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Relationships between phytoplankton growth and cell size in surface oceans: Interactive effects of temperature, nutrients, and grazing

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Abstract

We compile two data sets from ^{14}C uptake and dilution experiments conducted in surface waters of the global ocean to investigate the relationship between phytoplankton mass-specific growth rate and cell size. After temperature correction, both data sets suggest that this relationship might be described by a unimodal quadratic curve with the modal size (the size corresponding to the maximal growth rate) being 2.8 and 5.4 μm in the ^{14}C and dilution data sets, respectively. Nutrient enrichment does not change the qualitative nature of the relationships, and we conclude that inherently low maximal growth rates of picophytoplankton, not ambient nutrient effects, play the major role in determining the positive relationships over the size range where phytoplankton size is below the modal size. Temperature-corrected phytoplankton grazing mortality rate is positively correlated with phytoplankton average size, but the proportion of daily primary production consumed by microzooplankton is negatively correlated with cell size, suggesting a reduced grazing effect as size increases. The unimodal relationship between phytoplankton growth rate and cell size is consistent with theoretical considerations and might reflect an adaptive response of phytoplankton to varying extents of nutrient limitation and grazing effect in marine systems.

Estimating phytoplankton growth rates is of paramount importance in biological oceanography. A recently established theory proposes that size and temperature are two universal factors that influence metabolic rates of all organisms on Earth, including marine phytoplankton (Brown et al. 2004). Generally, individual mass-specific metabolic rate after temperature standardization is found to be a -0.25 power of organism body size (Brown et al. 2004), which has been robustly confirmed in terrestrial plants (Enquist et al. 1999).

In studies of eukaryotic algal cultures, it is generally the case that the slope of the log (maximal mass-specific growth rate)–log (size) relationship is not much different from or is slightly less negative than the classic -0.25 value in aquatic phytoplankton (Banse 1982; Tang 1995; Nielsen et al. 1996). Litchman et al. (2007), however, did not find any significant relationship between maximal growth rate and size. Following the classic allometric rule, Agawin et al. (2000) estimated that picophytoplankton contributed 39% to total global primary production, while they contributed only 8% of the total phytoplankton biomass, assuming that picophytoplankton had a higher turnover rate compared with larger cells. It is noteworthy that maximal mass-specific growth rates of prokaryotic phytoplankton, especially unicellular *Prochlorococcus* and *Synechococcus*, are usually lower than predicted from the classic allometric rule (Chisholm 1992), and this even applies to the smallest picophytoeukaryotes (Bec et al. 2008). In theory, this anomaly may be related to the increasing proportion of essential, nonscalable cellular components that reduces some part of the cellular machinery involved in growth when size decreases (Raven 1998). Using precise mathematical models, Verdy et al. (2009) have demonstrated that the mass-specific growth rates of large cells can be higher than those of small ones if storage capacity increases with cell size and phytoplankton growth is limited by internal nutrient assimilation. Therefore, an optimal cell size (2~3 μm) is often assumed to have the highest growth rate in marine phytoplankton (Jiang et al. 2005). Below this size range, phytoplankton growth rate will increase with cell size, while above this range, phytoplankton growth rate will decrease with cell size as predicted by classic allometry. Nutrient and light limitation can also alter the scaling of phytoplankton growth and photosynthesis. Both light and nutrient limitation can reduce the size scaling exponent of phytoplankton growth because of geometric constrains and package effects in light absorption and diffusion limitation of nutrient uptake, respectively (Finkel 2001; Mei et al. 2009).

When extrapolating the theory and laboratory findings to the real ocean, we must recognize that pico- and nanophytoplankton are the dominant groups in the vast, oligotrophic, open ocean. Although numerous measurements of phytoplankton growth, such as ^{14}C uptake rate, have been made around the global ocean, few studies (but *see* Marañón et al. 2007) have tried to test field data with existing allometric theory. Regardless of changes in phytoplankton community composition, Marañón and coworkers (Marañón et al. 2007; Marañón 2008) recently found that cell-specific ^{14}C uptake rate increased isometrically with cell size (i.e., phytoplankton mass-specific growth rate was independent of cell size), which appears to be consistent with Litchman et al. (2007). However, as the effects of environmental conditions such as temperature and nutrient were not thoroughly discussed in Marañón et

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al. (2007), in which a relatively small number of experiments were included, it still remains unclear what kind of theory can be applied to the phytoplankton assemblages in the real ocean.

