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Do marine phytoplankton follow Bergmann's rule *sensu lato*?

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ABSTRACT

Global warming has revitalized interest in the relationship between body size and temperature, proposed by Bergmann's rule 150 years ago, one of the oldest manifestations of a 'biogeography of traits'. We review biogeographic evidence, results from clonal cultures and recent micro- and mesocosm experiments with naturally mixed phytoplankton communities regarding the response of phytoplankton body size to temperature, either as a single factor or in combination with other factors such as grazing, nutrient limitation, and ocean acidification. Where possible, we also focus on the comparison between intraspecific size shifts and size shifts resulting from changes in species composition. Taken together, biogeographic evidence, community-level experiments and single-species experiments indicate that phytoplankton average cell sizes tend to become smaller in warmer waters, although temperature is not necessarily the proximate environmental factor driving size shifts. Indirect effects *via* nutrient supply and grazing are important and often dominate. In a substantial proportion of field studies, resource availability is seen as the only factor of relevance. Interspecific size effects are greater than intraspecific effects. Direct temperature effects tend to be exacerbated by indirect ones, if warming leads to intensified nutrient limitation or copepod grazing while ocean acidification tends to counteract the temperature effect on cell size in non-calcifying phytoplankton. We discuss the implications of the temperature-related size trends in a global-warming context, based on known functional traits associated with phytoplankton size. These are a higher affinity for nutrients of smaller cells, highest maximal growth rates of moderately small phytoplankton (*ca.* 10^2 μm^3), size-related sensitivities for different types of grazers, and impacts on sinking rates. For a phytoplankton community increasingly dominated by smaller algae we predict that: (*i*) a higher proportion of primary production will be respired within the microbial food web; (*ii*) a smaller share of primary production will be channeled to the classic phytoplankton – crustacean zooplankton – fish food chain, thus leading to decreased ecological efficiency from a fish-production point of view; (*iii*) a smaller share of primary production will be exported through sedimentation, thus leading to decreased efficiency of the biological carbon pump.

Key words: phytoplankton, body size–temperature relationship, Bergmann's rule, nutrients, grazing.

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I. INTRODUCTION

Bergmann's (1847) rule is one of the oldest manifestations of a 'biogeography of traits' *sensu* Barton *et al.* (2013). In its original form it states that endothermic animals become larger towards the poles. He provided the explanation that heat loss under cold conditions would be reduced and thermoregulation facilitated at lower surface area to volume ratios. Bergmann was not explicit as to whether this included both trends within species and replacements among similar species. In later applications, the term 'Bergmann's rule' has been applied to both of these phenomena, and also to latitudinal patterns in size of ectothermic organisms, although the thermoregulatory explanation cannot apply in the latter case. Blackburn, Gaston & Loder (1999) suggested using the term 'Bergmann's rule' for latitudinal replacements among closely related species (e.g. within genera) while 'James (1970) rule' should be used for intraspecific size trends. A more restricted case of body size–temperature relationships is predicted by Atkinson's (1994) 'temperature–size rule' (TSR) which stated that organisms experiencing higher temperatures during their ontogeny mature at a smaller body size, due to higher initial growth rates but lower asymptotic body sizes (Ohlberger, 2013). This implies that development is accelerated more strongly by higher temperatures than is body growth (Forster, Hirst & Atkinson, 2011). A response in the sense of the TSR is strictly phenotypic and does not involve species replacement or changes in gene frequencies within species. Therefore, it should also be apparent in clonal cultures, as shown for a multitude of auto- and heterotrophic protists in a review by Atkinson, Ciotti & Montagnes (2003). In spite of these conceptual differences, it is still widespread practice to use the term 'Bergmanns' rule' *sensu lato* as a 'concept cluster' (Hessen, Daufresne & Leinaas, 2013) relating an increased body size to lower temperatures or colder climates, as we do herein.

The study of size–temperature relationships has experienced a revival under the umbrella of Global Change research (Daufresne, Lengfellner & Sommer, 2009). There is growing, although not un-contradicted evidence, that declining body size might be a third universal biotic response to global warming, after latitudinal and seasonal shifts (Gardner *et al.*, 2011).

This review focuses on marine phytoplankton for three reasons. First, marine phytoplankton contribute *ca.* 50% of global primary production. Second, there is a well-known biogeographic trend in marine phytoplankton body size (Barton *et al.*, 2013), ascribed by many authors to variation in nutrient supply (Marañón *et al.*, 2015, and citations therein). A similar biogeographic trend seems to be lacking for lake phytoplankton. Third, several important ecosystem functions of marine phytoplankton, such as provisioning the food source of fisheries and carbon sequestration by sedimentation depend critically on body size. We pay particular attention to the distinction between community-level size changes driven by species replacements and size changes within species. Following the suggestion of Hessen *et al.* (2013) we also focus on the distinction between direct temperature effects and those of other environmental factors coupled to temperature in the natural environment or in experimental systems.

II. METHODOLOGICAL CONSIDERATIONS

(1) Field *versus* experimental studies

This review includes studies at three levels of complexity: field studies, single-species experimental studies, and experimental studies with plankton communities. While field studies cover the full complexity of natural ecosystems with a multitude of environmental factors influencing the responses of organisms, experimental systems can separate the effects of individual factors when relevant environmental factors are correlated *in situ* (e.g. temperature and nutrient supply in the ocean; Kamykowski & Zentara, 1986; Agawin, Duarte & Agusti, 2000). This reduction of complexity is not a shortcoming but the very purpose of such ecological experiments. The reaction norms of different genotypes to temperature, nutrients, light, etc., are retained when the physical complexity of the environment is reduced in an experimental system, e.g. when the complex but also site-specific interplay between temperature, vertical mixing, light supply and nutrient supply are not present in an experimental enclosure. However, the temporal and spatial scale of such studies has consequences for the processes involved in determining phytoplankton size. Phytoplankton culture experiments are usually based on clones, i.e. single genotypes which might be atypical

for the species or the functional group they represent. Responses of size to temperature or other environmental factors in short-term experiments based on clonal cultures are strictly phenotypic. Experiments based on naturally mixed phytoplankton communities include the potential for shifts in species and genotypic diversity available at the scale of litres (microcosms) or cubic metres (mesocosms), representing a high number of individuals (usually $>10^3$ ml^{-1}). However, temporal restrictions of the study period (usually a few weeks, i.e. 10–100 generations) provides little scope for evolutionary adaptation and the spatial confinement excludes re-arrangement of the species pool, e.g. by immigration. Therefore, it is unlikely that we will find quantitative agreement between the effect sizes of size–environmental factor responses between field and experimental studies; although we can be confident that the response is real if the effect is in the same direction at all levels of experimental complexity.

(2) Metrics of phytoplankton size

Experimental and oceanographic field research have different traditions in characterizing the cell or colony size of mixed phytoplankton assemblages, which are not always directly comparable.

Size fractionation by filtration is the most widespread technique used in field studies in biological oceanography. The limits of size fractions usually follow conventional classification (Sieburth, Smetacek & Lenz, 1978): picoplankton (<2 μm), nanoplankton (2–20 μm) and microplankton (20–200 μm; in many practical applications >20 μm). The biomass of the size fractions is then measured as chlorophyll *a* concentration or particulate organic carbon. In some cases, primary production of the size classes is measured. Characterizing phytoplankton size structure this way is efficient in terms of labour requirements per sample but provides only coarse resolution.

Size–abundance spectra (SAS) are based on calculating the cell number per logarithmically scaled size class of phytoplankton (size defined as cell volume; usual class width: one $\log_2$ or one $\log_{10}$ unit) and plotting log abundance of each class against log size (e.g. Cermeño *et al.*, 2008). This method was used to analyse the biomass distribution of all pelagic organisms from bacteria to whales (Sheldon, Prakash & Jr Sutcliffe, 1972; Platt & Denman, 1978). In most cases, a linear regression with a negative slope can be fitted through these double-logarithmic SAS plots. A more negative slope indicates stronger dominance by small phytoplankton. A slope of $b_A = -1.0$ indicates that all size classes have the same total biovolume. In principle, logarithmically scaled abundance and biomass-related size spectra are easily interconvertible, as the slope of the biomass-based spectrum (b_B) is $b_A + 1$, but care must be taken if carbon density changes systematically with size. Abundance and size measurements needed to construct such spectra are either based on flow cytometry or on microscopy or a combination of these (flow cytometry for small phytoplankton; microscopy for large phytoplankton).

