Environmental control of marine phytoplankton stoichiometry in the North Atlantic Ocean

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The stoichiometric coupling of carbon to limiting nutrients in marine phytoplankton regulates the magnitude of biological carbon sequestration in the ocean. While clear links between plankton C:N ratios and environmental drivers have been identified, the nature and direction of these links, as well as their underlying physiological and ecological controls, remain uncertain. We show, with a well-constrained mechanistic model of plankton ecophysiology, that while nitrogen availability and temperature emerge as the main drivers of phytoplankton C:N stoichiometry in the North Atlantic, the biological mechanisms involved vary depending on the spatiotemporal scale and region considered. We find that phytoplankton C:N stoichiometry is overall controlled by nitrogen availability below 40° N, predominantly driven by ecoevolutionary shifts in the functional composition of the phytoplankton communities, while phytoplankton stoichiometric plasticity in response to dropping temperatures and increased grazing pressure dominates at higher latitudes. Our findings highlight the potential of "organisms-to-ecosystems" modeling approaches based on mechanistic models of plankton biology accounting for physiology, ecology, and trait evolution to explore and explain complex observational data and ultimately improve the predictions of global ocean models.

phytoplankton stoichiometry | marine ecology | biogeochemical cycles | community ecology

The elemental composition of phytoplankton biomass, particularly its C:N:P:Fe ratio, is a crucial aspect of ocean biogeochemistry (1–4). The stoichiometry of biological uptake—relative to the ratio of supply—determines which nutrients are limiting to growth. Additionally, the ratio of carbon to the limiting nutrient in organic matter determines the maximum amount of carbon that can be fixed and exported for a given nutrient supply. Phytoplankton stoichiometry is therefore a key component of the efficiency of the biological carbon pump, and as such, understanding its sensitivity to environmental change is key to understanding ongoing changes to the marine ecosystem and climate (3, 4).

Although phytoplankton stoichiometry appears to be relatively well constrained when averaged over the global ocean, trends have been observed across a range of spatiotemporal scales (1–7). This suggests some level of environmental control, with significant correlations between the stoichiometry of marine organic matter and environmental and biological factors (4–9). However, strong intercorrelations between light, temperature, nutrient availability, and planktonic diversity makes it difficult to identify which (if any) of these relationships are causal (4). This is also partially attributable to an incomplete understanding of the biological mechanisms involved. For example, it remains unclear whether the observed variations result from the physiological (plastic) response of phytoplankton organisms to the variability of their environment, from ecological shifts between competing phytoplankton populations, or from the adaptive evolution of phytoplankton traits.

To address these questions, we use a simple model of plankton ecophysiology. Based on experimental observations (10–13), the model resolves how temperature and nutrient availability shape the physiology of phytoplankton organisms depending on their size (i.e., how they influence nutrient uptake and division rates and hence phytoplankton stoichiometry—see model description and *SI Appendix, Supplementary Discussions* SI1 and SI2). Nitrogen (N) being the most limiting nutrient to phytoplankton growth over most of the global ocean, including in the North Atlantic (14, 15), we here focus on C:N stoichiometry. Based on this parametrization of phytoplankton physiology, the model resolves the ecology and evolution in size of phytoplankton and zooplankton populations involved in competitive and trophic interactions. This formulation allows the emergence of the functional composition of plankton communities according to well-established ecophysiological constraints and environmental conditions (16–19).

We use this model to disentangle the respective role of N availability, temperature, and additional environmental drivers in controlling the C:N ratio of phytoplankton biomass and to identify the biological mechanisms involved at different temporal and spatial scales by confronting the model predictions with multiple observational datasets.

