

# Geophysical Research Letters<sup>®</sup>

## RESEARCH LETTER

10.1029/2024GL110065

## An Impact of Cobalt on Freshwater Phytoplankton in Warming Polar Regions?



### Key Points:

- Concentrations of macro- and micro-nutrients in a selection of Greenland and Antarctic lakes indicated cobalt deficiency for phytoplankton
- Bioassay incubation results showed cobalt potentially co-limited phytoplankton in three of the eight sites tested
- A time-series of measurements in Greenland runoff suggested high manganese:cobalt and zinc:cobalt ratios could impede cellular cobalt acquisition

### Supporting Information:

Supporting Information may be found in the online version of this article.

### Correspondence to:

K. Zhu and M. J. Hopwood,  
[Zhuke@sustech.edu.cn](mailto:Zhuke@sustech.edu.cn);  
[mark@sustech.edu.cn](mailto:mark@sustech.edu.cn)

### Citation:

Zhu, K., Krause, J., Marín-Arias, C., Mestre, M., Höfer, J., Browning, T. J., et al. (2024). An impact of cobalt on freshwater phytoplankton in warming polar regions? *Geophysical Research Letters*, 51, e2024GL110065. <https://doi.org/10.1029/2024GL110065>

Received 5 MAY 2024

Accepted 18 OCT 2024

### Author Contributions:

**Conceptualization:** Mark J. Hopwood

**Formal analysis:** Kechen Zhu

**Funding acquisition:** Mark J. Hopwood

**Investigation:** Kechen Zhu, Jana Krause, Camila Marín-Arias, Mireia Mestre, Juan Höfer, Thomas J. Browning, Eric P. Achterberg, Mark J. Hopwood

**Visualization:** Kechen Zhu

**Writing – original draft:** Kechen Zhu, Mark J. Hopwood

**Writing – review & editing:** Kechen Zhu, Jana Krause, Camila Marín-Arias, Mireia Mestre, Juan Höfer, Thomas J. Browning, Eric P. Achterberg, Mark J. Hopwood

© 2024. The Author(s).

This is an open access article under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Kechen Zhu<sup>1,2</sup> , Jana Krause<sup>2</sup>, Camila Marín-Arias<sup>3,4,5</sup>, Mireia Mestre<sup>5,6,7</sup>, Juan Höfer<sup>4,5</sup> , Thomas J. Browning<sup>2</sup> , Eric P. Achterberg<sup>2</sup> , and Mark J. Hopwood<sup>1</sup> 

<sup>1</sup>Department of Ocean Science and Engineering, Southern University of Science and Technology, Shenzhen, China,

<sup>2</sup>GEOMAR Helmholtz Center for Ocean Research Kiel, Kiel, Germany, <sup>3</sup>Programa de magíster en oceanografía, Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile, <sup>4</sup>Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile, <sup>5</sup>Centro FONDAP de investigación en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Valdivia, Chile, <sup>6</sup>Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain, <sup>7</sup>Centro de Investigación Oceanográfica COPAS COASTAL, Universidad de Concepción, Concepción, Chile

**Abstract** Polar freshwater ecosystems are sensitive to climate change, facing increasing temperatures and its consequences such as glacier retreat. Phosphorus and/or fixed nitrogen are widely expected to limit primary production in most freshwater environments, however the role of micronutrients is largely un-characterized. We measured dissolved nitrate and nitrite, phosphate, cobalt, iron, manganese and zinc in a selection of Greenland and Antarctic lakes, and report the first evaluation of cobalt regulating phytoplankton growth in these systems using bioassay incubations. Results showed cobalt potentially co-limited phytoplankton in three of the eight sites tested. A time-series of dissolved cobalt measured in Kobbefjord (southwest Greenland) runoff corroborated low cobalt availability during summer. This was in contrast to manganese and iron which remained at high concentrations throughout summer. We hypothesize that high manganese:cobalt and/or zinc:cobalt ratios in runoff, may impede cellular cobalt acquisition, meaning cobalt co-limitation of primary production is plausible in many polar freshwater environments.

**Plain Language Summary** Primary production in aquatic environments relies on supplies of bio-accessible nitrogen and phosphorus in addition to light availability. Glacier melt and permafrost degradation have accelerated worldwide over the past two decades, inducing changes in these resources with ensuing ecological impacts. The potential ecological role of bio-essential metals such as cobalt has however been sparsely tested in polar aquatic environments. Here we conducted nutrient addition bioassay incubations in a selection of Greenland and Antarctic lakes, and found phytoplankton growth was potentially co-limited by dissolved cobalt availability in three of the eight tested sites. Manganese, zinc and cobalt can compete for cellular uptake, therefore we further analyzed dissolved concentrations in runoff across a multi-year time-series, finding that the ratios of these elements are potentially conducive to inhibition of cobalt uptake. We hypothesize that cobalt may more broadly co-limit aquatic primary production as a result of high manganese:cobalt and/or zinc:cobalt ratios, with potential impacts on microbial community composition.

