

Cell size as driver and sentinel of phytoplankton community structure and functioning

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Abstract

1. Body size is a decisive functional trait in many organisms, especially for phytoplankton, which span several orders of magnitude in cell volume. Therefore, the analysis of size as a functional trait driving species' performance has received wide attention in aquatic ecology, amended in recent decades by studies documenting changes in phytoplankton size in response to abiotic or biotic factors in the environment.
2. We performed a systematic literature review to provide an overarching, partially quantitative synthesis of cell size as a driver and sentinel of phytoplankton ecology. We found consistent and significant allometric relationships between cell sizes and the functional performance of phytoplankton species (cellular rates of carbon fixation, respiration and exudation as well as resource affinities, uptake and content). Size scaling became weaker, absent or even negative when addressing C- or volume-specific rates or growth. C-specific photosynthesis and population growth rate peaked at intermediate cell sizes around $100 \mu\text{m}^3$.
3. Additionally, we found a rich literature on sizes changing in response to warming, nutrients and pollutants. Whereas small cells tended to dominate under oligotrophic and warm conditions, there are a few notable exceptions, which indicates that other environmental or biotic constraints alter this general trend. Grazing seems a likely explanation, which we reviewed to understand both how size affects edibility and how size structure changes in response to grazing. Cell size also predisposes the strength and outcome of competitive interactions between algal species. Finally, we address size in a community context, where size-abundance scaling describes community composition and thereby the biodiversity in phytoplankton assemblages.

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4. We conclude that (a) size is a highly predictive trait for phytoplankton metabolism at the cellular scale, with less strong and nonlinear implications for growth and specific metabolism and (b) size structure is a highly suitable sentinel of phytoplankton responses to changing environments.

KEYWORDS

biovolume, growth, meta-analysis, metabolism, nutrients, systematic review, trait-based ecology, warming

1 | INTRODUCTION

Body size is a decisive element of functional ecology as its implications propagate from basic physiology to the organization of ecological communities and ecosystems as well as evolution (Gould, 1966; LaBarbera, 1989; Peters, 1983). Allometric scaling of basal metabolic rates (Brown et al., 2004; Elgar & Harvey, 1987; West et al., 1997) extends to predict population growth or mortality rates (Marba et al., 2007), maximum abundances (Belgrano et al., 2002; Damuth, 1981) and home range sizes (McNab, 1963). Size is also decisive in structuring interspecific interactions, especially consumer–resource relationships (Brose et al., 2006; Cohen et al., 2003), and community properties such as species diversity (Cermeño & Figueiras, 2008; Ryabov et al., 2021).

The role of size is especially pervasive in pelagic ecosystems (Andersen et al., 2016) as pelagic food webs are strongly size-structured down to the primary producers (Brooks & Dodson, 1965). Whereas the carnivore–prey body size ratio is comparable across ecosystem types (Brose et al., 2006), aquatic and terrestrial systems differ especially at the herbivore–autotroph link (Lindeman, 1942; Shurin et al., 2006; Trebilco et al., 2013). Pelagic systems show heterotroph to autotroph biomass ratios of 1 (Cebrian et al., 2009), which is much higher than most other aquatic and all terrestrial ecosystem types, and reflects that a higher proportion of primary production is consumed by herbivores in pelagic systems than in those with ‘macrobial’ autotrophs (Cebrian, 1999; Cyr & Pace, 1993). Part of this difference is based on the smaller size of microalgae compared to terrestrial plants and macroalgae (Shurin et al., 2006), which coincides with higher growth rates, higher nutrient content and higher palatability (Cebrian et al., 2009).

Assessing phytoplankton size structure therefore is key to understand pelagic food web organization and flows of energy and matter, as these depend on the carbon fixed by phytoplankton. At the same time, phytoplankton span an extraordinary range of size classes: Largest linear dimensions cover 5 orders of magnitude across phytoplankton (Finkel et al., 2010) and volumes more than 8 orders of magnitude (Ryabov et al., 2021), which is 100–1,000 times the size range of terrestrial mammals or birds (Maurer et al., 1992). Consequently, the analysis of size classes has a long

tradition in phytoplankton ecology, often with cut-offs between pico-, nano- and microplankton based on filter sizes (Legendre & Rassoulzadegan, 1996). Analyses of size-fractionated primary production and element cycles have been and still are an important tool in biological oceanography (Durbin et al., 1975; Larsson & Hagström, 1982). In more detailed analyses of nutrient uptake, respiration, photosynthesis and growth, continuous estimates of cell size have been used (Agusti et al., 1987; Banse, 1976; Taguchi, 1976). These often derive from microscopic measurements and approximations as biovolume or cell volume (Hillebrand et al., 1999). Understanding cell size as a predictor of functional aspects of pelagic microalgae has gained additional momentum in the light of establishing a trait-based phytoplankton ecology (Litchman & Klausmeier, 2008; Litchman et al., 2007).

In this review, we bring the rich literature on phytoplankton cell size together by adopting a systematic literature review process (Hillebrand & Gurevitch, 2016; Lortie, 2014) to build a comprehensive basis for our synthesis. We report the steps of this approach according to PRISMA (preferred reporting items for systematic review and meta-analysis) principles (Moher et al., 2015) to enhance reproducibility of the review. We use this literature basis to assess both consequences of cell size and causes of cell size. The former focuses on cell size as a driver of phytoplankton performance (primarily at the species level) and also addresses the importance of cell size in species interactions and community contexts. The latter focuses on how cell size responds to environmental factors and therefore can act as a sentinel of changing conditions.

This effort stands on the shoulders of previous reviews, starting with Banse's review of how photosynthesis and respiration and, consequentially, growth rate of phytoplankton scale to size (Banse, 1976). With a similar aim, Sommer et al. (2017) summarized the importance of size for phytoplankton population dynamics, especially growth rate and loss-related processes (sedimentation, grazing). Finkel et al. (2010) added a review on how cell size influences elemental composition and stoichiometry of phytoplankton and how this might change in a changing ocean. The relationship between global warming, temperature and phytoplankton cell size is also at the core of a recent freshwater review (Zohary et al., 2021). Perhaps most comprising to date is a review that addresses both functional and numerical responses of marine phytoplankton species in relation

to their cell size (Marañón, 2015), but extends towards community composition and macroecology.

While these thorough reviews successfully synthesized qualitative and sometimes quantitative information on how cell size relates to ecological and physiological processes, they often relate to marine or freshwater systems or focus on specific processes (growth, stoichiometry or response to warming). Here we provide a highly comprehensive systematic review and meta-analysis on phytoplankton cell size that incorporates both marine and freshwater data and spans levels of organization from cellular processes to communities. In a rapidly changing field, we provide quantitative size scaling rules across the diversity of phytoplankton taxa for cell size as a driver of physiology, connect these findings to species performance and interactions along environmental gradients and scan the horizon for recently emerging and future research questions. More specifically, we aim at understanding how cell size functionally constrains the performance of algae in terms of photosynthesis, nutrient uptake and growth (Aim 1). Here, we provide a cross-system quantitative meta-analysis summarizing the current evidence for the relationship between cell size and (a) physiological rates at the cellular level as well as (b) specific physiological rates scaled to unit carbon or biovolume. Considering cell size as a response, we bring together information from previous synthesis and modelling work to address how cell size changes with nutrient supply, temperature and dispersion (Aim 2). Whereas these two aims mainly address species-level information (individual to population), we continue by extending towards interspecific and community consequences of size. Here, we first ask how cell size relates to two major types of interspecific interactions, grazing and competition (Aim 3). Finally, we discuss cell size in a community context, relating size to biodiversity, abundance and biomass of phytoplankton (Aim 4). In contrast to Aim 1, where the slope between cell size and physiological rates served as consistent effect size for a quantitative summary, we refrained from adding a quantitative meta-analysis for Aims 2–4 as the underlying studies comprised a plethora of approaches and measured variables that were not easily convertible to common effect metrics. We end the review with considering future avenues for phytoplankton ecology that consider the links between cell size and genetic traits, feedbacks between the dual role of cell size as driver and response, and aspects of intraspecific versus interspecific changes in cell size.

