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Comment: Temperature, nutrients, and the size-scaling of phytoplankton growth in the sea

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Chen and Liu (2010) investigated the effects of cell size on phytoplankton-mass–specific growth rate using a compilation of field measurements from surface waters around the world. After correcting for the effects of temperature, their analysis indicates that there is a modal size around 2.8–5.8 μm where mass-specific growth is maximal. As Chen and Liu (2010) acknowledge, their analysis contrasts with allometric scaling theories that predict a continuous decrease of mass-specific growth rate with increasing size (Brown et al. 2004; López-Urrutia et al. 2006). In contrast, Chen and Liu's (2010) analysis shows that bellow the modal size, that is in the pico- to nanophytoplankton size range, growth rate increases with cell size. They argue that the unimodal pattern stems from picoplankton having evolved to have inherently low growth rates, independently of nutrient availability. Here we argue that the unimodal pattern they obtain might be due to an incorrect temperature correction and to an internal inconsistency in their database because a large portion of their picoplankton data contain a correction for photoacclimation effects, while the rest of their data do not.

To carry out their study, Chen and Liu (2010) used two data sets, one from ^{14}C incorporation and a second from dilution experiments. In both data sets, a unimodal pattern between mass-specific growth rate and cell size emerges. In these two data sets, however, cell size is correlated with nutrient availability, so it could be argued that, rather than a direct effect of cell size, the lower growth rates of smaller phytoplankton could be due to these organisms living under resource limitation (Raven 1998), (*see* fig. 1C in Chen and Liu 2010). Chen and Liu (2010) tried to resolve these confounding effects due to correlation between nutrient availability and cell size by using a data set of phytoplankton growth rates measured under nutrient enrichment. The unimodal pattern still apparent in this nutrient-saturated dilution data set is probably the most striking result in their analysis. Chen and Liu (2010) concluded that the lower growth rates in the picoplankton size range are an adaptive feature rather than a direct consequence of nutrient limitation.

We consider whether this pattern is due to a bias in the data compilation. In an effort to get the best data available, Chen and Liu (2010) used phytoplankton growth rates with a correction for photoacclimation for the two data sources that had this information available, while the rest of their nutrient-enriched dilution data are uncorrected. These corrected data happen to correspond to most of the low values in the picoplankton size range (Fig. 1A). If we take this nutrient-enriched dilution data set and replace these photoacclimation-corrected data with the uncorrected values comparable to the rest of the data set, the unimodal pattern is no longer evident (Fig. 1B). The quadratic term in the unimodal fit is no longer significant (t-test, $t = -1.255$, df = 255, $p = 0.211$). Although now a linear fit is more appropriate, the linear relationship obtained is not what the metabolic theory of ecology (MTE) predicts. MTE predicts that metabolic rates and organism biovolume (BV) should scale as rate $\propto BV^{3/4}$ (West et al. 1999; López-Urrutia et al. 2006). Hence, size-specific metabolic rates (rate $\times BV^{-1}$), such as individual growth rate, should scale as $BV^{3/4} \times BV^{-1} = BV^{-1/4}$. Chen and Liu (2010) define cell size as the carbon content. López-Urrutia et al. (2006) have shown that, when phytoplankton cell size is expressed in units of carbon instead of biovolume, phytoplankton growth-rate scales isometrically with cell size (rate $\propto$ carbon^1), so carbon-specific growth rate (rate $\times$ carbon^{-1}) should be independent of cell carbon. This is due to phytoplankton carbon content and biovolume scaling as BV $\propto$ carbon$^{4/3}$ (Strathmann 1967), so rate $\propto BV^{3/4} \propto (\text{carbon}^{4/3})^{3/4} \propto$ carbon.