An obstacle when trying to apply metabolic theory in field studies is that usually only a bulk growth rate is measured for a parcel of water, as it is impractical to estimate growth rates for each species in many experiments. Therefore, we adopted the approach already taken by Marañón et al. (2007) to treat each water parcel as an individual sample and estimate the average phytoplankton size and specific bulk growth rate. Our objectives are to investigate the relationship between phytoplankton specific growth rate and cell size in field measurements and to see whether the field pattern can be interpreted by existing theory. The effects of temperature and nutrients are considered. We restrict the effects of light by including only surface data. We use two large, independent data sets compiled from the global ocean that are based on the dilution technique (Landry and Hassett 1982) and the ^{14}C uptake method, respectively (*see* Methods). The dilution technique is a nonisotopic method that can also provide reliable estimates of growth rate (Calbet and Landry 2004). Meanwhile, it also provides estimates of nutrient-saturated growth rate and microzooplankton grazing rates on phytoplankton, allowing us to investigate the effect of nutrient availability on phytoplankton growth rate and how phytoplankton grazing mortality rate varies with cell size.

Methods

We compiled two independent data sets containing phytoplankton in situ growth rate measurements in surface waters of the global ocean (*see* Web Appendix, http://www.aslo.org/lo/toc/vol_55/issue_3/0965a.html). One includes 322 data points from 21 studies including some of our own unpublished data (B. Chen unpubl.; H. Liu unpubl.) that used the dilution technique to estimate phytoplankton in situ mass-specific growth (μ_{dil}; d^{-1}) and microzooplankton grazing mortality rates (m; d^{-1}). The study locations ranged from polar (Arctic and Antarctic) to tropical and subtropical regions, mostly in the open ocean, but also included some coastal sites. The other data set includes 434 primary productivity measurements based on ^{14}C uptake from a dozen of United States Joint Global Ocean Flux Study (US JGOFS) cruises that surveyed the equatorial Pacific, Arabian Sea, Southern Ocean, and Antarctic waters. We included only experiments conducted in surface waters where the light intensity was $\geq$ 10% of surface irradiance to restrict the effect of light limitation. We also compiled accompanying temperature, initial chlorophyll *a* (Chl *a*) concentration ($\mu g\ L^{-1}$), nitrate concentration (S; $\mu mol\ L^{-1}$), and ultraphytoplankton ($< 5\ \mu m$; Murphy and Haugen 1985) abundance (N; cells L^{-1}) for each experiment. S was assigned to be 0.01 if reported as zero. We estimated total autotrophic carbon (AC; $\mu g\ C\ L^{-1}$) content whenever possible. If the data for AC were not available, we used the average C : Chl ratio reported in the literature to estimate AC. For a few studies in which no information of AC or C : Chl ratio was provided, we assigned the C : Chl ratio to be 50.

For the data set based on the dilution technique, μ_{dil} and m were directly estimated by linear regression between net phytoplankton growth rate, which was calculated based on the changes in Chl in each dilution treatment, and the proportion of unfiltered seawater of each corresponding treatment (Landry and Hassett 1982). Phytoplankton growth rates were corrected for photoacclimation in some studies based on the cellular fluorescence changes measured by flow cytometry (Chen et al. 2009; Sherr et al. 2009), and we used the corrected rates. Microzooplankton grazing rates are not affected by photoacclimation. In most dilution experiments, nutrients were added to the bottles to satisfy the assumption of constant phytoplankton growth, and a pair of control bottles without any nutrient amendment was set up. By this approach, two phytoplankton mass-specific growth rates, nutrient amended (μ_{diln}) and non-amended (μ_{dil}), could be derived. μ_{dil} represents phytoplankton in situ growth rate, while μ_{diln} can be regarded as a nutrient-saturated growth rate. Microzooplankton grazing rate (m) was assigned to be 0.01 if reported as zero.

For the data set based on ^{14}C uptake, the data were all based on 24-h incubation to keep consistency. The phytoplankton in situ mass-specific growth rates (μ_{PP}; d^{-1}) were calculated as the ratio PP : AC, where PP was the reported daily primary productivity ($\mu g\ C\ L^{-1}\ d^{-1}$).

We estimated average phytoplankton size (M; $\mu g\ C\ cell^{-1}$) by dividing total phytoplankton carbon with total numerical abundance approximated by ultraphytoplankton abundance (AC : N), as total phytoplankton abundance is mostly contributed by ultraphytoplankton that can be counted by flow cytometry (Li 2002). Even in highly eutrophic waters, the numerical abundances of ultraphytoplankton are usually an order of magnitude higher than those of other larger phytoplankton. Assuming that phytoplankton growth rate is a Michaelis–Menten function of ambient nitrate concentration, the half-saturation constant for phytoplankton growth on nitrate (K_N; $\mu mol\ L^{-1}$) was estimated as $10 \times M^{0.27}$ using a simple carbon-to-volume ratio of 0.28 pg C μm^{-3} based on the empirical equation given in Litchman et al. (2007). We chose the Michaelis–Menten function simply because only ambient nitrate data were often reported. To standardize the effect of temperature (T; °C), we used a Q_{10} of 1.88 (Eppley 1972; Bissinger et al. 2008) so that $\log_{10}(\mu) - 0.0275T$ is the temperature-corrected phytoplankton specific growth rate.