2 | SYSTEMATIC LITERATURE REVIEW AND META-ANALYSIS

2.1 | Systematic literature review

We searched ISI Web of Science on 10th February 2021, using a search term which in the title required 'phytoplankton OR algae' and 'cell OR size OR volume' and in the (more general) topic 'cell size OR cell volume OR size structure'. This combination was chosen as it retrieved studies that primarily addressed size issues (hence the 'size or volume' in the title), but reduced the number of papers to screen

by the more phytoplankton specific terms in the topic. Thereby, we avoided papers dealing with sizes in other organisms (zooplankton, fish) or using 'size' in the context of experiment size or ecosystem size. Our search retrieved 455 studies (see Figure S1), which we screened based on title and abstract. Papers not dealing with phytoplankton cell size as a functional trait or response were excluded at this stage (196 studies). For the remaining 259 we retrieved full-text versions, which we could not obtain for nine articles. 132 papers were excluded after inspecting the full text, as they described size-fractionated biomass or primary production (mainly chlorophyll on different filter sizes) or they did not report cell sizes in a functional context but presented, for example, methods how cell sizes could be calculated.

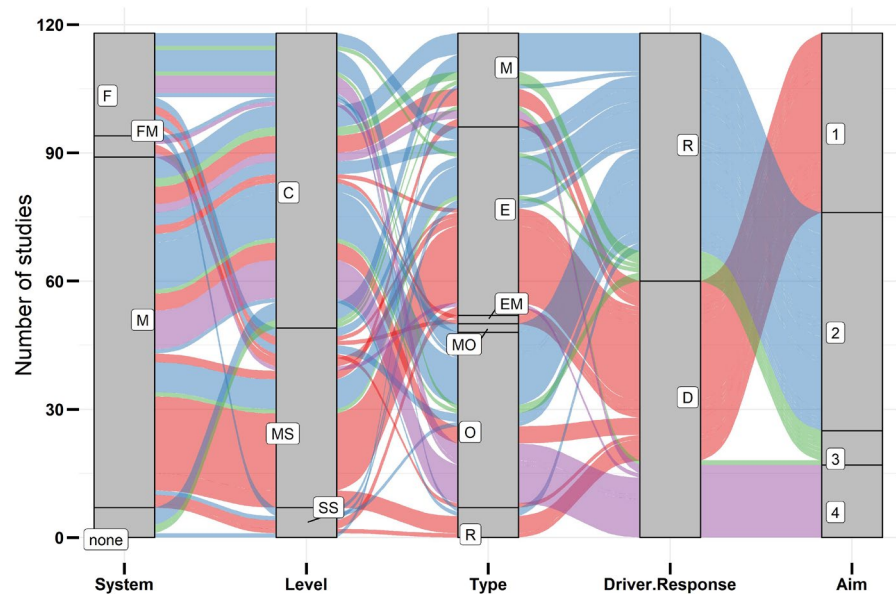
The remaining 118 papers were categorized by their *system* (marine or freshwater), the *study type* (model, experiment, observation or review) and the *organizational level* (single species, multiple single species or communities). Additionally, we categorized the *response scale* as either absolute or specific, the former including processes measured at the cellular level and the latter processes per unit carbon or biovolume. Finally, the use of cell size as driver (predominantly Aim 1) or response (most of Aims 2–4) was noted (Table S1).

A majority of these studies derived from marine systems, whereas a few modelling studies did not specify whether marine or freshwater phytoplankton was addressed (Figure 1). The study level was dominated by community-wide studies, but (multiple) single species were addressed in a range of contexts, especially in experiments. Observational studies, which were as frequent as experimental, were more directed towards communities (Figure 1). These empirical categories dominated the dataset over models or reviews. The studies split roughly into equal proportions using cell size as driver or response. The former per definition was strongly associated with Aim 1 (scaling the physiological and numerical responses to cell size), the latter to Aim 2 (cell size in response to the environment). For interactions (Aim 3), cell size occurred as both a driver of edibility and competitiveness and as a measure of the response to the presence of other species. Aim 4 was addressed with studies that used cell size as a component of community composition.

2.2 | Meta-analysis

For the quantitative meta-analyses, we focused on cell size as a driver of functional and numerical responses (Aim 1). In all, 22 studies of the 118 studies provided data in the form of diagrams, which we digitized using WebPlotDigitizer (Rohatgi, 2019), or in the form of data tables. Between studies, we checked whether data were used more than once (i.e. data from one study also used in a different review or comparison). Within studies, scatterplots in some very data-rich articles were dense and some data points might have been masked by overlaying symbols. Therefore, the number of observations in our analyses can marginally diverge from the actual number of observations in the original study. All cell volumes were transformed into log₁₀-transformed μm^3 . Response variables were

FIGURE 1 Alluvial plot summarizing the outcome of the systematic review and describing the database for this review. The number of studies are given based on system (F = freshwater, FM = freshwater and marine, M = marine, none = none), level of organization (C = community, MS = multiple individually cultured species, SS = single species), type of study (M = model, E = experiment, O = observation, R = review, double letters indicating the respective combination) and whether cell size has been assessed as a driver (D) or response (R). Colour code corresponds to the four aims of this review, cell size as driver of functional and numerical responses (Aim 1) and as sentinel to the environment (Aim 2), grazing (Aim 3) and compositional constraint (Aim 4)



divided into four categories (C fixation [including photosynthesis, respiration and exudation], resource uptake, cellular content and growth), the first three categories contained both absolute (per cell) and specific (per unit carbon or biovolume) functional responses. For growth, we obtained growth rates and sedimentation rates (in m per day), which we included in this category as it represents a loss rate. Within categories, we converted response variables into common units as far as possible and log₁₀-transformed these. Only growth rates were not log-transformed as they are defined as exponents with $\mu = \frac{\log(N_2) - \log(N_1)}{\Delta t}$, where N₂ and N₁ are abundances at two time points and Δt the time difference. Per day, for $\Delta t = 1$, this is equivalent to $\mu = \log\left(\frac{N_2}{N_1}\right)$.

For C fixation, studies reported *C-fixation* as rate per cell or per unit cell carbon, *carbon affinity* as fixation per unit light or available CO₂, and *critical demand* as minimum irradiance for zero net photosynthesis and CO₂ half-saturation constant. The loss of carbon was measured as *respiration* rate (O₂ respiration rate per cell, respired J per day per cell or respired C per fixed C), whereas *exudation* was given as C release rate per cell or as the fraction of C released per C fixed. For resource uptake, we obtained nitrogen uptake rates per cell and per available N as well as N or P affinity (N or P uptake per unit available N or P). For elemental content, we analysed cellular content of C, N, P and chlorophyll as absolute responses as well as N storage (ratio of maximal to minimal N quota), N:C molar ratio and chlorophyll per biovolume as specific responses.

We regressed the response variables (log-transformed rate) against the log-transformed cell size separately for each dataset as well as response category and scale, using

$$\log(\text{rate}) = a + b \times \log(\text{size}).$$

We used the slope *b* as effect size for the meta-analysis and the standard error of the slope as its sampling variance. First, we

obtained grand mean effect sizes (i.e. weighted mean slope per response category and scale), and their 95% confidence intervals (CIs) from a random effects meta-analysis. If the latter did not include zero, we identified these grand mean effect sizes as being significantly positive or negative. We also analysed whether the grand mean effects differed from 1, which would indicate an isometric relationship between size and response (Marañón, 2015). Second, we calculated phylum-specific slopes by splitting each case (as above) further by phylum, if the number of observations per phylum was >3 and the log-transformed size difference >1 order of magnitude. Four different phyla fulfilled these criteria in the data (Bacillariophyta, Chlorophyta, Dinophyta and Haptophyta). If studies did not report the phylogenetic identity of a result, we lumped these into the category 'other'. From these slopes, we obtained phylum-specific mean effect sizes and their CIs for each response category and scale. Third, we also tested for significant differences between systems (freshwater, marine, both) by splitting each case by system, but no significant differences were observed and we defer these results to the supporting material (Figure S2).

3 | CELL SIZE AS A DRIVER OF FUNCTIONAL AND NUMERICAL RESPONSES (AIM 1)

3.1 | Carbon fixation

All aspects of absolute (per cell) carbon metabolism scaled allometrically to cell size, including fixation (photosynthesis) and respiration rates as well as organic carbon exudation and C-affinity (Figures 2a and 3a–d). The consistent scaling of C acquisition processes with size (grand mean slope = 0.77, 95% CI 0.60–0.93) was congruently <1 across different studies involving different taxa. Size dependence was similar for the rate of carbon fixation and the rate of carbon

loss (respiration and exudation rates). The same relationship is potentially true within species, as Malerba et al. (2021) experimentally evolved a nearly 10-fold size difference in the marine green algae *Dunaiella tertiolecta*, finding size scaling for CO₂ affinity, external carbonic anhydrase, and maximum carbon fixation (all positive) and half-saturation constants (negative).

