Meta-analysis of multiple driver effects on marine phytoplankton highlights modulating role of pCO$_2$

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Abstract
Responses of marine primary production to a changing climate are determined by a concert of multiple environmental changes, for example in temperature, light, pCO$_2$, nutrients, and grazing. To make robust projections of future global marine primary production, it is crucial to understand multiple driver effects on phytoplankton. This meta-analysis quantifies individual and interactive effects of dual driver combinations on marine phytoplankton growth rates. Almost 50% of the single-species laboratory studies were excluded because central data and metadata (growth rates, carbonate system, experimental treatments) were insufficiently reported. The remaining data (42 studies) allowed for the analysis of interactions of pCO$_2$ with temperature, light, and nutrients, respectively. Growth rates mostly respond non-additively, whereby the interaction with increased pCO$_2$ profusely damps growth-enhancing effects of high temperature and high light. Multiple and single driver effects on coccolithophores differ from other phytoplankton groups, especially in their high sensitivity to increasing pCO$_2$. Polar species decrease their growth rate in response to high pCO$_2$, while temperate and tropical species benefit under these conditions. Based on the observed interactions and projected changes, we anticipate primary productivity to: (a) first increase but eventually decrease in the Arctic Ocean once nutrient limitation outweighs the benefits of higher light availability; (b) decrease in the tropics and mid-latitudes due to intensifying nutrient limitation, possibly amplified by elevated pCO$_2$; and (c) increase in the Southern Ocean in view of higher nutrient availability and synergistic interaction with increasing pCO$_2$. Growth-enhancing effect of high light and warming to coccolithophores, mainly *Emiliania huxleyi*, might increase their relative abundance as long as not offset by acidification. Dinoflagellates are expected to increase their relative abundance due to their positive growth response to increasing pCO$_2$ and light levels. Our analysis reveals gaps in the knowledge on multiple driver responses and provides recommendations for future work on phytoplankton.

KEYWORDS
additivity, antagonism, environmental drivers, growth rate, interaction effect size, phytoplankton groups, primary production, synergism
INTRODUCTION

Marine primary producers contribute about half of the global net primary production (~50 Pg C/year), whereof oceanic phytoplankton makes up the main share (~47 Pg C/year) (Middelburg, 2019) forming the base of the marine food web. The fixation of CO$_2$ into biomass and the subsequent transport to depth (biological carbon pump) maintains depth gradients of dissolved inorganic carbon (DIC, i.e., the sum of CO$_{2\text{aq}}$, bicarbonate, and carbonate ions), which facilitates the oceanic uptake of atmospheric CO$_2$. Phytoplankton functional types (PFTs; Le Quéré et al., 2005) like calcifiers, silicifiers, and nitrogen fixers contribute in different magnitudes and by different means to the biological carbon pump. Changes in the dominant PFT can thus significantly alter its strength, especially in terms of export production, even without changes in total production.

Anthropogenically induced climate change causes marine ecosystems to undergo substantial shifts in temperature, CO$_2$ (and thereby pH), nutrients, and light, which are the most important environmental factors in controlling the growth of marine phytoplankton (Pörtner & Karl, 2014). The latter two factors are often correlated with variability in the mixed-layer depth (MLD; Gruber, 2011). In the following, we use the neutral term “drivers,” as organisms can suffer, benefit from, or not respond to these environmental changes. Whether a driver turns into a “stressor,” that is has a negative impact, depends on driver value and sensitivity of the organism of interest (Boyd & Hutchins, 2012).

All of the mentioned drivers have either already or are projected to change within years or decades with regionally different manifestations of multiple driver changes (Henson et al., 2017; Pörtner & Karl, 2014), even in low emission scenarios (Bindoff et al., 2019). It is a common notion that organisms are sufficiently adapted to the drivers’ seasonal extrema within their habitat. The emergence of a new driver environment can cause acclimation and evolutionary adaptation, migration, and community shifts, but also extinction, depending on the spatiotemporal distribution and intensity of the change (e.g., Barton et al., 2016; Brennan et al., 2017; Cairns, 2013; Henson et al., 2017). Understanding the effect of changes in multiple drivers on marine PFTs as a result of climate change is fundamental to robustly project the future of the biological carbon pump.

The warming of the oceans is projected to continue, with strongest trends expected for the tropics and the northern high latitudes (Bindoff et al., 2019; Gruber, 2011; Kwiatkowski et al., 2020; Meredith et al., 2019). Changes in pCO$_2$ (or pH) are evident in many oceanic regions and are projected to be strongest in the Arctic Ocean (Bindoff et al., 2019; Bopp et al., 2013; Kwiatkowski et al., 2020; Meredith et al., 2019). Stratification is anticipated to increase in most parts of the ocean, causing an intensification of light exposure and a reduction in nutrient supply to phytoplankton (Gruber, 2011). In parts of the Southern Ocean, where the stratification is expected to weaken because strengthening winds counteract warming effects (Hauck et al., 2015; Panassa et al., 2018), phytoplankton will likely be exposed to lower light and higher nutrient conditions.

Each driver affects cell functioning of phytoplankton in different ways. As a universal driver, temperature affects the rates of all biochemical reactions. Rates increase with warming until an optimum temperature, beyond which they typically decrease sharply. Generally, species from thermally stable environments like polar or tropical regions have narrow thermal windows and are, thus, more sensitive to warming (Pörtner & Karl, 2014). As the ocean takes up atmospheric CO$_2$, aqueous CO$_{2\text{aq}}$ and bicarbonate concentrations increase while the carbonate concentration and pH decrease (Zeebe & Wolf-Gladrow, 2001). The higher availability of inorganic carbon species might favor species that are less efficient in assimilating carbon (Basu & Mackey, 2018; Rost et al., 2008), whereas a lower pH can reduce growth performance in species sensitive to higher proton levels (Gao et al., 2012; Kottmeier et al., 2016a). As the only source of energy, light fuels process in phytoplankton, but can also induce damage. Species that are more tolerant to high-light stress or more efficient under often prevailing low-light regimes can outcompete other species under these conditions (Basu & Mackey, 2018; Litchman & Klausmeier, 2008). In a nutrient-limited environment, species with more efficient nutrient uptake mechanisms or lower nutrient requirements have advantages over other species (Moore et al., 2013). All of these driver responses are linked via the energy status of the cell.

When acting together, the effect of drivers may not necessarily equal the sum of their individual effects (additive effects). Instead, the combined effect can either be smaller or greater than the additive effect, that is antagonistic or synergistic (Boyd & Hutchins, 2012; Folt et al., 1999; Przeslawski et al., 2015). Additivity has recently been defined as noninteractive (Boyd et al., 2018), but is also commonly subsumed together with synergy and antagonism as interactive effects (Boyd & Hutchins, 2012; Crain et al., 2008; Feng et al., 2020). While additivity is barely observed in phytoplankton, and synergistic or antagonistic interactions are rather the rule than the exception (Gruber, 2011), there is currently no large-scale ocean biogeochemical model that is accounting for the entire set of the interactions between the most relevant environmental drivers (Laufkötter et al., 2015).