Nonparametric Spearman rank correlations were used to estimate correlation coefficients between each variable using the SPSS 13.0 software (SPSS). Linear and quadratic regressions were also performed with SPSS 13.0. The figures were made by the software SigmaPlot 10.0 (Systat Software).

Results

In the dilution data set, T ranges from −1.7 to 30.6°C, while Chl *a* concentration ranges from 0.03 to 24.3 $\mu g\ L^{-1}$, spanning three orders of magnitude. The range of N also

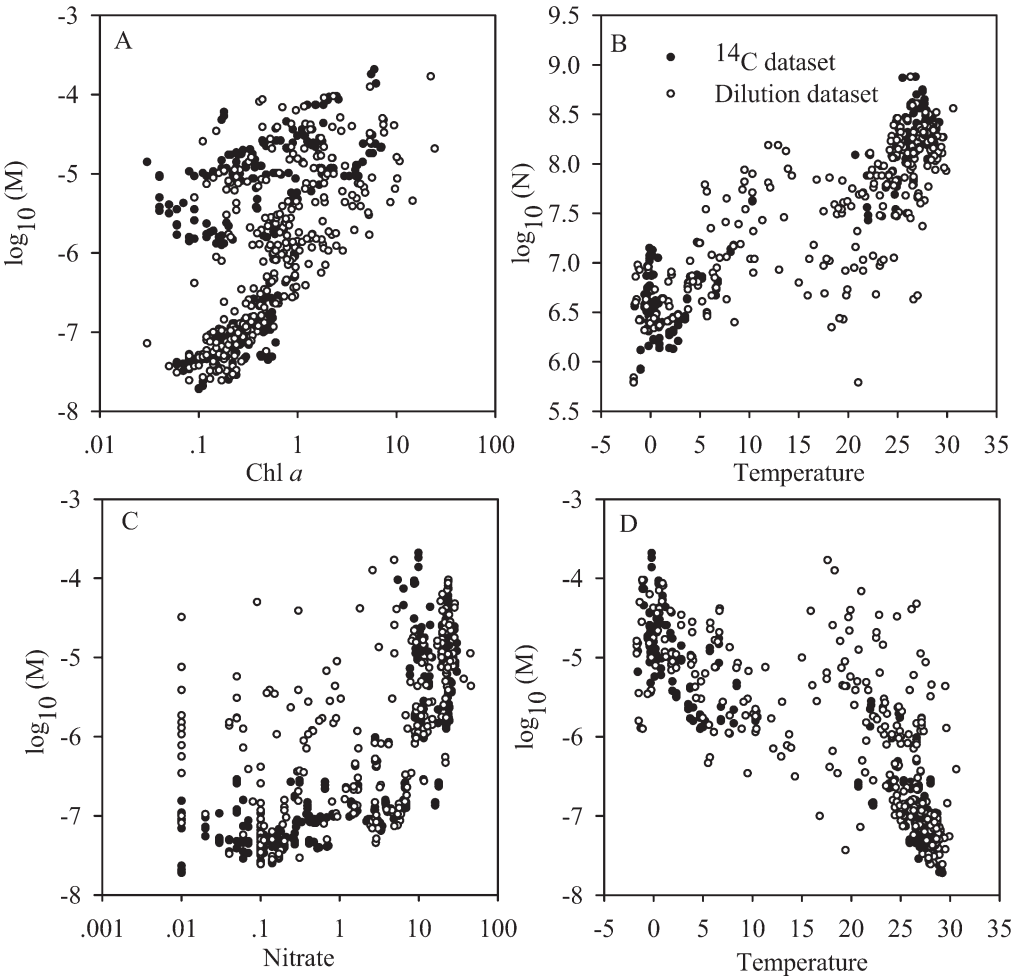

Fig. 1. (A) Scatter plot of log-transformed average cell size ($\log_{10}$ (M)) vs. Chl *a* concentration in both ^{14}C uptake and dilution data sets. (B) Scatter plot of log-transformed phytoplankton numerical abundance ($\log_{10}$ (N)) vs. temperature. (C) Log_{10} (M) vs. nitrate concentrations. (D) Log_{10} (M) vs. temperature. Units are M: μg C cell^{-1}; Chl *a*: μg L^{-1}; N: cells L^{-1}; temperature: °C; nitrate: μmol L^{-1}.

