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# Protists decrease in size linearly with temperature: *ca.* 2.5% °C$^{-1}$

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An inverse relationship between organism size and rearing temperature is widely observed in ectotherms ('the temperature–size rule', TSR). This has rarely been quantified for related taxa, and its applicability to protists also required testing. Here, we quantify the relationship between temperature and mean cell volume within the protists by a meta-analysis of published data covering marine, brackish water and freshwater autotrophs and heterotrophs. In each of 44 datasets, a linear relationship between temperature and size could not be rejected, and a negative trend was found in 32 cases (20 gave significant negative regressions, $p < 0.05$). By combining 65 datasets, we revealed, for each 1 °C increase, a cell-size reduction of 2.5% (95% CI of 1.7–3.3%) of the volume observed at 15 °C. The value did not differ across taxa (amoebae, ciliates, diatoms, dinoflagellates, flagellates), habitats, modes of nutrition or combinations of these. The data are consistent with two hypotheses that are capable of explaining the TSR in ectotherms generally: (i) resource, especially respiratory gas, limitation; and (ii) fitness gains from dividing earlier as population growth increases. Using the above relationship we show how changes in cell numbers with temperature can be estimated from changes in biomass and *vice versa*; ignoring this relationship would produce a systematic error.

**Keywords:** cell size; primary production; protozoa; phytoplankton; model

## 1. INTRODUCTION

The widespread ecological and economic implications of organism size are well known (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown & West 2000). In protists, for example, size affects sedimentation rate, feeding pressures from zooplankton, ability to capture prey and metabolic rate (Sournia 1982; Raven & Kubler 2002). Cell size also correlates with protist production, as production rate can be determined as the product of biomass and specific growth rate, $\mu$.

As protists play important roles in virtually all aquatic environments, assessing the impact of temperature on protist production is essential to understanding the functioning of many ecosystems. However, while the effects of temperature on growth and grazing are well established (e.g. as $Q_{10}$ values; Eppley 1972; Hansen *et al.* 1997), size changes are rarely considered in ecological models of production (Montagnes & Lessard 1999; Brush *et al.* 2002). To establish parameter values for models of production, the relationship between the size of a wide range of protists and ambient temperature needs to be assessed comprehensively and quantitatively.

In the temperature range normally encountered by a genotype or population of an ectothermic species (zone N, figure 1), there is usually an inverse relationship between rearing temperature and final body size (the 'temperature–size rule', TSR; Atkinson 1994; Atkinson & Sibly 1997). Inverse-size responses were observed, for example, in 83% of 109 datasets (Atkinson 1994), which included bacteria, protists, metazoa and metaphyta. An inverse relationship has also been commonly observed between temperature and metazoan cell size (Azevedo *et al.* 2002) and offspring size (Atkinson *et al.* 2001).

However, a simple pattern of size response, such as the TSR, can be hard to detect, even under controlled experimental conditions. For example, at low sublethal temperatures (zone L, figure 1) a further decrease can cause a reduction in size. This occurs below 10 °C for the ciliate *Euplotes balteatus*, which is presumably adapted to the higher temperatures of Florida, from where it was collected (Lee & Fenchel 1972). Such effects are most likely to occur under conditions that are so cool that population growth is prevented. At high sublethal temperatures (zone H, figure 1), a wide range of responses has been observed (between lines I and II, figure 1). For instance, in some diatoms, vegetative enlargement occurs at high temperatures (line I, figure 1) to increase viability without inducing sexual reproduction (see Gallagher 1983; Nagai *et al.* 1995; Montagnes & Franklin 2001). However, reductions in size (line II, figure 1) may be more common for ectotherms at high temperatures, as resource availability fails to keep up with increased metabolic demands, as enzymes become denatured and/or as membranes undergo phase transitions (Cossins & Bowler 1987; Criddle *et al.* 1997). At high sublethal temperatures, the usual increase in specific growth rate with temperature can be reversed, as occurred concomitantly with vegetative enlargement in a study of *Coscinodiscus* sp. (Montagnes & Franklin 2001). Quantitative comparisons between datasets will, therefore, be confounded if extreme temperatures (zones L and H, figure 1) are included in some studies but not in others. In this study we used

