

LETTER

Evidence of partial thermal compensation in natural phytoplankton assemblagesKailin Liu ¹, Bingzhang Chen ^{2,4}, Hongbin Liu ^{1,3,4*}

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Scientific Significance Statement

Temperature sensitivity of phytoplankton is critical to predicting the response of marine productivity to climate warming. It has been found in laboratory studies that the temperature sensitivity across phytoplankton species was lower than that within-species, which suggests the capacity of phytoplankton thermal adaptation. However, this pattern of thermal adaptation is yet to be confirmed in natural phytoplankton assemblages. We provide the first empirical evidence of the “hotter is partially better” in natural phytoplankton communities. The short-term temperature sensitivity within communities was higher than that across communities during an annual cycle. These results are consistent with laboratory findings and highlight the difference in temperature sensitivity of phytoplankton at different timescales, which will affect how we predict the effect of warming on plankton ecosystems in the sea.

Abstract

Whether phytoplankton growth is solely constrained by temperature (hotter is better) or compensated by thermal adaptation is still under debate. We measured the temperature sensitivity of natural phytoplankton communities at both short-term and seasonal timescales using temperature manipulation experiments. The activation energy across communities (mean \pm SE: $E_i = 0.51 \pm 0.12$ eV, $Q_{10} = 1.98$) is significantly lower than that within communities ($E_a = 0.80 \pm 0.10$ eV, $Q_{10} = 2.80$). Moreover, using a larger dataset of phytoplankton growth rates measured in (sub) tropical waters, we estimated the across-community activation energy as 0.33 ± 0.06 eV ($Q_{10} = 1.56$), which is also lower than E_a . Our study is the first to suggest the “hotter is partially better” for natural phytoplankton communities, indicating that the phytoplankton communities can show some thermal adaptation capability. Our results highlight the importance of incorporating the differential temperature sensitivities at different timescales into the biogeochemical models to better evaluate how marine ecosystems will respond to climate changes.

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Marine phytoplankton contribute to about half of global primary production and are critical in the ocean biogeochemical cycles (Falkowski et al. 1998). Reliably quantifying their responses to the projected ocean warming is vital to predicting the effect of climate change on marine ecosystem functioning, such as CO₂ uptake and sequestration (Vasseur and McCann 2005; Fussmann et al. 2014). The effect of temperature on marine phytoplankton is characterized by thermal performance curves (TPCs), which depicts the physiological response of a single phytoplankton taxon to the temperature at short-term timescales (minutes to days). However, the temperature sensitivity of phytoplankton in terms of activation energy (E , eV) or Q_{10} applied in most biogeochemical models is derived from the relationship of the maximum growth rates against temperature across various phytoplankton species, encompassing the difference in the adaptation to diverse habitats at longer timescales (months, seasons, or years) (Eppley 1972; Yool et al. 2013; Laufkötter et al. 2015).

Short-term thermal response of phytoplankton growth is typically unimodal with negative skewness, depicted by the TPC (Fig. 1a; Thomas et al. 2012). The growth rates of phytoplankton increase with rising temperature up to the maximum (μ_{\max}) at the optimal temperature (T_{opt}) and rapidly decrease when temperature surpasses T_{opt} (Schoolfield et al. 1981; Angilletta 2006). The thermal traits of phytoplankton growth (e.g., T_{opt} and μ_{\max}), which are embodied in the TPC and have the imprint of previous environments, are used to link the short-term thermal response to the long-term response involving adaptation (Knies et al. 2009; Kontopoulos et al. 2020). Nonetheless, the adaptation patterns revealed by the relationship between thermal traits (T_{opt} and μ_{\max}) remain debatable in the evolutionary biology literature. The “hotter is better” hypothesis posits that μ_{\max} should increase with T_{opt} in a similar manner to the short-term response within one certain species as the organisms residing in cold environments cannot overcome the thermodynamic constraints of their biochemical kinetics and inevitably have a lower μ_{\max} than those from warm environments (Frazier et al. 2006; Knies et al. 2009). Thus, the short-term temperature sensitivity of phytoplankton growth rate within species should not differ from the long-term temperature sensitivity across species (see Fig. 1b). This hypothesis is implicit in estimating temperature sensitivity from the Eppley curve (Eppley 1972), which is usually applied in marine biogeochemical models (Yool et al. 2013; Laufkötter et al. 2015).

However, some studies argued that the adaptation of biochemical machinery could reduce or minimize the influence of thermodynamic constraints, allowing the organisms in cold environments to upregulate their performances (Clarke and Fraser 2004; Angilletta 2009). An extreme hypothesis is the “biochemical adaptation,” which states that the maximum performance of cold-adapted organisms can be upregulated to the levels of the warm-adapted organisms—consequently, the μ_{\max} should be independent of temperature (see Fig. 1c). An

intermediate scenario is also posited as the “partial compensation” hypothesis (i.e., “hotter is partially better”) in which the influence of adaptation is weaker than what the “biochemical adaptation” hypothesis predicts, resulting in a weaker thermal response of μ_{\max} to the increase in T_{opt} than the physiologically thermal response within species (see Fig. 1d). Recent studies have found that the adaptation of phytoplankton to the thermal environments is in the absence of hard “hotter is better” constraints but more aligned with the “partial compensation” hypothesis (Barton and Yvon-Durocher 2019; Kontopoulos et al. 2020). Thus, the short-term thermal response would be partially compensated by adaptation at the species levels, leading to a lower across-species temperature sensitivity than within-species (Barton and Yvon-Durocher 2019). Nevertheless, it remains unexplored whether this pattern also applies to natural phytoplankton assemblages as cultivated species or strains in the laboratory cannot fully represent the communities in the real ocean.

