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Temperature influence on phytoplankton community growth rates

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Abstract A large database of field estimates of phytoplankton community growth rates in natural populations was compiled and analyzed to determine the apparent temperature effect on phytoplankton community growth rate. We conducted an ordinary least squares regression to optimize the parameters in two commonly used growth-temperature relations (Arrhenius and Q_{10} models). Both equations fit the observational data equally with the optimized parameter values. The optimum apparent Q_{10} value was 1.47 ± 0.08 (95% confidence interval, CI). Microzooplankton grazing rates closely matched the temperature trends for phytoplankton growth. This likely reflects a dynamic adjustment of biomass and grazing rates by the microzooplankton to match their available food source, illustrating tight coupling of phytoplankton growth and microzooplankton grazing rates. The field-measured temperature effect and growth rates were compared with estimates from the satellite Carbon-based Productivity Model (CbPM) and three Earth System Models (ESMs), with model output extracted at the same month and sampling locations as the observations. The optimized, apparent Q_{10} value calculated for the CbPM was 1.51, with overestimation of growth rates. The apparent Q_{10} value in the Community Earth System Model (V1.0) was 1.65, with modest underestimation of growth rates. The GFDL-ESM2M and GFDL-ESM2G models produced apparent Q_{10} values of 1.52 and 1.39, respectively. Models with an apparent Q_{10} that is significantly greater than ~1.5 will overestimate the phytoplankton community growth response to the ongoing climate warming and will have spatial biases in estimated growth rates for the current era.

1. Introduction

In order to accurately simulate marine carbon cycling, it is essential for models to accurately simulate marine net community production and export production. As global climate models and Earth System Models continue to grow in complexity, it is beneficial to revisit parameterizations as new data and findings come forth. A study comparing simulated marine primary production from numerical models of varying complexity has concluded that to improve modeled primary production there needs to be a better understanding of the temperature effect on photosynthesis and better parameterization of the maximum photosynthetic rate [*Carr et al.*, 2006]. The temperature influence on community phytoplankton growth rates is fundamental to simulating current and future marine primary production, and a reevaluation of this parameterization is needed to constrain how productivity will respond to climate change [*Taucher and Oschlies*, 2011].

The influence of temperature on growth rates exists due to the control temperature exerts over metabolic rates [*Raven and Geider*, 1988; *Brown et al.*, 2004]. A commonly used function that describes the relation between temperature and growth rate is the Q_{10} model,

$$g = g_o \cdot Q_{10}^{\frac{T - T_o}{10}}, \quad (Q_{10} \text{ Model})$$

where g_o is a reference growth rate (day^{-1}) at the reference temperature $T_o = 303.15$ K (30°C), and the Q_{10} value gives the factor change in growth rate for a 10° change in temperature. All temperatures used in the Q_{10} model are in Kelvin. Another commonly used function is the Arrhenius equation,

$$g = A \cdot e^{-E/kT}, \quad (\text{Arrhenius})$$

where A is an adjustable constant (day^{-1}), E is the activation energy (eV), and k is the Stefan-Boltzmann constant (8.617×10^{-5} eV K^{-1}). In both equations the temperature, T, is measured in Kelvin. Both equations can be used to describe the influence of temperature on phytoplankton growth assuming other factors such as light and nutrients are held constant.

Table 1. Phytoplankton Growth Experiments With and Without Nutrient Additions

	All	BothAdd	BothNoAdd
N	835	203	209
Temp (C°)	16.9626	20.9541	21.4408
Chl (µg/L)	1.3963	1.4475	1.2243
Nitrate (µM)	5.4873	5.0837	4.7001
Growth (day^{-1})	0.7055	0.9367	0.6526
Grazing (day^{-1})	0.4685	0.4939	0.5137
Grazing/growth	0.6641	0.5272	0.7872
Fitted Q_{10}	1.47	1.48	1.42
Fitted Q_{10} ref. growth rate	0.89	1.1	0.65
Fittted Q_{10} RMSE	0.4465	0.4541	0.4467
Fitted A coefficient	3.5315×10^4	5.9886×10^4	1.2013×10^4
Fitted E	0.2770	0.2852	0.2568
Fitted Arrhenius RMSE	0.4462	0.4541	0.4468
Imposed Q_{10} 2.0	2.0	2.0	2.0
Imposed Q_{10} 2.0, Fitted Reference Growth Rate	1.33	1.41	0.88
Imposed Q_{10} 2.0, RMSE	0.4619	0.4619	0.4882

Shown are the mean values and fitted growth equations for the entire observational database and for the BothAdd and BothNoAdd subsets. These subsets include results from the field where experiments were conducted both with and without nutrient addition. BothAdd represents experiments where nutrients were added. BothNoAdd are experiments where nutrient additions were omitted.

One key early study, compiling mostly laboratory growth rate data, suggested a phytoplankton Q_{10} value of 1.88 [*Eppley*, 1972], while another suggested a value of 2.08 [*Goldman and Carpenter*, 1974]. At the time, growth rate data were scarce and mostly from lab cultures. As a result, the sample size of early synthesis efforts was relatively small and limited to species in culture. Thus, the described temperature effects may not be representative of in situ rates for natural populations. *Calbet and Landry* [2004] compiled field estimates of phytoplankton community growth rates and showed increasing growth rates as one moved from polar to tropical waters. However, the change in growth rate implied a weaker temperature effect than a Q_{10} value of 1.88 or 2.0 would imply. This study attempts to build on these efforts by collecting and analyzing a large database of field observations of phytoplankton community growth rates, in comparison with satellite and Earth System Model (ESM) estimates.

