Temperature increase – an uncertain stimulant of algal growth and primary production in fresh waters

J.F. Talling

Hawthorn View, The Pines, Bongate, Appleby, Cumbria CA16 6HR, UK. Email: jaidtalling@btinternet.com

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Abstract

Temperature profoundly influences the occurrence and organic production of algae in inland waters. Correlations deduced from seasonality of species are limited by numerous interactions. The kinetics of growth and photosynthesis are more unequivocal, although light and nutrient conditions affect rate-response to temperature, with reduced sensitivity at low irradiance. Specific growth rates, species-characteristic, have rarely been measured systematically with numerous common species and short intervals over an extended range of temperature.

Different bases of quantitative analysis are cited; they include cardinal points, neo-Blackman behaviour, and the van’t Hoff ($Q_{10}$), Arrhenius (degrees K) and Bělehrádek (with ‘biological zero’) formulations. Temperature-limits of specific growth rate are widely found, and variable with species, outside the 10–20 °C range. Low-temperature stenothermy is apparently uncommon, and high temperature (35+ °C) species and strains are known. Maximum rates fall below an upper limiting envelope. In nature, species are only rarely most abundant at their optima for specific growth rate. Differences of temperature have indirect effects on algal distribution in a stratified water-column. Geographical distributions partly relate to temperature, although experimental elucidation is rare; there is indirect influence through ice-cover and altitude. Some prediction of rate-limitation is possible, both with latitude and globally.

Keywords: algae; cardinal points; diatoms; eurythermy; growth rate; stenothermy; temperature coefficient; thermal strains.

Introduction

As a familiar environmental factor, temperature has long attracted those concerned with the occurrence and production of organisms within fresh waters. Analysis has been helped by the relative damping of range in temperature excursions, both day–night and seasonal, compared with most terrestrial habitats. It has been a measured variable in probably all serious studies of planktonic (and other micro-algal) seasonal occurrence. Interpretation by correlation has been widespread, dating from early studies of algae (reviewed for plankton by Hutchinson, 1967) and then favoured by the ready availability of thermometers but lack of reliable analysis of plant nutrients in low
concentration. Later there was reduced confidence in deducing factor-action from correlations in time-series, although improved statistical methods and very long time-series brought some advantages (e.g. Lehman et al., 2004; Tadonléké, 2010). More unequivocal physiological information has derived from experimental work with growth kinetics in algal cultures; with laboratory and field work on the kinetics of photosynthesis by phytoplankton; and on the role of temperature in regulating loss-processes that include respiration, sinking, grazing and parasitism. It is with these topics, and cautious interpretation of geographical distribution, that this review is largely concerned. There is added relevance from the central role of temperature in current climatic change; its possible consequences, given certain assumptions, have been explored by modelling (e.g. Elliott et al., 2006). Given the wide scope, the bibliography is far from comprehensive. Illustrated examples are taken from work with which I was directly associated. Sub-cellular mechanisms (Raven & Geider, 1988) and cryothermal preservation are excluded.

**Temperature-sensitivity of primary properties**

Here it is convenient to list some primary properties that are sensitive to temperature and liable to be influential in ecological situations.

1. The density (specific gravity) of water changes non-linearly with temperature, showing a maximum near 4 °C and an increasingly negative relationship at higher temperature. Values are influenced systematically by pressure – atmospheric and hydrostatic – and solutes.

2. Liquid water has a solid phase boundary near 0 °C and a vapour phase boundary near 100 °C, limiting the range available for freshwater organisms.

3. Rates of photochemical reactions are typically temperature-insensitive whereas those of most other chemical reactions in aqueous phase increase with temperature, the gradient related exponentially (Arrhenius formulation) to absolute temperature (degrees Kelvin, K):

   \[ r = Ae^{-E/RT} \]  

   where \( r \) = rate of reaction, sec\(^{-1}\) (first-order reaction)  
   \( E \) = activation energy, J mol\(^{-1}\)  
   \( R \) = the universal gas constant, J mol\(^{-1}\)K\(^{-1}\)  
   \( A \) = a constant, sec\(^{-1}\)  
   \( T \) = absolute temperature.

