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Intraspecific Diversity in Thermal Performance Determines Phytoplankton Ecological Niche

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ABSTRACT

Temperature has a primary influence on phytoplankton physiology and ecology. We grew 12 strains of *Gephyrocapsa huxleyi* isolated from different-temperature regions for ~45 generations (2 months) and characterised acclimated thermal response curves across a temperature range. Even with similar temperature optima and overlapping cell size, strain growth rates varied between 0.45 and 1 day^{-1}. Thermal niche widths varied from 16.7°C to 24.8°C, suggesting that strains use distinct thermal response mechanisms. We investigated the implications of this thermal intraspecific diversity using an ocean ecosystem simulation resolving phytoplankton thermal phenotypes. Model analogues of thermal 'generalists' and 'specialists' resulted in a distinctive global biogeography of thermal niche widths with a nonlinear latitudinal pattern. We leveraged model output to predict ranges of the 12 lab-reared strains and demonstrated how this approach could broadly refine geographic range predictions. Our combination of observations and modelled biogeography highlights the capacity of diverse groups to survive temperature shifts.

1 | Introduction

Temperature critically influences organism size (e.g., Forster, Hirst, and Esteban 2013; Winder and Sommer 2012; Zohary, Flaim, and Sommer 2021), development (e.g., Gillooly et al. 2002), distribution (e.g., Somero 2005; Jeffree and Jeffree 1994) and metabolic rate (e.g., Savage, Van, et al. 2004). Many organisms are reliant on environmental temperature, ranging from microorganisms (e.g., Jansson and Hofmockel 2020; Singh et al. 2010) to corals (e.g., Carballo-Bolaños, Soto, and Chen 2019; Bairos-Novak et al. 2021), and fish (e.g., Dahlke et al. 2020). The strong relationship between physiology and temperature indicates that higher average ocean water temperature will impact the abundance and distribution of species (Cavicchioli et al. 2019; Lesser 2007; Vaquer-Sunyer and Duarte 2011; Abirami et al. 2021). Climate change is also expected to increase temperature variability (Rummukainen 2012; Arnell et al. 2019), which impacts organisms proportionally to their tolerable thermal range (Thornton et al. 2014). Increasing climate variability and extremes are predicted to shape ecology, including phenology, species interactions and dominant community assemblages (Vasseur et al. 2014; Parmesan and Yohe 2003; Tylianakis et al. 2008; Lavergne et al. 2010; Mock et al. 2016).

Phytoplankton are vital to global primary production and carbon biogeochemistry (Strickland 1965). Their abundance and distribution correlate with temperature (Righetti et al. 2019), and thermal response has multiplicative interactions with other drivers of phytoplankton fitness (Eppley 1972; Rhee and Gotham 1981). Thermal reaction norms describe the effect of temperature on growth rate, are measured for individual taxa in the laboratory, and indicate potential evolutionary trade-offs between adaptive thermal mechanisms (such as the use of proteins with different temperature sensitivities (Somero 1995)), the rate or regulation of resource use (Thompson, Guo, and Harrison 1992; Sayegh and Montagnes 2011; Baker and Geider 2021)) and fitness (Angilletta et al. 2003).

The deviation of thermal reaction norms of individual strains or ecotypes from a ‘standard’ form is suggested to be among the most important markers of the role of phytoplankton diversity in shaping thermal response (Kingsolver et al. 2015; Izem and Kingsolver 2005; Zhang et al. 2014), but its ecological implications have not been explored in ecosystem models to date. The width of a thermal reaction norm indicates the trade-off between being a temperature ‘generalist’ capable of growing successfully over a wide temperature range, or a ‘specialist’ with a narrower temperature range, but potentially with a growth rate advantage (Angilletta et al. 2003). The commonly used Eppley–Norberg model (Grimaud et al. 2017) parameterises thermal reaction norm width explicitly (Grimaud et al. 2017; Kremer, Thomas, and Litchman 2017; Norberg 2004). Thermal reaction norm width has broad relevance to ecology and species biogeography. Janzen's rule (Janzen 1967; Sheldon et al. 2018) hypothesises that at higher latitudes and elevations, higher thermal variability leads to wider thermal niche widths. Past work has found that phytoplankton frequently do not adhere to this expectation that thermal width increases with latitude (Chen 2015). The diversity of phytoplankton makes it difficult to extrapolate point measurements of thermal width and local temperature to community trends, which is key to interpreting phytoplankton studies in the context of ecological theory.

To directly interrogate the effect of diversity on thermal response, we used *Gephyrocapsa* (formerly *Emiliania*) *huxleyi* as a model system. *G. huxleyi* is frequently grown in the laboratory as a model phytoplankter due to its global distribution and ease of culturing (Wheeler, Sturm, and Langer 2023) as well as its developed molecular resources (Read et al. 2013). Moreover, intraspecific diversity within *G. huxleyi* is well-described, including in calcite elemental composition, growth rate, C:N ratio and thermal response (Blanco-Ameijeiras et al. 2016; Rosas-Navarro, Langer, and Ziveri 2016; Conte et al. 1998; Fielding 2013; Wheeler, Sturm, and Langer 2023). Distinct *G. huxleyi* isolates have unique thermal reaction norms (Zhang et al. 2014; von Dassow et al. 2021), and strain diversity can shift thermal reaction norms in ecologically significant ways (Anderson and Rynearson 2020). Strain identity thus may determine viral resistance via lipid remodelling (Kendrick et al. 2014), alkenone composition (Conte et al. 1998), elemental composition and change (Sheward et al. 2023) and trace metal speciation and use (William G. Sunda and Huntsman 1995; Strzepek, Boyd, and Sunda 2019; Echeveste, Croot, and von Dassow 2018), all of which may determine both phytoplankton community composition and nutrient export. The *G. huxleyi* species complex is unusually resilient to temperature among coccolithophores (Frada et al. 2022), which may further increase its importance as global mean temperatures rise. *G. huxleyi* also has a level of diversity appropriate to test hypotheses about coccolithophore and general phytoplankton thermal physiology. Coccolithophores are frequently cited as suited to low temperature, low turbulence and oligotrophic conditions, which drives predictions of declines in this group as a consequence of climate warming (Anderson et al. 2021). Despite this prediction, *G. huxleyi* expansions have recently been observed in situ (Rivero-Calle et al. 2015; Krumhardt et al. 2016). There is a pressing need to examine undersampled thermal niche traits in *G. huxleyi* and other phytoplankton, as niche width and strain diversity could impact group coexistence and overall biomass and hence explain unexpected trends in the success of competing phytoplankton taxa.