Mean cell size is the usual metric reported from experimental studies. It is usually calculated as abundance-weighted mean cell volume (V_A): $V_A = B_{tot}/N_{tot}$, where B_{tot} is total biomass and N_{tot} is total abundance. More rarely it is reported as biomass-weighted mean cell volume V_B, calculated as: $V_B = \sum V_i \cdot p_i$, where V_i is the cell volume of an individual species and p_i its relative proportion of total biomass. In the few cases where both V_A and V_B have been reported, there were order-of-magnitude differences in their numerical values, but their response to environmental drivers was in the same direction (Rüger & Sommer, 2012).

While a direct conversion of V_A and V_B into the SAS slope is not possible, they use the same primary database (cell counts and measurements). A comparison of these measurements with fractionation data can only be an approximation, because the relationship between retention by filters/nets of a defined pore or mesh size and cell size is not predictable for non-spherical particles. In an experiment by Runge & Ohman (1982), retention either depended on the longest axis (chain-forming diatoms) or on the second longest axis (*Ceratium fusus*).

(3) Metrics of resource richness

Assessing the relative role of nutrients (or more generally resources) *versus* temperature as driving factors for oceanic phytoplankton cell size makes it necessary to scrutinize how the resource richness or productivity of a water body is defined. Some authors use dissolved nitrate and/or phosphate concentrations (e.g. Cavender-Bares, Rinaldo & Chisholm, 2001; Cermeño *et al.*, 2008; Hilligsøe *et al.*, 2011) as a proxy for nutrient richness, while others use bulk measurements of phytoplankton biomass (often chlorophyll levels) or primary productivity (Marañón *et al.*, 2012; López-Urrutia & Morán, 2015). Use of dissolved nitrate and phosphate levels alone often means ignoring other potentially limiting factors (mainly iron and light) and is highly dependent on sampling time. At the start of a bloom, dissolved nutrient concentrations are high but later become depleted, sometimes to undetectable levels at the peak of the bloom, despite unchanging productivity of the water body. Using bulk phytoplankton variables avoids neglecting other limiting factors, but also involves the problem of time dependence, with order-of-magnitude differences in biomass between pre-bloom and bloom periods. To overcome these problems, Marañón *et al.* (2014) developed a resource index (RSI) based on nutrient levels just below the euphotic zone that includes the ratio of the euphotic depth [z_{eu}; defined as the depth where photosynthetically active radiation (PAR) is 1% of surface irradiance] to the mixing depth [z_m; defined as the depth where the density difference between the surface and 1% PAR depth ($\Delta\sigma T$) exceeds 0.125]: RSI = (NO_3 at 1% PAR/$\Delta\sigma T$) × (z_{eu}/z_{mix}). This index could be modified for other limiting nutrients by including physiologically optimal ratios.

III. GLOBAL TRENDS IN THE OCEAN

(1) Size variation assessed by fractionation of phytoplankton

The global trend towards larger phytoplankton cells in colder seas has become commonplace knowledge in biological oceanography. It is also accepted that the shift towards larger mean sizes is due to a greater contribution of large phytoplankton in colder waters rather than disappearance of smaller ones (Chisholm, 1992; Irigoien, Huisman & Harris, 2004). The trend towards smaller cell sizes at higher temperatures is also apparent in the fossil record of diatom frustules (Finkel *et al.*, 2005).

However, it is by no means clear whether the global trend towards larger phytoplankton is a temperature effect or a result of the global negative correlation between sea-surface temperatures and nutrient supply to the euphotic zone, i.e. to the well-illuminated surface zone where phytoplankton grow (Kamykowski & Zentara, 1986; Agawin *et al.*, 2000). This negative correlation results from the fact that the water below the euphotic zone is the most important source of nutrient supply to the surface, either by deep convective mixing promoted by surface cooling or by upwelling along continental margins bringing cold, nutrient-rich water to the surface even at low latitudes (e.g. Peru upwelling). At low nutrient availability, small phytoplankton are at a competitive advantage due to their high surface area to volume ratio facilitating nutrient uptake at low concentrations (Chisholm, 1992; Kiørboe, 1993; Raven, 1998; Marañón *et al.*, 2007, 2012). Under the umbrella of Global Change research, present-day biogeographic patterns in phytoplankton size distribution have been extrapolated to predict smaller phytoplankton in a future, warmer climate (Morán *et al.*, 2010).

It remains, however, legitimate to question the extent to which temperature has a direct, nutrient-independent effect on phytoplankton cell size. Attempts to answer this question using statistical analysis of global databases have either failed because of the strong correlation between temperature and nutrient levels ($r = -0.95$; Agawin *et al.*, 2000), or have found a dominant effect of nutrients alone (Marañón *et al.*, 2012, 2014) or a similar contribution from both factors (Hilligsøe *et al.*, 2011). The data compilation of Marañón *et al.* (2012) was re-analysed by López-Urrutia & Morán (2015) who found a nutrient-independent temperature effect: the proportion of picoplankton increased with temperature in the low-productivity subset ([chlorophyll *a*] $<1\,\mu g\,l^{-1}$) while the proportion of microplankton decreased with temperature in the high-productivity subset ([chlorophyll *a*] $>2\,\mu g\,l^{-1}$). However, in their reply Marañón *et al.* (2015) showed that size was also correlated with resource supply within the subsets defined by chlorophyll *a* concentrations.

Unfortunately, the databases do not provide a balanced representation of all combinations of nutrients and temperature, because few data represent 'cold–nutrient-poor' and 'warm–nutrient-rich' sites. This reflects the low contribution of such regions to the total area of global ocean, and becomes problematic when using multiple regression analysis or comparable statistical procedures to disentangle the roles of temperature and nutrient levels.

The 'warm–nutrient-rich' combination is mainly represented by areas affected by coastal eutrophication or coastal upwellings in tropical areas. However, frequent summer blooms of dinoflagellates, often red-tide species (Cloern *et al.*, 2005; Edwards *et al.*, 2006) in warm, eutrophicated coastal seas also underpin the role of nutrients. While these bloom-forming dinoflagellates clearly fall into the microplankton category, they are not the largest marine phytoplankton (cell volume of 10^3–$10^4\,\mu m^3$ as opposed to 10^5–$10^6\,\mu m^3$ for the largest diatoms). However, this difference would not be detected by the usual protocols of size fractionation.

The 'cold–nutrient-poor' combination is mainly represented by iron-limited polar waters. Here, there is a dominance of small phytoplankton; experimental *in-situ* iron-fertilization experiments caused a shift towards larger phytoplankton (Gall *et al.*, 2001). This size increase was relative to both pre-fertilization starting conditions and to the water outside the fertilized patch. While picoplankton showed only a weak response, the mean cell size of nanoplankton increased, and the proportion of the large microplanktonic diatom *Fragilariopsis kerguelensis* also increased. A similar response was reported from iron-fertilization experiments in the high nitrate/low chlorophyll (HNLC) zones of the equatorial pacific (Martin *et al.*, 1994; Coale *et al.*, 1996).

(2) Size variation assessed by size–abundance spectra

We searched *Web of Science* using the search items 'size abundance spectra', 'SAS', 'marine phytoplankton', 'temperature', 'upwelling', 'coastal', 'HNLC', 'nutrient', 'chlorophyll', 'warm', 'cold' and 'ocean'; alone or in combination. We selected papers that contained phytoplankton size–abundance spectra based on lumped abundances of size classes (usually $\log_2$-scaled). The slopes of the log-abundance *versus* log-size regressions ranged from approximately −1.3 to −0.7; more negative slopes characterizing open-ocean oligotrophic stations while less negative slopes characterized more eutrophic coastal and upwelling stations (Reul *et al.*, 2005; Marañón *et al.*, 2007; Barnes *et al.*, 2011; Huete-Ortega *et al.*, 2012, 2014). Moreno-Ostos *et al.* (2015) compared SAS from three Atlantic cruises spanning latitudes from 35°S to 35°N. The slopes ranged from −1.19 to −0.91, but the variance of slopes could not be explained by phytoplankton biomass nor by latitude/temperature, possibly because of the restricted range of these variables. In a multi-annual, seasonal study Huete-Ortega *et al.* (2010) separated the annual cycle at a shelf station in the Bay of Biscay into five periods: winter, upwelling I (start of bloom), upwelling II (peak of bloom), summer stratification, and downwelling. In four of the five periods the slope ranged from −1.1 to −0.94 with no significant differences between periods. Only upwelling

II had significantly less negative slopes (−0.82 to −0.88). Upwelling II was intermediate in terms of temperature and was one of the two high-biomass periods (together with summer stratification which was characterized by strongly negative slopes). Barnes *et al.* (2011) analysed size spectra from 362 samples from open Atlantic Ocean transects (50°S to 48°N) and coastal stations from the Benguela Upwelling to the Irminger Sea. The sea-surface temperatures ranged from 6 to 26°C, chlorophyll concentrations ranged from 0.03 to 2 mg m^{-3}. The final SAS regression model contained only chlorophyll *a* levels as a predictor variable ($b_A = -1.196 + 0.099$ [Chl *a*]) while the final model used to predict the cell size which divided biomass into two (M_{B50}) also contained sea-surface temperature (SST): $M_{B50} = 1.34 - 0.043$ SST (°C) + 0.929 [Chl *a*] (mg m^{-3}).

