



Temperature and the size of freshwater phytoplankton

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Abstract We review the literature on the relationship between water temperature and size of freshwater phytoplankton, to examine the hypothesis that freshwater phytoplankton, like marine phytoplankton and many other groups of organisms, conform to Bergmann's Rule and become smaller with warming. We provide both experimental and field evidence in support of the above hypothesis, much of this evidence was hidden in studies focused on other issues, but presenting temperature and phytoplankton size data. Freshwater phytoplankton size shrinks with increasing temperature at both the species level (by cells or colonies becoming smaller) and at the community level (shift to smaller species). Exceptions to the Rule

do occur but in most cases those exceptions can be explained by indirect effects of temperature on phytoplankton size, via processes such as grazing or nutrient availability. With global warming, freshwater phytoplankton are likely to be of smaller size. This article is dedicated to Colin S. Reynolds, who has had a leading role in our personal education and understanding of phytoplankton ecology.

Keywords Cell size · Colony size · Intra-specific · Inter-specific · Seasonal

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Introduction

Size is an important feature of all organisms across diverse taxa, with widespread ecological and economic implications (Peters, 1983; Calder, 1984). The phenomenon of shrinking body size with increasing temperature is well-known from large animals, as expressed already > 170 years ago by Bergmann (1847) and known as Bergmann's Rule. This rule states that within a broadly distributed taxonomic clade, species of larger size are found in colder environments, while species of smaller size are found in warmer regions. Bergmann provided the explanation that heat loss under cold conditions would be reduced and thermoregulation facilitated at lower surface area to volume ratios. Bergmann's Rule was originally based on field observations on warm-

blooded species (endotherms), within the same genus or higher taxonomic group (family, order), demonstrating latitudinal or altitudinal gradients in body size. These were mostly mammals and birds, e.g., bears, kangaroos, penguins (Yom-Tov & Nix, 1986; Blackburn & Gaston, 1996; Ashton et al., 2000). Subsequently, Bergmann's Rule was applied to races/strains/phenotypes within the same species (Rensch, 1938; James, 1970). It was tested with ectotherms (organisms that rely on external sources for body heat), such as amphibians, turtles, fish, and insects (Lindsey, 1966; Atkinson, 1994; Sheridan & Bickford, 2011; Horne et al., 2017). It was tested at a range of temperature gradient types such as altitudinal (Berven, 1982; Atkinson, 1994), seasonal (Horne et al., 2017), inter-annual (Abonyi et al., 2020), and paleoclimatic (Falkowski & Oliver, 2007), and scaled down to protists, including diatoms and dinoflagellates (Ray, 1960; Atkinson et al., 2003). Recently, Sommer et al. (2017b) reviewed the literature and concluded that the rule holds for marine phytoplankton. This implies that Bergmann's Rule would likely apply also to freshwater phytoplankton—which is the hypothesis we set out to explore.

Water temperature affects phytoplankton both directly, by impacting its physiology and metabolic rates, as well as indirectly, by impacting its aquatic growth environment and other members of its community. The basic metabolic processes of a phytoplankton cell, such as photosynthesis, respiration, growth, nutrient uptake, are all temperature dependent (Chisholm, 1992), with rates increasing with temperature over a range of suitable temperatures but then usually declining sharply as the temperature optimum is exceeded and enzymatic systems break down (Eppley, 1972; Huey & Kingsolver, 1980; Atkinson, 1994). Water temperature also determines water viscosity and density, thus directly impacting the sinking rates of small suspended particles such as phytoplankton. Changes in sinking rates could be crucial for remaining in suspension and therefore for phytoplankton survival (Naselli-Flores et al., 2020).

Indirect temperature effects on phytoplankton may act through the environment or the community. Warming causes lakes to stratify earlier in spring and de-stratify later in autumn (Adrian et al., 2009), lengthening the duration and increasing the stability of stratification (Kraemer et al., 2015), with potentially longer optimal growth periods for eurythermic

plankton (Winder & Sommer, 2012). For example, long-term warming of surface water in tropical and deep Lake Tanganika, Africa, caused a sharper temperature gradient that reduced vertical mixing leading to declining primary production (Livingstone, 2013; Verburg et al., 2003). In lakes with winter ice-cover, warmer temperatures lead to later ice-on and earlier ice-off, and therefore a longer ice-free period (Hewitt et al. 2018). These factors strongly influence phytoplankton species composition and succession, and consequently also their size structure.

