

## REVIEW

# Using $Q_{10}$ : Can growth rates increase linearly with temperature?

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**ABSTRACT:** For autotrophic and heterotrophic protists, we reviewed growth rate versus temperature data (92 cases, 74 species, 36 studies), using non-linear curve-fitting methods to determine whether relationships were linear. Of the 92 cases, 67 contained sufficient data for analysis; 61 did not significantly differ from a linear response (mean slope:  $0.064 \pm 0.005 \text{ d}^{-1} \text{ } ^\circ\text{C}^{-1}$ ). Of the 25 cases that were not statistically analysed, 18 appeared linear. The mean slope of the 79 data sets considered to be linear was  $0.07 \pm 0.005 \text{ (d}^{-1} \text{ } ^\circ\text{C}^{-1})$ . We suggest that growth rate usually responds linearly to temperature, the use of  $Q_{10}$  may be inappropriate, and a  $Q_{10}$  of 2 may arise due to this linear relationship and inappropriate experimental design.

**KEY WORDS:** Arrhenius · Ciliate · Diatom · Dinoflagellate · Flagellate · Meta-analysis · Model · Protist

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It is commonly assumed that growth rates increase exponentially with temperature. However, for aquatic, free-living protists there are many data suggesting that a linear response of growth rate to temperature is the more parsimonious interpretation. Undoubtedly, underlying processes (e.g. respiration) can have exponential responses, but here we suggest that the application of exponential (e.g.  $Q_{10}$ ) or power functions to model growth rate for aquatic protists may be incorrect.

It is well established that the specific growth rate ( $\mu$ ) of protists increases with temperature, within a defined temperature range (Fig. 1). Most aquatic ecologists expect this rate to increase exponentially with temperature over the portion of the response curve that excludes thermal extremes (e.g. Eppley 1972) (see Fig. 1), and the  $Q_{10}$  model (Van't Hoff 1884) is often employed to describe this and many other responses:

$$Q_{10} = (\mu_2/\mu_1)^{10/(\theta_2 - \theta_1)} \quad (1)$$

where  $\mu_2$  and  $\mu_1$  are growth rates at 2 temperatures,  $\theta_2$  and  $\theta_1$ , respectively. Many processes follow this model, often with a  $Q_{10}$  near 2 (Cossins & Bowler 1987). Alter-

natively, power functions can be used to model the response of growth rate to temperature (see Ahlgren 1987). But in either case (power or exponential functions), it is assumed that there is a greater than first order dependence of growth rate on temperature.

However, growth rate is a combination of processes, the sum of which might not yield an exponential- or power-response. There is, in fact, a history of reports suggesting a linear response of rate processes to temperature (see Bělehrádek 1926, Cossins & Bowler 1987), and there are strong suggestions that protistan growth rate increases linearly with increasing temperature (e.g. Ahlgren 1987, Thompson et al. 1992, Weisse & Montagnes 1998, Montagnes & Lessard 1999, Strzepek & Price 2000, Montagnes & Franklin 2001). Here, we take a parsimonious approach and test whether existing data deviate significantly from the mathematically simplest form of a relationship (i.e. a linear one). We do this by testing linearity versus a power function, which is more tractable than testing an exponential relationship, and results in a similar conclusion (i.e. the response is, or is not, curved).

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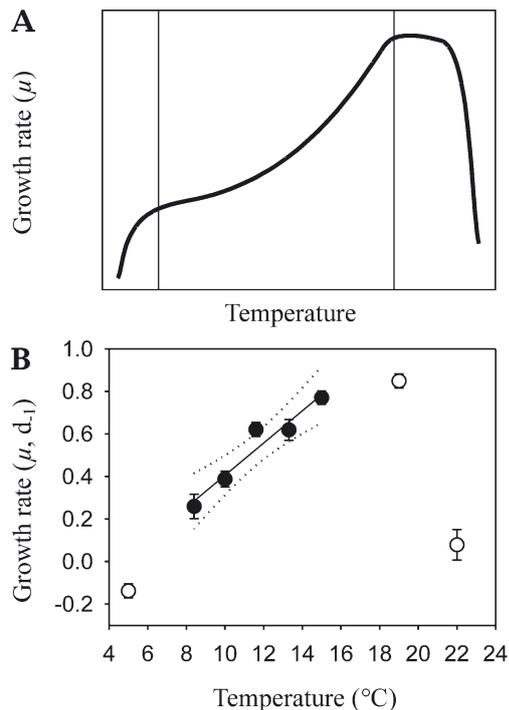


