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Temperature dependence of CO2-enhanced primary production in the European Arctic Ocean

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Abstract :

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 CO2 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 CO2 on primary production in the Arctic has not been conducted. Here we test the expectation that CO2-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 CO2 enhances GPP (by a factor of up to ten) over a range of 145-2,099 mu atm; 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 CO2-enhanced primary production has significant implications for metabolic balance in a warmer, CO2-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 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 and uptake from the atmosphere into surface waters with already low $p\mathrm{CO}_2$ [9]▪ , and ice-melt introduces freshwater with low alkalinity and dissolved inorganic carbon further lowering 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), pCO_2 varies seasonally more than 200 µatm, with values as low as 100 µatm in spring months[11] due 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 favor 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 currently consider (e.g.[3,14]▪).

Predicting future primary production in a changing Arctic is not straightforward; models diverge strongly on their predictions depending on the region and drivers for change (i.e. sea ice, light, nutrients, warming, etc.)[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 likely species-specific due to varying efficiencies of cellular carbon concentration mechanisms[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. Based on 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 likely dependant on the availability of nutrients[20].

In order to test our hypotheses, we examined *in situ* relationships of GPP, pCO_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 later we bubbled CO_2 at concentrations ranging from 145 to 2099 µatm in three-controlled temperature treatments (1, 6, & 10ºC). We exposed the spring community to 5 fixed CO_2 treatments ranging from 143 to 1097 µatm over 24 hours. We did not include temperature treatments in spring 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 S2).

Examination of *in situ* data revealed that GPP and pCO_2 are positively related, with GPP increasing at the 1.50 ± 0.46 power of pCO_2 (Figure 1a; Supplementary Table S1). However, temperature is also strongly related with pCO_2 (Figure 1b; Supplementary Table S1), as CO_2 is more soluble at higher temperatures, confounding the relationship of GPP and CO_2 *in situ*. To test for an interaction we with temperature we standardized

pCO_2 to 1ºC, the approximate mean temperature in the data set, so as to remove the thermodynamic effect of temperature from pCO_2. We found a stronger relationship of GPP with pCO_2 at 1ºC—increasing at 1.83 ± 0.54 power of pCO_2 (Figure 1c; Supplementary Table S1)—suggesting that an interaction with temperature blurs the relationship between GPP and pCO_2 *in situ*. Whereas GPP and chlorophyll *a* concentration were independent of nutrient concentration ($p > 0.05$, Supplementary Figure S2), pCO_2 showed a strong positive relationship with nutrient concentrations (Supplementary Figure S3), illustrating that CO_2 drawdown is directly connected with nutrient uptake. The intercepts of the pCO_2-nutrient relationships (141.9 ±8.9 and 157.9 ±8.2 µatm pCO_2 for pCO_2-phosphate and pCO_2-nitrate, respectively, Supplementary Figure S3) indicate a threshold pCO_2 of about 150 µatm below which nutrient limitation will preclude GPP from responding to CO_2 increase.

Controlled temperature treatments with the summer community reveal that GPP increases with pCO_2, but only significantly in the 1 and 6ºC temperature treatments specifically, GPP increased as the 1.40 ± 0.36 power of pCO_2 at 1ºC, almost twice that of the slope at 6ºC (0.87 ± 0.37), while no relationship was observed at 10ºC. (Figure 2a; Supplementary Table S3). Subsequent analysis of covariance revealed that the relationship between GPP and pCO_2 was significantly affected by an interaction with temperature, whereas GPP was not significantly affected by temperature alone (Supplementary Table S4). Finally, in the spring experiment GPP doubled from an *in situ* pCO_2 of 143 to 225 µatm. While fertilization did not increase further beyond this threshold (Figure 2b, Supplementary Table S5), The maximum $p\mathrm{CO}_2$ and temperature tested exceed the range currently recorded in the European sector of the Arctic, while the minimum values tested were above reported minima (45 to 700 µatm $p\mathrm{CO}_2$ [21] and −1.85 to 7 ºC [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 with those derived from *in situ* empirical relationships. While experiments may be limited in terms of size and time scales 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 predictive power of modelled relationships[22].