spans three orders of magnitude, from 6.1×10^5 to 7.6×10^8 cells L^{-1}. The range magnitude of M is even larger than that of N, from 2.4×10^{-8} to 1.7×10^{-4} μg C cell^{-1}, corresponding to an equivalent spherical diameter (ESD) from 0.6 to 10.5 μm. The two ends of M signify two typical oceanic environments: the warm and oligotrophic subtropical or tropical waters dominated by *Prochlorococcus* and cold and nutrient-rich polar waters dominated by nanophytoplankton. As expected, T is negatively rank correlated with both Chl *a* and nitrate concentration (Spearman correlation $r = -0.38$ and -0.62, $p < 0.001$, $n = 322$ and 291, respectively) but is positively rank correlated with $\log_{10}$ (N) (Spearman correlation $r = 0.81$, $p < 0.001$, $n = 322$; Fig. 1B). Log_{10} (M) is positively rank correlated with Chl *a* and nitrate concentration (Spearman correlation $r = 0.68$ and 0.64, $p < 0.001$, $n = 322$ and 291, respectively; Fig. 1A,C) and is negatively rank correlated with T and $\log_{10}$ (N) (Spearman correlation $r = -0.78$ and -0.89, respectively, $p < 0.001$, $n = 322$; Fig. 1D). Similar results are also obtained for the PP data set (Fig. 1). All the previously noted tight correlations suggest that the environmental factors are highly intertwined and strongly regulate the phytoplankton average cell size.

Two scatter plots of temperature-corrected logarithmic phytoplankton mass-specific growth rates vs. $\log_{10}$ (M) are shown in Fig. 2A,B. In the dilution data set, temperature-corrected logarithmic phytoplankton mass-specific growth rates ($\log_{10}$ (μ_{dil}) $-$ 0.0275T) are positively rank correlated with $\log_{10}$ (M) (Spearman correlation $r = 0.59$, $p < 0.001$, $n = 322$). If fitted with a linear regression line, the slope is 0.19 ± 0.02 (mean $\pm$ SE; ANOVA: $p < 0.001$, $R^2 = 0.23$, $n = 322$). The linear regression model can be slightly improved by a quadratic model with the equation $\log_{10}$ (μ_{dil}) $-$ 0.0275T $= -(0.071 \pm 0.02)$ [$\log_{10}$ (M)]^2 $-$ (0.65 ± 0.25) $\log_{10}$ (M) $-$ 2.08 (ANOVA: $p < 0.001$, $R^2 = 0.25$, $n = 322$; Fig. 2A). In the ^{14}C data set, $\log_{10}$ (μ_{PP}) $-$ 0.0275T are also positively rank correlated with $\log_{10}$ (M) (Spearman correlation $r = 0.34$, $p < 0.001$, $n = 434$). For this data set, a quadratic model ($\log_{10}$ (μ_{PP}) $-$ 0.0275T $= -(0.12 \pm 0.02)$ [$\log_{10}$ (M)]^2 $-$ (1.32 ± 0.20) $\log_{10}$ (M) $-$ 4.25 (ANOVA: $p < 0.001$, $R^2 = 0.16$, $n = 434$)) is much better than a linear model ($\log_{10}$ (μ_{PP}) $-$ 0.0275T $= (0.071 \pm 0.02)$ $\log_{10}$ (M) $-$ 0.25 (ANOVA: $p < 0.001$, $R^2 = 0.06$, $n = 434$); Fig. 2B). Although average cell size alone explains a small proportion of total variance observed in temperature-corrected phytoplankton mass-specific growth rate, a unimodal

relationship appears to exist between $\log_{10}(\mu) - 0.0275T$ and $\log_{10}(M)$ for both data sets. Based on the previously mentioned quadratic models, μ_{dil} peaks at an M of 2.28×10^{-5} μg C cell^{-1}, corresponding to an ESD of 5.4 μm, while μ_{PP} peaks at an M of 3.16×10^{-6} μg C cell^{-1}, corresponding to an ESD of 2.8 μm.