Results

Ecophysiological Basis of Phytoplankton C:N Ratio. To illustrate the ecophysiological mechanisms underlying the environmental control of phytoplankton stoichiometry, we simulate a highly idealized, initial scenario: a single population of phytoplankton

Significance

As they grow, die, and sink into the ocean's interior, oceanic phytoplankton drive the so-called biological carbon pump, one of the main biological processes regulating atmospheric carbon concentrations. The biological carbon pump is, therefore, key to climate regulation. Its efficiency is largely determined by the coupling of marine biology to ocean geochemistry through the C:N:P:Fe stoichiometry of phytoplankton biomass, yet what determines this stoichiometry remains poorly understood. Based on a model of plankton biology, we characterize control mechanisms of the C:N ratio of phytoplankton biomass in the North Atlantic, which explain extensive sets of apparently conflicting observations. These findings could improve the predictive ability of global ocean models regarding climate change and the role of marine biology in its mitigation/aggravation.

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with a fixed size (from now on expressed as equivalent spherical diameter, or ESD), exploiting a steady influx of nutrient. If nutrients are scarce, uptake by the phytoplankton is slow relative to the maximum achievable rate of cell division. As a result, the phytoplankton nutrient content drops, and the C:N ratio increases (Fig. 1A). Conversely, if nutrients are abundant, uptake is fast, and division becomes limiting to phytoplankton growth. Nutrients accumulate within the cell, and the C:N ratio drops. Variation of phytoplankton C:N stoichiometry is bounded by maximal and minimal values, respectively, determined by the minimal structural content of the phytoplankton cell in nutrient, Q_{min}, and by the intracellular dynamical equilibrium between saturated uptake (V_{max}) and division (μ_{max}) rates in conditions of nutrient excess (*SI Appendix, Supplementary Discussion* SI1). The size dependence of phytoplankton physiological properties predicted by the model can be summarized as follows: 1) the larger phytoplankton is characterized by a higher stoichiometric plasticity, 2) the maximum C:N ratio increases log linearly with phytoplankton size (as Q_{min} decreases with size), and 3) the minimum C:N ratio is maximized by intermediate cell sizes.

Although this stoichiometric plasticity is not directly influenced by temperature, indirect effects emerge as nutrients are drawn down to lower levels in warmer environments (as represented by their temperature-dependent R_N^* value—see *SI Appendix, Supplementary Discussion* SI1). By accelerating phytoplankton metabolism, higher temperatures result in 1) larger ranges of viable phytoplankton sizes, 2) overall lower R_N^*, and 3) R_N^* being minimized by phytoplankton of smaller size (ESD of 2 to 3 μm at 5 °C and 0.3 to 0.4 μm at 25 °C; Fig. 1B).

As it sets equilibrium conditions of nutrient availability (Fig. 1B), we predict phytoplankton size to have an indirect effect on phytoplankton stoichiometry (Fig. 1C). Small phytoplankton can deplete inorganic N to very low R_N^* values but are characterized by low stoichiometric plasticity and low, structural C:N ratios. On the other hand, large phytoplankton can exhibit very high C:N ratios in nutrient-depleted conditions but have a limited ability to generate such conditions. As a result, and as previously observed in laboratory experiments (10), C:N ratios (in monocultures at equilibrium) are maximal for phytoplankton of intermediate sizes, who have both the capacity to deplete N and the physiological plasticity to be affected by it. The size associated with maximal C:N, furthermore, shifts toward larger organisms at higher temperature (Fig. 1C), as the capacity of larger phytoplankton to deplete nutrients increases with temperature (Fig. 1B).

When comparing our predictions to previous observations (10, 20–22), we note that attempts to characterize the in situ link between cell size and C:N stoichiometry may often be confounded by uncontrolled variations in environmental conditions and taxonomic differences across size classes. For instance,

results from Lomas et al. (20) and Martiny et al. (6) suggest that cyanobacteria exhibit in average higher-C:N ratios than the larger eukaryotes they coexist with, while Baer et al. (21) seem to show the opposite, and Garcia et al. (22) remain inconclusive regarding the existence of a link between size and C:N stoichiometry among eukaryotes. Those claims can, however, be reconciled when considering that larger eukaryotes can exhibit both very high or very low C:N ratios depending on the environmental conditions, which is both confirmed by the review by Tanioka et al. (23) and predicted by our model. Additionally, our predictions are both supported by experimental data presented in the Marañon et al. study (10) used to parametrize the size dependence in our model and conserved when using alternative datasets (11) to parametrize size dependence (*SI Appendix, Supplementary Discussion* SI5).