Hence, following MTE, a plot of carbon-specific growth rate should yield no significant relationship with cell-carbon, whereas Fig. 1B shows a positive relationship. We think that this trend could be due to the temperature correction used. Chen and Liu (2010) used a Q_{10} of 1.88 (Eppley 1972; Bissinger et al. 2008) so that $\log(\mu) - 0.0275 \times T$ is the temperature-corrected phytoplankton-specific growth rate, where T is the temperature in Celsius. On the other hand, MTE uses the Van't Hoff–Arrhenius equation (Arrhenius 1915) to describe the effects of temperature on metabolic rates:

$$\text{Rate} \propto e^{-E/kT_a} \quad (1)$$

where k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}), T_a is the absolute temperature (in Kelvin) and E is the average activation energy for the metabolic process under study. For autotrophs the effective activation energy for photosynthetic reactions should be close to 0.32 eV (Allen et al. 2005). In the case of photosynthesis, the Van't Hoff–Arrhenius equation is just an approximation to a more complex process (Farquhar et al. 1980). The activation energy of 0.32 predicted by MTE is based on data from the effects of temperature on several photosynthetic processes (*see* appendix in Allen et al. 2005). López-Urrutia et al. (2006) obtained an effective activation energy for phytoplankton growth rates of 0.29 eV, not significantly different from the predicted value of 0.32 eV.

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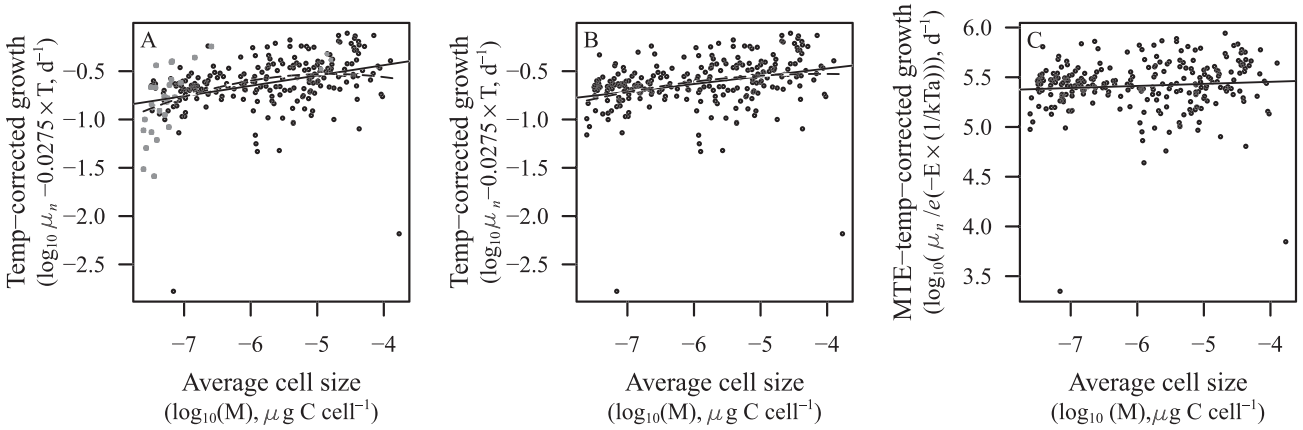

Fig. 1. Relationship between temperature-corrected growth rate and average cell size (M) for the nutrient-enriched dilution data set. (A) Chen and Liu (2010) data. Grey-filled symbols correspond to photoacclimation-corrected data. The solid line corresponds to a linear fit ($\log_{10}(u_n) = 0.11 \log_{10}(M) - 0.01$; ANOVA: $r^2 = 0.14$, $n = 261$, p-value < 0.001). The dashed line corresponds to a quadratic fit ($\log_{10}(u_n) = -0.05 [\log_{10}(M)]^2 - 0.48 \log_{10}(M) - 1.67$; ANOVA: $r^2 = 0.17$, $n = 261$, p-value < 0.001). (B) Same as (A) but with all data uncorrected for photoacclimation. The solid line corresponds to a linear fit ($\log_{10}(u_n) = 0.08 \log_{10}(M) - 0.15$; ANOVA: $r^2 = 0.09$, $n = 258$, p-value < 0.001). The dashed line corresponds to a quadratic fit ($\log_{10}(u_n) = -0.02 [\log_{10}(M)]^2 - 0.18 \log_{10}(M) - 0.91$; ANOVA: $r^2 = 0.10$, $n = 258$, p-value < 0.001). (C) Same as (B) but using the temperature correction based on MTE. In this panel, just a linear fit is shown ($\log_{10}(u_n) = 0.02 \log_{10}(M) + 5.54$; ANOVA: $r^2 = 0.01$, $n = 258$, p-value $= 0.203$).

