

Do increasing CO₂ concentration impacted on changing phytoplankton assemblages?

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Abstract. The effect of seawater pCO₂ concentration of 280, 380, 550, 650, 750 and 1000 ppm on the changing of phytoplankton assemblage was determined through a mesocosm experiment at the Barrang Lompo Island. The experiment was run for 48 and 96 hours without nutrient enrichment. The aim of the study is to examine the effect of the increasing CO₂ concentration on the changing phytoplankton assemblages. The result showed that Bacillariophyceae has been the most important algal group accounting for 74.5% for 48 hours of incubation period. Moreover, Diatomaceae was the most dominant algal group for 96 hours of the incubation period, accounting for 50.9%. There was no clear trend of Shannon diversity (H') and the evenness values between CO₂ concentration and incubation period. There was a clear grouping of species assemblages between the incubation periods. ANOSIM result showed that there is no significant difference in species assemblage among CO₂ treatments. On the other hand, a significant difference in species assemblage between incubation periods between CO₂ concentration treatments was observed. The three taxa that are most responsible for the dissimilarity were *Rhizosolenia fragilissima* (10.1%), *Gyrosigma acuminatum* (9.3%), and *Biddulphia sinensis* (9.2%).

Key Words: phytoplankton assemblages, increasing CO₂ concentration, mesocosm experiment, Barrang Lompo Island.

Introduction. Globally, we face a serious environmental problem, which is an increasing CO₂ concentration in the atmosphere. Fossil fuel utilization, cement production, and biomass burning are a source of CO₂ emission (Gattuso et al 1998). This CO₂ emission will increase in atmospheric CO₂ levels that will affect seawater carbonate chemistry by decreasing the current sea-water pH of ~8.1 by 0.3 units (Feely et al 2009). The global ocean is a significant sink for atmospheric CO₂, currently absorbing almost one-third of it (Sabine et al 2004). As a consequence, surface ocean carbonate chemistry is considerably affected (direct impact), resulting in the redistribution of inorganic carbon species (Raven & Johnston 1991; Brewer 1997). Ocean acidification is the consequence of increasing atmospheric carbon dioxide (CO₂), which dissolves in seawater and subsequently increases seawater acidity and decreases carbonate ion concentration. Due to the wide variety of processes affected, responses to ocean acidification vary broadly across and even within taxa (Eggers et al 2014). Ocean acidification cause changing in ocean chemistry and has positive and negative effects on marine algae (Coad et al 2016). Most the responses of marine phytoplankton to increasing CO₂ are not yet fully understood. The marine phytoplankton community comprises diverse groups from different geographic locations, each possessing its own unique ecophysiology and biogeography (Biswas et al 2011). During the last decade, numerous discrete studies have been conducted on marine phytoplankton (laboratory pure cultures, shipboard and field experiments) to test the effects of increasing CO₂ and a wide range of responses have been observed (Riebesell et al 2000; Riebesell 2004; Riebesell et al 2007; Doney et al 2009).

Phytoplankton community composition profoundly affects the biogeochemical cycling of many elements, such as carbon, nitrogen, and phosphorus, because the major functional groups have different requirements and modes of acquisition of these elements

(Falkowski 1994). Shifts in phytoplankton community composition in response to rising CO₂ has been shown to be significant but highly varied across a diverse range of geographical regions (Tortell et al 2002; Kim et al 2006; Yoshikawa et al 2007; Tortell et al 2010). Most of the elevated CO₂ response studies on phytoplankton, whether for calcification (Ramos-Scharrón & MacDonald 2007; Langer et al 2006; Riebesell et al 2000), photosynthesis (Gattuso et al 1998; Rost et al 2008), or other physiological parameters, have been primarily focused on single organisms. Egger et al (2014) revealed that calcifying organisms generally exhibit larger negative responses to ocean acidification than non-calcifying organisms across numerous response variables. Phytoplankton species, community or functional groups showed a variety of responses to increasing CO₂ concentration, the response depending on plankton community composition and environmental conditions at the time of pCO₂ manipulation (Gear et al 2017). Craig et al (2015) found that succession and the seasonal evolution of phytoplankton communities correspond with various features in the bulk CO₂ system parameters. Studies testing the effects of elevated CO₂ on the entire phytoplankton communities are comparatively rare. The aim of the present study is to examine the effect of increasing CO₂ concentration on changing phytoplankton assemblages.