2. Methods

The goal of this study is to evaluate the temperature effect on phytoplankton community growth rates and to estimate optimal growth rate parameters for marine ecosystem models, based on either the Arrhenius equation or the Q_{10} model. To this end, we compiled from the literature a large data set of in situ phytoplankton community growth rates ($n = 835$, Table 1, Figure 1; building on a previous compilation by *Calbet and*
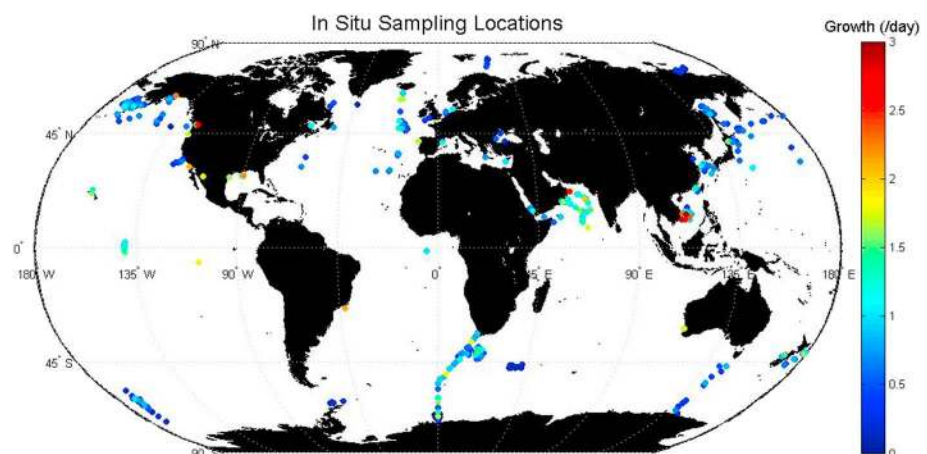

Figure 1. Spatial plot showing locations and observed phytoplankton community growth rates from the in situ data set.
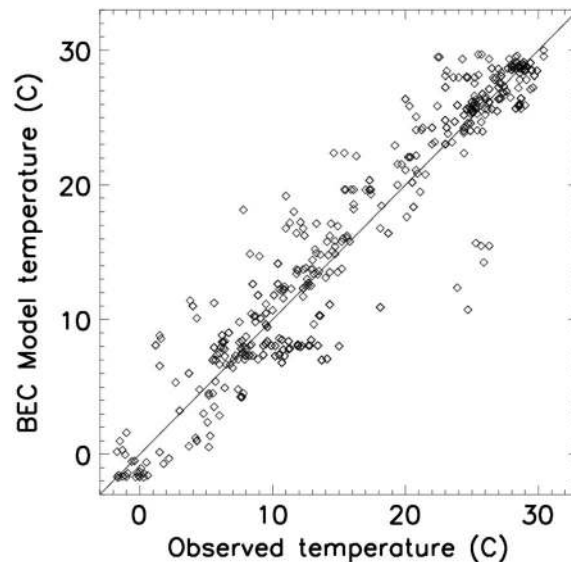
Figure 2. Scatterplot of BEC model sea surface temperature versus observed temperature for locations where temperature was reported in the field experiments.

Landry [2004]) measured using the dilution method [*Landry and Hassett*, 1982]. (Refer to supporting information for the compiled database). The dilution method of *Landry and Hassett* [1982] provides estimates of phytoplankton community growth rate and total microzooplankton grazing rate. Additional ancillary information was compiled where available, including geographic location, depth, chlorophyll concentration (mg/m^3), nitrate concentration (μM), temperature (°C), and sampling month. To minimize the role of light limitation, we only included upper water column experiments (<30 m depth). We also excluded experiments where the linear regression used to estimate phytoplankton growth rate had a low r^2 value (<0.33). Temperature was reported for 576 of these experiments and showed a good correlation with the sea surface temperature predicted from the Community Earth System Model (CESM)-Biogeochemical Elemental Cycling (BEC) ocean biogeochemical model [*Moore et al.*, 2004] ($r = 0.937$, Figure 2). Therefore, where temperature was not reported we substituted the monthly mean model sea surface temperature from the 1990s for that location (hereafter referred to as the combined temperature data set). The CESM sea surface temperatures are a good match to the observations for the 1990s [$r = 0.99$, *Moore et al.*, 2013].

The satellite product analyzed was from the Carbon-based Productivity Model (CbPM) and was extracted at the same geographic location and month as the in situ data [*Behrenfeld et al.*, 2005; *Westberry et al.*, 2008; www.science.oregonstate.edu/ocean.productivity/index.php]. A monthly climatology of CbPM growth rate estimates was created from 1999 to 2008. Growth rate estimates from the original CbPM from the *Behrenfeld et al.* [2005] study had a tendency to overestimate water column production from errors in photic zone depth. An updated version of the CbPM was used in this study [*Westberry et al.*, 2008]. The updated CbPM uses euphotic zone depths that are calculated from reconstructed profiles of irradiance based on profiles of chlorophyll/carbon and biomass. Temperature from our combined temperature data set and CbPM growth rates was used to find the apparent Q_{10} coefficient and reference growth rate for the CbPM, subsetting the satellite data at the same month and location as the data in our in situ database. The CbPM does not include an explicit temperature effect on growth rates but estimates growth as a function of the phytoplankton chlorophyll/carbon ratio [*Behrenfeld et al.*, 2005; *Westberry et al.*, 2008].

