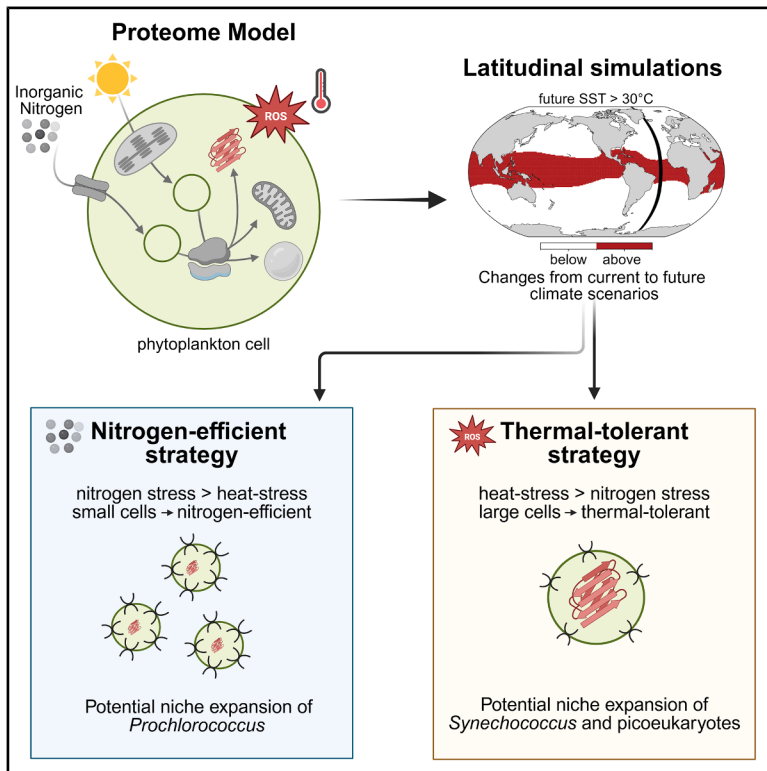


Heat stress drives increases in phytoplankton cell size in future oligotrophic oceans

Graphical abstract



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In brief

Leles et al. show that marine phytoplankton employ mutually exclusive metabolic and physiological strategies to cope with heat and nutrient stress. While small cells prioritize nutrient efficiency, larger cells better mitigate thermal stress. These findings raise questions about the predicted dominance of *Prochlorococcus* in future, ocean-warming scenarios.

Highlights

- Marine phytoplankton experience trade-offs under combined heat and nitrogen stress
- Nitrogen-efficient strategy requires smaller cell sizes at the cost of heat tolerance
- Thermal-tolerant strategy requires larger cell sizes at the cost of growth
- *Prochlorococcus* might not always dominate in the future warmest oceanic regions



Report

Heat stress drives increases in phytoplankton cell size in future oligotrophic oceans

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SUMMARY

Warming and nutrient limitation are major stressors that affect primary production in the ocean, with cascading impacts on the food web. Yet, we lack a mechanistic understanding of how phytoplankton manage multiple stressors and the implications of these responses for phytoplankton biogeography. By combining theory, proteome allocation modeling, and climate projections, we identified two potential competing strategies for multi-stressor growth: (1) nutrient efficient smaller cells or (2) heat-tolerant larger cells. We found that *Prochlorococcus* are more vulnerable in warmer, “heat-stressed”, tropical regions due to greater heat sensitivity and lower lipid storage capacity to buffer oxidative stress, indicating a potential ecological niche for larger phytoplankton with lower sensitivity to oxidative stress, such as *Synechococcus* and picoeukaryotes. Our findings advocate for the inclusion of phytoplankton heat-stress responses in global models to more accurately predict their ecological niches as the climate warms.

INTRODUCTION

Future climate scenarios project an average increase of 1.5°C by 2040 in the global ocean¹ with vast regions of the ocean warming to above 30°C by the end of the century.² Ocean warming is expected to promote stronger stratification, potentially decreasing the influx of nutrients from below the mixed layer.³ Changing ocean conditions have already resulted in decreased primary production⁴ and shifts in species distributions⁵ and size spectra.⁶ As phytoplankton drive ocean carbon cycling and fuel the ocean food web,⁷ understanding how these microbes respond to changes in temperature and nutrient availability is critical for predicting ecosystem function as the climate changes.^{8–10}

A key driver of microbial response to resource availability and temperature is cell size, more specifically surface area-to-volume ratio.^{11–14} Under low nutrient concentrations, uptake is limited by molecular diffusion. Thus, a phytoplankton cell can increase nutrient uptake by increasing the number of transporters

in the outer membrane.¹⁵ As there is a limit to the number of transporters a membrane can support, cells maximize the nutrient flux per unit of cellular volume by decreasing cell size and thereby increasing their surface area-to-volume ratio^{10,12,14} (Figure 1). While warming temperatures often result in smaller cell sizes,^{16,17} experimental^{18–21} and field²² studies have shown that phytoplankton increase their cell volume at critically high temperatures. In a previous study, we suggested that these larger cell sizes are a result of increased investment in energy metabolism and heat mitigation, both of which require a lower surface area-to-volume ratio, i.e., larger cell sizes, to accommodate carbon storage and antioxidant machinery²³ (Figure 1). This sets up a challenge for phytoplankton cells facing both nutrient and heat stress: invest in uptake which requires more transporters and higher surface area-to-volume ratios (smaller sizes) or invest in heat-stress mitigation strategies which require lower surface area-to-volume ratios (larger sizes) (Figure 1).

The global ocean has well-known biogeographical distributions of phytoplankton²⁴ with *Prochlorococcus* dominating the



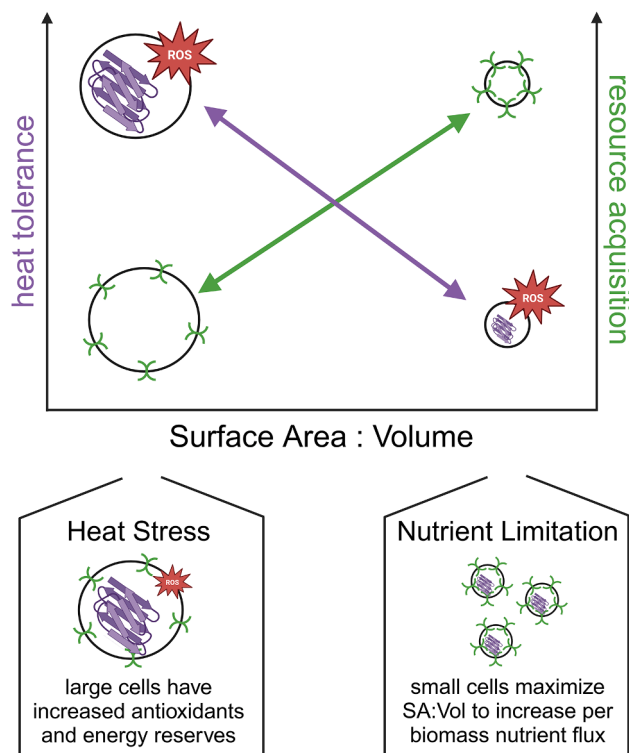


Figure 1. Predicted trade-off for phytoplankton under multi-stressor growth

Under nutrient limitation, phytoplankton need to invest more in transporters increasing their surface area-to-volume ratio, which requires smaller cell sizes. Under heat stress, the cell must invest in heat-mitigation strategies decreasing their surface area-to-volume ratio to accommodate antioxidants and other proteomic investments which requires larger cell sizes. A trade-off between decreasing cell size to optimize nutrient uptake and increasing cell size to optimize heat-mitigation emerges under the multiple stressor scenario.