Material and Method. Mesocosm experiment took place at the Barrang Lompo Island, Makassar City, South Sulawesi, Indonesia on July-August 2013. The natural phytoplankton community was used and exposed to six different CO₂ levels. There were two different incubation times for each treatment, such as 48 and 96 hours. Each treatment was quadruplicated, resulting in 24 experimental units comprising 2 L plastic bottles that were randomly deployed around a pier at a water depth of approximately 1 m.

Initial CO₂ was manipulated by adding NaHCO₃ and HCl following Schulz et al (2009). The six levels of CO₂ corresponded to 280 ppm (pH \approx 8.32), 380 ppm (pH \approx 8.25), 550 ppm (pH \approx 8.14), 650 ppm (pH \approx 8.01), 750 ppm (pH \approx 7.85) and 1000 ppm (pH \approx 7.74). Phytoplankton communities were obtained by collecting seawater from the integrated upper 5 m of the water column at the Barrang Lompo Island. To avoid grazing pressure by large zooplankton, the sea water was immediately filtered through a 200 μ m pore size mesh. Afterward, 48 L of seawater per site was distributed among 24 of 2 L bottles. Each CO₂ treatment was incubated at 1 m depth for 48 and 96 hours.

Phytoplankton assemblages. Samples were fixed in Lugol's iodine solution and counts of phytoplankton cell density were made from Sedgewick-Rafter Counting Cell and a minimum of 50 fields and 100 units (cells, trichomes or colonies). Sometimes more than 400 units were counted depending on the density. Identification was performed using the Olympus IX71 microscope with magnification 400X. Species richness (S), expressed as species number per sample (Pielou 1975), was estimated considering all species identified during the study period. Species diversity was calculated according to Shannon & Wiener (1963) ($H' = -\sum p_i \log p_i$, $p_i = N_i/N$, N_i number of cells of species i and N total number of cells/sample) and Evenness (J') as $H'/\log S$ (Pielou 1975), using log 2 in both formulations.

Statistical analysis. Multivariate statistical analysis was applied for identifying discrete groups and correlations between environmental and phytoplankton variables. These analyses were undertaken using PRIMER (v.6) software (Plymouth Routines in Multivariate Ecological Research, Plymouth Marine Laboratory, Plymouth, UK (Clarke et al 2006)).

ANOSIM test. The analysis of similarity, ANOSIM (Warwick & Clarke 1993; Clarke 1999) was performed to test statistical differences in environmental and phytoplankton data among incubation period of samples and CO₂ concentration treatments. A two-way crossed test, based on Bray-Curtis similarities (phytoplankton abundances, log (x+1) transformed) as our study focused on a fixed set of CO₂ concentration treatments, sampled at two incubation periods.

Non multidimensional scaling (nMDS). Multidimensional scaling, MDS, was applied to phytoplankton abundance ($\log(X+1)$ transformed). Similarities between species are obtained by Bray-Curtis similarity coefficient and the corresponding rank similarities used to construct MDS configuration. Stress levels of MDS representation less than 0.1 indicate good representation of the data. Also on the basis of Bray-Curtis similarities, the similarity percentages analysis (SIMPER) was applied to phytoplankton species abundance, in order to allow the separation of every two groups of CO₂ concentration treatments according to phytoplankton species.

Results

Composition and abundances of phytoplankton. Mean of phytoplankton abundance ranged from a minimum value of 1150 cell L⁻¹ at a 1000 ppm CO₂ concentration for the 48 hours incubation period to a maximum of 2425 cell L⁻¹ at 380 ppm CO₂ concentration for 48 hours incubation period (Figure 1). There was decreasing phytoplankton cell abundance with increasing CO₂ concentration for both incubation periods. Bacillariophyceae was the most important algal group accounting for 74.5% for 48 hours of incubation period. Moreover, Diatomaceae was the most dominant algal group for 96 hours of the incubation period, accounting for 50.9%.