(3) Intraspecific size variation

Studies on the intraspecific size variation of marine phytoplankton along natural gradients of latitude or temperature are rare. A *Web of Science* search with the key words 'marine', 'phytoplankton', 'size', 'latitude' or 'temperature' led to >600 hits, but only two studies reported intraspecific size variation *in situ*, and these were not biogeographic but seasonal studies. Jung *et al.* (2013) reported seasonal alternation between two distinct morphs of the diatom *Ditylum brightwellii* (T. West) Grunow 1885, with the large morph prevailing during cold seasons and the small morph during warm seasons. De Miranda, Gaviano & Serra (2005) found a negative correlation of cell length of the diatom *Cylindrotheca closterium* (Ehrenberg) Reimann & J.C. Lewin 1964 with temperature in a coastal, hypersaline lagoon.

Most studies of biogeographic gradients in phytoplankton size rely on size-fractionated biomass proxies, such as chlorophyll levels (Hilligsøe *et al.*, 2011) or, and to a much lesser extent, on Coulter-counter or flow-cytometric analyses. Such approaches are unable to disentangle the relative contributions of inter- and intraspecific size shifts, for which microscopic size measurements and identification are needed. However, few studies based on microscopy report size variation within species. At present, it seems safe to assume a stronger contribution of shifts in species dominance because the size range between the smallest species (*ca.* 0.6 μm) and the largest species (several millimetres; with colony sizes of several centimetres) by far exceeds intraspecific size variation.

IV. TEMPERATURE EFFECTS IN CLONAL CULTURES

Atkinson *et al.* (2003) reviewed a total of 73 size–temperature relationships from single-species (usually clonal) culture experiments with autotrophic and heterotrophic protists from freshwater, brackish and marine origin. Temperatures above the growth rate optimum and resource limitation conditions were excluded from analysis. Linear regression of cell volume *versus* temperature gave a relative temperature sensitivity (RST) expressed as the percentage change of cell volume per °C predicted for a standard temperature of 15°C. After excluding one study where the gas supply was changed between temperature treatments, the mean RST was −2.5% (95% CI: −1.7 to −3.3%). No significant influence of trophic mode (autotrophs *versus* heterotrophs), salinity group (fresh, brackish, marine) or higher taxon was found, but they did show (Fig. 3 in Atkinson *et al.*, 2003) that brackish water diatoms tended not to respond to temperature (mean RST = 0.1%; 95% CI: −2 to 1.8%). There are too few studies published since Atkinson *et al.* (2003) to warrant a new meta-analysis.

Atkinson *et al.* (2003) included only results relating to the size of single cells. However, shifts between single-cell and colonial life-cycle stages or changes in cell numbers per colony provide larger scope for size adjustments than changes to the volume of individual cells. The most extreme case in marine phytoplankton is represented by the prymnesiophyte genus *Phaeocystis* spp. which shows life-cycle shifts between unicellular flagellate stages (5–10 μm) and gelatinous colonies which can reach several millimetres or even centimetres. While the colonial stage is always diploid, flagellates can be haploid or diploid (Peperzak & Gaebler-Schwarz, 2012). While traditionally nutrient supply and zooplanktonic grazing have been considered cues for colony formation, a recent culture study by Wang *et al.* (2010) showed the colony size and the number of cells per colony decreased with increasing temperature in *Phaeocystis antarctica* Karsten 1905 and *P. globosa* Scherffel 1899, while Takabayashi *et al.* (2006) found an increasing number of cells per chain at higher temperatures in the diatom *Skeletonema costatum* (Grevillle) Cleve 1873.

V. SIZE EFFECTS IN COMMUNITY-LEVEL EXPERIMENTS

While experiments with clonal cultures detect strictly phenotypic responses to temperature, experiments with naturally mixed plankton communities have the potential to reveal size responses resulting from species sorting and from genotype sorting within species. However, the latter is only possible if cell sizes of different species are analysed separately for each experimental unit. This has only been done in some multispecies experiments because of labour constraints, because size shifts were not the main focus of these studies or because the effect of intraspecific size variation on total biomass and community mean cell size is usually considered negligible. Here we first review interspecific size effects and then concentrate on those studies which permit comparison of intra- and interspecific effects.

In most of the 12 experiments reviewed here, phytoplankton size variation was studied in response to temperature either alone or in combination with other environmental factors such as grazing by different types

Table 1. Mesocosm experiments where size shifts due to species shifts were recorded without analysis of intraspecific size changes. The experiments were performed in 1.5 m^3 mesocosms filled with natural late winter/early spring plankton from the Western Baltic Sea. Copepods (C_0) were added from net catches. Temperature followed the long-term mean seasonal sea-surface temperature starting from 4 February augmented by a temperature differential (Δt) for the different treatment levels. Light was programmed in order to maintain a constant ratio of initial light levels (I_0) and the seasonal progression of above-cloud irradiance. In 2006 two successive experiments were performed.

Year of experiment	Number of experimental units	Δt (°C)	I_0 (W h m^{-2} PAR)	C_0 (individuals l^{-1})
2005	12	0, 2, 4, 6	32.3	16
2006-1	12	0, 2, 4, 6	202	5.5
2006-2	12	0, 2, 4, 6	129	9
2007	12	0, 2, 4, 6	64.5	4.0
2008	12	0, 6	265, 318, 381	7.5
2009	12	0, 6	318	1.5, 4, 10

Sources: Sommer & Lengfellner (2008), Sommer & Lewandowska (2011) and Sommer *et al.* (2012). See Sommer *et al.* (2012) for a comprehensive meta-analysis of these experiments. PAR, photosynthetically active radiance.

of herbivores, nutrient limitation or addition of CO_2 (ocean acidification). The temperature effect was usually expressed as the slope of $\log_e$ cell size on temperature because log-transformation provided the best approximation to normal distributions. Where the original sources used other types of regression analysis (Peter & Sommer, 2012; Rüger & Sommer, 2012) the data were recalculated. When the original experiments manipulated additional environmental factors, their influence was either controlled for using multiple regression analysis or by performing separate $\log_e$ cell size regressions for each level of the additional factor. When only two levels of temperature were employed, the temperature effect size is expressed by the $\log_e$ ratio of cell sizes in the warm and cold treatments divided by the temperature difference. Depending on the original source, cell sizes are either expressed as cell volume (μm^3) or cell carbon content (pg).

(1) Interspecific size changes in multispecies experiments

Under the umbrella of Global Change research, multispecies experiments based on natural plankton communities, so-called mesocosm experiments, for the analysis of temperature effects on plankton biomass development, production, etc., were initiated in several regions worldwide. Among the marine studies, changes in phytoplankton cell size were reported only for six experiments on Baltic Sea phytoplankton performed in the mesocosms facility of GEOMAR, Kiel from 2005 to 2009 (summarized in Sommer *et al.*, 2012; Table 1), leading to a strong geographic bias in the available data. These experiments consisted of initially 8, later 12 mesocosms receiving graded temperature treatments from a control scenario for late winter/early spring (Kiel Fjord long-term mean 1993–2002) to up to 6°C warming. In 2008 interactions between the factors light and temperature and in 2009 interactions between the factors copepod density and temperature were studied. Incident light and initial inoculum composition (natural plankton from Kiel Bight) varied among experiments. A comparable freshwater experiment was performed in Dorset, UK (Yvon-Durocher *et al.*, 2011). Baltic Sea experiments after 2009 (Peter & Sommer, 2012, 2013, 2015; Rüger & Sommer, 2012) were designed to analyse both inter- and intraspecific size responses.