Fig. 1. (A) A generalised description of the response of specific growth rate ( $\mu$ ) to temperature. At low temperatures (below left vertical line), growth rate decreases rapidly, due to stressful conditions. At high temperatures (above right vertical line) growth rate does not increase and then decreases, due to stressful conditions. Between the 2 vertical lines, growth rate increases with temperature; this is typically expected to be an exponential increase (see text), and this is the data region used to determine the growth-temperature response (see text and Table 1). (B) An example of protistan specific growth rate versus temperature (data for the ciliate *Strombidinopsis multiauris*, modified from Montagnes & Lessard 1999), indicating the choice of data, as described above and 1 example of a linear relationship. Open data points were not used in the regression; solid points were used in the regression; the solid line is the linear response through the solid points and the dotted lines are 95% CIs (see Table 1 for parameters of this fit)

Specific growth rate ( $\mu$ ) data were collected from the literature;  $\mu$  being the slope of  $\ln$  cell-numbers versus time. Only studies stating that protists were grown under growth-saturating conditions ( $\mu_{\max}$ ) were used; i.e. conditions where light, nutrients, and/or food were considered to be non-limiting by the authors. A total of 92 data sets, representing 74 species from 36 studies, were examined, of which 28 were freshwater species, 53 were marine, and 11 were estuarine (Table 1). Temperature ranged from  $-1.5$  to  $30^{\circ}\text{C}$ . In all, 67 of the data sets were re-analysed by extracting data from tables or graphs, or obtaining data directly from the authors. Where values could not be obtained, growth-response shape was determined from written statements or visual interpretation.  $Q_{10}$  values were recorded, where available.

A response was evaluated for data where growth rate was positive and increased with temperature; data were not included when growth rate was adversely influenced at high and low temperatures (see Fig. 1). Data were fit to a power function (Eq. 2) using non-linear curve-fitting methods (SigmaPlot 5 and SigmaStat 2.03; SPSS):

$$\mu_{\max} = a\theta^b + c \quad (2)$$

where  $\mu_{\max}$  is growth rate ( $\text{d}^{-1}$ ),  $\theta$  is temperature ( $^{\circ}\text{C}$ ),  $c$  is the theoretical value of  $\mu_{\max}$  at  $0^{\circ}\text{C}$ , and  $a$  and  $b$  are constants. The analysis provides asymptotic standard errors for the parameters and a power of the test. The error term associated with  $b$  was used to test the hypothesis  $b = 1$ ; i.e. the relation between  $\mu_{\max}$  and  $\theta$  is linear ( $t$ -test,  $\alpha = 0.05$ ,  $\text{df} = n - 3$ ); this follows established methods (Montagnes & Lessard 1999, Montagnes & Franklin 2001). When the response did not differ from linearity, least squares regression was used to determine the slope of the response ( $\mu_{\max}$  vs  $\theta$ ).