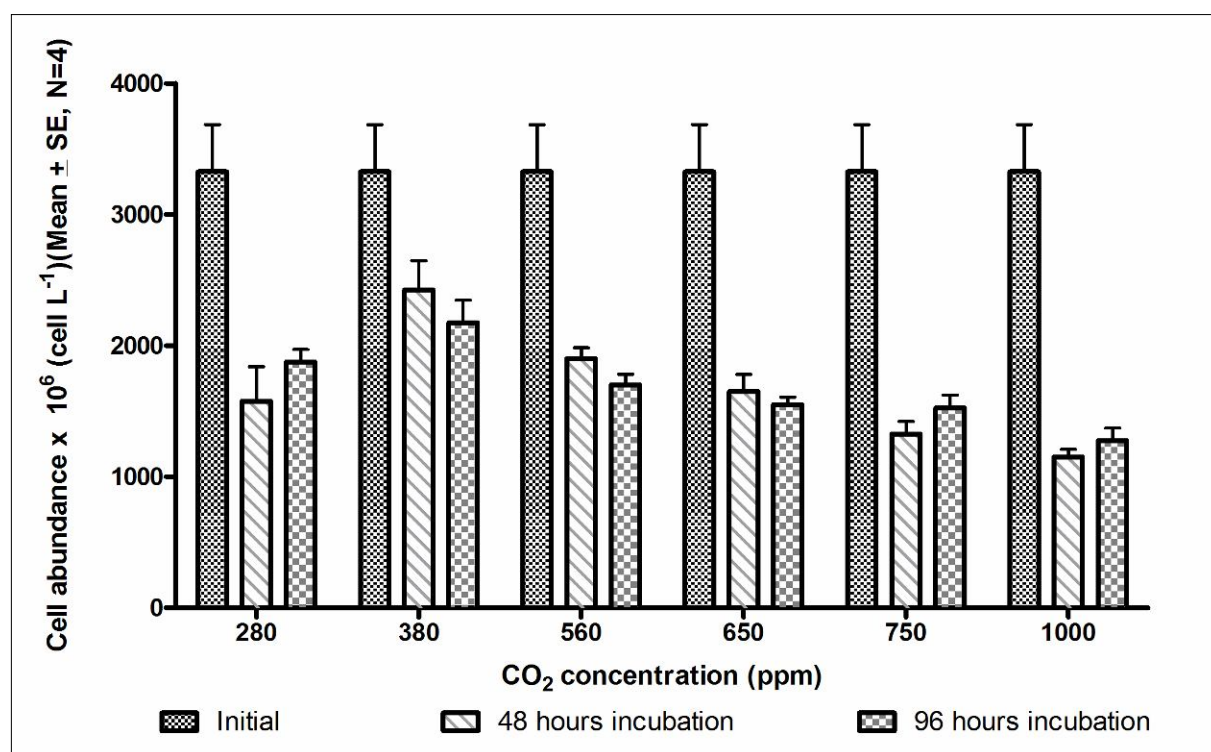


Figure 1. Cell abundance at six CO₂ concentration treatments for two incubation periods (Mean ± SE, N = 4).

Phytoplankton diversity. A total of 34 phytoplankton species was identified during the study period. However, species richness (S) was moderate and no clear trend was apparent between CO₂ concentrations and incubation periods (Figure 2a). There was no clear trend of Shannon diversity (H') and Evenness values between CO₂ concentration and incubation period (Figures 2b and 2c). Changes in J' closely mirrored changes in H'. The occurrence of a simultaneous reduction of H' and J', where phytoplankton maximum was attained, reflects the strong dominance of Bacillariophyceae.