The CESM-BEC model includes ecosystem and biogeochemical components. Three phytoplankton functional groups (diatoms, diazotrophs, and small phytoplankton) and the cycling of key biogeochemical elements (C, N, P, Fe, Si, and O) are represented [*Moore et al.*, 2004; *Moore and Braucher*, 2008]. The Q_{10} model is used to simulate the temperature dependence on phytoplankton growth rates (Explicit $Q_{10} = 2.0$). The BEC model runs within the Parallel Ocean Program model, which is a part of the larger Community Earth System Model (CESM 1.0) [*Gent et al.*, 2011; *Danabasoglu et al.*, 2012; *Moore et al.*, 2013]. The GFDL models also include multiple phytoplankton groups and a Q_{10} model of temperature impacts on growth (Explicit $Q_{10} = 1.88$) [*Bopp et al.*, 2013; *Dunne*, 2013]. We define the explicit Q_{10} as the value assigned to individual phytoplankton groups within the models. This can differ from the emergent, or apparent Q_{10} factor, for the influence of temperature on community growth rates when the model output is analyzed in the same manner as the field data.

The three ESM simulations used in this study are from the Coupled Model Intercomparison Project 5 (CMIP5). Model simulations were conducted following the CMIP5 guidelines (http://cmip-pcmdi.llnl.gov, see *Moore et al.* [2013] for details). Model resolution for the BEC is ~1°, and 1° for the GFDL models. Phytoplankton community growth rates were calculated by weighting the net primary production of each phytoplankton functional group (diatoms, diazotrophs, and small phytoplankton) and dividing by the fractional component

of community biomass in the upper 20 m of the water column. A monthly climatology for 1990s period was created for community phytoplankton growth rates from the CESM (see *Moore et al.* [2013] for additional details and validation comparisons with observed biogeochemical and physical oceanographic fields). Modeled growth rates were extracted at the same location and sampling month as the in situ observations. The same approach was used for the GFDL-ESM2M and GFDL-ESM2G models. Averaged historical CMIP5 output from years 1990 to 1995 was used to construct a monthly climatology. Primary carbon production by phytoplankton (CMIP5 variable "pp," (mol m^{-3} s^{-1})) was divided by phytoplankton carbon concentration (CMIP5 variable "phyc," (mol m^{-3})) at the in situ observational locations over the upper 20 m to estimate community net growth rates.

Using the temperature and the phytoplankton community growth rates (from the field data and from each model), we fit the temperature equations to determine the apparent phytoplankton community temperature-growth relationship. We define the apparent Q_{10} as the calculated optimal value fitting the Q_{10} model to the growth and temperature data. Thus, the apparent, community Q_{10} value is calculated in the same way for the field measurements and for the models (model output subsampled only at the locations of the field observations). The explicit Q_{10} is the parameter value specified in numerical models for individual plankton groups, which can differ from the phytoplankton community apparent Q_{10} value.

To estimate the parameters of the Q_{10} and Arrhenius models, we applied a logarithmic transformation to each model to make them linear in their adjustable parameters. We then used ordinary least squares to estimate $\ln(Q_{10})$ and $\ln(g_o)$ for the Q_{10} model and to estimate $\ln(E)$ and $\ln(A)$ for the Arrhenius model. For temperatures in the range found in the oceans, the curvature of the graph of $1/kT$ versus T (when T is measured in units of K) is negligible—for the temperature range between −2°C to 32°C the relative error made in approximating $1/kT$ by a linear function of T is less than one part in 10^5—so that the temperature dependence of both models is practically identical [*Dixon and Webb*, 1964]. This makes it impossible to select one model over the other based only on the quality of their respective fit to the in situ data. For the temperature range between −2°C and 32°C we can relate E to Q_{10} using $Q_{10} \approx \exp\left((\delta T\, E)/\left(k\overline{T}^2\right)\right)$, where $\delta T = 10$ K and $\overline{T} = 288.15$ K [*Dixon and Webb*, 1964].

To assign uncertainties to our estimates of the optimized parameter values, we assumed normally distributed errors for the logarithmically transformed growth rate data and reported 95% confidence intervals assuming uniform prior probabilities for the parameters. For the Arrhenius model there is a very strong correlation in the posterior probability of E and $\log(A)$, ($p = 0.9995$). This makes the optimal value of A extremely sensitive to the value of E. We have therefore reported the uncertainty for A conditioned on E fixed at its optimal value. The unconditional uncertainty for A, obtained after marginalizing out E, is $A = (3.5 \pm^{13.50}_{2.80} \times 10^4)$ day^{-1}.