In this study, we aim to evaluate the thermal response of phytoplankton community at both short-term and long-term (seasonal) scales. We used two datasets on the growth rate of natural phytoplankton community estimated by the dilution technique, which is the only widely used method for measuring phytoplankton specific growth rates in situ (Landry and Hassett 1982; Laws 2013). We compiled the data of short-term temperature manipulated dilution experiments which estimated the growth rate of the same phytoplankton community at different temperatures. We also calculated the long-term activation energy from a dataset of phytoplankton growth rates in the (sub)tropical regions where the optimal temperature of phytoplankton communities can be approximated by in situ temperature (Thomas et al. 2012; Liu et al. 2019). By analyzing the thermal response of phytoplankton growth rate within vs. across communities, we test whether the temperature sensitivity of phytoplankton growth rate across communities should be lower than that within communities but still significantly positive as described in the “partial compensation” hypothesis.

Methods and materials

Data compilation and description

We compiled the data of short-term temperature manipulated dilution experiments which measured the growth rate of natural phytoplankton communities at designated temperatures and estimated the short-term thermal response (within 1 d) of a phytoplankton community (Table S1). The experiments were conducted monthly for a year at three stations (Fig. 2), which allow us to estimate the thermal responses across communities at a longer timescale (i.e., seasonal). The details of the experiments are in Chen and Liu (2015) and Liu et al. (2019). Briefly, in each experiment, five sets of dilution experiments were conducted, and the bottles were incubated at five temperatures (in situ temperature T , $T - 5^{\circ}\text{C}$, $T - 3^{\circ}\text{C}$, $T + 3^{\circ}\text{C}$, $T + 5^{\circ}\text{C}$). For each dilution experiment, particle-free

