

REVIEWS

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Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters

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Abstract

Literature review and synthesis of growth rates of aquatic protists focused on the role of temperature in the formation of massive annual algal blooms in high-latitude ecosystems. Maximal growth rates of herbivorous protists equaled or exceeded maximal growth rates of phototrophic protists at temperatures above 15°C. Maximal growth rates of herbivorous protists declined more rapidly with decreasing temperature than did those of phototrophic protists, and at the very low temperatures common to high-latitude ecosystems, the maximal growth rates of herbivorous protists were less than half the maximal growth rates of phototrophic protists. Growth rates of herbivorous protists were consistently lower than those of bacterivorous protists and were unrelated to differences in cell volume between the two groups. Linear equations describing the relationship of the natural log of maximal growth rates of bacterivorous and herbivorous protists to temperature were generated and compared to published information for maximal growth rates of phototrophic protists and copepods. The three heterotrophic groups had similar slopes (0.12 for bacterivorous protists, 0.10 for herbivorous protists, and 0.13 for copepods) that were approximately double that of phototrophic protists (0.06). The massive annual algal blooms observed in high latitudes are due in part to a fundamental difference in the relationship between growth and temperature for phototrophic protists and their grazers.

Phytoplankton blooms are common occurrences in many aquatic ecosystems. These phenomena can positively or negatively affect food web structure and carbon flow in marine ecosystems. For example, spring blooms in temperate environments are often characterized by phytoplankton species that are subsequently grazed by larger zooplankton, resulting in the efficient transfer of energy to higher trophic levels and away from energetic losses within the microbial loop. Conversely, blooms of toxic or noxious species of phytoplankton can disrupt energy transfer in planktonic food webs and/or result in illness or death of mammals, birds, and commercially important fish and shellfish.

Formation of a phytoplankton bloom indicates a fundamental imbalance between growth and removal of phytoplankton. Assuming that grazing dominates other loss factors, this imbalance may be accomplished through the

stimulation of phytoplankton growth relative to extant grazing pressure, the inhibition of herbivory in the presence of phytoplankton growth, or some combination of the two. Most research has emphasized the importance of the stimulation of the intrinsic growth rate of phytoplankton as the primary underlying cause for massive accumulations of phytoplankton and has deemphasized the importance of removal processes (Verity and Smetacek 1996). This predilection is rooted in the preponderance of studies that have examined responses of phytoplankton growth to availability of nutrients and light (Riley 1942; Sverdrup 1953; Platt et al. 1991). Increases in phytoplankton standing stock can only occur if the algal population is growing. Nonetheless, reduced grazing pressure due to constraints on herbivory (e.g., as a result of low zooplankton abundance, low individual feeding rates, or the production of toxic or inhibitory compounds by phytoplankton) will yield a higher net population growth rate for a given intrinsic growth rate of the phytoplankton assemblage and thus can serve as an explanation for some phytoplankton blooms (Smayda 1997; Liu and Buskey 2000; Tagliabue and Arrigo 2003).

One classical explanation for the initiation of nontoxic (i.e., 'edible') phytoplankton blooms (e.g., the spring bloom of many temperate and polar ecosystems) is the temporal offset that occurs between onset of rapid phytoplankton growth in early spring and subsequent development of a zooplankton assemblage sufficient to affect phytoplank-

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ton standing stock. Historically, occurrence of these blooms has been explained by the fact that planktonic metazoan development is slow relative to maximal phytoplankton growth rates, particularly at very low temperature (Walsh and McRoy 1986; Huntley and Lopez 1992; Napp et al. 2000). This explanation has received less attention in recent years because of the recognition of the importance of herbivorous microzooplankton, which are eukaryotic consumers of phytoplankton and are in the size range of 20–200 μm , as defined by Sieburth et al. (1978). Herbivorous microzooplankton have demonstrated the potential for rapid growth rates and, thus, rapid response rates to increases in phytoplankton production. In fact, the absence of phytoplankton blooms in regions that would be expected to manifest these phenomena has been attributed to high microzooplankton standing stocks at those locations and times (Frost 1987; Parsons and Lalli 1988; Frost 1991).

If the latter scenario is a general principle of marine ecosystems, then one might ask “Why are blooms of nontoxic phytoplankton such a common event in the ocean?” Given the ubiquity of herbivorous microzooplankton and their potentially rapid intrinsic growth rates, what environmental factors constrain the growth and grazing rates of herbivorous microzooplankton (relative to phytoplankton growth rates) such that phytoplankton blooms are allowed to develop? We hypothesize that the extreme low temperatures characteristic of high-latitude environments provide a fundamental constraint on growth rates of microzooplankton relative to the effect of temperature on phytoplankton growth rates. Given favorable conditions for phytoplankton growth, this imbalance can result in a substantial net phytoplankton growth rate, thus contributing to massive bloom formation in these environments. Our hypothesis is supported by bloom dynamics and an extensive analysis of growth-rate data from the literature.

Massive annual algal blooms are common in high-latitude marine ecosystems. For example, the Ross Sea, the Bering Sea, and the high-latitude North Atlantic are characterized by seasonal algal blooms that are spatially extensive, with high maximal chlorophyll concentrations. Although bloom composition and specific timing vary with ice conditions and other annual variables, the overall dynamics of blooms in these environments are generally similar. Chlorophyll concentrations and algal cell abundances increase dramatically during late spring in conjunction with rapidly increasing light levels, day lengths, and ice retreat (Lochte et al. 1993; Stramska et al. 1995; Smith et al. 2000).