The much-used temperature coefficient \( Q_{10} (= \text{ratio of rates separated by a temperature interval of 10 °C}) \) can readily be shown algebraically to be related to activation energy \( E \) with close approximation by

\[ E = RT \log Q_{10} / 10 \]  

(Fig. 1. Temperature and ‘light intensity’ (illuminance) as interacting factors on the rate of photosynthesis of the planktonic diatom *Asterionella formosa*, sampled from a natural population in Windermere and exposed to fluorescent illumination. From Talling (1966).)
4. A variety of physical processes operative in a cell, including transport and viscosity, are temperature-sensitive, with temperature coefficients overlapping those of chemical reactions. Possible mechanistic implications for cellular growth are discussed by Raven & Geider (1988).

**Kinetics of algal growth and photosynthesis**

Items (iii) and (iv) above have extensions in the kinetics of algal growth, photosynthesis and respiration. Early views, here and in other branches of biology, were dominated by factor analysis in terms of minima, optima and maxima. These *cardinal points* are useful for general orientation, but are often difficult to define and locate on a temperature scale because of other factor-interactions. One is a frequent dependency on the time of exposure; another is the interacting control of rate of photosynthesis by radiant flux density (‘light intensity’). I have previously discussed (Talling, 1979) the limnological implications of Blackman and neo-Blackman kinetics, the latter with rate-ceilings imposed by factor-interaction. Thus the combined effect of two limiting factors can be far from multiplicative. Illustration is possible from my early work with a common planktonic diatom, in which two approaches (Talling, 1957a, 1966) showed the variable onset of light-saturation of photosynthesis – a key factor in natural populations – over an ecologically applicable range of temperature (Fig. 1).

![Figure 2](image-url)

*Fig. 2.* Growth, shown by semi-logarithmic plots, of three planktonic algae in culture exposed over the range of temperature indicated. Bars indicate standard deviations from three replicate cultures. From Butterwick et al. (2005).
The dependence of algal growth upon temperature is best expressed by the most fundamental measure, the specific (or relative or instantaneous) growth rate $\mu$. It is proportional to the slope or gradient of a plot of log biomass or its correlate cell numbers against time. It can be expressed, by a log, conversion, in terms of cell divisions or doublings of the biomass index in unit time (e.g., Fig. 5). It can be derived for a range of temperatures, at each of which growing replicated cultures are maintained at constant, approximately growth rate-saturating, illumination.

There are remarkably few published examples that encompass a wide range of ecologically familiar species tested at short intervals over a wide range of temperature. The fullest known to me, from Butterwick et al. (2005), is shown in Fig. 2 as growth-time graphs, with slopes of semi-logarithmic plots proportional to $\mu$ at or near light-saturation in nutrient-replete media. At the lowest and highest temperatures there is often irregular and negative behaviour, indicative of unfavourable conditions whose influence is time-dependent. Otherwise mean slopes are calculated as specific growth rates, depicted in Fig. 3 as fractions of maximum rates in relation to the temperature range tested. On this there are upper and lower limits of growth that are variable between species. Poor performance at low temperature, below 5 °C, is seen especially with the dinoflagellate *Ceratium furcoides*. Only one cyanoprobakryote (blue-green) grew sustainably at 35 °C, and only one diatom (of five tested) grew at 30 °C, at which all five green algae tested grew. Remarkably, but as reported earlier by Lund (1966), growth of the diatom *Asterionella formosa* cut off sharply above 25 °C. Besides lower or upper limits, the span of temperature for more active growth varied considerably, being particularly wide in the cryptoflagellate *Cryptomonas marssonii* – a species typically of wide seasonal occurrence. A considerable proportion of the species tested at 2 °C were there capable of sustained growth, close to the lower limit (0 °C) practicable in fresh waters. Some parallels could be drawn by Butterwick et al. (2005) with differences of the species occurrence in nature, seasonally or geographically.