Some previous evidence suggested isometric scaling exponents for phytoplankton metabolic rates including organic carbon exudation (Huete-Ortega et al., 2012, 2014; López-Sandoval et al., 2013, 2014; Marañón et al., 2007), whereas others suggested allometric relationships between cell size and photosynthesis, respiration and net-energy flux of a cell (Finkel et al., 2004; Malerba et al., 2017). The combined empirical evidence strongly suggests allometric, non-isometric scaling to be norm that seems to be consistent across algal phyla as indicated by their largely overlapping confidence intervals (Figure 2b).

In contrast to the results on absolute rates, specific rates for C-metabolism were weakly or nonlinearly related to cell size, resulting in a grand mean effect size not different from zero across and within phyla (Figures 2 and 3e–i). The compensation light intensity, the light level at which respiration balances photosynthesis, showed no significant relationship with cell size in our analysis (Figure 3e), indicating that other factors than size determine the minimum light intensity required for positive net production in phytoplankton. Malerba et al. (2017) attributed this size independency to the fact that larger cells produce more energy but also have higher energy costs due to respiration. Specific losses (fraction of C being exuded and C-specific respiration) were largely independent of cell size as well (Figure 3f,h) (López-Sandoval et al., 2013). Only C-specific C-fixation showed a consistent peak at intermediate sizes around 100 μm^3 (Figure 3g), leading to the lowest respiration to photosynthesis ratio at this size (Figure 3i). Such a unimodal relationship between specific

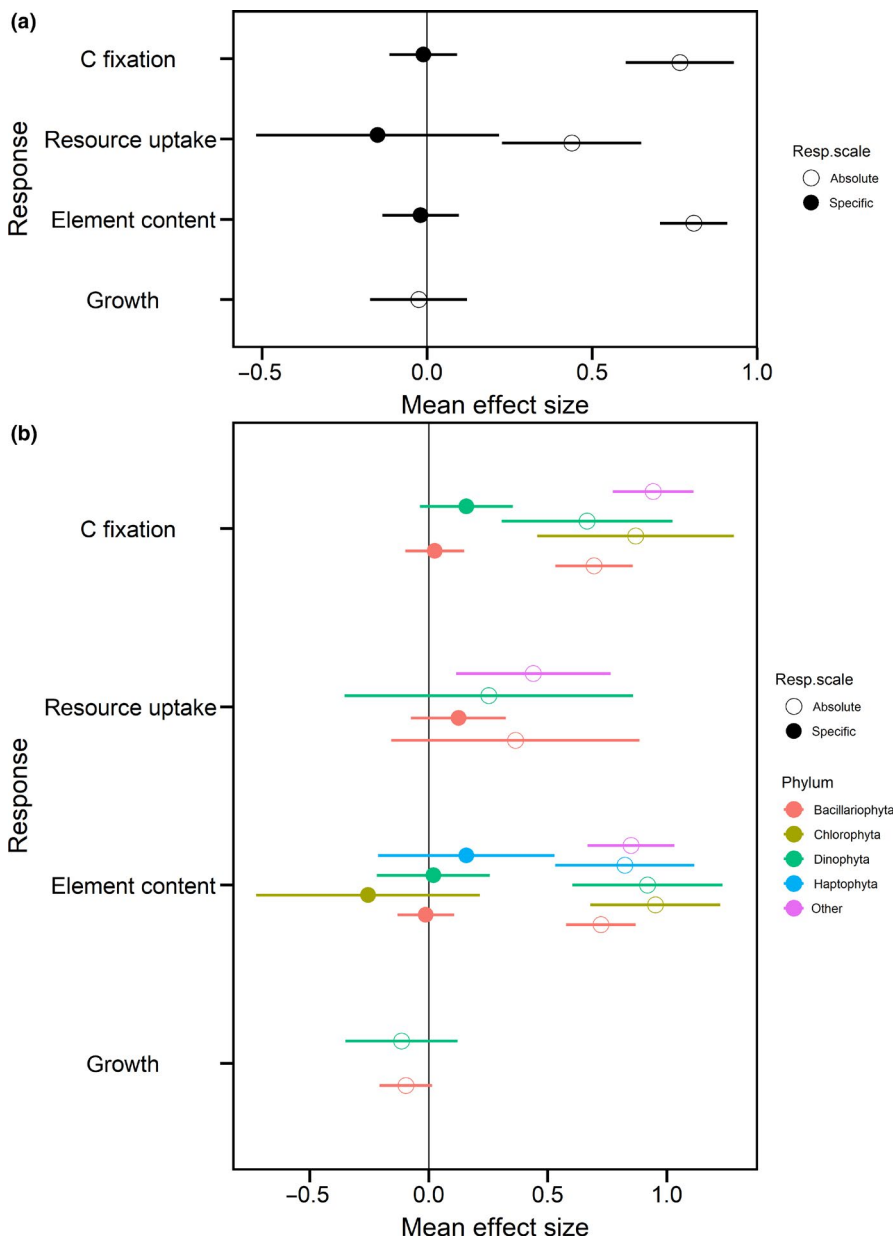


FIGURE 2 Results of meta-analysis on cell-size-driven response variables. For each response category and scale, the mean slope and its 95% confidence interval are represented. (a) Overall meta-analysis. (b) Meta-analysis with separate slopes per phylum, 'other' categorizing results that were not assigned to a specific phylum in the original study. Open symbols denote absolute variables (i.e. measured per cell), closed symbols specific variables scaled to per unit C or biovolume

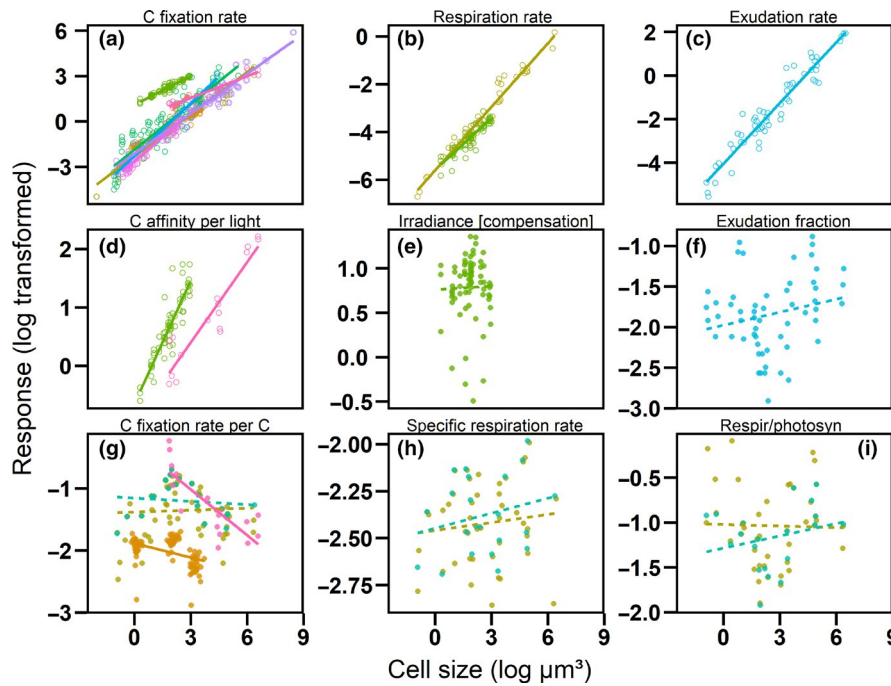


FIGURE 3 Digitized data on cell size as a driver of variables related to carbon fixation. Open symbols denote absolute variables (i.e. measured per cell, panels a–d), closed symbols specific variables scaled to per unit C or biovolume (panels e–i). (a) cellular carbon fixation rate [pgC hr^{-1}], (b) cellular respiration rate [olive symbols: $\text{pg O}_2 \text{ hr}^{-1}$; green: J day^{-1}], (c) carbon exudation rate [pgC hr^{-1}], (d) light-specific carbon affinity [green symbols: $\text{pg C } \mu\text{mol quanta}^{-1} \text{ m}^{-2}$, purple: $\text{pg C W}^{-1} \text{ m}^{-2}$]. (e) compensation irradiance [$\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$]. (f) fraction of carbon fixed released through exudation [%] (g) carbon-specific carbon fixation rate [$\text{pgC pgC}^{-1} \text{ hr}^{-1}$], (h) carbon-specific respiration rate [$\text{pgC pgC}^{-1} \text{ hr}^{-1}$], (i) ratio respiration to photosynthesis rates [dimensionless]. Response variables are log-transformed. Colour codes for study identity according to Table S1 and the data repository. Solid lines indicate significant regressions ($p < 0.05$), dashed lines non-significant relationships at the case level

C-fixation and cell size has been previously reported (Marañón, 2015 and references therein) and indicates stronger growth constraints on small and large cells compared with intermediate-sized cells (see 'Growth').

