Interactive effects of iron and temperature on the growth of *Fragilariopsis cylindrus*

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**Scientific Significance Statement**

Understanding how phytoplankton growth could react to future climate conditions will improve our knowledge of important marine ecosystem processes such as nutrient cycling and the ocean’s ability to absorb atmospheric CO₂. We currently do not understand how the projected simultaneous changes in two major drivers of phytoplankton growth, temperature and iron, will influence phytoplankton productivity in the future. In this study, we show that an ecologically important polar diatom can maximize growth under warming conditions by reducing its iron requirements. We observe morphological and physiological characteristics that may permit this species to take advantage of increased thermal energy under low iron.

**Abstract**

Iron and temperature are important drivers controlling phytoplankton growth in the Southern Ocean (SO). Most studies examining phytoplankton responses to these variables consider them independently, testing responses to changing temperature under constant iron and vice versa. Consequently, we lack a phenomenological and mechanistic understanding of how concurrent changes in these variables influence primary productivity. Here, we used a matrix of three temperatures and eight iron levels to examine changes in growth rate, photophysiology, and size in *Fragilariopsis cylindrus*. Temperature and iron interactively influenced growth; warming decreased iron demand, allowing cells to maintain half-maximal growth rate at lower iron concentrations. We also observed possible mechanisms underpinning this phenomenon: warming increased light-harvesting cross section and reduced cell size, thereby increasing light energy availability and iron uptake efficiency. These results suggest that interactive iron-warming effects could lead to larger increases in SO phytoplankton growth than those currently predicted by marine ecosystem models.

**Data Availability Statement:** Data and metadata are available at [https://doi.org/10.5061/dryad.np5hqbzq3](https://doi.org/10.5061/dryad.np5hqbzq3).

Additional Supporting Information may be found in the online version of this article.

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Diatom assemblages, which include *Fragilariopsis cylindrus*, contribute to the Southern Ocean’s (SO) ability to absorb 40% of all anthropogenic CO₂ (Frölicher et al. 2015). Future climate scenarios forecast changes in the SO environment, including average warming trends and uncertain modifications in iron availability (Turner et al. 2005; Tagliabue et al. 2017; Moore et al. 2018). Iron and temperature are two important drivers of phytoplankton growth; iron-specific growth rates increase with iron concentration until saturation (Sunda and Huntsman 1995a; Hutchins et al. 2002) and temperature-specific growth rates increase with warming until optimum (Eppley 1972). Most studies examining phytoplankton responses to these two variables examine them independently, and the few studies seeking to examine responses of temperature and iron simultaneously have featured experimental designs that test temperature responses under two iron
conditions, replete and limiting (e.g., Zhu et al. 2016; Boyd 2019). While these studies have yielded important insights into interactions between temperature and iron, they lack power to examine changes in growth kinetics and trends in the underpinning physiological responses. Consequently, we still lack a framework describing if temperature and iron interactively or independently influence growth. In an independent (additive or multiplicative) relationship, a change in one variable (i.e., temperature) does not influence how another variable (i.e., iron) affects growth. In an interactive relationship, a change in one variable influences another variable’s effect on growth. Understanding temperature-iron relationships in phytoplankton is imperative for understanding controls on SO primary productivity on physiological time scales.

Marine ecosystem models (MEMs) that simulate primary productivity typically assume that temperature \( T^F \) and nutrients \( N_{\text{lim}} \) influence growth in an independent, multiplicative manner (Laufkötter et al. 2015) (Eq. 1).

\[
\mu = \mu_{\text{max}} \cdot T^F \cdot N_{\text{lim}} \cdot L_{\text{lim}} \tag{1}
\]

where \( \mu \) = specific growth rate \( (\text{d}^{-1}) \), \( \mu_{\text{max}} \) = maximum growth rate, \( T^F \) = temperature coefficient = Q_{10} relationship, \( N_{\text{lim}} \) = nutrient factor = Monod function, and \( L_{\text{lim}} \) = light factor = function of light saturation.