During the planning phase of the experiments at Kiel, the main focus was on biomass, species composition and the timing of the bloom. However, the first results (Sommer *et al.*, 2007) showed the presence of a strong size effect with completely different types of phytoplankton in the coldest and the warmest treatments (Fig. 1). In the control treatments, chain-forming, medium-sized diatoms (e.g. *Chaetoceros* spp.) dominated biomass while nanoflagellates and picoplankton dominated in the treatments with 6°C warming. Since this shift in phytoplankton composition strongly resembled previously observed top-down effects of copepods on phytoplankton size structure (Sommer *et al.*, 2005), the hypothesis was put forward (Sommer *et al.*, 2007; Sommer & Lengfellner, 2008) that enhanced grazing by overwintering copepods could explain this shift. This hypothesis was confirmed using a factorial combination of copepod density and temperature (in 2009; Table 1): adding copepods had the same effect on cell size and species composition as warming (Sommer & Lewandowska, 2011). Analysis of the experiments performed from 2005 to 2009 (Sommer *et al.*, 2012) used the following approach: log community mean cell size (in pg C) was regressed against temperature separately for each experiment (for the 2008 and 2009 experiments the different light or copepod levels were treated as separate experiments). Then the cell sizes (S_P) predicted for the grand mean experimental temperature (5.28°C) and the slopes (b_T) of the individual regressions were used as dependent variables in a multiple regression analysis with stepwise variable selection. The candidate variables were initial phytoplankton biomass ($B_{P,0}$), initial phytoplankton cell size (S_0), initial copepod density (C_0), initial mean microzooplankton biomass ($B_{MZ,0}$) and incident light levels (I_0).

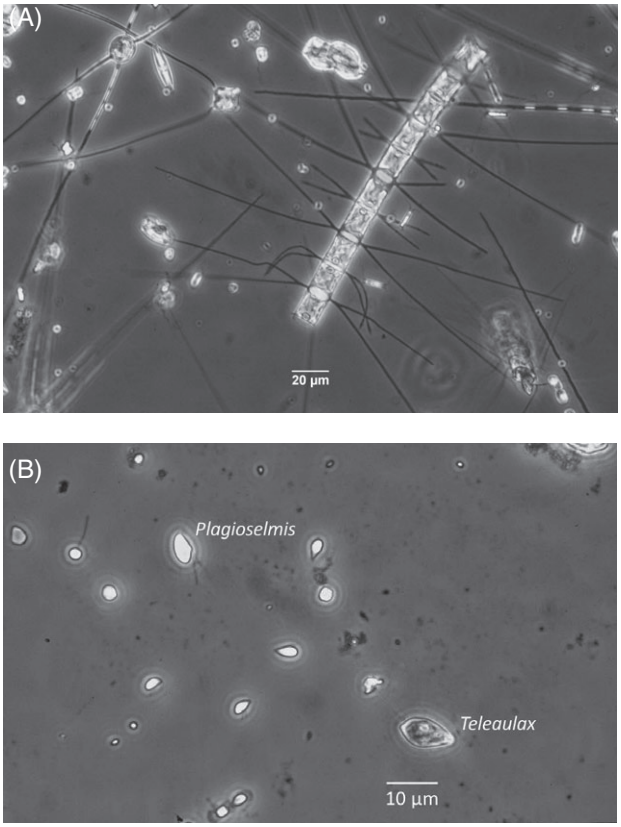

Fig. 1. Phytoplankton during the biomass maximum at the spring peak in the 2005 Kiel mesocosms experiment (Sommer *et al.*, 2007). Micrographs from a 50 ml Utermöhl chamber. (A) Natural temperature treatment; dominance by medium-sized diatoms (mainly *Chaetoceros curvisetus*). (B) 6°C-warmed treatment; dominance by nanoflagellates (*Teleaulax acuta*, *Plagioselmis prolonga*).

The size at the mean experimental temperature (S_P) was found to correlate positively with daily light levels (I_0 in W h m^{-2} PAR) and negatively with initial copepod density (C_0 in individuals l^{-1}):

$$\log_e S_P = 0.575\ (\pm 0.64\ \text{S.E.}) + 0.763\ (\pm 0.099\text{S.E.})\ \log_e I_0 - 0.261\ (\pm 0.123\ \text{S.E.})\ \log_e C_0\ (r^2 = 0.91;\ P < 0.0001;\ N = 10).$$

The slope b_T was found to correlate positively with light levels and initial phytoplankton biomass (B_0 in mg C l^{-1}):

$$b_T = -1.506\ (\pm 0.177\ \text{S.E.}) + 0.22\ (\pm 0.034\ \text{S.E.})\ \log_e I_0 + 0.054\ (\pm 0.024\ \text{S.E.})\ \log_e B_0\ (r^2 = 0.85;\ P = 0.0005;\ N = 10).$$

A positive correlation between the slope b_T and light intensity indicates decreasing temperature sensitivity of cell size with increasing light levels. The range of b_T values between individual experiments was rather wide, from −0.02 to −0.585 pg C °C^{-1}, with a mean of −0.194 pg C °C^{-1}. The temperature effect size in the freshwater study of Yvon-Durocher *et al.* (2011; see their Fig. 2) can be recalculated as −0.562 pg C °C^{-1} which is similar to the highest b_T values in the Baltic Sea experiments.

(2) Comparing intra- and interspecific size effects in multispecies experiments

The Kiel experiments summarized in Sommer *et al.* (2012) were only analysed for intraspecific size changes. A series of micro- and mesocosm experiments subsequently was set up with the aim of comparing intra- and interspecific size shifts in phytoplankton (Table 2). These were conducted using plankton from the western Baltic Sea. Typically, cell size was measured at the peak abundance for the species studied or at the end of the experiments, assuming that any temperature effect would increase with time. Only Rüger & Sommer (2012), using mesocosms for a late-spring community from the western Baltic Sea, failed to find decreased community mean cell size at higher temperatures, while the other studies did find a significant relationship (Table 2). Temperature was combined with other experimental factors in these studies, including zooplankton grazing (Peter & Sommer, 2012), nutrient limitation (Peter & Sommer, 2013, 2015), and CO_2 enrichment (Sommer *et al.*, 2015), because of field evidence suggesting a strong role of nutrients and because the earlier mesocosm studies suggested an indirect effect of temperature *via* grazing (Sommer & Lewandowska, 2011).

(*a*) *Temperature and grazing*

Peter & Sommer (2012) combined a range of temperatures with different types of grazers in two different experiments. In a first, bottle-scale (700 ml), microcosm experiment, the grazer communities consisted of nanoflagellates (pre-filtration by 20 µm mesh), nano- and microzooplankton (pre-filtration by 200 µm mesh), and the copepod *Acartia tonsa* Dana 1849 (added from cultures). In a subsequent mesocosm experiment (300 l) two types of grazer guilds [protists (after 200 µm pre-filtration) and *Acartia tonsa*] were combined with temperature. From existing knowledge on the size selectivity of different grazer types and their impact on the size spectrum of prey trophic levels (Stibor *et al.*, 2004; Sommer *et al.*, 2005; Sommer & Sommer, 2006; but see Calbet, 2008, for counter examples) it was hypothesized that increased grazing rates induced by warming should be advantageous for smaller algae under copepod grazing, while the reverse effect should be true under protist grazing, because they feed preferentially on small phytoplankton. Contrary to this hypothesis, no such reversal of the temperature effect was found. However, the intraspecific size decline with warming was strongest under copepod grazing (most negative value of slope b_T, Table 2), intermediate under microzooplankton (mainly ciliates) grazing and weakest or non-significant under nanozooplankton grazing (*cf*. the significant interaction terms in Fig. 2). Peter & Sommer (2012) concluded a

Table 2. Micro- and mesocosm experiments where intra- and interspecific size variation was studied. Effect sizes of temperature on phytoplankton cell size are as follows: E_{min}, temperature effect size for species with least-negative response to temperature; E_{max}, temperature effect size for most sensitive species; E_{mean}, mean intraspecific effect size for all species; E_C, temperature effect size for community (interspecific) mean cell size. −/ns/+, numbers of significantly negative, non-significant and significantly positive responses; significant effect sizes ($P < 0.05$) are printed in bold. Significance was either assessed by regression analysis of $\log_e$ size on temperature (>2 temperature levels, significance of the slope) or by ANOVA (two temperature levels). In the case of regression analyses effect sizes were defined as the regression coefficient b_T, in the case of ANOVAs effect sizes where defined as the $\log_e$ of the ratio between the mean cell volume at the higher and the lower temperature divided by the temperature difference. Experimental factors crossed with temperature had either significant main effects or significant interaction effects together with temperature on community mean cell size. For effects on individual species see text and the original literature