Seasonal Control of Phytoplankton C:N Ratio in Oligotrophic Systems. Having established the principal physiological mechanisms in play at the cellular level at equilibrium, we next consider the implications of these mechanisms within a seasonally varying environment, here an idealized representation of the seasonal cycle at the Bermuda Atlantic time series study site [BATS dataset (24); Fig. 2]. This overall oligotrophic system is characterized by a mild seasonal variation of temperature (Fig. 2A) and by generally nutrient-depleted conditions interrupted by a nutrient pulse during wind-driven winter mixing (Fig. 2B). Observations show that the C:N stoichiometry of the particulate organic matter is at its lowest during the winter (January through March) and at its highest during the nutrient-depleted summer (June through September; Fig. 2C). These observations thus suggest either a negative relationship between the N availability and the C:N ratio or a positive relationship with temperature. As shown by our exploration of the ecophysiological basis of phytoplankton stoichiometry, our model provides a mechanistic explanation for both those relationships. Increasing the model complexity only minimally, we simulated the dynamics of a single population of small nanoplankton [representing the ∼2-μm diameter phytoplankton that dominate this habitat (25)] controlled by a single population of zooplankton. With seasonal temperature and nutrient input forcing parametrized according to field data (24), our model predicts the C:N stoichiometry of the phytoplankton to match almost perfectly with the monthly median of the observations. We then ran the model with each of the two environmental drivers varying in isolation throughout the year (the other one remaining constant). We found that while seasonal variations of nutrient alone could reproduce the observed variations in C:N stoichiometry, those of temperature could not (*SI Appendix, Supplementary Discussion* SI6). This suggests a predominant role of N availability relative to temperature in controlling the C:N stoichiometry of phytoplankton biomass.
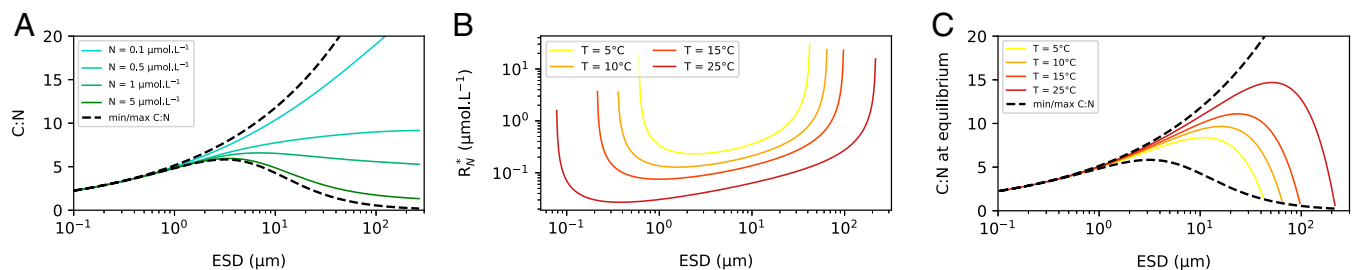