Of the 92 data sets (Table 1), 84 visually appeared to be linear, but only 12 studies explicitly mentioned a linear response. In all, 67 of the 92 data sets contained sufficient data for analysis ( $n > 3$ ); 61 of these were not significantly different from a linear response, and 1 was a significant power function with the exponent ( $b < 1$ , i.e. it was convex not concave). Of the 25 data sets that could not be statistically analyzed, 18 were linear, visually. The average slope from the 79 (61 + 18) data sets that were considered linear (statistically and visually) was  $0.070 \pm 0.005$  (SE) ( $\text{d}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ ). The average slope from the 61 data sets considered linear (statistically) was  $0.064 \pm 0.005$  ( $\text{d}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ ). A total of 52 data sets provided estimates of  $Q_{10}$  (assuming an exponential response); 34 of these were suitable for statistical analysis, and 29 were not different from a linear response. For these studies,  $Q_{10}$  was reported to range from 1.1 to 89.6 (mean = 2.7). Of the studies that provided  $Q_{10}$  estimates, 32 used the entire temperature range while 20 (38%) established  $Q_{10}$  from pairs of points.

Our analysis suggests that for protists, the predictive relationship between  $\mu_{\max}$  and temperature is typically linear, with an average slope of  $\sim 0.07$  ( $\text{d}^{-1} \text{ } ^{\circ}\text{C}^{-1}$ ). Although this may not be surprising for data sets containing few points, the studies with the greatest number of points ( $>10$ ) also showed good linear fits (Table 1). These findings, thus, indicate a simpler mathematical description than that previously provided, which assumed that protist growth rates increase as a power function or exponentially with temperature, and often quote a  $Q_{10}$  of 2 to 3 (e.g. Eppley 1972, Goldman & Carpenter 1974, Choi & Peters 1992, Lomas & Gilbert 1999). Admittedly, under some conditions the response of some protists may follow an exponential or power re-

Table 1. Species used to investigate the relationship between protist growth rate ( $\mu_{\max}$ ) and temperature ( $\theta$ ). Slope = the slope of the response ( $\mu_{\max}$  vs  $\theta$ ). n = number of data points used to assess the response. Power = power of the test for linearity; where power is not provided, the regression was not tested (i.e.  $n < 4$ ) or the response was not linear. Response = whether the response was linear (L) or a power function (P). When  $n < 4$ , data were visually examined to determine whether the relationship was linear; when it was considered linear, the slope was determined as above (see text for details). The slope is not provided when the response was considered to be a power function, either visually or statistically. Note: in 1 case (P-convex), the response was a power function but convex when viewed from below (i.e.  $0 < b < 1$ , see Eq. 2)