At the same time, the literature review generated evidence that environmental conditions strongly influence the relationship between size and specific physiology. Large-sized phytoplankton cells exhibited higher C-specific photosynthetic rates at high irradiance and nutrient conditions in coastal surface waters than smaller cells; however, these differences vanished under light limitation (Cermeño et al., 2005a, 2005b). The size scaling exponent decreased also under nutrient-depleted conditions (Marañón et al., 2007). These effects were attributed to the enhanced package effect in larger cells under light limitation (intracellular self-shading, Finkel et al., 2004; Mei et al., 2009) and the downregulation of metabolic processes under resource limitation, respectively. However, not all studies found different size scaling exponents for photosynthesis with nutrient and light availability (Malerba et al., 2017).

3.2 | Nutrient uptake

When molecular diffusion limits nutrient acquisition, theory predicts that smaller cells should have an advantage in the acquisition rate

relative to the required amount of nutrients for growth (Pasciak & Gavis, 1974; Yoshiyama & Klausmeier, 2008). Larger cells tend to have greater maximum uptake rates on a per-cell basis (Edwards et al., 2011, 2012; Litchman et al., 2007) and may have larger nutrient storage capacity relative to minimum nutrient requirements (Grover, 1991; Litchman et al., 2009; Stolte & Riegman, 1995). These predictions were well reflected in our quantitative analyses across a range of studies (Friebele et al., 1978; Marañón et al., 2013; Zaoli et al., 2019) as absolute (per cell) nutrient uptake rate scaled with size, whereas specific uptake rates did not (Figures 2 and 4). For the latter, the grand mean effect size was not significantly different from zero (mean = -0.15 , 95% CI -0.52 to 0.22), which reflected differences between N-specific N uptake (Figure 4a) and biovolume-specific P uptake (Figure 4e). Only for P, specific uptake rates tended to clearly decline with cell size, which indicated that small cells take up phosphorus faster per cell volume (Friebele et al., 1978).

The grand mean effect size (mean slope = 0.44 , 95% CI = 0.23 – 0.65) for absolute resource uptake was positive, but significantly <1 and smaller than for C-fixation. The latter mainly reflects that despite strong size scaling for absolute nutrient uptake rates (Figure 4b,f) we observed positive but weaker relationships between cell size and the half-saturation constant for N (Figure 4c) and P (Figure 4g) or the affinity for N (Figure 4d). Still, as predicted by theory (Smith et al., 2014), half-saturation constants increase with size.

3.3 | Carbon, nutrient and chlorophyll content

Absolute cellular contents (cell carbon, nitrogen and phosphorus as well as chlorophyll) increased allometrically with cell size (Figure 2a, grand mean effect size = 0.81, 95% CI 0.71–0.91). Slopes were similarly strong for C, N and P content (Figure 5a–c) as well as cellular chlorophyll content (Figure 5d). As slopes were significantly <1, smaller cells have lower C, N and P content per cell, but higher content per volume. This fact has been considered important early on (Mullin et al., 1966) as size (biovolume derived from microscopic analyses) is transferred into carbon (for mass balances and biogeochemical models) based on such allometric relationships (Menden-Deuer & Lessard, 2000; Montagnes et al., 1994). Whereas Menden-Deuer and Lessard (2000) found clearly different slopes of this relationship between phyla, we found that the scaling of absolute nutrient content with size was consistent across all taxonomic groups (Figure 2b). Likewise, Montagnes et al. (1994) pointed out that there was variance in the relationships between C, N and cell volume; however, the variation did not appear to be taxa related. The N:C ratio did not

substantially change with cell size in the data we obtained (Figure 5f) as had been described previously (Montagnes et al., 1994). But it should be noted that others proposed that C:N ratios increased with cell size (Marañón et al., 2013; Taguchi, 1976), arguing that small cells contain higher relative abundance of nitrogen-containing molecules, such as nucleic acids and membrane proteins, while they possess a reduced storage of carbon-rich compounds such as lipids and carbohydrates. As for bulk carbon, the volatile and semi-volatile carbon content also allometrically scaled to cell size (Bonsang et al., 2010; Ruiz-Halpern et al., 2014).

Although some studies point at rather isometric relationships for chlorophyll content (Marañón et al., 2007; Montagnes et al., 1994), which would mean that C:chlorophyll ratios are independent of cell size (Taguchi, 1976), the sampled data rather suggest an allometric relationship (Figure 5d) with lower specific chlorophyll content in larger cells (Figure 5g; Agustí, 1991; Key et al., 2010). Pigment ratios can be size dependent as well, reflecting that different scaling slopes exist for different pigments, for example, photo-protective versus photosynthetically active pigments (Fujiki & Taguchi, 2002;