oligotrophic gyres and larger eukaryotic phytoplankton thriving in more nutrient-rich temperate and coastal regions.²⁵ Current models predict that, as the climate warms, the oligotrophic gyres will expand poleward resulting in an expanded ecological niche for *Prochlorococcus*.^{26,27} However, these predictions are based on a simplified representation of phytoplankton physiology that does not account for cellular strategies to mitigate heat stress and store carbon, both of which can promote increases in cell volume.^{19,21,22,28–31} These predictions contrast with recent field data which demonstrates that *Prochlorococcus* abundance declines substantially in waters above 30°C.³² However, the mechanism for this constraint and why *Prochlorococcus* has not been able to evolve to manage elevated temperatures remains unknown. Constraining how cells respond to multi-stressor environments and how physiological responses interact to shape phytoplankton biogeography is critical for robustly predicting future ocean ecosystems.

Here, we investigate underlying mechanisms behind phytoplankton responses to co-occurring heat stress and nutrient limitation using a proteome allocation model. We demonstrate that the thermal optimum for cells (T_{opt}) can shift to either warmer or cooler temperatures under nitrogen limitation and that this shift is

modulated by the heat-mitigation capacity of the cell. We then expand our theoretical predictions by calibrating the model to data for relevant phytoplankton functional types and simulate optimal growth strategies across a latitudinal transect under current and future projections of temperature and nitrate concentrations in the ocean. While we observe that the niche of cyanobacteria expands poleward, we also find that *Prochlorococcus* are more vulnerable in the warmer tropical seas due to their low heat-mitigation capacity and small cell sizes. We thus identify a critical niche in warm tropical seas where phytoplankton with larger cell sizes, such as *Synechococcus* or even small eukaryotes, might thrive due to their larger flexibility in cell size and thermal tolerance. Our results suggest that representing the interaction between heat stress and nutrient limitation in climate models is paramount for predicting species extinction and succession.

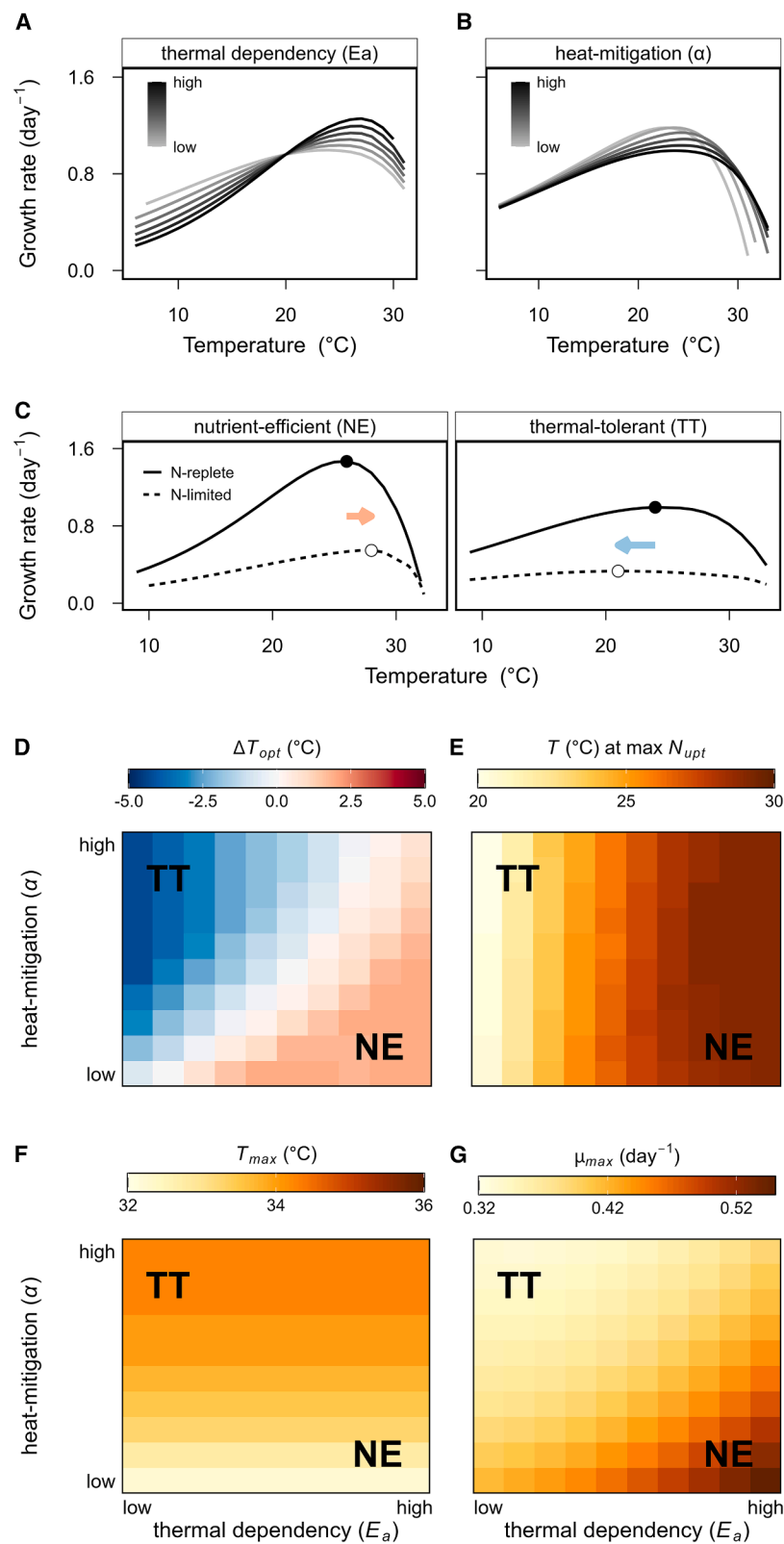
RESULTS

The proteome allocation model

We used a generic phytoplankton proteome allocation model to understand the molecular mechanisms behind changes in T_{opt} and cell size under multi-stressor growth (Figure 1). Here, we expand the model by Leles and Levine²³ to simulate a range of phytoplankton phenotypes under the multiple stressor condition of heat stress and resource limitation. The model can be generalized to all single-celled phytoplankton (prokaryotes and eukaryotes), but in its current form does not capture flexible metabolic strategies, such as osmotrophy and mixotrophy. Given that nitrogen is often the most limiting nutrient within oligotrophic gyres,³³ we investigated phytoplankton responses to nitrogen limitation. However, the model dynamics of resource limitation are broadly applicable to other limiting nutrients (e.g., phosphorus). We then validated the model against thermal growth curve data and proteomic datasets for a range of phytoplankton species and use the model to simulate phytoplankton growth along a latitudinal gradient under current and future ocean conditions (see STAR Methods).