The effects of multiple drivers on marine phytoplankton have been reviewed in the past (e.g., Deppeler & Davidson, 2017; Edwards et al., 2016; Gao et al., 2012, 2018, 2019; Hätter & Gao, 2015). Meta-analyses, however, deal either with single driver effects (e.g., Dupont et al., 2010; Dutkiewicz et al., 2015; Hancock et al., 2020; Kroecker et al., 2013), only two specific drivers (e.g., Harvey et al., 2013), or only specific phytoplankton groups (e.g., Brandenburg et al., 2019; Crain et al., 2008; Daufresne et al., 2009; Przeslawski et al., 2015). In short, all these investigations reveal substantial nonadditive interactions of multiple drivers on the growth, photosynthesis, and functional traits such as cell size or calcification. High light seems to have a negative effect on phytoplankton growth under high pCO$_2$ (Gao et al., 2012, 2018), but a positive effect under high temperature (Edwards et al., 2016). High pCO$_2$ and elevated temperature have an interactive effect on phytoplankton with the response direction depending on the species (Gao et al., 2019; Kroecker et al., 2013), but
nonadditivity might only affect photosynthesis, and not the growth rate (Harvey et al., 2013). Different functional traits can be influenced differently by the same drivers within the same organism (Rokitta & Rost, 2012; Weithoff & Beisner, 2019). In fact, rates of photosynthesis often respond to environmental variability, while organisms maintain relatively constant growth rates, that is, photosynthesis and growth can be uncoupled (Rost & Riebesell, 2004). Growth rate is yet fundamental for both biogeochemistry and ecology as this trait does not directly translate, but relate to primary production over a wide range of environmental conditions and, importantly, it approximates the fitness of a cell most closely (Collins et al., 2014).

Consequently, our meta-analysis focuses on growth rates of phytoplankton, going beyond the scope of previous studies by covering the broadest set of drivers and their interactions. We aim to assess the effects of single and multiple environmental drivers on the globally most abundant phytoplankton groups by effect sizes and statistical models. Chosen driver levels for pCO$_2$ and temperature mirror present-day and projected future conditions for the end of this century. We address the following hypotheses that are based on the aforementioned studies as well as our current understanding of the mode of action for each driver-response interdependence: (a) The interaction between pCO$_2$ and temperature is additive, because nonadditive interaction typically only applies to traits other than growth (several references in Gao et al., 2012; Harvey et al., 2013); (b) high pCO$_2$ and light act antagonistically, with high-light stress setting on at lower light levels under high pCO$_2$ conditions (Gao et al., 2012, 2018); (c) nonadditive interactions can be observed between low nutrient conditions and other drivers, as more energy is needed for nutrient acquisition, and depending on whether the increase in the second driver needs or saves energy for the organism, the interaction can either be synergistic or antagonistic (Charalampous et al., 2018; Maranõń et al., 2018).

Two research questions will guide us through the meta-analysis: How does the manipulation of one driver alone (pCO$_2$, temperature, light, nutrients) affect the phytoplankton specific growth rate relative to a control level (individual effect size)? What is the net effect of dual drivers compared to a hypothetical additive outcome (interaction effect size)? By this means, additivity, synergy, and antagonism can be determined for the combined effects of both drivers on growth. With our analysis, we also aim to reveal gaps in knowledge and to identify shortcomings in multiple driver studies.

## 2 | METHODS

### 2.1 | Strategy

We reviewed available literature on the effect of dual drivers on marine phytoplankton groups, namely calcifiers, silicifiers, nitrogen fixers, dinoflagellates, and *Phaeocystis* spp. We chose these phytoplankton groups based on their ecosystem relevance and service (Le Quéré et al., 2005), and included organisms from all geographic habitats. We focus on specific growth rates as this is the trait most reliably reported in laboratory studies, which furthermore most closely relates to the “fitness” of phytoplankton (Collins et al., 2014). While there are several methods to determine specific growth rates, we used the increments of cell concentrations based on cell counts or chlorophyll measurements.

For each environmental driver we decided on one pair of values, and we defined “high” and “low” values as follows: High and low temperatures were taken as categorized by the authors of the respective article, and/or by comparing with the estimated temperature in the habitat where the tested species was isolated from. Low pCO$_2$ values were representative for the present-day pCO$_2$ range (300–500 µatm). As future pCO$_2$ values, we decided on a range of 700–1,200 µatm. Regarding nutrients (nitrate, phosphate, iron), we used replete and deplete nutrient concentrations as defined by the respective authors. We did not distinguish between different chemical forms of nutrients. If two nutrients were manipulated simultaneously in one single experiment, we excluded the study from the analysis. We used high and low light as categorized by the authors of the article.

### 2.2 | Literature search

A literature search for peer-reviewed articles was performed in April/May 2019 with a first set of search terms, and in September/October 2019 with a second set of search terms on the databases ISI Web of Science and Scopus. On ISI Web of Science, the “Topic” search scanning titles, abstracts, and author keywords was used. On Scopus, article title, abstract, and keywords were directly used as search targets. The results of both databases were sorted by relevance, see webpages for details (https://images.webofknowledge.com/images/help/WOS/hs_sort_options.html and https://service.elsevier.com/app/answers/detail/a_id/14182/supporthub/scopus/). The first set of search terms included eight queries (see Figure S1), yielding a total of 5,100 articles on ISI Web of Science and 2,477 articles on Scopus. As the first search queries missed important publications, we extended the literature search by including synonyms of the previously mentioned keywords. The second set of search terms comprised six search queries (see Figure S1). In total, 7,110 articles were found on ISI Web of Science and 5,623 on Scopus. In addition to the literature search in online databases, we screened the bibliographies of selected review articles on the effects of multiple environmental drivers on marine phytoplankton (Gao & Campbell, 2014; Gao et al., 2012, 2018; Häder & Gao, 2015; Harvey et al., 2013; Kroeker et al., 2013; 856 articles in total). In the following, we use the term “article” to refer to a published paper, and “study” to a set of experiments within a paper.

In the first selection step, we reviewed titles and abstracts from the first 100 hits of each search query as well as the bibliographies of the review articles, adding up to 3,656 articles. Articles were excluded based on the following criteria: (i) no primary data: applies for, for example, reviews, meta-analyses, and model studies; (ii) not marine: study on freshwater species; (iii) wrong group:
study on a group of organisms that is not target of this meta-analysis, for example bacteria, zooplankton, benthic organisms; (iv) one driver: study where only one driver was manipulated; (v) wrong driver: study that is not based on a combination of the desired drivers; (vi) no laboratory: study based on field data or mesocosm experiments. Articles from the review bibliographies could additionally be excluded if they only served to elucidate the review’s background (i.e., on physiological processes of phytoplankton cells). This resulted in 171 articles from ISI Web of Science, 149 articles from Scopus, and 75 articles from the review bibliographies remaining for further analysis, which is 10% of the initial results.