Although herbivorous microzooplankton can be relatively abundant in these ecosystems, field studies indicate that grazing pressure is insufficient in spring to prevent the formation of large phytoplankton blooms during late spring and summer (Burkill et al. 1993; Gifford et al. 1995; Caron et al. 2000). This mismatch between production and consumption appears to be temperature related. In the Ross Sea, where extreme low temperatures ($\leq 0.5^\circ\text{C}$) persist year round, observed rates of herbivory (d^{-1}) were consistently low (Caron et al. 2000). Rates of microzooplankton herbivory in the Bering Sea were

positively correlated (albeit weakly) with temperature (Olson and Strom 2002), whereas in the North Atlantic at 59°N , microzooplankton herbivory had relatively little effect on the phytoplankton assemblage during spring, yet removed most of the potential daily chlorophyll production during summer (Gifford et al. 1995). Analysis of a much larger data set on the relationship between phytoplankton grazing and temperature has indicated a positive relationship between these parameters (Caron et al. 2000). This relationship may in part be due to differences in phytoplankton community composition at different temperatures, but these observations may also indicate the potential for a fundamental difference in the effect of temperature on the growth of phototrophic and heterotrophic protists. Here we examine this difference as a factor in the formation of phytoplankton blooms at high latitude.

The relationship between growth rate and temperature for temperate and tropical species of phytoplankton is well established. Eppley (1972) reviewed published growth rates for marine phytoplankton available up to that time and demonstrated that the upper limit for phytoplankton growth rate was exponentially and positively correlated with temperature. Goldman and Carpenter (1974) derived a similar relationship between temperature and phytoplankton growth rate based on data derived from continuous-culture experiments using a variety of algal species. The Goldman–Carpenter curve had a lower y intercept but a slope similar to that of Eppley.

The relationships described by Eppley (1972) and Goldman and Carpenter (1974) were based almost entirely on data derived from temperate and tropical phototrophic protists. Thus, the applicability of these data to extrapolation of potential maximal growth rates of polar phytoplankton species is questionable. In addition, a large number of studies to date have examined the relationship between temperature and growth rate for a wide spectrum of heterotrophic protists, but relatively few studies have examined this relationship for more than a few species at one time (Finlay 1977; Baldock et al. 1980; Muller and Geller 1993). To date, no comprehensive review has examined the effects of temperature on growth rates of heterotrophic protists.

Here we address these issues by expanding the analysis of phytoplankton growth rate, using information available since the publication of Eppley’s review more than 30 yr ago, to examine (1) its usage as a descriptor of phytoplankton maximal growth rate and (2) its applicability to describing maximal growth rates of phototrophic protists in permanently cold environments. In addition, we examine the relationship between temperature and growth rate for heterotrophic protists and, specifically, compare the temperature dependence of phototrophic and heterotrophic protists in order to examine the contribution of extreme low temperature to phytoplankton blooms in high-latitude environments.

Methods

Initially, protistan growth rates were compiled and organized into groups based on the local environment

from which cultures were isolated (temperate/tropical vs. polar). Temperate and tropical protists were grouped together since the limited data available for protists from tropical regions did not provide enough information for a meta-analysis. Next, protists were further grouped according to mode of nutrition (phototroph vs. heterotroph), and then heterotrophs were divided into groups according to prey type (bacterivore vs. herbivore). Growth rates measured on cultured protists were included, but rates measured on mixed plankton assemblages were not considered. The total data set consisted of 3,374 growth rates, representing a wide taxonomic range of protists isolated from water samples obtained throughout the world, including samples from both limnetic and marine systems. The data and list of references are available in Web Appendix 1 (http://www.aslo.org/lo/toc/vol_52/issue_2/0886a1.pdf). The data set contained 2,867 growth rates of protists from temperate and tropical regions and 483 growth rates of protists from polar regions. There were 2,041 growth rates of phototrophic protists (1,589 temperate and 452 polar) from 58 published reports and 1,308 growth rates of heterotrophic protists (1,277 temperate and 31 polar; 597 bacterivores and 711 herbivores) from 53 publications.

All growth rates were converted to intrinsic growth rate (d^{-1}) using the equations:

$$\mu = \ln 2 \times t_g^{-1}$$

$$t_g^{-1} = \text{doublings } d^{-1}$$

where μ = intrinsic growth rate (d^{-1}) and t_g = generation time (days). Numerical values for growth rates published in graphical form were acquired using the freeware program Data Thief (Kees Huyser)

Results and discussion

The entire data set of protistan growth rates compiled from the literature spanned the temperature range from -3°C to 40°C . This range was chosen because our primary interest was the response of growth rate to temperatures that occur within typical marine and limnetic systems. Growth rates have been measured at temperatures below -3°C , but this measure requires highly saline conditions found only in unusual environments such as brine channels. Eppley's (1972) published curve covered the temperature range from 0°C to 45°C and was calculated using algal growth rates in doublings d^{-1} . We extrapolated the curve to -3°C using the equation reported in his paper ($\text{doublings } d^{-1}; \log_{10} \mu_{\max} = 0.0275T - 0.070$, where T = temperature in $^{\circ}\text{C}$), converted to intrinsic growth rate (d^{-1}).

