

Predicting marine phytoplankton maximum growth rates from temperature: Improving on the Eppley curve using quantile regression

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Abstract

The Eppley curve describes an exponential function that defines the maximum attainable daily growth rate of marine phytoplankton as a function of temperature. The curve was originally fitted by eye as the upper envelope of a data set, and despite its wide use, the reliability of this function has not been statistically tested. Our analysis of the data using quantile regression indicates that while the curve appears to be a good estimate of the edge of the data, it may not be reliable because the data set is small ($n = 162$). We construct a contemporary, comprehensive data set ($n = 1,501$) and apply an objective approach, quantile regression, to estimate its upper edge (99th quantile). This analysis yields a new predictive equation, $\mu_{\max} = 0.81e^{0.0631T}$, that describes the maximum specific growth rates (μ_{\max} , d⁻¹) of marine phytoplankton as a function of temperature (T , °C). The Liverpool phytoplankton database (LPD) curve is higher than the Eppley curve across all temperatures, and at temperatures below 19°C, the Eppley curve falls below the lower 95% confidence interval of the LPD curve. However, the LPD Q_{10} value (1.88) is identical to that of the Eppley curve and thus supports the use of models that incorporate this as an estimate of phytoplankton growth-rate response to temperature change. To assess the potential effect of the LPD curve on primary production, we embedded the LPD function into a one-dimensional numerical model of a temperate, pelagic ecosystem. This analysis suggests that models using the Eppley function will underestimate primary production by as much as 30%.

Models of aquatic primary production are useful tools to predict global biogeochemical fluxes and better inform those involved in aquatic resource management. Marine phytoplankton are a key component of many of these models both because of their carbon assimilation (Behrenfeld et al. 2001) and because of their effect on other ecosystem components (Ryther 1969). Because the utility of such models hinges on the quality of the parameters, we need to be confident in their reliability. Thus, here we apply a statistical technique to assess the reliability of a parameter that relates phytoplankton maximum growth rates to temperature, which is a key component of numerous aquatic production models (e.g., Tett et al. 1985). Furthermore, the difference between this relationship and the growth-rate response of heterotrophic protists to temperature has been implicated in the formation of algal blooms in high-latitude ecosystems (Rose and Caron 2007).

Thus, the consequences of correctly interpreting the data are considerable.

In dynamic ecosystem production models, a temperature function is often used to set the upper limit of phytoplankton growth rates. From this theoretical maximum, growth rates are then reduced by applying coefficients relating to environmental limiting factors such as day length, photon flux density, and nutrients (Bowie et al. 1985). One temperature function commonly used is that developed by Eppley (1972):

$$\mu_{\max} = 0.59e^{0.0633T} \quad (1)$$

This exponential relationship defines the maximum attainable daily growth rate (μ_{\max} , d⁻¹) of phytoplankton as a function of temperature (T , °C) and has the advantage over more complex functions of being able to generate predictions in the absence of other data, such as community composition or phytoplankton size. The relationship was formulated from a compilation of data from laboratory culture studies in which light and nutrients were considered replete. Eppley (1972) indicated that the data fell within an upper envelope and drew a line by eye that defined the maximum expected growth at any given temperature between 0°C and 40°C (Fig. 1).

The citation history (>800) of Eppley (1972) suggests that its strong influence is as pronounced today as it was

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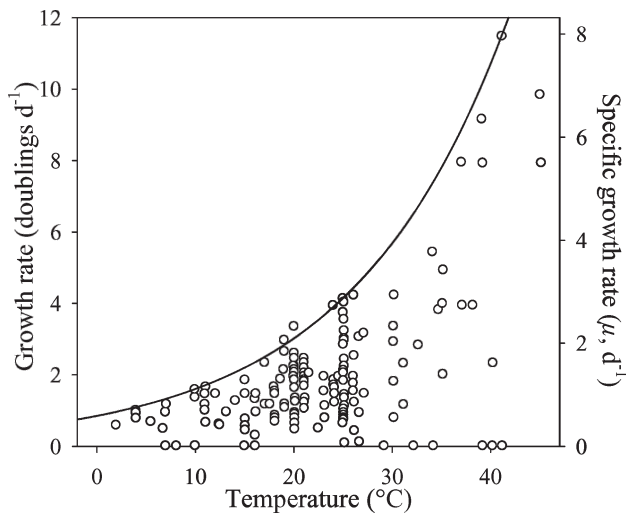