With global warming, the implications of warmer water in inland waters are of increasing concern. Based on the above relationships between temperature and body size, Daufresne et al. (2009) proposed that body size reduction is the third universal response to global warming, after changes in phenology (e.g., shifts in the timing of life cycle events; shift to phenotypes that can withstand higher temperatures) and in geographical distribution (migration to higher latitudes/altitudes) (Durant et al., 2007; Visser & Both, 2005; Gardner et al., 2011). The reduction in body size tends to be stronger in aquatic than in terrestrial systems, and greater in freshwater compared with marine environments (Forster et al., 2012). While this topic is drawing increasing scientific interest as attested by the number of publications during 1991–2019 with 'cell size' and 'phytoplankton' as key words, only a small fraction of these articles address freshwater or lake systems (Fig. 1).

Our objective was to review the literature on the relationships between phytoplankton cell or colony size and water temperature in inland waters, at both the species and community levels. To achieve this

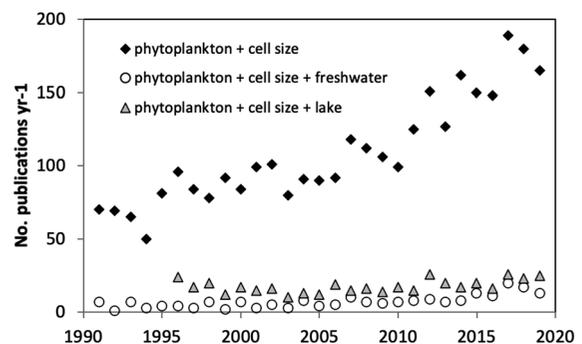


Fig. 1 Results of a web-of-science search for the number of articles published each year from 1991 to 2019, with keywords as indicated in the symbol legend

objective, we have searched the literature for studies directly addressing our hypothesis, that freshwater phytoplankton are smaller under warmer growth conditions. We further searched for studies focusing on other issues while presenting data on phytoplankton size and temperature that could be re-examined and interpreted in view of our hypothesis. We conclude that it is likely that the same principle, linking body size with the temperature of the environment, holds also for freshwater phytoplankton.

We, the authors, dedicate this article to the memory of Colin S. Reynolds, who has had a leading role in our personal education and understanding of phytoplankton ecology, through his seminal books (Reynolds, 1984, 1997, 2006) and hundreds of research and review articles, and personal interactions. His work has influenced the way of thinking of a whole generation of freshwater phytoplankton scientists. Our review of how the size of freshwater phytoplankton responds to changing temperatures falls in line with his overview of phytoplankton ecology.

Temperature effects on phytoplankton size: experimental evidence

Laboratory studies under controlled conditions allow us to isolate the specific effects of temperature on body size, hence their important contribution to exploring the relationship between organism size and cultivation temperature for different species, a single species at a time and also for assemblages of different species incubated together. Below we summarize evidence from experiments on clonal cultures (within-species effects), looking first at changes in the size of individual cells, and then at the size of colonies or filaments. We then proceed with experiments on natural assemblages (indoor or outdoor incubations in microcosms and mesocosms), to examine inter-species effects.

Experiments on clonal cultures (within-species effects)

Modifying size by changing the linear dimensions of individual cells

Already in the 1950s, Margalef (1954) studied the impact of temperature on cell size of *Scenedesmus*

(Chlorophyta) in a series of clonal culture experiments. In his words “Experimental work was started as an attempt to obtain further evidence of the estival [i.e. relating to summer, TZ] reduction of size observed in diverse freshwater organisms”. No citations were given. It seems that Margalef considered the decline in size with increasing temperature to be a well-known phenomenon, one that does not even require a citation. Culturing *Scenedesmus obliquus* (Turpin) Kützing (currently *Tetradesmus obliquus* (Turpin) M.J. Wynne), he noted that the linear dimensions of cells reared at 13.5°C increased over 2 weeks, whereas the dimensions of cells of the same clone reared under identical conditions but at 23°C declined over the same period. Furthermore, a 10°C difference of the cultivation temperature was associated with a 90% difference in mean cell length (12.9 µm at 17°C vs. 6.8 µm at 27°C) and 24% difference in mean cell diameter (3.6 µm at 17°C vs. 2.9 µm at 27°C). Other physio-chemical and density-dependent factors examined had similar but smaller effects. Margalef (1954) concluded that the alteration of cell size is a non-heritable, direct response to changing environmental parameters. Following Margalef, Ray (1960) incubated 4 species of the chlorophyte *Chlamydomonas* under controlled laboratory conditions at different temperatures and recorded their cell length. Three of the species exhibited a significant decline in body size with increasing temperature that averaged 10.7% per 10°C. The fourth species was isolated from the Alpine Lake Tovel, Italy, at almost 1200 m elevation, so originally from a colder environment than the other three species. This cold-water species did not show a change of size with increasing temperature from 12 to 30°C, but it was the largest of the four species, conforming with the hypothesized increase in size with increasing geographical altitude, i.e., colder conditions. Possibly, this alga was grown outside its optimal temperature range. Later, Schaum et al. (2017) showed a strongly significant negative linear correlation between growth temperature and cell size of *Chlamydomonas* cultures grown at 8 temperatures ranging 16–42°C.