Growth rates reported for cultures of phototrophic protists from polar, temperate, and tropical regions were nearly all less than or equal to Eppley's predicted maximum over the entire temperature range (thick solid line; Fig. 1). Thus, the overall effect of temperature on maximal growth rates of phototrophic protists appears to be consistent with Eppley's original findings. Out of a total of 2,048 compiled growth rates of phototrophic protists, 157 ($\sim 8\%$) were

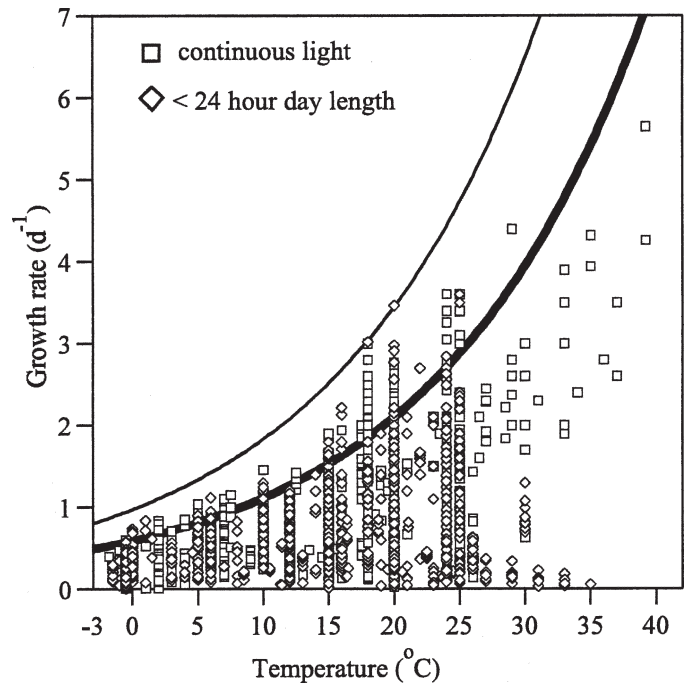


Fig. 1. Summary of the relationship between published growth rates of phototrophic protists and temperature. Thick solid line represents the Eppley (1972) curve of maximal predicted growth rates of phototrophic protists. Thin solid line represents the curve from Brush et al. (2002).

greater than the maximum predicted by the Eppley curve. Brush et al. (2002) noted published growth rates in excess of the Eppley curve. They suggested that the use of Eppley's maximal growth rate equation resulted in an underestimation of primary production in mathematical models of this process. Brush et al. (2002) argued for an alternative to the Eppley curve based on their new data set and recommended increasing the y intercept of the Eppley curve by roughly 60%. The new predictor (henceforth called the Brush curve) is depicted as the thin solid line in Fig. 1. Although the Eppley curve may underestimate the absolute maximal growth rate that can be attained by the fastest growing phototrophic protists, it still exceeds $>90\%$ of all the growth rates in our compiled data set. Moreover, the extrapolation of Eppley's curve below 0°C appears to closely bound growth rates of polar phototrophic protists at extreme low temperature. Although the exact placement of Eppley's line depicting maximal growth rate may be debated, it is clear that the shape of the curve is still appropriate for most of the data available before and since 1972.

The data sets of Eppley (1972) and Brush et al. (2002) were based primarily on growth rates of cultured protists measured under continuous illumination, since these authors were interested in obtaining the maximal possible growth rate for any phototrophic protist at each temperature. This approach may be appropriate for extreme high-latitude ecosystems, where protists will experience annual periods of continuous illumination, but at lower latitudes the annual maximal photoperiod will be reduced sub-

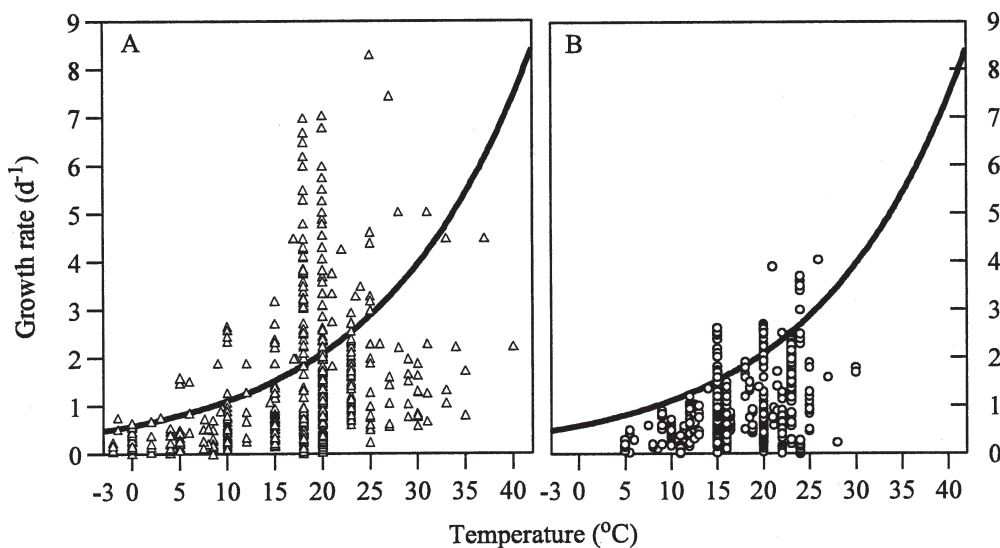


Fig. 2. Summary of the relationship between growth rates and temperature for (A) bacterivores and (B) herbivores. Solid line represents the Eppley curve for phototrophic protists from Fig. 1.

stantially from 24 h. Therefore, we divided our data set into growth rates measured under continuous versus <24-h illumination to look for differences in maximal growth rates between these two groups (Fig. 1). No discernable differences were apparent between phototrophic protists grown in continuous or <24-h illumination.