Species	Slope	n	Power	Response	Source
<b>Ciliates</b>					
<i>Balanion</i> sp.	0.118	4	0.5	L	Stoecker et al. (1983)
<i>Chilodonella uncinata</i>	0.073	3		L	Finlay (1977)
<i>Colpidium campylum</i>	0.085	3		L	Finlay (1977)
<i>Cyclidium glaucoma</i>	0.185	3		L	Finlay (1977)
<i>Favella</i> sp.	0.052	4	0.87	L	Aelion & Chisholm (1985)
<i>Favella</i> sp.	0.077	3		L	Stoecker et al. (1983)
<i>Loxocephalus plagius</i>	0.081	3		L	Finlay (1977)
<i>Paramecium aurelia</i>	0.070	3		L	Finlay (1977)
<i>Paramecium bursaria</i>	0.054	3		L	Finlay (1977)
<i>Pelagostrombidium fallax</i>	0.055	6	1.00	L	Müller & Geller (1993)
<i>Pseudobalanion planctonicum</i>	0.078	5	0.98	L	Müller & Geller (1993)
<i>Spirostomum teres</i>	0.017	3		L	Finlay (1977)
<i>Stentor polymorphus</i>	0.024	3		L	Finlay (1977)
<i>Strombidinopsis multiauris</i>	0.072	29	1.00	L	Montagnes & Lessard (1999)
<i>Strombidium sulcatum</i>	0.11	6	0.83	L	Martinez (1980)
<i>Tetrahymena pyriformis</i>	0.132	3		L	Finlay (1977)
<i>Tintinnopsis acuminata</i>		3		P	Verity (1985)
<i>Tintinnopsis vasculum</i>	0.069	3		L	Verity (1985)
<i>Urotricha farcta</i>	0.108	12	1.00	L	Weisse & Montagnes (1998)
<i>Urotricha furcata</i>		6		P	Müller & Geller (1993)
<i>Urotricha furcata</i> (Lake Constance Clone a)	0.081	9	1.00	L	Weisse & Montagnes (1998)
<i>Urotricha furcata</i> (Lake Constance Clone b)	0.063	15	1.00	L	Weisse & Montagnes (1998)
<i>Urotricha furcata</i> (Lake Constance Clone c)	0.074	12	1.00	L	Weisse & Montagnes (1998)
<i>Urotricha furcata</i> (Lake Constance)	0.075	12	1.00	L	Weisse & Montagnes (1998)
<i>Urotricha furcata</i> (Lake Schönsee)	0.070	12	1.00	L	Weisse & Montagnes (1998)
<i>Vorticella microstoma</i>	0.200	3		L	Finlay (1977)
<b>Dinoflagellates</b>					
<i>Alexandrium ostenfeldii</i>	0.019	4	1.00	L	Jensen & Moestrup (1997)
<i>Amphidinium klebsii</i>	0.025	5	0.84	L	Morton et al. (1992)
<i>Coolia monotis</i>	0.024	4	0.42	L	Morton et al. (1992)
<i>Gambierdiscus toxicus</i>	0.014	5	0.96	L	Morton et al. (1992)
<i>Gonyalux tamarensis</i>	0.016	7	0.97	L	Watras et al. (1982)
<i>Gonyalux tamarensis</i>	0.028	3		L	Langdon (1988)
<i>Gymnodinium catenatum</i>	0.048	4	0.53	L	Bravo & Anderson (1994)
<i>Heterocapsa triquetra</i>	0.025	5	1.00	L	Aelion & Chisholm (1985)
<i>Olisthodiscus luteus</i>	0.065	3		L	Langdon (1988)
<i>Ostreopsis heptagona</i>	0.016	4	0.70	L	Morton et al. (1992)
<i>Ostreopsis siamensis</i>	0.027	4	0.64	L	Morton et al. (1992)
<i>Oxyrrhis marina</i>	0.077	10	0.91	L	Kimmance (2001)
<i>Prorocentrum concavum</i>	0.023	4	0.40	L	Morton et al. (1992)
<i>Prorocentrum lima</i>	0.029	4	0.55	L	Morton et al. (1992)
<i>Prorocentrum mexicanum</i>	0.029	4	1.00	L	Morton et al. (1992)
<i>Prorocentrum minimum</i>		4		P	Lomas & Gilbert (1999)
<b>Flagellates</b>					
<i>Chroomonas salina</i>	0.07	4	0.77	L	Hobson (1974)
<i>Cryptomonas erosa</i>	0.036	4	0.94	L	Morgan & Kalff (1979)
<i>Cryptomonas ovata</i> var. <i>palustris</i>		3		P	Cloern (1977)
<i>Dunaliella tertiolecta</i>	0.075	5	0.55	L	Thompson et al. (1992)
<i>Dunaliella tertiolecta</i>	0.088	6	1.00	L	Eppley & Sloan (1966)

(Table continued on next page)

Table 1 (continued)