In the previous analysis, the effect of nutrients is inherently associated with the effect of M, as the two are positively correlated. We tried to separate the effect of nutrients by estimating K_N as a function of M (*see* Methods) and to estimate the phytoplankton nutrient-saturated growth rate as μ:$(S/(S + K_N))$. K_N ranges from 0.1 to 1 μmol L^{-1} in both data sets. However, the estimated nutrient-saturated growth rate is highly overestimated when S approaches zero, which is common in oligotrophic oceans, and finally we gave up this approach. Nonetheless, the estimations of K_N suggest that most rates of phytoplankton growth are already nearly saturated by nitrate in our data set given that the median values of $S/(S + K_N)$ are 0.94 and 0.95 in the dilution and the PP data set, respectively.

To further resolve the problem of compounding effects of nutrients and cell size on phytoplankton growth, we use a reduced dilution data set in which μ_{diln} estimates are available. Again, $\log_{10}(\mu_{diln}) - 0.0275T$ are positively rank correlated with $\log_{10}(M)$ (Spearman correlation $r = 0.38$, $p < 0.001$, $n = 261$). The quadratic model describing this relationship is $\log_{10}(\mu_{diln}) - 0.0275T = -(0.05 \pm 0.02)[\log_{10}(M)]^2 - (0.48 \pm 0.22)\log_{10}(M) - 1.68$ (ANOVA: $p < 0.001$, $R^2 = 0.17$, $n = 261$) with the modal ESD 4.8 μm (Fig. 2C).

Using the same Q_{10} to standardize the temperature effect on phytoplankton grazing mortality rates, we find that $\log_{10}(m) - 0.0275T$ is positively rank correlated with $\log_{10}(M)$ (Spearman correlation $r = 0.27$, $p < 0.001$, $n = 322$; Fig. 3A). Grazing rate is a function of grazer biomass, which is related with phytoplankton biomass and average size. However, the grazing pressure on phytoplankton, that is, the log daily primary productivity consumed by grazers ($\log_{10}(m : \mu_{dil})$), is negatively rank correlated with $\log_{10}(M)$ with statistical significance (Spearman correlation $r = -0.33$, $p < 0.001$, $n = 322$; Fig. 3B).

Discussion

Methodology concerns—Unlike lab cultures, there is still not a perfect way to measure the growth rate of phytoplankton under ambient field conditions. The most widely used ^{14}C method neglects several carbon loss pathways such as respiration, dissolved organic carbon exudation, grazing, and viral infection and measures a value between a gross and net production (Laws et al. 2000). Further, a conversion from total community production to mass-specific growth rate requires additional information on C : Chl, which may vary from 15 to 176 in the field (Sathyendranath et al. 2009). The dilution technique, originally designed to estimate community microzooplankton herbivory rates, measures net mass-specific growth rate directly but is also subject to other potential error sources such as photoacclimation (changes