Comparison of relationships between GPP and $p\mathrm{CO}_2$ derived *in situ* and experimentally is, however, confounded by the vast difference in the $p\mathrm{CO}_2$ and temperature ranges; the range of $p\mathrm{CO}_2$ *in situ* (135-386 µatm) is much narrower than in experiments (143-2099 µatm), and temperature *in situ* (–1.5-7.0 ºC) did not reach 10ºC, 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 falls within the confidence limits of the experimentally-derived relationship of GPP and $p\mathrm{CO}_2$ (Figure 3). We did not include spring experimental results in this combined analysis as GPP was measured using the ^{18}O technique while 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 Arctic Ocean when inorganic nutrients are not yet depleted and temperature remains below 6 ºC.

Similar to previous research[4]▪, our results demonstrate that CO_2 limits primary production, an idea that has been largely ignored in the past due 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 pCO_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 only act within a low range of CO_2 concentrations until 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 deplete in CO_2 due to strong net community production during the bloom[2,13]▪ and freshening by sea-ice melting[10]▪, resulting in the lowest pCO_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 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 in seawater density across the range (-1ºC to 7ºC) 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 due 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 $p\mathrm{CO_2}$ 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 $p\mathrm{CO_2}$ limiting, but that effect will decline with increasing temperature. During spring in the Marginal Ice Zone (MIZ) density changes stabilize the water column as sea ice melts, allowing for nutrient replete conditions conducive to forming phytoplankton blooms resulting in mass CO_2 drawdown in the surface layers. According to our results, with just a moderate 83 µatm increase in $p\mathrm{CO_2}$ in the MIZ during the spring, the rate of GPP (in µmol O_2 day^{-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 6ºC, increasing primary production at a rate between 0.9 and 1.4 µmol O_2 µg Chl a^{-1} day^{-1} per µatm CO_2. That is until increasing temperatures due to climate warming reduces any fertilization effect. In the annually ice-free ocean, characterized by high primary productivity due to extensive vertical mixing and light availability, warming will likely preclude any fertilizing effect of increased CO_2 on primary productivity all together. Thus, the area prone to a CO_2 fertilization response will likely be restricted to the MIZ, which will migrate poleward, 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 due 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 Barrents Sea and the Fram Strait[28].

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

Competing financial interests

Authors declare no competing interests as defined by Nature Publishing Group, or other interests that might be perceived to influence the results and/or discussion reported in this article

Figure legends

Figure 1. Gross primary production (GPP; µmol O_2 µg Chl a^{-1} day^{-1}) and pCO$_2$ (µatm) measured during four spring-summer cruises in the European Arctic Ocean. GPP increases with pCO$_2$ (a). However, pCO$_2$ and temperature (ºC) are strongly related in a half-logarithmic relationship (b). When pCO$_2$ is standardized to 1ºC (See Supplementary Methods), the power relationship between GPP and pCO$_2$ steepens (c). Black lines represent significant regression relationships (Supplementary Table 2).

Figure 2. Power relationships of gross primary production (GPP; µmol O_2 µg Chl a^{-1} day^{-1}) and pCO$_2$ (µatm) across the experimental range (a). Blue, green, and red points represent 1, 6, and 10ºC 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 S3). GPP (µmol O_2 µg Chl a^{-1} day^{-1}) in spring bloom experiment increases compared to control 143 µatm treatment in all treatments besides 571 µatm (b). Letters inside bars indicate groups that are significantly different according to a Tukey's HSD post hoc test.

Figure 3. Power relationship of combined *in situ* (●) and experimental (○) gross primary production (GPP; µmol O_2 µg Chl a^{-1} day^{-1}) and *in situ* and experimental pCO$_2$ (µatm) values. Solid line represents the relationship of the experimental data from the1ºC and 6ºC temperature treatments (GPP= $-4.44(\pm1.64) * p\mathrm{CO}_2^{1.04(\pm0.26)}$; $R^2= 0.40$; p=0.0005),

and the dashed blue and red curves represent the 95 % confidence limits for the regression equation and regression estimates, respectively.

