrumental record over

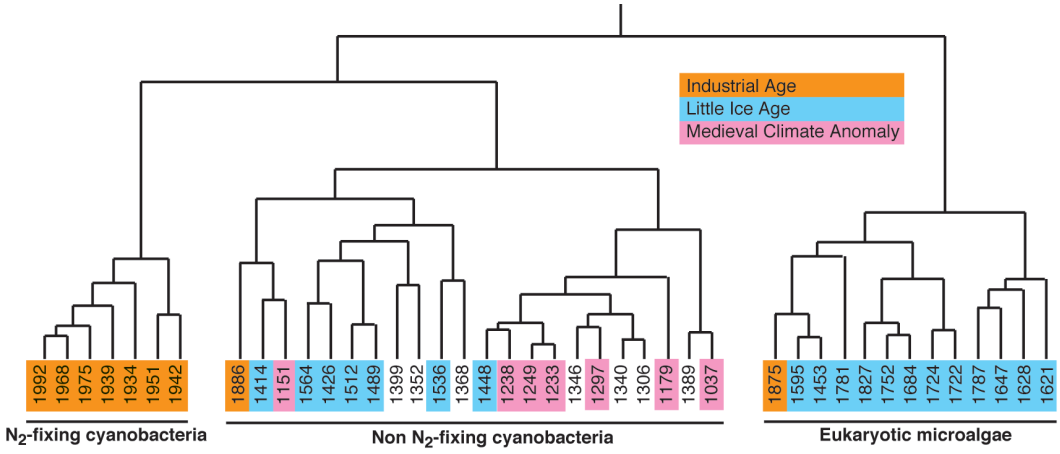

Fig. 4. Phytoplankton regime shifts recorded in deep-sea corals. Shown is a dendrogram of similarity in exported plankton carbon utilized by deep-sea corals over the past 1000 years, based on an average-link hierarchical cluster analysis. The dendrogram is separated into three significantly different clusters according to multiscale bootstrapping with approximately unbiased *P* values >0.95. The dates (CE) are colored based on overlap with well-known Northern Hemisphere climate phenomena (*18*).

the past ~20 years (*2*, *22*). Currently declining P inventories and increasing N:P ratios in the mixed layer at the HOT-ALOHA (Hawaiian Ocean Time-series–A Long-Term Oligotrophic Habitat Assessment) oceanographic station are thought to reflect this decades-long increase in N_2 fixation (*1*, *2*, *8*), an idea that is further supported by recent literature suggesting that canonical Redfield ratios in the NPSG may be more plastic than previously realized (*23*, *24*).

Our $\delta^{13}C_{EAA}$ fingerprinting data, which show a 47% increase in N_2-fixing cyanobacteria carbon in exported POM since the end of the LIA, correspond well with recent evidence of a 17 to 27% increase in NPSG N_2-fixation since ~1850 CE, determined from amino acid–specific nitrogen isotopes ($\delta^{15}N_{AA}$) in the same suite of *K. haumeaae* specimens as used in this study (*8*). These studies represent fully independent lines of evidence supporting the hypothesis that recent decreases in $\delta^{15}N_{bulk}$ values of exported POM in the NPSG are related to increases in diazotrophic plankton within a microbial loop–driven system (*11*).

By offering the first direct phylogenetic context for long-term shifts in isotopic records of exported POM, our data provide a major new constraint in understanding the evolution of NPSG biogeochemistry. For example, a recently proposed alternate hypothesis contends that advection of ^{15}N-depleted nitrate from the Eastern Tropical Pacific, associated with a reduction in denitrification (*25*), might explain recent low $\delta^{15}N$ values in the NPSG; similarly, Kim *et al.* (*26*) suggested that atmospheric N deposition is the dominant factor driving increases in values of N* (a nitrate- and phosphate-based tracer of N_2 fixation and denitrification) across the Pacific. However, the $\delta^{15}N$ value of N entrained in the mixed layer should not, by itself, affect planktonic community structure. Our new evidence for a profound phylogenetic community shift is fully consistent with increasing N_2 fixation, probably linked to overall increased stratification and reductions in upwelled nitrate, over the past 100 years.

Taken together, our data show that phytoplankton community structure in the NSPG is subject to multicentennial shifts that are broadly linked to climate conditions. They also reveal that the present-day cyanobacterial community, which is characterized by strongly enhanced N_2 fixation, is unprecedented within at least the past 1000 years. The transition to the current cyanobacterial regime (<200 years) was much faster than the transition from cyanobacterial dominance during the MCA to eukaryotic dominance during the LIA (>600 years). Both the nature and the rate of change of the current dominant autotrophic assemblage strongly suggest continuing rapid changes in NPSG plankton community structure associated with anthropogenic climate change and are consistent with the predicted expansion of N_2-fixing cyanobacteria habitat (*27*).