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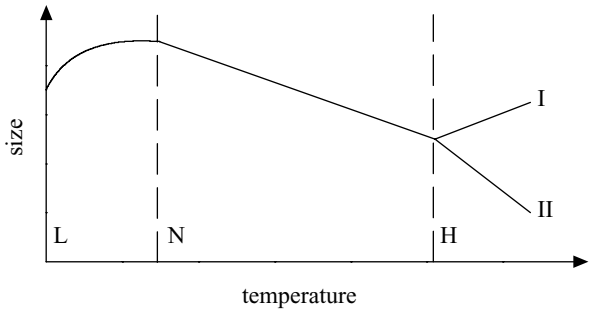


Figure 1. Plasticity of maximum size in response to rearing temperature in ectotherms: a proposed general relationship. At extremely low temperatures (zone L), size increases with increasing temperature. In the thermal range normally encountered by a population or genotype (zone N), an inverse relationship between size and temperature is expected. At extremely high temperatures (zone H) the response is more variable, and size may increase (line I) or decrease (line II) with increasing temperature. See § 1 for further discussion.

population-growth criteria to exclude extreme temperatures (see § 2), and thus focused on zone N (figure 1), where a constant inverse response was sought.

Early studies of protist species found a phenotypically plastic size response, which was usually inversely related to temperature (reviewed in Atkinson 1994). More recently, an inverse relationship was observed in several, but not all, diatoms studied by Montagnes & Franklin (2001), yet other studies on various protists have found either a positive relationship or no clear size response to temperature (Baldock *et al.* 1980; Thompson *et al.* 1992).

This paper, therefore, seeks to establish the extent to which inverse or positive temperature–size relationships occur, and the shape of these relationships, by a meta-analysis of published data covering a diverse range of marine, brackish water and freshwater autotrophs and heterotrophs. From this analysis we derive a single predictive relationship that should improve our ability to predict protist production. Finally, we suggest two possible reasons for this response that could apply widely to protists and other ectotherms.

## 2. MATERIAL AND METHODS

Data on size responses to temperature were extracted from tables or enlargements of figures in the published literature. To avoid confounding effects of other factors, such as light, nutrients and predation, we excluded studies in which temperature was not varied independently of other variables. Cases of obvious resource limitation were excluded. Only measurements of cell size made during the log growth phase were used, and when a range of conditions was studied, those giving maximum growth rate were selected. Extreme low temperatures were excluded by accepting data only where the specific growth rate was greater than 0. Extreme high temperatures were excluded by accepting data only where the specific growth rate did not decline with temperature. This method for eliminating extreme values accounted for differences in thermal tolerances between species, and, by selecting a temperature-limited growth range, avoided temperatures at which severe resource limitation occurred.

To allow comparison between studies, data were converted to cell volumes ($\mu m^3$) by assuming standard geometric shapes (Hillebrand *et al.* 1999; Montagnes & Franklin 2001) or, where size measurements were unavailable, by using conversion factors from dry weights or cell carbon (Gates *et al.* 1982; Montagnes *et al.* 1994).

The linearity of the relationship between cell volume and temperature was tested using iterative curve-fitting software (SIGMAPLOT v. 5, SPSS, Chicago, IL) to fit a three-parameter power equation to the data as follows:

$$V = a\text{Ø}^b + c,$$

where $V$ is the volume of a cell, Ø is the temperature (°C) and $a$, $b$ and $c$ are constants. We used $t$-tests to examine whether the predicted exponent $b$ significantly differed from unity (Zar 1974; Montagnes & Lessard 1999; Montagnes & Franklin 2001). When a linear relationship could not be rejected, linear regression techniques were used to fit straight lines between the cell volume and temperature—testing for significant slopes using $t$-tests. The regression coefficient or slope, $a$, was the thermal sensitivity of cell volume.

Then, to obtain a single predictive relationship for all datasets for which a regression coefficient could be calculated, we scaled the data; this took account of the 2300-fold variation in mean volume. To achieve this we divided the regression coefficient, $a$, for each dataset by the cell volume predicted for a common reference temperature (15 °C, $V_{15}$) from the same dataset. This reference temperature (15 °C) was chosen so as to be within the temperature ranges of as many studies as possible to allow estimation of each reference cell volume by interpolation of each fitted straight line.