These models are based largely on work describing an independent temperature-macronutrient utilization relationship (Goldman and Carpenter 1974; Ahlgren 1987; Marañón et al. 2018), even though temperature has been shown to influence macronutrient utilization in several phytoplankton groups (Rhee and Gotham 1981; Bestion et al. 2018). Moreover, MEMs do not incorporate temperature-micronutrient (e.g., iron) interactions, yet evidence shows that warming can influence iron utilization in *Trichodesmium* (Jiang et al. 2018).

An interactive temperature-iron relationship is possible due to phytoplankton’s ability to adjust morphological and physiological characteristics in response to environmental change. For example, cell size ubiquitously decreases at a rate of 2.5% °C\(^{-1}\) warming in many protist taxa (Atkinson et al. 2003), whereas cell volume increases with iron availability (Allen et al. 2008). Iron and temperature also influence photosynthetic parameters where photosynthetic efficiency increases with iron availability and light harvesting capacity increases with temperature (Maxwell et al. 1994; Strzepek et al. 2019). Changes in morphology and physiology could influence iron uptake rates, iron use efficiencies, and energy production, all of which can affect growth under different temperature and iron regimes.

The inability of current model formulations to capture potentially important interactive effects may contribute to their uncertainties (Laufkötter et al. 2015) and could hamper our ability to accurately predict future marine primary productivity. Our goal here is to characterize the short-term temperature effects on phytoplankton growth using an experimental design that would facilitate the examination of changes in growth kinetic responses to iron availability under different temperatures. We grew the polar diatom, *F. cylindrus*, under a gradient of ecologically relevant temperatures \( (1 \, ^\circ\text{C}, 3 \, ^\circ\text{C}, 6 \, ^\circ\text{C}) \) and eight iron conditions, and measured its growth rate, size, and photosynthetic health \( (F_{\text{r}}/F_{\text{m}}) \). Our results reveal a change in the kinetic constants that describe the relationship between iron availability and growth, and demonstrate that *F. cylindrus* can sustain half maximal growth rate at much lower iron concentrations under elevated temperature.

**Methods**

Experimental setup

We grew *F. cylindrus* (NCMA-1102, see Supporting Information Methods) in ethylenediaminetetraacetic acid (EDTA)-buffered media under a range of total iron concentrations \( (\text{Fe}_{\text{total}}: 0, 3.75, 10, 15, 20, 35, 50, 100, \text{ and } 500 \, \text{nmol L}^{-1}) \) at \( 1 \, ^\circ\text{C}, 3 \, ^\circ\text{C}, \text{ and } 6 \, ^\circ\text{C} \). *F. cylindrus* is successful in a wide span of SO environments including cold \( (< 0 \, ^\circ\text{C}) \) high-salinity sea ice to warmer \( (~5 \, ^\circ\text{C}) \) lower salinity open waters (Sackett et al. 2013), making it an ecologically and biogeochemically important species. The growth temperatures we used encompass a typical range of water temperatures during the current Antarctic growth season and possible future temperatures under warming (Boyd et al. 2015). Iron treatments ranged from severely limiting to replete, and were chosen based on previous work (Pankowski and McMinn 2009). Average dissolved free inorganic iron concentrations \( [\text{Fe}^{*}] \) were calculated by applying temperature-adjusted dissociation factors from Sunda and Huntsman (2003) to eq. 2 from Sunda et al. (2005) (see Supporting Information Methods, Table S1, and Fig. S1).

\[
[\text{Fe}^{*}] = \frac{[\text{FeEDTA}^{*}] \cdot (K_{\text{diss}} \cdot I_{\text{hv}} \cdot K_{\text{hv}} h/24)}{[\text{EDTA}^{*}]} \tag{2}
\]