Regime shifts in plankton community composition have far-reaching implications for productivity, food-web dynamics, biogeochemical cycling, and the efficacy of the biological pump (*22*, *28*, *29*). The fact that dominant cyanobacterial signatures were recorded in deep-sea corals from the mesopelagic zone strongly suggests that continuing shifts to an N_2-fixing prokaryotic regime have fundamentally altered the main sources of exported POM. These observations also support recent evidence (*3*, *30*) that small-cell picoplankton production, free-living and/or in cyanobacteria-diatom symbioses (*11*, *22*), may be a more important component of export production in oligotrophic gyres than traditionally recognized. Further, recent studies have shown that plankton elemental stoichiometry is more variable than previously assumed under the classical Redfield paradigm, with C:P ratios being several times higher in the oligotrophic gyres than in upwelling regions (*23*, *24*). This suggests that carbon export could actually be more efficient (per mole of P) in the oligotrophic gyres, despite their lower overall productivity, and, furthermore, that increasing nutrient limitation in warmer and more stratified oceans over the past 100 years may have served as a major negative feedback on rising CO_2 concentrations (*23*, *24*). Our finding that the phylogenetic origin of export production in the NPSG has trended toward N_2-fixing prokaryotes over the past century strongly supports this idea. If small-cell export does in fact act as a more efficient carbon pump, our new records suggest that this carbon cycle feedback has already been operating for the past 100 years. For this feedback loop to persist into the future, the system cannot become phosphate-limited.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/350/6267/1530/suppl/DC1
Materials and Methods
Figs. S1 and S2
Tables S1 and S2
References (*31*–*68*)

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MARINE CALCIFERS

Multidecadal increase in North Atlantic coccolithophores and the potential role of rising CO_2

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As anthropogenic carbon dioxide (CO_2) emissions acidify the oceans, calcifiers generally are expected to be negatively affected. However, using data from the Continuous Plankton Recorder, we show that coccolithophore occurrence in the North Atlantic increased from ~2 to more than 20% from 1965 through 2010. We used random forest models to examine more than 20 possible environmental drivers of this change, finding that CO_2 and the Atlantic Multidecadal Oscillation were the best predictors, leading us to 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.

Marine organisms that produce external features made of calcium carbonate are susceptible to harmful consequences from ocean acidification (*1*). Coccolithophores, the main calcifying phytoplankton, are unicellular algae surrounded by calcite plates called coccoliths, whose photosynthesis is strongly carbon-limited (*2*). Coccoliths are a major source of oceanic particulate inorganic carbon (PIC) and serve as ballast for sinking aggregates (*3*), thus accelerating carbon export (*4*). 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 effects on ocean carbon fluxes, dimethyl sulfide fluxes (*5*), carbonate geochemistry (*6*), and phytoplankton community structure (*6*). Current evidence regarding how increased pCO_2 will affect coccolithophores is contradictory (*7*–*10*). 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 past five decades.

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

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 (*11*). Sample preservation methods (using Borax-buffered formalin) and analysis have remained unchanged since 1958 (*12*), producing a unique, consistent, multidecadal data set. Although the CPR filtering system was designed to sample larger microplankton, coccolithophores are trapped, particularly in the intersection of the silk fibers (*12*). It is not possible to accurately quantify organisms that are smaller than the mesh size, but we can use the data set to estimate the probability of coccolithophore occurrence. Although our sampling underestimates natural abundances, this probability is a proxy for changes in coccolithophore abundance (fig. S1).

We calculated the annual probability of coccolithophore occurrence as the fraction of samples per year containing coccolithophores. The CPR data show an increase in occurrence of coccolithophores across the North Atlantic from ~2% of samples in the 1960s to more than 20% of samples with coccolithophores in the 2000s (Fig. 1, A to F, and fig. S2). Regional abundances of coccolithophores in the 2000s are at least 10 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 (*13*), satellite evidence of global poleward expansion of *Emiliania huxleyi* (*14*), and recurring blooms in areas where coccolithophores were previously absent or sparse (*14*–*17*).

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 data set. Additionally, the effects of different environmental forcings on phytoplankton groups are nonlinear and interdependent. After evaluating a suite of statistical methods (see the supplementary materials), we selected RF models (*18*), 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 nonlinearities, 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° area each month, as a function of more than 20 biological and physical predictors. Because the CPR data set is already complex and discontinuous, we only used in situ measurements of biological and physical parameters without interpolating data. The complete data set included 81,340 observations from 1965 to 2010. The importance of each variable in predicting coccolithophore

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