Growth rates of heterotrophic protists in culture were compared to maximal growth rates of cultured phototrophic protists over the temperature range of -3°C to 40°C (Fig. 2). Heterotrophic protists were divided according to prey type, separating bacterivores from herbivores. Bacterivores were capable of extremely rapid maximal growth rates at high temperatures (Fig. 2A), such as 8.3 d^{-1} at 25°C reported for a strain of *Uronema marinum* (Martinez 1980) and 6 d^{-1} at 20°C reported for an unidentified species within the genus *Paraphysomonas* (Caron et al. 1991). In general, the fastest growth rates of bacterivores were far in excess of Eppley's curve at similar temperatures. As the Eppley curve represents the theoretical maximal growth rates that can be achieved by phototrophic protists at any temperature, the data in Fig. 2A indicate that in the presence of high prey abundances, bacterivores have the potential for much higher growth rates than phototrophic protists. At temperatures of $<18^{\circ}\text{C}$, maximal published growth rates of bacterivores declined sharply, and below 5°C , their growth rates were less than or equal to the maximal observed growth rates of phototrophic protists. Q_{10} values were calculated for bacterivorous protists from the maximal reported growth rate at each temperature with the standard equation $Q_{10} = (\mu_1 \times \mu_2^{-1})^{(10/[t_1 - t_2])}$, where μ is specific growth rate (d^{-1}) and t is temperature ($^{\circ}\text{C}$). Q_{10} for maximal growth rates of bacterivorous protists between 5°C and 25°C was 2.4, compared to a value of 1.88 for the Eppley (1972) curve. Between the temperature ranges of $0-10^{\circ}\text{C}$ and $10-20^{\circ}\text{C}$, the Q_{10} values for maximal growth rates of bacterivorous protists were even higher: 2.68 and 2.97,

respectively. The differences in Q_{10} values between phototrophic and bacterivorous protists imply a fundamentally different relationship between temperature and growth rate for these two protistan groups.

Growth rates of herbivorous protists have been reported over the temperature range of $5-30^{\circ}\text{C}$. We are unaware of published growth rates of cultured herbivorous protists below 5°C or of growth rates of cultured herbivorous protists from polar environments measured at any temperature. In general, growth rates of herbivores were lower than those of bacterivorous protists (Fig. 2B). The maximal observed growth rate for an herbivorous protist at any temperature was 4.04 d^{-1} , compared to the maximal rate of 8.32 d^{-1} observed for a bacterivorous protist. The Q_{10} value derived from maximal growth rates of herbivores between 10°C and 20°C (Fig. 2B) was 3.75, which is larger than the Q_{10} value obtained by Eppley for phototrophs and the Q_{10} value observed in this review for bacterivores (Fig. 2A). Maximal growth rates of herbivorous protists were in excess of those of their prey at temperatures common to temperate and tropical regions ($20-30^{\circ}\text{C}$; Fig. 2B). As temperature decreased, maximal growth rates of herbivorous protists decreased more rapidly than those of their algal prey. At the lowest temperature for which data are available (5°C), the highest reported growth rate for an herbivorous protist was 0.3 d^{-1} , less than half the value of 0.81 d^{-1} predicted by the Eppley curve for phototrophic protists at the same temperature.

Differences between maximal growth rates of bacterivorous and herbivorous modes of nutrition observed in the multitaxa data sets of Fig. 2 were also apparent for a narrower data set examining omnivorous species of the genus *Paraphysomonas* grown primarily on phototrophic protists or bacteria (Fig. 3). Isolates of *Paraphysomonas* spp. fed bacteria grew at rates far in excess of the Eppley curve at temperatures representative of temperate and tropical regions ($20-28^{\circ}\text{C}$; Fig. 3A), while *Paraphysomonas*

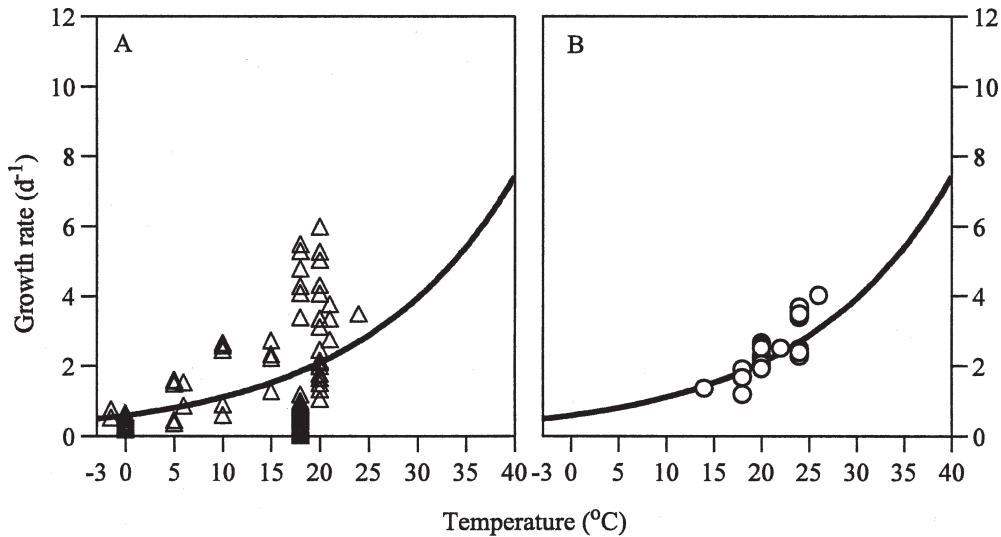


Fig. 3. Effect of temperature on the growth rate of (A) bacterivorous and (B) herbivorous *Paraphysomonas* spp. Solid line represents the Eppley curve.