	E_{min}	E_{max}	E_{mean}	−−/ns/+	E_C
Multispecies mesocosm experiment (1.4 m^3): three temperatures from 4°C to 12°C, copepods added as nauplii, nutrient replete, 14–19 April 2010, $N = 9$ (Rüger & Sommer, 2012)[a]					
	0.0482	**−0.0403**	0.0183	2/4/1	−0.0126
Multispecies microcosm experiment (700 ml): three temperatures from 4.5°C to 10.5°C combined with three grazer communities, 1–28 April 2011, $N = 27$ (Peter & Sommer, 2012)[b]					
Nanozooplankton grazing	0.0129	**−0.109**	−0.0488	4/1/0	**−0.268**
Microzooplankton grazing	−0.0059	**−0.133**	−0.0471	4/1/0	**−0.278**
Copepod grazing	**−0.0096**	**−0.176**	−0.0686	4/1/0	**−0.339**
Multispecies mesocosm experiment (300 l), four temperatures from 8°C to 18.5°C combined with two grazer communities, 5–28 July 2011, $N = 24$ (Peter & Sommer, 2012)[a]					
Protist grazing	0.0113	**−0.0985**	**−0.0498**	7/2/0	**−0.227**
Copepod grazing	0.0036	**−0.14**	**−0.073**	6/3/0	**−0.249**
Multispecies microcosm experiment (700 ml), three temperatures from 13.5°C to 19.5°C combined with three levels of N-limitation, 9–30 August 2012, $N = 27$ (Peter & Sommer, 2013)					
Weak N-limitation	0.0122	−0.0168	0.0009	0/15/0	**−0.0477**
Medium N-limitation	0.0012	**−0.0705**	**−0.0201**	9/6/0	**−0.189**
Strong N-limitation	−0.0032	**−0.259**	**−0.072**	13/2/0	**−0.613**
Multispecies microcosm experiment, two temperatures (1°C and 7°C) combined with two levels of nutrient limitation and three N:P ratios, 6–28 April 2013, $N = 36$ (Peter & Sommer, 2015)					
Low nutrient stress	**−0.0060**	**−0.0187**	−0.0125	7/0/0	**−0.0166**
Strong limitation, N:P = 16:1	**−0.0358**	**−0.0541**	−0.0469	7/0/0	**−0.0581**
Strong limitation, N:P = 40:1	**−0.0447**	**−0.0717**	−0.0573	7/0/0	**−0.0740**
Strong N-limitation, N:P = 4:1	**−0.0602**	**−0.0942**	−0.0777	7/0/0	**−0.111**
Multispecies mesocosm experiment (1.4 m^3) with two temperatures (9°C and 16°C) combined with two CO_2 levels (460 and 1040 µatm), 19 October to 12 November 2012, $N = 12$ (Sommer, Paul & Moustaka-Gouni, 2015)					
Low CO_2	0.00187	**−0.1475**	−0.0604	11/3/0	**−0.182**
High CO_2	−0.0029	**−0.1357**	−0.0448	11/3/0	**−0.118**

[a]In the original publication log volume–log temperature regressions were used.
[b]In the original publication second-order polynomials were fitted to the data.

grazing-independent temperature effect on phytoplankton cell size because the working hypothesis derived from existing knowledge about grazer size selectivity had predicted that protist grazing would lead to a positive temperature effect on phytoplankton size as opposed to a negative temperature effect under copepod grazing. A further observation was that under all grazing regimes, the relative size change (expressed as the slope of regressions of log-transformed size data on temperature, b_T) was more pronounced for larger algae than for small ones (examples in Fig. 2), as shown by regression analysis in Peter & Sommer (2012):

$$b_T = 0.14 - 0.32\ (\pm 0.08)\ \log V_M\ (r^2 = 0.41;\ P = 0.0001;\ N = 33),$$

where V is the grand mean cell volume (in μm^3) of each species.

(b) *Temperature and nutrients*

Peter & Sommer (2013) used three temperature levels with three levels of N-limitation. Nutrient limitation was manipulated by semi-continuous dilution, with lower dilution rates leading to stronger nutrient limitation. A two-factor ANOVA for 15 species showed seven significant ($P < 0.05$) negative temperature effects on cell size, 13 significant negative effects of the intensity of N-lmitation and nine significant temperature*nutrient limitation interactions. A separate analysis for the three nutrient levels showed an increasing number of significant cases with increasing intensity of nutrient limitation.

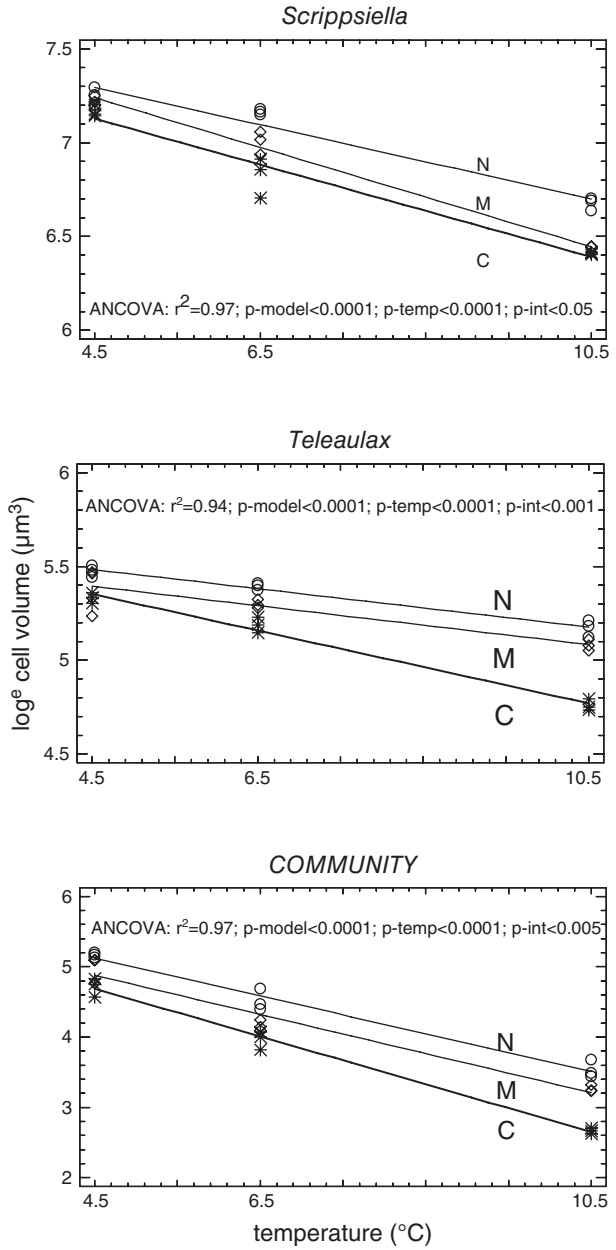

Fig. 2. Intraspecific temperature response of cell volume ($\log_e \mu m^3$) of the dinoflagellate *Scrippsiella trochoidea* (Stein) Loeblich III 1976 (top) and the cryptophyte *Teleaulax amphioxeia* (W. Conrad) D.R.A. Hill 1992 (middle), and interspecific (community) mean cell size (bottom) response to temperature under three different grazing regimes: nanoplankton grazing (N, thin line, open circles), microzooplankton grazing (M, medium line, diamonds), copepod grazing (C, thick line, asterisks) (data from Peter & Sommer, 2012). The r^2 and the significant P-values [for the entire model (P-model), for temperature (P-temp), and for the temperature × grazing interaction (P-int)] from ANCOVAs with temperature as a continuous factor and grazing type as a categorial factor are also shown.

However, in addition to a direct effect of the dilution regime all nutrient indicators (dissolved nutrient concentrations, biomass C:N ratios) showed that temperature intensified nutrient limitation. In order to disentangle nutrient effects from temperature effects, the C:N ratio of the particulate matter was used as a numerical proxy for the intensity of N-limitation because of published linear negative correlations between C:N or C:P and the quotient between nutrient-limited and maximal growth rates (Goldman, McCarthy & Peavey, 1979). Thus, temperature effects were distinguished from nutrient effects by multiple regression analysis of $\log_e$ cell volume V (in μm^3) on temperature (t) and log C:N ratios according to the model: $\log_e V = a + b_T\ t + b_{C:N}\ \log_e$ (C:N). Note that $\log_{10}$ cell volume (in μm^3) was used in Peter & Sommer (2013) but we use $\log_e$ here for consistency with other regression analyses within this review.