Fig. 1. (A) Size dependence of phytoplankton stoichiometric plasticity in response to nutrient availability. Nutrient availability at equilibrium in axenic ecosystems as a function of phytoplankton size (expressed as its equivalent spherical diameter, ESD, in μm) and local temperature (B) and corresponding C:N phytoplankton stoichiometry (C). The dashed black lines in A and C correspond to the maximum and minimum values of the C:N stoichiometry of phytoplankton set by the parameters of the physiological model ($^1/_{Q_{min}}$ and $^{V_{max}}/_{\mu_{max}}$ respectively; see *SI Appendix, Supplementary Discussion* SI1).
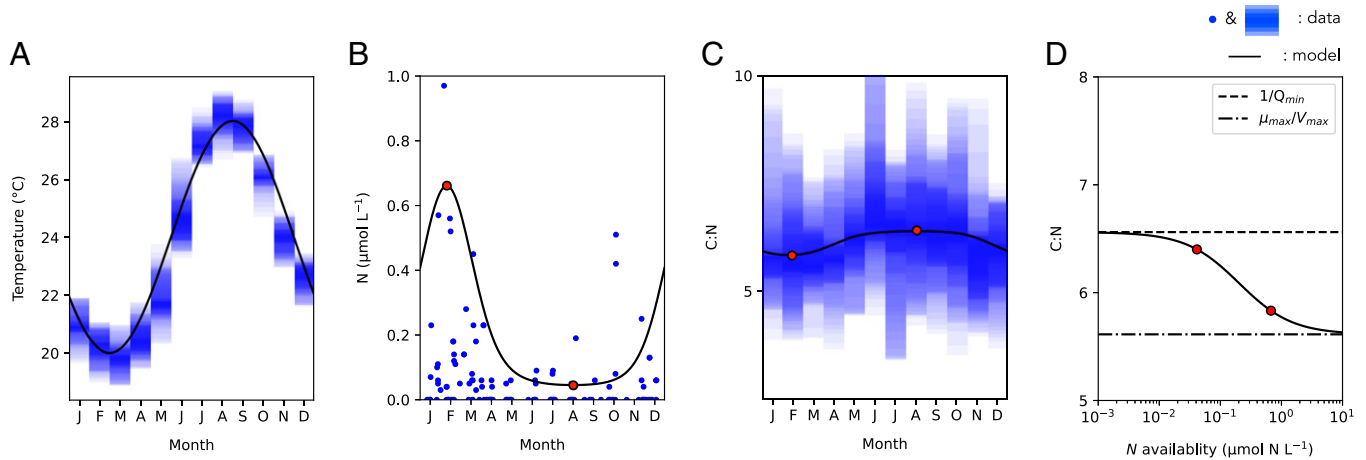
Fig. 2. The blue shaded areas and dots corresponds to the annual variation of the temperature (*A*), N availability (*B*), and the C:N ratio of the organic matter (*C*) observed in the Bermuda station [data from the 1988 to 2019 (24)]. Red dots highlight the most and least nutrient-rich period of the year. Each of the superimposed blue layers corresponds to the interval between the x and 1-x quantiles of the distributions (with x ranging from 0.05 to 0.49), the "bluest" section therefore representing the medians. The inputs of our model in terms of temperature (*A*) and its prediction in terms of nutrient availability (*B*) and C:N stoichiometry of a single population of small phytoplankton (equivalent spherical diameter of ~2 μm) (*C*) throughout the year and as a function of one another (*D*) and are represented with black solid lines.

Our results, therefore, confirm the previously described (23, 26–29) negative relationship between nutrient availability and C:N ratio in oligotrophic systems and highlight stoichiometric plasticity as the most plausible biological mechanism. It has been previously suggested that this relationship could be used to extrapolate the spatial distribution of phytoplankton stoichiometry in the ocean (27–29). This can be reasonably done only if the plastic response of the phytoplankton to N availability is the principle driver of phytoplankton stoichiometry across large spatial scales. In the following section, we will test whether this is the case.