Irradiance was supplied through white LED lights (LEDMO-EZ550) and was kept constant at \( \approx 50 \, \mu\text{mol phot}^{-1} \text{-s}^{-1} \). Cells were first acclimated to all iron concentrations until growth rates were stable at \( 3 \, ^\circ\text{C} \) (5 transfers \( \approx 15-20 \) generations). Cells from each iron concentration—except 0 nmol L\(^{-1}\) Fe, which failed to grow—were further acclimated to \( 1 \, ^\circ\text{C} \) and \( 3 \, ^\circ\text{C} \) through a full growth cycle and then used to inoculate triplicate 28 mL polycarbonate tubes (Nalgene) for each iron concentration at \( 1 \, ^\circ\text{C}, 3 \, ^\circ\text{C}, \text{ and } 6 \, ^\circ\text{C} \). Our results reveal a change in the kinetic constants that describe the relationship between iron availability and growth, and demonstrate that *F. cylindrus* can sustain half maximal growth rate at much lower iron concentrations under elevated temperature.
Media preparation

Synthetic ocean water was prepared in a trace-metal-clean manner following the Aquil™ recipe (Price et al. 1988; Sunda et al. 2005). Vitamins and macronutrients were prepared and added to the media following the Aquil™ recipe (Sunda et al. 2005). An iron-free, EDTA-buffered trace metal mixture (modified from Sunda and Huntsman 1995b) was added to the media with various concentrations of Fe$_3$Cl (Fe$_{total}$) dissolved in acidified ultrapure water to attain the desired iron treatments (see Supporting Information Methods).

Media preparation and cell culture work were conducted in a purpose-built clean room under positive pressure high efficiency particular air. Labware was rigorously cleaned through a series of soaks in 0.1% Citranox solution and 1.2 mol L$^{-1}$ trace-metal grade HCl, followed by rinsing with ultrapure pH 3 Milli-Q water.

Growth rates

In vivo relative chlorophyll $\alpha$ fluorescence units (RFUs) were measured directly from 28 mL culture tubes using a 10-AU Fluorometer (Turner Designs). Cell counts were also measured on the day of inoculation and 2–3 times throughout exponential growth using a BD Accuri™ C6 flow cytometer (BD Biosciences). RFUs correlated linearly with cell counts, measured on the day of inoculation and 2 times throughout exponential growth using a BD Accuri™ C6 flow cytometer under the same settings as Cyte for all cells.

The most appropriate $\frac{\text{d}}{\text{d}t}$was estimated using the method described above (see Supporting Information Methods, Tables S3, S4). The linear nature of the growth rate fits was assumed for all cells.

Photophysiology

Photochemical efficiency of PSII ($F_o/F_m$), relative functional absorption cross-section of PSII ($\sigma_{PSII}$), and PSII reaction center abundance (RC$_{II}$) were measured using a FIIRe Fluorometer System (Satlantic). Measurements were conducted during mid-exponential growth after 30 min of dark acclimation at the respective culture temperatures. The generated fluorescence profiles were fitted using Fireworx code (Barnett 2017). $F_o/F_m$ was calculated as the ratio of variable to maximum fluorescence, where $F_o = F_m - F_v$, and $\sigma_{PSII}$ was estimated using the slope between $F_o$ and $F_m$. RC$_{II}$ was calculated as $F_o$/cells mL$^{-1}$ to account for varying cell densities under the different treatments (Oxborough et al. 2012).

Curve fitting and statistical analysis

All statistical analyses were conducted using R version 3.6.0, and are discussed at significance level of $p < 0.05$. To characterize the temperature and iron effects on growth, we fitted growth rates vs. iron to a Monod equation (Eq. 3) using a nonlinear mixed effects model via “SSmimcmen” in R package “nlme,” where $\mu_{max} = $ maximum growth rate and $K_{Fe} = $ iron half-saturation coefficient.

$$
\mu = \frac{\mu_{max} \cdot [Fe]}{K_{Fe} + [Fe]} 
$$

We then investigated the temperature effect on model coefficients ($\mu_{max}$ and $K_{Fe}$) by treating temperature as a fixed three-level factor (1, 3, 6) and replicates as random effects. Nested models containing temperature effect on both, one, or none of the parameters were compared through likelihood ratio tests and Akaike information criterion (AIC) scores, and parameter estimates were determined using maximum likelihood (see Supporting Information Methods, Tables S3, S4).