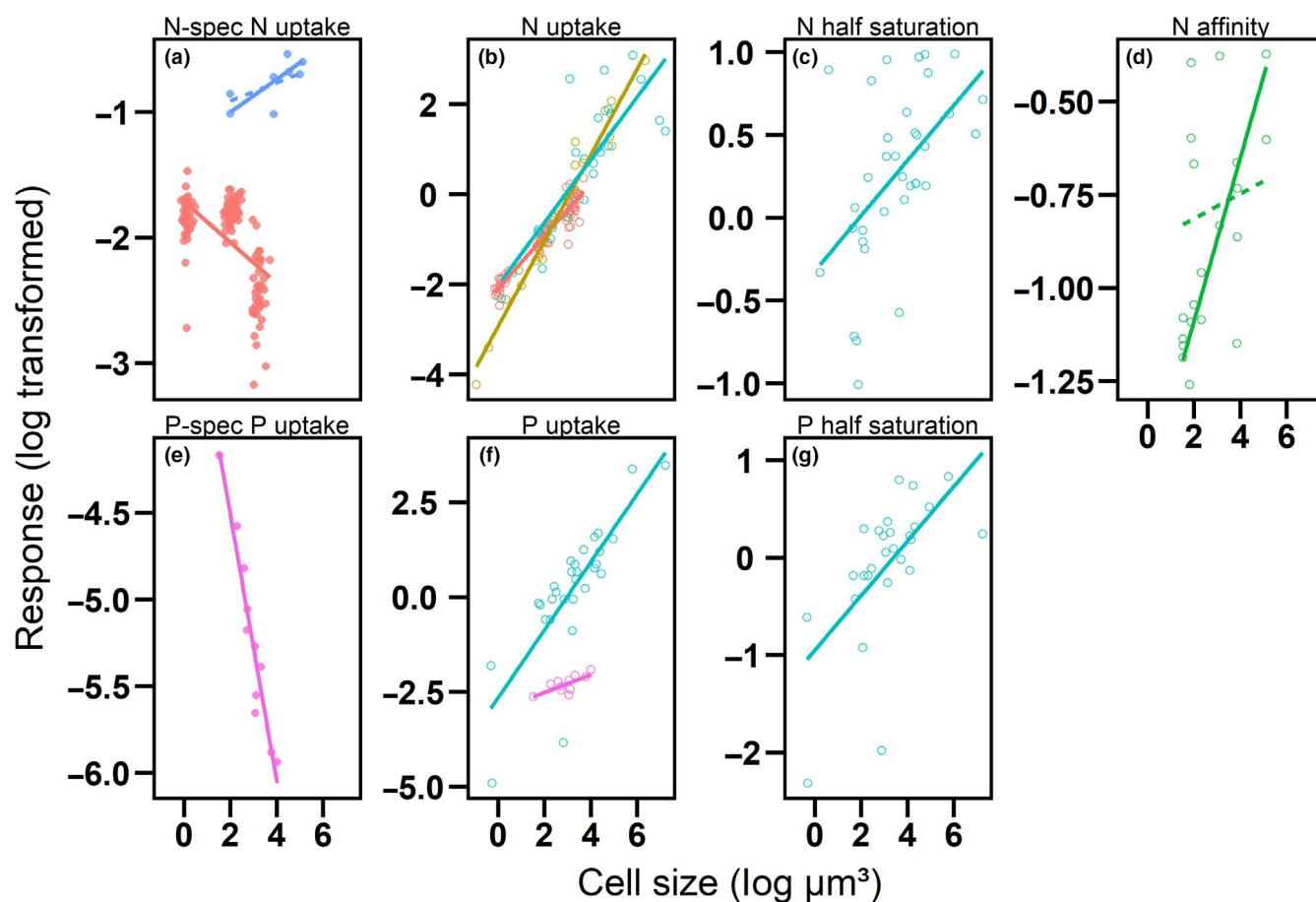


FIGURE 4 Digitized data on cell size as a driver of variables related to nutrient uptake. Open symbols denote absolute variables (i.e. measured per cell, panels b–d, f–g), closed symbols specific variables scaled to per unit N or P (panels a, e). (a) nitrogen-specific nitrogen uptake [$\mu\text{g N } \mu\text{g N}^{-1} \text{ hr}^{-1}$], (b) cellular nitrogen uptake [$\mu\text{g N } \text{hr}^{-1}$], (c) half saturation constant for nitrogen [μM], (d) nitrogen affinity [$\mu\text{g cell}^{-1}$], (e) specific phosphorus uptake [$\mu\text{g P } \mu\text{m}^{-3} \text{ hr}^{-1}$], (f) cellular phosphorus uptake [$\mu\text{g P } \text{hr}^{-1}$] (g) half saturation constant for phosphorus [μM]. Response variables are log-transformed. Colour codes for study identity according to Table S1 and the data repository. Solid lines indicate significant regressions ($p < 0.05$), dashed lines non-significant relationships at the case level

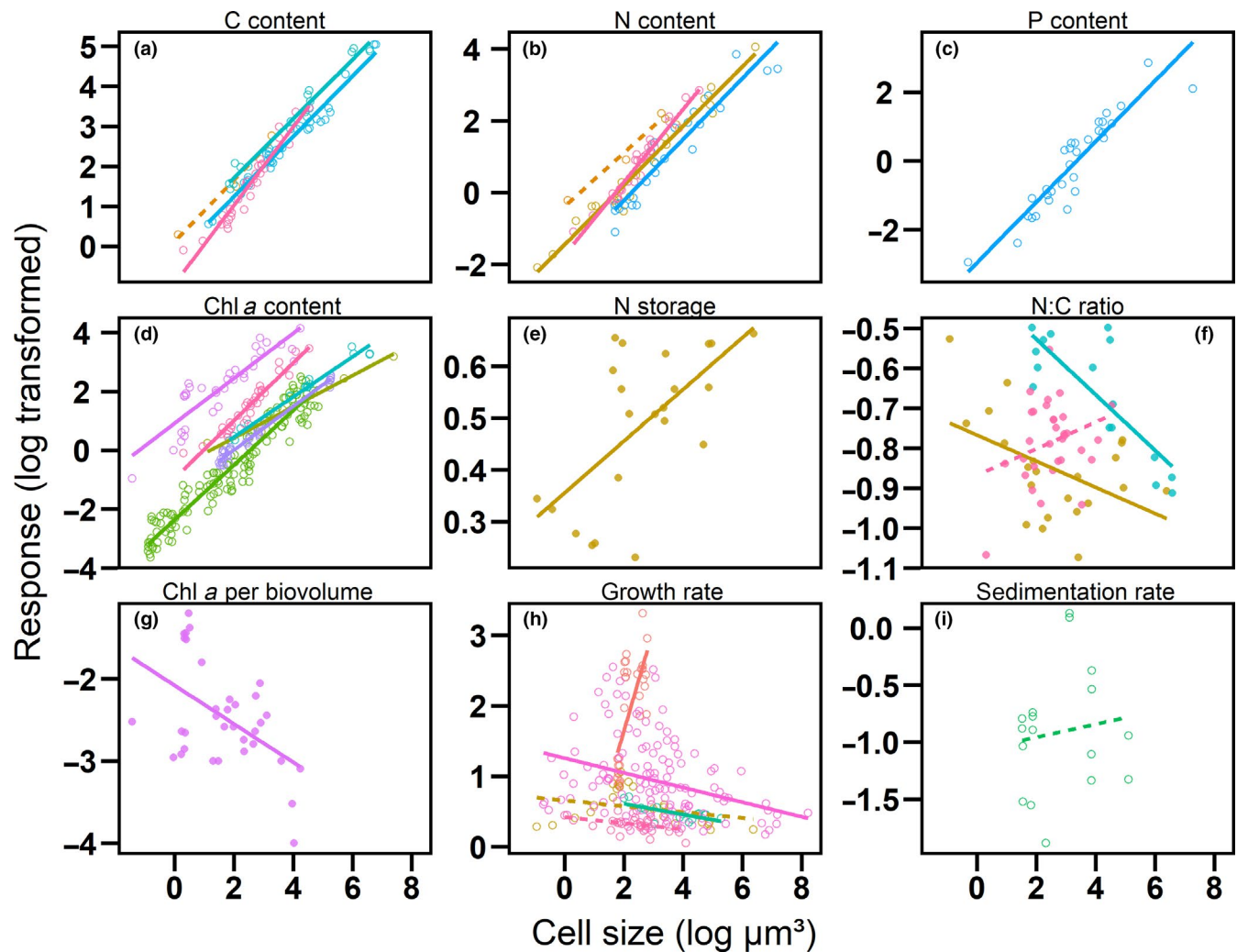


FIGURE 5 Digitized data on cell size as a driver of variables related to cellular composition and growth. Open symbols denote absolute variables (i.e. measured per cell, a–d, h–i), closed symbols specific variables scaled to per unit C, N or biovolume (e–g). (a) cellular carbon content, (b) cellular nitrogen content, (c) cellular phosphorus content, (d) cellular chlorophyll a content [units for a–d: $\mu\text{g cell}^{-1}$]. (e) N storage as ratio of maximal to minimal cell quota [dimensionless]. (f) molar N:C ratio. (g) chlorophyll content per biovolume [$\mu\text{g } \mu\text{m}^{-3}$], (h) growth rate [day^{-1}], (i) sedimentation rate [m day^{-1}]. Colour codes for study identity according to Table S1 and the data repository. Solid lines indicate significant regressions ($p < 0.05$), dashed lines non-significant relationships at the case level. Please note that growth rate (panel h) has not been log-transformed

Key et al., 2010). It is important to note that Chl *a* content and total cellular pigment content in phytoplankton are highly light dependent and decrease sharply with increasing irradiance at low light but more gradually at higher irradiances (Key et al., 2010).

3.4 | Growth

While absolute metabolic rates consistently scale allometrically to cell size, growth and sedimentation rates did not (Figure 2). Growth rates showed a peak at intermediate sizes around a cell size of $100 \mu\text{m}^3$ and lower growth rates at small and large extremes of the size spectrum (Figure 5h). This unimodal relationship between size and growth rate, when including all size classes, explains why the overall effect size in our meta-analysis (Figure 2) did not differ from zero. Previous experimental

work suggested a negative and monotonic relationship between cell size and maximum growth rates in phytoplankton, especially when focused mainly on nano- and microphytoplankton (Banse, 1976; Finkel et al., 2010; Sommer, 1989; Sunda & Huntsman, 1997). This led to a general assumption that growth rates decrease with greater cell size, as would be expected from power law scaling predictions of metabolic theory (e.g. Mei et al., 2011). However, recent theoretical (Ward et al., 2017; Wirtz, 2013) and empirical (Chen & Liu, 2010; Marañón et al., 2013; Sal et al., 2015) evidence suggests that picophytoplankton have reduced maximum growth rates compared with taxa of more intermediate size, such that a unimodal size-growth pattern emerges across all taxa. Only Montagnes et al. (1994) indicated that picophytoplankton growth rate does not increase with size.

The potential mechanisms for a unimodal relationship have been discussed previously (Marañón, 2015; Sommer et al., 2017)

and are effectively an integration of all size-based cellular functions, including nutrient uptake rates (V_{\max}), nutrient content (Q_{\min} and Q_{\max}) and light absorption (as discussed above), as well as intracellular transport distances. Briefly, for small cells (< c. 100 μm^3), growth rates are reduced due to limited nutrient uptake rates relative to minimum requirements (i.e. low $V_{\max}:Q_{\min}$ ratios) and a relatively high proportion of 'non-scalable components' like membranes and nucleic acids, which limit space for the biosynthetic machinery needed for rapid growth (Raven, 1998). Larger cells, on the other hand, face limited assimilation due to greater distances within cells. These size-mediated growth patterns can then have cascading influences on community and ecosystem properties from size-abundance-spectra to primary productivity and responses to environmental change.