Latitudinal Control of Phytoplankton's C:N Ratio in the North Atlantic. To test this hypothesis, we looked at the spatial variation of the C:N stoichiometry across the North Atlantic based on a large collection of data broadly distributed across the North Atlantic basin compiled by Martiny et al. (7) from several studies, completed with Atlantic Meridional Transect (AMT) data, including observations made at higher latitudes (*SI Appendix*, Fig. 6*A*). Fig. 3 shows the observed C:N ratio as a function of latitude in the North Atlantic. The C:N ratio shows an oscillating latitudinal pattern, with peaks at 0 and 40° N and much lower values found in the oligotrophic subtropical gyre at 20° N (*SI Appendix*, Fig. 6*B* and *SI Appendix, Supplementary Discussion* SI7) and in the polar and subpolar regions. This latitudinal pattern reveals a more complex relationship between nutrient availability and C:N stoichiometry than a straightforward negative link to nutrient supply—the N to C:N relationship appears to be positive between 0 and 40° N, becoming negative at higher latitudes. Two potentially complementary hypotheses can explain this apparent contradiction between observations made at the local and global scales. First, other environmental factors, not contributing to variability in the Bermuda system, could be at play when considering the ocean-wide distribution of the C:N stoichiometry. Could temperature, for instance, play a role in the latitudinal control of phytoplankton stoichiometry? Second, phytoplankton plasticity might not be the only biological mechanism involved in the environmental control of phytoplankton stoichiometry. The shifts in the size composition of the phytoplankton with latitude in response to latitudinal shifts in environmental conditions is a well-studied phenomenon (30). Can ecoevolutionary shifts in the size composition of plankton communities then be responsible for the

observed pattern of latitudinal variation of the phytoplankton C:N ratio?

We ran our model of the plankton community to simulate the ecoevolutionary emergence of the size composition of those communities along an idealized, environmental gradient representative of the North Atlantic transect (31) (Fig. 3*B*). Our model predicts how the environmental conditions (temperature and nutrient availability) dictate the range of viable phytoplankton size (i.e., that could colonize the system in the absence of competitors and predators) along the gradient (Fig. 3*C* and *SI Appendix, Supplementary Discussion* SI3). It then predicts how ecoevolutionary processes drive the emergence within this size range of the size distribution of the phytoplankton community (see model description; Fig. 3*D*). Those predictions are in line with field observations (30). The size composition of the phytoplankton community determines, with the local temperature, the phytoplankton ability to exploit the local nutrient input, hence, the nutrient availability at equilibrium R_N^* along the transect (Fig. 1*B* and 3*B*). The local R_N^*, in turn, determines the stoichiometry of each phytoplankton population given its characteristic cell size (Fig. 3*C*). When averaged over the whole community, the latitudinal variation of the phytoplankton C:N stoichiometry predicted by our model qualitatively matches the observations (Fig. 3*A*).

Below 40° N, we find regions characterized by higher-nutrient influxes (equatorial upwelling and northern boundary of the subtropical gyre) to exhibit higher C:N ratios because they are dominated by phytoplankton of intermediate to large cell sizes (Fig. 3*D*) experiencing low R_N^* conditions, hence, characterized by large C:N ratios (Fig. 3*C*). Those low R_N^* are the result of warm temperatures, increasing the overall ability of the phytoplankton, and of the larger size-classes especially, to consume nutrient (Fig. 1*B*). Regions characterized by low nutrient influxes (subtropical gyres, i.e., ~20° N) show lower C:N ratios because the larger size classes, capable of achieving higher C:N ratios, are excluded because of the nutrient scarcity (Fig. 3*D*). This result, therefore, suggests that, contrary to the seasonal variation of C:N in oligotrophic systems, the latitudinal variation of the C:N ratio is driven by ecoevolutionary shifts in the phytoplankton functional composition, leading to the opposite relationship between the N availability and C:N ratio.