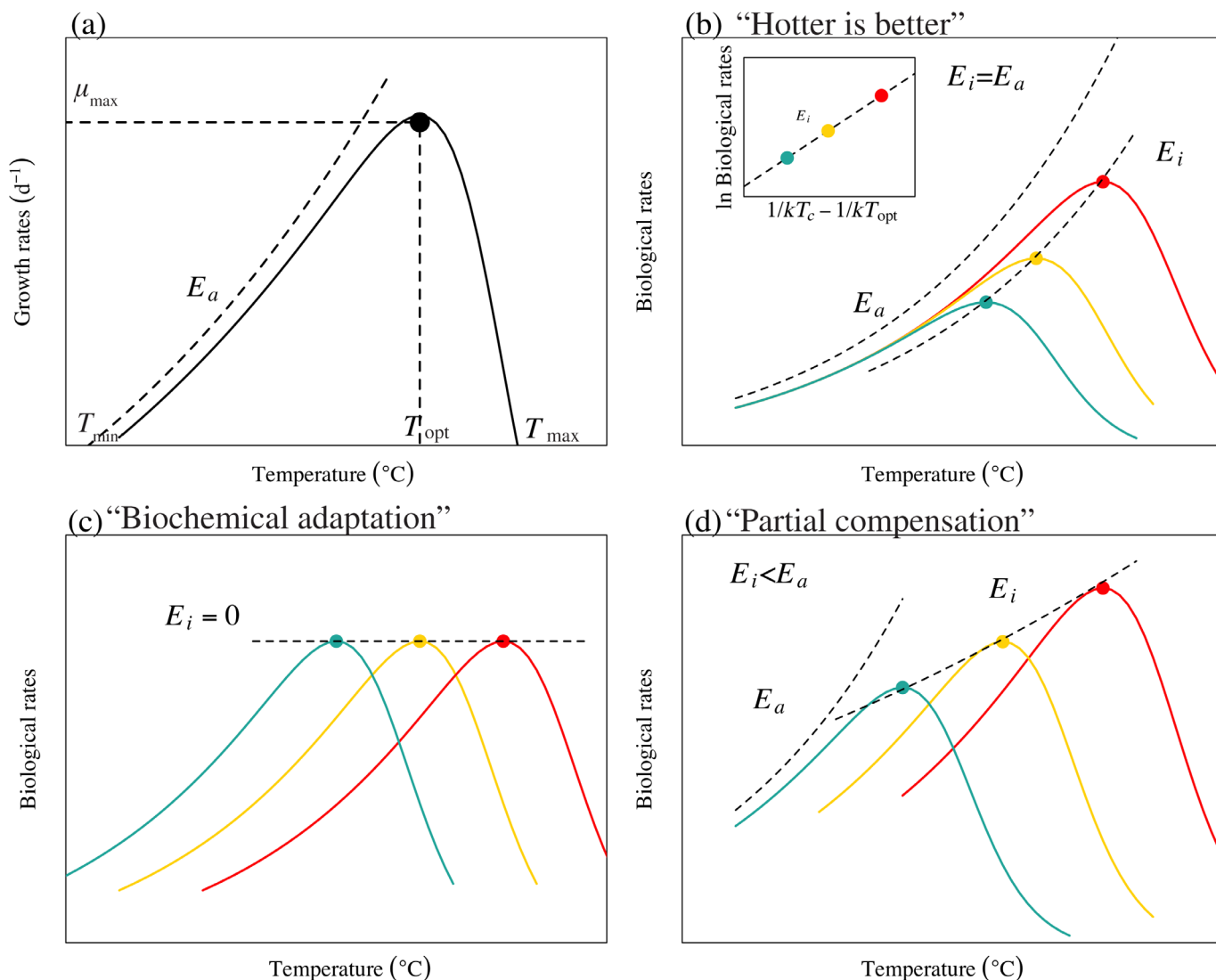


Fig. 1. An illustration of the TPC and three hypotheses for the thermal adaptation (modified from Barton and Yvon-Durocher 2019). **(a)** The relationship between biological rates and temperature (the thermal performance curve). T_{opt} is the temperature at which the rates are maximal (μ_{max}), E_a is the temperature sensitivity describing the curve rise below T_{opt} . **(b)** The “hotter is better” scenario for thermal adaptation. The curves represent the thermal responses of different communities. Under such a scenario, the μ_{max} increases with T_{opt} with the same temperature sensitivity (E_a) due to the thermodynamic constraint. **(c)** The “biochemical adaptation” hypothesis, whereby the long-term adaptation will override the effects of thermodynamic constraint such that μ_{max} is invariant with T_{opt} . **(d)** The “partial compensation” hypothesis, whereby the μ_{max} increases with increasing T_{opt} with a lower temperature sensitivity because of the partial thermal adaptation.

seawater was prepared by filtering through a 0.2 μm filter capsule into 1.2-liter PC bottles and mixed with the natural seawater to a designated proportion (15% natural seawater). Another pair of 1.2-liter PC bottles were filled with natural seawater (100% natural seawater). Nutrients (NO_3^- : 10 $\mu\text{mol L}^{-1}$, PO_4^{3-} : 1 $\mu\text{mol L}^{-1}$ in final concentration) were added into all bottles to ensure enough nutrients for phytoplankton growth. All bottles were incubated at the designated temperature for 24 h under simulated light conditions. At the beginning and the end of the incubation, the chlorophyll *a* concentration (Chl *a*) of each bottle were measured

(Supplementary Information). By assuming an exponential growth model for phytoplankton communities, the net growth rate of phytoplankton (k) in each bottle was then calculated as $k = (1/t) \ln(P/dP_0)$, where P_0 and P are the initial and final Chl *a* in each bottle, d is the dilution factor, and t is the incubation time. The growth rate of phytoplankton community was estimated as the intercept of the linear regression of the net growth rate (k) and dilution factor (d).

As such short-term experiments were conducted in the subtropical waters, where the T_{opt} of phytoplankton has been found to be close to the environmental temperature (Thomas

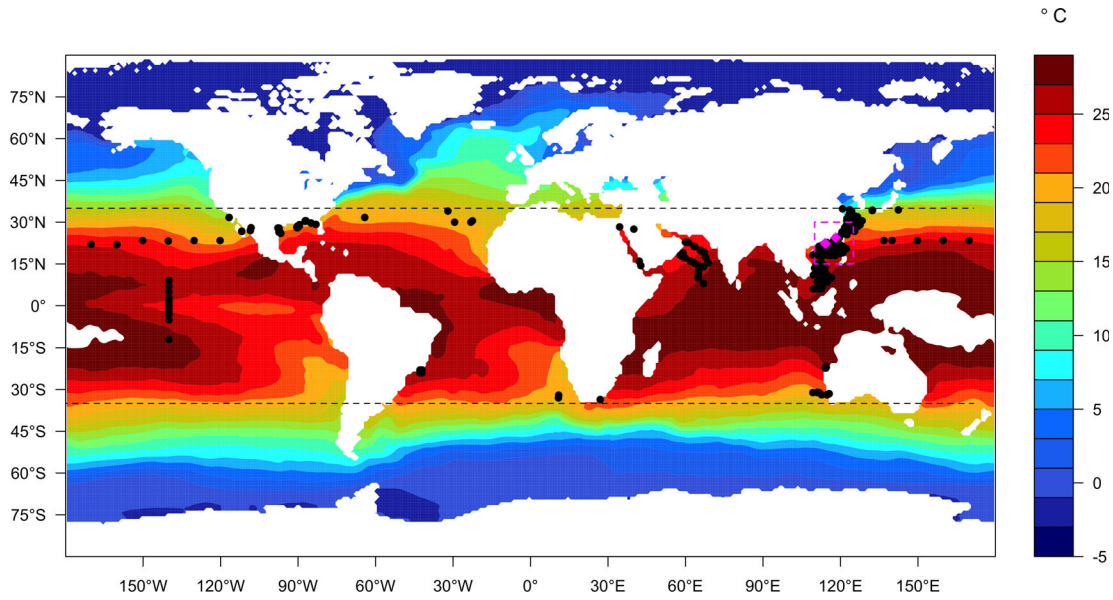


Fig. 2. Global map with annual mean sea surface temperature (SST, °C). The purple diamonds show the sites ($n = 3$) where the short-term temperature modulated dilution experiments were conducted. The black dots show the stations ($n = 319$) where the phytoplankton community growth rate was measured using the dilution technique in the (sub)tropical waters.

et al. 2012; Liu et al. 2019; see Fig. S1), we also compiled a larger dataset of in situ phytoplankton growth rates in the surface waters of (sub)tropical regions ($|\text{latitude}| < 35^\circ$; Fig. 2; Table S2). In this dataset, phytoplankton growth rates were estimated by the dilution experiments described above and conducted in various locations and seasons (Supplementary Information), allowing us to evaluate the thermal responses across various phytoplankton communities at seasonal time-scales. In these experiments, nutrients were also added to the experimental bottles to ensure sufficient nutrients for phytoplankton growth. Considering the effect of light intensity, we selected the data from experiments conducted in surface layers, and the corresponding photosynthetically active radiation (PAR, mol photons $\text{m}^{-2} \text{d}^{-1}$) was collected from the Goddard Earth Sciences Data and Information Service Center (<http://disc.sci.gsfc.nasa.gov/>).