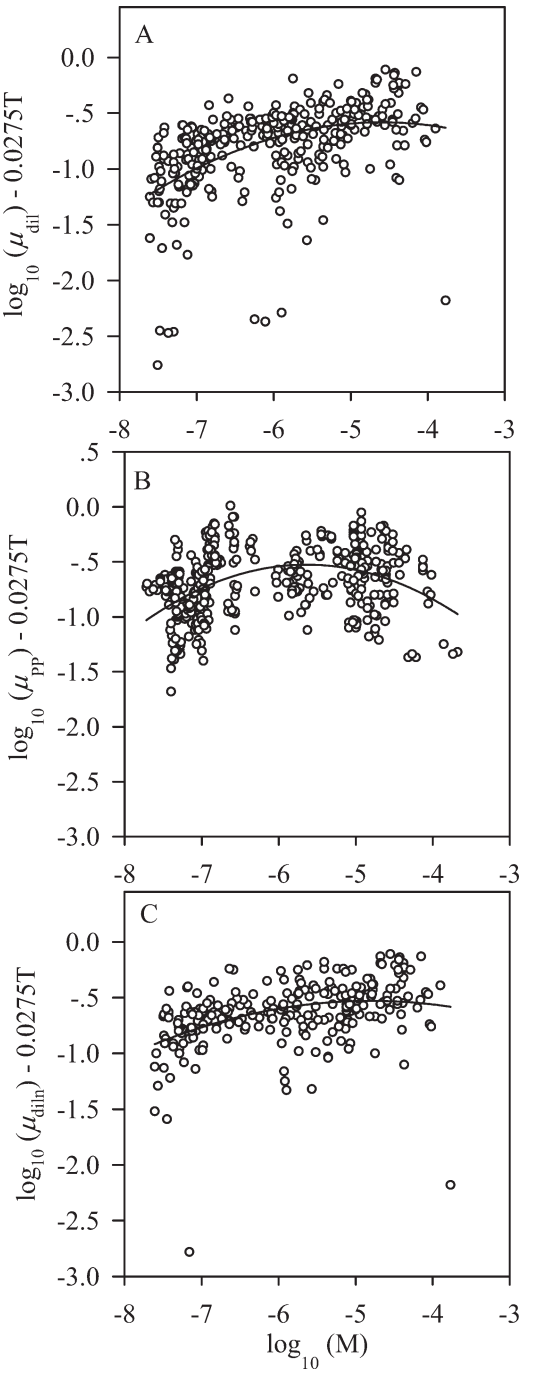

Fig. 2. Scatter plots of (A) temperature (T, °C) corrected log-transformed phytoplankton growth rate ($\log_{10}(\mu_{dil}) - 0.0275T$) based on the dilution data set, (B) temperature-corrected log-transformed phytoplankton growth rate ($\log_{10}(\mu_{PP}) - 0.0275T$) based on the ^{14}C uptake data set, and (C) temperature-corrected log-transformed phytoplankton nutrient-saturated growth rate ($\log_{10}(\mu_{diln}) - 0.0275T$) based on the dilution data set vs. log-transformed average cell size ($\log_{10}(M)$). The curves are the fitted quadratic equations to the data points, which are all significant at the $p < 0.001$ level (*see* text for detailed explanations). The units for μ_{dil}, μ_{PP}, and μ_{diln} are d^{-1}. M: μg C cell^{-1}.

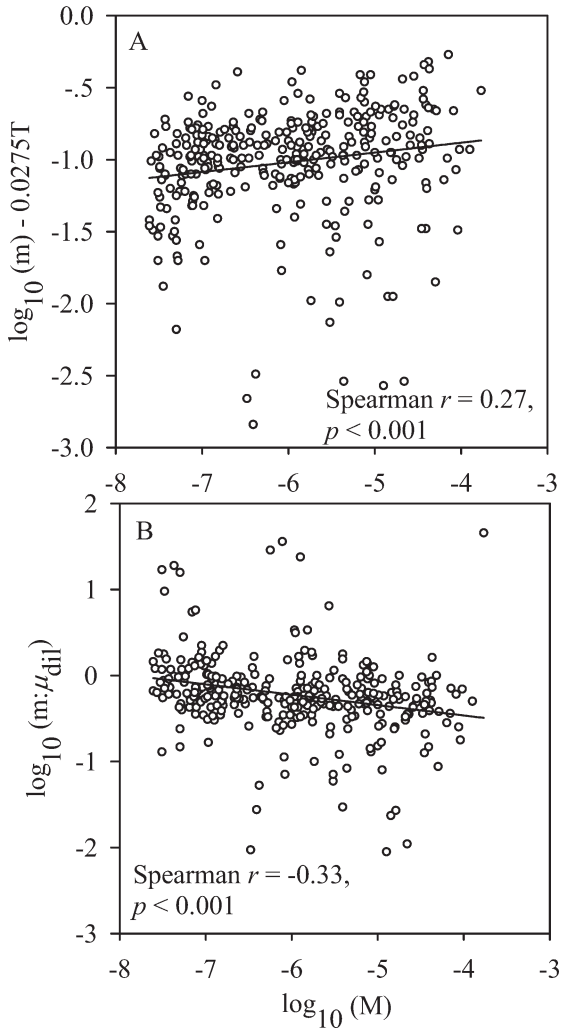

Fig. 3. Scatter plots of (A) temperature (T, °C) corrected log-transformed phytoplankton grazing mortality rate ($\log_{10}$ (m) − 0.0275T) based on the dilution data set and (B) log-transformed daily proportion of primary production grazed by microzooplankton ($\log_{10}$ (m : μ_{dil})) vs. $\log_{10}$ (M). The ratio m : μ_{dil} is a dimensionless variable. Units are m: d^{-1}; M: μg C $cell^{-1}$. The fitted straight line is an ordinary linear regression curve. The Spearman rank correlation coefficients and significance levels are also shown.

in pigment per cell before and after incubation) and uncertainties in satisfying the methodological assumptions (Landry and Hassett 1982; Dolan and McKeon 2005; Landry and Calbet 2005). In spite of the various problems, studies from US JGOFS cruises found a fairly good agreement of phytoplankton production rates between the ^{14}C method and the dilution technique (Calbet and Landry 2004), and therefore we think that both data sets are valuable in finding the underlying factors that affect phytoplankton growth.