Polewards of 40° N, however, we see the opposite trend, with C:N ratios declining as nutrient levels increase. We find this
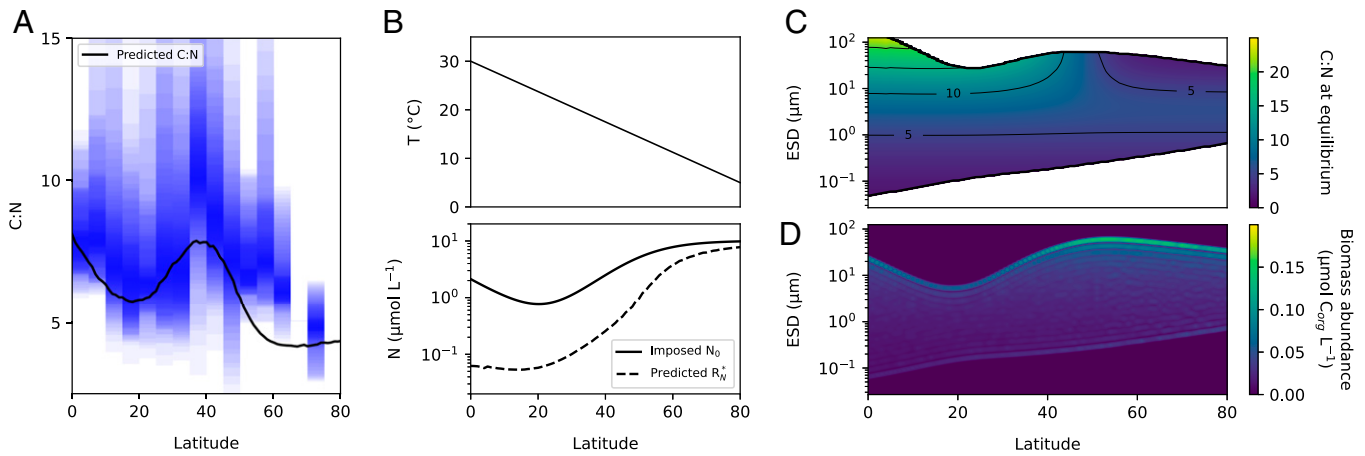
Fig. 3. (*A*) Latitudinal variation of the C:N stoichiometry of the organic matter along the North Atlantic transect as measured in the first 100 m of the North Atlantic ocean and reported in ref. 7 (blue shaded area) and as predicted by our model (solid black line). (*B*) Idealized environmental gradient (temperature, richness of the nutrient influx N_0, and nutrient availability at equilibrium R_N^*) along the North Atlantic transect injected in (solid lines) and predicted by (dashed lines) the model. The thick dark line in *C* corresponds to the range of phytoplankton size (expressed as its equivalent spherical diameter, ESD, in μm) for which local environmental forcing (N_0 and temperature) is viable. The actual size distribution of the phytoplankton community emerging within that range as a result of the local ecoevolutionary processes is shown in *D*. The nutrient concentration at equilibrium R_N^* in *B* is set by the whole community, depending on its size composition and the local temperature, which in turn determines the C:N stoichiometry of each population within the community (color gradient in *C*).

trend to be driven by the poleward decline in temperatures and increase in grazing pressure. Although the size composition of the phytoplankton communities varies relatively little north of 40° N (Fig. 3*D*), the metabolism of the phytoplankton slows down as temperature drops, and phytoplankton populations decline in their ability to exploit incoming nutrients (regardless of their size; Fig. 1*B*). Similarly, the increase in nutrient input with latitude strengthens the top-down control of the phytoplankton by the zooplankton, and nutrient assimilation by the phytoplankton becomes less effective proportionately to the nutrient input (32) (see a more detailed discussion regarding the latitudinal distribution of those two effects in *SI Appendix, Supplementary Discussion* SI8). Nutrient concentrations at equilibrium are, therefore, predicted to be higher in polar latitudes, which in turn results in a lower C:N stoichiometry of the phytoplankton (Figs. 1*C* and 3*C*).

We therefore find the North Atlantic latitudinal transect to be structured in three distinct regimes: 1) regions characterized by high-nutrient influxes and by moderate to high temperatures—in which the C:N ratio is high (equator and latitudes between 35 and 45°); 2) regions of low C:N ratios due to low nutrient influx (subtropical gyres); and 3) regions of low-C:N ratios due to low temperatures and strong grazing pressure (high latitudes). Temperature and grazing pressure are, alongside N availability, prevalent factors of determination of phytoplankton stoichiometry in the North Atlantic.

