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No detectable effect of ocean acidification on plankton metabolism in the NW oligotrophic Mediterranean Sea: Results from two mesocosm studies

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ABSTRACT

Oligotrophic areas account for about 30% of oceanic primary production and are projected to expand in a warm, high-CO_2 world. Changes in primary production in these areas could have important impacts on future global carbon cycling. To assess the response of primary production and respiration of plankton communities to increasing partial pressure of CO_2 (pCO_2) levels in Low Nutrient Low Chorophyll areas, two mesocosm experiments were conducted in the Bay of Calvi (Corsica, France) and in the Bay of Villefranche (France) in June–July 2012 and February–March 2013 under different trophic state, temperature and irradiance conditions. Nine mesocosms of 50 m^3 were deployed for 20 and 12 days, respectively, and were subjected to seven pCO_2 levels (3 control and 6 elevated levels). The metabolism of the community was studied using several methods based on *in situ* incubations (oxygen light–dark, ^{18}O and ^{14}C uptake). Increasing pCO_2 had no significant effect on gross primary production, net community production, particulate and dissolved carbon production, as well as on community respiration. These two mesocosm experiments, the first performed under maintained low nutrient and low chlorophyll, suggest that in large areas of the ocean, increasing pCO_2 levels may not lead to a significant change in plankton metabolic rates and sea surface biological carbon fixation.

1. Introduction

Oceanic primary production represents about 50% of global primary production (Field et al., 1998) and plays a key role in climate regulation. The balance between gross primary production (GPP) of autotrophic organisms and community respiration (CR) of both autotrophic and heterotrophic organisms determines the net community production (NCP), revealing the capacity of a system to sequester carbon via the biological pump. Production and consumption of organic matter depend on the composition of the plankton community and are constrained by environmental parameters such as nutrient availability (i.e., nitrogen, phosphorus, silicon concentration, ratios and chemical forms), light availability and temperature. The increase in the partial pressure of CO_2 (pCO_2) in the ocean and the consequent decrease in seawater pH, so-called ocean acidification (Gattuso and Hansson, 2011), might also influence the metabolism of plankton organisms and marine communities.

Many laboratory studies, focused on phytoplankton strains maintained in culture, have been performed to test the response of primary production to increased pCO_2, but present two major downsides. First of all, they do not take into account any potential compensation between species. Although laboratory studies have shown that diatoms appear to generally benefit from an increase in CO_2 and that the response of coccolithophores is more variable (from increased production to neutral or even inhibitory effects under nitrogen limitation; see comprehensive review by Riebesell and Tortell, 2011), the global response of the community might not be the sum of these individual effects. Another drawback of single strain culture experiments is that the heterotrophic component of plankton communities is, for the most part, not taken

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into consideration. Yet, a possible indirect effect of elevated pCO_2 on bacteria has been suggested and linked to changes in phytoplankton activity (Grossart et al., 2006). Autotrophic organisms can indeed release dissolved organic carbon (DOC), which can in turn be used by bacteria for growth and respiration. An increase in DOC production under elevated pCO_2 could therefore have an impact on the bacterial community (see also Liu et al., 2010).

In order to measure plankton metabolic rates, several techniques are available although each of these methods presents some advantages and disadvantages. The radioactive ^{14}C incorporation technique (Steemann-Nielsen, 1952) has been widely used for many years. However, although this method is believed to provide accurate estimates of carbon incorporation rates (Williams et al., 1983), uncertainties still remain on what is actually measured, considered to be in between gross and net production (Peterson, 1980). The oxygen light–dark method (e.g., Riley, 1939) is also an accurate technique that has been used for a long time and that allows determining the metabolic state of the community (NCP). However, in order to estimate GPP rates, one has to assume that light respiration equals the measured dark respiration (CR), an assumption that is not always correct (e.g., Bender et al., 1987). In contrast, another method based on the heavy isotope of oxygen (^{18}O; Grande et al., 1982) provides very accurate and direct estimates of GPP. However, with this method all the O_2 produced is labelled even though not all this O_2 is directly linked to carbon assimilation, therefore GPP-^{18}O is believed to overestimate true GPP (Laws et al., 2000). Finally, all three methods present the disadvantage to be performed in closed small containers that might lead to some confinement effects and not completely reflect *in situ* conditions of light, nutrients, turbidity, etc. This is out of the scope of this paper to extensively discuss how these methods compare to each other; we therefore refer to detailed reviews and comparison analyses for further details (e.g. Bender et al., 1987; Gazeau et al., 2007; Regaudie-de-Gioux et al., 2014).