3. Results

There is a strong influence of temperature on growth rates apparent in the observational data set. Mean phytoplankton community growth rates, averaged within 3°C temperature bins, are plotted against temperature in Figure 3a. We estimated an optimal apparent Q_{10} value of 1.47 ± 0.08 (95% CI) with a reference growth rate at 30°C of 0.89 ($\pm^{0.08}_{0.07}$) day^{-1} (95% CI) (without log transformation the optimal Q_{10} value was 1.38). We estimate an optimal activation energy of $E = 0.28$ (±0.04) eV (95% CI) for the Arrhenius equation. The optimal value of A depends sensitively on the assumed choice for the activation energy. Conditioned on E fixed at its optimal value of 0.277 eV, we estimate $A = 3.5$ ($\pm^{13.50}_{2.80} \times 10^4$) day^{-1} (95% CI). Figure 3 shows that both optimized models fit the data equally well, with approximately the same root-mean-square error of 0.45 day^{-1} (Table 1).

Our estimated activation energy of 0.28 (±0.04) eV is in good agreement with other estimates. Previous studies have found activation energies that range from 0.29 eV to 0.32 eV [*Allen et al.*, 2005; *Lopez-Urrutia et al.*, 2006; *Regaudie-de-Gioux and Duarte*, 2012]. However, our apparent Q_{10} value of ~1.5 is significantly lower than the canonical value of 2.0 often used when assigning explicit Q_{10} values in models [*Eppley*, 1972; *Goldman and Carpenter*, 1974; *Bissinger et al.*, 2008]. An apparent Q_{10} value of 2.0 overestimates the effect of temperature on community phytoplankton growth rates. This is illustrated in Figure 3, which compares our optimized equations with the growth rate computed as a function of temperature for a fixed apparent Q_{10} value of 2.0 and an optimized reference growth rate of 1.33 day^{-1} (blue line). Note the much steeper slope compared with the observational data set.
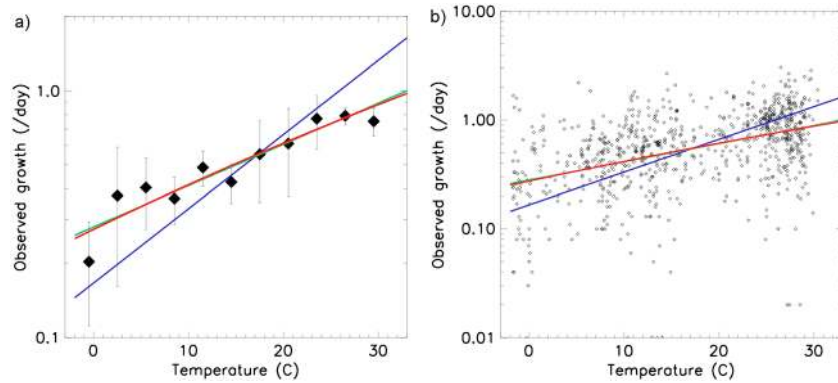
Figure 3. (a) Observed phytoplankton community growth rates are plotted versus temperature averaged within 3°C bins. Error bars show the 95% confidence intervals. The green line displays the modeled growth-temperature relation with the best fit to the Q_{10} equation (apparent Q_{10} value of 1.47). The red line (nearly identical to green) is the modeled growth-temperature relation with the best fit of the Arrhenius equation (activation energy of 0.28 eV, a coefficient value of 3.53×10^{4}, see text for details). The blue line shows the modeled growth-temperature relation with the best fit of the Q_{10} growth equation, imposing an apparent Q_{10} value of 2.0. (b) The original unbinned data with the same three trend lines.
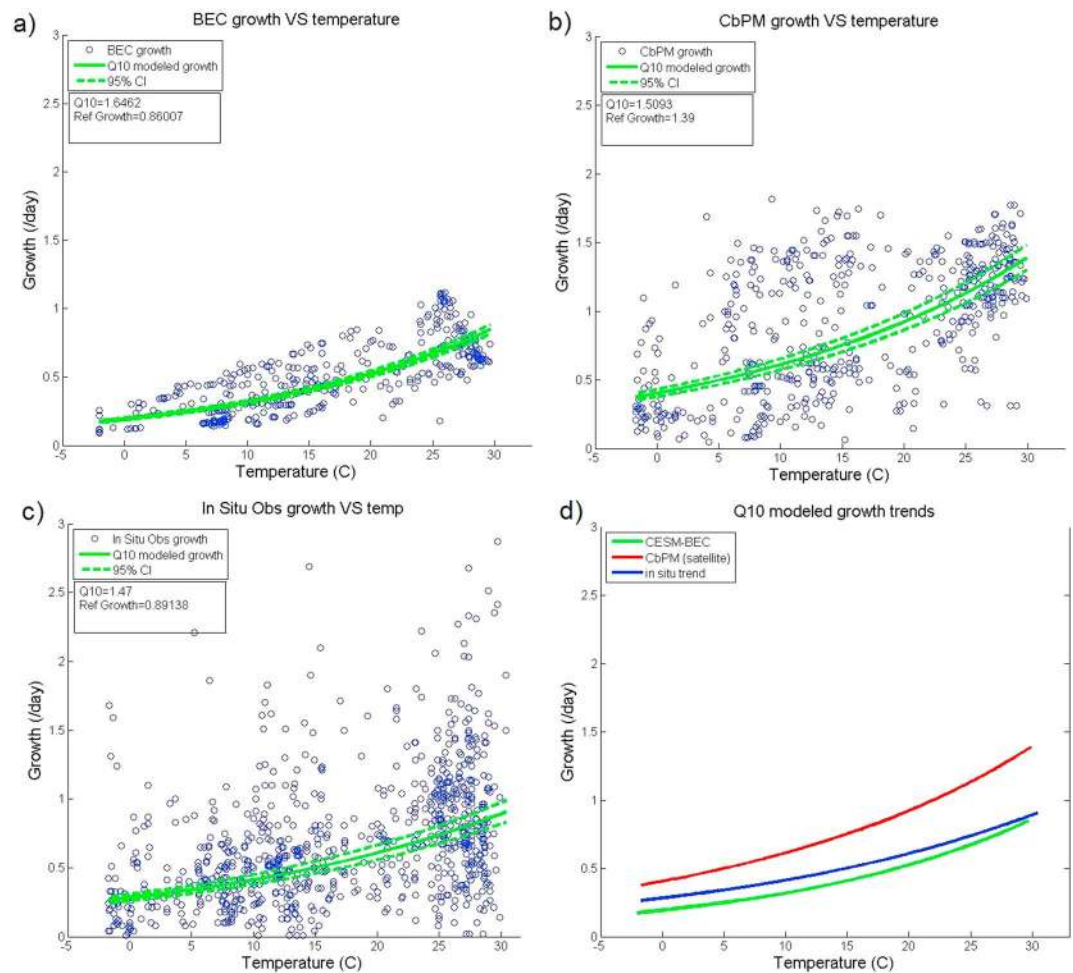