On the loss side (see 'Dispersion' under Aim 2 and 'Grazing' under Aim 3), sedimentation rates are typically assumed to increase with size (Kjørboe, 1993; Pančić & Kjørboe, 2018), especially when also leading to larger aggregate formation (Bach et al., 2016). The data we have at hand (Stolte et al., 1994) tested for effects of nitrogen nutrition on size-specific sedimentation rates and did not find different sedimentation rates with cell size (Figure 5i).

4 | CELL SIZE AS A SENTINEL OF ENVIRONMENTAL CHANGE (AIM 2)

4.1 | Nutrients

Varying nutrient conditions can influence phytoplankton cell sizes ranging from the individual to the community scale. Physiological adaptation of single species to nutrient conditions has been well documented, although the direction and magnitude of size change varies by taxa and the nutrient in question (Peter & Sommer, 2013, 2015; Yan et al., 2021). Peter and Sommer (2013, 2015) found that nutrient limitation uniformly decreases the cell volume of all species studied (as well as the community mean), and that N limitation causes stronger decreases in cell size relative to P limitation. By contrast, Yan et al. (2021) showed diverging cell shape and size responses as *Microcystis aeruginosa* decreased in volume while *Scenedesmus obliquus* increased when the severity of nutrient stress increased over time.

In addition to these physiological responses at the individual/population level, community assembly processes determine the relative abundance of species that differ in size and exhibit highly divergent growth responses to nutrient levels. Much work has focused in particular on how the size abundance spectrum (SAS) of whole communities is affected by variation in nutrient levels, especially in the context of eutrophic versus oligotrophic systems (Huete-Ortega et al., 2014; Lin et al., 2020; Montes-Pérez et al., 2020; Pomati et al., 2020; Pulina et al., 2019; Roselli & Basset, 2015). In this respect, nearly all studies find that a clear signature of eutrophic systems is a flatter SAS slope than for oligotrophic systems (i.e., indicating relatively higher abundances

of large cells in eutrophic vs. oligotrophic systems). These results are also supported by trait-based models that utilize empirical scaling relationships of metabolic parameters with cell size (Irwin et al., 2006; Kriest & Oschlies, 2007). This signature is clear enough that an assessment of size spectral slopes can then be used as predictive index to diagnose nutrient pollution and other anthropogenic impacts (Vadrucci et al., 2013). However, the total algal biomass cannot be inferred from the slope of the SAS relationship (Moreno-Ostos et al., 2015).

Nutrient-mediated effects rarely act alone to influence cell size. Complex interactivity among nutrients, temperature and grazing is common (Pomati et al., 2020), suggesting it may not be reasonable to expect a single dominating factor to drive observed size distributions in a given system. Peter and Sommer (2013, 2015) found consistent temperature-nutrient interactions by which temperature effects become much stronger with greater nutrient stress. Size spectra also exhibit interactive dependence upon nutrients and temperature, although the relative importance of each individual effect and their interactions varies substantially with system characteristics (Pomati et al., 2020).

As for macronutrients, the higher surface area:volume ratio of small cells leads to a higher uptake of micronutrients and also pollutants. Studies found higher accumulation of heavy metals such as methylmercury (Kim et al., 2014), whereas larger species tolerated higher concentrations of heavy metals (Echeveste et al., 2012) or organic substances such as polycyclic aromatic hydrocarbons (Ben Othman et al., 2012; Echeveste et al., 2010). Still, effects on size distributions may be subtle or absent, depending on toxicant (Baho et al., 2019; Biggs et al., 1978, 1979; Ting et al., 1991; Törnqvist & Claesson, 1987).

4.2 | Warming

Warming effects on cell size often occur in concert with other constraints such as nutrients (see above) or grazing (see below). For marine (Finkel et al., 2010) as well as freshwater phytoplankton (Zohary et al., 2021), previous reviews have concluded that with increasing temperature, cell size declines both within species (average cell size per species) and in communities (small species favoured over large species). These size reductions could be observed in warming experiments (Klauschies et al., 2012; Peter & Sommer, 2012; Yvon-Durocher et al., 2011) and observational studies (Abonyi et al., 2020; Chen & Liu, 2010; Hillebrand et al., 2022). The same relationship appears over geological time-scales, with declining temperatures over the Cenozoic coinciding with increasing cell size in dinoflagellates and diatoms (Finkel et al., 2007). Smaller cells under higher temperatures seem to be a general finding that meets model predictions (Chen et al., 2020) and macroecological patterns (Acevedo-Trejos et al., 2013, 2018). However, these patterns are not ubiquitous: Using the slope of biomass per size class distributions from multiple observations, Pomati et al. (2020) found small sizes to be favoured under low

temperature high nutrient conditions, contrasting the expected pattern. Likewise, 10 years of experimental warming also shifted size spectra towards larger species in a long-term mesocosm experiment (Padfield et al., 2018). Even if small size coincides with higher temperature in space or time, other correlated factors (nutrients, grazing) may cause the pattern (Marañón et al., 2012).

4.3 | Dispersion

The dynamics in a fluid depend on the so-called Reynolds number, which shows the relationship between inertial forces proportional to the cell mass and viscous forces proportional to the cell area (Purcell, 1977). The relative contributions of inertial and gravitational forces increase with cell size, which can lead to a size-dependent sinking rate (see above). Portalier et al. (2016) showed that large cells compared to small cells require a higher minimum turbulence level for survival. In addition, the maximum critical depth to survive exists for large cells at both low and high turbulence levels, whereas for small cells, due to their greater buoyancy, this depth is limited only at high turbulence level. As turbulence affects nutrient flow, we expect changes in size composition based on the vertical and horizontal water column hydrodynamics, as is reflected by flatter SAS in upwelling areas and steeper SAS in downwelling areas (Rodríguez et al., 2001).

These observations scale up from subregional to regional and global levels. For example, phytoplankton cell size distribution at spatial scales <10 km is influenced by the local circulation of water masses (Font-Muñoz et al., 2017; Waga et al., 2019), where gyres contain smaller cells towards their inner part and larger cells are displaced out of the gyres. By contrast, homogeneous cell size spatial patterns prevail when there are no gyres (Font-Muñoz et al., 2017). Such patterns can be modified by light, nutrient availability or temperature as detailed above such that phytoplankton community size structure at large scales can be predicted from hydrodynamics, nutrient concentrations and temperature (Acevedo-Trejos et al., 2015). Basin observations across the Atlantic Ocean corroborate the conclusions of Chen and Liu (2010) and others earlier (Cermeño et al., 2006) that the effects of these environmental conditions on the size composition of phytoplankton can be scaled to the global scale.

5 | CELL SIZE IN SPECIES INTERACTIONS (AIM 3)

5.1 | Competition

Based on the above described advantage in the acquisition rate relative to the required amount of nutrients for growth (Pasciak & Gavis, 1974; Yoshiyama & Klausmeier, 2008), small cells should have a competitive advantage for limiting nutrients. Edwards et al. (2011) predicted that these competitive abilities are correlated for phosphate and nitrate and smaller cells should be superior at acquiring both resources. By

contrast, larger cells should be more competitive under heterogeneous conditions as maximum cell quota increases faster with size than the minimum quota (Kerimoglu et al., 2012) and large cells thus have larger nutrient storage capacity relative to minimum nutrient requirements (Grover, 1991; Litchman et al., 2009; Stolte & Riegman, 1995). Large cell size has in fact been shown to be advantageous under fluctuating nitrate supply, as larger species had highest specific uptake rates (Edwards et al., 2011; Litchman et al., 2007; Stolte et al., 1994) and sustained uptake for longer time (Suttle et al., 1987). However, this advantage ceases if instead of uptake and storage the conversion from internal pools into biomass is the rate limiting step (Verdy et al., 2009). Moreover, differences in ammonium and nitrate transport rates can lead to high growth rates of small algae in ammonium-controlled systems, whereas large algae dominate under fluctuating nitrate supply due to a larger specific volume of vacuoles in which nitrate could be stored (Stolte & Riegman, 1995).