Short-term temperature sensitivity within the community

Based on the dataset of short-term experiments, the TPC for the growth rate of a phytoplankton community was quantified using a modified Sharpe–Schoolfield equation (Sharpe and Demichele 1977; Schoolfield et al. 1981) following the previous study (Chen and Laws 2017; Padfield et al. 2017):

$$\mu = \mu_c \frac{e^{\frac{E_a}{k_b} \left(\frac{1}{T_c} - \frac{1}{T} \right)}}{1 + \frac{E_a}{E_h - E_a} e^{\frac{E_h}{k_b} \left(\frac{1}{T_{\text{opt}}} - \frac{1}{T} \right)}} \quad (1)$$

where μ (d^{-1}) is the growth rate of phytoplankton at temperature T (K), μ_c is the growth rate normalized to a reference temperature T_c (here $T_c = 15^\circ\text{C}$), k_b is the Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$), T_{opt} is the optimal temperature at which the growth rate is the maximal, E_a is the activation energy (eV) within the same community which describes how fast the growth rate increase with increasing temperature below T_{opt} , E_h is deactivation energy induced by high-temperature inactivation. We fitted Eq. 1 to each phytoplankton community by the Levenberg–Marquardt nonlinear least-squares minimization algorithm, which was implemented using the *nlsLM* function in *minpack.lm* package in R (R Core Team 2017). The optimization process during the fitting was enforced by strict convergence criteria according to Kontopoulos et al. (2020). The fits were then filtered by criteria to ensure reliable parameter estimates. We removed the fits with $E_a < 0.01$, $E_h > 10$, or $E_h < 0.01$ to ensure that the TPCs are unimodal. The μ_{max} was calculated based on the estimated parameters by setting the temperature as T_{opt} .

As the estimates of thermal traits were affected by the different phytoplankton communities among months, we estimated the average value of each parameter in Eq. 1 using the nonlinear mixed-effect models allowing random effects on each parameter. The *Saemix* package based on the stochastic approximation expectation maximization algorithm was used for this analysis (Comets et al. 2017; Supplementary Information).

Long-term temperature sensitivity across communities

The temperature sensitivity across phytoplankton communities (E_i) was estimated based on the Boltzmann–Arrhenius

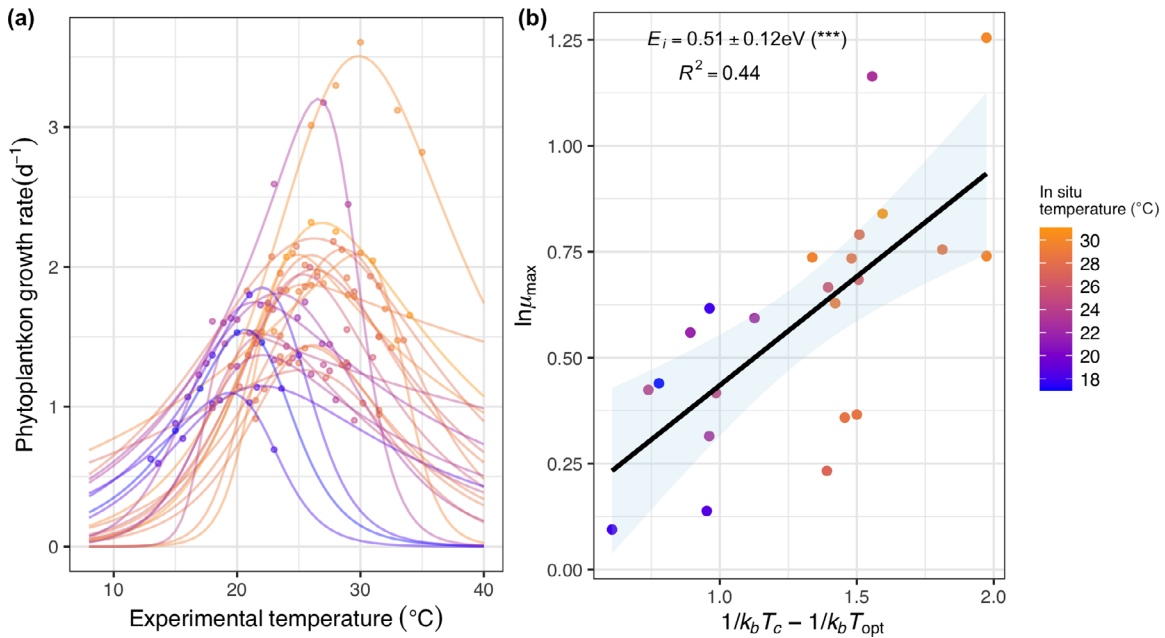


Fig. 3. (a) The thermal performance curves for the growth rate of natural phytoplankton community collected in different seasons spanning average temperature from 18°C (blue) to 30°C (orange). (b) Scatterplot of the natural logarithm of maximal growth rates (μ_{\max}) against Boltzmann optimal growth temperature ($1/k_b T_c - 1/k_b T_{\text{opt}}$). The line (the long-term thermal response) is the Boltzmann–Arrhenius model fitted using OLS regression. The color denotes the in situ temperature at sampling time.

equation (Chen et al. 2012; Padfield et al. 2017). As the phytoplankton growth may also be affected by size structure which changes with phytoplankton biomass (Chen et al. 2012), we also included the effect of biomass that represented by Chl *a* (*Chl*):

$$\ln \mu_{\max} = E_i \left(\frac{1}{k_b T_c} - \frac{1}{k_b T_{\text{opt}}} \right) + \ln \mu_c + \beta \ln \text{Chl} \quad (2)$$

where μ_{\max} is the maximal growth rate at optimal temperature T_{opt} estimated from Eq. 1 based on the dataset of short-term experiments; E_i is the activation energy across communities; other symbols are the same with Eq. 1.

