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Temperature dependence of CO_2-enhanced primary production in the European Arctic Ocean

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The Arctic Ocean is warming at two to three times the global rate[1] and is perceived to be a bellwether for ocean acidification[2,3]. Increased CO_2 concentrations are expected to have a fertilization effect on marine autotrophs[4], and higher temperatures should lead to increased rates of planktonic primary production[5]. Yet, simultaneous assessment of warming and increased CO_2 on primary production in the Arctic has not been conducted. Here we test the expectation that CO_2-enhanced gross primary production (GPP) may be temperature dependent, using data from several oceanographic cruises and experiments from both spring and summer in the European sector of the Arctic Ocean. Results confirm that CO_2 enhances GPP (by a factor of up to ten) over a range of 145–2,099 μatm; however, the greatest effects are observed only at lower temperatures and are constrained by nutrient and light availability to the spring period. The temperature dependence of CO_2-enhanced primary production has significant implications for metabolic balance in a warmer, CO_2-enriched Arctic Ocean in the future. In particular, it indicates that a twofold increase in primary production during the spring is likely in the Arctic.

Primary production in the Arctic Ocean supports significant fisheries[6] and renders it an important sink for anthropogenic carbon[2]; however, climate change has the potential to alter these capacities. Accelerated ice loss is opening surface area across the Arctic, resulting in observations of increased rates of primary production[7]. The reduced salinity caused by melting ice, combined with increasing temperatures, however, increases stratification, restricting turbulent nutrient supply to surface layers[8]. Ice loss also increases surface area for air–sea CO_2 exchange, causing an uptake from the atmosphere into surface waters with already low p_{CO_2} (ref. 9), and ice melt introduces freshwater with low alkalinity and dissolved inorganic carbon, further lowering the carbon content of surface waters[10]. The surface waters of the Arctic Ocean are largely undersaturated with respect to CO_2 throughout spring and summer[2]. In the European sector of the Arctic Ocean (Barents–Greenland Sea/Fram Strait), p_{CO_2} varies seasonally by more than 200 μatm, with values as low as 100 μatm in spring months[11] owing to strong net community production associated with the spring bloom of ice algae followed by that of planktonic algae in open waters[12,13]. Hence, increased CO_2 may stimulate primary production during spring and favour a greater CO_2 sinking capacity in the future[2,9], resulting in a feedback between increased CO_2 and primary production, which biogeochemical models do not consider at present (for example, refs 3,14).

Predicting future primary production in a changing Arctic is not straightforward; models diverge strongly in their predictions depending on the region and drivers for change (that is, sea ice, light, nutrients, warming, and so on)[15], and modelling studies including rising CO_2 concentrations are rare[15]. Experimental research from the European Arctic suggests that increasing CO_2 concentrations enhance primary production in nutrient-replete conditions[16], although this response is possibly species-specific owing to varying efficiencies of the mechanisms for concentrating cellular carbon[17]. However, the response to increased CO_2 when combined with warming may deviate from the expected additive effect.

Here we seek to determine if there is an interaction of increased CO_2 concentration and temperature on planktonic GPP throughout the spring and summer in the European Arctic region. On the basis of metabolic theory, we would expect a positive effect of both warming and higher CO_2 (a main substrate for autotrophic growth) on GPP rates[5,18]. Although previous studies have not found a strong effect of warming on GPP rates in the European Arctic[13,19], as such the effects of warming and increased CO_2 on primary production could cancel each other, leading to no increase in GPP in warmer, high-CO_2 conditions, signalling a temperature dependence for CO_2 fertilization in Arctic planktonic autotrophs. Nevertheless, the effect of enhanced CO_2 on primary production is probably dependent on the availability of nutrients[20].