Our proteome model consists of a system of ordinary differential equations defined as a constrained optimization problem (see Methods S1 for complete list of model equations). The model predicts cellular traits and physiological states by maximizing the steady-state growth rate of a phytoplankton cell under specific environmental conditions (i.e., irradiance, external inorganic nitrogen and carbon concentrations, and temperature). Specifically, the model simulates cellular resource allocation by optimizing the relative proteome investment across metabolic functions (e.g., nutrient uptake, biosynthesis, and respiration), intracellular macromolecular concentrations (e.g., proteins and carbon storage), and the surface area-to-volume ratio of the phytoplankton cell (Table S1). The model resolves carbon and nitrogen metabolisms, including transport of nitrogen into the cell and synthesis of all critical cellular components. Parameter values are given in the Methods S1 (Tables S2 and S4).

Temperature accelerates all enzymatic reactions in the model (Equation 3, STAR Methods; Figure S1) except photochemical reactions, which we assumed to be temperature independent.^{8,23} Nitrogen transporters have a lower thermal dependency than



(legend on next page)

other reactions in the model based on previous empirical^{34–37} and modeling²³ studies. All other processes are assumed to have the same thermal dependency (defined by the parameter E_a ; Figure S1). The emergent thermal sensitivities between phototrophic and heterotrophic processes in our model are consistent with previous experimental and theoretical results.^{8,23} Warming also results in protein damage in the model, thus mechanistically representing the decay in growth rates as temperatures increase beyond the optimum. To minimize heat damage, the model cell can invest in repair pathways and in heat-mitigation strategies, such as producing antioxidant enzymes and/or storing fatty acids.^{38–40} Heat-mitigation capacity is controlled by the model parameter α , with higher values enabling the cell to build more antioxidant machinery which, in turn, allows the cell to be more efficient at mitigating oxidative stress (Equation 4, STAR Methods). While high α values provide protection against oxidative stress, this strategy comes with a trade-off of requiring intracellular space and proteomic investment that divests resources away from nutrient acquisition and/or growth.

We solve the proteome model over a range of temperatures and nitrogen concentrations, allowing thermal growth curves to emerge as a function of molecular constraints. Key to our analysis is that we are able to evaluate the underlying physiological and molecular mechanisms driving changes in thermal traits (e.g., T_{opt}) and cell size. The optimal surface area-to-volume ratio of the cell is solved by the model as a function of surface area required for transporters in the cell membrane and cellular volume required for intracellular machinery, such as photosystems, nucleus, and antioxidants. Therefore, our model offers a platform to test, mechanistically, the cell size trade-off that phytoplankton face under the combined effects of heat stress and nitrogen limitation (Figure 1).

Understanding growth trade-offs under multi-stressor conditions

To understand the fundamental trade-offs associated with multi-stressor growth, we simulated phytoplankton cells with varying enzymatic thermal dependencies (E_a) and heat-damage mitigation ability (α) and analyzed the emergent thermal growth responses (see STAR Methods). For this analysis, the cells were otherwise equal (i.e., all other parameters were equal). The model captured the expected trade-offs where warm-adapted cells (higher E_a) have faster growth at higher temperatures but slower growth at lower temperatures (Figure 2A) and cells with higher heat-mitigation capacity (higher α) survive at higher temperatures at the cost of lower maximum growth rates (Figure 2B).

The model predicts both increases and decreases in T_{opt} under nitrogen limitation (Figures 2C and 2D), consistent with experimental results.^{41–43} The model suggests that warm-adapted cells (higher E_a) are more likely to increase their T_{opt} under ni-

trogen limitation (Figure 2D), allowing cells to maximize nitrogen uptake rates at higher temperatures (Figure 2E). Higher heat-mitigation capacity allows the cell to survive at higher maximum temperatures (Figure 2F), but it also results in a decrease in T_{opt} and lower maximum growth rates under nutrient stress (Figures 2D and 2G). Thus, two competing strategies for coping with multi-stressor conditions emerge from the model results: “nutrient efficient” or “thermal tolerant” (Figure 2C).

The “nutrient-efficient” strategy couples higher E_a values with lower α values. Higher E_a values allow cells to invest primarily in growth (ribosomes). In turn, lower α values results in less investment in heat-mitigation strategies which allows for smaller cell sizes and more efficient nutrient uptake. This comes with the trade-off that cells are more susceptible to heat damage and so have lower maximum growth temperatures. Alternatively, the “thermal-tolerant” strategy cells invest heavily in heat mitigation (higher α). This results in increased proteomic investment in heat mitigation proteins which diverts resources away from growth (ribosomes) and results in lower maximum growth rates (Figure 2G). This strategy also requires more antioxidant machinery that results in larger cells. However, this investment allows for a higher maximum critical thermal limit (Figure 2F). Because the “thermal-tolerant” strategy requires larger cell sizes, cells cannot be both thermally tolerant and nutrient efficient. Our model predicts that cells which combine low E_a and low α would be maladapted with a lower maximal survival temperature under nitrogen limitation, with no growth advantage, in agreement with the “metabolic meltdown” theory.⁴⁴

Predicting phytoplankton optimal growth strategies in a changing ocean

We investigate the implications of different growth strategies in a changing ocean using four contrasting phytoplankton functional types: *Prochlorococcus*, *Synechococcus*, warm-adapted diatom, and cold-adapted diatom. Cyanobacteria are small and optimized for high nutrient use efficiency,⁴⁵ while diatoms have substantially larger cell sizes and carry large numbers of genes for mitigating temperature and oxidative stress.^{46–48} However, differences are also observed within these two groups. Among the two cyanobacteria, *Synechococcus* have slightly larger cell sizes and are less sensitive to oxidative stress than *Prochlorococcus*.⁴⁹ Between the two diatoms, the warm-adapted type has the potential for faster maximum growth than the cold-adapted diatom.⁵⁰ Diatoms were selected as a representative bloom forming eukaryotic phytoplankton due to their abundance throughout the oceans, the critical role they play in marine ecosystems, and the availability of data to validate the model. The dichotomy between cyanobacteria and diatoms in our model also mirrors the way phytoplankton diversity is typically simplified in biogeochemical models (see discussion).⁵¹

Figure 2. Growth trade-offs as a function of thermal dependency (E_a) and heat-mitigation capacity (α)

(A and B) Thermal growth curves under nitrogen-replete conditions are given for (A) cells with variable E_a and (B) cells with variable α .
(C) Thermal growth curves indicate shifts in T_{opt} (open circles) from N-replete to N-limited conditions as a result of different metabolic strategies.
(D) The change in T_{opt} from N-replete to N-limited conditions (ΔT_{opt}) showing increases (positive and red values) and decreases (negative and blue values) in T_{opt} .
(E) Temperature (T) where nitrogen-uptake rates (N_{upt}) are maximized under N-limited.
(F) Maximal growth temperatures (T_{max}) under N-limited.
(G) Maximal growth rates (μ_{max}) under N-limited. The two competing strategies are highlighted: nutrient efficient (NE) and thermal tolerant (TT).