To corroborate the above estimate of E_i , we used the larger dataset of in situ phytoplankton growth rates by assuming that the T_{opt} of phytoplankton could be approximated by the environmental temperature and the growth rates were close to μ_{\max} in (sub)tropical waters (Thomas et al. 2012; Liu et al. 2019). We used generalized additive models (GAMs) to estimate E_i' . We considered the effect of biomass (*Chl*) and light intensity (PAR) on phytoplankton growth rate by constructing the following model:

$$\ln \mu_n = E_i' \left(\frac{1}{k_b T_c} - \frac{1}{k_b T_{\text{in situ}}} \right) + \ln \mu_c' + s(\ln \text{Chl}) + s(\text{PAR}) \quad (3)$$

where μ_n is the phytoplankton growth rate estimated at in situ temperature ($T_{\text{in situ}}$), μ_c' is the normalization constant, and

s is the smooth function (thin plate regression splines) in GAMs. As the growth rates were estimated under nutrient-enriched conditions, we did not add the effect of nutrients into the model. The *mgcv* package in R was used for the GAMs analysis (Wood 2006).

Comparing short- and long-term temperature sensitivities

To test whether the across- (E_i or E_i') and within-communities (E_a) activation energies were significantly different, we used bootstrap hypothesis testing following Efron and Tibshirani (1993) (Supplementary Information).

Results

Temperature sensitivity (E_a and E_i) estimated by temperature manipulated experiments

The phytoplankton community growth rates in most experiments showed unimodal patterns with increasing temperature and were fitted by the modified Sharpe–Schoolfield equation (Fig. 3a). The across-community activation energy E_i (mean ± SE: 0.51 ± 0.12 eV, the same below, equivalent to Q_{10} of 1.98; Fig. 3b) was significantly lower than the within-community E_a estimated by the nonlinear mixed-effect model (0.80 ± 0.10 eV, equivalent to Q_{10} of 2.80; Table 1; *bootstrap hypothesis testing*, $p < 0.05$). The Chl *a* does not significantly affect μ_{\max} (Eq. 2, $t = -0.59$, $p = 0.56 > 0.05$).

Table 1. The results of nonlinear mixed-effect models.

Parameter	Fixed effects			Variance of random effects		
	Estimate	SE	CV (%)	Estimate	SE	CV (%)
μ_c (d ⁻¹)	0.92	0.051	6	0.021	0.011	53
E_a (eV)	0.80	0.098	12	0.016	0.026	156
E_h (eV)	2.29	0.159	7	0.107	0.106	100
T_{opt} (°C)	25.35	0.538	2	5.725	1.838	32

CV, the coefficients of variation; E_a , the activation energy within the same community; E_h , the deactivation energy induced by high-temperature inactivation; SE, the standard error of the estimate; T_{opt} , the optimal temperature; μ_c , the growth rate normalized to a reference temperature T_c (15°C).

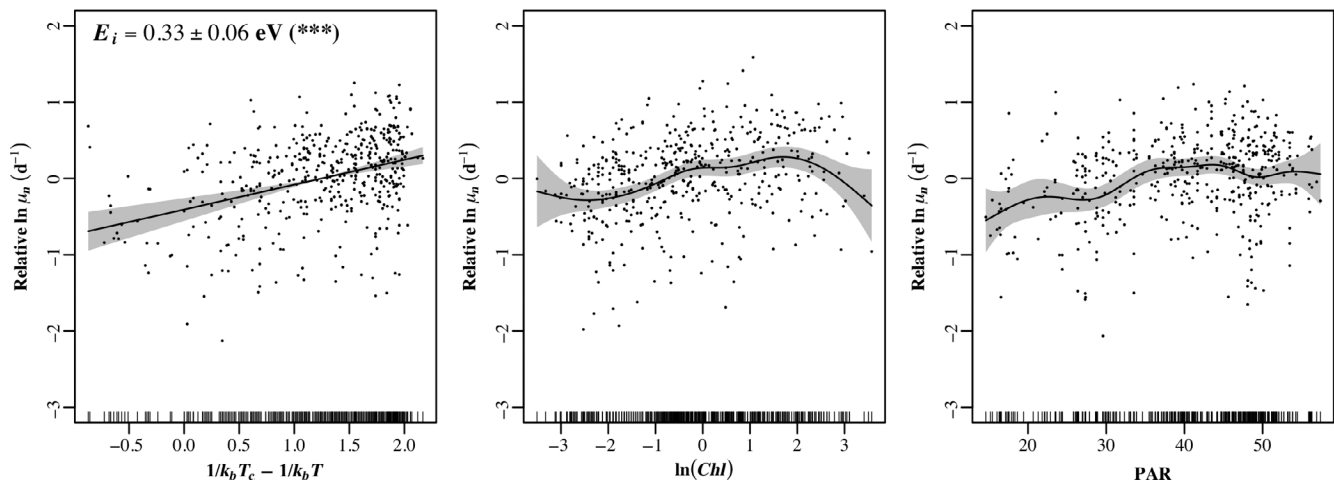


Fig. 4. Partial effects of Boltzmann temperature ($1/k_b T_c - 1/k_b T$), the natural logarithm of Chl *a* concentration ($\ln(\text{Chl})$), and the PAR on phytoplankton community growth rate based on a compiled dataset of dilution experiments conducted in the surface waters of (sub)tropical regions. Shaded areas denote 95% CI.