Fig. 1. Variation in the specific growth rate, μ , of photoautotrophic unicellular algae with temperature (redrawn from figure 1 of Eppley 1972).

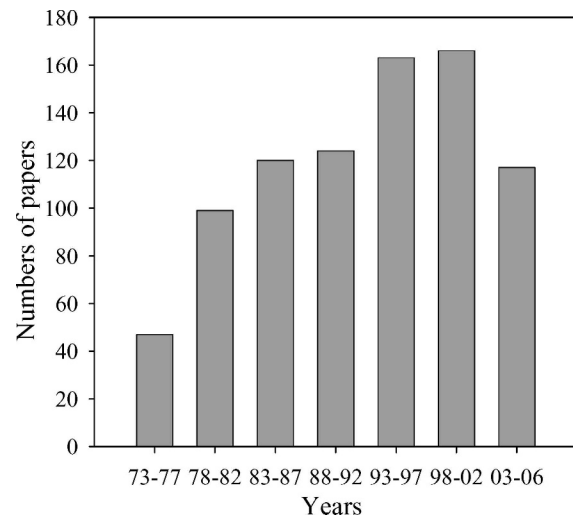


Fig. 2. Citation history (<http://wok.mimas.ac.uk/>) of "Temperature and phytoplankton growth in the sea" (Eppley 1972). Total number of citations = 835.

over 30 yr ago (Fig. 2). In a sample of 450 papers that cite Eppley (1972), 103 incorporate some aspect of the Eppley formulation in a model, i.e., either the function itself (e.g., Cugier et al. 2005) or the Q_{10} of 1.88 derived from the Eppley function (e.g., Tett et al. 1985). Another 85 studies compare their results to the theoretical maximum expected from the curve (e.g., Durbin 1974; Admiraal 1977); of these, 62 had results similar to or below the curve, and 15 had results that exceeded the theoretical maximum (e.g., Brush et al. 2002). In addition, some studies suggest that an exponential function is not the most appropriate model of the relationship across a wide range of temperatures (Moisan et al. 2002). Recognition of these discrepancies throws doubt on the applicability of the Eppley function and thus also on predictions of aquatic primary production.

Here, we focus on the exponential portion of the response, as Eppley (1972) did, and explore the outcome of a statistical approach that objectively defines the upper edge of a scatter graph, providing a quantitative measure of the reliability of the estimate obtained. Problems with fitting a line of maximum growth by eye include the subjectivity of the method, especially the risk that the relationship may be disproportionately affected by outliers, and the impossibility of quantitatively measuring the precision of the model parameter estimates. In the Eppley (1972) function, an estimate of μ_{\max} was inferred from a small sample ($n = 162$) without any measure of the confidence in that estimate. Furthermore, since Eppley (1972) produced his curve, numerous growth-rate studies have been published with data suitable for incorporation into a new analysis. Therefore, if we plan to use Eppley-like functions in modern aquatic ecosystem models, a quantitative assessment of the reliability of this relationship is needed.