## 1. Introduction

Seasonal growth of phytoplankton in most aquatic environments is moderated by a range of “bottom-up” factors including the availability of light and the elements nitrogen (N) and phosphorus (P). Polar freshwater ecosystems are commonly oligotrophic with low temperature and extreme seasonal light availability contrasting the polar summer and the polar night. N-, P- and/or light limitation of phytoplankton growth is often evident (Burpee et al., 2016; Olgun et al., 2024, see also Table S1 in Supporting Information S1). These climatically sensitive environments are experiencing rapid changes in the availability of these resources which may induce far-reaching biogeochemical feedbacks. Runoff from the world's ice sheets and glaciers has increased regionally since the 1980s (Bliss et al., 2014; Davison et al., 2024; Mankoff et al., 2020). As glaciers retreat inland, the development of lake systems moderates the downstream propagation of sediment and the dissolved constituents of meltwater (Anderson et al., 2017; Prater et al., 2022). Whilst chemical fluxes associated with transforming ice melt and glacier runoff are relatively well studied (Bhatia et al., 2021; Wadham et al., 2019), uncertainties remain concerning what bottom-up controls regulate phytoplankton growth at the interface between the cryosphere and other downstream aquatic environments (Burpee et al., 2018).

Freshwater lakes located in both Greenland and the Antarctic Peninsula have a short annual ice-free period, and limited exchanges of nutrients and organic matter with the surrounding environment. As aquatic environments where snow and ice melt may constitute a major source of external nutrients on annual timescales (Burpee et al., 2018), they represent interesting environments to test the proximal limiting factors for phytoplankton growth. The increasing duration of the ice-free summer period has enhanced exchange of atmospheric CO<sub>2</sub>, elevated temperature, and increased nutrient influx and primary productivity in lakes in the Antarctic (Choudhary et al., 2018a, 2018b). Around Greenland, higher turbidity combined with the influence of modest labile phosphorus and organic carbon inputs is thought to be a major driver of ecological dynamics in meltwater affected lakes (Burpee et al., 2018). A recent study using phytoplankton and macro- and micro-nutrient data from a range of freshwater environments indicated P-limitation in the lakes, ponds, and streams of King George Island (Antarctica) where the local phytoplankton community was dominated by pennate diatoms (Olgun et al., 2024). Similarly, P-limitation has been implicated as the proximal limiting nutrient in lakes across western Greenland during summer where the ambient phytoplankton community was dominated by small chrysophytes (Brutemark et al., 2006; Burpee et al., 2016; Whiteford et al., 2016). Whilst the role of P- and N- as proximal limiting factors for phytoplankton growth in aquatic environments has been well tested (Harpole et al., 2011), the role of micronutrients as potential limiting factors for phytoplankton growth has hardly been assessed in these environments because it is generally assumed micronutrient concentrations are replete in freshwater.

Cobalt (Co) is a bio-essential metal which, among other cellular functions, acts as a cofactor in vitamin B<sub>12</sub> (B<sub>12</sub>, Table S2 in Supporting Information S1), also called cobalamin. Whilst B<sub>12</sub> is an obligate nutrient for many phytoplankton, it is synthesized only by some bacteria and archaea, often leading to symbiotic relationships (Croft et al., 2005). The concentrations of dissolved Co (dCo) itself may be very low in some polar freshwater environments due to scavenging of dCo by high loads of iron (Fe) and manganese (Mn) oxides (Poulton & Raiswell, 2005; van Genuchten et al., 2022). Precipitation of dFe as oxyhydroxides is known to be a significant sink for phosphate in boreal lake environments (Norton et al., 2011). With both Mn and Fe oxides having a high scavenging capacity for dCo, a similar sink may exist for Co (Lienemann et al., 1997). Furthermore, other metals, particularly zinc (Zn) and Mn, can interfere with cellular dCo acquisition (Hawco & Saito, 2018). Therefore, environments with high ratios of dissolved Zn or Mn relative to dCo could be problematic for phytoplankton with absolute Co requirements. Whilst sparse measurements are available to date, glacier runoff does appear to have both high dissolved Zn:Co and high Mn:Co ratios (Hawkings et al., 2020; Mitchell et al., 2001).

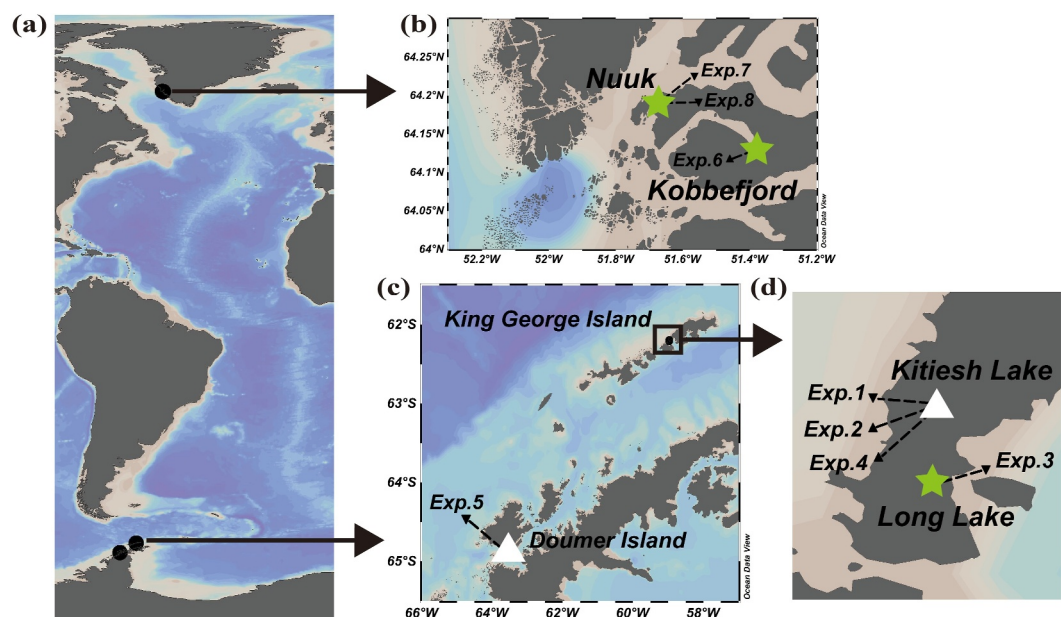
In order to investigate the potential “bottom-up” factors regulating phytoplankton growth in polar aquatic environments, we here measured dissolved nitrate and nitrite (NO<sub>3</sub> + NO<sub>2</sub>, hereafter referred to as simply as nitrate), phosphate (PO<sub>4</sub>), Co, Fe, Mn and Zn concentrations in two contrasting polar regions; southwest Greenland (SW Greenland) and the Western Antarctic Peninsula (WAP). In both regions, we conducted nutrient addition bioassay experiments to test the effects of increased macronutrient (N and P), and micronutrient (Co, Fe and Mn) availability on phytoplankton in a broad selection of proglacial lakes and streams. Herein “phytoplankton” are defined as filtered cells containing chlorophyll a (Chl a), which we use to assess the response in bioassay incubation experiments. A further analysis of dissolved trace metals collected in runoff from Kobbefjord (SW Greenland) was used to improve our understanding of the underlying processes potentially affecting dCo availability through the growth season.

