

Predictable ecological response to rising CO₂ of a community of marine phytoplankton

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Abstract

Rising atmospheric CO₂ and ocean acidification are fundamentally altering conditions for life of all marine organisms, including phytoplankton. Differences in CO₂ related physiology between major phytoplankton taxa lead to differences in their ability to take up and utilize CO₂. These differences may cause predictable shifts in the composition of marine phytoplankton communities in response to rising atmospheric CO₂. We report an experiment in which seven species of marine phytoplankton, belonging to four major taxonomic groups (cyanobacteria, chlorophytes, diatoms, and coccolithophores), were grown at both ambient (500 μatm) and future (1,000 μatm) CO₂ levels. These phytoplankton were grown as individual species, as cultures of pairs of species and as a community assemblage of all seven species in two culture regimes (high-nitrogen batch cultures and lower-nitrogen semicontinuous cultures, although not under nitrogen limitation). All phytoplankton species tested in this study increased their growth rates under elevated CO₂ independent of the culture regime. We also find that, despite species-specific variation in growth response to high CO₂, the identity of major taxonomic groups provides a good prediction of changes in population growth and competitive ability under high CO₂. The CO₂-induced growth response is a good predictor of CO₂-induced changes in competition ($R^2 > .93$) and community composition ($R^2 > .73$). This study suggests that it may be possible to infer how marine phytoplankton communities respond to rising CO₂ levels from the knowledge of the physiology of major taxonomic groups, but that these predictions may require further characterization of these traits across a diversity of growth conditions. These findings must be validated in the context of limitation by other nutrients. Also, in natural communities of phytoplankton, numerous other factors that may all respond to changes in CO₂, including nitrogen fixation, grazing, and variation in the limiting resource will likely complicate this prediction.

KEYWORDS

competition coefficient, global change, primary producers, taxonomic group

1 | INTRODUCTION

Atmospheric CO₂ concentrations recently exceeded a historic high of 400 parts per million (μatm), a level which has not been surpassed in at least the past 420,000 years (Griggs & Noguier, 2002). This increase in atmospheric CO₂ has led to a decrease in the ocean pH of 0.1 units since the onset of the Industrial Revolution (IPCC, 2014). The concentration of CO₂ in the atmosphere is expected to continue to increase at a rate which is ten times faster than has been recorded in the past 55 million years (Almén et al., 2016). Predictions suggest that by the end of this century, atmospheric CO₂ levels may reach between 700 and 1,000 μatm and ocean pH will decrease to ~7.8–7.7 (Brewer et al., 2014). These changes in atmospheric CO₂ concentration and in ocean pH combine to increase the availability of CO₂ for marine primary producers, hamper the ability of organisms to calcify and affect the growth rates of marine phytoplankton (Kroeker, Kordas, Crim, & Singh, 2010; Reinfelder, 2011).

Major phytoplankton taxonomic groups differ in the efficiency of their RuBisCO (Ribulose-1,5-bisphosphate carboxylase/oxygenase) activity and of their carbon concentration mechanisms (CCMs) and thus in their expected response to the rise in CO₂ and ocean acidification (Reinfelder, 2011; Tortell, 2000). Those phytoplankton that are more efficient at taking up and utilizing carbon (higher surface area to volume ratio, higher CCM efficiency, higher RuBisCO specificity, and/or lower carbon requirements) are hypothesized to benefit less from the increase in CO₂ as their growth is currently least CO₂-limited (Reinfelder, 2011). Cyanobacteria possess a highly specialized CCM involving carboxysomes to deal with low dissolved CO₂ levels and a RuBisCO with CO₂ specificity comparable to that of chlorophytes (Price, Badger, Woodger, & Long, 2008; Tortell, 2000). Cyanobacteria are capable of increasing the concentration of CO₂ at the site of photosynthesis over 1,000 times the levels of its surrounding environment (Badger & Price, 2003), which is an order of magnitude higher carbon concentration efficiency than the next most efficient major taxonomic groups (Tortell et al., 2008). Although cyanobacteria are capable of increasing their growth rate under elevated CO₂ [e.g., two species test in Fu, Warner, Zhang, Feng, and Hutchins (2007)], the magnitude of this increase in growth is generally considered to be small, and thus cyanobacteria would be expected to decrease in competitive ability under elevated CO₂ all else being equal. However, nitrogen-fixing cyanobacteria (diazotrophic cyanobacteria) are found to increase nitrogen fixation under elevated CO₂ and have a greater increase in growth rate than other groups of phytoplankton (Dutkiewicz et al., 2015). Diazotrophic cyanobacteria likely differ from other cyanobacteria in their carbon uptake and utilization, however, part of their larger response and thus part of this difference between diazotrophs and nonnitrogen-fixing cyanobacteria, may be attributed to culture conditions, in which nitrogen is completely omitted when culturing diazotrophs for the measurement of nitrogen fixation but other nutrients are supplied in abundance (e.g., Hutchins, Fu, Webb, Walworth, & Tagliabue, 2013). Similarly to expectations for cyanobacteria that do not fix nitrogen, some diatoms have been shown to exhibit a limitation response only

at CO₂ concentrations below present-day levels, suggesting that they also have a highly efficient CCM (Hopkinson, Dupont, Allen, & Morel, 2011), however, other diatoms do appear to have a large increase in growth under future CO₂ conditions (e.g., Wu et al., 2010). Chlorophytes and coccolithophores have a lower RuBisCO specificity than diatoms and lower CCM efficiency than dinoflagellates and cyanobacteria but comparable efficiency to that of diatoms (Price et al., 2008; Tortell, 2000). Chlorophytes and coccolithophores are therefore expected to be most limited by modern day CO₂ availability and would thus be expected to benefit most from the increase in CO₂ and increase in relative abundance. However, the benefits of higher CO₂ for the photosynthesis of coccolithophores may be offset by its effect on calcification. Calcification is made costlier by the decrease in pH associated with rising atmospheric CO₂ levels. Calcification in coccolithophores is generally hampered by the extent of acidification expected in this century, but the effects appear to be species-specific (Meyer & Riebesell, 2015), so that it is not clear that coccolithophores will have a consistent change in growth and abundance under elevated CO₂. Although there are substantive variation and uncertainty within major taxonomic groups for these traits, given the major taxa or species-specific differences in carbon uptake and utilization and the differences between calcifying and noncalcifying phytoplankton species in response to acidification, it may be possible to predict some of the shifts in community assemblages under increasing CO₂, with an expected decrease in nondiazotrophic cyanobacteria, an increase in chlorophytes and an intermediate response of diatoms.