spp. fed algal prey grew at maximal rates only marginally above the Eppley curve (Fig. 3B). Maximal growth rates of the flagellate fed bacteria decreased rapidly below 18°C (Fig. 3A). Maximal growth rates of bacterivorously grown *Paraphysomonas* appeared to cross the Eppley curve at polar temperatures (−1°C). However, *Paraphysomonas* spp. fed primarily phototrophic protists (including both axenic and nonaxenic cultures of prey) exhibited maximal growth rates that appeared to cross the Eppley curve at approximately 18°C (Fig. 3B). Q_{10} values for these species were similar between herbivorous and bacterivorous *Paraphysomonas* (2.57 between 14°C and 26°C for an herbivorous diet vs. 2.31 between 10°C and 20°C for a bacterivorous diet). Q_{10} values were higher for the bacterivorous *Paraphysomonas* between 0°C and 10°C than for those between 10°C and 20°C (3.97 vs. 2.31), but no information is available for herbivory by *Paraphysomonas* spp. below 14°C, so it is unclear whether this trend is true for both trophic modes.

We examined the possibility that the observed differences in maximal growth rates between herbivorous and bacterivorous protists might be explained by differences in average size of herbivores and bacterivores. Size has previously been correlated with zooplankton growth rate (Hansen et al. 1997), and since herbivorous protists are feeding on much larger prey, they could themselves have been larger on average. Growth rates of bacterivorous and herbivorous protists were compared on the basis of cell volume (Fig. 4). Volumes were calculated based on standard geometric shapes if cell measurements, but not cell volumes, were published. Cell volumes or measurements for the same species, published elsewhere, were used if neither volumes nor measurements were published with the growth rate data. The herbivorous dinoflagellate *Noctiluca* sp. was removed from the data set prior to analysis because its unusual morphology made its cell volume a clear outlier.

Cell volumes of species feeding herbivorously or bacterivorously overlapped considerably, and, thus, the more rapid growth rates of the bacterivorous protists were not due to smaller average cell volumes compared to those of herbivorous protists (Fig. 4). The largest cell volumes reported included both herbivorous and bacterivorous species. The smallest cell volumes strictly represented bacterivorous species. The average cell volume of bacterivores was $\sim 4,000 \mu\text{m}^3$. If cell volumes of $<100 \mu\text{m}^3$ were removed (thus, we were including only the range in which the herbivorous and bacterivorous protistan cell volumes

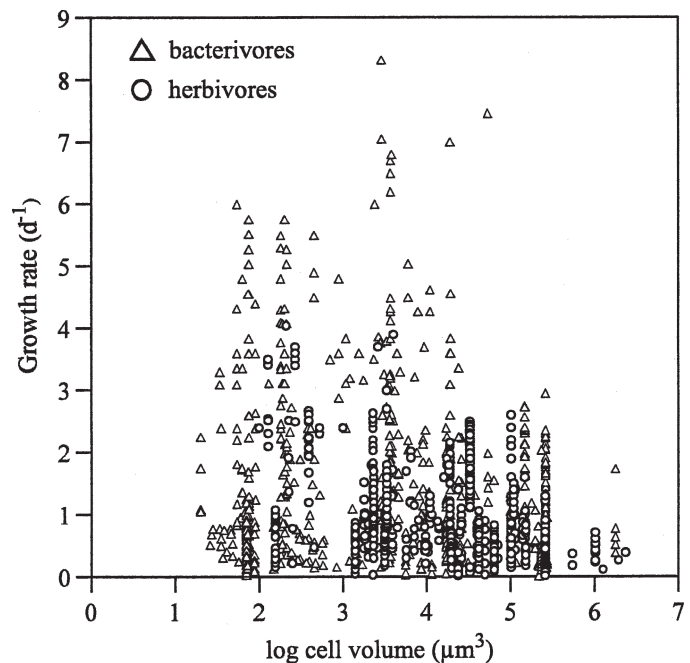


Fig. 4. Growth rates of bacterivorous and herbivorous protists as a function of cell volume.