Here, we selected 12 globally - distributed *G. huxleyi* isolates to assess the degree of thermal response curve variability across strains. To explore the impact of observed thermal trait diversity on total biomass and thermal type coexistence, we designed a model simulation for a general phytoplankter with varying thermal optima (following Dutkiewicz et al. (2020)) and included variable thermal response norm width among model ‘ecotypes’ (we use the term ‘ecotypes’ for the model organisms to differentiate from the empirically studied ‘strains’). The large, relatively geographically balanced collection of *G. huxleyi* strains that we collected in the laboratory expanded available thermal response data and provided sufficient resolution to implement a diversity-resolving model simulation. We combined the model simulation with the laboratory dataset to demonstrate that model output can predict and diagnose reasons for the success of dominant traits across ocean regions. Our study bridges increasing recognition of the importance of strain-specific processes with the impacts of intraspecific diversity on typical model representations of thermal response and global thermal range predictions.

2 | Materials and Methods

2.1 | Laboratory Culturing

Cultures were obtained from the Bigelow Laboratory for Ocean Science's National Center for Marine Algae and Microbiota (NCMA) for strains CCMP371, 374, 375, 379 and 2090 and from the Roscoff Culture Collection (RCC) for strains RCC874, 914, 1212, 3492, 3963 and 6071. Strain CCMP1516, which is a descendant of the same original isolation as Strain 2090, was obtained from the Dyhrman laboratory at Columbia University and has been observed to calcify, whereas strain CCMP2090 no longer calcifies in culture. Maintenance cultures of each of the twelve; RCC4567 was removed from the analysis strains were kept at 18°C under a 14:10 light/dark cycle and transferred approximately once per month. Four fluorescent tube bulbs were positioned below the culture vials such that each culture tube was situated directly above a bulb. Approximately 10 cm from the light source, a light level of approximately 24 μmol m^{-2} s^{-1} was measured. Natural seawater from Vineyard Sound, MA, USA was used as the base for all media recipes. Strains were maintained in standard L1 media without silica (reported herein as L1-Si; as per https://ncma.bigelow.org/algae-media-recipes). Strains CCMP1516 and 371 were maintained in low nutrient media to help retain their calcification state, where all nutrients, trace metals and vitamins were added at 1/25th of the standard concentration (reported herein as L1/25-Si; as per https://ncma.bigelow.org/algae-media-recipes).

An aluminium thermal block was used to achieve a thermal gradient over which strains could be incubated at increasing temperatures. The aluminium block has 80 openings across 4 rows and 20 columns for 25 mm diameter glass culture tubes. Thermal equilibrium is maintained using insulation, and a shared light source at the bottom of the thermal block enables constant light levels across the experiment (Blankley and Lewin 1976; Watras, Chisholm, and Anderson 1982). A circulating water bath was used to keep one side of the thermal gradient cool, while a heating element on the other side set the maximum temperature of the experiment; the low and high temperatures were selected for each set of measured strains based on their expected thermal tolerance. Temperature extremes were set according to realistic temperatures for the strain being tested, and temperatures were measured and recorded regularly throughout the experiments.

Each strain was transferred via 1 mL aliquots from the maintenance stock to 6–7 different temperatures spanning the thermal gradient at the beginning of the experiment. Strains CCMP1516 and 371, as well as strain CCMP2090 for intercomparability with a descendant of the same lineage strain CCMP1516, were transferred into and maintained in the L1/25-Si media, while the remainder of the strains were transferred into and maintained in L1-Si media for all subsequent transfers in the thermal experiment. Cell abundances and optical properties were measured daily using flow cytometry, with either a Guava easyCyte HT 2 or 3 (Luminex, USA; Strains RCC874, CCMP371, CCMP379 and CCMP374) or a BD Accuri C6 Plus equipped with a C-Sampler (BD, USA; Strains RCC1212, RCC6071, CCMP1516, CCMP2090, RCC3963, RCC914, RCC3492 and CCMP375). Each strain population was maintained in triplicate rows with identical temperatures in semi-continuous culture for a minimum of 45 generations, or approximately 2 months. Maximum growth rates were computed using the last recorded time point in the exponential phase and the first recorded time point in the exponential phase, identified manually to ensure that compatible points in the cell cycle were used for growth rate calculations, according to the equation:

$$\mu = \frac{ln(N_F) - ln(N_i)}{t}$$

where N_f is the final recorded concentration in the exponential phase as measured in cells per millilitre, N_i is the first recorded concentration and t is the duration in days. The final growth rate is expressed in dimensionless units per day. Final thermal reaction norms were constructed using growth rates computed from up to 3 semi-continuous transfers when data meeting the minimum quality thresholds were available.

2.2 | Thermal Response Curve Parameterisation

We used the equation from Norberg (2004) to parameterise phytoplankton growth rates across the strains we studied:

$$k(T) = a \times e^{bt} \times \left[1 - \left(\frac{T-z}{w/2}\right)^2\right] \qquad (1)$$

where T is temperature, $k(T)$ is specific growth rate, w is the estimated thermal niche width and a, b and z are parameters that determine the Eppley curve between temperature and growth rate encompassing the thermal optimum and niche width, commonly fit using methods like maximum likelihood estimation (Strock and Menden-Deuer 2021; Norberg 2004; Thomas et al. 2012). We used the bbmle package (version 1.0.25; Bolker and Bolker 2017) to estimate parameter values for this equation for each of the strains. We estimated the thermal optimum from the equation by using the optimise function in R with the maximum parameter set over an interval in temperatures from zero to 40°C. We recalculated the thermal width for the data from (Anderson et al. 2021) using 0.01 as a threshold value for when the growth rate was zero at the intersection points, since the parameterisations tended to have unrealistically high reported thermal widths when the estimated thermal performance curves had long tails with near-zero growth rates.

We calculated the 'plateau parameter' (the range of temperatures over which measured growth rate was within 80% of the maximum measured growth rate) using the same search procedure to determine the intersection points. The code used to calculate these quantities is available in the published GitHub repository.