Figure 1

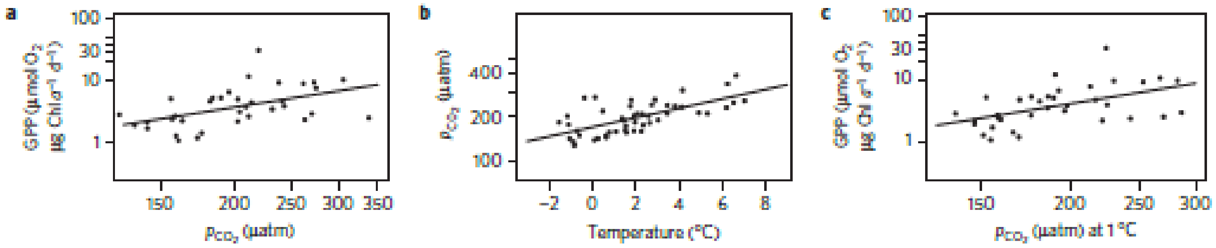


Figure 2

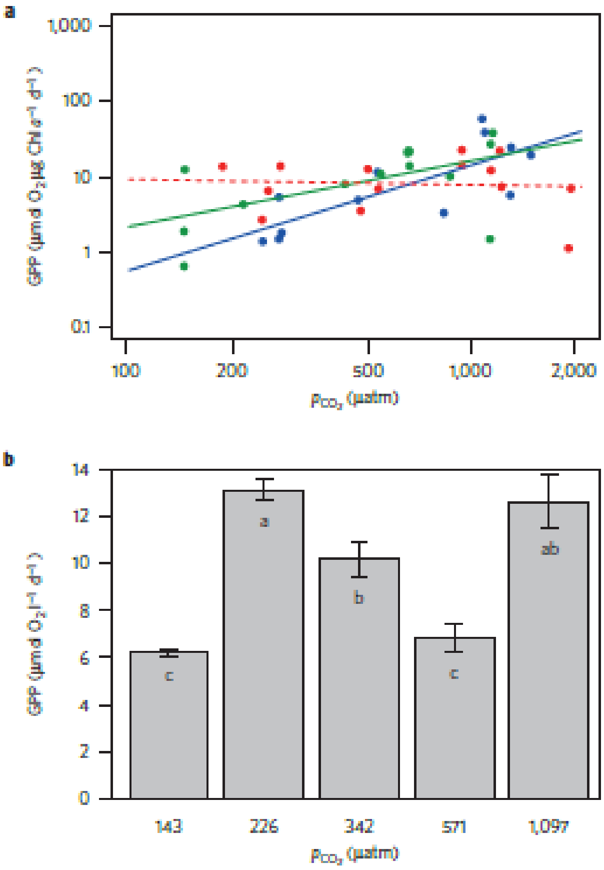
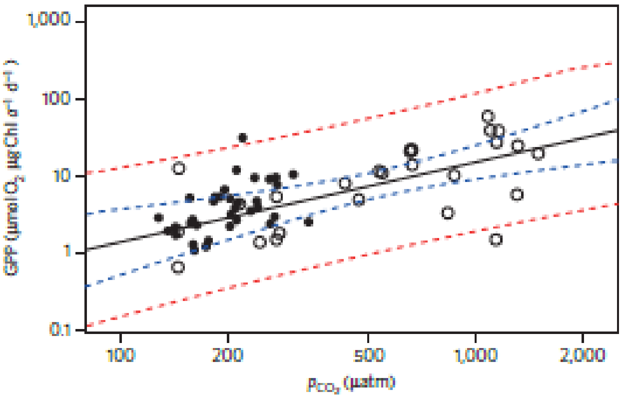


Figure 3


GPP (μmol O$_2$ μg Chl a^{-1} d^{-1})
1,000
100
10
1
0.1
100
200
500
1,000
2,000
p_{CO_2} (μatm)