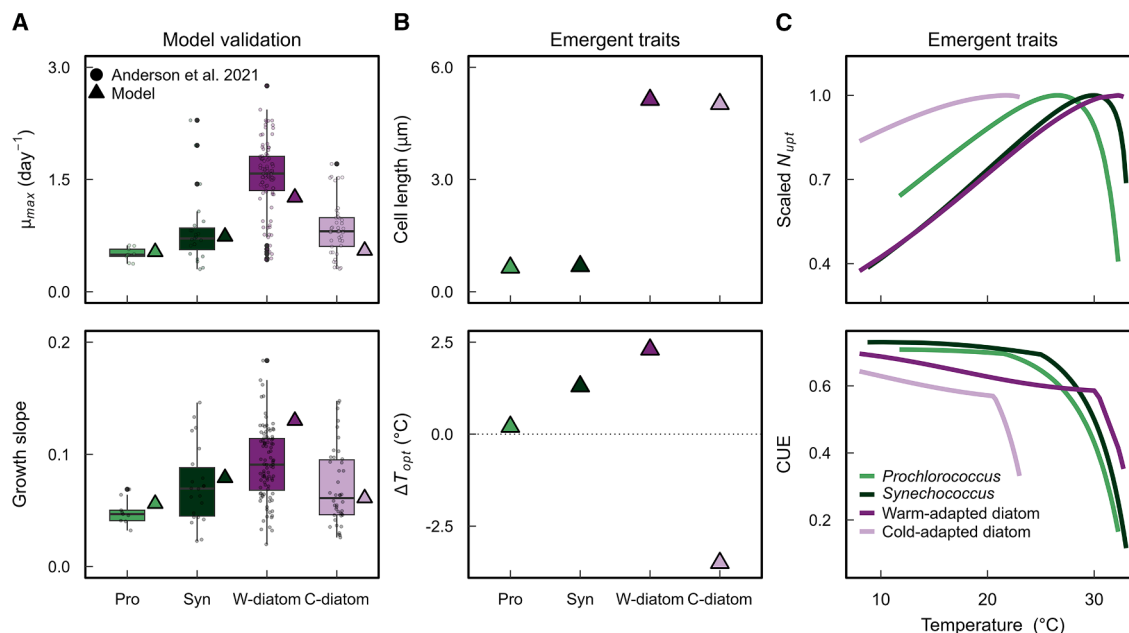


Figure 3. Emergent traits and trade-offs for different phytoplankton functional types

(A) Model validation against empirical thermal curve data from Anderson et al.⁵⁰ for the cyanobacteria *Prochlorococcus* ($n = 9$) and *Synechococcus* ($n = 23$) as well as cold-adapted ($n = 42$) and warm-adapted ($n = 93$) diatoms under nitrogen replete conditions. Maximum growth rates (μ_{max}) and the slope at which growth rates increase as a function of temperature are shown.

(B) Emergent model cell length at T_{opt} under nitrogen limitation (see Figure S3 for N-replete conditions) and the shift in T_{opt} from N-limited to N-replete conditions. (C) Model nitrogen uptake rates (N_{upt}) scaled by maximum observed rate and carbon use efficiencies (CUE) under nitrogen limitation. Carbon use efficiency is defined as $1 - \text{respiration/photosynthesis}$. See Figures S2 and S5 for full thermal curves and proteome investments in both nutrient regimes.

We parameterized the proteome model to represent these four strategies based on differences in nutrient uptake efficiency, thermal traits, and heat-mitigation capacity (Table S4, STAR Methods). We validated our model phenotypes against thermal growth data from 167 species obtained from Anderson et al.⁵⁰ The maximum growth rate and slope of the thermal curves for our model phenotypes (Figure S2) show good agreement with observed values (Figure 3A). In addition, the emergent cell sizes in the model were consistent with the expected differences between these two groups (Figures 3B and S3). Because we focused on the impact of co-occurring temperature and nutrient stress, we chose to represent pico- and nano-sized diatoms since they are the direct competitors with cyanobacteria in the nutrient-deplete oligotrophic gyres, which are projected to undergo significant warming in the next century.² However, we demonstrate that the model can also simulate larger phytoplankton (Figure S4). We also qualitatively validated modeled shifts in proteome investment under heat or nutrient stress using proteomic datasets, based on the up- or down-regulation of specific pathways (Tables S5 and S6, see STAR Methods). Unfortunately, no proteomic datasets were available to validate predictions under combined heat and nutrient stress.

Under heat stress, all phenotypes divested resources away from nitrogen transporters to invest in heat-mitigation strategies and glycolysis to support increased respiration demands (Figure S5). This trade-off is supported by observed proteomic shifts in the marine diatom *Chaetoceros simplex*,⁵² where popu-

lations down-regulated the investment in nitrogen transporters when grown at temperatures that induced heat stress, while up-regulating the investment in chaperones, reactive oxygen species (ROS) scavenging, heat shock proteins, and glycolysis (Table S5). Under nitrogen stress, all modeled phenotypes maximized the specific affinity for nitrogen uptake by decreasing cell size (Figure S5). Cells also divested resources away from photosystems, rubisco, ribosomes, and respiration under nitrogen limitation, while investing more in transporters (Figure S5). These metabolic shifts are overall consistent with empirical observations for both diatoms and cyanobacteria (summarized in Table S6).

Under multi-stressor growth, the “nutrient-efficient” strategy allowed *Prochlorococcus* to achieve the fastest maximum growth rates (Figure S2). However, at critically high temperatures, the “thermal-tolerant” strategy allowed *Synechococcus* and the warm-adapted diatom to achieve higher carbon and nitrogen use efficiency (Figure 3C), resulting in better survival at higher maximum temperatures (Figure S2). In turn, the lower thermal dependency of the cold-adapted diatom resulted in the slowest growth rates under multi-stressor conditions.

We then use these four phenotypes to investigate optimal growth strategies across a latitudinal transect in the Atlantic Ocean under present day (1980–2000) and future (2080–2100) conditions (see STAR Methods; Figure 4). For this analysis, we use temperature and nitrate concentrations for these two time periods from the CESM-WACCM model (Figure 4B). The