Temperature and iron effects on $F_o/F_m$ were also characterized via “SSmimcmen” in “nlme” using the method described above (see Supporting Information Methods, Tables S7, S8). The most appropriate “nlme” models were initially chosen based on lowest AIC scores following methods from Schaum et al. (2017).

Results

Growth kinetics

Growth rates ranged from 0.33 ± 0.19 d$^{-1}$ (mean ± standard error) at iron-replete 6°C, to no measurable growth in the 0 nmol L$^{-1}$ Fe$_{Total}$ treatment (i.e., dead cultures), which caused the 0 nmol L$^{-1}$ iron treatment to be excluded from further data analysis (Fig. 1). The iron half-saturation coefficient, $K_{Fe}$, decreased significantly (likelihood ratio test comparing models with and without temperature effect on $K_{Fe}, p = 0.021$) with warming following the Monod function $K_{Fe} = (20.38*T)/(-0.69 + T)$, where $T = $ temperature in °C. Maximum growth rate, $\mu_{max}$, also increased linearly with temperature (likelihood ratio test comparing models with and without temperature effect on $\mu_{max}, p < 0.001$), where $\mu_{max} = 0.03 + 0.16$ (Fig. 2A,B; Supporting Information Tables S3, S4). The linear nature of the
μmax-temperature relationship indicates that our growth temperatures were below $T_{opt}$ for $F. cylindrus$, which is typically 7–9°C (Mock and Hoch 2005).

Size

ECD ranged from 3.7 ± 0.04 μm in the most severely iron-limited cultures at 6°C to 6.29 ± 0.08 μm in iron-replete cultures at 1°C (Fig. 3A). Warming significantly reduced maximum size (likelihood ratio test comparing models with and without temperature effect on $Size_{max}$, $p < 0.0001$) and increased the rate at which cells became smaller under low iron (likelihood ratio test comparing models with and without temperature effect on $Size_{scale}$, $p = 0.002$, Supporting Information Tables S5, S6). Additionally, cells in iron replete treatments ($Fe_{Total} > 50$ nmol L$^{-1}$), reduced in size at a rate of

### Table 1. Increase in growth rate ($\Delta \mu$, d$^{-1}$) per 1°C warming at very low, intermediate, and replete iron conditions.

| $Fe_{Total}$         | $\Delta \mu$ (d$^{-1}$) per 1°C |
|----------------------|-------------------------------|
| Very low (<10 nmol L$^{-1}$) | 0.004 ± 0.003                |
| Intermediate (35 nmol L$^{-1}$) | 0.029 ± 0.006                |
| Replete (>50 nmol L$^{-1}$) | 0.028 ± 0.003                |

Fig. 1. Growth rates of $F. cylindrus$ under various temperatures and dissolved free iron (Fe') concentrations fitted using a Monod function. Each point at 1°C and 3°C represents measurements of three independent biological replicates. Each point at 6°C represents measurements of six independent biological replicates. $N_{total} = 96$, error bars represent 95% confidence intervals.

Fig. 2. (A) Changes in iron half saturation coefficient $K_{Fe}$ with temperature. $K_{Fe}$ is fitted using the Monod function $K_{Fe} = (20.38 * T) / (−0.69 + T)$, where $T$ = temperature in °C, and residual standard error (RSE) = 2.63. (B) Changes in maximum growth rate, $\mu_{max}$, with temperature. $\mu_{max}$ is fitted using the linear equation $\mu_{max} = 0.03 * T + 0.16$, $R^2 = 0.95$. In both (A) and (B), error bars represent 95% confidence intervals, line fits were estimated using R package nlMS (Supporting Information Table S9).