Quantile regression (Koenker and Bassett 1978) can be used to infer relationships from the edges of scatter graphs

(e.g., the upper edge of the Eppley [1972] data set; Fig. 1); for example, the 99th quantile describes a line below which are found 99% of the observations. This approach has already been applied to other problems in the aquatic sciences (e.g., the study of maximum bathymetric body-size gradients in gastropods carried out by McClain and Rex [2001], and the investigation of opportunistic predation in tuna by Menard et al. [2006]). Briefly, quantile regression is based on least absolute deviations (LAD) regression, which uses the median rather than the mean, and it is therefore less sensitive to extreme outlying values than ordinary least squares (OLS) regression. The quantile of interest (τ) is estimated using an optimization function that minimizes the sum of weighted absolute deviations (Koenker and Bassett 1978; Koenker and d'Orey 1987), and the solution to the minimization problem is achieved using an algorithm such as the simplex method (Cade and Noon 2003). Typically, like most modern statistics, these algorithms are available in software packages, for example, *R* (<http://www.r-project.org>).

Regression quantiles, unlike OLS regression, make no assumptions about the error distribution in the model and retain their statistical properties under any linear or nonlinear monotonic transformation (Cade and Noon 2003). Consequently, this method has the added benefit that it is possible to use a nonlinear transformation (e.g., logarithmic) to estimate the regression quantiles and then back-transform the estimates without loss of information (Cade and Noon 2003). Furthermore, estimation of the edges of scatter graphs using quantile regression is not burdened by arbitrary decisions about data partitioning and the numbers of size classes (Scharf et al. 1998), as is the case when binning approaches are used (e.g., Blackburn et al. 1992; Rose and Caron 2007). Since calculation of the standard error for the quantile of interest is dependent on variance in the sample distribution around this quantile (Cade et al. 1999), it is not possible to calculate an upper

confidence interval (CI) for a 100% quantile ($\tau = 1.0$). Therefore, the most reliable estimate of the edge of the data is that defined by the highest (i.e., nearest to 100%) quantile regression line with confidence intervals that do not include zero (Cade et al. 1999). Thus, in this type of analysis, there is often a trade-off between the maximum regression quantile (τ) that can be estimated and the confidence in that estimate.

In this study, five issues are addressed: we analyze the data compiled by Eppley (1972) using quantile regression and examine the statistics associated with the 99th quantile; we follow the approach of Eppley (1972) and obtain all suitable available data to construct a new, large ($n = 1,501$) database (Liverpool phytoplankton database, LPD) and then use quantile regression to establish a new predictive equation; we investigate if our new, comprehensive database produces a biased response due to a larger proportion of diatoms, since diatoms tend to exhibit high specific growth rates (Furnas 1990); we calculate and compare the Q_{10} of the observed responses, since Q_{10} is used regularly to predict primary production (e.g., Tett et al. 1985; Doney et al. 1996); and finally, we investigate if the quantile regression parameter estimates are influenced by growth-rate data at high temperatures, since there are indications that the growth-rate response should deviate from an exponential response at higher temperatures (Behrenfeld and Falkowski 1997).

Materials and methods

Quantile regression—We use quantile regression to estimate the maximum growth rates of phytoplankton at different temperatures together with a quantitative measure of the confidence in that estimate. Because linear quantile regression provides estimates of standard errors and confidence intervals (CI), the data were linearized by logarithmic transformation. However, log-transformation of the data to accommodate zero and negative growth values (e.g., $\log y + 1$) prevented direct comparison with the Eppley equation, so these few data (<1% of the LPD and ~5% of the Eppley data set) were not included. Quantiles and associated statistics were calculated using the “quantreg” (Koenker 2006) package in R, which employs a variant of the Barrodale and Roberts (1974) simplex algorithm (Koenker and d’Orey 1987).

When estimating extreme quantiles with confidence, a large sample size is required to provide a reasonable density of observations near the edge of the data (Cade et al. 1999). To ensure reliable estimates, Rogers (1992) suggested $n > 5/(1 - q)$ (where n is the sample size, and q is the quantile of interest); so, to estimate the 99th quantile, $n > 500$. In this study, the most reliable estimate of the edge of each data set was taken to be the highest possible quantile that complied with the sample size: quantile recommendation of Rogers (1992) and had a slope with 95% CI that excluded zero. In the following analyses, data sets are identified with subscripts, where (E) signifies the Eppley data, (LPD) signifies the Liverpool phytoplankton database, and (43% D) signifies the subset of the LPD data where diatoms

constitute 43% of the total (the same proportion as in the Eppley [1972] data set).