Discussion

Our results shed light on the complexity of the environmental control of phytoplankton stoichiometry. This control is characterized by a diversity of environmental drivers and biological mechanisms, interacting in a complex fashion that varies across spatiotemporal scales. Nitrate availability appears to be the main controller of phytoplankton stoichiometry in the North Atlantic, but temperature and grazing also play key roles across large spatial scales. Although plasticity emerges as an important component of the environmental control of phytoplankton stoichiometry, especially at the seasonal scale in oligotrophic systems, ecoevolutionary processes play a major role in determining basin-scale latitudinal patterns. We show that this complexity can be resolved by recreating key ecosystem features at

different spatial and temporal scales. We use a relatively simple empirically parameterized model of plankton physiology, ecology, and evolution. We demonstrate that those models can provide a sufficient mechanistic framework to reconcile and explain apparently conflicting observations.

In our analysis, we have assumed that N is the main limiting factor to phytoplankton growth. Under this simplifying assumption, we obtained a good, qualitative agreement with data from the North Atlantic, where this assumption holds for the majority of phytoplankton (15). We note that further investigations of the role of other mechanisms will be required to achieve more quantitative predictions regarding the determination of phytoplankton stoichiometry in the North Atlantic. For example, the contribution of N_2-fixing populations to biomass production and stoichiometry in the subtropical and tropical regions (33, 34) or the limitation by iron and phosphorus in the polar and subpolar North Atlantic (15, 35–37). More generally, while the mechanisms we propose here may be generalizable to other biogeochemically similar regions of the oceans, they will be less likely to hold in the many regions where other environmental factors, such as light, iron, or phosphate availability, become predominant limiting factors to phytoplankton activity. For example, a recently published dataset describes the latitudinal variation of environmental drivers and stoichiometry of the organic matter in the South Pacific (38). These data show a markedly different latitudinal relationship between N availability and C:N stoichiometry, probably as a result of phytoplankton biology being controlled by environmental drivers specific to the region—most likely iron limitation, as suggested by in situ experiments of enrichment (15), observations (35–37), and modeling studies (39). Limited to the influence of N availability and temperature on phytoplankton physiology, our modeling framework cannot, in its current form, accurately simulate those types of systems. The generality and explanatory power of our approach can nevertheless be improved. Indeed, additional colimitation factors (light, other macronutrients such as phosphate, or trace elements such as iron) can, in principle, be implemented in our model to allow accurate predictions of the physiological, ecological, and evolutionary responses of the marine phytoplankton to the variety of environmental regimes to which it is exposed. Although such developments are

technically feasible (40), a main obstacle is the lack of experimental data required for the parametrization of mechanistic models— for instance, regarding the influence of iron on phytoplankton physiology. We therefore think that further characterization of phytoplankton physiology in laboratories should complement the on-going improvement of ocean biogeochemical monitoring to achieve a better understanding of oceanic ecosystem function. Additionally, we are convinced that general circulation models (GCMs) accurately simulating the various environmental characteristics of oceanic ecosystems (e.g., light, macro- and micronutrient availabilities, temperature, pH, oxygenation, and water stratification) and their variations through time and space would provide an ideal framework to further investigate how environmental drivers other than N availability and temperature, but also the combination of those factors (e.g., colimitation of phytoplankton physiology by N, P, and Fe availability), influence phytoplankton stoichiometry in the North Atlantic and in the global ocean overall.

As the development of these "organisms-to-ecosystems" models goes on, their integration in GCMs will give access to predictions of a more quantitative and general nature than those presented in the present analysis. Moreover, such coupled models will allow addressing, quantitatively, the question of the effect of climate change on phytoplankton stoichiometry at the planetary scale (41, 42) and to predict more accurately the evolution of the carbon pump efficiency and of its role in mitigating climate change. Although previous analyses (42) of GCM results concluded that considering phytoplankton stoichiometric plasticity only changes marginally the global predictions of models, we think that this conclusion should be reevaluated in the light of the findings presented here.