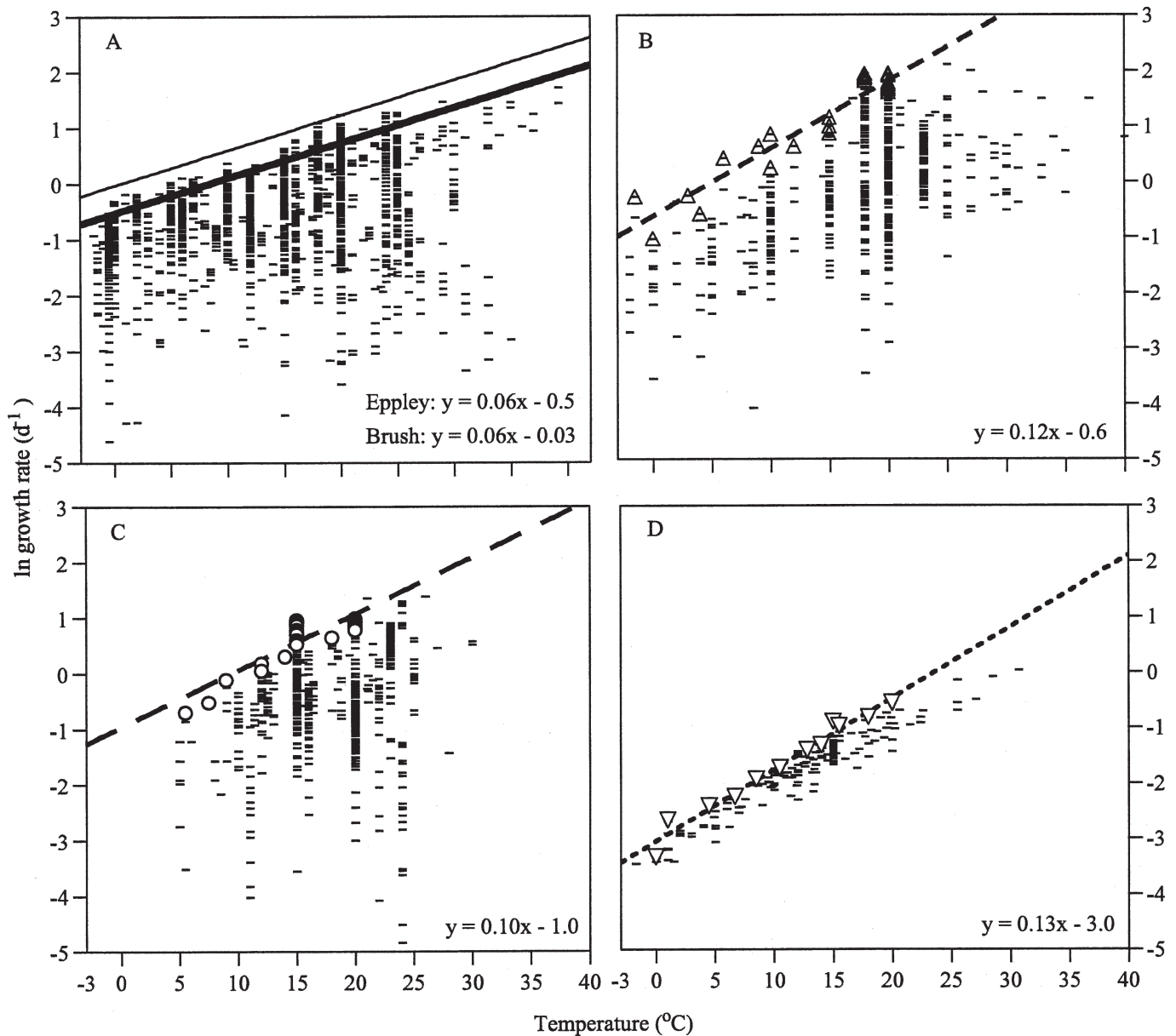


Fig. 5. Growth rates of (A) phototrophic protists, (B) bacterivorous protists, (C) herbivorous protists, and (D) copepods as a function of temperature. The thick solid line in (A) represents the Eppley curve, and the thin solid line represents the Brush curve. Lines in (B–D) represent predicted maximal growth rates at any temperature. Open symbols indicate the maximal values within each data set used to calculate the regression equations; bars indicate values not used in calculation of the regression equation.

overlapped), average cell volume was $\sim 13,000 \mu\text{m}^3$. Average cell volume of the herbivores was $\sim 14,000 \mu\text{m}^3$. Rapid growth rates ($>4 \text{ d}^{-1}$) were achieved solely by bacterivores and were attained by a wide range of sizes of bacterivorous protists ($55\text{--}54,000 \mu\text{m}^3$). Average growth rates of bacterivorous and herbivorous protists were compared over the entire range of volumes using a modified analysis of covariance (ANCOVA) test (Wilcox 2003). This test has the advantage over the standard ANCOVA of requiring no assumptions of normality, homoscedasticity, or linearity, nor does it require that the regression lines are parallel. This test used a running-interval smoother to approximate the regression lines for each set of points, then typical values for growth rate were compared (at a given value for

volume). Individual tests were performed using a modified, one-step M-estimator as a measure of location; the distribution of the data set was approximated using a percentile bootstrap method; and family-wise error rate was controlled by adjusting α values. The test was performed using the freeware statistical program R version 2.3 (<http://www.r-project.org/>). The modified ANCOVA found significant differences between the growth rates of bacterivores and herbivores across the entire range of volume at $\alpha = 0.05$.