Reanalyzing Eppley’s data—Eppley (1972) compiled phytoplankton growth-rate data from both primary and secondary sources and only included data from cultures that were grown in nutrient-replete conditions under continuous illumination, or at optimum day-length where a continuous photoperiod was detrimental to growth. Data points ($n = 153$ after zero values were removed) from Fig. 1 of Eppley (1972) were digitized using Grab It! data-capture software and converted from doublings per day to specific growth rates (μ , d⁻¹; Fig. 1). The 99th_(E) quantile was calculated as described previously and visually compared to the Eppley curve (Fig. 3A), since the sample size was too small for further analysis.

Analyzing the Liverpool phytoplankton database—The Liverpool phytoplankton database (LPD, $n = 1,501$ growth rates of marine taxa) only includes laboratory studies from the primary literature, i.e., field-based observations and compilations of growth-rate studies were not included. Data presented graphically were digitized using Grab It!, and growth rates expressed as doublings or divisions per day were converted to specific growth rates (μ , d⁻¹). Data from species that were originally isolated from the benthos were not included, and where experiments varied in salinity, only those growth rates with salinities ≥ 30 were included. Thus, the LPD is composed of studies that measured growth rates at only one temperature and those that collected growth rates over a number of different temperatures, in batch, continuous, and chemostat experiments, and for various day-length and photon flux density combinations. Consequently, the LPD includes data where conditions were not always replete and maximum growth rates were not always achieved. The LPD was compiled from 51 publications, is ~10 times larger than Eppley’s data set, and is composed of 92 species or strains from 62 genera (see Web Appendix 1, www.aslo.org/lo/toc/vol_53/issue_2/0493a1.pdf).

The influence of the percentage of diatoms in the data—Because regression quantiles are based on the percentage of data above or below the specified quantile, and the fast growth rates of diatoms (Furnas 1990) may mean that there is a greater percentage close to the upper envelope, we investigated whether the larger proportion of diatoms in the LPD (68% compared to ~43% in the Eppley data set) biased our analysis. We did so by randomly subsampling ($n = 828$) the LPD to create 30 subsets, where diatoms constituted 43% of the total in each subset. For each subset, we then calculated the 99th_(43% D) quantile with $\pm 95\%$ CI, and the mean of these was then compared to the Eppley curve and 99th_(LPD) quantile. To determine if differences existed between the slopes and intercepts of the log-transformed Eppley curve, 99th_(LPD), and 99th_(43% D) quantiles (i.e., three comparisons), t -tests were applied. To be conservative, these tests were Bonferroni corrected (Sokal and Rohlf 1995), giving an α value of 0.01.