2.3 | Parameterisation of Darwin 3-Dimensional Model Simulation

To simulate more diverse thermal response curve shapes, we modified the Darwin model (Follows et al. 2007; Dutkiewicz et al. 2020, 2015). The Darwin model is designed to be flexible in the number and types of plankton to include. Here, to focus on the relevance of thermal norm structure alone, we implement a setup where the phytoplankton types we include (either 10 or 60 types) are identical to each other except for their thermal norm and are grazed equally by the single zooplankton grazer without competition. The 10 or 60 phytoplankton functional types (which we refer to as 'ecotypes', while we refer to experimental variants as 'strains') had one of 10 thermal optimum values. We compared two simulation configurations: thermal optimum only, wherein only thermal optimum varied between 10 different types, and roughly linearly spaced optimum values varied between 0°C and 31.5°C corresponding to typical thermal optimum values for coccolithophores. In a second model configuration, the same 10 thermal optimum types were simulated between 0°C and 31.5°C, but each thermal optimum type also corresponded to 6 different thermal niche width values (16°C, 18°C, 20°C, 22°C, 24°C and

26°C). These thermal niche width values each corresponded to a different value of both the parameters a and w in the Norberg curve parameterisation of the thermal curve. We penalised the Eppley shape parameter a of each functional type by 0.05 for every degree Celsius wider its width was than the baseline specialist phytoplankton functional type. This imposed a cost to adopting the generalist lifestyle in the model. Because our strains varied in thermal niche width in the laboratory without predictable changes in maximum growth rate, we applied a uniform penalty rather than using an observed laboratory relationship between thermal width and maximum growth rate. A single grazer class was simulated in the model, with grazing rate scaled by temperature according to the expression:

$$e^{0.065\times(\text{Temperature}-24)}$$

In each of these two experiments, the phytoplankton types were initialised with identical biomass and the simulation was run for 10 years. The biogeography of the different phytoplankton types reaches a quasi-steady seasonal cycle after about 3 years of integration. We present results from the last year of this simulation.

2.4 | Analysis of Darwin Model Output

The Darwin model results were saved in time-averaged intervals of 1 month, and the surface layer of the simulation was extracted from the model output. Biomass was provided in the model in units of mg C/m^3 for each phytoplankton type. Biomass-weighted thermal niche width was calculated at each gridded latitude and longitude location according to the expression:

$$\text{Weighted Width (Long, Lat)} = \frac{\sum_{w=0}^{n} \text{biomass}[w] \times \text{widths}[w]}{\sum_{w=0}^{n} \text{biomass}[w]}$$

All maps were generated using the ggalt package (Rudis et al. 2017) and ggplot within the R statistical computing environment (version 4.1; Wickham n.d.; R Core Team 2022). The map projection was produced using the coord_proj function and parameters '+proj=robin +lon_0=0 +x_0=0 +y_0=0 +ellps=WGS84 +datum=WGS84 +units=m +no_defs'. RColorBrewer was used to create gradient colour fills for maps (Neuwirth and Brewer 2014).

The presence or absence of thermal niche widths was estimated by considering widths to be 'present' when they constituted at least 1% of total community biomass in at least one time-averaged month of the simulation.

2.5 | Projection of Thermal Habitat of Laboratory Strains

The maximum thermal habitat of each strain was calculated by taking all ecotypes that had ever constituted at least 1% of the community at each latitude and longitude point. Each combination of thermal width and optimum value was only included once in the distribution per latitude and longitude location based on its presence at any time in the final year of the situation. This was done to identify the locations in which a nonzero probability of ever finding the strain in question at that location. In other words, this value represents the probability of survival or persistence of that strain, rather than its likelihood of being particularly abundant or being present across seasons. Seasonality and relative abundance were only considered to the extent that they influenced whether or not each strain exceeded the abundance threshold for this reason, as constructed probabilities were designed to represent regions constituting viable habitats for the strain under consideration. The maximum and minimum temperature of each strain as assessed by the thermal width was extracted and used to build a bivariate normal distribution for each latitude and longitude point. Thermal minimum and maximum were identified from the Norberg curve parameterisation using an identical procedure for the modelled ecotypes as for the laboratory strains. Specifically, $\pm \frac{w}{2} + \text{opt}$ was calculated using the Norberg parameters to identify the upper and lower bounds of the thermal response curve. For each of the twelve strains, the probability density function value was calculated using a bivariate normal distribution constructed from the mean and standard deviation of the distribution of minimum and maximum values. The bivariate normal distribution probabilities were assessed using the pbinom function from within the VGAM package (version 1.1–11) in R (version 4.1.0). The probability of each strain being identified as surviving at any time of the year based on the distribution built from the modelled ecotype abundance cut-off in each model grid cell (referred to as 'model probability' in the Results and Discussion) was calculated using the cumulative distribution function (CDF) between 1.5° Celsius above and below the predicted thermal bounds for each strain to replicate the margin of error inherent in the spacing between adjacent columns of the thermal block setup during the experiments. The CDF was calculated using the bivariate normal distribution, with means and variances specified using the mean and variance of the lower and upper bounds of the modelled ecotypes present at a latitude-longitude grid point, with a covariance calculated between them and a small correction factor (0.0001) added or subtracted in case covariance was zero. We subtracted the CDF calculated using the temperature 1.5° Celsius below the lower/upper thermal limits of each strain subtracted from the CDF calculated at the temperature 1.5°C above the lower/upper thermal limits of each strain. We assessed whether the assumption of normality for the distribution of thermal minimum and maximum values was appropriate using a Shapiro–Wilk test, which qualified the distributions as not significantly different from normal at all but 7 of 35,865 combinations of latitude and longitude (and in no location did both the minimum and maximum distributions significantly deviate from normal).

3 | Results and Discussion

3.1 | *G. huxleyi* Thermal Reaction Norms Are Intraspecifically Variable

To quantify the intraspecific variability of phytoplankton thermal response due to local thermal habitat, we selected 12 strains of *G. huxleyi* isolated from across the global ocean and from a variety of global environmental regimes (Figure 1). We acclimated strains to temperatures in the lab for at least 2 months (~45 generations) and then characterised thermal reaction norms. This minimum time period was chosen because it was the common minimum time period by which all strains had stable acclimated growth rates. We did not evaluate whether any of the strains