In the second selection step, the full articles were reviewed for the criteria listed in the first selection step. Additionally, only studies on single species (and not on communities) were included further, and methods and results of each article were quality checked for the following criteria: (vii) experimental design: articles were excluded when the experiments were not performed under controlled conditions (e.g., unknown light intensity), or pCO₂ manipulations were outside the range of interest. Each driver must have been manipulated individually and together (multifactorial experiment) in at least three replicates; (viii) reported outcome: articles must report on the growth rate and use a unit that can be compared to the other studies. Furthermore, mean, standard deviation or variance, and sample size must be mentioned; (ix) CO₂ system: measurements of the carbonate system (DIC, pH, and/or pCO₂) from the beginning and the end of the experiments must be reported as raw data, or the drift of carbonate parameters during the experiment must have been mentioned. To be included, the maximum allowed drift over the experiment was 10% for DIC and 0.1 units for pH, respectively. If the carbonate system was not or not completely reported in the article or the supplementary material, we checked whether these data were supplied to the OA-ICC portal for ocean acidification biological response data on PANGAEA (http://oa-icc.ipsl.fr/).

We excluded 27% of the remaining articles based on criteria (i)–(vi) mentioned above, 23% due to experimental design, 13% due to the reported outcome, and 11% due to insufficient reporting of the carbonate system. The final literature set consists of 25 articles published during 2002–2019, containing 42 single studies. Figure S1 presents an overview on the literature search process and the number of studies obtained for each driver pair.

Most of the studies included in our literature set examine dual factors (10 studies), with more on pCO₂ (eight studies) and nutrient concentrations (seven studies). Only two studies examined the growth responses to different drivers in combination (one study with pCO₂ and nutrient concentrations, and one with pCO₂, temperature, and nutrient concentrations). In the studies that provided the origin of their phytoplankton cultures, the spatial distribution is clearly biased toward the northern hemisphere, with 11 studies for the tropical region (0–30°N), five studies for the temperate (30–60°N), and five studies for the Arctic region (north of 60°N; see Figure S2). There was no study on species from the southern tropical region (0–30°S). Five studies were performed on Southern Ocean species (south of 30°S), biased to the polar Southern Ocean (south of 60°S) with four studies, and only one study for the subpolar and temperate Southern Ocean (30–60°S). Nutrient manipulations were performed on nitrate (five studies) and phosphate supply (one study). Table S1 in the supplementary information lists the driver levels of the individual studies. In 21 out of 25 articles, levels of both drivers were explicitly related to present-day and climate change conditions. Be aware that initial nutrient concentrations are altered by phytoplankton growth, and the nutrient concentrations that the species experience over the course of the experiment are not necessarily equivalent to the initial concentrations.

### 2.3 | Data extraction

All studies used full-factorial designs, which include four experiments: both drivers at present-day level, one driver at present-day combined with the other driver at climate change level and vice versa, and both drivers together at climate change level. Present-day levels were taken as low and climate change levels as high temperature, pCO₂, and light, with present-day levels in the natural ranges of the organisms as defined by the authors. Nutrient concentrations were interpreted as being rather high under present-day and rather low under climate change conditions. Several studies, each in a full-factorial design, could be within an article when the experiments were either conducted with different species, same species from different habitats, or with a different driver combination. From each study, we extracted the growth rates and their standard deviations or variances. If three drivers were manipulated within one study, we extracted the growth responses of each driver pair at the present-day level of the third driver. We are aware that these data are then not entirely independent from each other. However, regarding the limited availability of multiple driver studies that met our criteria, we decided to use the selected studies as much as possible. If more than two scenarios of a parameter were applied (e.g., low–intermediate–high), we chose those two scenarios for our analysis that reflected present-day and climate change conditions best, and were comparable to the other studies.

Growth rates and their standard deviations or variances were taken as reported in the article or in PANGAEA. In cases where growth rates were only displayed in graphs, we had to use the graphical data retrieval tool WebPlotDigitizer (https://apps.automeris.io/wpd/). We only used the first two decimal digits of the retrieved values, as this is the accuracy reported in most studies. In cases when the growth rate and/or its variance was zero, we used a tiny number (10⁻¹⁵) because the denominator in the formula to calculate the effect size should not be zero. Additionally, the driver levels were extracted and converted to consistent units (µmol photons m⁻² s⁻¹ for light, °C for temperature, and µmol L⁻¹ for nutrients). For pCO₂, values in the units µatm and ppm were considered to be comparable, not taking into account the effects of air and water vapor pressures. Finally, we collected information on the experimental
setup (number of replicates, acclimation time, culture technique) and on the species (phytoplankton group, origin if available).

2.4 | Statistics

2.4.1 | Effect sizes

Effect sizes \( d \), defined as mean values \( \mu \) divided by the standard deviations \( \sigma \) of the statistical populations from which we sample, were proposed by Jeffreys (1961) to test whether environmental changes have an effect on certain quantities of interest. Effect sizes are, by definition, dimensionless quantities and their values allow intuitive interpretation: (a) effects with effect sizes of magnitude \( |d| \) much larger than one are easy to recognize and, thus, no formal testing is necessary, (b) effects with small effect sizes \( (-1 < d < +1) \) could be real, however might be difficult to recognize especially at small sample sizes and, thus, formal hypothesis testing is required. In the Bayesian context, effect sizes allow appropriate choice of priors (cf. Raftery et al., 2009).

In our meta-analysis, we used effect sizes to assess the effect of the combined change in two drivers in comparison to the effect of each driver alone, as well as to categorize possible interactions between various drivers. To this end, we applied an additive model, where a significant nonadditive interaction is observed by a significant deviation from the null model of additivity (Crain et al., 2008; Gurevitch et al., 2000). Another possibility to assess the impact of a driver are multiplicative models, which include log response ratios that are frequently used in single driver meta-analyses. Following Crain et al. (2008), we argue that experimental multiple driver studies are often based on ANOVA statistical analyses, which are likewise based on assumed additivity, and that it is therefore reasonable to apply an additive model also to our multiple driver studies.