The regression coefficient b_T was significantly negative for seven out of 15 species ($P < 0.05$) and coefficient $b_{C:N}$ was significantly negative in 13 cases. Both coefficients b_T and $b_{C:N}$ became more negative for larger species:

$$b_T = 0.103\ (\pm 0.006\ \text{S.E.}) - 0.0043\ (\pm 0.0009\ \text{S.E.})\ \log_e V_m\ (r^2 = 0.5;\ P < 0.001;\ N = 15)$$

and

$$b_{C:N} = 0.053\ (\pm 0.108\ \text{S.E.}) - 0.0123\ (\pm 0.016\ \text{S.E.})\ \log_e V_m\ (r^2 = 0.43;\ P < 0.001;\ N = 15)$$

where V_m is the grand mean cell volume for a given species. Thus, the cell sizes of larger species were more sensitive to warming and to nutrient stress than those of smaller species.

While the intraspecific temperature-related regression coefficients b_T varied between 0.0046 and −0.041 (mean: −0.0129) the value of b_T for community (interspecific) mean cell size was −0.214, i.e. over an order of magnitude larger than for the intraspecific mean. The regression coefficient $b_{C:N}$ characterizing the sensitivity to N-limitation ranged from −0.039 to −1.128 for individual species with a mean of −0.604, as opposed to the interspecific value of −5.11.

Peter & Sommer (2015) also investigated differences in the identity of the limiting nutrient (N *versus* P). Temperature (two levels) was combined with two levels of dilution (nutrient limitation) and three N:P ratios. Seven species were analysed. The effect of P-limitation was qualitatively similar to the effect of N-limitation, but it was less strong. The smallest cells were produced by a combination of high temperatures, low dilution rates and high N:P ratios and the largest cells at low temperature, high dilution rates and a balanced N:P ratio. At all combinations of temperature and dilution rates and for all species, a balanced 16:1 supply of N:P produced larger cells, the strongly P-limited medium (N:P = 40:1) produced intermediate-sized cells, and the

strongly N-limited medium (N:P = 4:1) produced the smallest cells. A three-factor ANOVA showed highly significant ($P < 0.001$) effects of temperature, dilution rates and N:P ratios for all species and for community mean cell size (Peter & Sommer, 2015).

(c) *Temperature and CO_2-enrichment*

Concern about ocean acidification motivated mesocosm experiments with a factorial combination of temperature (two levels) and CO_2 (550 *versus* 1040 ppm) levels (Sommer *et al.*, 2015). Fourteen species of phytoplankton and three heterotrophic flagellates were analysed. Nine phytoplankton species showed a significant, negative effect of temperature on cell size and nine showed a positive CO_2 effect. The negative effect of temperature on community mean cell size was weaker under high CO_2 (Fig. 3), leading to a significant interaction term ($P < 0.05$; Table 2 in Sommer *et al.*, 2015). Since CO_2 addition also enhanced total phytoplankton biomass, CO_2 was interpreted as a limiting nutrient. This interpretation was supported by the response of the heterotrophic flagellates; the response to warming of the two larger ones (*Telonema subtilis* Griessmann 1913: 5–8 µm, *Cryothecomonas* cf. *longipes* Schnepf & Kühn 2000: 8–15 µm) were like those of similar-sized algae, but they did not show a significant response to CO_2 limitation. Like pico-phytoplankton, the pico-sized heterotroph *Bolidomonas* sp. (average diameter 1.6 µm) did not respond to temperature.

The response to CO_2 might differ in calcifying algae, for which CO_2 is not only a resource for photosynthesis but also a potential inhibitor of calcification. In a factorially combined experiment, the coccolithophore *Emiliana huxleyi* showed a size reduction with increasing temperatures, but also with increasing CO_2 levels (De Bodt *et al.*, 2010).

VI. DIRECT *VERSUS* INDIRECT MECHANISMS OF SIZE CHANGE

There is overwhelming, but not unequivocal (*cf*. Rüger & Sommer, 2012) evidence that marine phytoplankton decrease in size with increasing temperature. However, most of the supporting evidence from community-level experiments comes from one marine locality (Kiel, western Baltic Sea) and one freshwater experiment from the UK. Nevertheless, until there is evidence to the contrary, we may assume that the fundamental mechanisms driving size changes apply throughout the globe, since all higher phytoplankton taxa except coccolithophores were present in the above studies. Biogeographic evidence for the mechanisms underlying the temperature effect on phytoplankton cell size is controversial. While many authors claim that the size–temperature trend is dominantly driven by a negative temperature–nutrient correlation (e.g. Marañón *et al.*, 2015) others claim that there is an additional, direct temperature effect (e.g. López-Urrutia & Morán,

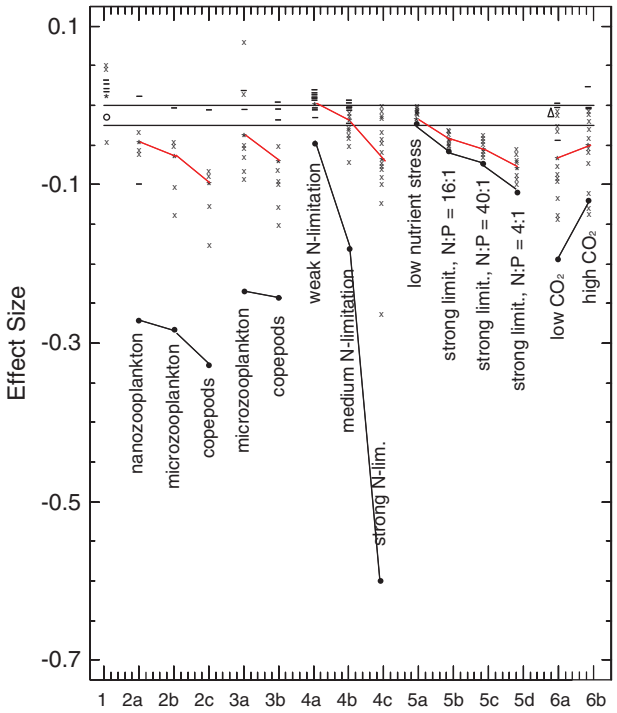

Fig. 3. Comparison of effect sizes in phytoplankton community experiments where intra- and interspecific temperature effects were compared: 1, Rüger & Sommer (2012); 2a, Peter & Sommer (2012) microcosm experiment with nanozooplankton grazing; 2b, Peter & Sommer (2012) microcosm experiment with microzooplankton grazing; 2c, Peter & Sommer (2012) microcosm experiment with copepod grazing; 3a, Peter & Sommer (2012) mesocosm experiment with protist grazing; 3b, Peter & Sommer (2012) mesocosm experiment with copepod grazing; 4a, Peter & Sommer (2013) weak N-limitation; 4b, Peter & Sommer (2013) medium N-limitation; 4c, Peter & Sommer (2013) strong N-limitation; 5a, Peter & Sommer (2015) low nutrient stress; 5b, Peter & Sommer (2013) strong limitation (N:P = 16:1); 5c, Peter & Sommer (2015) strong limitation (N:P = 40:1); 5d, Peter & Sommer (2015) strong limitation (N:P = 4:1); 6a, Sommer *et al.* (2015), low CO_2; 6b, Sommer *et al.* (2015), high CO_2. –, individual species, non-significant cases; ×, individual species, significant cases ($P<0.05$); red asterisk: intraspecific mean; open circle: interspecific effect, non-significant; black circle: interspecific effect, significant; connecting lines within experiments between means of interspecific effects (red) and intraspecific effects (black); horizontal lines: zero effect and 2.5% reduction in cell size per °C [derived from Atkinson *et al.*'s (2003) mean for clonal cultures].

2015). The successful use of a combined nutrient–light index in the meta-analysis of field data by Cermeño *et al.* (2006), Clarke *et al.* (2008), and Marañón *et al.* (2014) and the meta-analysis of mesocosm experiments in Sommer *et al.* (2012) indicate that increasing light levels also have a positive effect on cell size, as do levels of certain chemicals (N, P, CO_2).