Species	Slope	n	Power	Response	Source
<b>Flagellates (continued)</b>					
<i>Isochrysis galbana</i>		4		P	Hobson (1974)
<i>Isochrysis galbana</i>	0.035	5	0.14	L	Thompson et al. (1992)
<i>Parahysomonas imperforata</i>	0.158	5	0.93	L	Choi & Peters (1992)
<i>Parahysomonas imperforata</i>		3		P	Choi & Peters (1992)
<i>Pavlova lutheri</i>	0.118	5	0.53	L	Thompson et al. (1992)
<b>Diatoms</b>					
<i>Acnantes</i> sp.	0.048	17	1.00	L	J. Waring (unpubl.)
<i>Amphiprora</i> sp.		6		P	Admiraal (1977)
<i>Asterionella formosa</i>	0.042	4	0.84	L	Suzuki & Takahashi (1995)
<i>Aulacoseira granulata</i>	0.028	4	0.51	L	Coles & Jones (2000)
<i>Chaetoceros calcitrans</i>	0.139	5	0.54	L	Thompson et al. (1992)
<i>Chaetoceros gracilis</i>	0.028	4	0.66	L	Thompson et al. (1992)
<i>Chaetoceros simplex</i>	0.098	5	0.48	L	Thompson et al. (1992)
<i>Chaetoceros</i> sp.		4		P	Lomas & Gilbert (1999)
<i>Cylindrotheca closterium</i>	0.084	17	1.00	L	J. Waring (unpubl.)
<i>Detonula confervacea</i>	0.037	4	0.72	L	Suzuki & Takahashi (1995)
<i>Leptocylindrus danica</i>	0.118	4	0.51	L	Verity (1982)
<i>Navicula arenaria</i>	0.067	4	0.94	L	Admiraal (1977)
<i>Nitzschia americana</i>		3		P	Miller & Kamykowski (1986)
<i>Nitzschia dissipata</i>	0.073	6	0.99	L	Admiraal (1977)
<i>Nitzschia seriata</i>	0.021	6	0.45	L	Smith et al. (1994)
<i>Nitzschia sigma</i>	0.012	6	0.91	L	Admiraal (1977)
<i>Phaeodactylum tricorutum</i>	0.088	5	0.96	L	Fawley (1984)
<i>Phaeodactylum tricorutum</i>	0.055	5	0.62	L	Thompson et al. (1992)
<i>Phaeodactylum tricorutum</i>	0.042	4	0.56	L	Li & Morris (1982)
<i>Pseudo-nitzschia pseudodelicatissima</i>	0.103	6	1.00	L	Lundholm et al. (1997)
<i>Skeletonema costatum</i>	0.064	4	0.71	L	Jørgensen (1968)
<i>Skeletonema costatum</i>		5		P-convex	Suzuki & Takahashi (1995)
<i>Skeletonema costatum</i>	0.080	5	1.00	L	Langdon (1988)
<i>Skeletonema costatum</i>		3		L	Yoder (1979)
<i>Stephanodiscus hantzschii</i>	0.061	4	0.95	L	Suzuki & Takahashi (1995)
<i>Thalassiosira nordenskioeldii</i>	0.025	5	0.99	L	Suzuki & Takahashi (1995)
<i>Thalassiosira pseudonana</i>		3		P	Guillard & Ryther (1962)
<i>Thalassiosira pseudonana</i>	0.108	5	0.86	L	Thompson et al. (1992)
<i>Thalassiosira rotula</i>	0.066	3		L	Krawiec (1982)
<i>Thalassiosira weissflogii</i>		3		P	Lomas & Gilbert (1999)
<b>Gymnoamoebia</b>					
<i>Acanthamoeba polyphaga</i>	0.252	3		L	Baldock et al. (1980)
<i>Amoeba algonquinensis</i>	0.024	4	0.60	L	Baldock & Berger (1984)
<i>Cochliopodium minus</i>	0.123	4	0.99	L	Baldock et al. (1980)
<i>Glaeseria mira</i>	0.136	4	0.48	L	Baldock et al. (1980)
<i>Saccamoeba limax</i>	0.083	4	0.64	L	Baldock & Berger (1984)
<i>Saccamoeba limax</i>	0.134	3		L	Baldock et al. (1980)
<i>Vanella</i> sp.	0.089	4	0.97	L	Baldock et al. (1980)
<i>Vanella</i> sp. 1	0.075	4	0.64	L	Baldock & Berger (1984)
<i>Vanella</i> sp. 2	0.044	4	0.95	L	Baldock & Berger (1984)
<i>Vexillifera bacillipedes</i>		3		P	Baldock et al. (1980)

sponse. However, if the average response of many studies is actually linear, our observations will have important implications for modelers who use exponential or power relationships, reputedly obtained from average estimates, to predict (see Davidson 1996) or scale (e.g. Tang 1995, Hansen et. al. 1997) growth rates.