## 2. Materials and Methods

Macro- and micro-nutrient samples, and freshwater for nutrient bioassay incubation experiments, were collected from the surface of three lakes (in Kobbefjord and Nuuk) in SW Greenland in boreal autumn 2019; from Kitiash Lake on King George Island and one stream on Doumer Island in austral spring 2020; and from two lakes (Kitiash Lake and Long Lake) and one stream on King George Island in austral spring 2022 (see Figure 1, Table 1 and S3 in Supporting Information S1).

### 2.1. Determinations of Macro- and Micro-Nutrients

Dissolved macronutrient samples (nitrate and phosphate) were syringe filtered (Millipore, 0.22 μm, polyvinyl difluoride) and stored refrigerated in the dark until analysis. Samples that could not be analyzed within 2 days



**Figure 1.** Map of nutrient bioassay experiments conducted in southwest Greenland and the West Antarctic Peninsula, generated in Ocean Data View (Schlitzer, 2023). Sampling sites are presented with bioassay incubation results for southwest Greenland (panel b), Doumer Island (panel c) and King George Island (panel c, d). Green stars indicate sites of potential cobalt (co-/serial) limitation and white triangles indicate no effect of either cobalt or vitamin B<sub>12</sub> supply.

**Table 1**

Measured Freshwater Samples at the Nutrient Bioassay Sites in Southwest (SW) Greenland and the West Antarctic Peninsula (WAP)

Experiment	1	2	3	4*	5	6	7	8
	Western Antarctic Peninsula				southwestern Greenland			
Sites	Stream, Kitiesh Lake	Kitiesh Lake	Long Lake	Kitiesh Lake	Stream, Doumer Island	Lake, Kobbefjord	Lake 1, Nuuk	Lake 2, Nuuk
Long°E	-62.19	-62.19	-62.21	-62.19	-64.88	64.13	64.18	64.19
Lat°N	-58.97	-58.97	-58.97	-58.97	-63.58	51.39	51.66	51.67
Date	11/18 2022	11/26 2022	12/04 2022	01/10 2020	01/03 2020	08/16 2019	08/29 2019	09/02 2019
NO <sub>x</sub>	0.7	0.6	2	0.42	<LOD	<LOD	0.12	0.13
PO <sub>4</sub>	0.4	0.2	0.3	0.02	<LOD	<LOD	<LOD	<LOD
dCo	0.18 ± 0.02	0.08 ± 0.01	0.07 ± 0.0	0.01	0.19	0.38 ± 0.02	0.39 ± 0.01	0.37 ± 0.01
dFe	173 ± 21	55.2 ± 3.6	55.4 ± 1.7	20.8	66.3	521 ± 46.5	231 ± 1.5	280 ± 7.6
dMn	36.6 ± 0.95	45.6 ± 1.4	34.2 ± 1.7	0.55	2.27	12.5 ± 0.23	48 ± 1**	43 ± 4**
dZn	8.77 ± 2.7	22.3 ± 16.7	13.9 ± 10.7	7.25	14.1	5.45 ± 0.63	11.9 ± 1.1	11.0 ± 0.61
Co <sub>N</sub> *	0.172	0.073	0.046	0.005	NA	NA	0.389	0.368
Co <sub>P</sub> *	0.18	0.08	0.07	0.01	NA	NA	NA	NA
Co <sub>Fe</sub> *	-4.20	-1.32	-1.33	-0.516	-0.149	-12.8	-5.45	-6.71
Co <sub>Mn</sub> *	-2.30	-3.01	-2.25	-0.027	0.036	-0.466	-2.86	-2.54
Co <sub>Zn</sub> *	-1.90	-5.21	-3.23	-1.71	-3.15	-0.913	-2.43	-2.24
Chl a	0.46	0.2	0.16	0.08	<LOD	0.64 ± 0.06	0.14 ± 0.01	0.35 ± 0.01

