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

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The Arctic Ocean is warming at 2-3 times the global rate¹ and is perceived to be a bellwether for ocean acidification^{2,3}. Increased CO₂ concentrations are expected to have a fertilization effect on marine autotrophs⁴, and higher temperatures should lead to increased rates of planktonic primary production⁵. 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 (up to 10-fold) over a range of 145-2099 μ 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 future warmer, CO₂-enriched Arctic Ocean, in particular, it predicts a two-fold increase in primary production during the spring in the Arctic.

Primary production in the Arctic Ocean supports significant fisheries⁶ and renders it an important sink for anthropogenic carbon², 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 production⁷. 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 CO₂ exchange causing and uptake from the atmosphere into surface waters with already low p CO₂⁹, and ice-melt introduces freshwater with low alkalinity and dissolved inorganic carbon further lowering carbon content of surface

48 waters¹⁰. The surface waters of the Arctic Ocean are largely undersaturated with respect
49 to CO₂ throughout spring and summer². In the European sector of the Arctic Ocean
50 (Barents-Greenland Sea/Fram Strait), *p*CO₂ varies seasonally more than 200 μatm, with
51 values as low as 100 μatm in spring months¹¹ due to strong net community production
52 associated with the spring bloom of ice algae followed by that of planktonic algae in open
53 waters^{12,13}. Hence, increased CO₂ may stimulate primary production during spring and
54 favor a greater CO₂ sinking capacity in the future^{2,9} resulting in a feedback between
55 increased CO₂ and primary production, which biogeochemical models do not currently
56 consider (e.g.^{3,14}).

57 Predicting future primary production in a changing Arctic is not straightforward;
58 models diverge strongly on their predictions depending on the region and drivers for
59 change (i.e. sea ice, light, nutrients, warming, etc.)¹⁵, and modelling studies including
60 rising CO₂ concentrations are rare¹⁵. Experimental research from the European Arctic
61 suggests that increasing CO₂ concentrations enhance primary production in nutrient
62 replete conditions¹⁶, although this response is likely species-specific due to varying
63 efficiencies of cellular carbon concentration mechanisms¹⁷. However, the response to
64 increased CO₂ when combined with warming may deviate from the expected additive
65 effect.

66 Here we seek to determine if there is an interaction of increased CO₂
67 concentration and temperature on planktonic GPP throughout the spring and summer in
68 the European Arctic region. Based on metabolic theory, we would expect a positive effect
69 of both warming and higher CO₂ (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 CO₂ on primary production could cancel each other leading to no increase in GPP in warmer, high-CO₂ conditions, signalling a temperature dependence for CO₂ fertilization in Arctic planktonic autotrophs. Nevertheless, the effect of enhanced CO₂ on primary production is likely dependant on the availability of nutrients²⁰.

In order to test our hypotheses, we examined *in situ* relationships of GPP, *p*CO₂, 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 CO₂ concentrations. In the later we bubbled CO₂ at concentrations ranging from 145 to 2099 μatm in three-controlled temperature treatments (1, 6, & 10°C). We exposed the spring community to 5 fixed CO₂ 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 *p*CO₂ are positively related, with GPP increasing at the 1.50 ± 0.46 power of *p*CO₂ (Figure 1a; Supplementary Table S1). However, temperature is also strongly related with *p*CO₂ (Figure 1b; Supplementary Table S1), as CO₂ is more soluble at higher temperatures, confounding the relationship of GPP and CO₂ *in situ*. To test for an interaction we with temperature we standardized

$p\text{CO}_2$ to 1°C, the approximate mean temperature in the data set, so as to remove the thermodynamic effect of temperature from $p\text{CO}_2$. We found a stronger relationship of GPP with $p\text{CO}_2$ at 1°C—increasing at 1.83 ± 0.54 power of $p\text{CO}_2$ (Figure 1c; Supplementary Table S1)—suggesting that an interaction with temperature blurs the relationship between GPP and $p\text{CO}_2$ *in situ*. Whereas GPP and chlorophyll *a* concentration were independent of nutrient concentration ($p > 0.05$, Supplementary Figure S2), $p\text{CO}_2$ 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 $p\text{CO}_2$ -nutrient relationships (141.9 ± 8.9 and 157.9 ± 8.2 $\mu\text{atm } p\text{CO}_2$ for $p\text{CO}_2$ -phosphate and $p\text{CO}_2$ -nitrate, respectively, Supplementary Figure S3) indicate a threshold $p\text{CO}_2$ 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 $p\text{CO}_2$, but only significantly in the 1 and 6°C temperature treatments specifically, GPP increased as the 1.40 ± 0.36 power of $p\text{CO}_2$ at 1°C, almost twice that of the slope at 6°C (0.87 ± 0.37), while no relationship was observed at 10°C. (Figure 2a; Supplementary Table S3). Subsequent analysis of covariance revealed that the relationship between GPP and $p\text{CO}_2$ 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* $p\text{CO}_2$ of 143 to 225 μatm . While fertilization did not increase further beyond this threshold (Figure 2b, Supplementary Table S5),

The maximum $p\text{CO}_2$ 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 $\mu\text{atm } p\text{CO}_2$ ²¹ and -1.85 to 7°C 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 drivers²², 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 relationships²².

