



# Limited impact of ocean acidification on phytoplankton community structure and carbon export in an oligotrophic environment: Results from two short-term mesocosm studies in the Mediterranean Sea

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## ABSTRACT

Modifications in the strength of the biological pump as a consequence of ocean acidification, whether positive or negative, have the potential to impact atmospheric CO<sub>2</sub> and therefore climate. So far, most plankton community perturbation studies have been performed in nutrient-rich areas although there are some indications that CO<sub>2</sub>-dependent growth could differ in nutrient-replete vs. -limited regions and with different community compositions. Two *in situ* mesocosm experiments were performed in the NW Mediterranean Sea during two seasons with contrasted environmental conditions: summer oligotrophic stratified waters in the Bay of Calvi vs. winter mesotrophic well-mixed waters in the Bay of Villefranche. Nine mesocosms were deployed for 20 and 12 d, respectively, and subjected to seven CO<sub>2</sub> levels (3 controls, 6 elevated levels). Both phytoplankton assemblages were dominated by pico- and nano-phytoplankton cells. Although haptophyceae and dinoflagellates benefited from short-term CO<sub>2</sub> enrichment in summer, their response remained small with no consequences on organic matter export due to strong environmental constraints (nutrient availability). In winter, most of the plankton growth and associated nutrient consumption occurred during the 4-day acidification period (before the experimental phase). During the remaining experimental period, characterized by low nutrient availability, plankton growth was minimal and no clear CO<sub>2</sub>-dependency was found for any of the tested parameters. While there is a strong confidence on the absence of significant effect of short-term CO<sub>2</sub> addition under oligotrophic conditions, more investigations are needed to assess the response of plankton communities in winter when vertical mixing and weather conditions are major factors controlling plankton dynamics.

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## 1. Introduction

During the last 150 years, human activities, through the combustion of fossil fuels (oil, gas and coal), have led to a dramatic release of carbon dioxide (CO<sub>2</sub>) to the Earth's atmosphere. The accumulation of CO<sub>2</sub> impacts the radiative forcing, thereby warming the atmosphere and the ocean. The ocean acts as a climate integrator that absorbed 93% of Earth's additional heat since the

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1970s, offsetting much atmospheric warming but increasing ocean temperature and sea level and captured 28% of anthropogenic CO<sub>2</sub> emissions since 1750 (Gattuso et al., 2015). Although providing a valuable human service by moderating the rate and severity of global warming, the consequence of this oceanic CO<sub>2</sub> pump is the on-going increase in ocean acidity (i.e. decrease in pH). Surface ocean pH has already decreased by 0.1 units since the beginning of the industrial era (i.e. increased acidity of 30%; Ciais et al., 2013). According to recent projections and depending on the emission scenario considered, an additional decrease ranging between 0.06 and 0.32 units is expected by 2100 (Ciais et al., 2013).

The decrease in seawater pH leads to a decrease in the

concentration of carbonate ions ( $\text{CO}_3^{2-}$ ), one of the building blocks of calcium carbonate ( $\text{CaCO}_3$ ), and alters the ability of many calcifying organisms to precipitate  $\text{CaCO}_3$  (e.g. Kroecker et al., 2013). In addition, a decrease in seawater pH leads to an increase in dissolved  $\text{CO}_2$  and bicarbonate ( $\text{HCO}_3^-$ ) concentrations. Carbon fixation by marine photosynthetic organisms represents about 50% of global Earth primary production (Field et al., 1998), and the export of part of the produced organic matter from the sunlit surface layer to the deep-ocean (i.e. the biological or soft-tissue pump) is responsible for ~70% of surface to deep-ocean dissolved inorganic carbon ( $\text{C}_T$ ) gradients (Sarmiento and Gruber, 2006). Therefore, modifications in the strength of this biotically mediated carbon pump, whether positive or negative, have the potential to impact atmospheric  $\text{CO}_2$  and therefore climate (Riebesell et al., 2007).

$\text{CO}_2$  rather than the much more abundant  $\text{HCO}_3^-$  is the substrate used in the carbon fixation step of photosynthesis and RubisCO, the enzyme catalyzing this reaction, has a low affinity for  $\text{CO}_2$  (Badger et al., 1998; Giordano et al., 2005). As such, this enzyme is theoretically not saturated under current ambient  $\text{CO}_2$  levels (Badger et al., 1998). However, nearly all marine species have developed various mechanisms (carbon concentration mechanisms or CCMs) to compensate for this low  $\text{CO}_2$  availability through the energy-demanding use of carbonic anhydrase enzymes or active  $\text{CO}_2$  and/or bicarbonate transports through membranes (Raven et al., 2014). There is evidence that both the RubisCO affinity for  $\text{CO}_2$  as well as the efficiency of these CCMs differ widely among taxa, species or even strains (Tortell, 2000; Young et al., 2016), complicating the prediction of whether a cell's carbon fixation rate will respond directly to ambient changes in  $\text{CO}_2$  availability through increased  $\text{CO}_2$  diffusion and/or less energy expenditure needed to operate CCMs (Mangan et al., 2016; Raven and Beardall, 2014). Finally, although downregulation of CCMs at elevated  $\text{CO}_2$  has been observed, the significance of this downregulation to overall cell physiology and growth is not currently well constrained due to the presence of other limiting factors in the oceans such as macro- or micro-nutrients and light (Hennon et al., 2015; Young and Morel, 2015). All of this can partly explain the very diverse findings that have been documented on the effect of increased ambient  $\text{CO}_2$  availability on photosynthesis and growth of marine phytoplankton (Dutkiewicz et al., 2015).