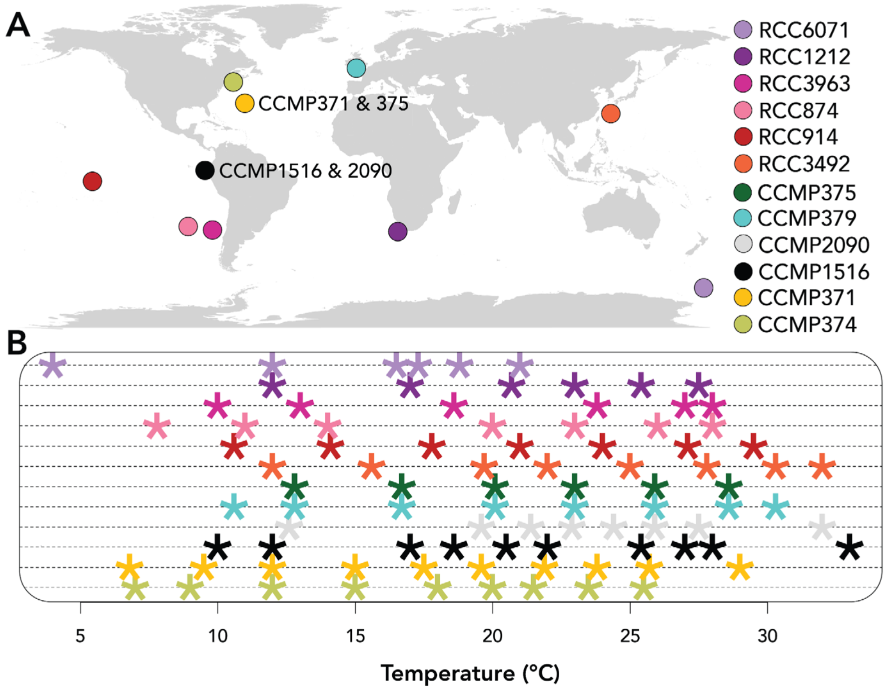

FIGURE 1 | Isolation location and measurement frequency of strains of *Gephyrocapsa huxleyi* tested. (A) Location of original isolation for each strain, which was retrieved from either the Roscoff Culture Collection (RCC) or the National Center for Marine Algae and Microbiota (NCMA). (B) Temperatures evaluated for each of the 12 strains.

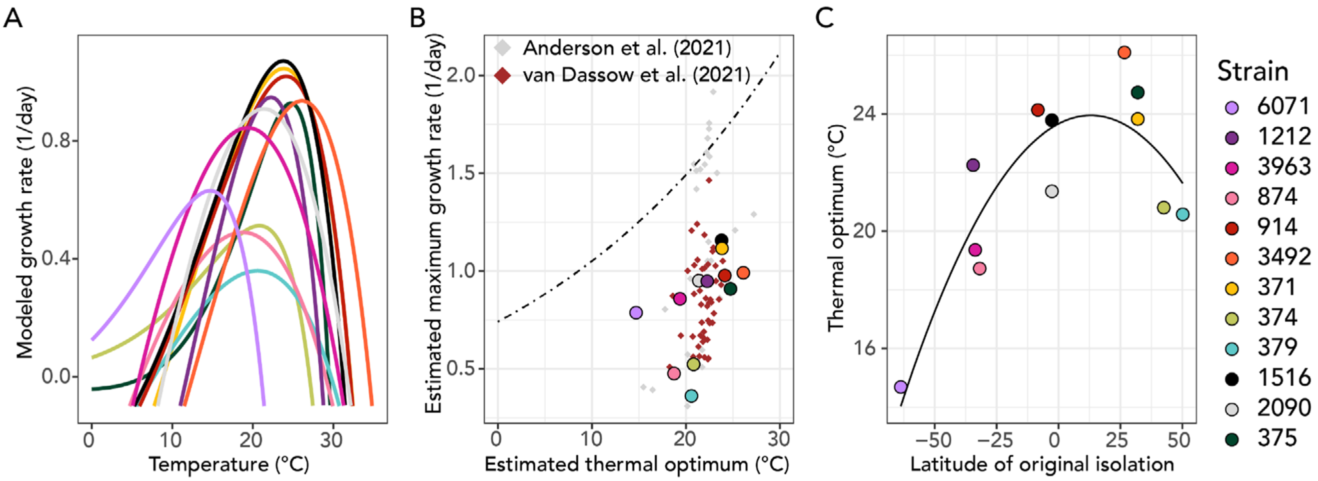

FIGURE 2 | Thermal response parameters for the 12 tested strains of *Gephyrocapsa huxleyi*. (A) Thermal response curves as parameterised by the Norberg equation for each strain. (B) Maximum growth rate compared to the estimated thermal optimum for each strain; the size of each point indicates its thermal width. The black dotted line indicates the hypothesised Eppley relationship for coccolithophores from Anderson et al. (2021). (C) Estimated thermal optimum by the latitude of isolation, where strains with a higher latitude of original isolation had higher thermal optimum values.

accumulated adaptations during the experiment and interpreted changes in each strain over the experimental period to be attributable to acclimation. The 12 strains of *G. huxleyi* in this study have distinct maximum growth rates, ratio between maximum growth rate and optimum temperature, and thermal range (Figure 2). The total range in measured thermal widths was 8.1°C, the range in thermal optimum was 11.4°C and the range between maximum growth rates at the thermal optima of the strains was 0.69 day^{-1}. We found no significant relationship between the thermal optimum and the growth rate at the thermal optimum (Kendall's tau: $T = 34$, $\tau = 0.03$, $p = 0.95$). Individual strains may respond differently to light and nutrient conditions, meaning that some trait heterogeneity may be the result of unevaluated light or nutrient limitation for particular strains under the conditions expected to be replete. Regardless, these results indicate that the strains we measured did not follow any straightforward scaling between average preferred temperature and either thermal range or maximum growth rate, highlighting the ecosystem relevance of intraspecific diversity under constant ambient environmental conditions. The 12 *G. huxleyi* strains examined here also had a broader range in thermal optimum than previously observed (Fielding 2013; von Dassow et al. 2021;

Anderson et al. 2021) due largely to our addition of a strain from the Southern Ocean (RCC6071). The data from the 12 strains we examined reaffirmed that coccolithophores have a wide range of maximum growth rates within a relatively small range of thermal optima (Figure 2B). The Southern Ocean strain also has a higher maximum growth rate than several strains with higher optimum growth temperatures (Figure 2B).