Statistical analyses were possible for the driver pairs \( p\text{CO}_2 \times \text{temperature}, p\text{CO}_2 \times \text{light}, \) and \( p\text{CO}_2 \times \text{nutrients, while too few studies on the other driver pairs did not permit further analysis (Figure S1). Effect sizes and additional information for each study are listed in Table S1. Two effect sizes were determined: the individual effect size \( d_{\text{Ind}} \) that is meant to demonstrate the effect on the response variable (here growth rate) of a change in each driver alone, and the interaction effect size \( d_{\text{Int}} \) that assesses the interplay of a change in both drivers together compared to an assumed additive outcome. Based on this, it was possible to determine the type of interaction (additive, synergistic, antagonistic; Folt et al., 1999; Przeslawski et al., 2015). A detailed description of the effect size calculation is presented in the supporting information. According to our interpretation of the effect sizes, an interaction is additive whenever nonadditivity cannot be proven statistically, that is, its 95% confidence interval overlaps with zero. An interaction is synergistic when it is promoting or dampening growth stronger than the assumed additive effect. In an antagonistic interaction, growth rates are not increasing or decreasing as strongly as expected from an additive interaction, or even have a different directionality than the theoretical additive outcome. Figure 1 schematically displays synergism and antagonism by means of hypothetical growth rates.

2.4.2 | Heterogeneity analysis

We used the R package “metafor” (version 2.1-0; Viechtbauer, 2010) in R version 3.6.1 (R Core Team, 2019) to test whether metadata of the studies were influencing the estimation of effect sizes, that is, having a significant effect on the heterogeneity of the data. A random-effects model with the restricted maximum likelihood (REML) estimator was fitted to the interaction and individual effect sizes and their variances by the rma.uni function. The REML estimator is recommended for meta-analytic variance estimation as it unites unbiasedness and efficiency (Viechtbauer, 2005). Publication year, number of replicates, acclimation time (in generations), article, number of studies stemming from one article, and the difference between elevated and control driver level were modeled as random effects (moderators). The model was initially applied without moderators to assess whether the effect sizes are significantly heterogeneous. Thereafter, the aforementioned moderators were included in the model. We reviewed the \( p \)-values of the test for heterogeneity \( Q \), the test for residual heterogeneity \( QE \), and the

![Figure 1](image-url)  
**FIGURE 1** Conceptual figure of growth rates representing synergism and antagonism in dual driver treatments. Dark gray bars display growth rates at present-day level, white bars the assumed additive outcome, and light gray bars the observed growth rates at climate change levels of both drivers. Circled arrows indicate an increase or decrease in the growth rate in comparison to the present-day level. Synergism applies when the observed interaction is increasing or decreasing the growth rate stronger than the theoretical additive outcome (A, B). Antagonism applies when the observed interaction is dampened in comparison to the assumed additive effect (C, D), or when the observed interaction has a different directionality than the assumed additive effect (E, F). Red arrows highlight the direction of growth responses of synergistic and antagonistic effects.
test of moderators QM to identify significance (level of significance \( \alpha = 0.05 \)).

## 3 | RESULTS

Individual effect sizes are displayed in Figure 2. Summarized over all studies, they show a positive effect of elevated pCO\(_2\) \((d_{\text{ind}} = 0.13 \pm 0.05, n = 36)\), elevated temperature \((d_{\text{ind}} = 1.16 \pm 0.24, n = 10)\), and high light \((d_{\text{ind}} = 1.40 \pm 0.09, n = 23)\) on the growth rates of phytoplankton. Decreasing nutrient concentrations result in a decrease in growth rates \((d_{\text{ind}} = -1.62 \pm 0.43, n = 6)\). Assessing the phytoplankton groups separately, high-light conditions increase the growth rates of all tested groups. The growth rate of coccolithophores is negatively affected by elevated pCO\(_2\), whereas the growth of diatoms and dinoflagellates benefits from higher pCO\(_2\). Only a few studies in our database examine the effect of temperature, therefore only effects on coccolithophores’ growth rates could be analyzed separately, yielding a clear increase in the growth rate with warming. Likewise, only diatoms could be analyzed separately with regard to the effect of decreasing nutrient supply, revealing a decrease in their growth rate (Figure 2). Information on the tested species and respective growth rates can be found in the supporting information (Table S1 and Figures S3 and S4). Individual effect sizes for pCO\(_2\) reveal a latitudinal pattern (Figure 3a). While the growth rate of species with polar origin on average decreases with increasing pCO\(_2\), average growth of temperate and tropic species increases or does not change. The underlying mechanisms, which could explain these latitudinal differences are illustrated in Figure 3b and discussed in Section 4.4.

Figure 4 presents the interaction effect sizes. A simultaneous increase in pCO\(_2\) and light exposure has an antagonistic effect on the growth of all phytoplankton groups together \((d_{\text{inter}} = -0.40 \pm 0.07, n = 23)\). This effect is mainly driven by diatoms, while dinoflagellates and coccolithophores respond additively to increasing pCO\(_2\) and light. Looking at the individual studies reveals that both drivers mostly have counteracting effects on the growth rates with high light increasing and elevated pCO\(_2\) decreasing growth, while in one third of the studies both drivers are growth enhancing (Table S1). Elevated pCO\(_2\) and temperature together are influencing growth rates antagonistically in the overall data \((d_{\text{inter}} = -0.36 \pm 0.18, n = 10)\), and additively in coccolithophores. In four studies, both single effects have the same growth-enhancing directionality, and in another four studies warming increases and elevated pCO\(_2\) decreases growth. In two studies, the interactive effect of both drivers leads to a reduction of growth although both single drivers alone promote growth (Table S1). Lowered nutrients and elevated pCO\(_2\) act additively on the overall growth rates \((d_{\text{inter}} = 0.08 \pm 0.29, n = 6)\), and synergistically on the growth rates of diatoms. In half of the studies, both drivers are growth dampening, and in half of the studies, elevated pCO\(_2\) is growth enhancing while nutrient limitation is growth dampening. Growth rates in the individual studies and the corresponding effect sizes are displayed in Figures S3 and S4.

Heterogeneity in the effect sizes is significant for all single drivers and driver combinations. It mainly stems from the single studies, while other moderators (publication year, number of replicates per study, acclimation time, number of studies stemming from one article, difference between elevated and control driver level) did not contribute significantly to heterogeneity. Results of the statistical tests are listed in Table S2. Thus, most effect sizes do not vary with metadata. Exceptions are the individual effect sizes of pCO\(_2\) and nutrients. Our

![Figure 2](image-url)  
**Figure 2** Individual effects and their 95% confidence interval of environmental drivers on the growth rates of phytoplankton groups. Effect sizes of groups are displayed separately when assessed for more than three studies. Note that the effect size of coccolithophores is biased toward *Emiliania huxleyi*. The number of studies included in the effect size calculations is given in parentheses.
heterogeneity analysis reveals that about half of the heterogeneity in pCO$_2$ effect sizes is caused by the genus, mostly by coccolithophores. Effect sizes quantifying nutrient deficiency are significantly biased by the number of studies stemming from one article and, thus, also the experimental conditions within each study. Only six studies were included in this effect size calculation, from which three come from one article.