Figure 4. (a) BEC community phytoplankton growth rates versus temperature at in situ sampling locations. (b) CbPM community phytoplankton growth rates versus temperature at in situ sampling locations. (c) In situ observations versus temperature. (d) The Q_{10} modeled growth from Figures 4a–4c plotted against temperature. Reported Q_{10} values are apparent values.
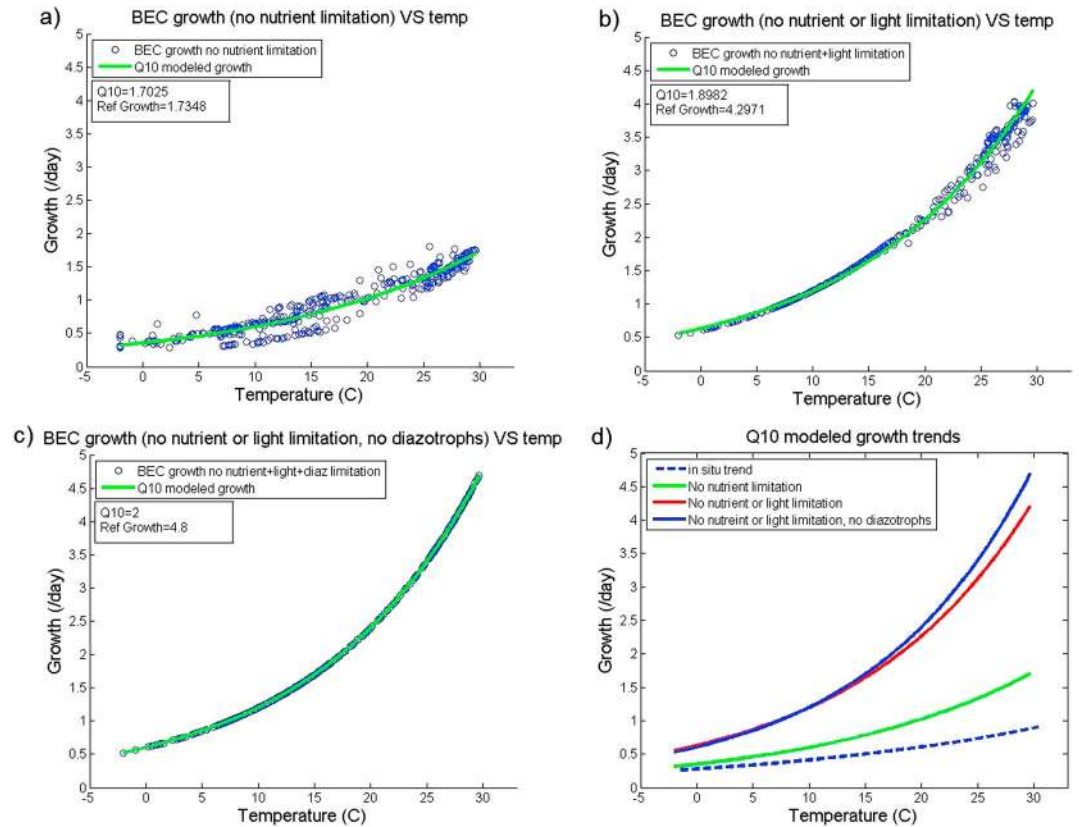
Figure 5. All growth rates shown are phytoplankton community growth rates. (a) BEC growth without nutrient limitation versus temperature. (b) BEC growth without nutrient or light limitation versus temperature. (c) BEC growth without nutrient, light, or diazotrophs versus temperature. (d) The Q_{10} modeled growth from Figures 5a–5c plotted against temperature. Reported Q_{10} values are apparent Q_{10} values.