With the specific goal of identifying generalists and specialists, we compared our thermal performance characterisations to a prior data compilation for coccolithophores (Anderson et al. 2021), and added a recent set of thermal characterisations of *G. huxleyi* (von Dassow et al. 2021; Figure 2B). Our globally sampled data affirm that thermal trait diversity within the cosmopolitan species *G. huxleyi* is representative of all known thermal response data for coccolithophores (Figure 2A,B; Figure S1), hence *G. huxleyi* is exceptionally phenotypically variable. However, the total diversity of coccolithophore thermal responses is undersampled–only four other species of coccolithophore were present in the two datasets combined (Anderson et al. 2021; von Dassow et al. 2021). Our work underscores the importance of considering intraspecific variability, in that characterising a single isolate is insufficient to capture the flexibility of phytoplankton thermal response and inform parameterisations of phytoplankton thermal limits in models (Demory et al. 2019; Ye et al. 2023; Bishop et al. 2022). This discovery and our results highlight the importance of quantifying uncertainty attributable to intraspecific diversity in future laboratory and modelling studies.

Generalist and specialist strategies may influence the ecology of phytoplankton within and between thermal types and determine the water temperatures at which they can be successful. We evaluated the thermal niche width of *G. huxleyi* in the laboratory experiments by recalculating the width of the thermal response curve using the temperatures at which the simulated growth rate via the Norberg parameterisation crossed zero. The 12 strains fell along a range of thermal width values, with strain RCC1212 being the most ‘specialist’, while strain RCC3963 was the most ‘generalist’ (Figure 2B). Given the relationship between maximum growth rate and thermal optimum and other factors influencing growth, it is difficult to ascertain from laboratory data whether a penalty that assigns a growth rate cost to have a wider thermal niche width exists. We could not assign a straightforward growth rate cost to a broader thermal niche width. Although more thermal range flexibility would likely necessitate a lower maximum growth rate (Angilletta et al. 2003; Gilchrist 1995), neither our data nor previous data compilations supported a significant penalty (Figure S25). The relationship between maximum growth rate and thermal optimum complicates the evaluation of the cost, and may be an artefact of using idealised conditions in the laboratory that may not accurately reflect the environmental condition of simultaneous nutrient (including light) and temperature limitation https://paperpile.com/c/S5bid7/61Mo (Thomas et al. 2017). It is likely that with a broader survey of strains or a shift in the experimental design (e.g., examination of thermal growth response under nutrient-limited conditions), a more direct relationship between growth rate and tolerable thermal range might be determined. While assigning a penalty is essential to set the feasibility of arbitrarily flexible thermal niche widths, because this penalty cannot currently be directly determined from empirical data, we can explore and evaluate different penalties in a theoretical framework. We will take this approach later in the manuscript in designing a model parameterisation for a growth rate penalty of thermal niche width.

We used a second thermal width parameter for the range of temperatures that fell within 80% of the maximum measured growth rate. We call this the ‘plateau parameter’, since it captures the scenario that we frequently observed in which a range of temperatures appeared to be close to equally suitable for growth (Figure S2). The plateau parameter had a range of 6.5°C between strains, and similarly had no significant relationship with optimum temperature (Kendall's tau: $T=22$, $\tau=-0.33$, $p=0.15$) or maximum growth rate at the thermal optimum (Kendall's tau: $T=25$, $\tau=-0.24$, $p=0.31$). The plateau parameter was weakly correlated with the thermal width (Kendall's tau: $T=47$, $\tau=0.42$, $p=0.063$). Strains with a high range of survivable temperatures tended to have high growth rates across that survivable temperature range, but their maximum growth rates did not occupy a uniform proportion of the range (Figure S2). A larger measured thermal niche width only partially explained the larger range of temperatures around the thermal optimum with similar, near-maximum growth rates. The phytoplankton thermal types we measured were hence diverse in thermal optimum, thermal niche width and range of temperatures with high, near-maximum growth rates.

3.2 | Varying Modelled Thermal Width Traits Predicts Distinct Biogeographies of Generalists and Specialists

Our observations of the thermal traits of *G. huxleyi* highlight the variability in thermal niche width present in a single marine species. To understand how this diversity may impact *G. huxleyi* and other phytoplankton distribution at the ecosystem scale, we took an ecological modelling approach. To isolate the role of thermal reaction norm in determining phytoplankton distribution and biomass, we used the Darwin model (Follows et al. 2007; Dutkiewicz et al. 2020), an ecosystem layer on the MIT general circulation model (Marshall et al. 1997). We resolved sixty identical phytoplankton ecotypes with the same light and nutrient requirements (operating under the assumption that these fundamental requirements did not vary significantly between empirically studied strains, though this was not tested in the laboratory study) and susceptibility to predation. These ecotypes only differed in their thermal optima and thermal niche widths. We chose six thermal widths that linearly spanned the approximate range of thermal niche widths we observed across *G. huxleyi* strains (Figure 3C). Both our experiments and a previous data compilation did not find a clear relationship between thermal niche width and growth rate (Chen 2015), but imposing a hypothesised growth rate penalty in the model ensured that a wider niche width would not be a universally beneficial trait (Figure S4). To interpret the impact of an imposed penalty on the growth rate for a wider thermal niche width, we compared our results to a no and a high penalty model scenario (Figure S4). Comparing the no- and high-penalty scenario to the intermediate penalty we used in this study revealed that while generalist biomass