The effects of mode of nutrition ('trophy': heterotrophy, autotrophy) and salinity (freshwater, brackish, marine) on $a/V_{15}$ were examined using a general linear model (GLM; MINITAB v. 13.2, Minitab Inc.). Some of the five major taxonomic groups in the total dataset were largely or totally confined to particular salinities or modes of nutrition (e.g. the diatoms and dinoflagellates were mainly marine autotrophs; all amoebae were heterotrophs), producing strong associations between taxon and salinity and/or mode of nutrition. The effect of 'taxon' (amoebae, ciliates, diatoms, dinoflagellates, other flagellates) was therefore examined in a separate GLM. Mean (± 1 s.e.) relative thermal sensitivities of the cell volume were calculated for each combination of taxon, salinity category and mode of nutrition (ecological taxonomic category). To ensure that apparent differences between categories did not rely on datasets derived from single studies, whose species would have experienced similar experimental regimes, a GLM was performed to compare relative thermal sensitivities among those ecological taxonomic categories whose datasets were derived from more than one study, with 'study' nested within the ecological taxonomic category.

## 3. RESULTS

Forty-four datasets showing size responses to temperature contained sufficient data points ($n = 4$ or more) to allow tests for curvilinearity. It was not possible to reject statistically a linear regression model in favour of a curvilinear model for any of these datasets (all $p > 0.05$). Twenty of these regressions showed a significant negative linear relationship between cell volume and temperature, and one showed a significant positive relationship (see electronic Appendix A available on The Royal Society's Publications Web site).

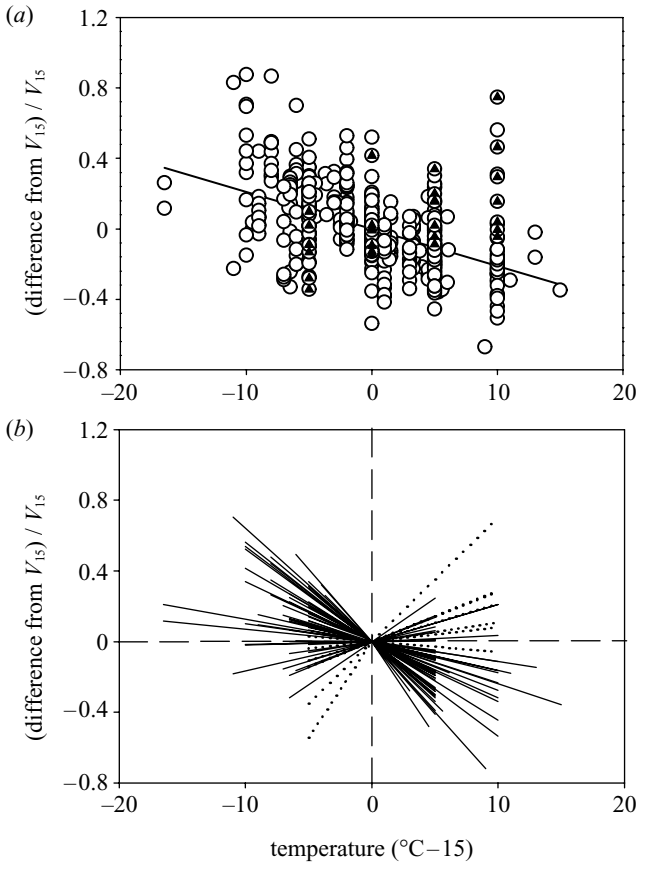


Figure 2. The relationship between protist cell volume and temperature. (*a*) Each of the 455 measurements from 72 datasets is expressed as the difference from the volume at 15 °C ($V_{15}$) divided by $V_{15}$ in the respective dataset. Temperature is expressed as the difference from 15 °C (see electronic Appendix A). Data from Thompson *et al.* (1992) (see § 3 for further discussion) are represented by solid triangles. (*b*) The distribution of relative thermal sensitivities of cell volume ($a/V_{15}$ = regression coefficient of cell volume against temperature, divided by cell volume at 15 °C). Each of the 72 regression lines is constrained to pass through the origin. Regression lines from Thompson *et al.* (1992) are represented by dotted lines (see § 3 for further discussion).