Fig. 3. (A) Estimated cell diameter vs. dissolved free iron concentrations (Fe') at the three tested temperatures. Each point represents measurements of three independent biological replicates, $N_{total} = 72$. X-axis is log-transformed for clarity. (B) The percent reduction in ECD per 1°C warming under various total iron ($Fe_{Total}$) conditions. This was calculated using the slope values of $\Delta ECD/\Delta$temperature under the various iron conditions. In both (A) and (B), error bars represent 95% confidence intervals.

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2.09% ± 0.29% 1°C⁻¹ warming, while iron stressed cells (3.75 nmol L⁻¹ < FeTotal < 50 nmol L⁻¹), reduced in size at a rate of 4.52% ± 0.11% 1°C⁻¹ warming (Fig. 3B).

Photophysiology

$F_v/F_m$ values ranged from 0.23 ± 0.03 in the most iron limited cultures, indicating severe iron stress, to 0.47 ± 0.01 in iron replete cultures at 6°C, a typical value for unstressed *F. cylindrus* (Arrigo et al. 2010) (Fig. 4A). Warming increased maximum $F_v/F_m$ values under iron replete conditions but not under iron stress (likelihood ratio test comparing models with and without temperature effect on $F_v/F_{m,max}$, $p < 0.0001$ and $F_v/F_{m-lowiron}$, $p = 0.27$, respectively, Supporting Information - Tables S7, S8). $\sigma_{\text{PSII}}$ showed a decreasing trend with iron availability at 3°C and 6°C and increased with warming only under iron-limited conditions (Supporting Information Fig. S3). $R_{C_{II}}$ increased significantly with iron availability, and decreased at 6°C under iron replete conditions (multiple linear regression using “lm” function, $p = 0.001$ and $p = 0.01$, respectively; $R^2 = 0.81$) (Supporting Information Fig. S4).

Discussion

The increase in growth rate with warming and increasing iron availability we observed has been well documented previously, and is captured in models that use an independent relationship between dependencies on iron and temperature (Laufkötter et al. 2015). However, we show an interactive temperature-iron relationship, where warming decreases the iron half-saturation coefficient ($K_{Fe}$), indicating that cells need less iron to sustain growth under warming. This interaction causes an increase in the nutrient(iron) term—$N_{lim(Fe)}$—(Eq. 1) even when iron is not increased. To quantify the effect of temperature on $N_{lim(Fe)}$ we can incorporate the temperature-$K_{Fe}$ relationship into the Monod equation (Eq. 3) to include a temperature-Fe interactive term (Eq. 5). Where $\mu =$ specific growth rate (d⁻¹), $\mu_{maxTemp} = 0.03 * T + 0.16$, [Fe] = iron concentration (pmol L⁻¹) and $K_{FeTemp} =$ temperature adjusted $K_{Fe} = (20.38*T)/(-0.69 + T)$, $T =$ temperature in °C.

$$N_{lim(Fe)} \equiv \mu = \frac{\mu_{maxTemp} \cdot [Fe]}{K_{FeTemp} + [Fe]}$$

An increase in $N_{lim(Fe)}$ with warming under low iron could translate to higher *F. cylindrus* primary productivity rates than current models predict. This short-term interactive response to temperature and iron could have important ramifications in the SO where iron is limiting throughout most of the year, and would be especially important if the response is maintained in the long term.

Our findings differ from studies where warming did not enhance phytoplankton growth under macronutrient limitation (Marañón et al. 2018). This discrepancy may be due to the different fundamental roles these two types of nutrients play within cells: macronutrients function as molecular “building blocks,” while iron functions as a cofactor in many enzymes used as “workers” to assemble these blocks. Under macronutrient limitation, warming increases enzymatic (worker) efficiency, but cell growth would be limited by the lack of building blocks. Conversely, in an iron-limited, macronutrient replete environment, warming increases enzymatic efficiency and thus decreases the number of iron-containing workers required to maintain growth. This would only be beneficial in regions like the SO, where there is an abundance of macronutrient building blocks. While the efficiency of iron-containing enzymes has been shown to increase with warming (Di Martino Rigano et al. 2006; Jiang et al. 2018), iron quota measurements and proteomic surveys under various temperature and iron conditions are needed to further examine this hypothesis.