*Note.* Dissolved nitrate (NO<sub>x</sub>), phosphate (PO<sub>4</sub>) (μmol L<sup>-1</sup>); dissolved cobalt (dCo), iron (dFe), manganese (dMn), zinc (dZn) (nmol L<sup>-1</sup>) and chlorophyll a (Chl a, μg L<sup>-1</sup>) concentrations correspond to measurements at the start of each bioassay experiment. “<LOD” measurements were below the limit of detection (~0.02 μmol L<sup>-1</sup> for NO<sub>x</sub>, 0.02 μmol L<sup>-1</sup> for PO<sub>4</sub>). Values are presented as mean ± standard deviation where triplicate samples were collected. \*Experiment 4 was conducted using 20% lake water mixed with 80% meltwater; \*\*dMn shown as total dissolved Mn (unfiltered) in Experiments 7 and 8. Co<sub>N</sub>\*, Co<sub>P</sub>\*, Co<sub>Fe</sub>\*, Co<sub>Mn</sub>\*, and Co<sub>Zn</sub>\* were calculated as described by Browning et al. (2018).

were frozen ( $-20^{\circ}\text{C}$ ). Macronutrient concentrations were measured via a Quattro 39 System (SEAL) segmented flow analyzer with a XY2 Autosampler (Hansen & Koroleff, 1999).

Dissolved micro-nutrients (i.e., dissolved Co, Fe, Mn and Zn) samples were syringe filtered (Millipore,  $0.22\ \mu\text{m}$ , polyvinyl difluoride) into trace metal clean 125 mL low density polyethylene bottles (Nalgene). Syringe filters were precleaned with  $1\ \text{mol L}^{-1}$  laboratory grade HCl then de-ionized water. All samples were then acidified to  $\text{pH} \sim 1.9$  by addition of  $180\ \mu\text{L}$  32%–35% HCl (ROMIL, UpA grade) per 125 mL within 1 day of sample collection and stored for  $>6$  months prior to analysis. Dissolved trace metal concentrations were determined by high resolution inductively coupled plasma-mass spectrometry (Element XR, Thermo Fisher Scientific) exactly as per Rapp et al. (2017). Though there is no specific reference material for freshwater, a certified coastal seawater standard (CASS) was preconcentrated via SeaFAST and analyzed with samples, in order to validate our trace metal measurements.

## 2.2. Bioassay Incubations

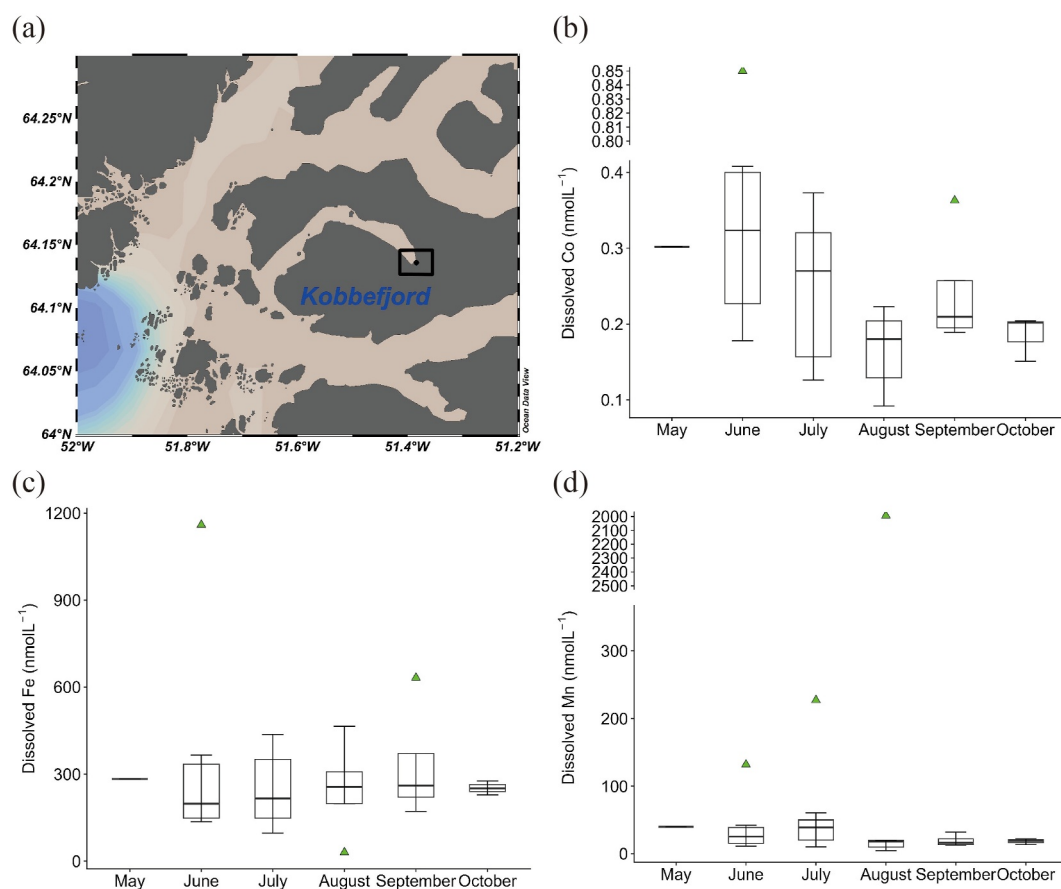
Nutrient addition bioassay experiments were conducted in trace metal clean, 500 mL polycarbonate bottles (Nalgene) which were filled with unfiltered freshwater. Freshwater was collected in acid cleaned polycarbonate carboys (20 L) from the surface of lakes/streams via acid cleaned 2 L bottles that were lowered into the water by hand. Three replicate 500 mL bottles were spiked with (micro)nutrient combinations for each treatment and three bottles were sealed with no amendment as controls. One set of bottles were subsampled immediately for assessment of the initial conditions (Chl a, macronutrients and micronutrients). Bottles were incubated in an on-land incubator (described below). After several days (3–5) of incubation time, the Chl a biomass response of each treatment was compared to the control treatment. The treatments for the eight experiments (Experiment 1–8) are shown in full (Table S3 in Supporting Information S1). Silica was also added in experiments 2 and 3 (as one treatment group added with all other nutrients plus silica), but is not discussed as a primary factor limiting phytoplankton growth herein as this is mainly expected to influence the growth of siliceous phytoplankton only. The fixed N, P and silica spike solutions were previously passed through a column of Chelex-100 to remove trace metals. The N spike solutions contained both nitrate and ammonium to fully alleviate N-limitation irrespective of whether nitrate or ammonium was a preferred N source.