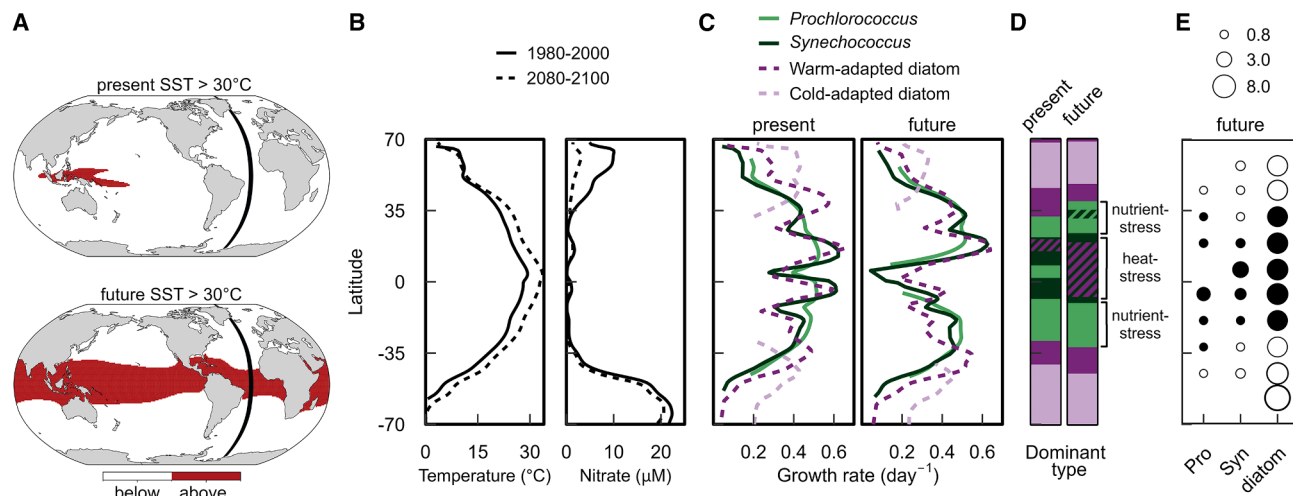


Figure 4. Phytoplankton optimal growth strategies across a latitudinal gradient

(A) Future projections from the CESM-WACCM model indicate that 34.5% of global surface waters will experience temperatures above 30°C.

(B) Simulations were run using current (1980–2000) and future (2080–2100) temperature and nitrate concentrations along a latitudinal transect in the Atlantic Ocean.

(C–E) Also shown are the optimal growth rates (C), dominant functional type by latitude (D), and optimal cell diameter (μm) under the future climate scenario (E), where white fill and black fill shows decreases and increases in cell size from present to future, respectively. See Figure S9 for modeled proteome investments.

proteome model captured present-day biogeographical distributions. Specifically, we observed the expected distributions of cold-adapted diatoms at the poles and warm-adapted diatoms in the temperate ocean due to their different thermal dependencies (Figures 4C and 4D). The cyanobacteria showed the highest growth potential in the oligotrophic gyres as expected (Figure S6), especially in the ultra-oligotrophic South Atlantic, due to their high-specific nutrient affinity (Figures 4C and 4D). The warm-adapted diatom dominated again near the Equator due to increases in nitrate concentrations, except in the latitudinal range 0°N–7°N where nitrate concentrations were minimal and temperatures were maximal (Figures 4C and 4D). We would like to note that our model only predicts potential growth advantage since we did not simulate ecological interactions and physical dynamics (see discussion).

Under the future climate scenario, the model predicts a drastic increase globally in surface waters experiencing temperatures above 30°C from only 2.7% under present day to 34.5% by the end of the century (Figures 4A and S7). Temperatures along the transect also warmed significantly with average increase of 2.8°C (maximum of 4.76°C) and nitrate concentrations were on average 33% lower (maximum of 86%). The poleward expansion of the oligotrophic gyres, where decreases in nitrate concentrations were greater than the increases in temperature, resulted in the poleward expansion of cyanobacteria due to their higher nutrient affinity, i.e., “nutrient-efficient” strategy (Figure 4D). The cold-adapted diatom phenotype still achieved the highest growth rates in the poles, however, the potential ecological niche for this group was narrower in the future projection due to the higher temperatures (Figure 4D).

The proteome model results also suggest a niche where the projected increases in temperature will have a larger impact in governing phenotype shift than the projected change in nutrients

(“heat-stressed regions”, Figure 4D). This niche occurred in regions of the ocean that are severely nutrient-limited under present-day conditions and were predicted to experience significant warming (e.g., 12°S–22°N). We hypothesize that the “thermal-tolerant” strategy rather than the “nutrient-efficient” strategy will have a competitive advantage in these regions, resulting in increases in cell size corresponding to the need to combat oxidative damage and meet dark respiration demands (Figure 4E). Thus, the *Synechococcus* and the warm-adapted diatom functional types are predicted to fair better in these “heat-stressed” regions than *Prochlorococcus*. This finding holds even when assuming the same heat-mitigation abilities between the functional types (Figure S8), because *Prochlorococcus* has a lower thermal dependency than *Synechococcus* (Table S4), implying that thermal stress develops at lower temperatures. While the specific latitudinal range over which these changes would occur depend on the CESM model projections for changes in temperature and nitrate concentrations, our hypothesized shift in ecological niches provide insight into how the phytoplankton community will respond to multi-stressor change.

The underlying metabolic shifts in response to future multi-stressor change varied across oceanographic regions and by phenotype (Figures S9 and S10). At the poles, all phenotypes invested more in transporters (Figure S9) and decreased their cell size (white filled symbols in Figure 4E) to maximize nitrogen use efficiency under future more nitrogen limited conditions. This result is consistent with empirical observations that nitrogen limitation plays a more important role than temperature in determining phytoplankton cell size.¹⁴ In the tropics, all phenotypes divested away from transporters and invested more in photosystems due to critical high temperatures, which increased respiration demands and oxidative stress, resulting in lower growth

rates relative to current conditions (Figures S9 and S10). This strategy required larger cell sizes relative to present conditions (black filled symbols in Figure 4E). While *Prochlorococcus* (“nutrient-efficient” strategy) increased cell size to accommodate intracellular energy storage compounds to manage increasingly high rates of heat damage and respiration, *Synechococcus* and the warm-adapted diatom (“thermal-tolerant” strategy) increased cell size to both store carbon for dark respiration and accommodate intracellular machinery for combating oxidative damage, thus better managing levels of heat stress. This difference explains why the growth potential of *Prochlorococcus* was lower in the tropics. Overall, *Prochlorococcus* must devote a larger fraction of the proteome to respiration relative to *Synechococcus* and diatoms due to their lower heat-mitigation capacity (Figure S10). As a result, our model suggests that cyanobacteria, in particular the streamlined ultra-oligotrophic “nutrient-efficient” *Prochlorococcus*, will have lower metabolic flexibility to manage a warmer climate.

DISCUSSION

By combining ecological theory, proteome allocation modeling, and future climate projections, we were able to identify proteomic and cell size constraints underlying phytoplankton response to multi-stressor change. Specifically, our approach allows us to differentiate between “hard constraints” imposed by physics (e.g., space and energy limitations) and “flexible constraints” due to biology (e.g., enzyme kinetics).²³ Unlike “hard constraints”, “flexible constraints” can be mitigated through adaptation. We identified two different strategies that allow phytoplankton to minimize the negative impacts of climate warming under nitrogen limitation: “nutrient efficient” and “thermal tolerant”. Due to hard constraints on cells, these two strategies are mutually exclusive—a cell cannot be both maximally nutrient efficient and have a high thermal tolerance. The cyanobacteria *Prochlorococcus* is a key example of the nutrient-efficient strategy. This strategy has allowed this group to thrive in present day oligotrophic gyres, and we predict that their niche will expand polewards under future conditions, consistent with previous studies.^{26,27} However, we demonstrate that evolving to become maximally nutrient efficient, as *Prochlorococcus* has done, comes at a cost of thermal tolerance. We therefore predict that future warming will result in the expansion of a “heat-stressed” niche in the tropics where “thermal-tolerant” phytoplankton will gain an advantage over “nutrient-efficient” phytoplankton, due to their higher cell size flexibility and ability to manage heat damage.