A model parametrized using a meta-analysis of growth response to increased CO₂ and assuming that this growth response will directly translate into proportional changes in community composition has led to the expectation that major changes in the composition of communities should be expected with rising CO₂ and that these changes will exceed those caused by warming or changes in nutrient availability (Dutkiewicz et al., 2015). The assumption that growth response will directly translate into proportional changes in community composition remains to be tested. Despite these important differences in CO₂-related physiology between major taxonomic groups, few studies have focused on how these differences will translate into changes in competition between groups and, ultimately, how they alter community composition with increasing CO₂.

Studies of natural assemblages of marine phytoplankton have found that high CO₂ resulted in an increase in the abundance of the cyanobacterium *Synechococcus* and a decrease in the abundance of the coccolithophore *Emiliania huxleyi* (Paulino, Egge, & Larsen, 2007). Similar experiments also found a decrease in fucoxanthin-containing phytoplankton including diatoms (Yoshimura et al., 2009) or that community composition remains unchanged (Bermúdez et al., 2016). Within taxonomic groups, an increase in CO₂ benefits larger over smaller diatoms (Tortell et al., 2008) as expected from facilitation of CO₂ diffusion with larger surface area to volume ratios. Changes in composition of marine phytoplankton communities associated with changes in CO₂ concentration could potentially be predicted from published information on the CO₂-related physiology

associated with major taxonomic groups (including CCM efficiency and RuBisCO specificity) or the measurement of growth response to CO₂ of the phytoplankton species present in the natural assemblage, but this has not been tested. Although this has not been explicitly tested, other physico-chemical conditions may alter the response to elevated CO₂. Notably the availability of nutrients can affect pH, thus the availability of CO₂, and growth rate or peak biomass, thus the drawdown and competition for CO₂.

In freshwater phytoplankton, it has been demonstrated that differences in the capacity to uptake and utilize CO₂ between major phytoplankton taxa can lead to predictable changes in their competitive ability in response to rising atmospheric CO₂ (Low-Décarie, Fussmann, & Bell, 2011). In contrast to most freshwater systems, marine environments have very little dissolved inorganic carbon (DIC) available as pCO₂, requiring specific investigation of the differences between major taxonomic groups in their growth response to CO₂ and predictability of associated shifts in community composition in marine systems.

This study aims to test whether information on differences between major taxonomic groups of marine phytoplankton are sufficient to predict the effect of increasing CO₂ on their capacity to compete. Taxonomic groups that are more efficient at concentrating and utilizing CO₂, such as the genus *Synechococcus*, would be expected to have a smaller growth response and a decreased ability to outcompete taxonomic groups that are less efficient at concentrating and utilizing CO₂, such as chlorophytes, under elevated CO₂ all else being equal. In contrast, taxonomic groups with specific functional traits, such as calcification in the coccolithophores, maybe deleteriously affected by the increase in CO₂. We measured how the growth rates, paired competitive abilities, and compositions of a community of seven phytoplankton species belonging to four major taxa (cyanobacteria, chlorophytes, diatoms, and coccolithophores) responded to an increase in CO₂. We test how robust our findings are to changes in the growth regime and nutrient concentration by replicating this study in both high-nitrogen batch cultures and lower-nitrogen semicontinuous cultures.

2 | MATERIALS AND METHODS

2.1 | Phytoplankton cultures

We studied seven species from four dominant marine phytoplankton groups: the cyanobacterium *Synechococcus* sp. (CCMP 2370, mean ± range 1.2 ± 0.4 μm diameter, Hughes, Franklin, & Malin, 2011); the chlorophytes *Dunaliella tertiolecta* (CCMP 1320, 11 ± 1 μm diameter) and *Prasinococcus capsulatus* (CCMP 1194, 4.5 ± 1 μm diameter); the diatoms *Phaeodactylum tricoratum* (CCMP 2561, ~21 μm by 3.5 μm) and *Thalassiosira weissflogii* (CCMP 1051, 15 ± 10 μm diameter); and finally, the calcifying coccolithophores *E. huxleyi* (PLY 1516, 4 ± 1 μm diameter) and *Coccolithus pelagicus* (PLY 183, 25 ± 15 μm diameter). Each major taxon, with the exception of the cyanobacteria, was represented by two species, each selected based on being ecologically relevant

and being clearly identifiable through morphological features visible under microscopy. There was a large difference in size between the pairs of species from a group (25% difference for diatoms, 240% for chlorophytes, and 625% for coccolithophores) so that there was an overlap in cell size (and associated surface area to volume ratio) between all groups, with the exception of the smaller cyanobacterium.