Trainor (1992a, b, 1993, 1998) studied the phenotypic plasticity of several species of *Scenedesmus* (currently *Desmodesmus*) grown in batch cultures at 10 and 22°C. He reported several cases of within-species temperature-related variability in size, which he attributed to cyclomorphosis (cyclic or seasonal

changes in the phenotype of an organism through successive generations). All species were larger at 10°C and smaller at 22°C, with some differences in the details of how the size changed with temperature. At the lower temperature, *Scenedesmus communis* E. Hegewald (currently *Desmodesmus communis* (E. Hegewald) E. Hegewald) cells were larger and four-celled colonies were up to 3.5 times wider than those at the higher temperature (Trainor, 1992a). During log growth, at 10°C *S. communis* developed multi-spined, eight-celled colonies rather than typical four-celled, four-spined colonies (Trainor, 1992a). Similarly, *Scenedesmus subspicatus* Chodat (currently *Desmodesmus subspicatus* (Chodat) E. Hegewald & A.W.F.Schmidt) was unicellular at 22°C whereas at 10°C colony production was stimulated, with up to 67% 4-celled or 8-celled colonies that developed during the early stationary phase of growth (Trainor 1993). For *Scenedesmus armatus* Chodat (currently *Desmodesmus armatus* (Chodat.) E.H. Hegewald) (Trainor (1992b), single cells as well as colonies were larger at the colder temperature. Cell length was not significantly different regardless of temperature, but cell width increased markedly at the lower temperature. In addition, an arcuate (curved), eight-celled, multi-spined ecomorph was produced at 10°C. *Scenedesmus abundans* (O. Kirchner) Chodat also had larger cells at the lower temperature (Trainor, 1998). Trainor concluded that these species show distinct cold-water and warm-water ecomorphs.

Coles & Jones (2000) grew unialgal cultures of *Microcystis*, *Merismopedia*, *Oscillatoria* and *Aulacoseira* isolated from the Potomac River at 15, 20, 25 and 30°C to determine their photosynthesis-light response and growth at the different temperatures. Cell diameter of *Microcystis* declined from 3.6 µm at the lower temperatures to 3.0 µm at 25 and 30°C, when intensive blooms developed. They reported only minor changes in cell size for the other 3 species. Neustupa et al. (2008) grew cultures of the desmid *Micrasterias rotata* Ralfs at different temperatures (10–30°C) and followed their morphology. They reported a decline in length and width of cells with increasing temperature from 15 to 30°C.

Jezberová & Komárková (2007) grew cultures of picoplanktonic cyanobacteria (*Synechococcus* and *Chroococcus*) at 8, 20 and 28°C. Single cells of all strains were larger at 8°C, although contrary to our hypothesis, two strains formed chains (i.e., larger

“algal units”) at 28°C. Other results that do not conform to Bergmann’s Rule are rare. An example is the psychrophilic dinoflagellate *Borghiella dodgei* Moestrup, Hansen et Daugbjerg grown in the laboratory by Flaim et al. (2010). Its cell size increased as temperature increased above the cell optimum of 5°C, while growth rate decreased.

Modifying size by changing the number of cells per colony

The published literature on size changes due to modifications to the number of cells per colony is extremely slim. In addition to the studies of Trainor (1992a, b, 1993) and Jezberová & Komárková (2007) reported above, who looked at both cell size and the number of cells per colony or filament, we found only one additional experimental study addressing colony size. Lürling & Van Donk (1999) cultured *Scenedesmus acutus* Meyen (currently *Tetradesmus obliquus* (Turpin) M.J. Wynne) at four temperatures (9.5°, 16.5°, 24°, and 29° C) and reported that the number of cells per colony increased with declining temperature.

Experiments on natural assemblages: inter-species effects

Moss et al. (2003) imitated shallow lake ecosystems using 3200-l mesocosms sunk into the ground with sediment on bottom, submerged macrophytes, and benthic invertebrates. Those mesocosms were either heated by 3°C (all year round or in summer only) or unheated (controls). Total biomass and chlorophyll showed no significant change with warming by 3°C. Warming modestly decreased the abundance of dinoflagellates and especially of cryptophytes, while other taxa were not impacted significantly and cyanobacteria did not become dominant with warming. They concluded that a 3°C temperature change may not have been large enough to cause major species shifts under the prevailing conditions. No size measurements were made, so we cannot assess whether warming impacted cell- or colony-size.