The Q_{10}, in turn, is an approximation to Van't Hoff–Arrehnius equation, so both temperature coefficients, E and Q_{10}, are interrelated by eq. $Q_{10} = e^{[-E/(kT_0^2)] \times 10}$, where T_0 is 273.15 K (*see* box 1 in Gillooly et al. 2002). Hence, the Q_{10} of 1.88 from Eppley (1972) is equivalent to an activation energy of ~ 0.405 eV, which is slightly higher than the activation energy predicted for autotrophs and the empirical value obtained by López-Urrutia et al. (2006). If growth rates from the nutrient-enriched dilution data set are plotted against temperature, the resultant activation energy is 0.36 eV (Fig. 2), which is not significantly different from the value predicted by MTE (t-test, $t = 2.08$, df $= 256$, $p = 0.15$) but significantly lower than the value used by Chen and Liu (2010) (t-test, $t = 12.522$, df $= 256$, $p < 0.001$).

This subtle difference between the two temperature corrections might be responsible for the pattern obtained in Fig. 1B. If instead of the temperature correction used by Chen and Liu (2010) based on Eppley's (1972) Q_{10}, we use the temperature correction based on MTE and the theoretical activation energy of 0.32 eV (equivalent to a Q_{10} of 1.64), we obtain no significant relationship between carbon-specific growth rate and average cell carbon (Fig. 1C), in agreement with MTE. The Q_{10} used by Chen and Liu (2010), is based on the studies of Eppley (1972) and Bissinger et al. (2008) that analyze the temperature dependence of phytoplankton maximal growth rates. It should be noted that the temperature dependence of this maximally attainable growth rate might be different from the temperature dependence of growth rate under optimal conditions. For example, in Fig. 2 we fit a line to the growth rates under nutrient- and light-saturated conditions, while Eppley (1972) and Bissinger et al. (2008) fits would represent the upper limit of the recorded growth rates. Our fit, therefore, attempts to predict the average growth rate of a population of phytoplankton living at optimum nutrient and light conditions, while Eppley (1972) and Bissinger et al. (2008) predict the maximum growth rate of the same population. Maximal and average metabolisms might have different temperature dependencies but it is the latter (such as the one shown in Fig. 2) that