To test our hypotheses, we examined *in situ* relationships of GPP, p_{CO_2} and nutrients using data from four oceanographic cruises in the European sector of the Arctic Ocean. We exposed a spring bloom and a summer post-bloom plankton community (inorganic nitrogen: 0.71 and 0.04 μmol N l^{-1} respectively) to increased CO_2 concentrations. In the latter we bubbled CO_2 at concentrations ranging from 145 to 2,099 μatm in three controlled temperature treatments (1, 6 and 10 °C). We exposed the spring community to five fixed CO_2 treatments ranging from 143 to 1,097 μatm over 24 h. We did not include temperature treatments in the spring

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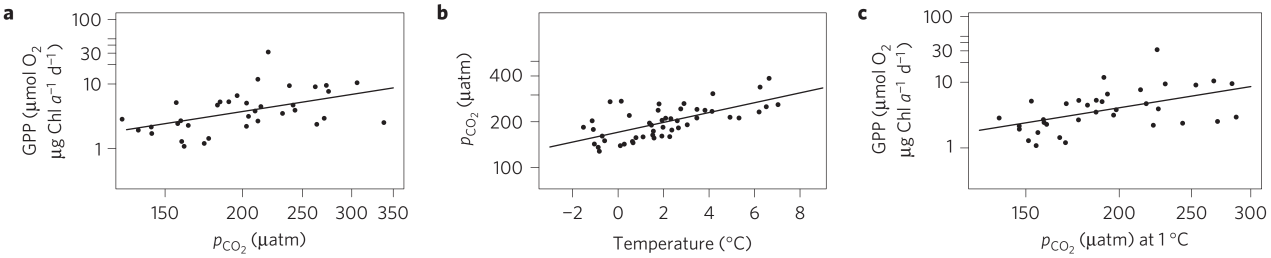

Figure 1 | Gross primary production (GPP) and p_{CO_2} measured during four spring–summer cruises in the European Arctic Ocean. a, GPP increases with p_{CO_2}. **b**, However, p_{CO_2} and temperature (°C) are strongly related in a half-logarithmic relationship. **c**, When p_{CO_2} is standardized to 1 °C (see Supplementary Methods), the power relationship between GPP and p_{CO_2} steepens. In **a–c**, black lines represent significant regression relationships (Supplementary Table 2).

experiment as temperatures in the spring are not expected to change with climate warming as long as sea ice is present. Over the course of the experiments we monitored the evolution of GPP, chlorophyll *a*, nutrients and carbonate system parameters (see Supplementary Table 2).

Examination of *in situ* data revealed that GPP and p_{CO_2} are positively related, with GPP increasing as the 1.50 ± 0.46 power of p_{CO_2} (Fig. 1a and Supplementary Table 1). However, temperature is also strongly positively related with p_{CO_2} (Fig. 1b and Supplementary Table 1), as gases expand with increasing temperature, confounding the relationship of GPP and CO_2 *in situ*. To test for an interaction with temperature we standardized p_{CO_2} to 1 °C, the approximate mean temperature in the data set, so as to remove the thermodynamic effect of temperature from p_{CO_2}. We found a stronger relationship of GPP with p_{CO_2} at 1 °C—increasing as the 1.83 ± 0.54 power of p_{CO_2} (Fig. 1c and Supplementary Table 1)—suggesting that an interaction with temperature blurs the relationship between GPP and p_{CO_2} *in situ*. Whereas GPP and chlorophyll *a* concentration were independent of nutrient concentration ($p > 0.05$, Supplementary Fig. 2), p_{CO_2} showed a strong positive relationship with nutrient concentration (Supplementary Fig. 3), indicating that CO_2 drawdown is directly connected with nutrient uptake. The intercepts of the p_{CO_2}–nutrient relationships (141.9 ± 8.9 and 157.9 ± 8.2 μatm p_{CO_2} for p_{CO_2}–phosphate and p_{CO_2}–nitrate, respectively, Supplementary Fig. 3) indicate a threshold p_{CO_2} of about 150 μatm below which nutrient limitation will preclude GPP from responding to an increase in CO_2.