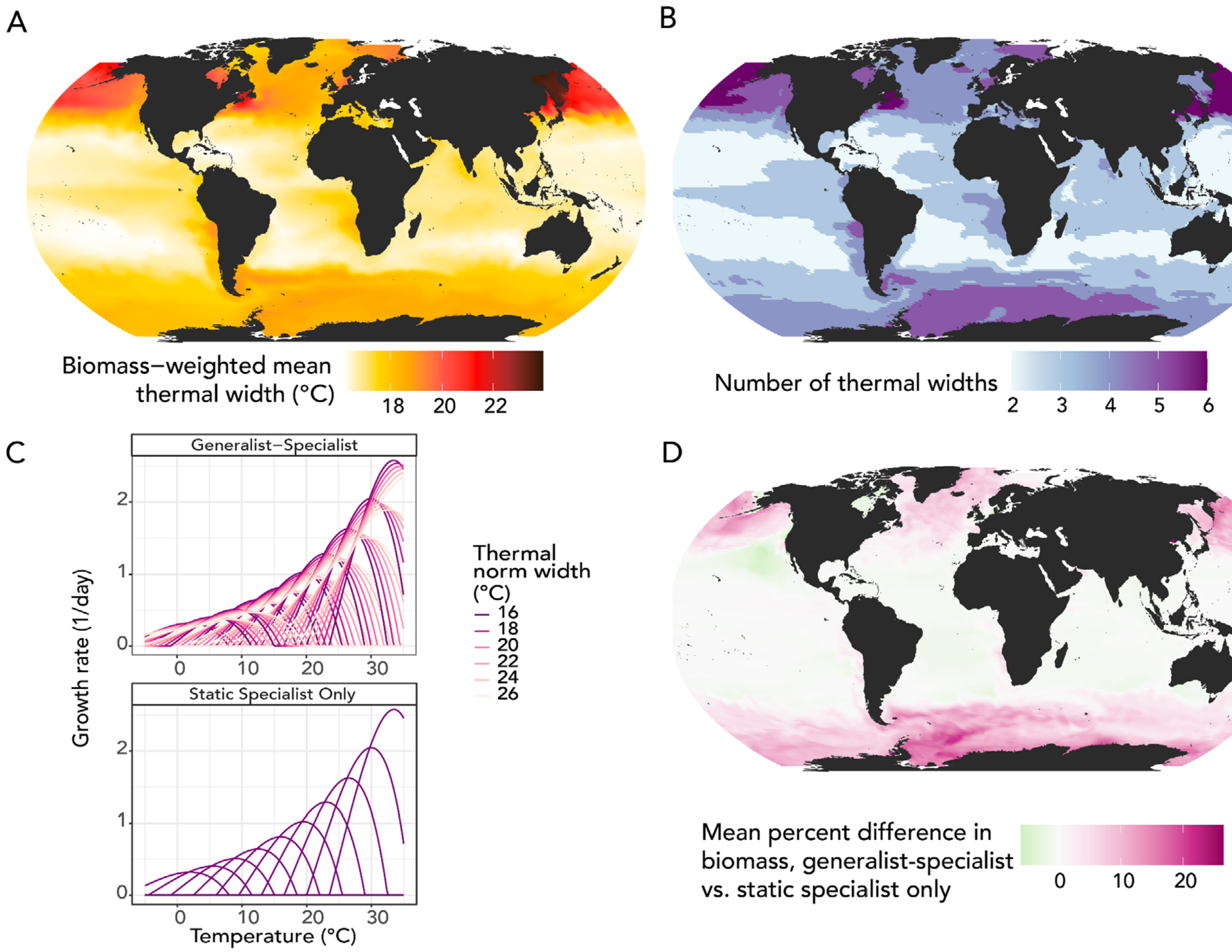

FIGURE 3 | Thermal niche width modifications to the Darwin model simulation reveal distinct global biogeography of phytoplankton generalists and specialists (A) Mean biomass-weighted thermal niche width of 60 phytoplankton functional types in the Darwin model simulation. Whereas theory suggests that specialists should dominate in high-latitude regions with high seasonality, we found that specialists tended to play a larger role in the total phytoplankton community in the subtropical gyres, whereas generalists with higher thermal niche widths thrived in temperate, mid-latitude regions. (B) Number of thermal niche widths observed with at least 1% biomass in the generalist-specialist simulation; more purple colours indicate more thermal niche widths present, up to a maximum of 6. (C) Static thermal niche width (left) vs. specialist-generalist (right) thermal reaction norms; each colour corresponds to a different thermal niche width, with lighter colours indicating a more generalist thermal niche width. (D) Percentage difference in mean modelled biomass in the final year of the simulation between the generalist-specialist simulation and the static specialist-only simulation. Darker pink colours indicate higher biomass in the generalist-specialist simulation, whereas green colours indicate higher biomass in the static specialist-only simulation.

correlates strongly with temperature variability in the no-penalty scenario (Figure S4A), there was low overall thermal niche width diversity, which contrasts with our laboratory observations. The high-cost scenario was completely specialist-dominated and showed the least correlation to temperature variability (Figure S4C). The intermediate penalty scheme that we adopted provided a reasonable trade-off between these two extremes that was consistent with the observation that many different thermal niche widths are indeed found in situ, suggesting that a penalty may exist even if not directly observed. Possible reasons for the lack of observed penalty in the laboratory experiments include the use of replete nutrient media or the differences between strains with respect to their specific nutrient requirements, which would moderate growth rate, and the specific selection of strains of *G. huxleyi* (i.e., that a penalty may be observed given a larger total sample size). Our experiments show that variability in thermal niche width exists between strains, which motivates a modelling approach (Darwin and MITgcm) that we use to explore the validity of a growth rate penalty on thermal niche width variation.

The largest relative populations of generalists were found in the north Pacific Ocean and northwest Atlantic (Figure 3A), which were areas of high-temperature variation in the model (Figure S3; Figure 3). However, some regions that favoured generalists, such as areas of the Southern Ocean, did not have high thermal variability. Further, regions enriched with specialists included oligotrophic gyres with low thermal variability (Figure 3A). The observation that regions with higher thermal variability tend to favour generalists in our model is partially compatible with generalisations of Janzen's hypothesis (Janzen 1967; Sheldon et al. 2018). However, the model reveals that physical features or the timing of seasonal changes in temperature and nutrient availability may result in an outsized role of resource availability (Tilman 1980) over thermal variability in some regions (e.g., Figures S4 and S5).

In this intermediate cost simulation, the mean thermal niche width and the number of coexisting thermal niche widths (Figure 3A,B) corresponded to ocean biogeochemical provinces, such as oligotrophic gyres and boundary currents. Due in part to these features, abundance patterns of individual thermal types did not necessarily correlate to thermal variability via standard metrics. In addition to non-temperature physiological influences on phytoplankton growth, these features may explain unexpected observations in thermal niche width relative to latitude or local temperature. For example, past work found that strains of *G. huxleyi* isolated from Bergen, Norway, a region with comparatively high thermal variability, had a lower mean thermal reaction norm width than isolates from Azores, Portugal, where thermal variability was lower (Zhang et al. 2014). The model predicts approximately the same mean thermal niche width (Figure 3A; Figure S5), and coexistence between generalists and specialists (Figure S8) at these two locations. This result indicates the flexibility of the model to predicting thermal niche width coexistence amid differences in temperature variability. While regions of very high thermal variability in the model had correspondingly high average thermal niche widths, average weighted thermal niche width more frequently corresponded to basin biogeography–hence local resource availability (Fu and Sun 2024; Tilman 1980; Sommer 1989; Tilman, Kilham, and Kilham 1982)–than absolute range or standard deviation in environmental temperature (Figures S4–S6). This could be due to geographic separation between basins, advection of specific water masses, nutrient availability or physical mixing.