4 | DISCUSSION

Single driver studies are important to understand how a driver is acting on an organism (Harvey et al., 2013). However, single driver effects are not sufficient to assess how a changing abiotic environment might affect the growth of marine phytoplankton. To achieve this, the interaction of effect sizes based on
the interplay of drivers needs to be evaluated. Experiments on phytoplankton addressing more than two drivers revealed that few drivers dominate the response of the organisms in the short-term (Brennan & Collins, 2015) and on evolutionary timescales (Brennan et al., 2017). While being restricted to dual driver interactions due to the lack of studies with more drivers, we are confident that we capture the most climate-relevant drivers (pCO$_2$, temperature, light, and nutrients) affecting phytoplankton growth. We therefore expect our findings to be valid also in situations where more than two drivers interact. Looking at these drivers, one has to be aware, however, that changes in pCO$_2$ and temperature can be more reliably projected on a global scale than changes in nutrient and light availability (Bindoff et al., 2019).

### 4.1 Growth-enhancing effects of increasing pCO$_2$, temperature, and light

We found that elevated pCO$_2$ slightly enhances growth rates (Figure 2; Figure S3), except for coccolithophores. This overall stimulating effect of elevated CO$_2$ is also supported by other single-species studies that were not included in our analysis, which observed an increase in growth rates of diatoms, dinoflagellates, Phaeocystis spp., and N fixers with increasing pCO$_2$ (e.g.,Errera et al., 2014;Hutchins et al., 2007;Kranz et al., 2010; Wu et al., 2014; Zhu et al., 2017). Regarding coccolithophores, the only calcifying group included in our analysis, we observe a decrease in their growth rates with elevated pCO$_2$ levels. Their exceptional response is also supported by the significant contribution to the effect size heterogeneity. Previous laboratory studies on the effects of ocean acidification on coccolithophores confirm the higher sensitivity of this group, but also reveal variable response patterns depending on the choice of species and experimental conditions (e.g., Hoppe et al., 2011; Iglesias-Rodríguez et al., 2008; Langer et al., 2006; Riebesell et al., 2000; Zhang et al., 2019). The response of coccolithophores (and supposedly also other phytoplankton groups) to increasing pCO$_2$ is significantly shaped by morphological parameters like cell size (Müller et al., 2017), the mode of carbon acquisition (Beardall & Raven, 2020; Kottmeier et al., 2016b), the ability to maintain pH homeostasis (Gafar et al., 2019; Taylor et al., 2011), and of course how other environmental drivers modulate the response (see Section 4.2). For community studies, effects of elevated pCO$_2$ are less conclusive, partly because other environmental drivers like changes in temperature or nutrient availability often dominated and thus masked pCO$_2$ effects (Eberlein et al., 2017; Feng et al., 2009, 2010; Neale et al., 2014; Tatters et al., 2013; Yoshimura et al., 2014). More importantly, however, ecological processes associated with the intra- and interspecific diversity within communities can modulate the overall effects in comparison to those observed in single strain studies, which are governed by physiology only. A shift in species composition together with physiological changes, for instance, can buffer the negative effects of pCO$_2$ on individual species (Hoppe, Flintrop, et al., 2018; Hoppe, Schuback, Semeniuk, Giesbrecht, et al., 2017; Sampaio et al., 2017; Sobrino et al., 2014), keeping community growth rather constant. Once the competitive ability of individual species or groups are significantly impacted, however, the community sensitivity toward ocean acidification can be even larger than would be predicted by single strain studies (Beaufort et al., 2011; Riebesell et al., 2017).

In our meta-analysis, increasing temperature generally has a growth-enhancing effect, especially for coccolithophores (Figure 2). In support, other studies found increasing temperatures to promote the development of earlier blooms and a different community structure in marine and freshwater phytoplankton (Boyd, 2019; De Senerpont Domis et al., 2014; Feng et al., 2009; Remy et al., 2017; Winder et al., 2012), where smaller phytoplankton groups including coccolithophores became more dominant (Coello-Camba et al., 2014; Feng et al., 2009; Hare et al., 2007). The benefit of primary production from warming can, however, be compensated as community respiration might increase more strongly than community production (López-Urrutia et al., 2006; Regaudie-de Gioux & Duarte, 2012). The biomass accumulation of phytoplankton can also be dampened as warming disproportionately promotes the grazing rate of herbivorous species (Laufkötter et al., 2015; Paul et al., 2015).

Our meta-analysis reveals that an increase in light intensity has an overall positive effect on the growth of phytoplankton species, where coccolithophores benefit most and dinoflagellates least. Such beneficial effects can be expected given that low and high-light levels in experiments are typically adjusted to represent light-limiting and saturating conditions, respectively. Elevated light intensities can cause a shift in the species composition of phytoplankton communities. The reasons why higher light conditions can be more beneficial to one species or group than to another are numerous; next to cell size and mode of photoacclimation, habitat depth and nutrient availability in different seasons and oceanic regions can matter (Burson et al., 2018; Donahue et al., 2019; Gao et al., 2012). Also the ability of several dinoflagellate species to switch to mixotrophy and being less dependent on light as an energy source can be important. Hence, growth response to increasing light availability depends on whether dinoflagellate species in cultures were grown phototrophically or mixotrophically (Hansen, 2011).

Finally, our analysis found decreasing growth rates with lower nutrient availability, which is rather expectable and raises confidence in our results despite the low availability of studies. Nutrient limitation can act on different processes within a phytoplankton cell, and the availability of nutrients can therefore modulate the response of an organism to other environmental drivers (Gao et al., 2018; Yoshimura et al., 2014). For example, the tolerance of phytoplankton to high temperatures decreases when the nutrient concentrations are low (Thomas et al., 2017).

### 4.2 Modulated growth responses in dual driver interactions with pCO$_2$

Rejecting our first hypothesis, which is based on earlier reviews and meta-analyses (Gao et al., 2012; Kroeker et al., 2013), we found clear antagonistic, growth-enhancing interactions between pCO$_2$...
and temperature (Figure 4; Figure S4). Findings from studies on single species (Errera et al., 2014; Milner et al., 2016; Qu et al., 2018; Tew et al., 2014) or communities (Collo-Canb et al., 2014; Paul et al., 2015) that were not assessed in our analysis illustrate the high variability in respective outcomes, with the majority tending toward antagonistic or additive reactions to increasing temperature and pCO₂. Hence, we challenge the assumption of purely additive interaction between increasing temperature and pCO₂ (Harvey et al., 2013) and instead would suppose a mutual dampening of their effects on phytoplankton growth (Sett et al., 2014). Experiments demonstrate that picoeukaryotes particularly benefit from warming and increasing pCO₂ levels (Hoppe, Flintrop, et al., 2018; Schaum et al., 2013) and become more abundant in communities under these future scenarios (Feng et al., 2009; Hare et al., 2007; Schütz et al., 2017). Our data show a similar response for coccolithophores that are rather small-sized cells compared to most other phytoplankton groups, with a positive (although additive) interaction effect size, in contrast to the antagonistic interaction of all phytoplankton groups together. In diatom-dominated communities, however, rising temperatures and pCO₂ concentrations can lead to a shift toward larger diatom species and faster bloom development (Sett et al., 2018), which argues against a pure size dependence for this interactive effect. Due to our limited data, we cannot draw conclusions for the effect of this driver interaction on diatoms and dinoflagellates.