Controlled temperature treatments with the summer community reveal that GPP increases with p_{CO_2}, but significantly only in the 1 and 6 °C temperature treatments—specifically, GPP increased as the 1.40 ± 0.36 power of p_{CO_2} at 1 °C, almost twice that of the slope at 6 °C (0.87 ± 0.37), whereas no relationship was observed at 10 °C. (Fig. 2a and Supplementary Table 3). Subsequent analysis of covariance revealed that the relationship between GPP and p_{CO_2} was significantly affected by an interaction with temperature, whereas GPP was not significantly affected by temperature alone (Supplementary Table 4). Finally, in the spring experiment GPP doubled from an *in situ* p_{CO_2} of 143 to 225 μatm, whereas fertilization did not increase further beyond this threshold (Fig. 2b and Supplementary Table 5).

The maximum p_{CO_2} and temperature tested exceed the range recorded at present in the European sector of the Arctic, whereas the minimum values tested were above reported minima (45 to 700 μatm p_{CO_2} (ref. 21) and −1.85 to 7 °C (ref. 13)). This is consistent with the intent to explore future scenarios, where warmer, high-CO_2 waters are expected, and highlights the importance of assessing the consistency between results obtained experimentally and those derived from *in situ* empirical relationships. Although experiments may be limited in terms of size and timescales for response as well as their ability to properly mimic environments exposed to multiple, interacting drivers[22], inferences drawn from field surveys are correlative and do not necessarily support mechanistic cause–effect interpretations, as variables may suffer from co-linearity. Integrating both experimental approaches and field observations provides confidence in inferences, and enhances the predictive power of modelled relationships[22].

Comparison of relationships between GPP and p_{CO_2} derived *in situ* and experimentally is, however, confounded by the vast difference in the p_{CO_2} and temperature ranges; the range of p_{CO_2} *in situ* (135–386 μatm) is much narrower than in experiments (143–2,099 μatm), and temperature *in situ* (−1.5–7.0 °C) did not reach 10 °C, the highest experimental temperature. Nonetheless, examination of the consistency of relationships derived *in situ* and experimentally within the same temperature boundaries revealed that *in situ* data indeed fall within the confidence limits of the experimentally derived relationship of GPP and p_{CO_2} (Fig. 3). We did not include spring experimental results in this combined analysis, as GPP was measured using the ^{18}O technique whereas GPP *in situ* and in the summer experiment were measured using the Winkler technique (see Supplementary Methods). The observation that experimental and *in situ* relationships are consistent in both magnitude and direction provides robust evidence of the strong control of CO_2 over primary production in the European sector of the Arctic Ocean when inorganic nutrients are not yet depleted and temperature remains below 6 °C.

Similar to previous research[4], our results demonstrate that CO_2 limits primary production, an idea that has been largely ignored in the past owing to high concentrations of dissolved inorganic carbon relative to other nutrients in the photic layer. Although inorganic carbon in the ocean exists mainly as bicarbonate (HCO_3^-), passive uptake of uncharged CO_2 molecules is generally preferred over uptake of bicarbonate, which requires active transport across membranes and conversion to CO_2 to be used for photosynthesis, an energy-consuming process[23]. Thus it would be expected that increased concentrations of CO_2 would exert a fertilizing effect on marine phytoplankton. Results from the spring experiment indeed suggest that phytoplankton may suffer from CO_2 limitation when p_{CO_2} concentrations in the photic zone are low, as is the case in the marginal ice zone (MIZ) during the spring bloom[11]. Results *in situ*, however, demonstrate that this limitation may act only within a low range of CO_2 concentrations, up to a threshold of about 150 μatm, below which nutrient depletion would outweigh CO_2 limitation. Surface water in the European Arctic in the spring is depleted in CO_2 owing to strong net community production during the bloom[2,13] and freshening by sea-ice melting[10], resulting in the lowest p_{CO_2} values reported anywhere in the ocean[11], with values as low as 135 μatm found in our field survey, and 45 μatm reported in the literature[21].