This and other experimental work is restricted regarding the levels of other ambient conditions, such as light regime. For example, Foy (1983) and Foy & Gibson (1993) have shown that photoperiod can modify response to temperature. Thus, at light saturation, a 12h light : 12h dark alternation yielded a lower value of $Q_{10}$ than that obtained with continuous light. There is evidence (Morgan & Kalff, 1979; Foy & Gibson, 1993) that inhibition of growth at high levels of radiant flux is accentuated at low temperature. Seasonal field observations (Heaney et al., 1983, 1989) and experiment (Figs 2, 3) have shown that with the related dinoflagellates *Ceratium hirundinella* and *C. furcoides* there are two dissimilar influences of temperature – a lower...
range (3 to 5 °C) promoting excystment to vegetative cells and a higher range (11 to 25 °C) active growth of the latter.

Although there is limitation of growth at low and high temperature, it is a commonplace experience that a wide range of freshwater algae grow in culture in the range 10 to 20 °C. A remarkable exception is the planktonic diatom *Aulacoseira baicalensis* studied by Richardson et al. (2000), which could not be induced to grow above 8 °C. Its highest growth rate was found at 2–3 °C, the lowest temperature tested. This species represents low-temperature stenothermy, apparently an exceptional characteristic of freshwater algae. In Lake Baikal, where it is seasonally abundant, it is followed by a picoplankter, *Synechococcus limnetica*. This Richardson et al. found in culture did not grow below 6 °C, with the maximum rate obtained at 8 °C and some growth up to at least 17 °C. The differences between species – at least with nutrient-replete cells – correspond with their sequence in the seasonal (spring) increase of temperature in the lake, here likely to be a major factor. In contrast, the much-cultivated green alga *Chlorella* was early found (e.g. Sorokin, 1959) to have a high-temperature strain capable of exceptionally rapid growth at 39 °C. Later experimentation extended to other thermal autotrophic organisms, such as those isolated from hot springs in the Yellowstone National Park (Brock, 1967) and elsewhere (Castenholz, 1969). The subsequently recognised Archaebacteria include notable thermophiles. Thermal waters apart, a temperature of 35 °C or above is rarely encountered in sizeable bodies of fresh water.

Three helpful general surveys of temperature / algae relations are by Eppley (1972), Ahlgren (1987), and Raven & Geider (1988), all centred on growth kinetics and with probable cellular mechanisms considered by the last. Eppley assembled specific growth rates (µ) deduced for numerous freshwater and marine algae on a temperature scale with a considerable scatter of points, and distinguished an upper bounding line that had a gradient of factor 1.88 (temperature coefficient, Q10) per 10 °C (Fig. 4). His approach was expanded by Goldman & Carpenter (1974) to records from additional algae, and the simple exponential (Q10) relation to temperature compared with the Arrhenius relationship. These two types of relationship can be found, respectively, in Fig. 5 and Reynolds (2006). A Q10 relationship is here shown in Fig. 5 in relation to the more typical members of the freshwater phytoplankton investigated by Butterwick et al. (2005).

The operating range of each species includes regions with temperature sensitivity far below that of the Q10 gradient shown. Such insensitive regions are known from work elsewhere (Seaburg & Parker, 1983), and appear to be of typically greater extent than found (with less acclimated material?) for rates of photosynthesis (Jitts et al., 1964).

Goldman & Carpenter (1974) further coupled an exponential temperature relation, multiplicatively, to the Monod relationship of growth rate µ and nutrient-substrate concentration. Experimentally, others have explored the interaction between variable temperature and nutrient limitation (e.g. Ahlgren, 1978; Rhee & Gotham, 1981), including that in the plankton diatom *Stephanodiscus minutus* under silicon depletion (Mechlin & Kilham, 1982). It was often found that accompanying nutrient depletion lessened the effect of temperature on µ and that temperature could influence the onset of nutrient limitation.

Ahlgren (1987) reviewed exponential plots of specific growth rate based on temperature scales in °Celsius and

![Fig. 4. The maximum specific growth rates (as doublings per day) of a diversity of cultured freshwater and marine algae, assembled by Eppley (1972) in relation to temperature and with an upper bounding envelope (Q10 = 1.88) inserted.](image)
Ahlgren (1987) and Butterwick et al. (2005) could successfully apply the Bělehrádek formulation to the growth of algae over spans of temperature of limited range below the upper decline of growth, and in which the familiar $Q_{10}$ coefficient was variable.