Apart from the above-mentioned variability in RubisCO affinity for  $\text{CO}_2$  and CCMs efficiency, a significant part of the observed discrepancies among available perturbation studies could be explained by differences in experimental setups and environmental conditions such as temperature, light conditions and nutrient availability. Phytoplankton growth obviously does not only depend on carbon availability but on a combination of physico-chemical-biological drivers such as macro- and micro-nutrient availability, temperature, light, competition and grazing. It is therefore very likely that the response of phytoplankton will differ depending on these environmental conditions (Verspagen et al., 2014). Furthermore, as this is the amount of organic matter that can escape the sunlit layer that determines the capacity of the surface ocean to pump atmospheric  $\text{CO}_2$ , there is a great need to evaluate the impact of  $\text{CO}_2$ , not only on phytoplankton growth but on the export of this organic matter to deeper layers. The build-up of organic matter and its potential export strongly depends on phytoplankton community composition (Eggers et al., 2014). Indeed, large cells (e.g. diatoms) account for a large proportion of export production and ultimate burial in sediments (Finkel et al., 2005). In contrast, small cells (nano- and pico-plankton) are particularly important in regions with limited nutrient availability with a close coupling between production and grazing through the microbial loop and a with low export capacity (Riebesell and Tortell, 2011). As already mentioned, differing responses to increased  $\text{CO}_2$  availability between different

functional groups, size classes and species (Dutkiewicz et al., 2015) have the potential to significantly alter community structure and functioning. In that sense, studies focused on plankton assemblages rather than on isolated single species and under very contrasted environmental conditions are very informative (Tarling et al., 2016).

During the last decade, there has been a noticeable increase in the number of experimental assessments of the sensitivity of plankton community compositions to the on-going increase in  $\text{CO}_2$ . These experiments were conducted in various areas of the world ocean using different approaches, from small bottle incubations to large mesocosm deployments, and over different time scales (few days to few weeks). Several of these experiments highlighted significant modifications of community compositions under elevated  $\text{CO}_2$  levels. For instance,  $\text{CO}_2$  enrichment has been shown to stimulate growth of large species such as diatoms (e.g. Domingues et al., 2014; Feng et al., 2009; Reul et al., 2014; Tortell et al., 2002, 2008; Wu et al., 2014). Several experiments suggested stimulating effects on small species (pico-phytoplankton; e.g. Newbold et al., 2012; Paulino et al., 2008; Schulz et al., 2013). In contrast, Richier et al. (2014) reported significant decrease in the growth of small phytoplankton species (<10  $\mu\text{m}$ ) suggesting that small species are less adapted to changes in their local pH while larger cells must face larger pH variations at short time scales (Flynn et al., 2012). Other studies showed differential responses between species from the same taxa (e.g. Endo et al., 2016; Feng et al., 2010; Kim et al., 2006; Meakin and Wyman, 2011) and finally among different phylotypes and phenotypes of the same species (e.g. Brading et al., 2011; Rickaby et al., 2016).

Whether or not these modifications of community structure (e.g. increase or decrease in cell size) can modify the amount of organic matter sinking to deeper layers can be evaluated through the use of mesocosms. They are defined as experimental enclosures from 1 thousand to several thousands of litres that allow the maintenance of natural communities under close-to-natural conditions and the collection of sinking organic matter (Riebesell et al., 2008, 2013a). In recent years, plankton community studies performed using such experimental systems have led to very contrasted outcomes in terms of community composition and carbon export responses to  $\text{CO}_2$  enrichment (see Table 1). Most of these experiments have been performed in nutrient-rich areas (or following artificial nutrient enrichment) dominated by large species and experiments conducted in areas limited by nitrate, phosphate and/or iron are currently lacking (Paul et al., 2015a). These areas represent a very large surface area of the ocean and are projected to expand in the coming decades because of enhanced thermal stratification and nutrient depletion (Irwin and Oliver, 2009; Polovina et al., 2008). As already mentioned, they are usually dominated by small cells adapted to low-nutrient conditions and have low export capacities. Recently, and in contrast to theoretical considerations (Verspagen et al., 2014), two mesocosm experiments suggested that communities exposed to low nutrient concentrations may be more responsive to  $\text{CO}_2$  enrichment than previously thought (Bach et al., 2016; Paul et al., 2015a). This was confirmed recently by Sala et al. (2016) based on indoor experiments in a coastal site of the Western Mediterranean Sea. During these experiments, effects of ocean acidification, i.e. positive effect on pico- and nano-phytoplankton, were more important when nutrient concentrations were low. However, it must be stressed that nutrient and chlorophyll levels observed during these experiments were representative of an urbanized coastal area and much higher than levels usually observed in the vast majority of the Mediterranean Sea.

The Mediterranean Sea is generally considered as oligotrophic but actually exhibits a gradient from mesotrophic-oligotrophic in the western basin to ultra-oligotrophic in the eastern basin (The

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