Results from the summer experiment add the observation that CO_2 limitation of Arctic GPP declines with increasing temperature, suggesting that CO_2 limitation is particularly acute at low temperatures. This finding is in agreement with recent experiments using cultured diatoms[24], and can be explained by the rapid increase

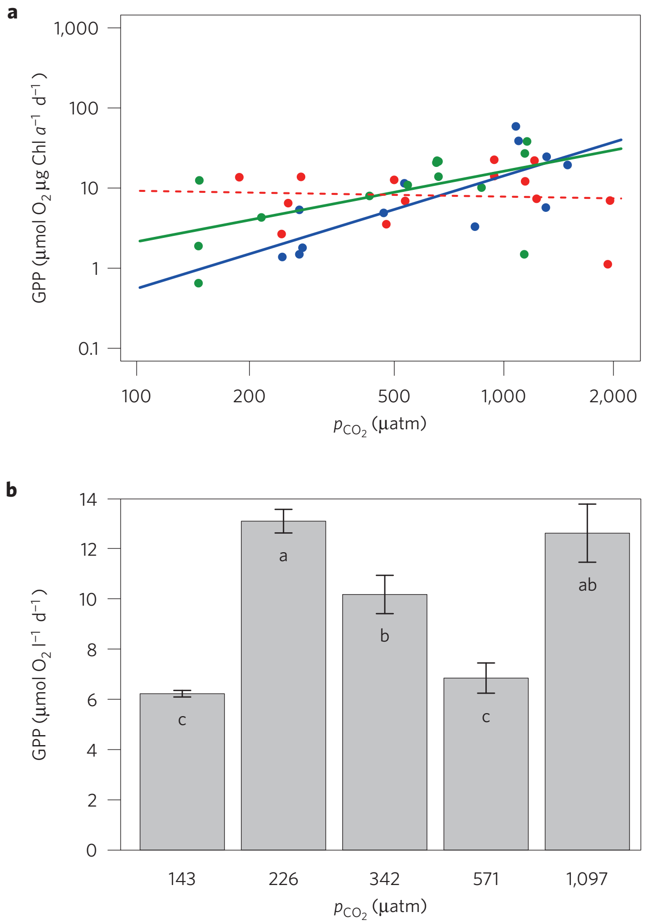

Figure 2 | GPP and p_{CO_2} measured during controlled temperature experiments. a, Power relationships of GPP and p_{CO_2} across the experimental range. Blue, green and red points represent 1, 6 and 10 °C temperature treatments, respectively. Solid lines represent significant regression relationships ($p > 0.05$) and dashed lines non-significant trends for respective temperature treatments (for regression parameters and R^2 see Supplementary Table 3). **b**, GPP in spring bloom experiment increases compared to control 143 μatm treatment in all treatments besides 571 μatm. Letters inside bars indicate groups that are significantly different according to a Tukey's HSD *post hoc* test.

in seawater density across the range (−1 to 7 °C) present in Arctic waters—as increasing density at low temperature leads to reduced diffusion rates of limiting substrates, enhancing resource limitation of planktonic osmotrophs[25]. Although focused on bacteria, the Pomeroy–Wiebe hypothesis[25] argues that polar osmotrophs require higher resource concentrations owing to reduced diffusion rates at low temperature and decreased fluidity over the cell membrane, causing a reduced affinity for substrates. Hence, CO$_2$ limitation of primary production is, as observed here, expected to be highest at low p_{CO_2} and low temperatures.