To further explore the benefit of being a generalist, we compared the simulation with both specialists and generalists (generalist-specialist experiment) to one with only specialists (Figure 3C). We found that total biomass was generally lower in the specialist-only simulation (Figure 3D). The largest changes in biomass occurred in generalist-dominated regions (Figure 3A,D). However, there were also some increases in biomass in regions that favoured specialists, suggesting that generalists were in fact less productive in these regions, but had nevertheless persisted in the generalist-specialist experiment. Hence, biogeochemical conditions promoted the existence of regional niches selecting for diverse thermal widths over maximised community growth rate. Notably, while many regions that had more generalists than specialists had higher total biomass in the generalist-specialist simulation as compared to the specialist-only simulation, change in biomass was not proportional to the relative abundance of generalists (Figure 3A,D). This suggests higher relative importance of other factors (e.g., nutrients, phenology or finer-scale population dynamics (Moisan et al. 2002)) in these regions.

We also compared the specialist-only simulation to a generalist-only simulation, which revealed different global patterns in the benefit of being a specialist versus a generalist (Figures S9 and S10). Most of the global ocean had higher biomass in the generalist-only simulation. However, regions like the northwest Pacific and Sargasso Sea had unexpectedly higher biomass in the specialist-only scenario (Figures S9 and S10) despite high thermal variability (Figure S3). Short-term bursts in specialist biomass are only beneficial when fully coupled to the timescale of temperature change, hence mismatch between these two timescales may explain the difference in the specialist-benefit trade-off between ocean regions. Expected impacts differed between the generalist-only and the generalist-specialist simulation, indicating that the presence of both specialists and generalists influences overall biomass. The simulation results reinforced the observation that thermal niche width influences overall predicted biomass in an ecosystem model simulation, despite not always correlating directly with local temperature.

3.3 | Strain Geographic Predictions Highlight the Role of Intraspecific Diversity in Biogeography

The ecosystem model simulation output can be leveraged to determine which thermal traits are likely to be most successful in each ocean region. We used the ecosystem model output to predict the distribution of the twelve strains of *G. huxleyi* that we measured in the laboratory (Figure 4). Using the minimum and maximum temperatures of the model thermal types that could survive at each latitude and longitude, we calculated the probability that a hypothetical 'thermal type' with the same thermal maximum and minimum of each of the measured laboratory strains could persist (hereafter 'model probability'; see Methods). We found agreement between the location of the original isolation of the strain and the predicted model probability that the strain would exist in that location. We consider agreement to be when the model probability was nonzero, indicating the possibility that the strain could be isolated from the environment at approximately the location at which the strain was collected. Some examples of nonzero agreement include that 6 of the strains had greater than 15% probability and 3 had greater than 50% probability (Figure S11). The 3 strains with less than 1% probability of existence in the model grid point corresponding to their isolation location (RCC6071, RCC914 and CCMP1516) had high probability values nearby (Figure S11). Latent diversity within *G. huxleyi* indicates the ability of the species to survive across virtually all global ocean regimes, yet no individual strain tested had a greater than 1% probability in all simulated ocean regions (Figure S12). This result indicates that intraspecific variability in thermal trait diversity can increase the overall success of a species in surviving a range of temperatures and may be a mechanism that underpins the coexistence of strains in situ.

3.4 | Implications for Modelled Current and Future Phytoplankton Habitat

Taken together, the model analysis and laboratory results demonstrate that the width of the thermal response curve can have a strongly deterministic influence on the simulated distribution of phytoplankton in a diversity-resolving ecosystem model. The varied thermal niche widths of the strains we measured in the laboratory suggest that individual strains may prioritise allocation to subcellular processes differently in response to temperature, have variable rates of temperature-controlled reactions or use entirely different mechanisms to cope with the environmental temperature. Genome sequencing paired with gene expression studies will illuminate what specific differences in biological