As phytoplankton growth depends on nutrient uptake as well as photosynthesis, the interplay between light and nutrients in natural environments further influences the competition outcome between small and large cells. Increasing cell sizes were found with increasing light intensities (Thompson et al., 1991). Small cells suffer less from self-shading, have less scattering of light, higher light absorption and faster nutrient transport affinities (Agustí et al., 1994; Chisholm, 1992). Therefore, a shift towards smaller cells in a warmer (see below), more stratified and less nutrient-rich ocean is expected (Finkel et al., 2005, 2007).

Given the size-specific competitive abilities, one should also expect that size differences constrain the strength of competition as well, but we found only one study addressing this. In an experimental study with differentially sized cyanobacteria, Gallego et al. (2019) found that increased size differences reduced competition as both niche and fitness differences increased; however, size differences were not sufficient to predict species coexistence.

5.2 | Grazing

As we did not find studies on size-specific parasitism and viral loads, the top-down section of species interactions focuses entirely on grazing. The size selectivity of many zooplankton grazers is well known to affect the size structure of phytoplankton communities (Bergquist et al., 1985; Tackx & Daro, 1993). Thus, phytoplankton size is used as a proxy for how palatable these organisms are to their grazers, where smaller cells are considered more edible than larger cells (Riegman et al., 1993), and constant predator-prey ratios in planktonic communities are generally suggested (but they are not the rule, see Sommer et al., 2017). To describe this interaction a simple growth-defence trade-off between the higher competitive ability to acquire nutrients by smaller cells and the lower vulnerability of larger cells is commonly suggested (Cottingham, 1999; Marañón, 2015; Sunda & Hardison, 2010) and implemented in theoretical models (Acevedo-Trejos et al., 2015; Cloern, 2018; Jiang et al., 2005; Wirtz, 2013). An alternative modification to this classical trade-off

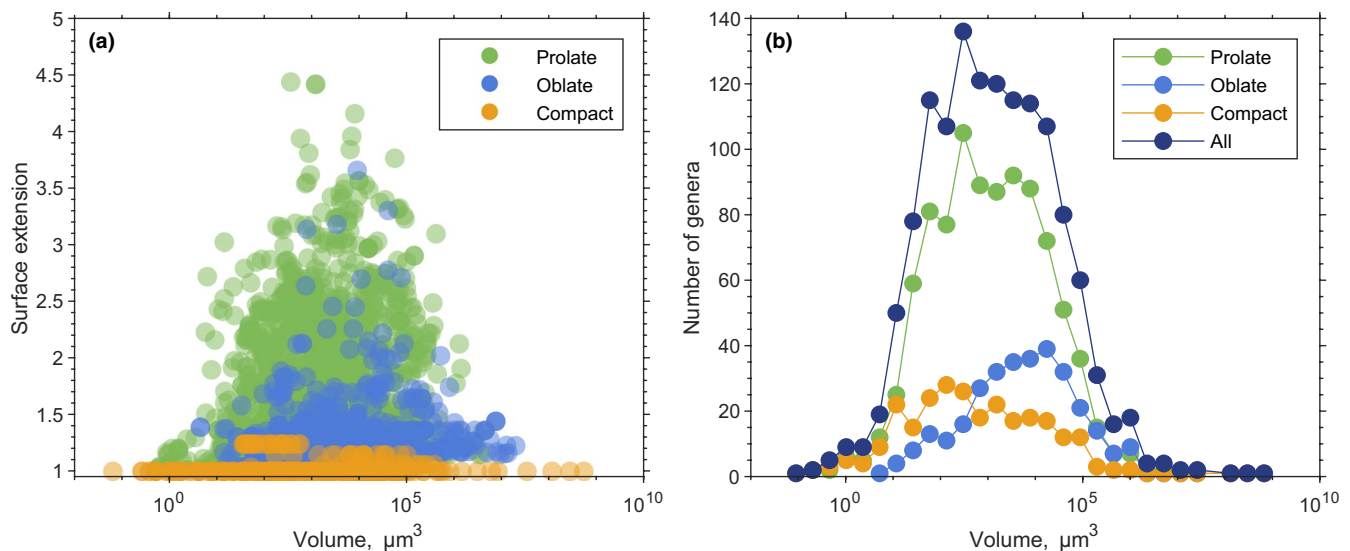


FIGURE 6 Geometry and diversity of unicellular phytoplankton. (a) Surface extension (compares a cell's surface to that of a sphere of equal volume) and (b) diversity (characterized as the number of genera) per volume bin. The colour coding indicates different shape classes: compact with aspect ratio equal to 1, prolate with aspect ratio >1 and oblate with aspect ratio <1 . Based on data from Ryabov et al. (2021)

relates phytoplankton nutrient quality with grazer selectivity towards high-quality food, where smaller undefended cells are assumed to have a richer nutritional value (Branco et al., 2020). However, the detectability and selectivity of food value by zooplankton grazers have been questioned and cell size is just one of many other relevant traits or strategies that phytoplankton can use to alter their palatability to grazers (see Pančić & Kjørboe, 2018 for a recent review on phytoplankton defence mechanisms).

A shift from smaller and less diverse communities to larger and more diverse communities is predicted via a size-selective grazing and nutrient acquisition mechanism (Acevedo-Trejos et al., 2015, 2018). Other observations at different scales seem to support this trade-off mechanism to explain the size composition of planktonic communities (Cloern, 2018; Irigoien et al., 2005). These observations suggest that large phytoplankton cells dominate under high nutrient conditions by exploiting a lag response of the predators. However, based on the studies described above (Aim 1), phytoplankton physiology provides another feasible explanation for the dominance of large-sized phytoplankton in resource-rich environments. In addition, natural community assemblage experiments testing the combined effects of grazing and temperature on the size structure of phytoplankton communities suggest that the presence of grazers can modify the response to warming but does not reverse its effect by, for example, shifting the phytoplankton community towards larger sizes (Klauschies et al., 2012; Peter & Sommer, 2012, 2013).

6 | CELL SIZE IN A COMMUNITY CONTEXT (AIM 4)

Phytoplankton cell size is a decisive aspect of community composition, reflecting the importance of size as driver of functional and

numerical responses (Aim 1), sentinel of the physical and chemical properties of the environment (Aim 2) and important trait in species interactions (Aim 3). The frequent use of species abundance scaling (see above) as well as community-weighted means and variances of cell sizes reflect this central role of size, which makes the diversity of morphological traits such as cell size and shape an integral part of phytoplankton diversity. Early observations by Semina et al. (1976) along the South African coast showed that even as the species composition varied, similar mean cell sizes and shapes ('Lebensformen') were observed under similar environmental conditions. A linear relationship between logarithm of cell size and taxonomic richness indicated high species richness for small sizes in the open ocean (Cermeño & Figueiras, 2008) and Aegean Sea (Ignatiades, 2017). But the same study showed that bell-shaped relationships between cell size and taxonomic richness can occur in coastal environments (Cermeño & Figueiras, 2008). Similar dominance of intermediately sized species was also found in Lake Kinneret (Kamenir et al., 2006). Support for these patterns comes from a recent compilation of phytoplankton morphological traits (surface area, aspect ratio, elongation and volume) and taxonomic diversity data across various coastal marine environments, which showed a unimodal relationship between species richness and cell size in coastal environments (Figure 6, Ryabov et al., 2021). The highest species diversity coincided with a high variability of cell shapes, both occurring at intermediate cell sizes (10^2 – $10^4 \mu\text{m}^3$), whereas both richness and shape diversity declined as cell volumes became smaller or larger because of spherical shapes dominating at both ends (Figure 6).

These emergent patterns imply fundamental physiological, ecological and evolutionary constraints to the size–shape relationships. Selection of certain shapes and sizes might be driven by fundamental physical laws that determine rates of energy–mass exchange and physical interaction between cells and environment (Naselli-Flores

et al., 2021; Niklas & Hammond, 2019), because the rates of these processes depend significantly on cell size and shape. For example, the rate of resource diffusion to the cell surface (Fick's law) depends on the cell shape and surface area, and the water drag force against a moving object depends on the object's projected sail area. Thus, the scaling of the metabolic rates depends directly on cell size and shape, but the details of these dependencies and their impact on phytoplankton diversity and abundance so far remain largely unexplored.