Incubation bottles were placed in open top containers which were filled and regularly (three times per day) flushed and re-filled with ambient freshwater. The incubator was shaded with blue screening (Lee Filter “Blue Lagoon”) to yield incubator light intensities  $\sim 35\%$  of surface values in the WAP, whilst experiments were conducted without additional shading in SW Greenland due to higher turbidity in ambient water. Samples were incubated for 4–6 days. At the start and end of experiments, 300–350 mL subsamples for Chl a were filtered (glass fiber filters,  $0.7\ \mu\text{m}$  nominal pore size, 25 mm diameter, Macherey–Nagel), extracted in the dark in 10 mL 90% acetone at  $-20^{\circ}\text{C}$  ( $\sim 12$  hr), then measured using a calibrated Turner Designs Trilogy fluorometer (Welschmeyer, 1994).

## 3. Results and Discussion

### 3.1. Low dCo Concentrations Were Widely Evident

We collected a series of freshwater samples from lakes and streams in SW Greenland and the WAP for the determination of macro- and micro-nutrients, and subsequently conducted nutrient addition bioassay incubations (Figure 1). The concentrations of dissolved nitrate, phosphate, Fe (dFe), Mn (dMn), Co (dCo) and Zn (dZn) are shown in Table 1. All freshwater samples had relatively low dCo concentrations, consistently  $<0.38\ \text{nmol L}^{-1}$ , in contrast to generally high concentrations of dFe ( $20.8\text{--}521\ \text{nmol L}^{-1}$ ), dMn ( $0.55\text{--}48.0\ \text{nmol L}^{-1}$ ) and dZn ( $5.45\text{--}22.3\ \text{nmol L}^{-1}$ ). The low dissolved Fe:Mn ratios found (range from 1.2 to 41.6, median = 5.1,  $n = 8$ ) in comparison to the mean upper continental crust ratio ( $\sim 50$ ) (Rudnick & Gao, 2003) are generally expected in glacier runoff due to the more prolific scavenging of dFe than dMn (Colombo et al., 2020; Zhang et al., 2015). Given the overall high concentrations of Fe and Mn across most of the sites, conditions were likely saturated with respect to Fe oxides as well as Mn oxides (Aciego et al., 2015). The sorption capacity of freshly precipitated Mn oxides is high for a variety of metal cations, including  $\text{Co}^{2+}$  (Murray, 1975), whilst both Co and Mn are strongly adsorbed by Fe oxides ( $\text{Co} > \text{Mn}$ ) (Bibak, 2008). The dissolved Mn:Co ratio (range from 12 to 570, median = 126,  $n = 8$ ) was often higher than that of continental crust ( $\sim 45$ ) (Rudnick & Gao, 2003), suggesting scavenging process by Fe oxides could have reduced dCo availability relative to dMn. Dissolved nitrate and phosphate concentrations were consistently below, or close to, the detection limit, with the only notable exception being moderately high



**Figure 2.** Temporal trends of dissolved cobalt (dCo), iron (dFe) and manganese (dMn) in runoff from an Arctic catchment, Kobbefjord. (a) Map of Kobbefjord, southwest Greenland, (b) concentrations of dCo, (c) concentrations of dFe, and (d) concentrations of dMn. Green triangles indicate outliers. Boxes show the mean, upper and lower quartiles. Whiskers show the minimum and maximum values excluding outliers.

nitrate concentrations in Long Lake ( $2.0 \mu\text{mol L}^{-1}$ ). Phosphate is also susceptible to co-precipitation with dFe as Fe oxyhydroxides are formed and so similar mechanisms may have contributed to the low phosphate concentrations observed across all sites (Norton et al., 2011).

To provide further insights into seasonal dCo dynamics, we collected water samples at weekly intervals from a proglacial stream in Kobbefjord, SW Greenland (Figure 2) close to the site of the corresponding nutrient addition bioassay incubation experiments (discussed below). Kobbefjord hosts a series of interconnected lakes, which receive freshwater input from snow melt in spring and early summer, and runoff from mountain glaciers through summer. The last lake before runoff enters the fjord was used for incubations herein and the timeseries refers to outflow from this lake as it integrates the effects of upstream processes. Throughout summer, dCo generally decreased from  $0.38 \pm 0.25 \text{ nmol L}^{-1}$  in June to  $0.17 \pm 0.05 \text{ nmol L}^{-1}$  in August and  $0.22 \pm 0.07 \text{ nmol L}^{-1}$  in September and October (Figure 2, panel b). These results were consistent with low dCo concentrations observed at the start of bioassay experiments (Table 1) and notably contrasted with the seasonal dynamics of dFe and dMn which showed no such depletion in boreal summer (Figure 2, panel c and d). A one-way Anova test confirmed a significant seasonal change in dCo concentration ( $p < 0.05$ ) with a Spearman's rank correlation showing a significant negative relationship between dCo and month (June–October). This suggested that whilst runoff maintained relatively elevated dFe and dMn concentrations during the meltwater season, dCo sources were insufficient to compensate for dCo sinks. We infer either a stronger inorganic removal mechanism in summer, perhaps dependent on freshly precipitated Mn/Fe oxides (van Genuchten et al., 2022), and/or increased biological demand relative to Co supply.