Rasconi et al. (2015) conducted a multi-seasonal (8 months) outdoor mesocosm experiment to test how increasing water temperature and brownification affect plankton community composition, phenology, and functioning. They filled 24 cylindrical polyethylene containers with 400 l of surface water from pre-

Alpine, oligotrophic Lake Lunz, Austria, added zooplankton, and conducted 2-weekly sampling for nutrients, zooplankton and phytoplankton. They split phytoplankton into 3 size classes: pico ($< 5 \mu\text{m}$), small (5–20), large (20–100 μm). They found a clear effect of higher temperature (+ 3°C) on phytoplankton size structure, with significantly higher abundance of the smaller size classes (pico- and nano-phytoplankton). The size shift was associated with lower phytoplankton community diversity but higher primary production, which were related to higher community turnover and faster growth rates rather than increasing photosynthetic efficiency.

Pulina et al. (2016) ran a 2-week indoor experiment, incubating brackish water from Cabras Lagoon, Sardinia in 10-l buckets at different temperatures. Three treatments were applied in triplicates: control (11°C), + 3°C increase (14°C), and + 6°C increase (17°C). They reported significant effects of warming on phytoplankton size structure: the abundance of smaller celled taxa (*Chlorella* sp. and *Planktothrix agardhii-rubescens* group) increased at 17°C, whereas the abundance of larger taxa (*Cyclotella* sp. and *Thalassiosira* sp.) decreased, compared with the controls.

Yvon-Durocher et al. (2011) conducted an outdoor mesocosm experiment at FBA, UK. Twenty outdoor mesocosms were filled with local water, organic matter, phytoplankton, zooplankton, and fish (Roach) half of which were warmed by 4°C. After 1 year, warming shifted the distribution of phytoplankton size toward smaller species and individuals with rapid turnover and low standing biomass, resulting in a restructured foodweb. Yvon-Durocher et al. (2015) conducted another outdoor mesocosm experiment, using the same experimental setup as in the 2011 paper, but now sampling after 5 years of experimental warming by 4°C. By then, the phytoplankton was adapted to the warmer temperatures. The results were contradictory to those of the former study: phytoplankton communities in the warmed treatments were more species rich, had larger standing stock of biomass and were dominated by species larger by order-of-magnitude. The authors attributed the size change to increased zooplankton grazing pressure. Using the same outdoor mesocosm experimental setup of Yvon-Durocher et al., Padfield et al. (2018) examined the response of phytoplankton communities after 10 years of experimental warming by 4°C. Warmed and ambient phytoplankton communities

differed substantially in their taxonomic composition and size structure, with warmed communities having larger species.

Temperature effects on phytoplankton size: field evidence

Field studies specifically examining the relationship between water temperature and phytoplankton size are rare, especially for freshwater (Sommer et al., 2017b). The few available studies are not only reviewed here, but we also found data hidden in studies addressing other issues but presenting cell size and water temperature data. Again, reported size changes occur at both the species (within-species) and community (between species) levels. At the community level, changes occur over temperature gradients that are either spatial (altitudinal, latitudinal) or temporal (seasonal, multiannual, geological time scales). We did not find studies reporting on size changes with altitudinal or longitudinal temperature changes, so all studies address temporal changes of temperature.

Seasonal

According to our hypothesis, in water bodies with large seasonal temperature gradients of $> 10^\circ\text{C}$, such as subjected to temperate and subtropical (but not tropical) climates, changes in phytoplankton cell size are expected to occur seasonally, with smaller sizes in summer, larger in winter. There is ample evidence to demonstrate this, by simply examining patterns of seasonal changes of cell or colony size, at both community and species and level.