Approximate E_i estimated based on (sub)tropical dilution dataset

The results of GAMs showed that the temperature, Chl *a*, and light were important factors affecting the phytoplankton growth rate in (sub)tropical waters (Fig. 4). After controlling the effects of Chl *a* and light, the E_i was 0.33 ± 0.06 eV, which equals a Q_{10} of 1.56 and was also significantly lower than the temperature sensitivity within communities ($E_a = 0.80 \pm 0.10$ eV; Table 1; *bootstrap hypothesis testing*, $p < 0.001$).

Discussion

The thermal responses of the phytoplankton community are complicated because of the influence of community compositional changes, making it difficult to scale up the temperature–rate relationship from individual species to the whole communities. The theory derived from species levels may not directly guide the thermal responses of complex communities in nature. Here, we

assessed the thermal response of phytoplankton communities using the data of short-term temperature manipulated experiments on natural phytoplankton communities, which incorporates the influence of community compositional shifts. Although the short-term temperature changes may induce the “thermal shock” to phytoplankton that may affect the estimate of temperature sensitivity, the value we estimated via nonlinear mixed-effect model (0.80 ± 0.10 eV) was in the range of literature reports on the within-species E_a of all kinds of organisms including microbes, plants, and animals (Dell et al. 2011). It was also close to the average activation energy of 18 phytoplankton species (i.e., 0.77 eV) examined in a recent study (Barton and Yvon-Durocher 2019). Therefore, the average short-term temperature sensitivity (E_a) in the current study should be robust to reveal the emergent thermal response of phytoplankton communities, which is vital in highly thermal dynamic environments.

Our results demonstrated that the short-term temperature sensitivity of growth rate for a certain phytoplankton

community ($E_a = 0.80 \pm 0.10$ eV; Table 1) was significantly higher than the temperature sensitivity of phytoplankton growth across communities at seasonal scale ($E_i = 0.51 \pm 0.12$ eV; Fig. 3). Moreover, it is also higher than the temperature sensitivity of phytoplankton across communities in the (sub)tropical waters ($E'_i = 0.33 \pm 0.06$ eV; Fig. 4), which were consistent with previous laboratory studies (Barton and Yvon-Durocher 2019; Kontopoulos et al. 2020). Collectively, the results support the “partial compensation” hypothesis (Fig. 1d) at the community level, suggesting that the effect of thermodynamic constraints on phytoplankton community growth could be only partially compensated. It questions the current monotonical temperature function of phytoplankton growth in biogeochemical models, which implicitly assumes that the temperature sensitivities within vs. across species are the same (Eppley 1972; Yool et al. 2013; Laufkötter et al. 2015).

The “partial compensation” pattern observed in phytoplankton communities reflects the seasonal succession of phytoplankton species (i.e., the succession of cold-adapted species in winter to warm-adapted species in summer). In winter, the phytoplankton community is dominated by cold-adapted species whose μ_{\max} at optimal temperature is constrained by low temperature. Thus, the μ_{\max} of winter community is significantly lower than the summer community (Fig. 3). This suggests that the thermal adaptation capacity of phytoplankton cannot fully compensate the thermodynamic constraint and is at least partly consistent with the “hotter is better” hypothesis which posits that organisms adapted to lower temperature have lower μ_{\max} (Fig. 1b; Frazier et al. 2006; Knies et al. 2009). When seasonal temperature changes, the phytoplankton community composition gradually shifts from cold-adapted species dominant to warm-adapted species dominant, leading to the increases in the T_{opt} and μ_{\max} of the whole community. If there are only cold-adapted and warm-adapted species in the winter and summer communities, respectively, the E_i across these communities may approach the E_a within the community. However, the mixture of various species during seasonal succession may lower the μ_{\max} of the community, which eventually results in a relatively low E_i . Indeed, some previous studies have found a low E_i for plankton community metabolism and growth rates (López-Urrutia et al. 2006; Chen et al. 2012; Regaudie-De-Gioux and Duarte 2012). One possible explanation for these observations could be the community composition shift among various species with different thermal traits (e.g., cold-adapted and warm-adapted species). Nevertheless, the underlying compensatory mechanisms for thermal responses of phytoplankton at both species and community levels indeed remain substantially understudied and badly in need of thorough investigations.

Even so, such a “hotter is partially better” pattern we observed in the phytoplankton community has far-reaching implications for predicting the effect of climate warming on primary production and relevant processes (e.g., carbon export), especially for regional-scale predictions. Our results emphasized

the difference in temperature sensitivity of phytoplankton growth within vs. across communities, as well as the difference between short-term and seasonal scales (i.e., E_a vs. E_i). Such a difference has long been neglected in the biogeochemical and ecosystem models (Eppley 1972; Laufkötter et al. 2015). Applying the compensated temperature sensitivity to the regional models may not accurately capture the thermal response of phytoplankton community, especially in waters with large temperature fluctuations (Strock and Menden-Deuer 2021). The phytoplankton communities in such regions may not have sufficient time to adapt to the temperature changes. Thus, their thermal response could be stronger than the adapted communities. It has been found that the estimate of daily primary production in the highly thermal dynamic coastal waters is very different when using the short-term response of phytoplankton instead of the thermal response with acclimated effects (Strock and Menden-Deuer 2021). As the thermal fluctuations in coastal regions are anticipated to intensify under the context of climate changes (Schär et al. 2004), the fluctuations and the corresponding short-term responses of phytoplankton should be considered when predicting the effect of warming on primary production and relevant processes, which has been pointed out by a growing number of studies (Vasseur et al. 2014; Schaum et al. 2018). Nevertheless, using the short-term temperature sensitivity will neglect the effect of adaptation, which would overestimate the impact of ocean warming over timescales of years to decades. Thus, the compensated long-term temperature sensitivity should be used in the global models when predicting the long-time impacts.