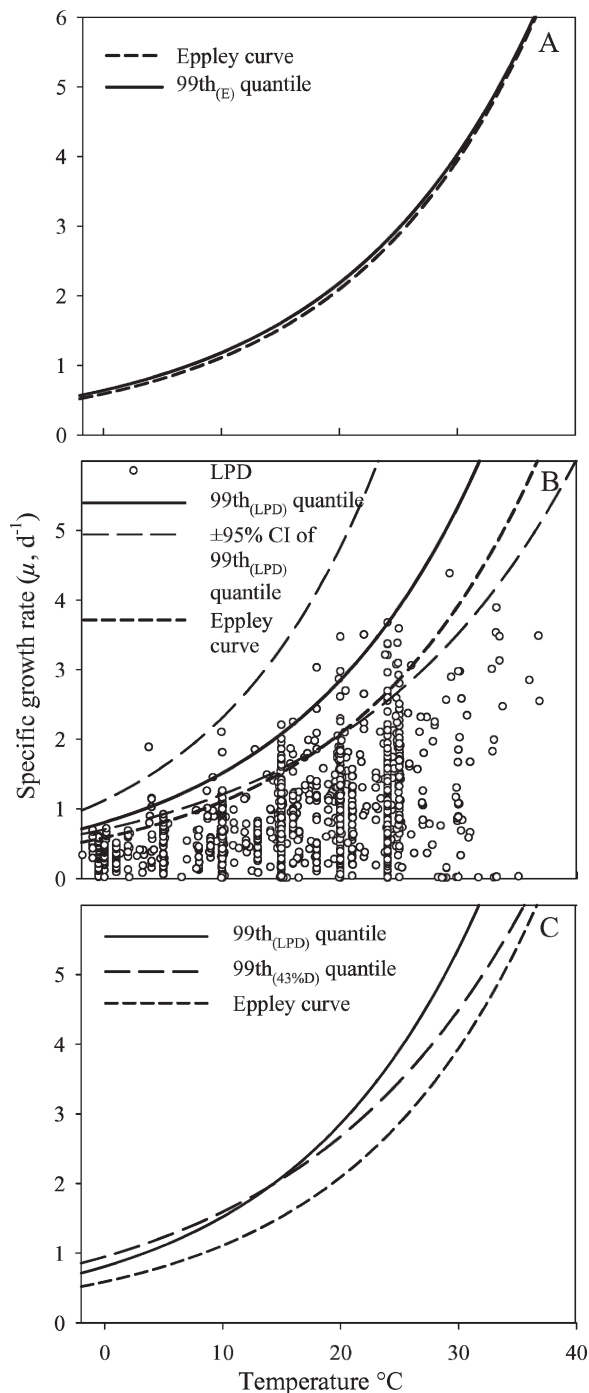


Fig. 3. Marine phytoplankton maximum growth rates (μ_{\max}) as a function of temperature. (A) A comparison of the two methodologies used to estimate the upper edge of Eppley's data. The Eppley curve, which was drawn by eye, is compared to the 99th(_E) regression quantile calculated from Eppley's digitized data ($n = 153$). (B) The 99th(_{LPD}) quantile and associated $\pm 95\%$ confidence intervals calculated from the Liverpool phytoplankton database (LPD) ($n = 1,501$). The Eppley curve is shown for comparison. (C) Normalization of the LPD data to account for differences in the percentage of diatoms in the data. Lines show the 99th(_{LPD}) and 99th(_{43%D}) ($n = 828$) quantiles, with the Eppley curve shown for comparison.

Calculating the Q_{10} value—We calculated the Q_{10} value of the LPD μ_{\max} and that derived from the subsets with 43% diatoms using the Q_{10} model of Van't Hoff (1884). Assumptions included an exponential response and no inhibition of growth rate at high temperatures, following the approach of Eppley (1972).

The influence of growth rates at high temperatures—At higher temperatures ($>29^{\circ}\text{C}$, Fig. 3B), data points were fewer and appeared to have maxima below the calculated 99th quantile. So, to alleviate any concerns that these high-temperature data may unduly influence the parameter estimates from the quantile regression analysis, a reduced data set was created that excluded growth-rate data at temperatures $>29^{\circ}\text{C}$. To determine if there were differences between the log-transformed regression parameters from the full and reduced data sets, t -tests were applied.

Results

Analysis of Eppley's data—Qualitatively, the 99th(_E) quantile appears to be similar to the Eppley curve (Fig. 3A). However, as only one positive residual point occurs above the 99th(_E) quantile, it was not possible to statistically analyze the differences between the 99th(_E) quantile and the Eppley curve. Thus, error estimates were not obtained for the Eppley curve using quantile regression.