Unimodal relationship between growth rate and size—In spite of the great variability of phytoplankton growth rates observed in both data sets, which is expected, as these studies cover a great range of geographic locations and environmental conditions and also include day-to-day variations, we find that a unimodal relationship appears to rise between log-transformed phytoplankton mass-specific growth rate and cell size after temperature standardization. Although some of the differences in the detailed curvilinear shape of the two data sets might be accounted for by methodology, the major cause of the difference should probably be different data sources. The curvilinear shapes are at least qualitatively similar in both data sets; phytoplankton growth rate increases with cell size when M is smaller than the modal size but decreases with size when M becomes larger. It is noteworthy that using the current approach, most of the calculated phytoplankton average sizes in the vast tropical and subtropical open oceans are smaller than the estimated modal size.

One potential factor that leads to such a unimodal relationship is that because M increases with ambient nutrient levels, it could be that M itself does not have any effect on growth rate but just reflects the effect of ambient nutrient levels. Acknowledging that this is probably true to some extent, we argue for several reasons that the effect of nutrients is relatively unimportant compared with that of cell size affiliated with taxonomic changes, although precisely quantifying the effect of nutrients on phytoplankton growth rate is difficult. Nutrient recycling, which can be represented by the *F*-ratio, supplies most of the nutrient requirement of marine phytoplankton in oligotrophic oceans (Eppley and Peterson 1979). The most abundant phytoplankter, *Prochlorococcous*, even lacks the ability to utilize nitrate (Moore et al. 2002). Therefore, even if nutrient levels are below detection limit in surface waters of the ocean, it does not necessarily mean that phytoplankton growth rate is very low. For example, *Prochlorococcus* grow at the rate of near one doubling per day in the oligotrophic western equatorial Pacific and subtropical North Pacific Ocean (Liu et al. 1997). Under such circumstances, the ratio $S/(S + K_N)$ has little utility. Furthermore, the diffusion constant increases with temperature, which can relieve the extent of nutrient limitation in warm, oligotrophic surface oceans (Mei et al. 2009). Using the data of μ_{diln}, which is supposed to approximate nutrient-saturated growth rate, the unimodal relationship still exists, with a significant positive correlation. Most of the values of $S/(S + K_N)$ calculated based on nitrate concentrations, which can be used as a rough index for the extent of nutrient limitation, are close to 1 in both data sets.

The observed unimodal relationship instead of a negative linear one is consistent with theoretical considerations that within the pico to nano range, phytoplankton growth rate should increase with size (Raven 1998; Raven et al. 2005). The mass-specific growth rate and nutrient (e.g., phosphate) uptake rate of the smaller cyanobacterium *Prochlorococcus* is often found to be lower than that of the larger *Synechococcus* (Zubkov et al. 2007; Chen et al. 2009). Within the eukaryotic component of ultraphytoplankton, Bec et al. (2008) found a similar unimodal relationship between growth rate and size. Apparently, the classic −0.25 rule cannot be directly applied to phytoplankton as a single group. It has been recognized that if assuming that maximal mass-specific growth rate (μ_m) can be described

as $\mu_m = a \times M^{-0.25}$ within a single phylogenetic group, larger phytoplankton especially diatoms usually possess a much higher a compared with smaller cells (Raven et al. 2005; Irwin et al. 2006) because of characteristics such as the vacuole, storage capacity, vertical migration, and surge uptake of nutrients (Stolte and Riegman 1995; Villareal et al. 1999; Verdy et al. 2009).

Besides the difference in using the temperature correction and in data sets themselves, another cause of the difference in the conclusions drawn between the present study and Marañón et al. (2007) is probably due to the different emphasis. We focus on the mass-specific growth rate, while Marañón et al. (2007) emphasized the cell-specific production rate. The scaling exponent of the mass-specific growth rate with size is 0.1 in fig. 1 of Marañón et al. (2007), which does not differ significantly from the scaling exponent (0.07) in our ^{14}C data set. However, such a linear model might overlook the subtle nonlinear relationships between mass-specific growth rate and cell size and give a misinterpreted impression that the mass-specific growth rate does not have any relationship with cell size. Other studies, such as Tang (1995) and Litchman et al. (2007), did not include any prokaryotic picoplankton, and therefore both negative and zero scaling exponents are possible in their data sets, in which most phytoplankton sizes might be larger than the modal size. Because of the great importance of picophytoplankton in the ocean, we conclude that the unimodal relationship is most appropriate in describing the scaling relationships between mass-specific growth rate and cell size.