In this study, both *in situ* and experimental results point to a temperature dependence of CO$_2$ fertilization on planktonic primary production in the European Arctic. In particular, our results imply that increasing CO$_2$ concentrations will have a fertilizing effect on primary producers when nutrients are available and p_{CO_2} is limiting, but that effect will decline with increasing temperature. During spring in the MIZ, density changes stabilize the water column as sea ice melts, allowing nutrient-replete conditions conducive to forming phytoplankton blooms and resulting in mass CO$_2$ drawdown in the surface layers. According to our results, with just a moderate 83 μatm increase in p_{CO_2} in the MIZ during the spring, the rate of GPP (in μmol O$_2$ d^{-1}) could as much as double, intensifying the bloom and leading to enhanced vertical export. During summer, when regenerated production and heterotrophic communities dominate in the MIZ, CO$_2$ fertilization may only affect areas where nutrients are still available and temperatures remain below 6 °C, increasing primary production at a rate between 0.9 and 1.4 μmol O$_2$ μg Chl a^{-1} d^{-1} per μatm CO$_2$; at least, until increasing temperatures due to climate warming reduce any fertilization effect. In the annually ice-free ocean, characterized by high primary productivity due to extensive vertical mixing and light availability, warming will probably entirely preclude any fertilizing effect of increased CO$_2$ on primary productivity. Thus, the area prone to a CO$_2$ fertilization response will probably be restricted to the MIZ, which will migrate polewards, following the ice edge, to occupy a diminishing fraction of the Arctic Ocean with climate warming and be replaced by an annually ice-free ocean[26,27]. Furthermore, CO$_2$ limitation is unlikely to affect the southern sector of the European Arctic owing to the invasion of the Arctic by increasingly warmer and CO$_2$-rich Atlantic waters through the two-branched inflow of Atlantic Water along the Barents Sea and the Fram Strait[28].

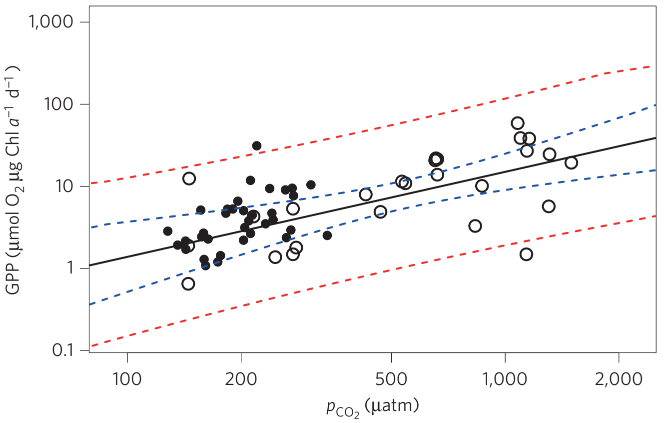

Figure 3 | Combined GPP and p_{CO_2} of both experiments and spring–summer cruises. Power relationship of combined *in situ* (filled circles) and experimental (open circles) GPP and *in situ* and experimental p_{CO_2} values. Solid line represents the relationship of the experimental data from the 1 and 6 °C temperature treatments (GPP $= -4.44(\pm 1.64) * p_{CO_2}{}^{1.04(\pm 0.26)}$; $R^2 = 0.40$; $p = 0.0005$) and the dashed blue and red curves represent the 95% confidence limits for the regression equation and regression estimates, respectively.

Although our study conducted in the European sector of the Arctic cannot be readily extrapolated to other regions, this region is responsible for approximately 50% of annual Arctic Ocean production[7], with a spring bloom estimated to account for about 26% of the annual primary production in the European Arctic and a productive season that lasts well into August[13]. Consequently, elevated CO$_2$ derived from increasing atmospheric concentrations of CO$_2$ which propels an increase in GPP at low temperatures during the late stages of the bloom may have a key impact on the entire ecosystem and carbon budget, with feedback effects not yet considered in future scenarios of the Arctic.

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Author contributions

C.M.D., J.M.A., I.E.H., M.S.-M., M.R., P.W. and S.A. were responsible for experimental design. J.M.A. led and oversaw the summer experiment. M.S.-M. was responsible for running the spring experiment. M.C. was responsible for carbonate system measurements during the spring 2014 experiment and cruise, and E.M. and A.D. were responsible for ^{18}O measurements. L.S.G.-C., M.S.-M. and A.R.-d.-G. contributed metabolism data from oceanographic cruises. J.M.H. was responsible for running the summer experiment as well as all data analysis and writing of the manuscript. All authors, especially C.M.D., contributed to the writing and editing of the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.M.H.

Competing financial interests

The authors declare no competing financial interests.