2.2 | Growth conditions

All phytoplankton species were grown in Enriched Seawater Artificial Water (ESAW) (Berges, Franklin, & Harrison, 2001) at 15 ± 0.1°C, under a 12:12 hr light:dark cycle at irradiance levels of 250.1 ± 4.5 μmol m⁻² s⁻¹. All cultures were kept in suspension on platform rockers set to 70 rotations per minute (rpm) in two CO₂-controlled growth chambers (Adaptis CMP6010, Conviron, Canada). The relative humidity levels across both chambers averaged 82 ± 6.3%. One chamber simulated ambient CO₂ conditions (506 ± 6 μatm, local conditions lead to higher than the global average of 400 μatm) and the other future CO₂ conditions (1,000 ± 7 μatm) predicted for the year 2100 (IPCC, 2014). The growth medium was first equilibrated in the chamber conditions for a period of 3 days prior to inoculating the phytoplankton in test tubes. Each of the phytoplankton species was acclimated for a period of 2 weeks (one transfer cycle) before experimentation by maintaining stock cultures in each CO₂ and nutrient treatment. Stock cultures were maintained in 50 ml of media within 150 ml glass flasks stoppered with air-permeable foam caps and were maintained in exponential growth with weekly 1:10 dilution.

2.3 | Growth and competition experiments

All experiments were conducted in 8 ml of medium in 15 ml test tubes fitted with polyurethane foam stoppers and initiated with a starting inoculation of 1 × 10⁵ cells/ml, taken from each of the single species cultures pre-acclimated under each nutrient and CO₂ regime. All cultures remained in exponential growth throughout each of the 5-day experiments. Triplicates of seven pure (individual species), 21 pairwise mixtures and one full community culture were inoculated for each condition (CO₂ treatment and culture regime). To account for any chamber effects, the experiments were repeated switching the CO₂ treatment between chambers and repeated twice in each chamber configuration (total replication if pooling across chambers is 12, for a total of 1,392 experimental cultures).

To test the effect of growth regime on the link between growth and community response, all experiments were conducted in two growth regimes that differed in nutrient concentration and maximal cell density. In the high-nitrogen batch culture regime, the standard ESAW medium (882 μmol/L nitrogen as in F/2 medium; Jutson, Pipe, & Tomas, 2016) was used and the culture was tracked for 5 days without replenishing the medium. Long-term culturing of species in our culture collection was carried out using ESAW ensuring acclimation to this media. In the lower-nitrogen semicontinuous culture

regime, the nitrogen concentration in the medium was 55 $\mu\text{mol/L N}$, all other nutrients were at the same levels as in the high-nitrogen batch culture regime (i.e., F/2 medium) and all cultures were replenished daily over the 5-day period with 1 ml of fresh lower nitrogen media (1:8 replenishment).

2.4 | Quantification

To track changes in the cultures throughout the experiment, samples were taken daily from all test tubes. Samples from both the single species cultures and the control tubes containing only the growth media (blanks) were taken on the final day of each run to measure both pH and alkalinity (Snoeyink & Jenkins, 1980) to permit the estimation of the level of dissolved CO_2 using the CO_2Calc application (Robbins, Hansen, Kleypas, & Meylan, 2010). Pure culture cell densities were measured daily from the day of inoculation until the final day through either haemocytometry or flow cytometry for the calculation of their respective growth rates. Fresh samples of all other pure cultures were passed directly through a flow cytometer (Accuri C6, BD Bioscience, USA). For flow cytometry, a protocol with a medium flow rate of 0.583 $\mu\text{l/s}$ and a total of 10,000 events recorded was used following the production of a template file using forward and side scatter profiles to standardize the cell counts. Due to flow cytometer use and set up, cyanobacteria could not be counted on the flow cytometer. Cyanobacteria samples were immediately fixed with Lugol's solution (1% final concentration) and injected into a haemocytometer slide and counted using microscopy. Samples from each of the competition mixtures were also immediately fixed with Lugol's solution and stored at 4°C until they were counted via microscopy, whereby the abundance of each species comprising the mixtures were counted using a total minimum count of 400 cells.

2.5 | Statistical analysis

To measure the response of growth to treatments, exponential growth rates of each culture were calculated as the ratio of the natural-log of cell densities over the 5-day experimental period. Predicted competition coefficients were calculated from pure culture growth rate, while realized competition coefficients were calculated from changes in frequency (Low-Décarie et al., 2011). A change in the sign of the competition coefficient indicates a change in competitive dominance, but a change in the competition coefficient that does not alter the sign indicates a change in the speed of competitive exclusion. Predicted (p) competition coefficient of species 1 (c_1) was calculated as the difference of its growth rate with the growth rate of a competing species (r_2) standardized by the growth rate of the entire competing community ($r_{\text{community}}$):

$$\text{Predicted competition coefficient } c_{1p} = \frac{r_1 - r_2}{r_{\text{community}}} \quad (1)$$

Realized (r) competition coefficients (Equation 2) were calculated from the change in the frequency (aka. relative frequency,

f) of each species through time accounting for the growth of the community overall (number of generations across the community $g_{\text{community}}$):

$$\text{Realized competition coefficient } c_{1r} = \frac{1}{g_{\text{community}}} \ln \left(\frac{\frac{f_1 \text{ final}}{f_2 \text{ final}}}{\frac{f_1 \text{ initial}}{f_2 \text{ initial}}} \right) \quad (2)$$

In the full community of seven species, f_2 was the frequency of all other species combined. Phytoplankton responses to CO_2 were calculated as the difference between growth rates or competition coefficients in ambient and high CO_2 treatments. The measured competition coefficient, based on change in frequency, integrates any effect of one species on the frequency of another species (whether through limited growth through resource competition or through some other ecological interactions, including facilitation or allelopathy).

The response of dissolved CO_2 in cultures, growth rates, and competition coefficients were assessed using an analysis of variance (ANOVA), in which the main effects and interactions of CO_2 treatment, culture regime, and major taxonomic group were tested, the main effect of species was also included. When needed, individual ANOVAs were conducted for the response of each separate taxonomic group, with the main effects and interactions of CO_2 treatment, culture regime, and species. Full community competitions were assessed using a multivariate analysis of variance (MANOVA) when phytoplankton were grouped by major taxa, and when grouped by species. Predictions of the response of competition to CO_2 from the response of growth rates was assessed by averaging the competition and growth response by species and fitting a linear regression.