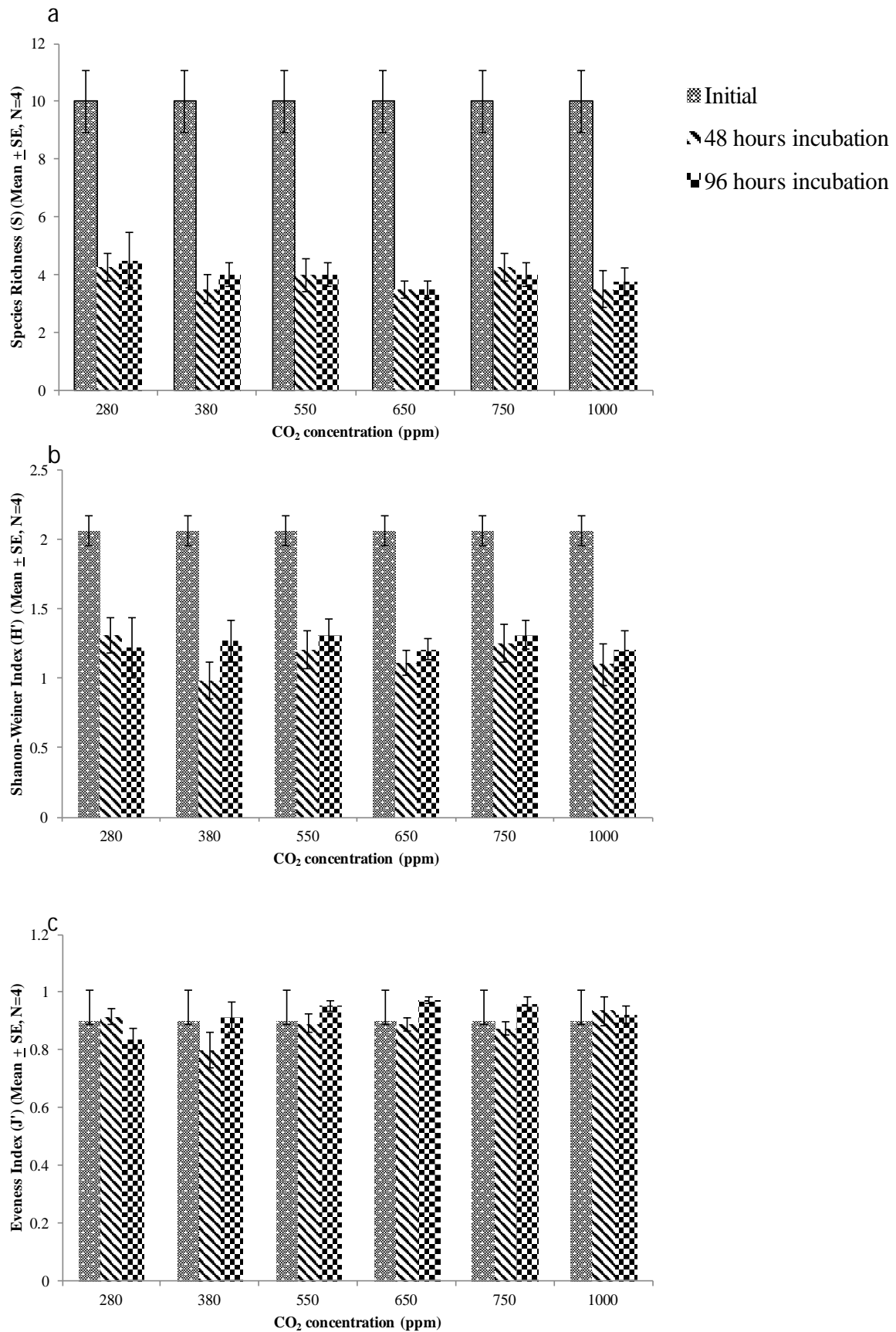


Figure 2. Species Richness (S), Shannon Diversity Index (H') and Evenness Index (J') at six CO₂ concentration treatments for two incubation periods (Mean \pm SE, N = 4).

Phytoplankton assemblages. The nMDS ordination of CO₂ concentrations and incubation periods generated by phytoplankton abundance was illustrated in Figures 3a and 3b. The stress value associated with this two-dimensional plot is 0.18, revealing that this representation of stations is still sound. However, there was not a clear cluster of species assemblages between CO₂ concentrations. Interestingly, there was a clear grouping of species assemblages between incubation periods. ANOSIM result showed that there was not a significant difference of species assemblages among CO₂ treatments. On the other hand, there was a significant difference of species assemblages among incubation periods (Table 1). In general, all communities were dominated by diatoms. The identities of the species, but not their contributions were similar in all communities.