Relationships between maximal growth rates and temperature were compared for phototrophic protists, bacterivorous protists, herbivorous protists, and copepods (Fig. 5). Copepod growth rates were obtained from

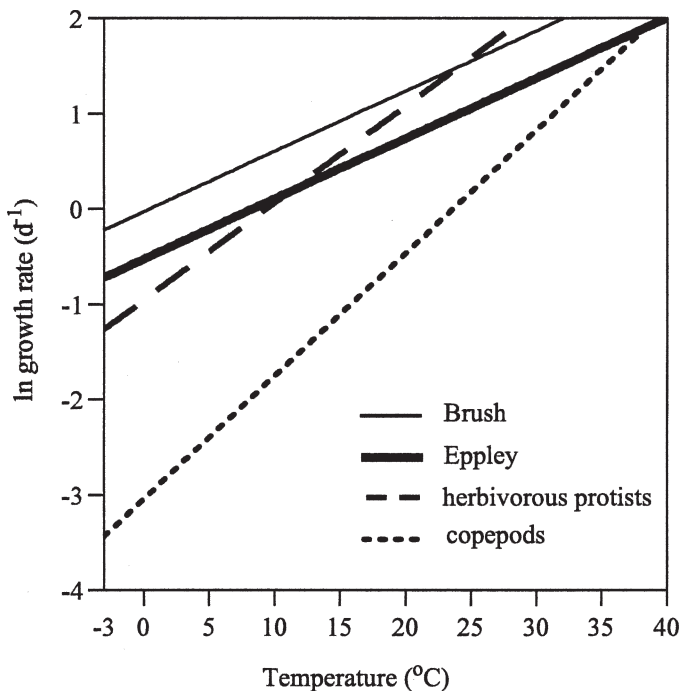


Fig. 6. Comparison of maximal growth rate predictor lines for phototrophic protists, herbivorous protists, and copepods generated in Fig. 5. The thick solid line represents the Eppley curve, the thin solid line represents the Brush curve, the dashed line represents maximal growth rates of herbivorous protists, and the dotted line represents maximal growth rates of copepods.

Huntley and Lopez (1992). The natural logarithms of all growth rates for each category were calculated and plotted against temperature. Eppley and Brush curves were converted to natural logarithms and plotted against growth rates of phototrophic protists (Fig. 5A). An upper envelope enclosing the maximal growth rates of bacterivorous and herbivorous protists and copepods was generated, similar to the Eppley and Brush curves for phototrophic protists (Fig. 5B–D). This envelope was generated for each subset as follows: growth rates were first separated into 2°C temperature bins, centered on odd numbers of °C, and growth rates within each bin were sorted according to magnitude. The top 5% of growth rates within each bin were included in the regression. At least one growth rate was included from each bin. If 5% of the total number of growth rates in a bin was not an integer, the number of growth rates included was rounded to the nearest whole number. The regressions obtained in this manner were $y = 0.12x - 0.6$ for bacterivorous protists (Fig. 5B), $y = 0.10x - 1.0$ for herbivorous protists (Fig. 5C), and $y = 0.13x - 3.0$ for copepods (Fig. 5D).

The Eppley and Brush curves describing the effects of temperature on maximal algal growth rates were then compared to the regressions generated in Fig. 5C and 5D for algal grazers (herbivorous protists and copepods; Fig. 6). This comparison indicated that the maximal growth rates of algal grazers decrease much more rapidly with decreasing temperature than do the maximal growth

rates of their algal prey. Furthermore, the slopes of the regressions of the herbivores (herbivorous protists and copepods) were quite similar to each other.

Maximal physiological rates (e.g., clearance rates, growth rates, and ingestion rates) have been demonstrated to vary among taxonomic groups of protists (Hansen et al. 1997). These authors specifically noted that ciliates had much higher maximal growth rates than did dinoflagellates. It is possible that the steep decline in maximal growth rate of herbivorous protists observed in this study might have been biased if the data set used to generate the regression was influenced at extreme low and high temperatures by different taxonomic groups of protists. For example, if the maximal growth rates published at high temperatures (20–25°C) were dominated by ciliates and the rates at low temperature (0–5°C) were dominated by dinoflagellates, then this bias could have skewed the regression of temperature versus maximal growth rate and resulted in a greater slope for the overall regression. In order to address this issue, we have included in Table 1 the specific data points used to form our regression equation for herbivorous protists. This subset of the herbivore data set was dominated by ciliates across the entire range of temperatures, with a few nanoflagellate growth rates. Since the data set used to generate the regression was not composed of different taxonomic groups at different temperatures, we conclude that our regression is not biased by confounding taxon with temperature.

We speculate that the more severe effect of decreasing temperature on the maximal potential growth rates of herbivorous protists (relative to its effect on maximal growth rates of their algal prey) may have major implications for microbial food web dynamics in cold-water ecosystems. We infer from our analysis that, all other conditions being optimal, growth rates of herbivorous protists in cold waters will be lower than rates for phototrophic protists. This effect may result in low grazing pressure on polar phototrophic protists in spring, when phytoplankton growth rates are rapid as a result of increasing light and nutrient availability. In northern temperate systems, grazing pressure on phototrophic protists may also be constrained (relative to phytoplankton growth rates) in early spring, when water temperatures are low. This situation appears analogous to the poor temporal coupling between bacterial production and primary production in some cold marine ecosystems (Pomeroy and Deibel 1986; Ducklow et al. 2001). The underlying physiological basis for this difference in maximal growth rates of phototrophs and heterotrophs is not clear. We speculate that the catabolic processes associated with heterotrophy would appear to be a likely source of the differences, because phototrophs and heterotrophs may contain similar suites of anabolic pathways.

Based on this reasoning, slow growth rates of herbivores relative to growth rates of phototrophic protists may allow phototrophs to temporarily escape top-down control and may contribute to the initiation of massive phytoplankton blooms. It is unfortunate that few to no data are available for growth and grazing rates of cultured herbivorous protists at the extremely cold (<5°C) temperatures at which

Table 1. Growth rates used to generate the upper envelope and regression for herbivorous protists.