Our results highlight that cell size constraints are an important driver of phenotype. All phenotypes were predicted to decrease cell size in the polar and temperate oceans in response to nutrient stress and increase cell size in the tropics due to temperature stress (Figure 4E). This increase in cell volume for our model diatoms is consistent with previous work which has shown that diatoms and other eukaryotes increase cell size when exposed to temperatures above their growth maxima^{18–20,22} and when deprived of nutrients during transient stress, due to an accumulation of carbohydrates^{29,31} and/or lipids.²⁸ Similarly, our model predicted that, in order to survive

in the tropics, the cyanobacteria functional types would need to significantly increase their cell diameter (up to 4-fold for *Prochlorococcus* and 3-fold for *Synechococcus*) to store carbon and support high respiration costs. This is consistent with recent laboratory^{20,21} and field manipulative experiments by Marañón et al.,³⁰ which found that cyanobacteria increased their cell diameter under warming conditions up to 2-fold in the Atlantic Ocean, and that increases in cell volume were associated with slow or negative growth rates.

Global climate models predict a drastic increase in ultra-warm oligotrophic waters,² from 2% to 34% by the end of the century (Figures 4A and S7). These projections are based on the average temperature and do not show additional effects of temporal variability such as heatwaves, which will further exacerbate the situation. The two closest analogies in the present day ocean for these future conditions are the South Pacific Gyre and the Red Sea. Although *Prochlorococcus* is abundant and the key contributor to carbon fixation around the rims of the South Pacific Subtropical Gyre, carbon fixation within the gyre is dominated by small photosynthetic eukaryotes.⁵³ An analysis of a large dataset (800 billion cells) from the Pacific demonstrated that *Prochlorococcus* is rarely found in waters above 30°C.³² Red Sea surface temperatures can reach record values of 33°C in the surface⁵⁴ and nutrient concentrations can be as low as 0.1 μM.⁵⁵ Field observations show that the larger, more thermally tolerant cyanobacteria *Synechococcus* can dominate over *Prochlorococcus* in the surface waters of the Red Sea,^{55,56} especially in the warmest (> 30°C) waters of the southern Red Sea.⁵⁷ While not conclusive, this does suggest that the Red Sea strains of *Prochlorococcus* have not been able to evolve to be competitive in the high temperature (> 30°C) niche.²¹ In contrast, *Synechococcus* was shown to be able to easily evolve to growth at elevated temperatures (> 30°C) by increasing cell size and chlorophyll per cell.²⁰ Thus, both our work and field and experimental evidence suggest that elevated temperatures in the equatorial and tropical regions may favor small eukaryotes and larger cyanobacteria relative to *Prochlorococcus*.

We hypothesize that the ability to manage oxidative stress will play a key role in the success of different phenotypes in the future oceans that experience high levels of warming. *Synechococcus* are less sensitive to oxidative stress than *Prochlorococcus*.⁴⁹ Overall, eukaryotes are better at sensing the environment and controlling oxidative stress relative to prokaryotes,⁴⁶ which is probably related to the lack of a large number of antioxidant genes in the latter, especially for *Prochlorococcus*.⁴⁷ Previous work suggested that *Prochlorococcus* may have lost many antioxidant genes because they are costly and, instead, rely on other microbes to degrade ROS for them.^{58,59} Our model did not account for the potential benefit of these “helpers”. Yet, relying on other microbes to perform this important function may pose a risk to the adaptive potential of *Prochlorococcus*, as the “helpers” will also rapidly evolve under changing ocean conditions with no guarantee that the current interactions will persist.^{60,61} Finally, diatoms and other eukaryotes have been found to associate symbiotically with nitrogen-fixing cyanobacteria, representing yet another strategy that enables larger eukaryotic cells to thrive under nitrogen depleted conditions.^{62,63} Exploring how these microbial

interactions will shift under multi-stressor changes is an important avenue for future work.

Here, we highlight the key importance that heat stress can play in determining biogeographical distributions of phytoplankton. Moreover, we hypothesize that due to inherent space and energy trade-offs, there are two alternative strategies for dealing with multi-stressor growth: “nutrient efficient” and “thermal tolerant”. Our work advocates for the inclusion of heat stress strategies, carbon storage, and changes in cell size into earth system models used for future climate predictions. The proteome-allocation model results elucidate the trade-offs related to different metabolic strategies thereby providing a road-map for how to represent these dynamics in large-scale models. This would allow for future studies to investigate the interactive effects of cellular-level responses to multi-stressor growth with population dynamics and ecological interactions.

The creation of a niche for larger phytoplankton in the equatorial and tropical ocean under warming conditions has the potential to reshape microbial interactions, food web structure, and nutrient cycling. Although we focused on pico- and nano- sized cells, we show that larger eukaryotes (Figure S4) are subjected to similar trade-offs (Figures S11 and S12). Eukaryotic phytoplankton typically release more diverse and abundant organic compounds than cyanobacteria, fueling heterotrophic bacterial growth and enhancing nutrient remineralization.⁶⁴ In addition, larger phytoplankton cells can support larger zooplankton, enhancing trophic transfer efficiency to larger predators.⁶⁵ Larger phytoplankton also have higher cellular carbon content, produce sticky exopolymers that promote particle aggregation,⁶⁴ and are consumed by zooplankton that generate denser fecal pellets. Together, these traits could increase the potential for vertical carbon export to deeper waters, altering the stoichiometry and depth of nutrient recycling. Integrating the insights from cellular scale models into biogeochemical models provides a powerful tool for synthesizing experimental and field data on cellular responses and scaling-up to understand large-scale climate impacts.

Limitations of the study

A key challenge faced broadly by numerical models is how to represent the vast diversity of marine microbes. For this study, we used diatoms as our example eukaryotic phytoplankton type to facilitate validation against experimental datasets and to be consistent with the simplified set of phytoplankton functional groups typically used in global biogeochemical models.² As we do not incorporate key diatom specific metabolisms such as silicate frustule synthesis into the proteome model, these findings are broadly applicable across bloom forming eukaryotic phytoplankton (e.g., haptophytes). However, our model currently does not resolve mixed forms of metabolisms, such as mixotrophy, which could be highly advantageous under multi-stressor environments. A key area for future research, both modeling and laboratory, is to understand the different strategies for coping with high temperature growth and oxidative stress in eukaryotic phytoplankton. Similarly, we focus on the upper water column (upper 20 m) where temperature and nutrient stress are greatest. However, there are sharp gradients within the euphotic zone and key differences between high and low light adapted

Prochlorococcus. An additional area for future work would be to explore how the environment at the deep-chlorophyll maximum is predicted to shift and the impact on the relative competitive advantage of different strategies.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Suzana G. Leles (suzana.leles@utexas.edu).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data: This work did not generate new data. Data used to support model validation can be found in the [key resource tables](#).
- Code: The model was written in Julia⁶⁶ and the code is deposited on Zenodo (DOI: <https://doi.org/10.5281/zenodo.21925253>) and is available on GitHub (<https://github.com/LevineLab/ProteomePhyto/tree/main>). The CESM2-WACCM model output used in this study is available via the Earth System Grid Federation (<https://esgf-node.ipsl.upmc.fr/projects/esgf-ipsl/>). Please see the [key resource tables](#) for more information.
- Any additional information required to reanalyze the data reported in this paper are available from the [lead contact](#) upon request.