All the datasets for which a (linear) regression coefficient could be calculated and that included 15 °C were then examined to assess whether a general relationship existed. This increased the number of datasets to 72, comprising 455 data points. The regression coefficients were more steeply negative for larger species, but became independent of log species size when divided by $V_{15}$ in the respective datasets ($F_{1,68} = 0.20$, $p = 0.66$). The mean (± s.e.) relative thermal sensitivity of cell volume ($a/V_{15}$) for the 72 datasets was –0.020 °C$^{-1}$ (± 0.004). This value changed to –0.023 °C$^{-1}$ (± 0.004) when the regression coefficients were weighted by the number of data points used to calculate each one (see electronic Appendix A). The relationship between relative thermal sensitivity of cell volume and temperature for all datasets (figure 2*a*) did not deviate from linear ($p > 0.4$).

The significant positive regression ($a/V_{15} = 0.070$) and five of the non-significant positive trends came from a single study, which differed from the others in that, apparently, more air was bubbled into vessels as the temperature increased (Thompson *et al.* 1992, see § 4). Exclusion of data from this study changed the mean (± s.e.) relative thermal sensitivity of cell volume to –0.025 °C$^{-1}$ (± 0.004) (unweighted data) and –0.026 °C$^{-1}$ (± 0.003) (weighted data) for the remaining 65 datasets.

The mean (± s.e.) relative thermal sensitivity of cell volume of the 20 datasets that gave significant linear negative regressions was –0.040 (± 0.006) °C$^{-1}$.

There were no significant effects of salinity, trophy, salinity × trophy interaction or taxonomic group on $a/V_{15}$ (GLM, $p > 0.27$ for each factor and for the interaction). The mean relative thermal sensitivities were negative for 11 out of the 12 ecological taxonomic categories (figure 3). The other category (heterotrophic freshwater amoebae) showed relative insensitivity to temperature, and was based on a single study (figure 3). The three marine autotrophic taxa whose relative thermal sensitivities were derived from more than one study (figure 3) did not differ in their relative thermal sensitivities (GLM, $F_{2,16} = 0.44$, $p = 0.65$).

## 4. DISCUSSION

### (a) *The nature of the temperature–size relationship*

We have quantified an inverse relationship between cell volume and temperature in a wide variety of aquatic protists: for every 1 °C increase, cells reduce in volume by *ca.* 2.5% of their cell volume at 15 °C.

This inverse relationship is consistent with the TSR, which applies to body size in ectotherms generally (Atkinson 1994; Atkinson & Sibly 1997) and may also apply to the sizes of metazoan cells (Atkinson 1994; Azevedo *et al.* 2002). However, few attempts have been made to quantify this relationship for groups of species (Chrzanowski *et al.* 1988; Montagnes & Franklin 2001). The present analysis appears to be the first study to derive a single predictive relationship that can be applied to diverse protist taxa, both autotrophic and heterotrophic, from various aquatic habitats. Such a relationship could be usefully incorporated in some ecosystem simulation models, and its recognition is a first step towards addressing its underlying causes.

The size responses appeared to be mainly caused by phenotypic plasticity rather than evolutionary change because most studies used either single clones or measurements made after only a few days at the experimental temperatures. Furthermore, a straight-line fit between cell volume and temperature appears to describe the relationship well for most species. While deviations from linearity were not expected in datasets with only a few points, the lack of deviation in any of the 44 datasets, including some with 25 points (see electronic Appendix A), or in the combined dataset supports the case that the relationship is generally linear.

To produce a single predictive relationship for all the protists, we chose cell volume at 15 °C as the reference value by which thermal sensitivities of volumes were divided. Another approach, used by Montagnes & Franklin (2001), is to divide the regression coefficient of cell volume against temperature by the *mean* cell volume of the respective dataset. Our use of volume at a single reference temperature has two advantages over the use of mean cell volume. First, the value of mean cell volume depends on