In text, values are expressed as means ± 1 standard deviation. Analyses were conducted within the R statistical coding package (R Development Core Team, 2013) and figures were produced in Microsoft Excel.

3 | RESULTS

3.1 | Dissolved CO_2 concentration

CO_2 concentration was controlled in the atmosphere and some CO_2 drawdown was expected in growing cultures, so the effect of treatment on DIC concentration needed to be tested. Changes in atmospheric CO_2 concentrations caused the expected changes in $p\text{CO}_2$ (Figure S1, 310.7 ± 23.5 – $711.2 \pm 94.4 \mu\text{atm}$, $F_{1,336} = 10,427$, $p < .001$) and pH (from 8.15 ± 0.02 to 7.85 ± 0.03). The concentration of nitrogen in each culture regime also had an effect on the pH (8.02 ± 0.16 in high-N vs. 7.88 ± 0.14 in lower nitrogen) and thus $p\text{CO}_2$ ($19.0 \pm 20.0 \mu\text{atm}$ higher in low-nitrogen, $F_{1,336} = 26.7$, $p < .001$). All cultures drew down on average $140.4 \pm 117.1 \mu\text{atm}$ of CO_2 compared to blank media over the 5-day experiment, but the difference between ambient and high CO_2 treatments remained throughout the growth of the cultures (average $198.3 \pm 76.2 \mu\text{atm}$

difference, $F_{1,336} = 2,389$, $p < .001$, Table S1 for drawdown for each species).

3.2 | Growth response

The effect of an increase in atmospheric CO_2 on phytoplankton growth rates was assessed. Growth rates recorded for each phytoplankton culture between chambers did not differ (Table S2), indicating that there was no confounding chamber effect upon their responses, so assays in each chamber were treated as replicates. Growth rates of all species increased with high CO_2 independent of culture regime, where on average an increase of $0.12 \pm 0.07 \text{ day}^{-1}$ was observed in phytoplankton exposed to high CO_2 compared to ambient conditions (Figure 1, $F_{1,336} = 106$, $p < .001$). The scale of this change was taxa- and culture-regime dependent ($F_{3,336} = 240$, $p < .001$). Chlorophytes had the largest average increase in growth rate between CO_2 treatments of $0.20 \pm 0.04 \text{ day}^{-1}$, whereas *Synechococcus* had the smallest increase of $0.06 \pm 0.01 \text{ day}^{-1}$. Species within each major taxon also differed in their response to high CO_2 (Table S3).

3.3 | Pairwise competitions

The effect of increasing atmospheric CO_2 upon the competitive ability of each species within each of the pairwise competitions was assessed across both culture regimes. There was a log-linear change in species frequency in each competition culture (Figures S2 and S3). On average, the response of competitions between species of the same taxonomic group was smaller than the average change in competition coefficient between species of different major groups (same group: average absolute change of 0.28 ± 0.23 , Figure 2a–c, different group: average absolute change = 1.02 ± 0.48 , $t_{144} = 11.78$, $p < .001$, Figure 2d–i). The competitive ability of *Synechococcus* declined under the high CO_2 treatment independent of the taxonomic group it was competing with (Figure 2d–f, average decrease of 1.24 ± 0.98 in competition coefficient, $F_{1,288} = 1,386$, $p < .001$). The chlorophytes on average competed better with increased CO_2

levels (Figure 2d,g–h, average increase of 1.1 ± 0.76 in competition coefficient, $F_{1,480} = 2,118$, $p < .001$), however, a partial reversal of this trend was observed under batch high-nitrogen conditions when competing against diatoms ($F_{2,480} = 96$, $p < .001$). The competitive response of the diatoms and coccolithophores to elevated CO_2 conditions was dependent on the competing taxonomic group (Figure 2e–f, diatom: average decrease of 0.32 ± 0.92 in competition coefficient, $F_{3,480} = 518$, $p < .001$, coccolithophore: average decrease of 0.28 ± 0.41 , $F_{3,480} = 183.7$, $p < .001$) and was species-specific when the coccolithophores competed with the diatoms ($F_{2,192} = 18.2$, $p < .001$).

3.4 | Full community competitions

The assembled community was not stable (extinctions were eventually expected but not observed) and there was a log-linear change in species frequency in the community comprising all seven species (Figure S4). These competitive dynamics in the full community were also altered by the CO_2 treatment. The competitive ability of *Synechococcus* decreased the most when CO_2 levels increased (Figure 3; average decrease of 0.77 ± 0.29 in competition coefficient, $F_{1,48} = 2,197.6$, $p < .001$), although it remained a dominant competitor with a positive competition coefficient, and the diatoms also decreased, although to a lesser extent (average decrease of 0.20 ± 0.21 in competition coefficient, $F_{1,96} = 194.4$, $p < .001$). The chlorophytes, on the other hand, were the only taxon which increased their competitive abilities (average increase of 0.44 ± 0.34 in competition coefficient, $F_{1,96} = 107.1$, $p < .001$) and the response of the coccolithophores was found to be species-specific (Table S3), where *E. huxleyi*'s competition coefficient increased by on average 0.19 ± 0.31 at elevated CO_2 levels ($p < .001$) but *C. pelagicus* was unaffected (average increase 0.01 ± 0.60 in competition coefficient, $p > .05$).