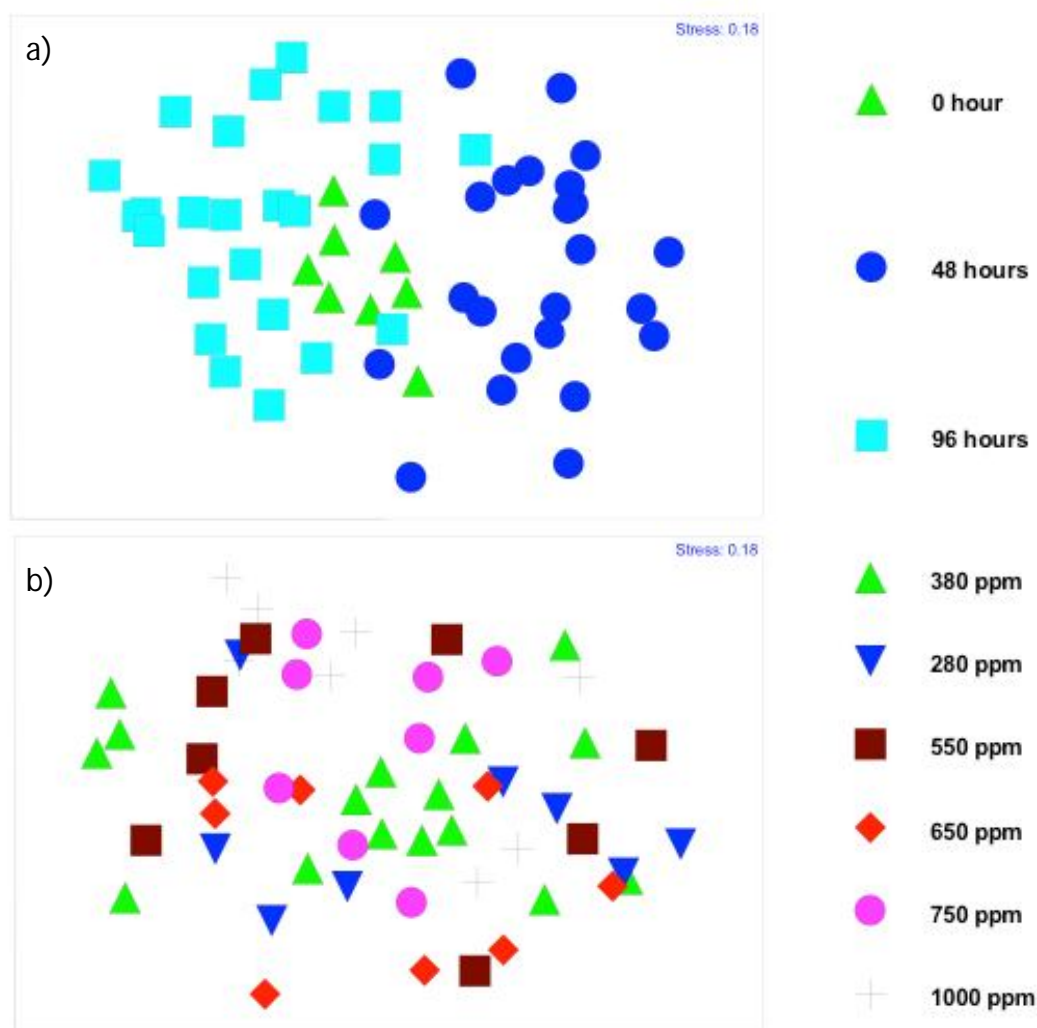


Figure 3. Non-metric multi-dimensional scaling plots of phytoplankton assemblages. a) incubation periods; b) six CO₂ concentration treatments.

The compositional dissimilarity between CO₂ concentration treatments, as well as between incubation periods was varied ranged from 69.24 to 90.14 (Table 1). The highest dissimilarity was found at a pair of 48 hours vs 96 hours of the incubation period, with taxa the most responsible for dissimilarity were *Rhizosolenia fragilissima*, *Biddulphia sinensis*, *Thalassionema nitzchioides*, with the percentage that contributes to dissimilarity were 11%, 8.6%, and 8.5%, respectively. In addition, between CO₂ concentration treatments, the highest dissimilarity was found in the pair of 650 ppm vs 1000 ppm, account for 83.15%. Three taxa that most responsible for dissimilarity were *Rhizosolenia fragilissima* (10.1%), *Gyrosigma acuminatum* (9.3%), and *Biddulphia sinensis* (9.2%).

Table 1

ANOSIM Pairwise tests and Groups that contributed to the dissimilarity between CO₂ concentration treatments and incubation, based on SIMPER analysis Bray-Curtis