The Eppley-type of scatter diagram, Bělehrádek formulation, and critical upper and lower limits of growth provide examples of biological limitation to a basic (chemical) form of exponential increase of rate with rising temperature (Arrhenius formulation) that can be summarised by a $Q_{10}$ value of extensive range. Any single species has an operating range for $Q_{10}$ of limited extent, coupled with absolute values of specific growth rates that fall below an upper limiting envelope as introduced by Eppley. In multiple natural populations of mixed species, a species-transition with temperature regime might confer a wider-ranging exponential response to temperature than is shown by any single species. In an even wider context, it has been used to support a metabolic-dominated theory of ecology (Brown et al., 2004).

Other biological phenomena of acclimation or ‘adaptation’ can govern a cell component (e.g. chlorophyll $a$) and hence metabolic rates referred to that component. Rhee & Gotham (1981) provide examples relevant to temperature response. However, specific growth rates have the dimension of time$^{-1}$ only, and if assessed over an extended time (as by use of a sensitive counting method: Fig. 2) will incorporate much potential acclimation of significance in nature.

If respiration is a major source of C loss relative to photosynthetic gain, resulting organic production in growth is likely to be influenced by sensitivity of respiration to temperature. At low photon fluxes this may confer a temperature-sensitivity of growth that is absent

Fig. 5. Temperature-dependency of a range of freshwater planktonic algae (Butterwick et al., 2005), shown as specific growth rates (doublings per day) on a logarithmic scale, in relation to the limiting envelope ($Q_{10} = 1.88$) distinguished by Eppley (1972).

the reciprocal of K (Absolute, Arrhenius plot), noted the lack of practical discrimination between them due to experimental variance, and championed application of equations proposed by Bělehrádek (e.g. 1926) to summarise rate–temperature relationships in various organisms. The additional assumption is made of a variable inception – a ‘biological zero’ – of growth inception on the temperature scale. It appears as $\alpha$ in the following equation, which relates specific growth rate $\mu$ to temperature ($t$) and where $a$ and $b$ are constants that can be calculated from a double logarithmic plot of experimental data with $\mu$ and $(t - \alpha)$:

$$\mu = a (t - \alpha)^b$$

whence

$$\log \mu = \log a + b. \log (t - \alpha)$$
in corresponding measures of ‘gross’ photosynthesis. However, there are examples of much overall parallelism between the growth and photosynthetic kinetics of algae (e.g. *Asterionella formosa*: Talling, 1955) in relation to varying photon flux and temperature in the ecological range. Although exceptions exist (e.g. for *Microcystis aeruginosa*: Kruger & Eloff, 1978), temperature-independence of growth at low irradiance has been recorded for some planktonic diatoms, and its generality discussed, by Gibson & Foy (1989). That of photosynthesis (Foy & Gibson, 1982) is also illustrated in Fig. 1.

In one lake, Windermere, the influence of physical factors on weekly specific growth (i.e. doublings of cell number) has been tested using dilute nutrient-replete cultures suspended over seasons at various depths over the euphotic (productive) zone (Lund, 1949; Talling, 1955, Cannon et al., 1961). Depth-profiles for specific growth rate were of a form intermediate between profiles of photosynthetic rate obtained under high and low solar radiation. Experience with *Asterionella formosa* exposed near the surface indicated a joint influence of temperature and daylength that was quantitatively compatible with the known kinetics of growth in laboratory culture (Talling, 1955). Since the spring–summer temperature increase lags behind that of daily radiation totals and daylength, the corresponding weekly growth was recognisably biased towards the higher-temperature summer compared to that in the seasonally earlier phase of highest mean daily radiation and daylength. This incidence is unlike that of the seasonal incidence of the weekly increase realised by the same species in its normal seasonal periodicity within the lake (Lund, 1950), terminated by nutrient limitation and sedimentation. In some similar tests with planktonic desmids the late-summer bias from temperature more corresponded to known periodicity in the lake (Canter & Lund, 1966; Lund, 1971). One species, *Staurastrum cingulum*, was found in laboratory culture to grow especially rapidly between 11 and 30 °C (Figs. 3, 5: Butterwick et al., 2005).

### Common interactions in ecology that involve several temperature-correlates

Temperature-correlates are common in ecological situations, and impede recognition of direct action of the temperature factor on growth-based occurrence.