The interactive temperature-iron relationship we show is also influenced by the degree of iron limitation. Growth rate increase
due to warming was an order of magnitude lower under severely iron-limiting treatments ($Fe_{\text{Total}} < 10 \text{ nmol L}^{-1}$) compared to moderately stressed and replete iron conditions (Table 1). The negligible temperature effect on growth at extremely low iron may be due to severe stress ($F_v/F_m = 0.23$) and failure to meet the minimum iron quota required to sustain basic metabolic function. Consequently, studies using only iron replete and deplete conditions could fail to observe much of the important interactive effects of temperature and iron on growth.

We observed several morphological and physiological characteristics that may allow *F. cylindrus* to reduce $K_{lc}$ and take advantage of warming. Photosynthetic efficiency ($F_v/F_m$) did not improve with warming under low iron, which suggests that other photosynthetic mechanisms may be responsible. The increase in $\sigma_{\text{PSII}}$ under warmer, low-iron conditions (Supporting Information Fig. S3) improves light harvesting and increases the energy available for photosynthesis. This decreases the demand for iron-containing photosynthetic proteins, as reflected in the reduced abundance of PSII reaction centers ($RC_{\text{II}}$) at 6°C (Supporting Information Fig. S4). However, larger $\sigma_{\text{PSII}}$ reduce the efficiency of light energy transfer to photosynthetic reaction centers, creating an inverse relationship between $\sigma_{\text{PSII}}$ and $F_v/F_m$ in SO algae grown at ~4°C (Strzepek et al. 2019). This inverse relationship was only apparent under elevated temperature in our experiment (Fig. 4B, Supporting Information Table S10), which further suggests that warming may assist iron-limited photosynthesis by increasing light harvesting.

The decrease in iron requirement with temperature was accompanied by a decrease in effective cell size. Smaller cells grow more favorably under iron limitation due to increased surface area to volume ratios and reduced nutrient and energy quotas per cell, allowing faster division/growth rates (Hudson and Morel 1990; Finkel et al. 2010). A decrease in size under increased temperature could then be a beneficial strategy to maximize growth while reducing iron demand. This would be especially advantageous in the SO, where higher water temperatures occur later in the summer and coincide with major iron drawdown by algal blooms (Wu et al. 2019). The decrease in size with temperature observed here (2.1% decrease°C$^{-1}$ warming) follows an established temperature-size rule in nutrient replete environments (Atkinson et al. 2003). Our results expand on this rule by showing that the decrease in size is magnified twofold under iron-limited growth conditions (4.5% decrease°C$^{-1}$ warming). This phenomenon further reduces iron demand per cell and enables increased growth with warming. However, since smaller cells also contain less carbon, it is possible that iron demand per carbon (Fe : C ratio) did not change. Interrogation of Fe : C ratios is required to understand the implications of these trends for iron use efficiency.

Our data show that temperature and iron interactively, not independently, influence the growth rates of *F. cylindrus*; the initial slope of the exponential phase of growth rate curves (Fig. 1) becomes steeper at higher temperatures, indicating a reduction in $K_{lc}$. This allows *F. cylindrus* to increase its iron-limited growth at a rate faster than is predicted by current models under warming. Regardless of mechanisms underlying this temperature-iron interaction, the morphological and physiological flexibility we observed here will influence the abundance and ecological role of *F. cylindrus* in SO microbial communities. This temperature-iron interaction may also be amplified in diatoms with lower iron demand than *F. cylindrus* (i.e., *Pseudo-nitzschia subcurvata*, Zhu et al. 2016). The resulting increase in primary productivity under warming would contribute to further drawdown of macronutrients and increase the SO trapping effect, where nutrients are exported and prevented from being redistributed to fuel productivity at lower latitudes (Moore et al. 2018). With increasing sea surface temperature trends, an interactive temperature-iron relationship could have important ramifications for SO primary productivity and global biogeochemistry.

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Conflict of Interest
None declared.