Analysis of Liverpool phytoplankton database—Since the $\pm 95\%$ CI of the 99th(_{LPD}) quantile slope estimate excluded zero and complied with the minimum size recommended by Rogers (1992) (Table 1), this quantile provided the most reliable estimate of the edge of the LPD data set. Back-transformation of the parameters from the 99th(_{LPD}) quantile yields:

$$\mu_{\max} = 0.81e^{0.0631T} \quad (2)$$

A comparison of the log-transformed quantile parameters to those of the Eppley curve indicates that the intercept of the 99th(_{LPD}) quantile is significantly greater than that of the Eppley curve ($t = 3.20$, $\text{df} = 1,499$, $p < 0.01$). Furthermore, at temperatures below 19°C , the Eppley curve falls below the lower 95% CI associated with the 99th(_{LPD}) quantile (Fig. 3B). However, the slope of the 99th(_{LPD}) quantile is not significantly different from that of the Eppley curve ($t = 0.53$, $\text{df} = 1,499$, $p > 0.01$). The slope and intercept of the 99th(_{43%D}) quantile are not significantly different from those of the Eppley curve ($t = 1.05$, $\text{df} = 826$, $p > 0.01$, and $t = 2.08$, $\text{df} = 826$, $p > 0.01$, respectively), or the 99th(_{LPD}) quantile ($t = 0.97$, $\text{df} = 2325$, $p > 0.01$, and $t = 0.66$, $\text{df} = 2325$, $p > 0.01$, respectively).

The Q_{10} value of the 99th(_{LPD}) quantile (1.88) is identical to that of the Eppley curve, whereas the Q_{10} value of the 99th(_{43%D}) quantile is 1.68. The log-transformed slope and intercept parameter estimates of the reduced ($\leq 29^{\circ}\text{C}$) data set are not significantly different ($t = 0.24$, $\text{df} = 2953$, $p > 0.01$, and $t = 0.18$, $\text{df} = 2953$, $p > 0.01$, respectively) from those of the full data set.

Table 1. 99th regression quantile slope parameter estimates and associated statistics for the Liverpool phytoplankton (LPD) data sets. The parameter values are calculated to a confidence level of $\alpha = 0.05$, and $n > 5/(1 - q)$ represents the minimum recommended sample size at the specified quantile (Rogers 1992). Note that the 43% D slope estimate and $\pm 95\%$ CI represent the mean value of 30 subsamples.

Data set	n	$n > 5/(1 - q)$	Estimate	−95% CI	+95% CI
LPD	1,501	500	0.0631	0.0535	0.0721
43% D	828	500	0.0518	0.0259	0.0668

Discussion

Using quantile regression, we recognized that the Eppley curve could be improved upon. To this end, we derived a new exponential function for marine phytoplankton growth rates as a function of temperature using the Liverpool phytoplankton database (LPD), and we compared it to that derived by Eppley (1972). However, the data set compiled by Eppley (1972) did not fulfil the minimum size recommendations of Rogers (1992) for calculating the 99th quantile with confidence. Calculating extreme quantiles with a small sample size may lead to a limited number of residuals, which renders methods for calculating standard errors unreliable (R. Koenker pers. comm.). Consequently, it was not possible to provide error estimates for the Eppley curve using quantile regression. Nevertheless, the visual fit of the 99th_(E) quantile to the original Eppley (1972) curve (Fig. 3A) suggests that the Eppley curve is a good estimate of the edge of the data. Furthermore, there is no significant difference between the log-transformed slopes of the LPD and the Eppley curve, indicating equivalence in Q_{10} values (1.88) and suggesting that the Eppley curve has been an appropriate estimate of the thermal sensitivity of phytoplankton growth rates. This result supports and complements studies that demonstrate fundamental differences in growth-rate thermal sensitivity between heterotrophs and phototrophs (Allen et al. 2005; López-Urrutia et al. 2006; Rose and Caron 2007), and it should also reassure those who have used the Q_{10} value of 1.88 in models over the last 35 yr.