Organism	Temperature (°C)	Growth rate (d ⁻¹)	Study
<i>Balanion planctonicum</i>	5.5	0.50	Weisse et al. (2001)
<i>Balanion planctonicum</i>	7.5	0.60	Weisse et al. (2001)
<i>Balanion planctonicum</i>	9	0.90	Weisse et al. (2001)
<i>Urotricha farcta</i>	12	1.20	Weisse et al. (2001)
<i>Urotricha farcta</i>	12	1.20	Weisse et al. (2002)
<i>Lohmanniella spiralis</i>	12	1.06	Jonsson (1986)
<i>Paraphysomonas imperforata</i>	14	1.37	Caron et al. (1986)
<i>Balanion comatum</i>	15	2.63	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	2.54	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	2.54	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	2.48	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	2.48	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	2.39	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	2.20	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	2.11	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	2.03	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	1.83	Pedersen and Hansen (2003)
<i>Balanion comatum</i>	15	1.74	Pedersen and Hansen (2003)
<i>Balanion planctonicum</i>	15	1.70	Weisse et al. (2001)
<i>Paraphysomonas imperforata</i>	18	1.92	Caron et al. (1986)
<i>Urotricha farcta</i>	20	2.70	Weisse et al. (2001)
<i>Favella taraikaensis</i>	20	2.60	Kamiyama (1997)
<i>Paraphysomonas imperforata</i>	20	2.55	Caron et al. (1985)
<i>Paraphysomonas imperforata</i>	20	2.52	Caron et al. (1985)
<i>Favella azorica</i>	20	2.40	Kamiyama (1997)
<i>Paraphysomonas imperforata</i>	20	2.31	Caron et al. (1985)
<i>Favella azorica</i>	20	2.20	Kamiyama (1997)

the disparity between maximal growth rate of herbivorous and phototrophic protists may be the highest and, thus, at which the potential for phytoplankton bloom formation is the greatest.

Of course, it is important to recognize that growth rates of heterotrophic protists do not translate directly into grazing pressure in marine systems. For example, it is possible that slow growth rates that are the result of rapid ingestion rates but low growth efficiencies could still yield high rates of prey removal. However, increasingly field and laboratory information supports the idea that temperature significantly constrains grazing rates. Burkill et al. (1993) measured low rates of herbivory in the Bellingshausen Sea, Antarctica. Caron et al. (2000) measured rates of herbivory during four cruises spanning three seasons in the polynya of the Ross Sea, Antarctica. Only 13 of 51 experiments yielded detectable rates of herbivory using the dilution method, and the highest rate observed was low in comparison to rates reported for temperate and tropical ecosystems. The low grazing rates in that study were not a consequence of low grazer abundance. Microzooplankton grazers (ciliates and heterotrophic dinoflagellates) varied considerably in abundance over the course of the experiments and were at times comparable in abundance to those abundances observed in locations such as the North Atlantic during the spring bloom as well as the Arabian Sea and the Equatorial Pacific. The authors also compiled a literature review of grazing rates from 19 published studies measured over a wide range of temperatures and from a variety of marine systems and found significantly lower grazing rates at temperatures below 2°C, compared

to rates measured at 10°C or above. Similarly, two studies that examined ingestion rates of microzooplankton on fluorescently labeled phytoplankton (FLP) in the Atlantic and Indian sectors of the Southern Ocean reported low uptake rates at ambient temperature (Becquevort 1997; Becquevort et al. 2000). Maximal ingestion rates in those studies were ≤ 2 FLP *Paraphysomonas antarctica* grazer⁻¹ h⁻¹, and ≤ 0.01 FLP *P. antarctica* grazer⁻¹ h⁻¹. Measurements of specific ingestion rates of individual ciliate taxa in natural plankton assemblages within the Ross Sea, Antarctica, as well as specific ingestion rates of an Antarctic *Strombidium* sp. culture in the laboratory support the idea of very low specific ingestion rates at natural prey abundances at ambient Antarctic temperatures (Rose 2006).

Some of the largest annual phytoplankton blooms in the world occur in cold waters. At the same time, neither polar nor temperate phototrophic protists in culture have demonstrated rapid growth at low temperature, based on the maximal growth rate information collected in this review. Our analysis indicates that the formation of these massive blooms may, in part, be related to the different effects of temperature on the growth rates of phototrophic and heterotrophic protists in these systems. The growth rates of heterotrophic protists in general appear to be more strongly constrained by decreasing temperature than the growth rates of phototrophic protists. Also, our data indicate that the growth rates of herbivorous protozoa are considerably lower than rates for bacterivorous protozoa for the same temperature, regardless of cell size and even among members of the same genus. Maximal growth rates

of herbivorous protozoa were similar to the maximal growth rates of phototrophic protists at moderate temperatures (20°C), but these rates decreased sharply with decreasing temperature to approximately half the maximal growth rates of phototrophic protists at the lowest temperature for which data are available (5°C). Published reports of grazing and ingestion rates of microzooplankton in cold waters also support our overall conclusion that temperature also exhibits a strong negative effect on herbivory. Slow growth and grazing by herbivores in cold waters may result in a reduction in top-down control of phytoplankton by micrograzers at a critical period when phytoplankton growth rates are stimulated. Reduced top-down control in cold waters due to low temperatures could be a strong contributing factor in the formation of algal blooms in these ecosystems.

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