Seasonality in temperate fresh waters provides several examples. Especially in deeper waters it is accompanied by density- as well as temperature-stratification that effectively subdivides the habitat and controls vertical circulation of water, nutrients and phytoplankton. One consequence is altered exposure of algal cells to light and to their sinking or buoyancy. Thus vertical profiles of species abundance are usually related to temperature stratification by mechanisms other than by direct relationship between temperature and growth – although such relationship has been suggested in some cases (Findenegg, 1943). Work on the equatorial Lake Victoria (Talling, 1957b, Fig. 3) has shown the significance of temperature differences under 1 °C on the vertical distributions of two blue-greens (buoyant), two diatoms (intermediate sinkers) and another diatom liable to deep accumulation (*Aulacoseira nyassensis* var. *victoriae*). The environmental and biological control of positive or negative sinking rates has received much attention; Reynolds (2006) provides a recent review. Implicated is the widely remarked but imperfect association, in temperate lakes, of planktonic diatoms with seasonally cooler conditions (and extended vertical circulation, also applicable to tropical lakes). Exceptions include *Fragilaria crotonensis*, a common summer form in the plankton of temperate lakes and recorded to grow in culture between 5 and 30 °C (Hartig & Wallen, 1986; Butterwick et al., 2005). Another association is that of many cyanoprokaryotes with warmer summer conditions. The measured enhancement of specific growth rate of *Oscillatoria agardhii* (Ahlgren, 1978) and *Microcystis aeruginosa* with rising temperature can be relevant for bloom-formation (Kruger & Eloff, 1978; Niklisch & Kohl, 1983), although water density-structure also contributes. Thus seasonal abundance and depth distribution may correlate with temperature, which relates to net heat gain.
or loss. Experimental evidence exists for some common summer-abundant species (e.g. *Microcystis aeruginosa*: Niklish & Kohl, 1983) and *Tychonema bourrellyi* (Heaney et al., 1996; Butterwick et al., 2005) that suggests a relation with enhanced growth rate at higher (>12 °C) temperatures. With phytoplankton in general there is also ample reason for suspecting other, indirect, relationships with season. Examples are nutrient depletion accompanying seasonal warming (e.g. Lund, 1950) and sinking out under increasing density stratification. Still more indirect and secondary is the common association of a ‘clear water phase’ and reduced algal abundance with relatively warmer weather that in the late spring–early summer also favoured the rapid parthenogenetic multiplication of cladoceran grazers (Lampert & Sommer, 1997), or that in winter favoured parasitism by chytrids (Ibelings et al., 2011).

There is somewhat better reason for operation of a direct relation of temperature and growth rate behind the widely observed increase in colonial mucilaginous algae (some historically over-attributed to *Sphaerocystis Schroeterii* Chod.) in the early summer plankton (e.g. Sommer et al., 1986), which also occurs in lakes lacking seasonal thermal stratification (e.g. Malham Tarn: Talling & Parker, 2002) and is supported by some experimental determinations of growth capacity – as of *Dictyosphaerium pulchellum* in culture at 25 and 32 °C (Ragsdale & Clebsch, 1970; Dauta, 1982). Among other green algae, there is experimental evidence for severe growth limitation at moderately low temperature for *Pandorina morum* and *Volvox* spp. (Senft et al., 1981).

Some evidence exists (e.g. Talling, 1957a, 1966; Bindloss, 1974, 1976) for a direct relationship between higher temperature and experimentally measured, light-saturated rates of photosynthesis per unit measure of biomass (e.g. chlorophyll *a*) obtained from successive field exposures over seasons. Here the most generally encountered interference is from a trend to lower specific rates of photosynthesis with increasing algal abundance in any one water-body, capable of several derivations. At higher temperature, as above 20 °C, depressed specific rates of photosynthesis can occur, as shown by Mariazzi et al. (1983), although high specific rates are widespread in tropical lakes (e.g. Talling, 1966; Lemoalle, 1981). Work on the equatorial Lake George by Ganf (1972) has shown a depression of photosynthetic rate above 35 °C and that of its ratio to respiratory oxygen uptake above 27 °C.