To assess the influence of nutrient limitation in the observational data set, we compare subsets of the data from the studies that estimated growth rates both with and without nutrient addition ($n = \sim 200$, Table 1). We calculated the apparent Q_{10} value for subsets of the data both with and without nutrient addition. The apparent Q_{10} value calculated from the experiments with nutrient additions is 1.48, and the apparent Q_{10} value calculated from the data without nutrient additions is 1.42, with overlapping 95% confidence intervals (Table 1). The very similar apparent Q_{10} values strongly suggest that spatial or temperature-correlated patterns in the degree of nutrient stress are not strongly skewing our optimized apparent Q_{10} values. However, the reference growth rate was higher in the nutrient-addition subset (1.1 day^{-1} versus 0.65 day^{-1} without nutrient addition, Table 1), demonstrating significant nutrient limitation of the in situ community growth rates. The estimated reference growth rate with nutrient limitation was 65% of the reference growth rate with no nutrient limitation value. These results together indicate that the degree of nutrient limitation was not correlated with temperature but was in fact very similar across different regions.

To further explore the role of nutrient and light limitation, we analyze output from the CESM-BEC model. We take the existing simulation results and calculate what the growth rate would have been without the nutrient and/or light limitation terms. This is a simplified approach, in that we assume that phytoplankton biomass and community composition are not changed, and by removing the light limitation term we assume a saturating light field 24 h per day. Then we refit the Q_{10} model with the modified growth rates. Modeled growth, both with and without nutrient limitation, was extracted at the same location and month as all of the in situ observations. Figure 4a shows BEC-simulated growth (with nutrient limitation) versus temperature. Figure 5a shows BEC-simulated growth without any nutrient limitation (assuming that phytoplankton biomass and community composition remain the same) versus temperature. The apparent Q_{10} value for CESM-BEC growth with nutrient limitation is 1.65($\pm$0.06) with a reference growth rate of 0.86($\pm^{0.10}_{0.09}$), while the apparent Q_{10} value
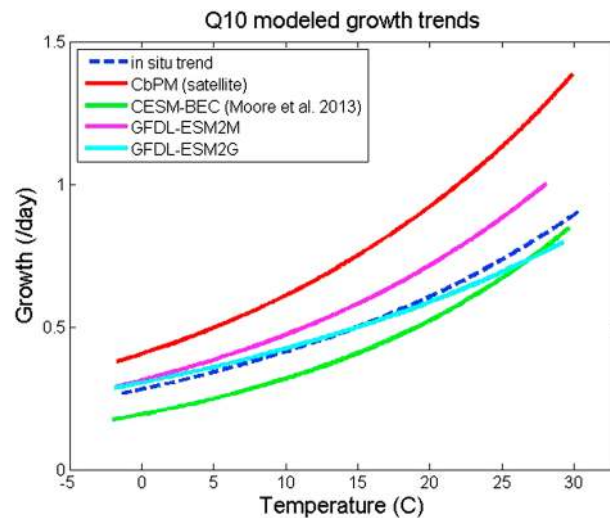
Figure 6. Q_{10} modeled growth, using respective apparent Q_{10} values and reference growth rates, for in situ observations, CbPM, CESM-BEC, GFDL-ESM2M, and GFDL-ESM2G.

without nutrient limitation is $1.70 \pm (0.02)$ with a reference growth rate of $1.73 \pm (0.03)$. Much like in the observational data set, we only see a modest nutrient influence on the apparent Q_{10} factor, but the reference growth rate is again significantly different. The reference growth rate with nutrient limitation for the BEC was 50% of the estimated rate without nutrient limitation. Overall, the CESM-BEC model (with nutrient limitation) slightly underestimates phytoplankton community growth rates in comparison to the in situ observations with the largest underestimation at low temperatures (Figure 4d).

Light limitation could potentially skew our analysis of the temperature influence on community phytoplankton growth rates. Figure 5b shows CESM-BEC community phytoplankton growth, at the in situ locations, without nutrient or light limitation. There is only a modest difference in apparent Q_{10} values without nutrient limitation (apparent $Q_{10} = 1.7025$) and without nutrient and light limitation (apparent $Q_{10} = 1.8982$). The large majority of the field dilution experiments were sampled near the surface (~5 m) and incubated on deck (we excluded deep euphotic zone experiments). We therefore believe light limitation is not significantly skewing our results. Growth rates calculated without light limitation assume a 24 h per day photoperiod, resulting in unrealistically high growth rates at low latitudes. Accounting for the latitudinal variations in summer season photoperiod length would tend to flatten the growth-temperature relation (longer photoperiod at high latitudes), which may partially explain the ~ 0.2 difference in apparent Q_{10} values noted above.

Diazotrophs have inherently slower growth rate than other phytoplankton [i.e., *Falcón et al.*, 2005; *Breitbarth et al.*, 2007], which has been incorporated in the CESM-BEC [*Moore et al.*, 2004]. The diazotrophs are excluded from high-latitude waters in the model by temperature constraints [*Moore et al.*, 2004]. If phytoplankton community biomass was weighted more toward diazotrophs in warmer regions, this may skew the apparent Q_{10} value low. Figure 5c shows BEC community phytoplankton growth rates without nutrient and light limitation while also excluding diazotrophs from the phytoplankton community at the in situ locations. Comparing the apparent Q_{10} value without nutrient and light limitation (apparent $Q_{10} = 1.8982$) and the apparent Q_{10} value without nutrient and light limitation and excluding diazotrophs (apparent $Q_{10} = 2.0$), we find the difference to be 0.1018. These results suggest that diazotrophs are not strongly skewing the in situ apparent Q_{10} estimation, which would still be an apparent Q_{10} value significantly lower than 2.0. The diazotrophs typically only account for 1–3% of primary production in the CESM, even in warm water, nutrient depleted regions. Diazotrophs would be included in the field estimates as well and may contribute to the apparent modest flattening of the growth versus temperature relation at the warmest temperatures (Figure 3).