Materials and Methods

Model. We consider an idealized model of a marine plankton ecosystem, characterized by a concentration in N (N) and an arbitrary number of phytoplankton (P_i) and zooplankton (Z_j) populations. Each of those populations is characterized by a specific set of ecophysiological traits. N is advected into the system at a rate I (in per day) and at a concentration N_0 (in micromoles of N per liter). It is then consumed by phytoplankton, which are themselves grazed by zooplankton. Nutrients are taken up by phytoplankton cells at a rate V, the biomass specific uptake rate of the phytoplankton (in mole of N per mole of organic carbon per day). Once taken in, nutrients enable phytoplankton growth μ (in per day).

$$V_i = V_{max,i} \frac{N}{N + K_i} \qquad [1]$$

and

$$\mu_i = \mu_{max,i} \frac{N}{N + \kappa_i}, \qquad [2]$$

where V_{max} and μ_{max} are the maximum uptake and growth rates, respectively, and K and κ the two half-saturation constants.

A widely used approach to modeling phytoplankton systems, based on the Monod model of growth, is to consider phytoplankton growth and nutrient uptake to be coupled and to use the Redfield ratio as a scaling factor, therefore assuming a fixed biomass stoichiometry (43, 44). Quota models (45, 46) instead consider those two mechanisms as uncoupled nutrients being stored inside the phytoplankton cells before being used for growth. Based on previous work (19, 47), we use Monod-like formulations to describe both uptake and growth (see a detailed presentation of the model in the *SI Appendix*,

Supplementary Discussion SI1). The stoichiometry of the phytoplankton cell of a population i is then described by its intracellular nutrient quota Q_i (in mole of N per mole of organic carbon), determined by the dynamical balance between uptake and growth. Therefore, in the following equation:

$$Q_i = \frac{V_i}{\mu_i} \qquad [3]$$

and ranges between the Q_{min} and Q_{max}, which respectively are approached when nutrients are scarce and in excess (*SI Appendix, Supplementary Discussion* SI1). It is well established that these physiological parameters are primarily correlated to organism size (10, 11, 19, 48–52). This size dependence is typically described by power–law relationships of the type $p(x) = a \cdot x^b$, with p the parameter value and x the organism's volume. Similarly, the kinetics of the phytoplankton metabolism typically increases with temperature (48), which is often described in plankton models by the Norberg–Eppley relationship $p(T) = p(T_{ref}) \cdot e^{\alpha(T - T_{ref})}$, with p the value of a given parameter—here uptake or growth—α the temperature exponent, and T_{ref} a reference temperature (12, 13). By implementing those temperature and size dependencies into the parametrization of the model (detailed in the *SI Appendix, Table S1*), we can evaluate analytically for a given environmental forcing of the ecosystem (i.e., for a given set of I, N_0, and temperature T); the range of viable phytoplankton cell sizes; and, for a single phytoplankton population within that range, the corresponding ecological attractor in terms of nutrient concentration, biomass, and C:N stoichiometry at equilibrium (the solving method and some biological implications are described in details in the *SI Appendix, Supplementary Discussion* SI1).

In addition to a basal mortality rate d (in per day), phytoplankton populations experience the grazing pressure from zooplankton populations, which increases with zooplankton size (53–55) and, with how well the size of a specific phytoplankton population fits the size preference of the zooplankton, the grazing pressure being maximized for a specific predator-to-prey size ratio (56). The emergence of the size distribution of the phytoplankton and zooplankton guilds is, therefore, the result of the community ecology (i.e., the variation of the abundance of the phytoplankton and zooplankton populations resulting from the competition and predation interactions between those populations) but also of adaptive processes. Indeed, each time new individuals are produced, mutations occur, and some of those individuals are characterized by sizes that are slightly different from that of their ancestor. Depending on their fitness, those mutants can either die without decent or reproduce and lead to the emergence of a new population (13, 14). Using the method described in Sauterey et al. (17), we resolve the ecoevolutionary dynamics of the ecosystem and its equilibrium characteristics in terms of nutrient abundance (R_N^*) and in terms of (phytoplankton and zooplankton) plankton density and size composition. A typical prediction of this type of model is that size-directed grazing drives the diversification of the plankton community, while the total number of coexisting populations is limited by resource availability (17, 57).

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