Experiments have recently been conducted to assess the effects of ocean acidification on natural plankton assemblages with results showing either increased photosynthesis and/or net community production with increasing pCO_2 (e.g., Riebesell et al., 2007; Egge et al., 2009) or no effect (e.g., Hare et al., 2007; Tanaka et al., 2013). Some of these experiments at the community level have been conducted using pelagic mesocosms. This approach is considered to be closer to the "real world" because large mesocosms enclose a significant volume of seawater containing an entire plankton community with environmental conditions (e.g., temperature, irradiance, water motion) within the mesocosm similar to those prevailing *in situ* (Riebesell et al., 2010, 2013). However, most of these experiments have been performed in high-nutrient or nutrient-enriched systems and very few experiments have been reported in low nutrient areas (Yoshimura et al., 2010). Yet, pelagic primary production is highly variable between oceanic provinces and more than 60% of the open ocean is considered to be oligotrophic (i.e. low chlorophyll). Despite their low nutrient concentration and relatively low productivity, these areas represent about 30% of oceanic primary production (Longhurst et al., 1995). Furthermore, it has been suggested that oligotrophic areas will expand as a result of ocean warming (Polovina et al., 2008), with potential implications for ocean biogeochemistry and primary production (Irwin and Oliver, 2009). Although the metabolic status of open ocean waters is still hotly debated (Duarte et al., 2013; Williams et al., 2013), any change due to ocean acidification and/or warming will undoubtedly have profound impacts on the biological carbon pump and carbon cycle. Most of the oligotrophic areas are in the open ocean where it is difficult to perform field experiments. The Mediterranean Sea, a semi-enclosed sea, gives the opportunity to overcome this problem as characterized by low nutrient and low chlorophyll (LNLC) concentrations, although depending on the location and season, trophic conditions can be defined as ranging from mesotrophic to ultra-oligotrophic (D'Ortenzio and d'Alcalà, 2009).

To test whether ocean acidification will affect plankton community composition and functioning in oligotrophic areas, two mesocosm experiments were performed in the North-Western Mediterranean Sea during two contrasting periods (winter *vs.* summer), in the framework of the European project 'Mediterranean Sea Acidification in a Changing Climate' (MedSeA; www.medsea-project.eu). Here, we report on the effects of ocean acidification on plankton metabolism (gross primary production, net community production, particulate and dissolved carbon production as well as community respiration), as measured using the methods briefly described above (the oxygen light–dark, ^{14}C and ^{18}O labelling techniques).

2. Material and method

2.1. Study sites and experimental set-up

One mesocosm experiment was conducted in the Bay of Calvi (BC; Corsica, France) in summer (June–July 2012) and the other one in the Bay of Villefranche (BV; France) during the transition between winter and spring (February–March 2013). The experimental set-up and mesocosm characteristics are fully described in a companion paper (Gazeau et al., sbm, this issue). Briefly, for each experiment, nine mesocosms of ca. 50 m^3 (2.3 m in diameter and 12 m deep) were deployed for 20 and 12 days in BC and BV, respectively. Once the bottom of the mesocosms was closed, CO_2 saturated seawater was added to obtain a pCO_2 gradient across mesocosms ranging from ambient levels to 1250 µatm (Table 1), with three control mesocosms (C1, C2 and C3) and six mesocosms with increasing pCO_2 (P1 to P6). Measurements of plankton metabolism started after the end of the CO_2 manipulation, on 24 June 2012 and 22 February 2013 for BC and BV, respectively corresponding to Day 0 in BC and Day 1 in BV. Before sunrise (04:00 in BC and 05:00 in BV; local times), depth-integrated sampling (0–10 m) was performed using 5 L Hydro-Bios integrated water samplers and distributed into various incubation bottles (see below). Processes influenced by light were incubated *in situ* on an incubation line, moored near the mesocosms, and incubations took place at the depth of mean irradiance over the 12 m depth of the mesocosms (6 m for BC and 4 m for BV; see section on irradiance below for more details). Other incubations were performed in a laboratory incubator at *in situ* temperature (ca. 21–25 °C for BC and ca. 13 °C for BV). During both experiments, net community production (NCP) and community respiration (CR) were determined using the oxygen light–dark method every two days. Gross primary production (GPP) was measured using the ^{18}O-labelling method (GPP-^{18}O) every 4 days during the BC experiment, while rates of particulate organic (PP-^{14}C) and dissolved organic carbon production (DO^{14}Cp) were determined every two days using the ^{14}C labelling technique during the BV experiment.

2.2. Irradiance and metabolic rates measurements techniques

2.2.1. Irradiance

Surface irradiance (photosynthetically active radiation; PAR) was measured continuously during the two experiments using a LI-COR LI-192SA 2-Pi sensor connected to a LI-1400 data logger (see Gazeau et al., sbm, this issue, for more details). The depth of mean irradiance was estimated at the start of each mesocosm experiment based on PAR profiles (0–12 m) performed using a Biospherical

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