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Carbon-13 labelling shows no effect of ocean acidification on carbon transfer in Mediterranean plankton communities

L. Maugendre [a, b, *], J.-P. Gattuso [a, b, c], A. de Kluijver [d], K. Soetaert [e], D. van Oevelen [e], J.J. Middelburg [f], F. Gazeau [a, b]

[a] Sorbonne Universités, UPMC Univ Paris 06, UMR 7093, LOV, Observatoire Océanologique de Villefranche, 06230 Villefranche-sur-Mer, France
[b] CNRS-INSU, UMR 7093, Laboratoire d'Océanographie de Villefranche, 06230 Villefranche-sur-Mer, France
[c] Institute for Sustainable Development and International Relations (IDDRI), Sciences Po, 27 rue Saint Guillaume, F-75007 Paris, France
[d] Deltares, Delft, The Netherlands
[e] Department of Ecosystems Studies, Royal Netherlands Institute for Sea Research (NIOZ), Yerseke, The Netherlands
[f] Department of Earth Sciences, Faculty of Geosciences, Utrecht University, The Netherlands

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ABSTRACT

Despite an increasing number of experiments, no consensus has emerged on the effect of ocean acidification on plankton communities and carbon flow. During two experiments, performed in the Bay of Calvi (France, Corsica; summer 2012) and the Bay of Villefranche (France; winter 2013), nine off-shore mesocosms (~50 m^3) were deployed among which three served as controls and six were enriched with CO_2 to reach partial pressure of CO_2 (pCO_2) levels from 450 to 1350 µatm and 350–1250 µatm in the Bay of Calvi and the Bay of Villefranche, respectively. In each mesocosm, inorganic ^{13}C was added in order to follow carbon transfer from inorganic via bulk particulate organic carbon and phytoplankton to bacteria by means of biomarkers as well as to zooplankton and settling particles. Despite very low plankton biomasses, labelled carbon was clearly transferred through plankton communities. Incorporation rates in the various plankton compartments suggested a slow-growing community based on regenerated production in the Bay of Calvi while in the Bay of Villefranche, fast-growing species were clearly dominating community production at the start with a shift toward slow-growing species during the experiment due to nutrient limitation. Both bulk and group-specific productions rates did not respond to increasing pCO_2 levels. These experiments were the first conducted in the Mediterranean Sea under low nutrient concentrations and phytoplankton biomasses and suggest that ocean acidification may not significantly impact plankton carbon flows in low nutrient low chlorophyll (LNLC) areas.

1. Introduction

The ocean is the largest active reservoir of carbon on Earth, absorbs about 2.6 ± 0.5 Pg C yr^{-1} (Le Quéré et al., 2014) and has a key role in regulating carbon flow on Earth. Carbon dioxide (CO_2) fluxes from the atmosphere to the ocean are partly controlled by primary production, community respiration and organic matter (OM) export to the deep-sea, the so-called biological pump. Primary production rates in the surface layer depend on environmental conditions such as temperature, water-column structure (mixed *vs.* stratified), irradiance levels and nutrient availability. The freshly produced OM can be consumed by zooplankton or exported to the deep-sea but a large fraction is respired and degraded by heterotrophic bacteria in the upper layer producing CO_2 as well as recycled inorganic nutrients brought back in the ecosystem (Rivkin and Legendre, 2001). The CO_2 equilibrium between atmosphere and ocean is then dependent on the trophic status and metabolic state of surface plankton communities.

Over the last century, CO_2 concentration in the atmosphere has increased at an unprecedented rate in the Earth's history due to human activities, warming the lower atmosphere and the ocean. Furthermore, 26% of the emitted CO_2 dissolves in seawater (Le Quéré et al., 2014) causing an acidification of the ocean with potential effects on plankton metabolic rates in the upper layer (Riebesell and Tortell, 2011). Dissolved CO_2 is the main substrate for

* Corresponding author. Sorbonne Universités, UPMC Univ Paris 06, UMR 7093, LOV, Observatoire Océanologique de Villefranche, 06230 Villefranche-sur-Mer, France.
E-mail address: laure.maugendre@gmail.com (L. Maugendre).

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photosynthesis but the activity of the RuBisCO, the enzyme necessary for carbon fixation, is suboptimal at CO_2 concentrations present in ocean surface waters (Reinfelder, 2011). Therefore, primary production rates might increase under elevated CO_2 levels resulting in carbon overconsumption relative to other nutrients (Riebesell et al., 2007). This could further alter phytoplankton-derived dissolved organic matter (DOM) production and composition (Engel et al., 2004; Riebesell et al., 2007), and consequently increase bacterial carbon consumption as DOM is the main substrate for their growth (Grossart et al., 2006). In parallel, the formation of C-rich aggregates could also increase carbon export and therefore the efficiency of the biological pump (Engel et al., 2004). Furthermore, due to differences in carbon fixation pathways between phytoplankton species, carbon export capacities of the surface ocean could be altered due to modifications of phytoplankton community size structure and sinking capacities (Klaas and Archer, 2002). An significant number of experiments have assessed the effects of ocean acidification on plankton composition and functioning. These studies provided variable and sometimes conflicting results, preventing the development of a general concept on the effects of ocean acidification (see Riebesell and Tortell, 2011 for review). For instance, in some studies, ocean acidification has been shown to modify the community structure towards more diatoms (Tortell et al., 2008, 2002) or towards smaller species (Brussaard et al., 2013). In other studies, no changes were found (Nielsen et al., 2010, 2012).