3.5 | Predicting phytoplankton community changes

Changes in competition and community dynamics in response to rising CO_2 were predictable from known difference in the CO_2 -related

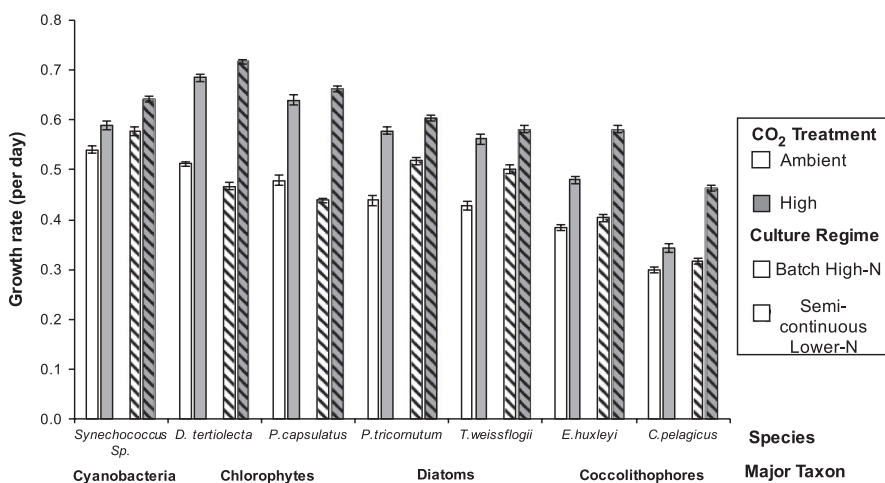


FIGURE 1 Phytoplankton growth rates across CO_2 and culture regimes. Plain bars are batch high nitrogen conditions (high and low CO_2), bars with stripes are semicontinuous lower nitrogen conditions (high and low CO_2), white bars are ambient CO_2 ($\sim 500 \mu\text{atm}$), and shaded bars are high CO_2 ($\sim 1,000 \mu\text{atm}$). Each bar shows the mean values with ± 1 standard deviation ($N = 12$). All species had a higher growth rate in high CO_2 compared to low CO_2 independent of culture regime

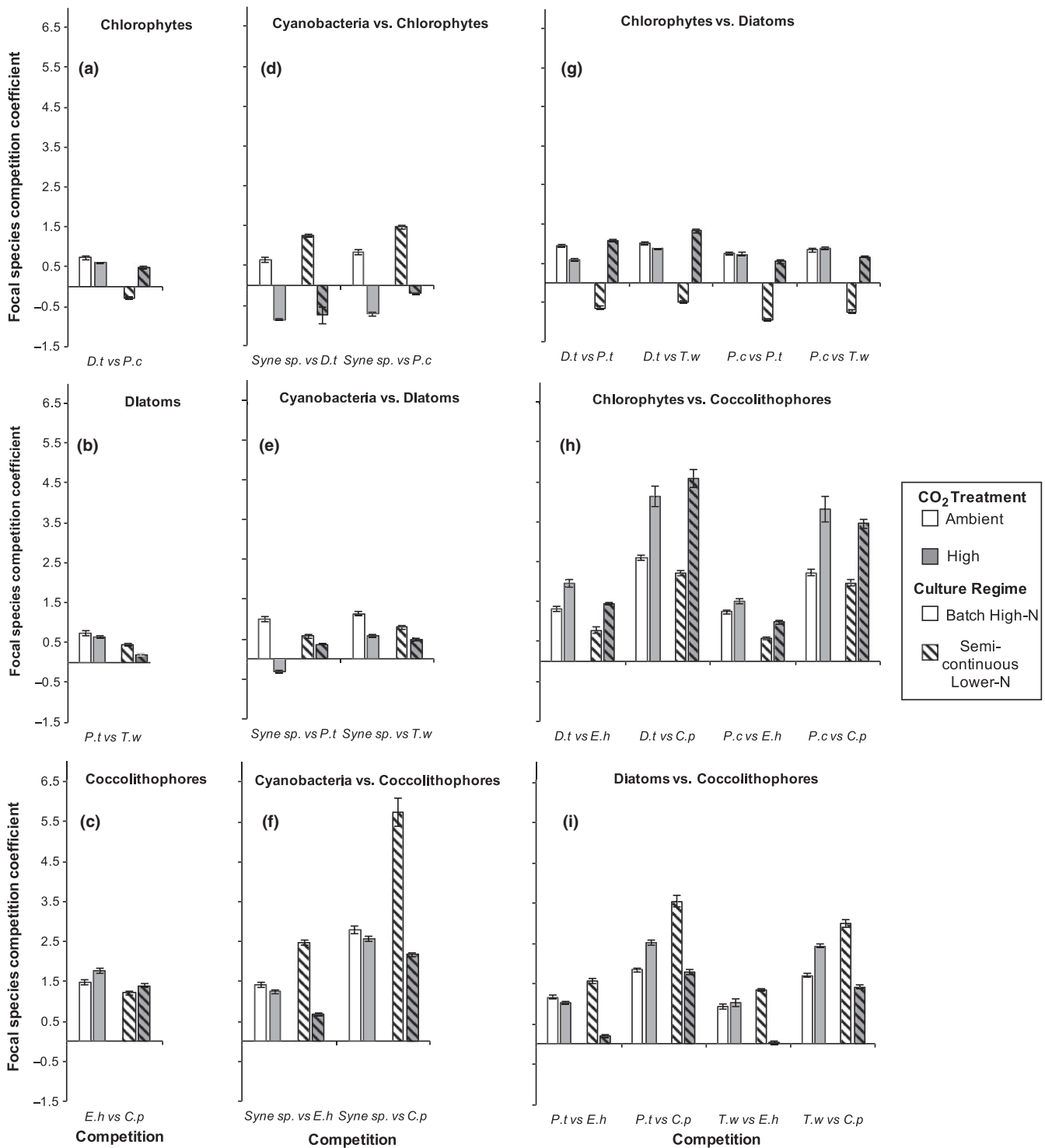


FIGURE 2 Competition coefficient in all pairwise competitions. (a–c) Competitions between members belonging to the same taxonomic group, (d–f) competitions where the focal competitor was *Synechococcus* sp. (*Syne* sp.; cyanobacterium), (g–h) competitions with chlorophytes (*Dunaliella tertiolecta*–*D.t.* and *Prasinococcus capsulatus*–*P.c.*) as focal competitors, (f) comparisons with diatoms as focal competitor species (*Phaeodactylum tricornutum*–*P.t.*, *Thalassiosira weissflogii*–*T.w.*). The coccolithophores are shown in competition but not as focal species (*Emiliania huxleyi*–*E.h.* and *Coccolithus pelagicus*–*C.p.*). Statistics and legend match Figure 1: shading (high CO₂), stripes (semicontinuous lower nitrogen), each bar shows the mean values with ±1 standard deviation (N = 12). High CO₂ decreases the competitive ability of *Synechococcus* while mostly increasing the competitive ability of chlorophytes