Community level size shifts

The temperature of the upper 10 m layer in Lake Washington, USA fluctuates between 7°C in winter and 21°C in summer (Arhonditsis et al., 2003). The lake experiences a typical annual pattern of phytoplankton community compositions that repeats from year to year, with a major diatom bloom (*Aulacoseira*, *Fragilaria*, *Asterionella*) in March–April each year, followed by low biomass in summer and dominance of small-sized chlorophytes and cyanobacteria (Arhonditsis et al., 2003). A similar annual pattern was typical in the 1970s and 1980s in Lake Kinneret, Israel (with a

15°C difference between winter and summer water temperatures), showing a recurring early spring bloom of the large dinoflagellate *Peridinium gatunense* Nygaard, that was replaced by small nanoplanktonic species in summer-fall (Zohary, 2004). Since the mid 1990s, the dominant species in Lake Kinneret have changed (Zohary et al., 2014), but the pattern of larger species in winter-spring and smaller in summer-fall still exists, although the size differences are not as extreme as in the past. Similarly, Sin et al. (2000) reported seasonal changes in the phytoplankton of York River, USA, with larger species in winter and smaller in summer. Pulina et al. (2019) analyzed multiannual (2006–2015) variability of single phytoplankton species and assemblage size structure in a man-made reservoir in Sardinia. They found that throughout the 10-year study smaller mean cell size dominated in summer whereas larger mean size dominated in winter. Apparently, this seasonal succession pattern is quite common.

Quite different patterns might be found in eutrophic lakes, where summer biomass is dominated by large colonies/filaments of cyanobacteria (*Microcystis*, *Dolichospermum*, *Aphanizomenon*) or large dinoflagellates (e.g., *Ceratium hirundinella* (O.F. Müller) Dujardin) (Sommer et al., 1986, 2012). Lake Constance underwent a recovery from eutrophication since the early 1980s. During peak eutrophication around 1980, the spring bloom occurring after the onset of stratification at temperatures from 7 to 12°C consisted primarily of nanoplanktonic diatoms (small *Stephanodiscus* spp.) and cryptophytes (*Rhodomonas*) while during summer at ~ 10°C higher temperatures there was a succession from a dominance of medium sized, colonial diatoms (*Asterionella*, *Fragilaria*, *Diatoma*, *Stephanodiscus*) over large green algae (e.g., *Pandorina*) to colonial and filamentous cyanobacteria and large dinoflagellates (Sommer, 1985). With recovery from eutrophication, medium-sized diatoms started to dominate during the spring bloom and the summer biomass of large cyanobacteria and dinoflagellates declined, thus leading toward a large to small seasonal size trajectory (Sommer et al., 1993).

Species level size shifts

Atkinson (1994) was probably the first to argue that for ectotherms, including plants, protists and the vast

majority of animals that rely on external sources for body heat, temperature was a good correlate of body size between seasons and from one generation to the next. Field studies demonstrating seasonal changes in body size with smaller morphs typically occurring in summer are quite frequent for a diversity of small animals, such as arthropods (Chown & Gaston, 2010; Horne et al., 2017).

Gibson (1975) reported seasonal fluctuations in filament length of *Oscillatoria redekei* Van Goor, with longest filaments in February–March, and shortest in June–July. But exceptionally, long filaments were also recorded in April and August. Zohary et al. (2017) analyzed a multiannual record (2004–2012) of cell size data for phytoplankton species from Lake Kinneret, Israel, sampled at 2-week intervals. Many of the species abundant enough to be counted year-round showed a typical seasonal cell size pattern that repeated from year to year: cell diameter was maximal in winter and minimal in summer. This pattern was shared by species of cyanobacteria, chlorophytes, and dinoflagellates. In some colonial species of diatoms, chlorophytes, and cyanobacteria, becoming smaller in summer was achieved by an alternative strategy: by having a smaller number of cells per colony. Similar data of seasonal shifts in cell size were reported by Naselli-Flores et al. (2020), for a chlorophyte and a diatom from a Sicilian Reservoir. Abonyi et al. (2020) studied long-term (1979–2012) trends of mean cell size of phytoplankton and of centric diatoms in the Danube River. In addition to a long-term trend of decline in average cell size, they reported that the phytoplankton was consistently of smaller average size in the summer than in the winter. Both the seasonal and long-term size changes were recorded at multiple assemblage levels: whole community, centric diatoms, as well as a specific diatom genus (*Stephanodiscus* spp.). They attributed the changes in phytoplankton size structure to longer water residence time, warming and decline in nutrients and suspended solids.

Multiannual (decades to centuries)

Winder et al. (2009) studied the diatoms of Lake Tahoe, USA from 1982 to 2006. They reported that over time, smaller species replaced larger species, and correlated this shift to increasing lake stability with reduced vertical mixing. While temperature data were

not presented, they explained the increase in stability by global warming. Other long-term studies on natural diatom populations, using paleolimnological methods to follow changes over the last 50–150 years, showed the same pattern, of replacement of larger diatom species by smaller ones as water temperature increased, ice cover became shorter while the growing season became longer (Rühland & Smol, 2005; Smol et al., 2005, Rühland et al., 2008).