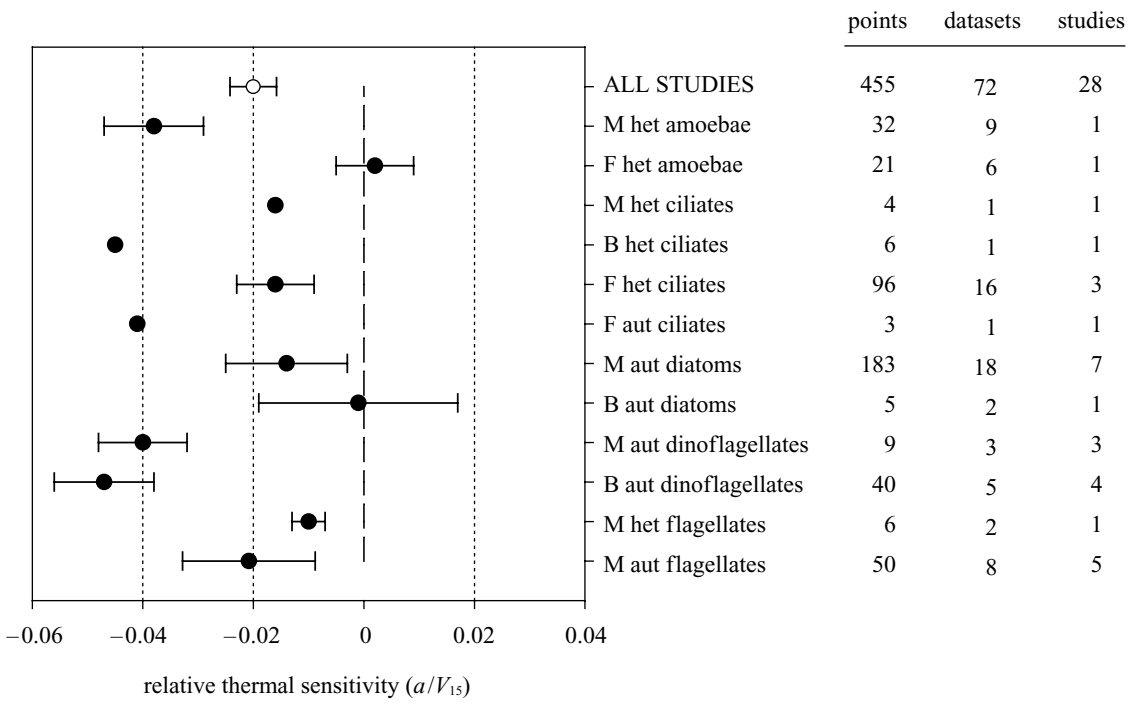


Figure 3. Mean (± s.e.) relative sensitivities of cell volume to temperature for all studies combined and for each of the 12 ecological taxonomic categories. The relative thermal sensitivity for each dataset was calculated as the regression coefficient of cell volume against temperature divided by the cell volume at a reference temperature (15 °C). The numbers of data points, numbers of datasets and numbers of studies contributing to the data in each category are shown. Abbreviations: F, freshwater; B, brackish; M, marine; aut, autotrophic; het, heterotrophic.

the choice of temperatures used in the experiment, and some studies may have had treatments mainly near one or other end of a species' thermal range (figure 1): $a/V_{\mathrm{mean}}$ is therefore a reference value that can vary simply with the choice of temperatures used in the different studies. Second, it is more pragmatic (in terms of time and resources) to predict the rate of production of a particular protist community when measurements need be made at only a single temperature, rather than over several temperatures to derive a mean. Despite these differences in the calculation of thermal sensitivity of cell volume, the means (± s.e.), estimated to the nearest 0.1%, were indistinguishable.

The mean relative thermal sensitivity of cell volume for the 20 datasets that showed significant ($p < 0.05$) negative regression coefficients was 4.0% (± 0.6%) of the reference cell volume $^{\circ}C^{-1}$. This value is similar to the 3.9% (± 0.8%) obtained by Montagnes & Franklin (2001) with a smaller sample (five diatoms and two flagellates). A negative trend was observed in 32 out of the 44 datasets, but the lack of a significant regression in more than half of the total datasets reduced the overall mean thermal sensitivity of cell volume. The lack of a significant relationship may reflect variation in the responses to temperature, or in some cases could have been caused by the inclusion of extreme low or high temperatures, which generate unusual responses (figure 1). Our use of specific growth rate to exclude extreme temperatures could not guarantee that all unnaturally low and high temperatures were excluded.