The evolutionary basis for the unimodal relationship between phytoplankton growth rate and cell size might be related with several selective forces such as nutrient limitation, grazing, high light, and ultraviolet radiation (UVR). Extremely low nutrient availability in surface waters of the oligotrophic, open ocean might drive dominant picophytoplankton cells evolving to reduce the energy allocation to size-scalable components and decrease their maximal attainable growth rate as a trade-off associated with the success being able to cope with low nutrient availability (Raven 1998). There is no benefit for picophytoplankton to grow fast in a nutrient-scarce environment, as their grazing loss rate is not high. Further, small cells are more vulnerable to photoinactivation by high light or UVR than large cells (Key et al. 2010). When nutrient availability and average cell size increase, the size-scalable fraction increases, and maximal attainable growth rate increases to some point where the fraction of the size-scalable component does not constrain the maximal attainable growth rate but other factors, such as the thickness of the diffusion layer, ratio of surface area to volume, and the package effect, start to limit the step of nutrient uptake and light acquisition and reduce the maximal attainable growth rate (Raven 1998; Mei et al. 2009; Verdy et al. 2009).

The increasing phase in the unimodal relationship between phytoplankton growth rate and cell size might be also related with the evolutionary race between predator and prey (Smetacek 2001). High growth rate may act as a defense strategy in marine phytoplankton to offset the effect of grazing. Compared with freshwater or terrestrial ecosystems, the uniqueness of the marine ecosystem is that phytoplankton biomass is limited mostly by grazing, especially in the open ocean, with most of the essential nutrients supplied by zooplankton recycling (Landry et al. 1997). On average, microzooplankton and mesozooplankton consume 67% and 23%, respectively, of daily primary production in surface oceans (Calbet 2001; Calbet and Landry 2004), and therefore a total 90% of the daily primary production can be consumed by herbivores in the ocean. While in terrestrial and freshwater ecosystems, herbivores consume on average only 18% and 51% of primary production, respectively (Cyr and Pace 1993). As resource supply increases, phytoplankton size, biomass, and primary productivity all increase, and the system will support more grazers, which, in turn, exert higher grazing rates on the phytoplankton community (Fig. 3A; Irigoien et al. 2005). As a protection strategy, larger phytoplankton increase growth rate to offset the enhanced grazing mortality rate. The slower growth rate of smaller phytoplankton helps to explain why picophytoplankton abundances decrease in eutrophic waters, as they cannot balance increased loss rates such as grazing or flushing in these environments (Li 2002; Irwin et al. 2006; Follows et al. 2007). As a consequence, the overall microzooplankton grazing effect decreases as M increases (Fig. 3B), while other losses, such as sinking, should become more significant as a result of larger M.

Within an oceanic framework where grazing plays a major role, the dominance of small phytoplankton in unproductive waters where loss rate is low and the dominance and high growth rate of large phytoplankton in relatively productive waters with high loss rate appears to suggest a size-dependent trade-off between minimal resource requirement (R^*; Tilman 1982) and maximal growth rate in phytoplankton (Chen et al. 2009). In other words, phytoplankton either evolve to be small to attain a low resource requirement to survive in oligotrophic, open ocean or become large to grow fast to counteract the high loss rate in productive waters. Litchman et al. (2007) found positive correlations between maximal nitrate uptake rate and half-saturation constant as well as minimal cell quota, all of which increase with cell size (Litchman et al. 2007). The large size per se can also become a defense strategy against grazing (Thingstad et al. 2005). Strategies adopted by marine phytoplankton to dominate in different environments could be highly size related.

Implications for future work—Our results suggest that size-structured models assuming classic allometric growth of phytoplankton (i.e., phytoplankton growth rate decreases with cell size) may need to incorporate phylogenetic differences (Armstrong 1994; Irwin et al. 2006). In fact, some models have been quite successful in predicting geographic distributions of phytoplankton by assigning higher growth rates to larger phytoplankton (Follows et al. 2007).

We admit that, in our data sets, average cell size explains only a small proportion of total variability in measured phytoplankton growth rates even after teasing out the effects of temperature and nutrients. Knowledge about the

scaling of growth rate within and among phylogenetic groups existing in the real ocean is still quite limited. To improve the situation, further efforts should be made to measure size-related growth rates in different phylogenetic groups in natural phytoplankton assemblages. Pigment analysis based on high-performance liquid chromatography is a widely used method for studying phytoplankton community composition but does not provide any information on size structure in each group. Some recently developed techniques, such as fluorescent in situ hybridization, might be able to provide size information in each phylogenetic lineage (Not et al. 2004). Such techniques, combined with the dilution or some other technique that can estimate cell-specific production rates, will help us understand phytoplankton growth in the ocean. Further progress, by taking into account the effect of stoichiometry, can be made by estimating in situ cellular nutrient quotas, which are in turn related to cell-specific growth rates in situ.

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