Abonyi et al. (2018) analyzed long-term (1980–2010) changes in the River Danube in phytoplankton traits in response to re-oligotrophication and climate change as expressed by extended time periods of low-flow conditions together with more frequent flood events. They reported the occurrence of a regime shift to which the planktonic community responded with decreasing cell size, as expected by our hypothesis. At the same time, the frequency of dispersed large-sized elements such as benthic diatoms and large filamentous limnophilic taxa increased, in response to more frequent floods following extended periods of low flow.

Geological time scale

For this much longer time scale we did not find evidence from the freshwater literature, and therefore cite marine studies. Falkowski & Oliver (2007) examined fossil records of diatoms preserved in marine sediments spanning the past 200 million years, and found that diatom frustule size changed with temperature, being smaller at warmer temperatures. Mousing et al. (2017) analyzed the sedimentary archive of dinoflagellate cysts in a sediment record taken from the West Greenland shelf and show that mean cell size decreased at both intra- and interspecific scales in a period of relatively warm temperatures compared with periods of colder temperatures (during the Little Ice Age). The share of intra-specific changes in size was greater than interspecific changes.

Physiological implications of changing size

While crucial to understanding the implications of declined size with increasing temperature in freshwater phytoplankton, the topic of physiological implications of changing size is well-reviewed (Chisholm,

1992; Litchman & Klausmeier, 2008; Marañón, 2015) and is therefore covered here only briefly.

Growth and resource acquisition

Smaller organisms have higher biomass-specific metabolic rates, which generally scale with the -0.25 th power (“allometry coefficient”) of body mass (Peters, 1983). This effect is reflected by population growth rates. Generally, phytoplankton studies demonstrating increasing maximal growth rates with declining algal size confirmed this trend qualitatively, though the value of the allometry coefficient varies widely among studies, from -0.06 (Finkel et al., 2010) to -0.32 (Schlesinger et al., 1981), as reviewed in Sommer et al. (2017a). However, it seems that the size dependence of maximal growth rates either breaks down or is even reverted for the smallest phytoplankton, those with volume $< 100 \mu\text{m}^3$ or having an equivalent sphere diameter of $\sim 6 \mu\text{m}$ (Marañón et al., 2013; Marañón, 2015). A unimodal response was also reported for mass-specific rates of photosynthesis and respiration (López-Sandoval et al., 2014).

Under limiting nutrient supply, smaller phytoplankton experience even further advantages because their favorable surface area:volume ratio reduces diffusion limitation of nutrient transport to the cells (Raven, 1998; Litchman et al., 2007). Similar to the advantage at lower nutrient availability, smaller phytoplankton also experience an advantage under low-light conditions because of higher cross-sectional area:volume ratios and a smaller package effect, i.e., less intracellular self-shading of chloroplasts (Finkel, 2001; Finkel et al., 2004; Malerba et al., 2018).

On the other hand, larger cells can better utilize pulses of elevated nutrient concentrations to build up intracellular storage pools, because maximal uptake rates per cell increase linearly with cell mass, while minimal cell quotas (the structural minimum of a limiting element per cell) increase less than linearly with cell mass (Edwards et al., 2012; Marañón et al., 2013; Marañón, 2015). This provides an advantage to larger phytoplankton, if nutrient supply is variable in space and time (Turpin & Harrison, 1979; Rothhaupt & Güde, 1992).

Exploitation of the spatial heterogeneity of resources becomes particularly important when prolonged stratification of the water column leads to

vertical segregation of light availability (declining with depth) and nutrients (increasing with depth), which becomes more pronounced in more eutrophic lakes. Under such circumstances, it is beneficial to perform diel vertical migrations, either by flagellar movements (Sommer & Gliwicz, 1986; Sommer, 1988) or by density regulation below and above the density of the surrounding water like in gas-vacuolated cyanobacteria (Walsby, 1972; Walsby & Reynolds, 1980). In both cases larger phytoplankton achieve larger diel vertical migration amplitudes, with reported maxima of 18 m in the case of the large, colonial flagellate *Volvox* and up to 50 m by large, colonial cyanobacteria. The diel migration amplitudes of flagellates were described by a continuous size–amplitude relationship, independent of the colony status, e.g., single-celled dinoflagellates and colonial *Volvox* (Sommer, 1988).

Losses (sinking and grazing)

The major loss processes of phytoplankton are sinking, grazing and parasitism *sensu lato* (e.g., fungi or by viruses). The size dependence of the former two is well-established knowledge (Reynolds, 2006), while at present too little is known about possible size relationships of parasitism to warrant a review.