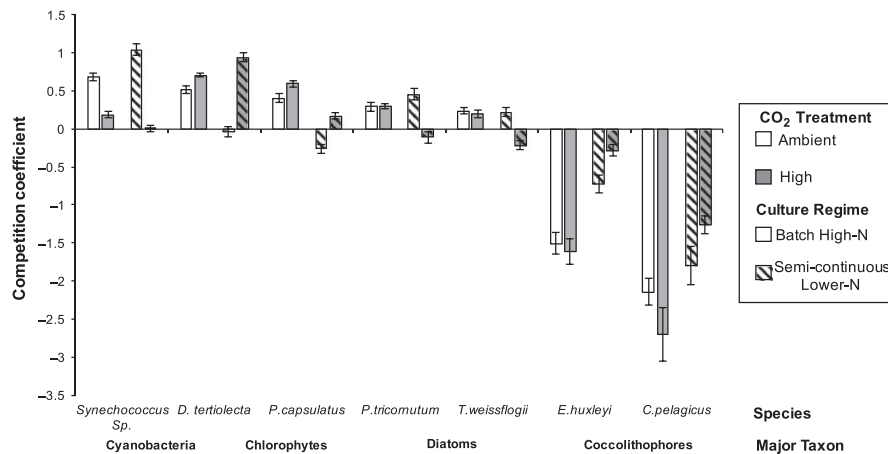


FIGURE 3 Full community competition coefficients. Elevated CO₂ decreases the competitive ability of *Synechococcus* and the diatoms, increases the competitive ability of the chlorophytes, but did not exhibit an overall effect on the coccolithophores unless interacting with culture regime, where their competitive ability within semicontinuous-lower nitrogen cultures increased but decreased in batch high-nitrogen cultures. Matches previous figures: gray (high CO₂), stripes (semicontinuous lower nitrogen), bar value (mean), and error bars (one standard deviation $N = 12$)

taxonomic traits and growth responses to elevated CO₂. The mean competitive response for each species within pairwise competitions was a good indicator of the competitive ability of each phytoplankton species within the full community (Figure S5), in batch high nitrogen ($R^2 = .75$, $p < .001$) and semicontinuous lower nitrogen conditions ($R^2 = .93$, $p < .001$).

Pure culture growth responses were also a good predictor of the overall competitive response of each species within pairwise competitions (Figure 4a) in both batch high nitrogen ($R^2 = .94$, $p < .001$) and semicontinuous lower nitrogen conditions ($R^2 = .93$, $p < .001$) and of the competitive response in the full community of seven species (Figure 4b), in batch high nitrogen ($R^2 = .73$, $p < .001$) and semicontinuous lower nitrogen conditions ($R^2 = .80$, $p < .001$).

4 | DISCUSSION

4.1 | CO₂ as a limiting resource

Marine environments are highly dynamic systems in which growth rate is an important parameter for phytoplankton population dynamics. In situ growth rates of communities of phytoplankton range from 0.1 to 3.6 doubling per day (Furnas, 1990). Even in conditions where other factors, such as grazing, pathogens, or maximum total biomass achievable, growth rates will influence dynamics and composition of communities. All phytoplankton species examined in this study had an increased growth rate when exposed to future atmospheric CO₂ levels across both culture regimes. This contrasts with expectations based on nutrient limitation in natural marine phytoplankton communities, where the main limiting resources are usually nitrogen and iron (Downing, Osenberg, & Sarnelle, 1999). However, they match extensive laboratory experiments looking at growth response to elevated CO₂ in nutrient-replete and nutrient-limited conditions (e.g., meta-analysis Dutkiewicz et al., 2015). The nitrogen

levels on our experiment did not limit growth in either treatment and were high compared to oceanic total nitrogen ranges between 21.9 and 41.0 $\mu\text{mol/L}$ (Guildford & Hecky, 2000), but the lower nitrogen treatment (55 $\mu\text{mol/L N}$) was within natural range for estuarine and coastal marine ecosystems in which total nitrogen can exceed 150 $\mu\text{mol/L N}$ (Smith, 2006). Biomass of primary producers in marine environments is generally expected to be limited by nitrogen or iron, although there is growing understanding that multiple nutrients, potentially nitrogen and CO₂, can limit primary production simultaneously (Harpole et al., 2011; Moore et al., 2013). CO₂ could play a role as a rate-limiting nutrient, limiting growth rate but not maximal biomass (Low-Décarie, Fussmann, & Bell, 2014), and thus, may exhibit a stronger limitation role in dynamic marine environments where maximal biomass is rarely reached and dynamics are in part controlled by growth rates. Increased CO₂ increases primary producer biomass in natural marine phytoplankton communities when other nutrients are added simultaneously (Riebesell et al., 2007) and even in low nutrient concentration and the absence of nutrient addition (Eberlein et al., 2017). However, understanding the role of CO₂ among other limiting resources requires further experimentation.