To derive predictive parameter relationship(s) for cell-volume sensitivity to temperature that could be applied to protists more generally, we included all studies for which an average regression coefficient could be calculated. The total sample of 455 data points from diverse taxa with differing modes of nutrition and habitats showed on average a reduction of 2.0% of cell volume at 15 °C per 1 °C. However, with the removal of one study, in which the rate of air bubbling appears to have been increased with increased temperature (see § 4b), this value changed to 2.5% (95% CI of 1.7–3.3%). The value that best reflects the overall reduction in size with temperature will depend on the extent to which experimental error or the inclusion of unnaturally low or high temperatures altered the regression coefficients in the datasets. The mean relative thermal sensitivity of cell volume did not differ significantly ($p > 0.05$) between ecological categories (salinities, modes of nutrition) or among the five taxonomic groups. Neither did it vary across the three categories of marine autotrophs whose datasets were derived from more than one study.

As the number of studies contributing to the datasets of individual ecological taxonomic groups was small (seven categories contained data from just single studies), it was not possible to distinguish real differences between ecological taxonomic groups from differences caused by variations in experimental protocols between individual studies. Therefore, more studies are required to determine any differences between ecological taxonomic groups.

The cell-volume change appears to be a response to temperature in all taxa, even in diatoms whose cells typically decrease in size with successive cell cycles irrespective of temperature (Edlund & Stoermer 1997). The idea that the inverse relationship in diatoms arose solely from the completion of more cell cycles at increased temperatures was evaluated by Montagnes & Franklin (2001); they found no evidence to support it from their experiments.

### (b) *What causes the temperature–size relationship?*

Several causes of the inverse relationship between organism size (including protist cell size) and temperature have been proposed, yet no single explanation is widely accepted (Atkinson 1994; Atkinson & Sibly 1997; Montagnes & Franklin 2001).

The possibility that the decrease in cell size with increasing temperature is an adaptation to reduce sinking rate could apply to planktonic protists, but cannot be applied to ectotherms in general (Atkinson 1994). This hypothesis has recently been evaluated quantitatively by applying Stokes' law to diatom data, but no differences in response to temperature were found between planktonic and benthic species (D. Franklin, personal communication). Next, we discuss two other hypotheses with potentially widespread application for which our analysis provides suggestive, rather than conclusive, evidence.

The first hypothesis assumes that the ratio of supply to potential consumption of limiting resources (e.g. energy, oxygen for heterotrophs, carbon dioxide or oxygen for autotrophs, nitrogen, phosphorus) is reduced by increased temperature; a reduced size can then compensate for this since resources can be acquired, and used in growth, more effectively in smaller than in larger cells (Margalef 1954; Von Bertalanffy 1960; Atkinson & Sibly 1996, 1997; Raven 1998; Woods 1999). An increased temperature reduces the concentrations of dissolved oxygen and carbon dioxide in water, and their rates of diffusion are relatively insensitive to warming ($Q_{10}$ *ca.* 1–2). By contrast, unrestrained metabolism is generally more sensitive to warming ($Q_{10}$ *ca.* 2–3) (Von Bertalanffy 1960; Woods 1999), which in autotrophs could increase the need for active uptake of carbon. Consequently, at an increased temperature the supply of these gases to the cell surface is reduced relative to the increased potential demand. Thus, at increased temperature, rate of diffusion, being relatively insensitive to temperature, could limit the rate at which these gases are replenished in the water immediately surrounding the cells. If other resources are limiting, temperature will again have little direct effect on their acquisition, but warming will still increase the rate at which resources are needed for both routine metabolism and for achieving maximum growth rate. Hence, warming will increase the demand for resources. One way to compensate for this is to reduce size, and hence increase the ratio of surface area (for resource uptake) to metabolizing cell mass.

Margalef (1954) did not consider this hypothesis to be important for the chlorophyte *Scenedesmus obliquus* because the ratio of oxygen assimilation to respiration declined with increased temperature despite the reduction in cell size. However, this merely begs the question, by how much more would the ratio have declined if cell size had not reduced?

In contrast to the conclusion of Margalef (1954), an observation from our data analysis suggests that exceptions to the TSR may be generated if these resource limitations are removed or reduced. Specifically, we discovered only one study (Thompson *et al.* 1992) that reported adjusting the rate at which air was bubbled through experimental flasks to maintain a constant pH, thereby preventing carbon limitation, which would otherwise have been likely since the cultures had 24-hour illumination. This study also produced the only significant positive regression between cell volume and temperature (for the diatom *Phaeodactylum tricornutum*) and five other positive (though not significant) trends (see electronic Appendix A). We assume that the delivery of air bubbles through the water body was increased with increased temperature to replenish carbon dioxide faster at the higher temperatures, thus compensating for faster consumption. Thus, we suggest that, by delivering air bubbles faster to the cells, the experimenters would have maintained the partial-pressure gradient in the immediate vicinity of the cell surfaces.