Other properties of the sinking particles being equal, sinking velocities increase quadratically with the diameter of a sphere of equal volume and linearly with the difference between the density of the sinking particle and the water (Stoke's law). The ascent velocity of algae lighter than water (see above: density regulation of cyanobacteria) follows the same law. Phytoplankton have adopted various types of extensions and pertuberances to reduce sinking velocities (relative to that of a sphere of the same volume), this is quantified by the 'form resistance' factor added to the Stoke's Equation (Padisák et al., 2003).

Also, according to Stoke's equation, sinking rates of particles are inversely related to viscosity and directly related to water density, both of which decline with increasing temperature, with different decreasing slopes. Therefore, as temperature changes, the sinking velocity of a phytoplankton cell changes, with implications for the need to remain entrained and avoid sinking out of the water column. According to Stoke's equation, the sinking velocity of a spherical algal cell with a radius of 20 μm will change by $\sim 30\%$

between 15 and 30°C, due to changes in water viscosity and density alone (Zohary et al., 2017). A summary of current knowledge on temperature and phytoplankton sinking rates was given by Naselli-Flores et al. (2020).

Realized sinking velocities of algae range from close to zero to ca. 10^{-4} m s^{-1} (equivalent to 8.6 m day^{-1}) for very large diatoms (Walsby & Reynolds, 1980). However, for most other diatoms sinking velocities of individual cells or colonies are in the order of 1 m day^{-1} or even less (Riebesell, 1989; Kiørboe, 1993) while non-silicified phytoplankton sink even slower. The population loss rate to sinking (s ; in day^{-1}) from a continuously mixed water layer can be approximated by the ratio of the sinking velocity (v ; in m day^{-1}) and the mixing depth (z_m ; in m): $s = v/z_m$ (Reynolds, 1984). This means that sinking can be a substantial population loss for large and heavy, non-flagellated algae during summer stratification, favoring their smaller or motile competitors, while this effect vanishes during deep mixing.

Size is also the dominant factor determining who eats whom in plankton. From the beginning of intensive grazing studies, it has been acknowledged that larger algae profit from being better protected from grazing than smaller ones (Gliwicz, 1980; Sommer et al., 1986). Overall, maximal sizes of edible algae increase with the body size of grazers. Thus, it is usually assumed that heterotrophic nanoflagellates (2 to 20 μm) graze primarily on picoplankton ($< 2 \mu\text{m}$), microzooplankton (20 to 200 μm , ciliates, heterotrophic dinoflagellates) on phytoplankton smaller than 5 to 10 μm (Sherr & Sherr, 2002) and filter-feeding cladocerans on phytoplankton $< 30 \mu\text{m}$ (Gliwicz, 1980; Geller & Müller, 1981). The lower size limits of these groups' feeding ranges do not differ very much from each other and extend to the lower end of the phytoplankton size spectrum. There are some exceptions, e.g., heterotrophic flagellates feeding on almost equal-sized prey (Moustaka-Gouni et al., 2016). Within the mesozooplankton grazer guild, copepods differ substantially from cladocerans. They feed inefficiently on phytoplankton smaller than 5 to 10 μm , and even release them from grazing pressure by feeding also on heterotrophic protists (Sommer & Sommer, 2006). Therefore, zooplankton taxonomic composition has a major impact on phytoplankton size distribution (e.g., Carpenter & Kitchell, 1984). For example, in a lake

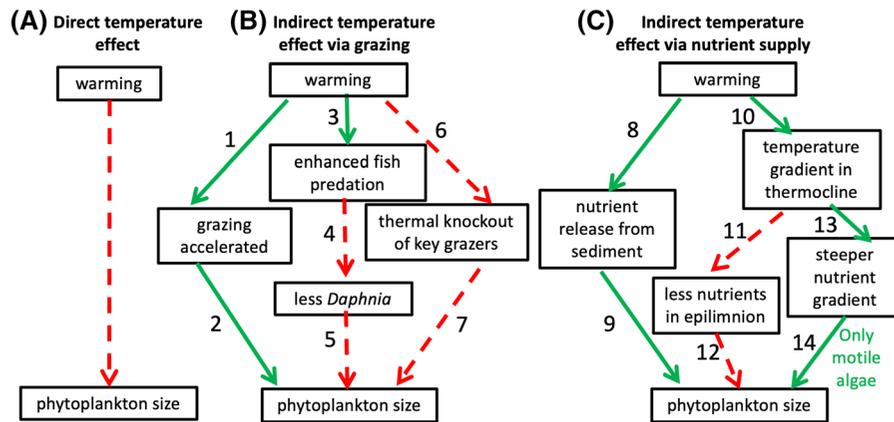


Fig. 2 Major pathways of direct and indirect temperature effects on phytoplankton size; green solid arrows: positive effects; red dashed arrows: negative effects. **A** The direct effect of temperature on phytoplankton size. **B** applies when *Daphnia* spp. dominates grazing on phytoplankton. Under copepod dominance the effects on phytoplankton size are reversed. In **C**, only motile species respond positively to steeper nutrient gradients. Numerical symbols for pathways: (1) higher grazing rates because of higher temperature; (2) stronger removal of small phytoplankton by filter feeding *Daphnia*; (3) higher feeding rates of zooplanktivorous fish; (4) selective removal of larger zooplankton, especially *Daphnia*; (5) less removal of