In our second hypothesis, we argue that high pCO₂ and high light interact antagonistically, with a higher risk of photoinhibition under high compared to ambient pCO₂ conditions (Gao et al., 2012, 2018; Hoppe et al., 2015). Indeed, our analysis shows growth-enhancing antagonism for all phytoplankton groups together as well as separately for diatoms (Figure 4). This antagonism may be traced back to a high pCO₂-induced downregulation of the carbon acquisition and a concomitantly increased sensitivity of phytoplankton toward high-light stress (Kottmeier et al., 2016a; Rost et al., 2008; Sobrino et al., 2014). This phenomenon gets even more pronounced under more realistic fluctuating light conditions (Hoppe et al., 2015). A recent laboratory study, however, indicates that the picoeukaryote Micromonas pusilla (Butcher) Manton and Parke can cope well with elevated CO₂ despite dynamic light simulating changing light intensities caused by mixing and day–night cycles (White et al., 2020). Due to the limited number of studies on dinoflagellates in our meta-analysis, the confidence interval is relatively large and, thus, overlaps with \( y = 0 \), indicating additive interaction (Figure 4). By their ability to switch to mixotrophy, some dinoflagellate species can lower their dependence on both light and pCO₂ for photosynthesis (Donahue et al., 2019) and therefore have a competitive advantage toward, for example, diatoms under these conditions. This is particularly relevant under nutrient-limited conditions in summer, a time when dinoflagellates often thrive. Two studies on Southern Ocean communities observed a decrease in diatom abundance under high light and high pCO₂ conditions (Donahue et al., 2019; Heiden et al., 2019). Other publications present a shift in the dominant diatom species in communities under high light and pCO₂ (Feng et al., 2010; Hoppe, Schuback, Semeniuk, Maldonado, et al., 2017). Such species shifts may increase the resilience of the phytoplankton community, as one species takes over the ecological role of the other species, maintaining, for example, primary production (Hoppe, Schuback, Semeniuk, Maldonado, et al., 2017), but at the same time can lead to large changes in the carbon export (Feng et al., 2010).

In our third hypothesis, we supposed a nonadditive interaction of nutrient limitation with other drivers, because the nutritional state influences the energy that is available for other cell functions. Because of the restrictions in our dataset, we could only analyze the interaction between nutrients and pCO₂. The interaction effect size of all phytoplankton groups together implies an additive outcome (Figure 4), and, thus, a similar effect of the nutrient treatment independently from increasing pCO₂, leading to a net decrease in growth. However, the effect sizes of each study separately are split into one-third additive, one-third synergistic, and one-third antagonistic interaction. For diatoms, our meta-analysis reveals an overall synergistic effect (Figure 4). From the five individual studies on diatoms, two showed synergism, one showed antagonism, and two showed additivity. Even though chemostat studies could not be included in our analysis as growth rates are fixed by the dilution rate, this approach is commonly used to study the effect of nutrient limitation. Under P or N limitation, elevated CO₂ caused particulate organic carbon quota to remain stable (Sciandra et al., 2003), to increase (Borchard et al., 2011; Müller et al., 2012), or to decrease (Eberlein et al., 2016), supporting the findings of our meta-analysis of diverse interaction of nutrients and pCO₂ and highlighting the need for further studies on this issue. Generally, CO₂ can be considered as a nutrient that regulates the growth of phytoplankton similar to other macronutrients such as nitrate and phosphate. Traditionally, this regulation is considered as being described by Liebig’s law of the minimum (von Liebig & Gregory, 1842), which makes the maximum growth rate of an organism only dependent from the most limiting nutrient. The occurrence of all possible interactions in our data, however, supports the opinion of other studies (Danger et al., 2008; Harpole et al., 2011) that the interaction between nutrients is much more complex.

### 4.3 The special role of coccolithophores

While there are not enough data to display the individual and interaction effect sizes for all phytoplankton groups separately, few groups can be compared to the mean effect sizes. Coccolithophores stand out in almost all individual and interaction effect sizes (Figures 2 and 4). In our literature dataset, seven out of eight studies have been conducted on the bloom-forming coccolithophore Emiliania huxleyi (Lohmann Hay and Mohler (Feng et al., 2008; Jin et al., 2017; Listmann et al., 2016; Rokitta & Rost, 2012; Schütter, 2014; Tong et al., 2019; Zondervan et al., 2002), and one study examined the responses of Gephyrocapsa oceanica Kamptrner (Zhang et al., 2015). Hence, there is a bias toward E. huxleyi which, despite being the most abundant living coccolithophore species (Hagino & Young, 2015) that occurs in almost
all oceanic habitats (Read et al., 2013), is a rather unusual representative for this phytoplankton group (Eikrem et al., 2016). Our analysis demonstrates that high pCO₂ conditions are detrimental to coccolithophores (more specifically to *E. huxleyi*, given the number of studies on this species in our analysis), while increasing the growth rates of other phytoplankton groups. Furthermore, warming causes a stronger increase in their growth rates compared to the other phytoplankton groups. Temperature and pCO₂ do not interact antagonistically as for the other groups, but additive or even synergistically (Figure 4), if one disregards the overlap of the relatively large confidence intervals with \( y = 0 \) due to the small sample size. In three out of four studies, this interaction is growth-enhancing. Our findings are in line with another study, which found warming to induce higher tolerance toward higher pCO₂ values in the coccolithophore species *G. oceanica* and *E. huxleyi* (Sett et al., 2014).

In conclusion, our study shows that the group of coccolithophores, dominated by *E. huxleyi*, differs from other groups because of their high sensitivity toward elevated CO₂ and how this interacts with higher light availability and warming. An exceptional feature of *E. huxleyi*, which could not be assessed in our meta-analysis due to the lack of multiple drivers studies, is the high tolerance toward low nutrient conditions, where essential cell functions can be sustained longer than in other phytoplankton groups (e.g., Löbl, 2010; Riegmian et al., 2000; Rokitta et al., 2016). Correspondingly, it was shown in a global model that coccolithophores can partly counteract the decrease in marine production under low nutrient conditions (Gregg & Rousseaux, 2019). Determining the effect of multiple drivers on calcification rates was beyond the scope of our meta-analysis, but we acknowledge that this trait may play a role for competitive abilities of coccolithophores and largely determine the magnitude of the calcium carbonate flux (e.g., Gafar & Schulz, 2018; Rost & Riebesell, 2004). Thus, in biogeochemical models where phytoplankton can only be considered down to the relatively broad level of PFTs, coccolithophores should be treated as a separate group.