Across all experiment sites, both the dMn:dCo and dZn:dCo ratios were consistently high (Table 1), which in a marine context has been shown to induce phytoplankton Co deficiency (Hawco & Saito, 2018). In prior work, *Prochlorococcus* growth rates were shown to decrease at high levels of both dZn and dMn due to a shared uptake transport mechanism for Zn, Mn and Co (Hawco & Saito, 2018). We calculated the theoretical deficiency of dissolved Co to nitrogen (N), phosphorus (P), Fe, Mn or Zn, taking into account assumed average requirements for these nutrients ( $Co_N^*$ ,  $Co_P^*$ ,  $Co_{Fe}^*$ ,  $Co_{Mn}^*$ ,  $Co_{Zn}^*$ , respectively); following the approach by Browning et al. (2018), shown as Equation 1. We found lower  $Co_N^*$  and  $Co_P^*$  values ( $<0.1 \text{ nmol L}^{-1}$ ) in most of the tested regions in the WAP (Table 1).

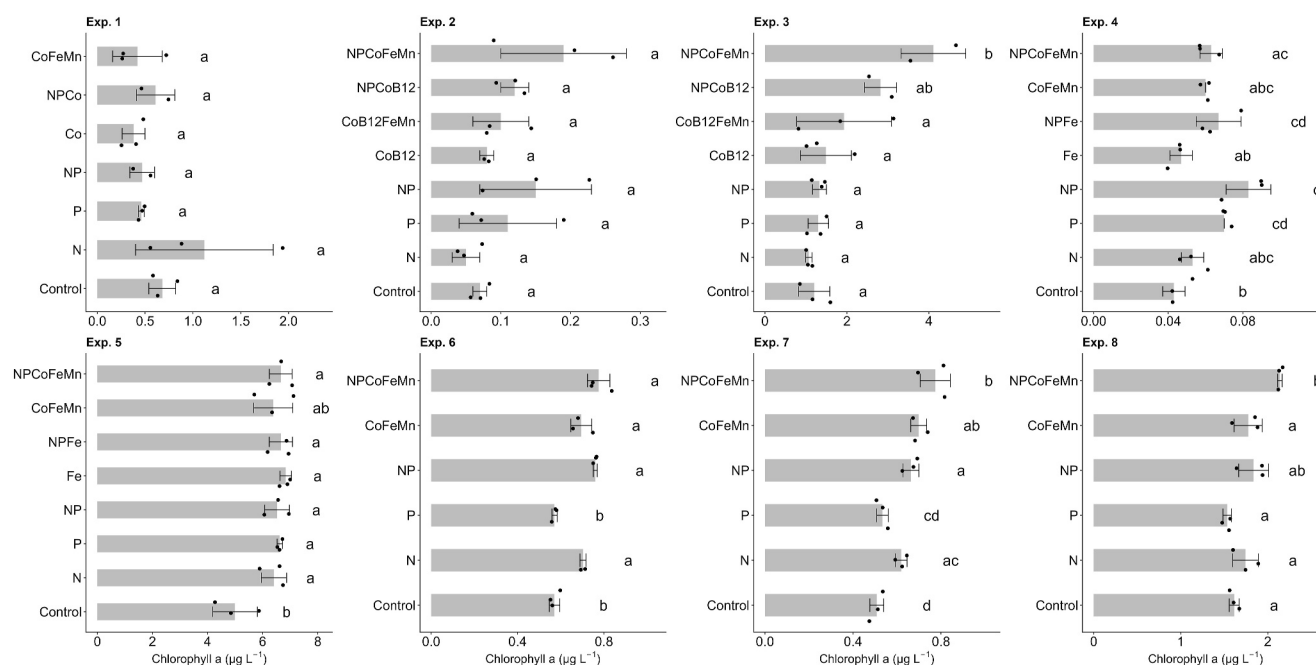
$$Co_{X^*} = Co - X * R_{Co:X} \quad (1)$$

Where X is either N, P, Fe, Mn or Zn concentration and  $R_{Co:X}$  is the assumed average phytoplankton dCo: nutrient X ratio (Moore et al., 2013). Higher  $Co_N^*$  values were found in SW Greenland ( $>0.1 \text{ nmol L}^{-1}$ ), where there was no available value for  $Co_P^*$ . In contrast,  $Co_{Fe}^*$ ,  $Co_{Mn}^*$  and  $Co_{Zn}^*$  values were nearly negative in all tested regions except one WAP site with a very low  $Co_{Mn}^*$  value ( $0.036 \text{ nmol L}^{-1}$ ) in the runoff near Yelcho station. These results imply Co was almost always more deficient in water for phytoplankton growth than Fe, Mn, or Zn. Calculated ratios suggest conditions approaching N-Co (and potentially N-P-Co) co-deficiency at WAP sites and corroborate that dissolved Co was likely the only trace element potentially at co-limiting levels.