There are also non-protistan examples of rate processes that exhibit a linear response to temperature, e.g. oxygen uptake by the Colorado potato beetle (Schmidt-Nielsen 1990), photosynthetic rate in leaves (Hochachka & Somero 1984), and metazoan development rate (Cossins & Bowler 1987). Thus, the linear

response is not only relevant to protistan growth rate, but may be a more common phenomenon. In fact, there may be parallels between the linear, thermal response of metazoan development and protistan growth rate, as cell division is central to both (Atkinson 1994).

As indicated above, many biological processes are expected to increase exponentially with temperature, so it is not surprising that many researchers assume growth rates should also be described by  $Q_{10}$ . However, the  $Q_{10}$  'rule' is a simplification, appropriate only for small temperature intervals, of a complex and accurate law, proposed by Van't Hoff (1884), theoretically elaborated by Arrhenius (1889), and generally used in chemistry (Bělehrádek 1935). The  $Q_{10}$  approximation can produce substantial errors; e.g. estimates of the relationship between mass-corrected development time of metazoa and temperature were 10 to 15% different from predictions derived from biochemical kinetics theory (Gillooly et al. 2002). Thus,  $Q_{10}$  is often given a precision and meaning which is unjustified (Cossins & Bowler 1987).

The use of  $Q_{10}$  in biology arose from the assumption that biological rates are limited by chemical processes (Bělehrádek 1935). By using this 'rule', aquatic ecologists have neglected the complexities of biological processes; i.e. we tend to apply  $Q_{10}$  to describe data without considering the theoretical implications or how well it fits the data. In fact, as indicated above, the growth rate of protists may increase linearly with increasing temperature, even though many studies assume an exponential ( $Q_{10}$ ) relationship and obtain  $Q_{10}$  values of 2 to 3. Below we propose why this might be.

Let us assume that growth rate increases linearly with temperature. Also, initially assume that for protists growth rate is zero at  $0^{\circ}\text{C}$ . Finally, take the context of an aquatic ecologist making growth measurements on a temperate species that lives at  $\sim 5$  to  $25^{\circ}\text{C}$ ; the ecologist then decides to only make measurements at 2 temperatures, 10 and  $20^{\circ}\text{C}$ , adequately representing the encountered temperature range. If the  $Q_{10}$  model (Eq. 1) is applied to these 2 points, then the calculated  $Q_{10}$  will be 2, by definition, regardless of the slope of the straight line. Perhaps this is obvious, but similar measurements have been presented in the literature, and not surprisingly the  $Q_{10}$  was  $\sim 2$ . Even when researchers make measurements at several temperatures, they often continue to use paired points to determine  $Q_{10}$  (38% of the cases mentioned above used paired points). However, the above analysis makes 2 assumptions: measurements are made  $10^{\circ}\text{C}$  apart, and the response passes through the origin.

What happens if the linear response still passes through the origin, but 2 measurements are not made

at 10 and  $20^{\circ}\text{C}$ ? The result is that  $Q_{10}$  ranges from 1.7 to 3.2 when the lower temperature ( $\theta_1$ ) ranges between 5 and  $13^{\circ}\text{C}$  and the higher temperature ( $\theta_2$ ) ranges between 14 and  $25^{\circ}\text{C}$  (Fig. 2a). Thus, changing the 2 temperatures does little to alter the  $Q_{10}$  from 2. What then happens if the linear response does not pass through the origin? For this analysis, the slope of the linear response was assumed to be  $0.07 \text{ d}^{-1} \text{ }^{\circ}\text{C}^{-1}$  (i.e. that found for protists). The intercept was allowed to range between  $-0.2$  and  $0.2 \mu_{\text{max}}$ ; this corresponds to a base temperature, where no growth occurs, of  $-2.9$  to  $2.9^{\circ}\text{C}$ . If measurements are then made at 10 and  $20^{\circ}\text{C}$ ,  $Q_{10}$  ranges from 1.8 to 2.4 (Fig. 2b), again near 2.