In conclusion, to our knowledge, our study is the first to provide empirical evidence for the “partial compensation” pattern of the natural phytoplankton community, supporting the previous studies on phytoplankton species (Barton and Yvon-Durocher 2019; Kontopoulos et al. 2020). Our results emphasize the difference in temperature sensitivity at different timescales (short-term vs. seasonal scales) and highlight the importance of comparing the short- and long-term effects for predicting the ecosystem responses to ocean warming. We also suggest incorporating the short-term thermal response of phytoplankton into the regional models in highly thermal dynamic coastal ecosystems. Besides, it is worth noting that the phytoplankton growth rates in the current study were measured under the conditions of replete nutrient and simulated in situ surface light intensity, which should be sufficient for phytoplankton growth (Edwards et al. 2016). It allows us to study the thermal response of the phytoplankton without considering the complex effects of resource availability. However, resource availability usually affects the thermal response of the phytoplankton (Thomas et al. 2017; Liu et al. 2021), which entails further investigation of their interactive effects.

References

- Angilletta, M. J. 2006. Estimating and comparing thermal performance curves. *J. Therm. Biol.* **31**: 541–545. doi:[10.1016/j.jtherbio.2006.06.002](https://doi.org/10.1016/j.jtherbio.2006.06.002)

- Angilletta, M. J. 2009. *Thermal adaptation: A theoretical and empirical synthesis*. Oxford Univ. Press. doi:[10.1093/acprof:oso/9780198570875.001.1](https://doi.org/10.1093/acprof:oso/9780198570875.001.1)
- Barton, S., and G. Yvon-Durocher. 2019. Quantifying the temperature dependence of growth rate in marine phytoplankton within and across species. *Limnol. Oceanogr.* **64**: 2081–2091. doi:[10.1002/lno.11170](https://doi.org/10.1002/lno.11170)
- Chen, B., M. R. Landry, B. Huang, and H. Liu. 2012. Does warming enhance the effect of microzooplankton grazing on marine phytoplankton in the ocean? *Limnol. Oceanogr.* **57**: 519–526. doi:[10.4319/lno.2012.57.2.0519](https://doi.org/10.4319/lno.2012.57.2.0519)
- Chen, B., and E. A. Laws. 2017. Is there a difference of temperature sensitivity between marine phytoplankton and heterotrophs? *Limnol. Oceanogr.* **62**: 806–817. doi:[10.1002/lno.10462](https://doi.org/10.1002/lno.10462)
- Chen, B., and K. Liu. 2015. Responses of autotrophic and heterotrophic rates of plankton from a subtropical coastal site to short-term temperature modulations. *Mar. Ecol. Prog. Ser.* **527**: 59–71. doi:[10.3354/meps11218](https://doi.org/10.3354/meps11218)
- Clarke, A., and K. P. P. Fraser. 2004. Why does metabolism scale with temperature? *Funct. Ecol.* **18**: 243–251. doi:[10.1111/j.0269-8463.2004.00841.x](https://doi.org/10.1111/j.0269-8463.2004.00841.x)
- Comets, E., A. Lavenue, and M. Lavielle. 2017. Parameter estimation in nonlinear mixed effect models using saemix, an R implementation of the SAEM algorithm. *J. Stat. Softw.* **80**: 1–41. doi:[10.18637/jss.v080.i03](https://doi.org/10.18637/jss.v080.i03)
- Dell, A. I., S. Pawar, and V. M. Savage. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl. Acad. Sci. USA* **108**: 10591–10596. doi:[10.1073/pnas.1015178108](https://doi.org/10.1073/pnas.1015178108)
- Edwards, K. F., M. K. Thomas, C. A. Klausmeier, and E. Litchman. 2016. Phytoplankton growth and the interaction of light and temperature: A synthesis at the species and community level. *Limnol. Oceanogr.* **61**: 1232–1244. doi:[10.1002/lno.10282](https://doi.org/10.1002/lno.10282)
- Efron, B., and R. Tibshirani. 1993. *An introduction to the bootstrap*. Chapman and Hall/CRC.
- Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* **70**: 1063–1085.
- Falkowski, P. G., R. T. Barber, and V. Smetacek. 1998. Biogeochemical controls and feedbacks on ocean primary production. *Science* **281**: 200–206. doi:[10.1126/science.281.5374.200](https://doi.org/10.1126/science.281.5374.200)
- Frazier, M. R., R. B. Huey, and D. Berrigan. 2006. Thermodynamics constrains the evolution of insect population growth rates: “Warmer is better”. *Am. Nat.* **168**: 512–520. doi:[10.1086/506977](https://doi.org/10.1086/506977)
- Fussmann, K. E., F. Schwarzmuller, U. Brose, A. Jousset, and B. C. Rall. 2014. Ecological stability in response to warming. *Nat. Clim. Change* **4**: 206–210. doi:[10.1038/nclimate2134](https://doi.org/10.1038/nclimate2134)
- Knies, J. L., J. G. Kingsolver, and C. L. Burch. 2009. Hotter is better and broader: Thermal sensitivity of fitness in a population of bacteriophages. *Am. Nat.* **173**: 419–430. doi:[10.1086/597224](https://doi.org/10.1086/597224)
- Kontopoulos, D. G., E. van Sebille, M. Lange, G. Yvon-Durocher, T. G. Barraclough, and S. Pawar. 2020. Phytoplankton thermal responses adapt in the absence of hard thermodynamic constraints. *Evol.* **74**: 775–790. doi:[10.1111/evo.13946](https://doi.org/10.1111/evo.13946)
- Landry, M., and R. Hassett. 1982. Estimating the grazing impact of marine micro-zooplankton. *Mar. Biol.* **67**: 283–288. doi:[10.1007/bf00397668](https://doi.org/10.1007/bf00397668)
- Laufkötter, C., and others. 2015. Drivers and uncertainties of future global marine primary production in marine ecosystem models, *Biogeosciences*, **12**: 6955–6984. doi:[10.5194/bg-12-6955-2015](https://doi.org/10.5194/bg-12-6955-2015)
- Laws, E. A. 2013. Evaluation of in situ phytoplankton growth rates: A synthesis of data from varied approaches. *Ann. Rev. Mar. Sci.* **5**: 247–268.
- Liu, K., B. Chen, S. Zhang, M. Sato, Z. Shi, and H. Liu. 2019. Marine phytoplankton in subtropical coastal waters showing lower thermal sensitivity than microzooplankton. *Limnol. Oceanogr.* **64**: 1103–1119. doi:[10.1002/lno.11101](https://doi.org/10.1002/lno.11101)
- Liu, K., Suzuki, K., Chen, B., and Liu, H. 2021. Are temperature sensitivities of *Prochlorococcus* and *Synechococcus* impacted by nutrient availability in the subtropical northwest Pacific?. *Limnol. Oceanogr.* **66**: 639–651. doi:[10.1002/lno.11629](https://doi.org/10.1002/lno.11629)
- López-Urrutia, Á., E. San Martín, R. P. Harris, and X. Irigoien. 2006. Scaling the metabolic balance of the oceans. *Proc. Natl. Acad. Sci. USA* **103**: 8739–8744. doi:[10.1073/pnas.0601137103](https://doi.org/10.1073/pnas.0601137103)
- Padfield, D., and others. 2017. Metabolic compensation constrains the temperature dependence of gross primary production. *Ecol. Lett.* **20**: 1250–1260. doi:[10.1111/ele.12820](https://doi.org/10.1111/ele.12820)
- R Core Team. 2017. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from <https://www.r-project.org>
- Regaudie-De-Gioux, A., and C. M. Duarte. 2012. Temperature dependence of planktonic metabolism in the ocean. *Global Biogeochem. Cycles* **26**: GB1015. doi:[10.1029/2010gb003907](https://doi.org/10.1029/2010gb003907)
- Schär, C., P. L. Vidale, D. Lüthi, C. Frei, C. Häberli, M. A. Liniger, and C. Appenzeller. 2004. The role of increasing temperature variability in European summer heatwaves. *Nature* **427**: 332–336. doi:[10.1038/nature02300](https://doi.org/10.1038/nature02300)
- Schaum, C. E., A. Buckling, N. Smirnov, D. J. Studholme, and G. Yvon-Durocher. 2018. Environmental fluctuations accelerate molecular evolution of thermal tolerance in a marine diatom. *Nat. Commun.* **9**: 1719. doi:[10.1038/s41467-018-03906-5](https://doi.org/10.1038/s41467-018-03906-5)
- Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. Nonlinear regression of biological temperature dependent