Intra- and interspecific size effects of temperature usually have the same sign (negative), but the interspecific effect size tends to be larger than the mean intraspecific effect and in most cases than the intraspecific effect for the most

sensitive species (Figs 2 and 3). This is predictable because size variation among different species spans approximately four orders of magnitude in linear dimensions, while intraspecific size ranges are much smaller, especially in species with single-cell life stages. If size changes are driven by selection from existing variance, it is also expected that inter- and intraspecific trends are in the same direction. Atkinson *et al.* (2003) gave two hypotheses for a reduction in size as an adaptive character with increasing temperature: (*i*) the metabolic demand for gases (CO_2, O_2) increases with temperature two- to threefold for a temperature increase of 10°C (Q_{10}), while diffusion rates are less temperature sensitive ($Q_{10} = 1–2$). This should lead to a reduction in availability of gases at higher temperatures and thus an increasing advantage to smaller cell size in terms of gas uptake. (*ii*) The relative fitness advantage of reproducing earlier at a smaller body size increases with increasing population growth rates ('combined interest hypothesis' *sensu* Stearns, 1976; Atkinson, 1994).

To date, the evidence supports the assumption that there are both direct and indirect effects of temperature on phytoplankton cell size. The indirect effects act *via* the proximate factors of grazing and nutrient limitation. However, several alternative causal pathways lead to changes in these proximate factors with temperature. Temperature affects grazing both *via* a generally positive relationship between *per capita* grazing rates and temperature (functional effect) and *via* effects on the density of grazers (numerical effect). Negative numerical effects are expected if increased metabolic demands outweigh food supply (Brown *et al.*, 2004; O'Connor, 2009; O'Connor *et al.*, 2009) or if predation rates on grazers increase at higher temperatures. Moreover, it is expected that different grazers could have different effects on the size spectrum of phytoplankton (Sommer & Stibor, 2002; Katechakis *et al.*, 2004; Sommer *et al.*, 2005; Sommer & Sommer, 2006). Copepods tend to remove larger algae (except for the largest ones) and to benefit smaller ones by suppressing their protist grazers. However, a negative impact on picophytoplankton might also occur because of a four-link trophic chain (copepods – ciliates – heterotrophic nanoflagellates – picoplankton) (Zöllner *et al.*, 2009). Contrary to copepods, other grazer guilds, such as pelagic tunicates and protists tend to shift the size spectrum towards larger phytoplankton by feeding on smaller ones, but some protists, in particular heterotrophic dinoflagellates, feed on algae of almost their own size (Calbet, 2008). However, protists are themselves under top-down control by copepods (Stibor *et al.*, 2004) and pelagic tunicates are subject to egg predation by copepods (Sommer *et al.*, 2003). Further complications arise from warming-driven top-down effects of zooplanktivorous fish on copepods, predatory fish on zooplanktivorous fish etc.

An expected reversal of temperature–size effects between copepod and protist grazing was a working hypothesis of Peter & Sommer (2012). This was not found, even if the grazer community was restricted to nanoplanktonic protists. However, at each temperature most of the individual species and community mean cell size were smaller under copepod grazing than under protist grazing (Figs 2 and 3). The absence of a reversal between copepod and protist grazing may be interpreted as evidence for a grazing-independent temperature effect: without an independent temperature effect an increase in protist grazing rates at warmer temperatures should have led to greater removal of smaller phytoplankton, i.e. an increase of community mean cell size with warming.

Similarly, the experimental combination of temperature and nutrient limitation demonstrated an effect of nutrients, but did not rule out an independent temperature effect (Peter & Sommer, 2013, 2015). At present, it is not possible to explain why the effects of nitrogen limitation appeared greater than the effect of phosphorus limitation. This might result from differences in the uptake systems for these elements, or in their different roles: the bulk of N in organic matter being found in amino acids, while most P exists in nucleic acids, ATP and phospholipids. CO_2 can also be a limiting nutrient with influences on cell size, but CO_2 limitation differs from that of N and P because HCO_3^- ions provide an inexhaustible alternative source. A smaller cell size will always be advantageous under conditions of limiting supply (Reinfelder, 2011).

VII. ECOLOGICAL IMPLICATIONS OF SIZE CHANGE

(1) Size, growth and losses

Size is one of the dominant traits influencing the physiological performance and environmental requirements of organisms (Brown *et al.*, 2004; Litchman & Klausmeier, 2008). While it is generally assumed that biomass-specific metabolic rates and, therefore, also growth rates decline as body mass$^{-0.25}$, recent analyses of growth rate data have shown that phytoplankton show a unimodal response to cell size with maximal growth rates at approximately 100 μm^3 cell volume (Marañón *et al.*, 2013; Wirtz, 2013; Marañón, 2015). Surprisingly, in some biogeochemical models (e.g. Dutkiewicz, Scott & Follows, 2013), larger phytoplankton are assigned a higher maximal growth rate. While smaller cells are generally assumed to achieve better nutrient uptake at low concentrations (Chisholm, 1992; Kiørboe, 1993; Raven, 1998; Marañón *et al.*, 2007, 2012) larger cells have an advantage at higher concentrations, because maximal uptake rates increase linearly with cell size while nutrient demands expressed by the minimal cell quota (Droop, 1973) increase with a lower exponent (Marañón *et al.*, 2013; Marañón, 2015).

Size is not only important to resource acquisition and growth, but also to loss processes, i.e. predatory grazing by zooplankton and sinking from the illuminated surface layer. Smaller phytoplankton are consumed primarily by heterotrophic protists while larger ones are consumed by herbivorous metazoans, dominantly copepods in most oceans (Sommer & Stibor, 2002; Sommer *et al.*, 2005; Boyce, Frank & Leggett, 2015). However, exceptions occur:

highly specialized dinoflagellates feed on large diatoms (Calbet, 2008; Sherr & Sherr, 2009) and filter-feeding planktonic tunicates feed on picoplankton (Acuña *et al.*, 2002; Katechakis *et al.*, 2004). Interestingly, pelagic tunicates are the fastest growing metazoans with population growth rates almost equalling protists (Acuña, 2001): biomass can more than double in a day, which is an order of magnitude faster than the growth of copepods (Hopcroft & Roff, 1995). As a consequence, mass growth ('blooms') of pico- and smaller nanophytoplankton are usually prevented by their rapidly growing consumers, while the slower growth response of copepods and other crustacean zooplankton allow the potential for bloom development of phytoplankton >5–10 μm (Kiørboe, 1997; Irigoien, Flynn & Harris, 2005). The effects of copepod grazing on planktonic size are usually stronger than effects on total phytoplankton biomass, because by removing larger phytoplankton copepods release smaller phytoplankton from grazing pressure by protists (Sommer & Sommer, 2006). Indirect evidence in support of this can be found in a comparison of Micheli's (1999) review with Frank *et al.* (2005). Based on total chlorophyll *a* concentration, Micheli (1999) found evidence for a top-down effect of mesozooplankton on phytoplankton in only 1 of 50 studies. Frank *et al.* (2005) claimed a top-down effect using the colour index as a proxy for phytoplankton biomass. However, the colour index is based on plankton capture by a mesh screen and, therefore, does not include most nano- and picoplankton. These results provide evidence for changes in population size structure but not for impact on total biomass.

Another loss factor, sinking, is probably less related to cell size than traditionally assumed. Stoke's law states that the sinking velocity of particles of similar shape and density should increase with the square of the radius (Reynolds, 1984). However, only a minute proportion of phytoplankton sedimentation losses from the surface layer can be ascribed to sinking of single cells or colonies; most sedimentation occurs *via* much bigger aggregates ('marine snow') held together by transparent extracellular polymeric substances (TEPs; Alldredge, Passow & Logan, 1993). The formation of such aggregates depends on turbulent shear, excretion of exopolymers by phytoplankton, cell density and stickiness, and TEPs, and only to small extent on cell size (Kiørboe & Hansen, 1993).