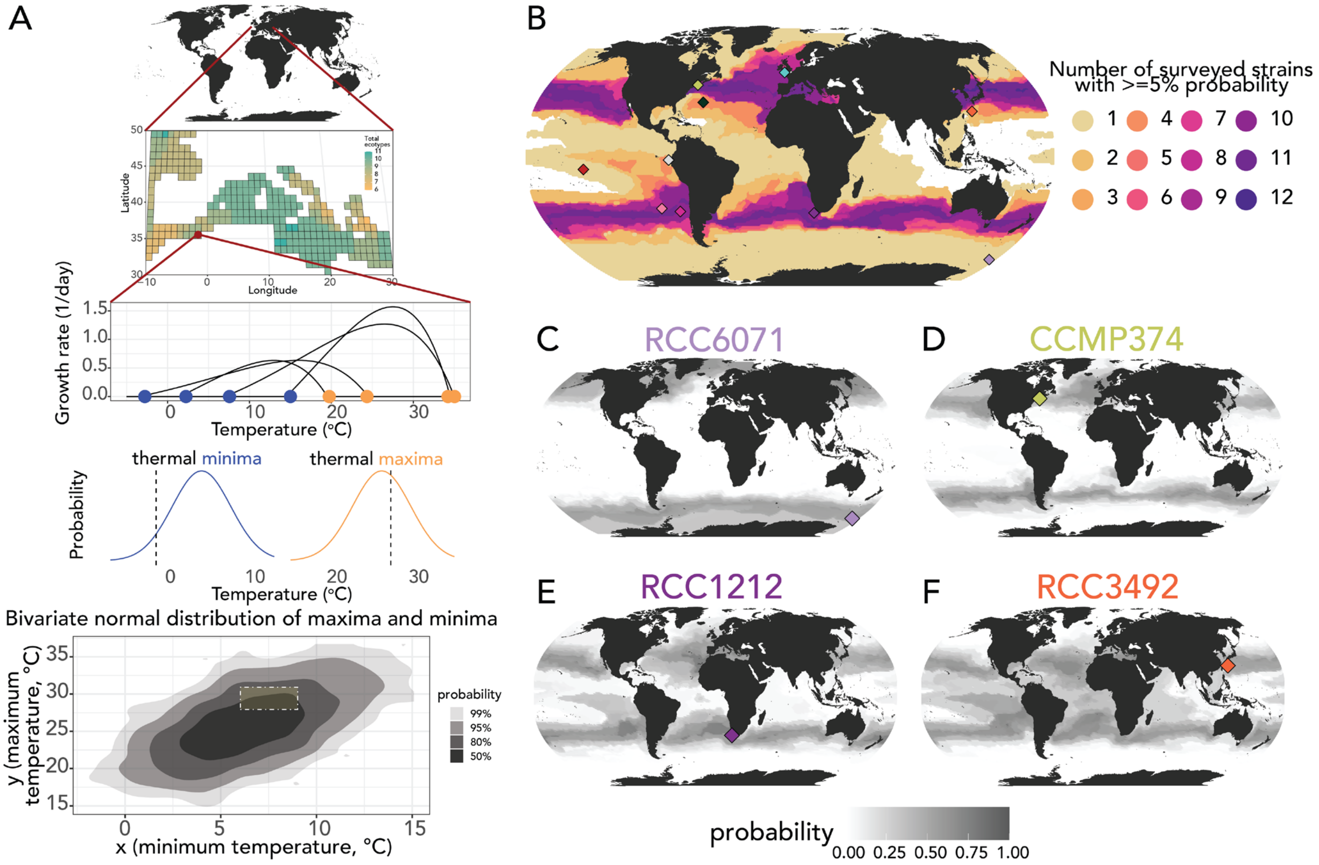

FIGURE 4 | Probabilistic projections of the environmental distributions of each of the strains of *Gephyrocapsa huxleyi* measured in the laboratory. (A) A representation of the methodology used to calculate probabilities; a bivariate normal distribution was built from the thermal minima and maxima of all strains that existed at each gridded latitude and longitude point in the model and constituted at least 1% of the population. Probability was calculated using the cumulative distribution function for the bivariate normal distribution within a range of 3° Celsius around the minimum and maximum values (the difference between the cumulative distribution function result and 1.5° Celsius above and 1.5° Celsius below the thermal minimum and maximum values). The 2D bivariate normal distribution at the bottom of panel A has a box surrounded by a dashed line that shows the region of the bivariate normal distribution in which this probability would be calculated. (B) The number of strains in each latitude and longitude point with at least a 5% probability of occurring from 0 (white) to 12 (dark purple); coloured diamonds indicate the isolation locations of each of the 12 strains and are identical to the gridded locations and colours of Figure 1A. (C) Predicted model probability using the method from 4A for strain RCC6071 (D) Strain CCMP374, (E) Strain RCC1212 and (F) Strain RCC3492.

pathways may be responsible for different observed thermal parameters between strains (Toseland et al. 2013). Thermal response mechanisms may also have variable responses under different resource conditions, which could reduce, eliminate or augment each strain's thermal response, including shifting the shape or centring of the thermal response curve (Andersson et al. 2022; Sunda 1989; Boyd et al. 2013; Thomas et al. 2017; Bestion et al. 2018; Litchman and Thomas 2022; Barton and Yvon-Durocher 2019; Rhee and Gotham 1981; Dedman et al. 2023). The importance of more complex temperature-resource availability relationships in moderating phytoplankton distributions could be tested by future laboratory experiments that consider the combined effects of temperature and the availability of one or more additional resources (Kremer, Thomas, and Litchman 2017). Future work on the thermal sensitivity of phytoplankton to other environmental drivers (e.g., trace metal availability) should also consider intraspecific variation. Additionally, it should be noted that the inclusion of other phytoplankton competitors, especially with different nutrient requirements, and more complex trophic strategies could impact the thermal niche distributions suggested in the model. Future modelling studies including additional complexity of the ecosystem, and more complex thermal-resource functions could explore these many interacting facets further.

Our observation that generalist-specialist simulations show greater biomass in thermally variable ocean regions may impact predicted phytoplankton resilience to future climate, including increasing thermal variability (Rummukainen 2012; Vasseur et al. 2014; Easterling et al. 2000) and marine heat waves (Meehl and Tebaldi 2004). For example, slowly increasing maximum growth rates among isolates at their optimum temperatures and diversity of thermal niche widths may enable coccolithophores to persist during short-term heat waves, which may increase stored resources and resilience to temperature fluctuation (Mason-Jones et al. 2022; Malik et al. 2019). Because *G. huxleyi* tends to be comparatively resilient to warming temperatures and fluctuating nutrients among coccolithophores (Keuter et al. 2023; Frada et al. 2022), the intraspecific diversity in the thermal niche (e.g., generalist v. specialist) observed here may offer a still greater mechanistic advantage against temperature warming and variability. While there is geographic separation of strain isolates in this study, intraspecific diversity is expected to exist both via allopatric and sympatric sub-populations (Kashtan et al. 2014; Anderson and Rynearson 2020; Godhe and Rynearson 2017). Fully characterising this diversity in the laboratory is not feasible. However, the current intraspecific resolution of culture studies is insufficient to estimate what proportion of the total range of trait values within species is covered by cultured isolates. Future work will measure trait variation in the laboratory among a statistically robust sampling of isolates, connect those traits to -omic variation (e.g., gene content or expression), use environmental meta-omics to predict access of individual species to those same traits in the field, and increase flexibility in modelled trait parameters accordingly. This workflow will be useful for predicting future shifts in the environmental range of species, but also for estimating present differences and future diversification of allocation strategies and resultant shifts in marine nutrient availability, storage and export, and identifying the level of resolution appropriate to model these features. Measuring the phenotypic flexibility that confers diverse thermal traits and encoding it in models is hence essential to projecting future climate-driven changes in the relative abundance and biogeography of phytoplankton functional types.

Author Contributions

Arianna I. Krinos: conceptualization, methodology, software, validation, formal analysis, investigation, data curation, writing – original draft, writing – review and editing, visualization. **Sara K. Shapiro:** investigation, writing – review and editing. **Weixuan Li:** formal analysis, writing – review and editing. **Sheean T. Haley:** resources, writing – review and editing. **Sonya T. Dyhrman:** resources, project administration, writing – review and editing, funding acquisition. **Stephanie Dutkiewicz:** software, methodology, resources, data curation, writing – review and editing. **Michael J. Follows:** conceptualization, resources, writing – review and editing, supervision, project administration, funding acquisition. **Harriet Alexander:** conceptualization, resources, writing – review and editing, supervision, project administration, funding acquisition.

Data Availability Statement

All codes used to create figures are available on GitHub at https://github.com/AlexanderLabWHOI/2024-Krinos-Ghux-Darwin. All growth rate data used in the model and the thermal parameters calculated for each strain are uploaded to the online Open Science Framework (https://osf.io/53bzp/?view_only=0cffef5f0a8c41749ff1d22367511488) and GitHub repository as well as available in Tables S1–S3.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.