The significant difference between the intercept of the log-transformed 99th_(LPD) and the Eppley curve supports studies that suggest that the Eppley curve is too low (e.g., Brush et al. 2002). However, in our new relationship (Eq. 2), the intercept value (0.81) is lower than the value (0.97) derived by Brush et al. (2002). We suggest that this discrepancy is due to the different methodologies adopted in defining the edge of the upper envelope. In their analysis, Brush et al. (2002) adopted the same slope value as Eppley (1972) and determined the upper edge of their data by eye. As discussed earlier, in relation to Eppley (1972), there are possible problems with this approach, e.g., the subjectivity involved and the lack of quantitative measures of reliability.

Construction of the LPD subset containing 43% diatoms, i.e., an equivalent proportion to that of Eppley (1972), allowed us to further investigate whether differences between the LPD envelope and the Eppley curve could be

attributed to the greater percentage of diatoms in the LPD, since diatoms typically have disproportionately high growth rates (Furnas 1990). However, because there were no significant differences between the intercepts of the 99th_(43% D) quantile and the 99th_(LPD) quantile, the dissimilarities between the Eppley curve and the 99th_(LPD) quantile cannot be solely attributable to differing proportions of diatoms in the two data sets. Consequently, the LPD function (Eq. 2) is an appropriate model when a single theoretical maximum function is required, e.g., when the only data available are biomass, or Chl *a* and temperature.

A good example of where a single temperature function has been repeatedly employed is in pelagic ecosystem models (e.g., Balch and Byrne 1994; Antoine et al. 1996; Sharples et al. 2006). To assess the extent to which our function may alter model results, we compared the output of one temperate shelf-sea ecosystem model (Sharples et al. 2006) using our new function and that of Eppley (1972). This simple analysis suggests that models that incorporate the Eppley function may underestimate primary production in cooler temperate waters by ~30%. This underestimate applied to both the 99th_(LPD) quantile and the 99th_(43% D) quantile, since these two responses are similar at lower temperatures (Fig. 3C). Consequently, assessments of the thermal influence of primary production on ecosystem services such as oxygen production, carbon sequestration, and biogeochemical cycling may also require revision.

Our analysis of the influence of diatom percentage abundance on the upper envelope, and, in particular, the differences in slope parameter estimates between the 99th_(43% D) quantile and the 99th_(LPD) quantile (Table 1), indicates how other variables may be incorporated into a more accurate model. Size (Savage et al. 2004) and taxonomic affiliation (Banse 1982), for example, may explain much of the remaining variation in μ_{\max} among phytoplankton. Building on our revised general growth rate–temperature relationship, we are currently developing new predictive models, using the LPD, that incorporate these and other variables, such as community composition and habitat.

Finally, in this study, we concentrated on producing a relationship that is directly comparable to the Eppley curve, but we acknowledge that there are limitations with the applicability of this function in warm or oligotrophic oceanic areas, where the maximum growth rates of phytoplankton may always be limited by factors other

than temperature. Furthermore, this analysis has highlighted two issues that need to be addressed in the future. First, while our analysis of the reduced data set ($\leq 29^\circ\text{C}$) indicates that the use of the full data set to determine the upper envelope is valid, we note that the relationship is not exponential at very high temperatures. We will address the shape of the maximum envelope in future models, and we caution against using our existing model (Eq. 2) at temperatures $>29^\circ\text{C}$. Second, a Q_{10} value of 1.88 is somewhat higher than predicted by the metabolic theory of ecology (Brown et al. 2004; Allen et al. 2005), which gives a Q_{10} value of between 1.62 (for $0\text{--}10^\circ\text{C}$) and 1.52 (for $20\text{--}30^\circ\text{C}$), derived from a predicted activation energy of 0.32eV for rates controlled by photosynthesis. This discrepancy clearly merits further scrutiny.

In conclusion, while recognizing the utility and robustness of the Eppley curve over the last 35 yr, the quantitative measures of reliability associated with our LPD function (Eq. 2) should give users greater confidence in its value and suitability in situations where a single exponential growth-rate relationship is sought.

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