(2) Changed ecosystem functions of phytoplankton in a warmer ocean

In temperate and warm seas, the anticipated direct effects of global warming and its indirect effects on nutrient supply operate in the same direction. In such areas, temperature and nutrient supply are coupled *via* the mixing and upwelling regime. Away from coastal areas with land-based nutrient sources, winter mixing and upwelling at continental margins are the prime source of mineral nutrients from the euphotic zone, leading to a global negative correlation between temperature and nutrient supply (Kamykowski & Zentara, 1986; Agawin *et al.*, 2000). Global warming is expected to decrease vertical mixing and upwelling. However, intensified wind stress might counterbalance the negative effects of temperature on upwelling (Bakun *et al.*, 2010). The expected changes for the open ocean, but not necessarily for upwelling zones, are expected to lead not only to reduced phytoplankton standing stock (Boyce, Lewis & Worm, 2010; Hofmann *et al.*, 2011; Lewandowska *et al.*, 2014) but also to reduced phytoplankton cell size (Morán *et al.*, 2010; Sommer *et al.*, 2012). This shift will have consequences on the partitioning of phytoplankton primary production between the different pathways of carbon and energy transfer in the pelagic ecosystem. The situation is different for polar seas, where increased stratification and melting of sea ice will increase light availability and productivity and permit increased biomass and larger phytoplankton cell sizes. However, the majority of global models predict a globally declining phytoplankton biomass and production in spite of increases in polar regions (e.g. Bopp *et al.*, 2001; for contrasting predictions see Taucher & Oschlies, 2011) and some other seas (Chust *et al.*, 2014). A decrease in phytoplankton cell size is also predicted by global models (e.g. Bopp *et al.*, 2005; Dutkiewicz *et al.*, 2013).

One of the main ecosystem services provided by marine phytoplankton is as the nutritional basis for fish production. There is a clear overall positive correlation between primary production and fish production (Iverson, 1990). However, this relationship is not linear, with a slope of 1.65 in a log–log regression. At the lower end of the productivity gradient, fish production amounts to 0.375% of primary production while it reaches 1% at the upper end of the productivity gradient. This difference can be explained by phytoplankton size structure and the resulting food chain length (Sommer *et al.*, 2002). In unproductive waters, phytoplankton <5 μm dominate. They cannot be eaten by crustacean zooplankton (mainly copepods), the main food of zooplanktivorous pelagic fish. Instead, they are consumed by heterotrophic protists which themselves are consumed by copepods. Depending on the number of food-chain links within the different microbial food webs (i.e. small phytoplankton – heterotrophic nanoflagellates – microzooplankton – copepods *versus* small phytoplankton – microzooplankton – copepods) copepods have a trophic level (TL) of 3 or 4 and zooplanktivorous fish a TL of 4 or 5. This differs from the classic food-web paradigm based on upwelling zones and the boreal ocean, where microphytoplankton occupy TL1, copepods TL2 and zooplanktivorous fish TL3. If, under productive conditions, phytoplankton >5 μm dominate, a larger share of phytoplankton can be consumed directly by copepods, giving them a trophic level close to 2 (Fig. 4), but see also Irigoien *et al.* (2014) who claim high food-chain efficiency of oligotrophic oceans based on high biomass levels of mesopelagic fish. Decreased trophic transfer efficiency under warmer conditions is also predicted by the modelling study of Chust *et al.* (2014) which predicts globally a stronger percentage decrease in zooplankton biomass than phytoplankton biomass.

This redistribution of matter and energy fluxes between the microbial food web (feeding by protists) and the classic grazing food chain (feeding by copepods) also has

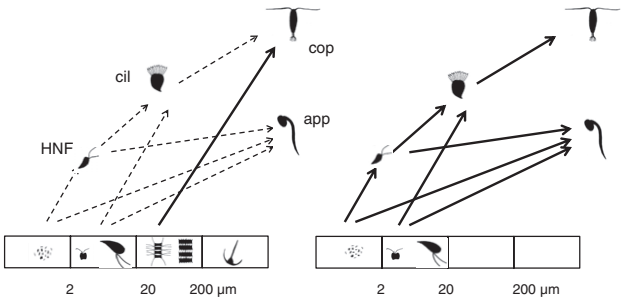

Fig. 4. Idealized planktonic food web fuelled by phytoplankton dominated by micro- and larger nanophytoplankton (left) or by pico- and smaller nanophytoplankton (right). Thick arrows: dominant pathways of energy and carbon flow, broken arrows: subordinate pathways. HNF, heterotrophic nanoflagellates; cil, ciliates; cop, copepods; app, appendicularians. The size limits for phytoplankton demarcate picophytoplankton (<2 µm), nanophytoplankton (2–20 µm), microphytoplankton (20–200 µm). Original drawing after Fig. 5 in Sommer *et al.* (2002) and Fig. 3 in Sommer & Stibor (2002).

consequences for the biological carbon pump, i.e. the sequestration of CO_2 by phytoplankton sinking into the deep ocean. If small phytoplankton dominate, they will be rapidly consumed by planktonic protists, most of the biologically fixed carbon will be respired again in the surface layer and no dense blooms will form which could facilitate aggregate formation and subsequent sinking. If large phytoplankton dominate, the slow growth response of copepods will permit the formation of blooms (Irigoien *et al.*, 2005), subsequent aggregate formation (Alldredge *et al.*, 1993; Kiørboe, 1993) and sinking of particulate organic carbon below the permanent thermocline. It is generally assumed (Smetacek, 1999; Dugdale *et al.*, 2002) that downward export of particulate organic carbon is primarily driven by medium- to large-sized diatoms because of their tendency to aggregate towards the end of blooms, and to contribute to carbon export as fast-sinking fecal pellets when eaten by copepods. Since large diatoms will be impacted negatively by ocean warming, a major mechanism of CO_2 sequestration in the ocean might be impaired which could result in a vicious circle in climate change (Wohlers *et al.*, 2009). A decrease in the efficiency of the biological pump is predicted by most global models (e.g. Bopp *et al.*, 2001, 2005), even those which predict increasing net primary production (Taucher & Oschlies, 2011).

In eutrophicated coastal seas with a shallow thermocline, the situation is quite different. Here, intensified vertical stratification leads to a steeper nutrient gradient in the thermocline during bloom periods, when surface nutrients are exhausted by algal consumption. If this nutrient gradient is within reach for vertically motile flagellates they experience a selective advantage, because they can use the nutrient-depleted surface water for photosynthesis and the nutrient-rich water below the thermocline for nutrient uptake. This advantage increases with flagellate size, because of the positive correlation between cell size and vertical migration amplitudes, which can reach *ca.* 10–20 m (Sommer, 1988). In coastal seas, flagellates profiting from nutrient gradients in a shallow thermocline include dinoflagellates, of which several species form toxic blooms (Graneli & Turner, 2007). Typical bloom-forming dinoflagellates have cell sizes of 10^3–10^5 µm^3, thus representing relatively large phytoplankton. Their expansion in response to global warming or to climate anomalies has been documented for the northeast Atlantic Ocean, including the North Sea (Edwards *et al.*, 2006), San Francisco Bay (Cloern *et al.*, 2005), and numerous other sites (Hallegraeff, 2010), and was supported experimentally by Peperzak (2003). The increasing importance of dinoflagellate blooms under intensified summer stratification in nutrient-rich coastal seas is the most important exception to the general prediction that cell size of the marine phytoplankton community should become smaller under climate warming. Because of the high prevalence of toxic or otherwise harmful species among dinoflagellates that bloom under such conditions, no advantages to fish production can be expected. On the contrary, fish kills and human poisoning by invertebrate seafood are to be expected (Graneli & Turner, 2007).

VIII. CONCLUSIONS

(1) The cell size of phytoplankton tends to decrease with increasing ocean temperature. While the role of nutrient supply (which increases in cooler oceans) is beyond doubt, an independent, direct contribution of temperature to the observed pattern is still controversial. The size trend is well documented at the community level while examples at the intraspecific level are still scarce.

(2) In clonal cultures of phytoplankton, warming leads to a reduction of cell sizes by 2.5% per °C on average.

(3) In multispecies experiments both interspecific mean cell size and intraspecific cell sizes tend to become smaller at higher temperatures. Interspecific size changes are larger than intraspecific changes.

(4) The effects of temperature on size can be attributed both to direct temperature effects and to indirect effects mediated by grazing and nutrient supply. Under different grazing regimes, the effect of temperature on size is strongest under copepod grazing and tends to decrease for smaller-sized grazer guilds. Under different regimes of nutrient limitation, it is strongest under nitrogen limitation and tends to vanish in the absence of nutrient limitation.

(5) The changed size structure of phytoplankton expected for a warming ocean will lead to a decreased ratio of fish production to primary production with possible exceptions in polar seas and wherever increased wind-stress enhances coastal upwelling.

(6) The changed size structure of phytoplankton expected for a warming ocean will lead to a weakening of the biological carbon pump in open non-polar oceans.

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