### 3.2. Impact of Cobalt on Regulating Freshwater Phytoplankton Growth

In previous work, evidence of  $B_{12}$  serial limitation was observed in the Southern Ocean (Bertrand et al., 2007) and it has been speculated that increased terrestrial Fe supply could drive coastal Antarctic systems toward lower Co availability (Chmiel et al., 2023). Moreover, prior work found that Co supplied from subsurface waters may have some impact on community growth and  $B_{12}$  production in Antarctic sea ice (Bertrand et al., 2007). Whilst to our knowledge, no bioassay experiments have been conducted to assess the effects of micronutrient additions to polar freshwater environments, there have been a restricted number of reports of Co co-limitation in other diverse freshwater environments. Cobalt addition was found to stimulate primary production during a bloom of heterocytous cyanobacteria in Lake Waiholo, New Zealand (Downs et al., 2008). Similarly, Co was shown to limit cyanobacterial growth in a shallow eutrophic lake Taihu, China (Fan et al., 2021).

Here we conducted eight bioassay incubations in order to test our hypothesis of Co limitation of phytoplankton growth. Measurements of Chl a from all bioassay incubations are shown in Figure 3. In a number of experiments Co additions were made with simultaneous addition of Fe and Mn; however, given the strongly elevated concentrations of Fe and Mn in initial waters and theoretical excess relative to Co (i.e., negative  $Co_{Fe}^*$  and  $Co_{Mn}^*$  at all sites apart from  $Co_{Mn}^*$  in Experiment 5; Table 1), these elements were not considered to have regulated the magnitude of the Chl a response and are ignored in the following discussion. In SW Greenland, one of the freshwater lakes from Nuuk (Experiment 7) showed that N addition (alone or in combination with P) led to a statistically significant increase in Chl a relative to controls, whereas the combined addition of Co + N + P enhanced this further. In contrast, another experiment at the same site (Experiment 8) showed that the Chl a response to the combined addition of Co + N + P was significantly higher than the control, but statistically indistinguishable from the N + P treatment. In a freshwater lake in Kobbefjord (Experiment 6), N, N + P, Co (+Fe + Mn) or N + P + Co(+Fe + Mn) additions each led to significant increases in Chl a over the control or + P treatments. In one of the WAP lakes (Long Lake; Experiment 3), Chl a concentrations increased significantly only following combined N + P + Co(+Fe + Mn) treatment. No enhancement of Chl a following Co addition was evident elsewhere in the WAP (Experiments 1 and 2), with  $B_{12}$  additions similarly not indicating any stimulation of phytoplankton growth (Experiments 2 and 3). In the stream water near Yelcho station (Experiment 5), Chl a enhancements were observed in all nutrient treatments relative to the control, whilst enhancements of P additions (alone or in combination with N) were found in Kitish lake (Experiment 4). The majority of results were therefore consistent with the existing paradigm that P and/or N availability limits productivity in aquatic environments. However, at three locations positive effects of dCo were found suggesting a potential role for Co limitation in some cases. More broadly, the low dCo concentrations and calculated Co deficiencies relative to other micronutrients implied dCo was not available in a large excess of phytoplankton demands at any site.



**Figure 3.** Chlorophyll a (Chl a,  $\mu\text{g L}^{-1}$ ) responses to nutrient additions (see Table S3 in Supporting Information S1). Dots indicate the concentrations measured in the triplicate biological replicates and error bars indicate the range. Treatment means were compared using a one-way analysis of variance and a means comparison test based on the Studentized range statistic, Tukey's "Honest Significant Difference" method (indistinguishable means are labeled with the same letter,  $P < 0.05$ ).

### 3.3. Environmental Implications

Three different microalgae; snow algae, ice algae and phytoplankton have been found in Kitiash lake on King George Island (Montecino et al., 1991). Croft et al. (2005) found that nearly half of the 326 algae species surveyed required exogenous  $B_{12}$  for growth. Few measurements of  $B_{12}$  have been made in freshwater so it is not yet possible to construct a  $B_{12}$  budget for any polar freshwater environments. Yet given the high energetic cost of  $B_{12}$  synthesis, it would be expected that  $B_{12}$  concentrations would reflect primary productivity levels. A survey at monthly resolution in the English Lake District suggested a link between overall productivity and  $B_{12}$  concentrations (Daisley, 1969). It is plausible that either low Co or low  $B_{12}$  concentrations could (co)-limit primary production in polar freshwater environments. Experiments herein were insufficient to determine the underlying cause of the positive response. Nevertheless, the systematically low dCo concentrations across all fieldsites suggest that strength of Co (co)-limitation could easily be affected by other biogeochemical perturbations that affect productivity. For example, whilst fluxes of bio-essential elements including Fe and Mn may increase with freshwater discharge and/or sediment load (Krause et al., 2021; Overeem et al., 2017), dCo could have a fundamentally different relationship in some downstream environments due to its high affinity for Mn and Fe oxide surfaces which are continuously formed in these environments (Schroth et al., 2014; Zhang et al., 2015). Potential impacts of Co on freshwater phytoplankton growth alongside very high concentrations of Fe ( $>200 \text{ nmol L}^{-1}$ ) were found in SW Greenland in this work, similar to the Co stimulation of phytoplankton growth alongside high Fe concentrations in Lake Waihola, New Zealand (Downs et al., 2008). Noting the high absorption capacity of Fe oxides for Co, this may relate to an inorganic sink for Co (Ainsworth et al., 1994).