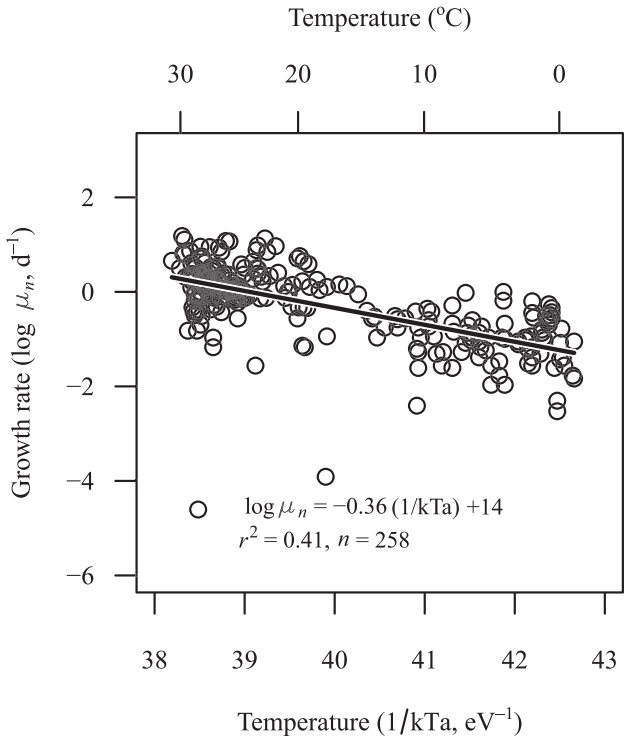

Fig. 2. Effect of the temperature function ($1/kT_a$, lower axis) on log-transformed nutrient-saturated growth rate ($\log_e(u_n) = -0.36(1/kT_a) + 14$; ANOVA: $r^2 = 0.41$, $n = 258$). The corresponding temperatures in degrees Celsius are presented in the upper axis for reference.

needs to be used to obtain growth rates corrected for the effects of temperature.

When inferring the effect on metabolic processes of variables that might be correlated with temperature, such as body size or nutrients, it should be borne in mind that the value used for the temperature correction might introduce some bias. We believe that the value used for the temperature correction should be derived theoretically, such as the one used in Fig. 1C, and not empirically, because solely based on a field data set such as the one under analysis, it is impossible to discern the magnitude of the effects of temperature and of variables correlated with it. For example, it could be argued that the temperature coefficient we obtain in Fig. 2 is dependent on the assumption that weight-specific growth rate is independent of cell size, and that if we had corrected growth rate by the cell-size effects obtained in Fig. 1B, we would have obtained a temperature coefficient closer to Eppley's (1972). To avoid this caveat, the temperature coefficient used should be based on some theory, such as the one we used based on MTE, or corroborated by experimental work where the effect of the other variables can be controlled.

Such a criticism can be applied also, for example, to the activation energy of 0.29 eV for cell-size–corrected phytoplankton growth rate obtained by López-Urrutia et al. (2006). This value is, to some extent, dependent on the assumption that growth rate scales with cell size to the 3/4 power. Because cell size and temperature are correlated, taking a theoretical value for the effects of cell size to evaluate the effects of temperature, conditions in some way the activation energy obtained.

Theory and experiments should have a major say in elucidating whether phytoplankton growth rates scale according to models of resource distribution networks as proposed by MTE or are constrained by surface diffusion. As explained above, MTE predicts that rate $\propto BV^{3/4}$, while nutrient uptake area considerations suggest that the scaling between primary production and BV should be rate $\propto BV^{2/3}$ (Aksnes and Egge 1991). In terms of surface area, assuming $S \propto BV^{2/3}$, MTE predicts that rate $\propto S^{9/8} = S^{1.12}$, while surface diffusion theories predict that rate $\propto S^{1}$.

Paradoxically, a recent comprehensive study measuring metabolic rates of protists (Johnson et al. 2009) obtained a size-scaling exponent of $S^{1.057}$, at the midpoint between resource distribution and surface-area theories. Johnson et al. (2009) incorrectly argued that, although they obtained a scaling between cell volume and metabolic rate of 0.72 with a 95% confidence interval of 0.65–0.79 (*see* their fig. S2), cell volume is not the appropriate metric for metabolic scaling and cell carbon should be used instead. And because rate scales as *carbon*[1] they argue that metabolic scaling theories can't be applied to protists. This last argument by Johnson et al. (2009) is not correct; metabolic scaling theories derive the 3/4 scaling exponent on biovolume (West et al. 1999). MTE theories then assume that mass and biovolume scale isometrically (*see* assumption 6 in Banavar et al. [2010] and eq. 8 in West et al. [1999]) to derive the mass scaling exponent. Metabolic rates scale as $BV^{3/4}$; therefore, the experimental data in Johnson et al. (2009) also agree with MTE. In summary, data to allow a clear decision on which theory is correct are still lacking. In fact, the two theories might not be independent (Mei et al. 2009). Maybe organisms have to deal with both constraints (limitations on diffusion across surfaces and limitations on resource distribution networks), and that is why the measured scaling exponent is at the midpoint (Banavar et al. 2010).

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