Although there is no explicit temperature effect included in the CbPM, there is a positive correlation between temperature and phytoplankton growth rates. The CbPM growth rates are driven by the satellite estimates of the phytoplankton chlorophyll/carbon ratio. It appears that this ratio must correlate strongly with temperature at the global scale. We estimated an apparent Q_{10} value of $1.51(\pm0.06)$ with a reference growth rate of $1.39\left(\pm^{0.10}_{0.09}\right)$ at 30°C. Figure 4b shows CbPM growth rates versus temperature and estimated growth rates using the Q_{10} model and apparent CbPM Q_{10} value and reference growth rate values. The CbPM matches well the growth-temperature relation seen in the field data but consistently overestimates community growth rates (Figure 4d).

Using data from the CMIP5 archives, we also calculated apparent Q_{10}s and reference growth rates for the GFDL-ESM2M and GFDL-ESM2G models (Figure 6). The GFDL-ESM2M apparent Q_{10} is $1.52 \pm (0.02)$ with a
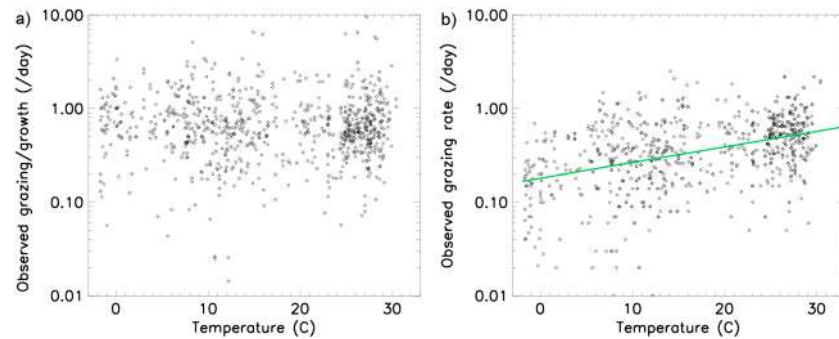
Figure 7. (a) The ratio of observed microzooplankton grazing rate/phytoplankton community growth rate is plotted as a function of temperature. (b) The microzooplankton grazing rate as a function of temperature, with an optimal fit of the Q_{10} equation (here as the Q_{10} function multiplied by a reference grazing rate at 30°C, see text for details).

reference growth rate of $1.08 \pm (0.03)$. This apparent Q_{10} value closely matches the observation-based estimate of 1.47; however, the reference growth rate is higher than in the observations, leading to a modest overestimation of community phytoplankton growth rates that increases with temperature (Figure 6). The GFDL-ESM2G apparent Q_{10} is $1.39 \pm (0.02)$ with a reference growth rate of $0.82 \pm (0.02)$.

Chen et al. [2012] reported a positive correlation between increasing temperatures and microzooplankton grazing rate/phytoplankton community growth rate for eutrophic conditions. Contrary to the findings of *Chen et al.* [2012] and *Rose and Caron*'s [2007] trophic decoupling by temperature theory, we found no temperature influence on the ratio of microzooplankton grazing rate/phytoplankton community growth rate (Figure 7a). We note that our examination of microzooplankton grazing rate/phytoplankton community growth rate was not assessed with respect to chlorophyll concentrations as was done in *Chen et al.* [2012].

There was a strong temperature trend for the microzooplankton grazing rates, nearly exactly matching that observed for phytoplankton growth rates (Figure 7b). Fitting our Q_{10} equation to the grazing rates gives an apparent Q_{10} value of 1.47 ± 0.08 with a reference grazing rate at 30°C of $0.57 \pm 0.05 \, \text{day}^{-1}$. This likely reflects not only the temperature sensitivity of the grazer populations, whose respiration likely scales more strongly with temperature [*Lopez-Urrutia et al.*, 2006; *Regaudie-de-Gioux and Duarte*, 2012], but also a dynamic adjustment of grazing pressure (by modifying microzooplankton biomass and grazing rates) to match available food resources (a function of phytoplankton growth and biomass) [*Peters*, 1994]. Most of the time, over much of the ocean, there is a relatively tight coupling between primary production and grazing [*Calbet and Landry*, 2004, and references therein]. There was no correlation observed between phytoplankton community growth rates and nitrate or chlorophyll concentrations for the subset of studies that reported ambient nitrate and chlorophyll (Table 1 and Figure 8).

The global mean growth rate for all the field observations was $0.71 \, \text{day}^{-1}$, and the mean grazing rate was $0.47 \, \text{day}^{-1}$, indicating that on average about 66% of daily production was grazed by the microzooplankton.
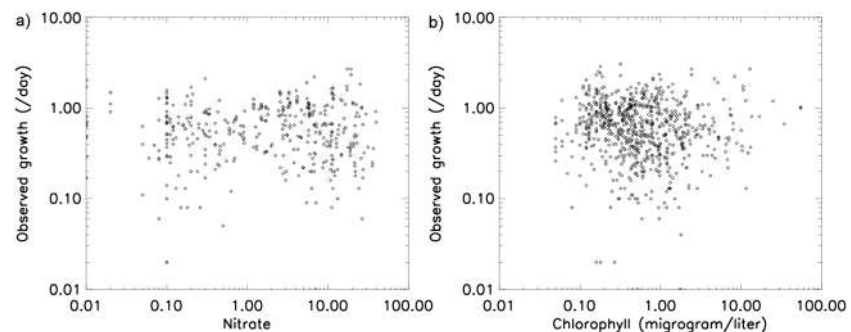

Figure 8. (a) Observed phytoplankton community growth rates are plotted against observed nitrate and (b) observed phytoplankton community growth rates are plotted against observed chlorophyll concentrations.