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AUTHOR CONTRIBUTIONS

S.G.L. and N.M.L. conceptualized this study and wrote the initial manuscript. S.G.L. developed the model, run simulations, and performed the data analyses. L.B. developed the code to improve the optimization algorithm. A.K. developed the code to perform the analyses with the empirically derived thermal growth data. L.F. provided the CESM2-WACCM model output. M.A.G. analyzed the proteomic dataset. H.A., H.V.M., C.L., E.L., and other authors revised the initial draft contributing to the final version of this manuscript.

DECLARATION OF INTERESTS

The authors declare that they have no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Compilation of thermal growth curves data across 167 species of diatoms and cyanobacteria	Anderson et al. ⁵⁰	Zenodo: https://zenodo.org/records/5507532
Data for proteomic responses of <i>Prochlorococcus marinus</i>	Domínguez-Martín et al. ⁶⁷	PRIDE database with the identifier PXD005745
Data for proteomic responses of <i>Chaetoceros simplex</i>	Aranguren-Gassis et al. ⁵¹	https://doi.org/10.1101/2024.11.27.625584
Data for proteomic responses of <i>Phaeodactylum tricornutum</i>	Yang et al. ²⁸	https://doi.org/10.1007/s10811-013-0050-3
Data for proteomic responses of <i>Thalassiosira pseudonana</i>	Chen et al. ⁶⁸	PRIDE database with identifier PXD011133
Data for proteomic responses of <i>Phaeodactylum tricornutum</i>	Remmers et al. ⁶⁹	https://doi.org/10.1016/j.algal.2018.08.012
Phytoplankton proteome model output simulated data	This paper	https://github.com/LevineLab/ProteomePhyto/tree/main
Software and algorithms		
Phytoplankton proteome model	This paper	https://doi.org/10.5281/zenodo.21925253 https://github.com/LevineLab/ProteomePhyto/tree/main
Julia	https://julialang.org/	N/A
JuMP	https://jump.dev/JuMP.jl/stable/	N/A
Ipopt	https://github.com/jump-dev/Ipopt.jl	N/A
Omicsbox software (version 1.4.12)	https://www.biobam.com/omicsbox/	N/A
R	https://www.r-project.org/	N/A

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

This study did not involve any new experiments and exclusively relies on computer simulations. Simulations were compared against empirical data previously published in the literature as described in the Key resources table.

METHOD DETAILS

The model

We use a proteome allocation model modified from Leles and Levine²³ to predict the optimal metabolic strategy and cell size of a phytoplankton cell under the multi-stressor growth condition of heat and nutrient stress. We further integrate the model to empirical data from 167 species previously compiled by Anderson et al.⁵⁰ to model the optimal strategies of different phytoplankton functional types across a latitudinal transect under current and future ocean conditions. Our coarse-grained model is defined as a constrained optimization problem that maximizes the steady-state growth of the cell. Here, we give the general equations governing the model behavior and focus on the processes relevant for the present work. For the full model equations and list of optimized variables (Table S1) and parameter values (Tables S2 and S4), we refer the reader to the Methods S1 and the code available on GitHub (<https://github.com/LevineLab/ProteomePhyto/tree/main>).

The model assumes a cell that is growing exponentially given a certain temperature and nitrogen concentration. The macromolecular concentrations (c) can thus be obtained assuming that the sum of the syntheses rates ($v_{\text{synthesis}}$) minus the sum of the degradation rates ($v_{\text{degradation}}$) are balanced by the cellular growth rate, μ :

$$\frac{dc}{dt} = \sum v_{\text{synthesis}} - \sum v_{\text{degradation}} - \mu c = 0 \quad (\text{Equation 1})$$

Each reaction rate catalyzed by a given protein i is described following a Michaelis-Menten type equation:

$$v_i = k_i p_i \frac{S_i}{S_i + K_i}, \quad (\text{Equation 2})$$

where k_i is the maximum turnover rate per protein, S_i is the substrate concentration, K_i is the half-saturation constant, and p_i is the concentration of protein i . k_i is derived from literature values and corrected to a reference temperature of 20°C. We assume all reaction rates in the cell increase with temperature following the Arrhenius equation, such that:

$$k_i = k_{ref,i} \gamma_{Ta},$$

$$\gamma_{Ta} = \exp \left(\frac{E_a}{R} \left(\frac{1}{T_{ref}} - \frac{1}{T} \right) \right) \quad (\text{Equation 3})$$

where $k_{ref,i}$ is the maximum turnover rate at a reference temperature T_{ref} (in Kelvin) for a given protein i , E_a is the thermal dependency of metabolic rates (eV), R is the Boltzmann's constant (eV K⁻¹) and T is the actual temperature (K). The only exception is the maximum rate of photosynthesis, which we assume to be independent of temperature.⁸ All reactions were assumed to have the same E_a , with the exception of nitrogen uptake, for which we halved the thermal dependency relative to other reactions in the model according to previous empirical^{34–36} and modeling²³ studies.

Warming also results in protein damage v_d which increases with increasing temperature, however, cells can invest in heat-mitigation strategies that reduce the impact of heat damage:

$$v_d = k_{ref,d} \gamma_{Td} \frac{\alpha}{p_{ox}},$$

$$\gamma_{Td} = \exp \left(\frac{E_d}{R} \left(\frac{1}{T_d} - \frac{1}{T} \right) \right) \quad (\text{Equation 4})$$

in which $k_{ref,d}$ is the maximum rate of damage at a given temperature, E_d is the thermal dependency of protein damage, α is the heat-mitigation capacity of the cell, and p_{ox} is the pool of antioxidant machinery. p_{ox} is constrained to be lower or equal to α . Thus, higher α enables the cell to build more antioxidant machinery p_{ox} , which increases the efficiency of the cell in managing oxidative stress, but it comes at the cost of lower maximum growth rates (Figure 2B) due to higher intracellular space and proteomic costs required to build p_{ox} that are ultimately divested away from growth. Our model can represent two different strategies in which a cell can mitigate heat damage: storing lipids to sequester reactive oxygen species³⁹ or producing antioxidant enzymes to decrease oxidative stress.⁴⁰ Here, we present the results for the model version in which a cell utilizes lipid storage. The results for antioxidant enzymes are quantitatively the same and are provided in the Supplemental Materials (Figure S13).