Consequently, size distribution modelling is an important task in predicting global ecosystem response and satellite-based phytoplankton stock assessment (Laiolo et al., 2021; Montes-Hugo et al., 2008; Waga et al., 2019). The size distribution of biomass is roughly described by the so-called Sheldon spectrum, a roughly uniform distribution of biomass density as a function of logarithmic body mass (Gaedke, 1992; Sheldon et al., 1972), although the observed distribution may depart from it to a large extent when large or small cells dominate. Trait-based modelling approaches typically use empirical dependencies of metabolic parameters of nutrient and light uptake as well as sinking and grazing on phytoplankton size (Portalier et al., 2016; Ward et al., 2014). Zero and one-dimensional mechanistic models with bottom-up control help to understand the influence of natural conditions on the dominance of size classes. However, one of the main problems with this approach is the low biodiversity and competitive exclusion of most species. Aggregated or adaptive dynamic models (Acevedo-Trejos et al., 2015; Chen et al., 2020; Jiang et al., 2005; Wirtz, 2013) allow capturing mean size and size variance by focusing on the adaptive capacity of phytoplankton communities as a whole. However, this approach omits adaptive processes at the individual/population level and requires an external mechanism to sustain diversity. These models often predict lower size variability than observed in nature.

Another approach to reconstructing the phytoplankton size spectrum includes losses, which can result either from background mortality or from grazing. With increasing cell size, trophic function changes smoothly from small autotrophic species through intermediate mixotrophic to large heterotrophic species. The formation of the phytoplankton size spectrum apparently cannot be considered in isolation from top-down control as large organisms grow not only from inorganic resources, but also by feeding on smaller organisms, with some of them being both prey and predators (Guiet et al., 2016; Sprules & Barth, 2015). While most spectral models explain the biomass distribution of multicellular organisms, Cuesta et al. (2018) presented a model explaining the biomass spectrum of unicellular phytoplankton. The stable solution of this model gives a power law of the Sheldon biomass distribution, but requires incorporating allometric scaling of metabolic parameters of nutrient consumption, explicit consideration of cell size growth and cell division, and a non-linear dependence of predation rate on prey density.

Perhaps the most promising approach is global ecosystem models that explicitly account for spatial environmental heterogeneities and differences in the scaling of metabolic rates of different phylogenetic groups and zooplankton grazing pressure (Ward et al., 2014). Developing such an approach, Dutkiewicz et al. (2020) showed an

increase in cell size diversity with increasing rate of limiting nutrient supply, and a decrease in phytoplankton biodiversity with decreasing predator biodiversity. Summarizing a set of computer experiments, they conclude that phytoplankton diversity, and hence size spectrum, is a complex function of four major driving forces: rate of supply of limiting resource, imbalance in resource ratios relative to the competitor requirements, size-dependent grazing control and transport processes.

7 | CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

We conducted a systematic literature review on phytoplankton size as a driver and sentinel of its performance. Following the protocol enhanced the breadth of the literature basis for this review and brought aspects to our attention that often sail in the shadow of a few highly cited papers. Based on this database, we can conclude that size pervades levels of organization and spatial-temporal scales as a predictive trait for phytoplankton. Cellular uptake of resources, elemental content, photosynthesis and C-loss all monotonically and allometrically scale with size (Aim 1). However, specific C-fixation and the respiration:photosynthesis ratio are unimodally related to size, which coincides with fastest growing species being found at intermediate size around $100 \mu\text{m}^3$. Given these strong functional dependencies, changes in the environment (nutrients, temperature, physical processes) as well as biotic interactions leave clear imprints on the phytoplankton size structure (Aims 2 and 3). Selection for smaller sized phytoplankton under warm, nutrient-poor and more stratified conditions seems to prevail, whereas top-down effects of grazers on phytoplankton size depend on feeding type and resource conditions. Most importantly, the different impacts are strongly interactive, as temperature, light, nutrients, and grazer presence and compensation affect phytoplankton simultaneously. Therefore, size is ultimately linked to phytoplankton diversity and biogeography, which makes it a central item of models on the role of phytoplankton from local ecosystems to the global ocean (Aim 4). In addition to these overarching conclusions, our systematic review also obtained a range of knowledge gaps and needed next steps. While we cannot provide a fully exhaustive horizon scan, we focus here on three major aspects.

7.1 | Genetic traits (Aims 1 and 4)

Much of the size-related phytoplankton literature deals with morphological and physiological consequences and causes of size differences. Much less is known about the relationship between cell size and molecular traits. Genome size generally increases with cell size in eukaryotes (Gregory, 2005), which has also been demonstrated for numerous phytoplankton taxa, including chlorophytes (Malerba

et al., 2020; Smith et al., 2013), diatoms (Connolly et al., 2008) and chrysophytes (Olefeld et al., 2018). The positive relationship between cell size and genome size in eukaryotes has been suggested to be the product of conflicting evolutionary pressures, on the one hand, to minimize redundant DNA and maximize performance, but on the other hand to maintain a minimum level of essential function (Malerba et al., 2020). For prokaryotes, no significant correlation between cell size and genome size was found in bacteria and archaea (Westoby et al., 2021), but some evidence exists that it does for cyanobacteria. Analysing 58 cyanobacteria genomes, Larsson et al. (2011) demonstrated that strains with a genome size of >3.3 Mbp were more variable in terms of cell size and included all filamentous taxa, while all genomes <3.3 Mbp in size represented unicellular taxa. However, to our knowledge, there has still been no systematic analysis on the relationship between genome size and cell size in cyanobacteria. Smith et al. (2013) also found plastid DNA to scale with cell size and complexity in chlorophytes, yet, other studies provided mixed evidence for this pattern and emphasized a lack of plastid genome data for many major algal groups (Smith, 2017). Filling in this information by cross- and within-species surveys would be a first step towards understanding the genome-size relationship, but to bring this information into algal biogeography and trait-based global models requires also the understanding of its ecological and evolutionary constraints (see table 1 in Green et al., 2008, which also lists genetic traits other than genome size). For example, Olefeld et al. (2018) demonstrated for chrysophytes that genome size may differ depending on the nutritional mode of a species, with phototrophs having larger cell volumes and genomes than heterotrophic strains, while intermediate-sized mixotrophs exhibited smaller genomes than expected based on cell size. The authors attributed this finding to the evolutionary reduction of the energetically costly photosynthetic apparatus in phototrophs to the reduced apparatus in mixotrophs and a further reduction in pure heterotrophs.

7.2 | Feedbacks and interactions (Aims 1, 2 and 3)

Most data we obtained by our survey consisted of bivariate relationships using cell size either as driver or response in correlation to another variable. Consequently, the effect sizes obtained for the meta-analysis were slopes of such bivariate relationships. Such bivariate approaches tend to ignore feedbacks, though, which are likely to occur in nature (see Aim 2 for example of low nutrient availability selecting for smaller cells, but smaller cells reducing nutrient concentrations more by their higher affinity). Such feedbacks and the already shown strong interdependency of cell size responses to nutrients, light, temperature, hydrodynamics and grazing call for different statistical analyses that allow disentangling these aspects. Structural equation models come to mind as they allow quantifying reciprocal relationships where cell size can be a cause and a consequence of observed patterns at the same time (see Grace et al., 2016 for an example of how SEM can provide insights regarding

biodiversity effects). Thereby, the field can move to acknowledge the multivariate nature of cell size as a driver and a response and to assess the relative role of top-down and bottom-up forces under different conditions.

7.3 | Intraspecific variance (Aims 1 and 4)

Whereas the amount of cell-size-related information on different species is massive, intraspecific plasticity in cell size and variance in size-scaling has rarely been addressed except for some specific size-selection experiments (Malerba et al., 2021). However, intraspecific changes in mean size were major in a long-term phytoplankton monitoring programme (Hillebrand et al., 2022). Additional flexibility arises from colony formation, where size and number of cells per colony may vary. Intraspecific trait variation has become a cornerstone of trait-based approaches (Bolnick et al., 2011), but has only recently been assessed more systematically for phytoplankton (Fontana et al., 2018). Here we recommend assessing not only the magnitude of this plasticity, but also its importance for competitive (Gallego et al., 2019) and trophic interactions (as size links to trophic strategy, see Andersen et al., 2016; Chakraborty et al., 2017).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

H.H. designed the review; M.-L.S. conducted the systematic review; H.H. and M.-L.S. conducted the meta-analysis; H.H. outlined the manuscript, substantial parts were written by P.T., E.A.-T., S.D.M., A.R. and M.S. All authors revised the manuscript.

DATA AVAILABILITY STATEMENT

No new data were collected for this paper; however, all data sources used are digitized and deposited on Zenodo together with the R code (<https://doi.org/10.5281/zenodo.5727728>).

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