Dividing our computed reference grazing rate (0.57 day^{-1}) by the reference growth rate (0.89 day^{-1}) gives a similar value of 64% of daily production being grazed. The *Calbet and Landry* [2004] data set had similar mean values of 0.67 day^{-1} for growth and 0.41 day^{-1} for grazing, which implies 61% of daily production on average being grazed. There are additional mortality terms in the model including a nongrazing mortality loss meant to account for losses to viruses, excretion, and respiration, and an additional loss to aggregation and sinking [*Moore et al.*, 2004].

4. Discussion

It is perhaps not surprising that a weaker temperature-growth relation is observed in natural phytoplankton communities across ecosystems than has been observed in culture studies with single species. At the global scale, the dominant component of phytoplankton communities will be well adapted to ambient temperatures. For example, phytoplankton can adapt to low temperatures by modifying internal resource allocations to compensate for some of the most temperature sensitive metabolic reactions [*Raven and Geider*, 1988]. Our results indicate that such adaptations may weaken but certainly do not erase the temperature influence on metabolism and growth. It is important to keep in mind that our findings apply to the phytoplankton community growth rate at the global scale. It is possible that individual species, which typically thrive only in a fairly narrow temperature range [i.e., *Eppley*, 1972], but are well adapted for those temperatures, could all exhibit growth-temperature relations with an apparent Q_{10} value of 2.0, but when combined at the community level produce a weaker apparent growth-temperature relation as we report here. Phytoplankton may have more mechanisms to optimize and acclimate for growth at low temperatures than for high temperatures, for example, by producing more substrates for the most temperature-sensitive metabolic reactions [*Raven and Geider*, 1988]. The longer summer season photoperiod at high latitudes likely also plays a role in weakening the growth-temperature relation.

There was considerable spread in the data for any given temperature range (about 1 order of magnitude; Figures 3a and 3b). This could be due to several factors, including the seasonally varying nutrient and light fields, species-specific differences, bloom progression status, and experimental error in the measurements. One might expect the warmer waters to be more strongly nutrient limited, with a stronger suppression of growth rates. There is little indication of the growth rates falling off the optimal trend line, except at the very highest temperatures in the binned data (Figure 3a).

It appears that as community composition shifts in response to nutrient availability, often correlated with temperature, the resulting community growth rates and the relative degree of nutrient stress are similar across marine ecosystems at the global scale, even as ambient nutrient concentrations and total phytoplankton biomass vary widely. This effect is seen in the relatively constant apparent Q_{10} values with and without nutrient stress in both the field observations and the CESM-BEC model output. The very small phytoplankton that dominate the community in warm, stratified regions, where nutrients are typically scarce, are extremely efficient at taking up nutrients [*Agawin et al.*, 2000; *Raven*, 1998]. This allows them to grow relatively quickly even when ambient nutrient concentrations are quite low. In regions with higher ambient nutrient concentrations, a larger fraction of the phytoplankton community will be made up of larger species, such as diatoms, that are much less efficient at nutrient uptake. The shifting community structure appears to adjust so that the relative degree of nutrient stress for the community is similar across biomes.

Our results show that the apparent Q_{10} value for phytoplankton community growth rates for natural populations is approximately 1.5. Utilizing the Arrhenius equation with an activation energy of ~0.28 eV would be equally good at predicting the growth response to changing temperatures. Global scale marine ecosystem models with only one phytoplankton group, or a few phytoplankton functional types, should strive to match the apparent Q_{10} value seen in our observational data set. This may require explicit Q_{10} values imposed in the model that are less than the values of 1.88 or 2.0 often used today (or an equivalent Arrhenius model). Models that include a large number of phytoplankton types, or that explicitly account for internal resource allocation strategies to adapt to low temperatures, could a include a range of group-specific explicit Q_{10} values, but their integrated community growth rates should be compared with the observational data set compiled here to ensure that the phytoplankton community growth rate displays a temperature sensitivity equivalent to an apparent Q_{10} value of ~1.5.

Parameterization of the temperature effect on phytoplankton growth rates is important for simulating net primary production, especially under climate change scenarios [*Taucher and Oschlies*, 2011]. *Laufkötter et al.* [2015] examined a suite of the CMIP5 ocean biogeochemical models and suggested that the temperature-growth relationship could be as important as nutrient concentrations in driving NPP-climate interactions at the lower latitudes. Models with stronger temperature sensitivity (i.e., apparent Q_{10} value = 2.0) in their phytoplankton community growth rates will overestimate the response to ongoing ocean warming and will have strongly biased growth rates in some regions for the current era.

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Erratum

In the originally published version of this article, there was an error in one of the equations in the second to last paragraph of the Methods section. The equation has since been corrected, and this version may be considered the authoritative version of record.