**Evidence from geographical distribution**

With higher and terrestrial forms of vegetation, tolerances of temperature range are undisputed partial determinants of gross latitudinal distribution. With the algae of fresh waters, the effective range is curtailed to 0 °C and above, and in these small forms dispersal is probably exceptionally effective due to the abundance of individuals (Finlay, 2002). A consequent tendency to cosmopolitanism would be enhanced by eurythermy. Association of these characteristics is indicated by the diatom *Aulacoseira* (formerly *Melosira* *granulata*, as noted by Pearsall (1923), although his deduction was based upon taxonomically flawed examples.

Restriction of geographical occurrence by temperature tolerance can be deduced by experimental testing or from the characteristics of a well-known geographical range. Experimental tests of relevance exist for very few species of tropical and circumpolar regions. For an Antarctic region, Seaburg et al. (1981) describe the growth performance of many local species isolated in culture, in relation to temperature. These showed no evidence of obligate low temperature limitation of range; on the contrary, the temperature optima for growth (here not resolved as specific rates) were generally near 20 °C, and over one-third of species tested grew at 30 °C, a temperature not occurring at the place of origin.

There appears to have been no comparable testing of tropical isolates. However, as already mentioned, a temperate isolate of the temperate-cosmopolitan diatom *Asterionella formosa* was found to have an abrupt upper limit for growth, between 25 and 26 °C. Unless other thermal strains exist – as is known for some species, e.g. *Spirulina* (*Arthrospira*) *fusiformis*: Kebede & Ahlgren, 1996 – this would imply its exclusion from the lowland tropics where the range 25–30 °C is general,
as appears in the known geographical distribution of the species (Lund, 1966; Butterwick et al., 2005).

Further evidence can be obtained from an examination of the transition between temperate and tropical floras, extended to high altitudes with low temperature range atypical of the tropics (Fig. 6). A variety of studies cited by Talling & Lemoalle (1998), of the biota of high-altitude tropical fresh waters, have concluded that low temperature is mainly responsible for floristic and faunistic peculiarities – especially absences – distinct from the surrounding low-altitude tropics. It seems that quantitative work with protozoans, rotifers and micro-crustaceans (Green 1994, 1995) has not extended to algal assemblages. However, Thomasson (1965) has noted the greater frequency of normally temperate species at high tropical altitudes, compared to waters in the tropical lowlands in which there are some distinctively tropical species. Temperature is the most probable altitudinal differential responsible.

**General remarks**

This review surveys an overall interactive situation far removed from an overall impression in terms of cardinal points – minimum, optimum, maximum – with average temperature coefficient ($Q_{10}$) of about 2.0. Nevertheless, there is the useful proposition (of Eppley) that the scatter of growth rate variation lies below such an upper exponential relationship, limiting maximum rates at low temperatures. We may remember the summary of experience by Klevaness (1988), that ‘it is a common experience that temperature optima found in the laboratory do not coincide with observations on occurrence or dominance in nature’. However, this does not hold for the abundant *Aulacoseira baicalensis* in Lake Baikal (Richardson et al., 2000), and is doubtfully applicable to tropical regions.

But quantitative prediction using the $Q_{10}$ coefficient is not unhelpful, as exemplified by the recent bold global estimate of freshwater primary production by Lewis (2011). His approach combines estimates of latitudinally predictable and other irregular factors, such as lake numbers, area and depth, with productive efficiency linked to maximum quantum efficiency and light-saturation behaviour in a water-column where there is competition between photosynthetic and residual energy absorption plus scattering, and duration aspects linked to daylength and seasonal ice-free period. Temperature-independent behaviour linked to photo-reactions is not directly represented. The whole illustrates, like the survey here, the chemically and physically influential and highly interactive role of temperature in governing primary production in fresh waters.

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**Fig. 6.** Decrease with altitude of near-bottom temperature (insensitive to diurnal changes) measured in various tropical African water-bodies. Bars indicate seasonal ranges. From Talling (1992).
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Temperature increase and primary production

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### Author Profile

Jack Talling has been engaged, since 1950, in studies on the physiological ecology of freshwater algae and the associated physical and chemical behaviour of lakes and rivers. A special interest in tropical limnology developed from early experience in Africa at Khartoum and in East Africa. All these research topics were maintained during work over more than 50 years with the Freshwater Biological Association at Windermere, including a late period there as an Honorary Research Fellow.