ANOSIM Pairwise Test			SIMPER Results	
Pair	Global R statistic	Significance level (%)	Dissimilarity (%)	Taxa most responsible for dissimilarity (%)
<i>Incubation period</i>				
0 hour vs 48 hours	0.342	0.1	77.01	<i>Thalassionema nitzchioides</i> (7.8%), <i>Gyrosigma acuminatum</i> (7.8%), <i>Hemiaulus sinensis</i> (7.3%)
0 hour vs 96 hours	0.058	23.7	69.24	<i>Gyrosigma acuminatum</i> (8.3%), <i>Perinidium conicoides</i> (7.9%), <i>Hemiaulus sinensis</i> (7.1%)
48 hours vs 96 hours	0.616	0.1	90.14	<i>Rhizosolenia fragilissima</i> (11%), <i>Biddulphia sinensis</i> (8.6%), <i>Thalassionema nitzchioides</i> (8.5%)
<i>CO₂ concentration</i>				
280 ppm vs 380 ppm	0.032	29.3	76.28	<i>Lauderia borealis</i> (7.8%), <i>Chaetocerus lauderi</i> (7.0%), <i>Rhizosolenia fragilissima</i> (6.9%)
280 ppm vs 550 ppm	-0.062	71.9	77.81	<i>Lauderia borealis</i> (9.3%), <i>Biddulphia sinensis</i> (8.7%), <i>Rhizosolenia fragilissima</i> (8.4%)
280 ppm vs 650 ppm	-0.001	41.9	79.89	<i>Lauderia borealis</i> (9.7%), <i>Gyrosigma acuminatum</i> (8.9%), <i>Biddulphia sinensis</i> (8.6%)
280 ppm vs 750 ppm	0.099	15.1	77.84	<i>Lauderia borealis</i> (9.3%), <i>Rhizosolenia fragilissima</i> (9.1%), <i>Biddulphia sinensis</i> (8.9%)
280 ppm vs 1000 ppm	0.069	17.7	81.27	<i>Lauderia borealis</i> (9.6%), <i>Rhizosolenia fragilissima</i> (9.3%), <i>Hemiaulus sinensis</i> (7.8%)
380 ppm vs 550 ppm	0.030	29.7	76.86	<i>Rhizosolenia fragilissima</i> (7.7%), <i>Lauderia borealis</i> (7.0%), <i>Biddulphia sinensis</i> (6.7%)
380 ppm vs 650 ppm	0.045	26.5	77.49	<i>Gyrosigma acuminatum</i> (7.9%), <i>Thalassionema nitzchioides</i> (7.6%), <i>Rhizosolenia fragilissima</i> (7.4%)
380 ppm vs 750 ppm	0.050	25.6	75.85	<i>Biddulphia sinensis</i> (8.4%), <i>Rhizosolenia fragilissima</i> (8.3%), <i>Hemiaulus sinensis</i> (7.2%)
380 ppm vs 1000 ppm	0.102	10.7	79.21	<i>Rhizosolenia fragilissima</i> (8.3%), <i>Biddulphia sinensis</i> (7.4%), <i>Hemiaulus sinensis</i> (6.9%)
550 ppm vs 650 ppm	0.000	40.6	80.30	<i>Gyrosigma acuminatum</i> (9.1%), <i>Rhizosolenia fragilissima</i> (9.0%), <i>Thalassionema nitzchioides</i> (8.8%)
550 ppm vs 750 ppm	0.092	15.5	77.62	<i>Rhizosolenia fragilissima</i> (9.7%), <i>Biddulphia sinensis</i> (8.5%), <i>Hemiaulus sinensis</i> (8.4%)
550 ppm vs 1000 ppm	0.024	30.4	80.04	<i>Rhizosolenia fragilissima</i> (9.7%), <i>Biddulphia sinensis</i> (9.1%), <i>Hemiaulus sinensis</i> (7.8%)
650 ppm vs 750 ppm	0.075	20.5	77.92	<i>Biddulphia sinensis</i> (10.7%), <i>Rhizosolenia fragilissima</i> (9.9%), <i>Thalassionema nitzchioides</i> (9.0%)
650 ppm vs 1000 ppm	0.102	14.3	83.15	<i>Rhizosolenia fragilissima</i> (10.1%), <i>Gyrosigma acuminatum</i> (9.3%), <i>Biddulphia sinensis</i> (9.2%)
750 ppm vs 1000 ppm	-0.120	90.1	69.26	<i>Rhizosolenia fragilissima</i> (11.4%), <i>Biddulphia sinensis</i> (10.3%), <i>Hemiaulus sinensis</i> (9.9%)