The model optimizes for the surface area-to-volume of the cell. We assume a spherical cell for simplicity and our model does not describe chains or filaments. The cell size is a trade-off between 1) surface area required for nitrogen transporters and 2) intracellular space required for intracellular machinery, including photosystems, carbon storage, nucleus, and antioxidants (see Methods S1). The model can be applied to simulate a phytoplankton cell of any shape, but here we assume a spherical cell for simplicity.

Sensitivity analyses

Empirical observations show that phytoplankton species display diverse thermal growth curves^{5,50} and sensitivities to oxidative stress.^{46,70} To capture such trait diversity, we varied two parameters in our simulations: the thermal dependency of metabolic reactions (E_a) and the heat-mitigation capacity of the cell (α). We leveraged 167 phytoplankton thermal growth curves from previous compilations^{5,50} to select the range of E_a values to test in our sensitivity analyses. Note that the value for E_a in our model corresponds to the metabolic reaction and not necessarily the E_a for growth rates, which is the commonly described parameter in the literature.

In turn, the value of α is poorly constrained in the literature. The range of α values used in our simulations was guided by a previous study, which found that phytoplankton sensitivity to oxidative stress can vary up to 10-fold between species.⁴⁶ This sensitivity was evidenced by elevated F_0 and decreased oxygen production under H₂O₂ exposure, consistent with PSII photoinhibitory damage. Our model captures this differential sensitivity through the modeled concentrations of damaged photosystems (Figure S14). We further assumed that, the higher the maximum concentration of antioxidants α , the lower the energetic cost associated with protein damage e_d ; all remaining parameter values were held constant for these analyses (Table S2).

We performed simulations for 100 different cells based on a 10x10 grid combining different E_a and α values. We solved the model across a wide range of temperatures for every 0.25°C to capture the full thermal growth curves and derive the T_{opt} for each phenotype from our simulations. We repeated this process for two different nutrient regimes to simulate nitrogen-replete (DIN = 20 μM) and nitrogen-deplete (DIN = 0.1 μM) conditions. In total, we simulated 200 thermal growth curves and found optimal solutions for approximately 10,000 combinations of temperature, DIN, E_a and α (see Methods S1).

Model comparison against proteomic data

We validated the heat-stress predictions from our model against data from an experimental evolution study that quantified the proteomic responses of the marine diatom *Chaetoceros simplex*.⁵² In the experiment, protein differential expression was compared between three different populations: ancestral population acclimated to control temperature (25°C), ancestral population acclimated to heat-stress (31°C), and warm-evolved population acclimated to heat-stress (34°C). Functional annotation of all identified proteins and gene ontology (GO) enrichment analysis were conducted using the Omicsbox software (version 1.4.12), employing the Fisher exact test with a false discovery rate (FDR) of 0.05. The analysis utilized the reduced option to provide more specific GO terms (Table S5). We compared our simulations against the proteomic dataset qualitatively, based on the up-regulation or down-regulation of specific pathways. This expands our previous work by providing empirical evidence that supports the modeled trade-off between nutrient acquisition and heat-mitigation for both ancestral and evolved populations. The responses of *Prochlorococcus* to warming have been validated previously in Leles and Levine²³ against transcriptomic datasets.⁷¹ To validate the model predictions between the two different nutrient regimes, we compared model output to literature values for the proteomic responses of different phytoplankton species between nitrogen-replete and nitrogen-deplete conditions (Table S6; Methods S1). No proteomic datasets were available to validate predictions under combined heat and nutrient stress.

Phytoplankton functional types and latitudinal simulations

We solved the proteome model across a latitudinal transect in the Atlantic Ocean, spatially averaging over the longitude range of 330°–335°E, after verifying that temperature and nutrient conditions within this narrow range are relatively uniform. We selected the Atlantic transect for this analysis as it is less dominated by iron limitation compared to the Pacific and therefore offers a more representative environment for examining responses to nitrate limitation. We used historical and future SSP5-8.5 simulations from the CESM2-WACCM model⁵¹ to construct present-day (1980–2000) and future (2080–2100) averages for temperature and nitrate concentrations, both averaged over the upper 20 m of the water column. Since changes in irradiance were not the focus of this study, we used a constant light dose of 300 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ as representative of average mixed layer conditions.

We parameterized the model to represent four phytoplankton functional types: *Prochlorococcus*, *Synechococcus*, warm-adapted diatom and cold-adapted diatom. We chose these four types given their importance to global primary production⁷² and their differences in three key properties: 1) nutrient uptake efficiency,⁴⁵ 2) thermal traits,⁵⁰ and 3) heat-mitigation capacities.⁴⁶ Given the wide thermal range of diatoms, we simulated two phenotypes to capture cold- and warm-adapted species. Parameter values were chosen based on previous literature and details are given in the Methods S1 (Table S4).

We then expanded our model validation with further experimental data. To confirm that our parameter choices mimic the general physiology of the four types, we validated the emergent maximum growth rates (μ_{max}) and growth (left) slopes of the thermal curves from our model against data from 167 species previously compiled by Anderson et al.⁵⁰ Diatom species within this dataset with a T_{opt} lower than 20°C were assigned as cold-adapted. All *Prochlorococcus* and *Synechococcus* species in the dataset had a T_{opt} higher than 20°C. To make this comparison (Figure 3A), we fitted the data to the Norberg equation. We used a log likelihood function to fit the parameters of the Norberg equation for each experimental dataset from,⁵⁰ then estimated the upper and lower temperature values at which the modeled growth rate was 20 % of its maximum value following.⁵⁰ We calculated the lower and upper slopes of the thermal curve by dividing the difference between the maximum growth rate and 20 % of the maximum growth rate value by the difference between the thermally optimum temperature and the identified temperatures at which growth rate was 20 % of maximum.

To parameterize the differential heat-mitigation abilities (α) between our functional types, we demonstrate that the modeled concentration of damaged photosystems is approximately 10 times higher for *Prochlorococcus* relative to the warm-adapted diatom, consistent with the findings of Drábková et al.⁴⁶ (Figure S14). We also performed a sensitivity analysis for the heat-mitigation ability of *Prochlorococcus* for the latitudinal runs (Figure S15), demonstrating that our key finding, i.e., the potential niche for larger phytoplankton in multi-stressor regions where heat-stress dominates, holds even if we assume equal heat-mitigation abilities among the functional types, but the exact latitudinal range where this happens is variable (Figure S8). Because *Prochlorococcus* has a lower thermal dependency than *Synechococcus* (Table S4), thermal stress develops at lower temperatures when assuming equal heat mitigation abilities. We also compared the emergent averaged cell size and nutrient uptake affinities from our model between cyanobacteria and diatoms to make sure these reflected differences observed empirically (Figure 3B). Finally, we also evaluated if the highest optimal growth rate between cyanobacteria and diatom at any given latitude, as predicted by the proteome model, reflected in higher biomass for that group using simulations from a global model that also considered the different thermal dependencies between these two functional types²⁵ (Figure S6).

QUANTIFICATION AND STATISTICAL ANALYSIS

The computational approach is fully described above and more details can be found in the supplement. Optimization was performed using Ipopt via the JuMP interface in Julia. All data analyses and graphs were performed in R. All code is available in Zenodo.