If the demand for a resource is generally more sensitive to temperature than is the supply of that resource, this would then cast doubt on the assumption that resources are non-limiting at all temperatures, both in experiments and in the field. Merely providing and maintaining a surfeit of food and nutrients may not actually prevent limitation of *all* resources (e.g. respiratory gases) at increased temperature. This argument implies, for instance, that air bubbling *per se* may not always maintain a non-limiting supply at the cell surface, and may need to be accelerated with increased temperatures. The same principle applies in the field: even when the growth of a heterotroph is not food-limited at any temperature, oxygen limitation is more likely at increased temperature. Even if increased temperature yields daytime supersaturation of oxygen owing to photosynthesis, the hypothesis predicts that without a size reduction these heterotrophs could be oxygen limited during warm nights owing to increased net oxygen consumption in the habitat.

A second hypothesis to account for the inverse temperature–size relationship in protists is derived from evolutionary theory. Rapid reproduction is typically advantageous. However, there is additional selection for earlier reproduction (completion of cell cycle in protists), which increases as population growth increases, since offspring 'born' early will form a larger fraction of the total population than those born later, and hence will have a higher Darwinian fitness (Lewontin 1965). This has been called the 'compound interest hypothesis' owing to its parallel with putting money quickly into a high-interest account to accumulate compounding interest (Stearns 1976; Atkinson 1994). This accelerated completion of the cell cycle will occur even at the expense of cell size.

When resources are abundant and densities are low, an increase in temperature in the range normally encountered will increase population growth. This increase was found in all our datasets because we accepted, as a way of excluding thermal extremes, only positive growth rates that increased with temperature. Thus, the reduction in cell size at increased temperatures that we observed could be an adaptive plastic response to conditions that indicate increasing population growth rate.

### (c) *A potential application of the temperature–size relationship*

The inverse relationship between size and temperature will extend the predictions made by some dynamic ecosystem simulation models of aquatic primary production. Many such models begin with the calculation of the

maximum attainable daily rate of production from forced environmental variables, most commonly temperature (Brush *et al.* 2002; Moisan *et al.* 2002). This maximum rate of production is then reduced by factors that prevent the phytoplankton from realizing this hypothetical maximum, such as day length, light intensity and nutrient concentrations (Brush *et al.* 2002). Simulation models commonly use formulations for the response of maximum specific growth rate to temperature, such as the 'Eppley curve' (Eppley 1972) or modifications of this for particular ecosystems or taxa (Brush *et al.* 2002; Moisan *et al.* 2002). The production rate can then be determined as the product of biomass and specific growth rate. However, biomass is the product of cell number and specific cell mass. Assuming that the cell volume : cell mass ratio is temperature-invariant, then the temperature–size relationship provides a quantitative link between (i) temperature effects on maximum production, and (ii) temperature effects on maximum numbers. Thus the temperature–size relationship may be applied to predict changes in cell numbers with temperature from biomass estimates made at several temperatures and cell numbers at one temperature. Moreover, if the temperature–size relationship is ignored, predictions of temperature effects on production based on a biomass estimate at a single temperature and cell numbers at several temperatures would overestimate potential production by *ca*. 2.5% of that at 15 °C with every 1 °C increase in temperature. Of course, this argument applies to short-term warming or cooling at particular locations. By contrast, comparisons over large geographical distances (e.g. poles versus tropics) or timescales (e.g. winter versus summer) will be influenced more by changes in species composition than by phenotypic plasticity.

In conclusion, we have established that an inverse relationship between protist cell size and temperature, resulting mainly from a plastic phenotypic response, is widespread. We have quantified this relationship, and found that it does not differ among diverse taxa, habitats or modes of nutrition. The relationship has the potential to improve predictions in some aquatic-ecosystem simulation models. The data are consistent with two hypotheses that are capable, in principle, of explaining the TSR in ectotherms in general. The extents to which resource limitation and 'compound interest' affect the temperature–size relationship in protists will determine when our broad 2.5% prediction should be applied, and when and how it should be modified. It is, therefore, ecologically important that these hypotheses are tested.

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