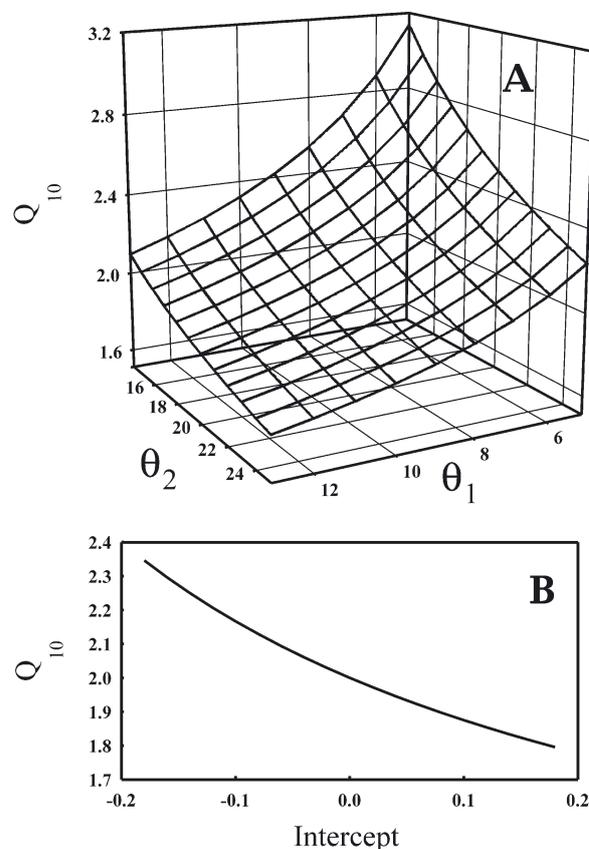


Fig. 2. Estimates of  $Q_{10}$  calculated by Eq. (1). (A) Estimates of  $Q_{10}$  (response plane) were made using measurements at 2 temperatures: first and second ( $\theta_1$  and  $\theta_2$  respectively). These calculations assume that the underlying relationship between temperature and the measured parameter (e.g. growth rate) is linear and the value of the parameter at  $0^{\circ}\text{C}$  is zero. See text for an explanation of the underlying assumptions. (B) Estimates of  $Q_{10}$  when measurements are made at 10 and  $20^{\circ}\text{C}$ , the true relationship is linear (following the equation  $\mu_{\text{max}} = 0.07\theta + b$ ), and the straight line has different elevations ( $b$ ), ranging from  $-0.2$  to  $0.2 \mu_{\text{max}}$ ;  $\mu_{\text{max}}$  = maximum specific growth rate;  $\theta$  = temperature. See text for an explanation of the underlying assumptions

Thus, based on some simple assumptions, by imposing an exponential response on a linear relationship, and making only 2 measurements, values of  $Q_{10}$  between 1.7 and 3.2 are likely to be obtained. This may shed light on why literature values of  $Q_{10}$  are often near 2, and, at the very least, this analysis indicates that  $Q_{10}$  should not be determined from only 2 points.

In conclusion, we raise 2 points: (1) protistan growth rate responds linearly to temperature, with a slope of  $\sim 0.07 \text{ d}^{-1} \text{ } ^\circ\text{C}^{-1}$ , and (2)  $Q_{10}$  is widely used as a descriptive and predictive model even though the protist temperature-growth responses may be linear. These points are particularly important, as using an exponential response to scale growth data to a single temperature (e.g. for allometric relationships or in food web models) may be inappropriate. Finally, we offer a cautionary note: this work examines species, not community, responses. Models that place a species assemblage into a trophic 'black box' and then impose a single temperature function on the box will be potentially inaccurate, regardless of the temperature-growth function, as the species composition within the box may be altered by the temperature shift. Assessing this response of trophic assemblages to temperature is yet another challenge to modelling.

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