Discussion. In general, a variation of the composition and density of phytoplankton were determined by their physical and ecological features, and the environmental factors such as temperature, salinity gradient, and nutrients (Cuici et al 2006). Furthermore, there is a beneficial factor that is often considered for phytoplankton, which is ocean acidification. Increasing CO₂ concentration by 50% may lead in increasing primary productivity of phytoplankton (Schipper et al 2004), but there is an inhibition of photosynthesis and growth in diatom due to increasing CO₂ levels that combined with increasing light exposure (Gao et al 2012). Our experiments clearly showed a negative effect of high CO₂ concentration on phytoplankton abundance; however, our study was focused on changing phytoplankton assemblage due to increasing CO₂ concentration. In this study, we clearly observed that an increase in CO₂ concentration (decrease in pH) increased the abundance of Diatomae. The increase in free CO₂ concentration combined with ocean acidification has been commonly believed to increase the rate of photosynthesis of phytoplankton, and to what extent varies depending on the efficiency of CCM (Riebesell 2004; Rost et al 2008).

Our result also found that three most abundant species which contribute to the dissimilarity between CO₂ concentration treatments were from a bigger size of the phytoplankton of Bacillariophyceae/Diatom group. This finding is in line with Reinfelder (2011) who found that larger cells were subjected to greater reaction-diffusion limitation due to increasing CO₂ concentration; consequently, it caused the greater growth of larger cells than small cells. pCO₂ treatments affected neither species composition nor aggregated growth rate in the > 20 µm size class (Gear et al 2017). Tortell et al (2010) found that elevated pCO₂ from 100 µatm to 380 µatm and to 800 µatm leads to increase colonial diatom assemblages. Reinfelder & Larger (2011) explained that inorganic carbon concentration mechanisms (CCM) has been possessed by nearly all marine phytoplankton to support photosynthetic carbon fixation at the concentration of CO₂ present in ocean surface waters. Furthermore, Raven & Johnston (1991) stated that a significant portion of cellular energy expenditure was by CCM through active transport of inorganic carbon. Eggers et al (2014) mentioned that ocean phytoplankton has to adjust with increasing CO₂ over the next century through acclimation process, which involved a saving from CCM down-regulation.

We found that increasing CO₂ concentration showed a negative effect to cell abundance and it also changed the dominant species. This finding was supported by previous studies of Tortell et al (2010) who found that CO₂ elevation caused a shift in the relative abundance of species within a major taxon and shift of major taxa within a community (Tortell et al 2002; Paulino et al 2008). Our study also showed that the outcome of competition in pairwise mixtures rarely changed in response to elevated CO₂, but CO₂ did alter the dynamics of the species succession in ways consistent with knowing the differences among taxa in their ability to take up and use CO₂ (Tortell et al 2000).

Elevated atmospheric CO₂ is expected to drive a decrease in pH, an increase in temperature and a host of indirect changes in natural aquatic systems (Orr et al 2005; IPCC 2007). Furthermore, at any given CO₂ concentration many factors can influence the availability of CO₂ to phytoplankton, such as temperature and biological activity, and the ability of phytoplankton to take up the CO₂, such as nutrient availability and light limitation (Beardall et al 1998). Our experiment was designed to manipulate CO₂ alone in order to isolate the effect of elevated CO₂ on species and communities. Much more extensive experiments to evaluate phytoplankton growth and competition under varying levels and combinations of global change factors (Rost et al 2008) and experiments long enough to allow for evolutionary adaptation and its interaction with ecological responses (Collin & Bell 2004; Collins & Gardner 2009) will be necessary to predict with more confidence in the state of phytoplankton communities of the future. Moreover, the experiment explored only a small fraction of either the major taxa or (especially) the species diversity within major taxa that are present in natural phytoplankton assemblages. The importance of major taxa in predicting CO₂ response and of the predictive chain from physiological to competitive response to elevated CO₂ needs to be tested in a larger diversity of species and major taxa. We believe that the experimental approach is the most powerful way of inferring the response of ecological communities to

environmental changed. Future studies will need to examine the effects of finer scale CO₂ variation on the species composition of marine phytoplankton communities. In addition, more information is needed on the physiological mechanisms of inorganic C acquisition in a variety of marine phytoplankton taxa. Such information will inform our understanding of how phytoplankton species may respond differentially to natural and anthropogenic CO₂ variation in the oceans.

Conclusions. Phytoplankton assemblages did not change with increasing CO₂ concentration, however this CO₂ increasing showed a negative effect to cell abundance of natural phytoplankton. There was a changing on dominant species of phytoplankton with increasing of CO₂ concentration, which was dominated by diatoms.

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