### 4.4 Growth response to high pCO₂ is altered by latitude

Our individual effect sizes of pCO₂ reveal a latitudinal pattern with negative effect sizes at the poles and positive effect sizes in the tropical areas (Figure 3a), implying a higher vulnerability to elevated pCO₂ values of polar species. While our dataset for the northern polar region is dominated by coccolithophores that were found to be more sensitive to an increase in the pCO₂ concentration, the individual effect size for pCO₂ in the southern polar region is mainly based on diatoms.

The solubility of CO₂ is highly temperature-dependent: Despite having the same pCO₂, a decrease in water temperature from 20°C (temperate or tropical regions) to 2°C (polar regions) increases \([\text{CO}_2]_{\text{aq}}\) by 80% (e.g., at 400 ppm, 2°C water holds 23 µmol kg⁻¹ CO₂aq compared to 13 µmol kg⁻¹ CO₂aq in 20°C water). While increasing \([\text{CO}_2]_{\text{aq}}\) (accompanied by increasing \([\text{HCO}_3]\) known as carbonation) can have a growth-enhancing effect, the concomitant increase in \((\text{H}^+\)) that causes the pH to drop (acidification) often has detrimental effects (Bach et al., 2013; Kottmeier et al., 2016a). For the given example, increasing pCO₂ from 400 to 1,000 ppm causes the H⁺ concentration to increase by 113% at 20°C, and by 135% at 2°C. Changes in pH in the time period between 1770 and 2000 were largest in polar regions due to a higher solubility of CO₂ at lower temperatures (Jiang et al., 2019). Whether the different magnitudes in the shift of the carbonate system with increasing pCO₂ can solely trigger a different growth response of phytoplankton, or only in combination with the different water temperatures needs to be investigated further. Figure 3b conceptually illustrates how temperature dependence in solubility could modulate the pCO₂ dependence and explains why polar species are already negatively impacted by pCO₂ levels that are not detrimental to species thriving in warmer waters. A recent meta-analysis on the effect of ocean acidification on Southern Ocean phytoplankton indeed shows that pCO₂ levels higher than 1,000 µatm become detrimental for most of the investigated traits (Hancock et al., 2020). Half of the Southern Ocean studies included in our meta-analysis were conducted at 800 µatm, indicating that growth-dampening effects can already occur within this century even under CO₂ emission scenario SSP3-7.0 that is less extreme than the “worst-case” scenario (SSP5-8.5; O’Neill et al., 2016). Studies on Arctic single species or communities, however, revealed a relatively high tolerance toward ocean acidification over a wide range of temperature and light conditions (Hoppe, Wolf, et al., 2018; Wolf et al., 2019). Interestingly, the only ocean acidification treatment in Hoppe, Wolf, et al. (2018) in which negative effects have been observed was conducted at the lowest temperatures. Further investigations are needed to reveal whether lower temperatures generally aggravate the impact of increasing pCO₂ in polar regions, or whether they manifest differently in the Arctic versus the Southern Ocean.

### 4.5 Implications for future global primary production

In this chapter, findings from our meta-analyses on growth responses are embedded in projected changes of the global ocean caused by climate change to qualitatively assess the impact of multiple drivers on the ocean’s primary production. Even though growth is not always equivalent to primary production, it is the key trait that allows phytoplankton to disperse and successfully compete for resources. Earth system models show that changes in ocean acidification and warming emerge earlier than changes in primary production (Bindoff et al., 2019; Frölicher et al., 2016). Figure 5 illustrates which changes in the driver environment of the oceanic regions are to be expected within this century.

Our statistical meta-analysis shows that the interaction of two future driver levels causes growth rates to increase for the driver combinations high pCO₂ × high temperature and high pCO₂ × high
light, and to decrease for the driver combination high $pCO_2 \times$ low nutrients. The first two driver combinations interact antagonistically, while $pCO_2$ and a decreasing nutrient supply interact additively to synergistically (Figure 4). In view of the projected deepening of the mixed layer in the Southern Ocean (Hauck et al., 2015; Panassa et al., 2018), we also tested for the effect of lower light and higher nutrient conditions as future scenarios with the full dataset. Increasing nutrient availability and $pCO_2$ have a clear synergistic and growth-enhancing effect. Decreasing light and increasing $pCO_2$ interact additively to antagonistically, and act growth-decreasing. This includes an average positive $pCO_2$ individual effect size on growth (Figure 2). However, the latitudinal analysis reveals a negative individual effect size of $pCO_2$ in the Southern Ocean. Due to data limitations, we could not determine the interaction effect sizes specifically for the Southern Ocean.

We evaluate the expected modification in primary production caused by bottom-up effects in view of the projected driver changes as follows (Figure 5): Principally, the growth-decreasing effect of the combination of increasing $pCO_2$ and nutrient deficiency affects primary production much stronger due to the additive to synergistic interaction than the antagonistic growth-enhancing driver combinations $pCO_2 \times$ temperature and $pCO_2 \times$ light. Dinoflagellates, however, benefit more than other phytoplankton groups from the new conditions, as $pCO_2 \times$ light interact additively and promote their growth, therefore counteracting the dampening effect of reduced nutrient supply. Besides, dinoflagellates can make better use of increasing $pCO_2$, and their ability to switch to mixotrophy may broaden their nutritional spectrum, making them more competitive in post-bloom situations. A recent meta-analysis found that, next to dinoflagellates, cyanobacteria also benefit from elevated $pCO_2$ and lowered nutrient availability in the future because of their high plasticity in carbon acquisition and ability to fix $N_2$ under otherwise $N$-limiting conditions (Van de Waal et al., 2019). Our meta-analysis reveals that, when exposed to elevated $pCO_2$ alone, coccolithophores decrease their growth, which might be important under stronger acidification in subpolar and polar waters. However, similar to dinoflagellates, the interaction with high-light conditions cause the growth rate of coccolithophores to increase stronger than growth rates of other phytoplankton groups, a circumstance that becomes more relevant with stronger stratification. In line with this, *E. huxleyi* showed a lower sensitivity toward ocean acidification under saturating light (Rokitta & Rost, 2012). Diatoms could be the group that benefits least under climate change conditions, because they can make less use of the growth-enhancing interaction of increased $pCO_2$ and light availability. Furthermore, it
is not clear in which way the interaction of high \( pCO_2 \) and low nutrient supply affects diatom growth. A recent publication proposes, however, that larger phytoplankton cells like diatoms partly overcome the disadvantage of taking up nutrients less efficiently when considering the entire suite of interactions of environmental drivers (Van de Waal & Litchman, 2020). The authors hereby argue that rising \( pCO_2 \), temperature, and light levels can lead to a reduction of metabolic and photosynthetic costs, leaving more energy to be allocated to nutrient acquisition. While we did not include picoeukaryotes as a separate phytoplankton group in our meta-analysis because of limited data, they can cope much better with nutrient-limited conditions than larger phytoplankton groups, and were also found to benefit in experiments under other global change conditions (e.g., Feng et al., 2009; Hare et al., 2007; Hoppe, Flintrop, et al., 2018; Schaum et al., 2013; Schulz et al., 2017). Therefore, picoeukaryotes may become more important in the future ocean.