As the functioning of plankton communities depends on many ecological interactions between biotic and abiotic compartments, there is a strong need to study natural assemblages rather than individual species or strains. Carbon flow within natural plankton communities has been studied using stable isotopes labelling coupled with biomarkers (Middelburg et al., 2000; van den Meersche et al., 2011). The addition of ^{13}C dissolved inorganic carbon and subsequent transfer to phytoplankton, heterotrophic bacteria as well as zooplankton and sinking particles, allows following carbon transfer through plankton communities. The estimation of carbon incorporation in various taxonomic groups can be performed through the analysis of ^{13}C enrichment in phospholipids derived fatty acids (PLFA) biomarkers. PLFA are cell membrane components, produced by phytoplankton and heterotrophic bacteria, which occur in relatively fixed proportion in cells and allow distinguishing among groups of organisms (Middelburg, 2014). As PLFA degrade rapidly after cell death, they therefore largely reflect the activity of living cells (Boschker and Middelburg, 2002). The combination of ^{13}C stable isotope labelling with biomarkers analyses and particulate organic carbon has been used to determine production rates at taxon-specific (Dijkman et al., 2009) and community level (Van den Meersche et al., 2004, 2011; De Kluijver et al., 2010, 2013).

To date, two experiments have focused on the effect of ocean acidification on the flow of carbon within plankton communities through the use of ^{13}C stable isotope labelling combined with biomarkers analyses. The first experiment was performed in the frame of the PeECE III project (Riebesell et al., 2008) in land-based mesocosms following initial nutrient additions (N and P). Group specific primary production rates increased with elevated pCO_2 during the post-bloom period, while no effects were found on phytoplankton-bacteria coupling nor on export rates (De Kluijver et al., 2010). The second experiment was performed in Arctic waters using large offshore mesocosms (Riebesell et al., 2013). Heterotrophic bacteria and two phytoplankton groups were distinguished based on their PLFA composition: mixotroph and autotrophic phytoplankton (De Kluijver et al., 2013). While no effects of CO_2 on particulate organic carbon (POC) production rates were detected before nutrient addition, POC production rates decreased with increasing partial pressure of CO_2 (pCO_2) after nutrient addition. In contrast, no CO_2 effects on bacterial production were highlighted both under nutrient-depleted or -replete conditions. Depending on the experimental period considered, positive or negative effects of CO_2 on phytoplankton and mixotroph production rates, zooplankton grazing and export of detritus were highlighted. The effects of ocean acidification during this experiment were subtle and different for each phase (before and after nutrient addition).

Most of the experiments conducted at community level (including mesocosm experiments) have been performed during a natural or artificial phytoplankton bloom that only occurs during a restricted period of the year and may not reflect the physiological state of plankton community and ecosystem trophic state for most of the year. There is therefore a strong lack of data for warm, low nutrient and productivity regions although these areas represent a vast majority of the surface ocean (>60%, Longhurst et al., 1995). However, a recent study in the Northwestern Mediterranean sea has shown a substantial effect of ocean acidification on plankton communities (phytoplankton abundances and bacterial activities and abundances) under very low nutrient concentrations (Sala et al., 2015) in 200 L laboratory mesocosms (controlled temperature, light intensity and light–dark cycles).

The Mediterranean Sea is oligotrophic for most of the year although several biogeographical provinces have been identified (D'Ortenzio and D'Alcalà, 2009). The pH decrease in this region has been estimated to be ~0.15 pH units since the industrial revolution (Touratier and Goyet, 2009) and an additional decrease of 0.3–0.4 units is foreseen for the end of the century (Geri et al., 2014). The effect of ocean acidification on plankton communities has been investigated based on mesocosm experiments conducted in two different sites of the Northwestern Mediterranean Sea (Gazeau et al., 2017a). This manuscript reports on the first ^{13}C labelling study on Mediterranean plankton communities in the frame of a mesocosm experiment focused on ocean acidification.

2. Material and methods

2.1. Study sites, experimental set-up and sampling

Two mesocosm experiments were carried out: one in the Bay of Calvi (BC; Corsica, France) in June–July 2012 and the other in the Bay of Villefranche (BV; France) in February–March 2013. The experimental set-up and mesocosm characteristics are described in Gazeau et al. (2017a). In brief, for each experiment, nine mesocosms of ca. 50 m^3 (2.5 m in diameter and 12 m maximum depth) were deployed for 20 and 11 days in BC and BV, respectively. Once the bottom of the mesocosms was closed, acidification of the mesocosms was performed over 4 days by homogenous addition of various volumes of CO_2-saturated seawater to obtain a pCO_2 gradient from ambient levels to an intended 1250 µatm, with three control mesocosms (C1, C2 and C3) and six mesocosms with increasing pCO_2 (P1 to P6). In BC, the six targeted elevated pCO_2 levels were P1: 550, P2: 650, P3: 750, P4: 850, P5: 1000 and P6: 1250 µatm. In BV, the levels were P1: 450, P2: 550, P3: 750, P4: 850, P5: 1000 and P6: 1250 µatm. Mesocosms were grouped in clusters of 3 with each cluster containing a control, a medium and a high pCO_2 level (cluster 1: C1, P1, P4; cluster 2: C2, P2, P5 and cluster 3: C3, P3, P6). During the last day of CO_2 saturated seawater addition, ^{13}C sodium bicarbonate ($NaH^{13}CO_3$; 99%) was added to each mesocosm to increase the isotopic level ($\delta^{13}C$ signature) of the dissolved inorganic carbon pool ($\delta^{13}C$-DIC) to ca. 200‰ in BC and 100‰ in BV. In BC, on day 11, a second addition of $NaH^{13}CO_3$ was performed to better constrain production rates and this resulted in a further enrichment of the DIC pool to ca. 270‰.