Comparison of relationships between GPP and $p\text{CO}_2$ derived *in situ* and experimentally is, however, confounded by the vast difference in the $p\text{CO}_2$ and temperature ranges; the range of $p\text{CO}_2$ *in situ* (135-386 μatm) is much narrower than in experiments (143-2099 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 falls within the confidence limits of the experimentally-derived relationship of GPP and $p\text{CO}_2$ (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 CO₂ over primary production in the European Arctic Ocean when inorganic nutrients are not yet depleted and temperature remains below 6 °C.

Similar to previous research⁴, our results demonstrate that CO₂ 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 (HCO₃⁻), passive uptake of uncharged CO₂ molecules is generally preferred over uptake of bicarbonate, which requires active transport across membranes and conversion to CO₂ to be used for photosynthesis, an energy consuming process²³. Thus it would be expected that increased concentrations of CO₂ would exert a fertilizing effect on marine phytoplankton. Results from the spring experiment indeed suggest that phytoplankton may suffer from CO₂ limitation when *p*CO₂ concentrations in the photic zone are low, as is the case in the marginal ice zone (MIZ) during the spring bloom¹¹. Results *in situ* however, demonstrate that this limitation may only act within a low range of CO₂ concentrations until a threshold of about 150 µatm, below which nutrient depletion would outweigh CO₂ limitation. Surface water in the European Arctic in the spring is depleted in CO₂ due to strong net community production during the bloom^{2,13} and freshening by sea-ice melting¹⁰, resulting in the lowest *p*CO₂ values reported anywhere in the ocean¹¹, with values as low as 135 µatm found in our field survey, and 45 µatm reported in the literature²¹.

158 Results from the summer experiment add that CO₂ limitation of Arctic GPP
159 declines with increasing temperature, suggesting that CO₂ limitation is particularly acute
160 at low temperatures. This finding is in agreement with recent experiments using cultured
161 diatoms²⁴, and can be explained by the rapid increase in seawater density across the
162 range (-1°C to 7°C) present in Arctic waters, as increasing density at low temperature
163 leads to reduced diffusion rates of limiting substrates, enhancing resource limitation of
164 planktonic osmotrophs²⁵. Although focused on bacteria, the Pomeroy-Wiebe
165 hypothesis²⁵, argues that polar osmotrophs require higher resource concentrations due to
166 reduced diffusion rates at low temperature and decreased fluidity over the cell membrane
167 causing a reduced affinity for substrates. Hence, CO₂ limitation of primary production is,
168 as observed here, expected to be highest at low pCO₂ and low temperatures.

169 In this study, both *in situ* and experimental results point to a temperature-
170 dependence of CO₂-fertilization on planktonic primary production in the European
171 Arctic. In particular, our results imply that increasing CO₂ concentrations will have a
172 fertilizing effect on primary producers when nutrients are available and pCO₂ limiting,
173 but that effect will decline with increasing temperature. During spring in the Marginal Ice
174 Zone (MIZ) density changes stabilize the water column as sea ice melts, allowing for
175 nutrient replete conditions conducive to forming phytoplankton blooms resulting in mass
176 CO₂ drawdown in the surface layers. According to our results, with just a moderate 83
177 µatm increase in pCO₂ in the MIZ during the spring, the rate of GPP (in µmol O₂ day⁻¹)
178 could as much as double, intensifying the bloom and leading to enhanced vertical export.
179 During summer, when regenerated production and heterotrophic communities dominate
180 in the MIZ, CO₂ 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 $\mu\text{mol O}_2 \mu\text{g Chl } a^{-1} \text{ day}^{-1}$ per $\mu\text{atm CO}_2$. 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 Strait²⁸.

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 production⁷ 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 August¹³. 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., J.A., 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; $\mu\text{mol O}_2 \mu\text{g Chl } a^{-1} \text{ day}^{-1}$) and $p\text{CO}_2$ (μatm) measured during four spring-summer cruises in the European Arctic Ocean. GPP increases with $p\text{CO}_2$ (a). However, $p\text{CO}_2$ and temperature ($^{\circ}\text{C}$) are strongly related in a half-logarithmic relationship (b). When $p\text{CO}_2$ is standardized to 1°C (See Supplementary Methods), the power relationship between GPP and $p\text{CO}_2$ steepens (c). Black lines represent significant regression relationships (Supplementary Table 2).

Figure 2. Power relationships of gross primary production (GPP; $\mu\text{mol O}_2 \mu\text{g Chl } a^{-1} \text{ day}^{-1}$) and $p\text{CO}_2$ (μatm) across the experimental range (a). 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 S3). GPP ($\mu\text{mol O}_2 \mu\text{g Chl } a^{-1} \text{ day}^{-1}$) in spring bloom experiment increases compared to control $143 \mu\text{atm}$ treatment in all treatments besides $571 \mu\text{atm}$ (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* ($\bullet$) and experimental ($\circ$) gross primary production (GPP; $\mu\text{mol O}_2 \mu\text{g Chl } a^{-1} \text{ day}^{-1}$) and *in situ* and experimental $p\text{CO}_2$ (μatm) values. Solid line represents the relationship of the experimental data from the 1°C and 6°C temperature treatments ($\text{GPP} = -4.44(\pm 1.64) * p\text{CO}_2^{1.04(\pm 0.26)}$; $R^2 = 0.40$; $p = 0.0005$),

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

325