4.2 | Predictability of changes in the composition of communities to a changing environment

Our results on the ecological response to increased CO₂ in marine phytoplankton align with previous studies of change in competition in freshwater phytoplankton (Low-Décarie et al., 2011) and with expectation based on the CO₂-related physiology of the major taxonomic groups (e.g., Reinfelder, 2011). *Synechococcus*, which has the most efficient uptake and utilization of CO₂, lose out mostly at the benefit of chlorophytes under high CO₂ as chlorophytes have likely invested in functional traits not related to carbon utilization and acquisition such as nitrogen scavenging or light harvesting. However,

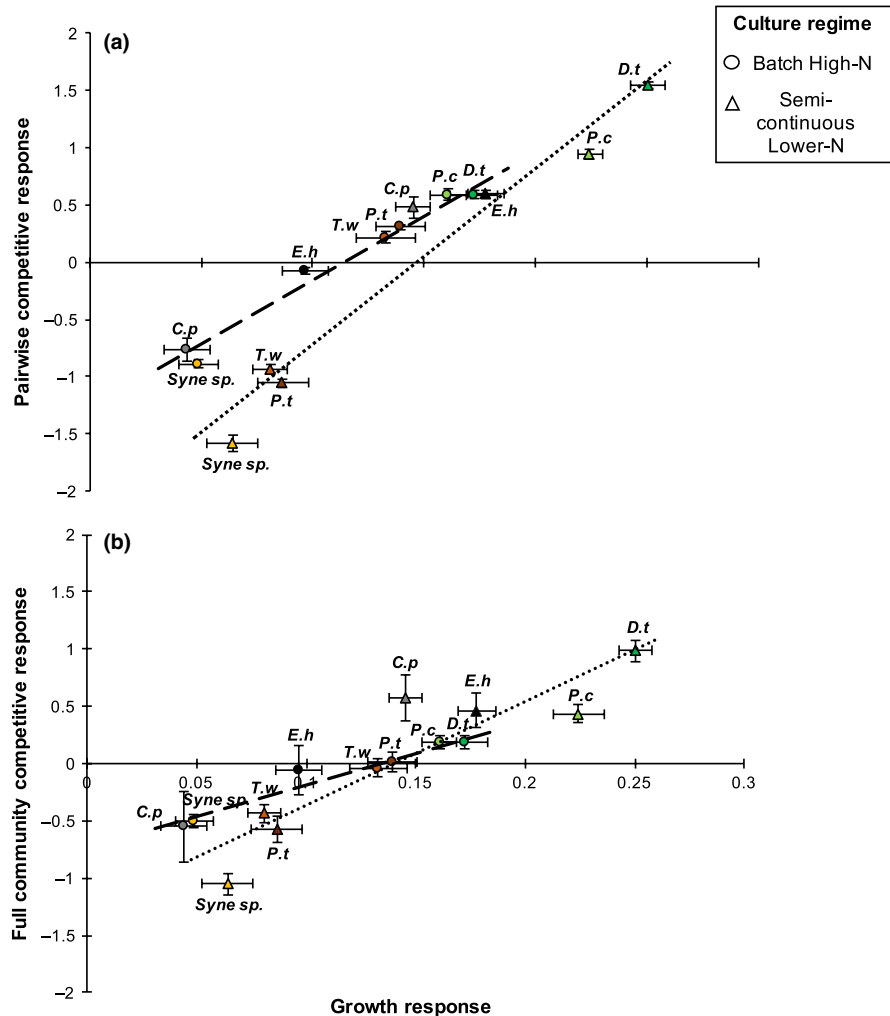


FIGURE 4 Predicting responses from pure culture growth responses. The growth response of each phytoplankton species was used to predict the average competitive response (a) in pairwise competitions and (b) in the full community comprised of all seven species. Circles are batch high-nitrogen with dashed line for the regression [(a) $R^2 = .94$ and (b) $R^2 = .73$] and triangles are semicontinuous lower nitrogen with dotted line for the regression line [(a) $R^2 = .93$ and (b) $R^2 = .80$]. All values are labeled with the first letter of its genus and species names, and are colored according to both taxonomic group and species. The chlorophytes are shown as dark (*Dunaliella tertiolecta*) and light green (*Prasinococcus capsulatus*), the diatoms as dark (*Phaeodactylum tricornutum*) and light brown (*Thalassiosira weissflogii*), the coccolithophores as black (*Emiliania huxleyi*) and gray (*Coccolithus pelagicus*), and the cyanobacteria are shown as orange (*Synechococcus sp.*). All points displayed are the mean for a species with ± 1 standard deviation ($N = 12$). The greatest responses were always exhibited by the chlorophytes, followed by the diatoms (in batch high-nitrogen conditions) or coccolithophores (in semicontinuous lower nitrogen conditions) and the lowest responses were generally exhibited by *Synechococcus*

this change in competitive ability did not prevent *Synechococcus* from increasing in frequency in the full community under elevated CO_2 . The change in competition between groups that have more similar capacities for carbon utilization and acquisition (chlorophytes vs. diatoms or diatoms vs. coccolithophores) is less predictable (more species-specific or depends more on culture regime). Other traits that are not specific to any major groups, such as size and associated surface area to volume ratio, could also influence the expected response to increasing CO_2 , with larger taxa benefiting most from the increase in CO_2 . However, changes in competition under elevated CO_2 between species of the same group was not consistent, this difference was small when present and it did not align with predictions made by size (smaller species tended to benefit from the increase

in CO_2). Our findings contrast with findings from some studies of in situ natural marine phytoplankton assemblages, including a study showing an increase in the cyanobacterium *Synechococcus* (Paulino et al., 2007) and a decrease in auroxanthin-containing phytoplankton (diatoms, Yoshimura et al., 2009). In these experiments on natural communities, as in our experiments, growth response is expected to dominate the community dynamics and as these experiments track the response in a bloom elicited through the addition of nutrients. A mesocosm experiment without the addition of nutrients did find a decrease in *Synechococcus* and an increase in major groups of chlorophytes (Crawford, Alvarez-Fernandez, Mojica, Riebesell, & Brussaard, 2017). Difference in the response of natural assemblages and those of simplified laboratory communities are not surprising,

and can be explained by factors including interactions with other treatments (including nutrient addition), changes in communities selective grazer or pathogens in response to the CO₂ treatment or greater importance of heterotrophic and mixotrophic processes utilizing existing organic carbon stocks. In natural marine communities, competitive dynamics and the response to CO₂ may also be controlled by the capacity to reach maximal biomass (carrying capacity) or other types of interactions between competitors (e.g., through allelopathy or facilitation). Results of both controlled laboratory studies and natural phytoplankton assemblages are likely to be dependent on the experimental duration due to the interplay of plastic and evolutionary responses of individual species.