- rate models based on absolute reaction-rate theory. *J. Theor. Biol.* **88**: 719–731. doi:[10.1016/0022-5193\(81\)90246-0](https://doi.org/10.1016/0022-5193(81)90246-0)
- Sharpe, P. J. H., and D. DeMichele. 1977. Reaction kinetics of poikilotherm development. *J. Theor. Biol.* **64**: 649–670. doi:[10.1016/0022-5193\(77\)90265-X](https://doi.org/10.1016/0022-5193(77)90265-X)
- Strock, J. S., and S. Menden-Deuer. 2021. Temperature acclimation alters phytoplankton growth and production rates. *Limnol. Oceanogr.* **66**: 740–752. doi:[10.1002/lno.11637](https://doi.org/10.1002/lno.11637)
- Thomas, M. K., Aranguren-Gassis, M., Kremer, C. T., Gould, M. R., Anderson, K., Klausmeier, C. A., and Litchman, E. 2017. Temperature–nutrient interactions exacerbate sensitivity to warming in phytoplankton. *Glob. Chang. Biol.* **23**: 3269–3280. doi:[10.1111/gcb.13641](https://doi.org/10.1111/gcb.13641)
- Thomas, M. K., C. T. Kremer, C. A. Klausmeier, and E. Litchman. 2012. A global pattern of thermal adaptation in marine phytoplankton. *Science* **338**: 1085–1088. doi:[10.1126/science.1224836](https://doi.org/10.1126/science.1224836)
- Vasseur, D. A., and K. S. McCann. 2005. A mechanistic approach for modeling temperature-dependent consumer–resource dynamics. *Am. Nat.* **166**: 184–198. doi:[10.1086/431285](https://doi.org/10.1086/431285)
- Vasseur, D. A., and others. 2014. Increased temperature variation poses a greater risk to species than climate warming. *Proc. R. Soc. B* **281**: 20132612. doi:[10.1098/rspb.2013](https://doi.org/10.1098/rspb.2013)
- Wood, S. N. 2006. *Generalized additive models: An introduction with R*. Chapman and Hall.
- Yool, A., E. E. Popova, and T. R. Anderson. 2013. MEDUSA-2.0: An intermediate complexity biogeochemical model of the marine carbon cycle for climate change and ocean acidification studies. *Geosci. Model Dev.* **6**: 1767–1811. doi:[10.5194/gmd-6-1767-2013](https://doi.org/10.5194/gmd-6-1767-2013)

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