On the large scale, we hypothesize production to be reduced in the mid-to-low latitudes due to lowered nutrient availability, which dominates over the beneficial effect of warming and improved light conditions (Figure 5). Upwelling regions would need separate consideration because of their sensitivity to changes in winds and eddy activity, which makes their response to climate change more complex compared to the open ocean (Xiu et al., 2018). Generally, the interactions between the drivers light, temperature, and nutrients might become more important in mid-to-low latitudes, as acidification is less prevalent than that in the polar regions. Unfortunately, we could not test these interactions due to limited data availability. Based on our data and the order of emergence of driver changes, we expect an initial increase in productivity for the Arctic Ocean due to the improved light availability followed by a decrease in productivity once nutrient limitation becomes dominant (Figure 5), complying with recent model projections and measurements (Randelhoff et al., 2020; Vancoppenolle et al., 2013). In regions of the Southern Ocean where the MLD is deepening (Hauck et al., 2015; Panassa et al., 2018), the nutrient supply is projected to increase, and the interaction with \( pCO_2 \) is synergistic. This can override the growth-dampening (although mostly antagonistic) effect of decreasing light availability and increasing \( pCO_2 \) on Southern Ocean species. Altogether, we hypothesize that primary production will increase in the Southern Ocean due to increased nutrient supply. The relative abundance of dinoflagellates in the Arctic and mid-to-low latitudes will likely increase. Coccolithophores might benefit in the mid-to-low latitudes due to less pronounced acidification, while the fate of coccolithophores in subpolar and polar regions depends on which of the changes in drivers dominate. The restrained response of diatoms to higher light availability with increasing \( pCO_2 \) likely makes them less competitive than other phytoplankton groups in the future ocean. The evaluation of top-down control by zooplankton is beyond the scope of our meta-analysis, but might even dominate over bottom-up effects in controlling phytoplankton biomass at times. Warming-enhanced grazing in low latitudes can, for instance, be equally important as nutrient control (Laufkötter et al., 2016).

4.6 | The value of multiple driver research and recommendations for laboratory studies

Our meta-analysis proves statistically that the interaction of environmental drivers cannot be assumed to be additive by default. In fact, most of the interactions result in synergistic and antagonistic growth rate responses. While our results are valid for the specifically tested driver values, other types of interaction are possible when driver values are higher or lower. We restricted ourselves to single-species laboratory experiments as they represent the largest number of studies with controlled conditions. This approach has drawbacks, as the interaction of organisms within a community, the dynamic condition within a natural habitat, and top-down control by grazing can add important controls to the response of phytoplankton growth rates to climate change (Gao et al., 2018). Species shift and evolutionary adaptation can, for instance, change the response of phytoplankton over time (e.g., Brennan et al., 2017; Hoppe, Schuback, Semeniuk, Maldonado, et al., 2017; Schaum et al., 2017), making the experimental outcome dependent on the length of the treatment (Darling & Côté, 2008; Taherzadeh et al., 2019). Fluctuating levels of environmental drivers, being closer to natural conditions, trigger different physiological responses than constant driver levels applied in most experiments (Schaum et al., 2016). Thus, multiple driver studies on single species tend to oversimplify the complex interaction between organisms and their environment (Boyd et al., 2018; Przeslawski et al., 2015). Nonetheless, those laboratory studies represent the best available tool to understand patterns in the organism’s physiological responses to conditions the oceans are facing. Hence, if interpreted with the necessary caution, we believe that multiple driver studies, summarized in meta-analyses like the one presented here, are valuable approaches to improve the projection of the ocean’s primary productivity and serve as an essential amendment to field and physiological studies.

Although many studies on multiple driver effects on marine phytoplankton have been conducted in the last years, we had to exclude a large number of articles because of missing metadata. Extensive advice on how to design and report multiple driver experiments is given in the “Best Practice Guide for ‘Multiple Drivers’ Marine Research” (Boyd et al., 2019), and in a meta-analysis on early life stages of marine species (Przeslawski et al., 2015). The “Guide to best practices of ocean acidification research and data reporting” (Riebesell et al., 2010) describes in detail which metadata have to be documented with a publication. Nonetheless, most multiple driver studies do not report the full set of recommended metadata.

To guide future multiple driver studies, we here highlight the most common reasons why articles were excluded or were of limited use for our meta-analysis. (a) Several articles did not (or not sufficiently) report on the carbonate system. We require either measurements of the carbonate system from the beginning and the end of the experiment, or the drift in carbonate system parameters during the experiment. (b) Not all multiple driver studies
were conducted in multifactorial experiments (testing the effect of each driver alone and in common with another driver), but only for a present and a future scenario (collapsed design). This does not allow attributing responses to the individual drivers. (c) To evaluate regionally different effects, it is important to report the origin of the species, the time of isolation and, if not freshly isolated, the conditions under which they were cultured before the experiment. (d) The reasons why certain driver levels were chosen in each treatment should be reported (e.g., following the projections of the Intergovernmental Panel of Climate Change). Ideally, control conditions should fall into the natural range of a species, whereas the altered driver levels should not a priori be chosen to be harmful but to follow certain future scenarios.

5 | CONCLUSION

Our results highlight the importance of considering the effects of dual driver interactions on the growth of marine phytoplankton. While the isolated impact of pCO₂ on phytoplankton growth is generally smaller than effects of changes in temperature and light, pCO₂ is tipping the scale by antagonistically dampening the growth-enhancing effects of warming and higher light availability. Despite using the tool of a meta-analysis, it remains challenging to compare a bouquet of studies conducted by different authors on a multitude of species, driver combinations, and driver ranges originating from all oceanic regions—an “apples and oranges” problem (Boyd et al., 2019). Nonetheless, it is urgent to gain knowledge on the global consequences of environmental changes for primary producers to improve our ability to project climate change impacts on the oceanic ecosystem (Bindoff et al., 2019; Crain et al., 2008). The largest source of uncertainty in model projections of marine net primary production stems from the model uncertainty, that is from gaps in our understanding (Frölicher et al., 2016). Robustness of model projections can only be increased by improving the mechanistic understanding of underlying processes, which can be achieved by a prudent selection and evaluation of existing literature. However, interactive effects are barely considered in the current generation of biogeochemical models. With our meta-analysis, we hope to give a handle to modelers and ecologists for the consideration of multiple driver effects.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information of this article.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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