4.3 | Plasticity and evolution

Phytoplankton are able to regulate their CCMs, such that in high CO₂ conditions they are able to reduce their activity and therefore energy consumption (Giordano, Beardall, & Raven, 2005; Reinfelder, 2011). High CO₂ exposure is suggested to be accompanied by a down-regulation of the genes involved with these cellular CCMs (Crawford, Raven, Wheeler, Baxter, & Joint, 2011; Van de Waal et al., 2013). Different life stages do not have the same responses to rising CO₂, for example, haploid and diploid stages in coccolithophores do not have the same response to acidification (Rokitta, John, & Rost, 2012), therefore, a plastic response could arise from a change in life-history strategy. If these plastic responses in gene regulation are not captured by the time scale of our experiments (5 days) and differ markedly between taxa, they could affect the predictability of the changes in competitions under elevated CO₂.

Marine phytoplankton may eventually adapt to higher CO₂ concentrations. As for plasticity, potential differences in the rate of adaptation or scale of adaptive gains between major taxonomic groups or species may alter the expected changes in competition. However, freshwater phytoplankton were not found to specifically adapt to elevated CO₂ (Collins & Bell, 2004, 2006; Collins, Sultemeyer, & Bell, 2006; Low-Decarie, Jewell, Fussmann, & Bell, 2013), although prolonged exposure to elevated CO₂ can lead to a decreased ability to grow under lower CO₂ (Collins & Bell, 2004). These findings in freshwater phytoplankton may not be transferable to marine algae. In calcifying phytoplankton, the change in pH associated with higher CO₂ concentrations could be expected to act as a strong selective pressure leading to faster evolution in this group (Collins, Rost, & Rynearson, 2014). The coccolithophore *E. huxleyi*, a calcifying phytoplankton, has been shown to adapt to high CO₂ conditions in marine systems within 500 generations (Lohbeck, Riebesell, Collins, & Reusch, 2013; Lohbeck, Riebesell, & Reusch, 2012). Another coccolithophore species, *Gephyrocapsa oceanica*, did evolve under high CO₂, although it is not clear that observed changes were an adaptive response to CO₂ (Tong, Gao, & Hutchins, 2018). Beyond calcifying phytoplankton, the evolutionary implications of elevated CO₂ for marine phytoplankton, and thus its potential effect on the predictability of changes in competition and community composition, is not well resolved. An

experiment with the cyanobacterium *Trichodesmium*, a globally important diazotroph, showed adaptation to elevated CO₂ conditions when maintained at high CO₂, but it was not CO₂ specific, with lines evolved at elevated-CO₂ growing better than the ambient selected lines independent of CO₂ concentrations (Walworth, Lee, Fu, Hutchins, & Webb, 2016). To test for the impact of adaptation on the predicted changes in competitive dynamics under elevated CO₂, the experiment presented in this study could be repeated with high CO₂-adapted lines of each major taxonomic group if the required long-term selection experiments are conducted.

4.4 | Implications of changes in community composition

In addition to differing in the carbon acquisition and use, the major taxonomic groups of phytoplankton have different ecological roles. On average, diatoms have some of the fastest sinking rates (Fahnenstiel et al., 1995) and play a major role in exporting primary productivity from the euphotic zone. Coccolithophores release CO₂ through calcification and decrease the DIC pool so that the increase in coccolithophores with higher CO₂, seen for at least the species from this study (*E. huxleyi* which is most abundant and widespread coccolithophores in the ocean), could lead to a feedback and a further increase in dissolved CO₂ concentration. The association of CO₂ response and ecological role of marine phytoplankton taxonomic groups lead models to suggest that the repercussions of change in the community composition for ecological function will exceed the effects of warming and reduced nutrient supply arising from global change (Dutkiewicz et al., 2015).

Our laboratory experiments and the resulting predictions of major ecosystem level repercussions from the change in phytoplankton communities with rising CO₂ ignore numerous ecological complexities. In addition to the limitation already raised about high-nutrient concentrations and a small set of laboratory strains, further caveats include that the natural phytoplankton communities are embedded in complex food webs, in which each trophic level, or even each species, may respond to ocean acidification, and thus modulate the response of phytoplankton to rising CO₂. Rising CO₂ could thus still affect phytoplankton in ways that do not depend on the capacity of major taxonomic groups of phytoplankton to uptake and utilize CO₂. In addition, ocean acidification is only one of many current anthropogenic changes affecting our world's oceans. Nonetheless, that the change in community composition with rising CO₂ of a functionally diverse community of phytoplankton can be predicted from growth response of individual species suggests that some useful inferences can be made from the study of individual taxa for the prediction of how marine communities will respond to global changes.

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CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTIONS


Jacob Pardew designed and conducted the experiment, analyzed the results, and drafted portions of the manuscript. Macarena Blanco Pimentel conducted a pilot experiment and contributed to the experimental design. Etienne Low-Décarie advised on the design of the experiment, its analysis, and drafted portions of the manuscript. All authors contributed to the review and editing of the complete manuscript.

DATA ACCESSIBILITY

Data and analysis script are available on Zenodo (<https://doi.org/10.5281/zenodo.1172665>).

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