mesocosm experiment, Sommer et al., 2001 found that copepods drove phytoplankton size structure toward a dominance of small taxa while grazing by the cladoceran *Daphnia* drove it toward dominance of large taxa.

Conclusions

Apparently, information considered accepted and well known in the 1950s, that diverse freshwater organisms are smaller in summer than in winter (Margalef, 1954), has been more or less forgotten over time, or at least received negligible attention, until global change research initiated renewed interest in this topic. The issue of temperature effects on size became superseded by the issues of size-selective grazing, size–nutrient relationships and size–sedimentation relationships. Only recently it is beginning to receive renewed attention in both experimental and field studies (Sommer et al., 2017b; Zohary et al., 2017). Our survey of the literature suggests that there is quite a strong support for the hypothesis that freshwater phytoplankton, like marine phytoplankton and like

smaller phytoplankton; (6) transgression of thermal tolerance limits of *Daphnia*; (7) less removal of small algae; (8) warming increases the release rates of nutrients from sediments; (9) more nutrients reduce the competitive advantage of smaller phytoplankton; (10) warming leads to a steeper thermocline; (11) a steeper thermocline reduces upward vertical nutrient transport; (12) more stringent nutrient limitation in the epilimnion increases the competitive advantage of smaller phytoplankton; (13) a steeper thermocline leads to a steeper vertical nutrient gradient; (14) large motile algae can exploit deep water nutrient reservoirs by vertical migration

other ecological groups of organisms, tend to become smaller with warming. Most studies reported here supported this conclusion although we did report on a few exceptions to the rule. Temperature changes of only 2–3°C result in body size changes of only a few %, that are often within the measurement error of light microscopy, especially for data collected in pre-digital times, and therefore were often left unnoticed or unrecorded. Selection between differently sized species produces effects that are easier to notice, but indirect temperature effects via nutrients or grazing might supersede direct selection by temperature. Figure 2 depicts two major complexes of indirect temperature effects alongside the simple direct effect. The indirect effects apply to seasonal, geographic and climate change-related temperature changes. The indirect effects acting via the grazing pathway (Fig. 2B) depend on the dominant crustacean zooplankton group (Sommer & Sommer, 2006). Under *Daphnia* dominance, like in many temperate lakes, accelerated physiological rates of grazers will benefit the larger algae, while accelerated fish predation and transgression of thermal optima of *Daphnia* and in particular knock-out by transgression of lethal limits

will favor the smaller algae. If copepods dominate, as seen in marine environments, the size effects on phytoplankton will be the opposite. The indirect pathways acting via nutrient supply (Fig. 2C) contain two major pathways: nutrient release from the sediment that is accelerated by warming—favors larger phytoplankton. Concurrently, warming causes a stronger temperature gradient at the thermocline, leading to more stringent nutrient limitation in the epilimnion (beneficial for small algae) with steeper nutrient gradients across the thermocline (beneficial for large algae). The relative importance of those main pathways is highly dependent on lake morphometry and trophic state. Shallowness increases the importance of internal nutrient loading from the sediment. Under strong stratification, the ‘less nutrients in epilimnion’ effect prevails under oligotrophic conditions and the steeper nutrient gradient effect prevails under eutrophic conditions (Sommer et al., 2017a).

From the practical point of view, it is becoming obvious that phytoplankton biomass estimates should be based on seasonally determined biovolume per species data rather than fixed values. This is a direct outcome of our understanding that cell size of many phytoplankton species fluctuates seasonally in most regions of the world (excluding the tropics). It is therefore crucial to measure regularly the dimensions of the dominant taxa and consider their biovolume per cell for biomass calculations.

From a global perspective, we would expect to see small-sized freshwater phytoplankton in the future as global warming changes ambient temperatures. This means lower algal biomass for the same cell density, with likely implications for higher trophic levels and specifically less food for grazers, and possibly less fish production. This could lead to more frequent occurrence of “clear-water phases” in large, human-impacted lakes and rivers under global change.

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