Not only does increased meltwater discharge affect the flux of bio-essential metals, but also the physico-chemical properties of metal transport and thus their availability. Herein we have only determined the dissolved concentration of trace metals, yet metal availability is strongly influenced by pH, temperature and dissolved organic matter which may all have strong gradients in proglacial environments (de Paiva Magalhães et al., 2015). Organic cobalt complexation tends to be predominant in aquatic environments, with 80%–96% of total dCo in freshwater samples found to be organically complexed in Switzerland (Qian et al., 1998). Changing pH or DOC levels would thereby affect dCo availability. Because meltwater typically has low alkalinity concentrations (Fransson et al., 2015), meltwater affected lakes are weakly buffered and can be subject to strong pH changes. For example, the average pH of several lakes on the Fildes Peninsula (Antarctica) increased from 6.0 in 1998 (Préndez &

Adriana Carrasco, 2003), to 8.2 in 2017 (Olgun et al., 2024). One of the few studies on freshwater Co speciation, in Linsley Pond, USA, further showed that increasing pH decreased the solubility of Co due to CoS precipitation (Xuan & Benoit, 2023). Both low DOC and weak buffering in polar freshwater environments, in addition to changing chemical weathering or biological activity (Zaini et al., 2024), could therefore strongly affect dCo dynamics. Future work could therefore investigate how Co speciation and availability changes across these dynamic zones.

#### 4. Conclusions

Our findings contribute to greater understanding of the bottom-up mechanisms regulating primary production in polar freshwater ecosystems, particularly during summer when oligotrophic conditions prevail and result in relatively low primary production despite high light availability. Concentration analyses of both macro- and micro-nutrients and a set of bioassay nutrient addition experiments results, re-affirm N and P availability as major drivers of phytoplankton growth, yet simultaneously suggest that low dCo availability could also be (co-)limiting in some polar freshwater environments. Low dCo concentrations in summer might be maintained in proglacial aquatic environments partially due to the enhanced supply of Fe and Mn oxides that are typically present in glacier discharge and have a high scavenging potential for Co. Furthermore, phytoplankton acquisition of dCo could simultaneously be kinetically impeded by high dissolved ratios of Mn:Co and Zn:Co. The sensitivity of dCo to these factors may make Co regulation of these environments highly dynamic in space and time, and particularly sensitive to rapid environmental changes such as increasing runoff, changes in suspended sediment load and glacier retreat. Further work is clearly necessary to assess the impact of changing micronutrient availability on phytoplankton growth and community composition alongside other factors influencing ecological dynamics (Cauvy-Fraunié & Dangles, 2019).

#### Data Availability Statement

All data reported in this study are available at Zhu et al. (2024).

#### Acknowledgments

The authors thank colleagues at the Greenland Institute of Natural Resources (GINR) and the Instituto Antartico Chileno (INACH) for facilitating fieldwork. André Mutzberg (GEOMAR) is thanked for macronutrient analysis. MH was supported by the DFG (award number HO 6321/1-1) and the NSFC (RFIS-II 42150610482). Work in Antarctica was possible through FONDAP-IDEAL 15150003 and FONDECYT 1211338 (JH). Field access to Kobbefjord (southwest Greenland) was possible through European Union Horizon 2020 project INTERACT (Grant 730938).

#### References

- Aciego, S. M., Stevenson, E. I., & Arendt, C. A. (2015). Climate versus geological controls on glacial meltwater micronutrient production in southern Greenland. *Earth and Planetary Science Letters*, 424, 51–58. <https://doi.org/10.1016/j.epsl.2015.05.017>
- Ainsworth, C. C., Pilon, J. L., Gassman, P. L., & Van Der Sluys, W. G. (1994). Cobalt, cadmium, and lead sorption to hydrous iron oxide: Residence time effect. *Soil Science Society of America Journal*, 58(6), 1615–1623. <https://doi.org/10.2136/sssaj1994.03615995005800060005x>
- Anderson, N. J., Saros, J. E., Bullard, J. E., Cahoon, S. M. P., McGowan, S., Bagshaw, E. A., et al. (2017). The Arctic in the twenty-first century: Changing biogeochemical linkages across a paraglacial landscape of Greenland. *BioScience*, 67(2), 118–133. <https://doi.org/10.1093/biosci/biw158>
- Bertrand, E. M., Saito, M. A., Rose, J. M., Riesselman, C. R., Lohan, M. C., Noble, A. E., et al. (2007). Vitamin B12 and iron colimitation of phytoplankton growth in the Ross Sea. *Limnology & Oceanography*, 52(3), 1079–1093. <https://doi.org/10.4319/lo.2007.52.3.1079>
- Bhatia, M. P., Waterman, S., Burgess, D. O., Williams, P. L., Bundy, R. M., Mellett, T., et al. (2021). Glaciers and nutrients in the Canadian Arctic Archipelago marine system. *Global Biogeochemical Cycles*, 35(8). <https://doi.org/10.1029/2021gb006976>
- Bibak, A. (2008). Cobalt, copper, and manganese adsorption by aluminium and iron oxides and humic acid. *Communications in Soil Science and Plant Analysis*, 25(19–20), 3229–3239. <https://doi.org/10.1080/00103629409369261>
- Bliss, A., Hock, R., & Radić, V. (2014). Global response of glacier runoff to twenty-first century climate change. *Journal of Geophysical Research: Earth Surface*, 119(4), 717–730. <https://doi.org/10.1002/2013jf002931>
- Browning, T. J., Rapp, I., Schlosser, C., Gledhill, M., Achterberg, E. P., Bracher, A., & Le Moigne, F. A. C. (2018). Influence of iron, cobalt, and vitamin B12 supply on phytoplankton growth in the tropical east Pacific during the 2015 El Niño. *Geophysical Research Letters*, 45(12), 6150–6159. <https://doi.org/10.1029/2018gl077972>
- Brutemark, A., Rengefors, K., & Anderson, N. J. (2006). An experimental investigation of phytoplankton nutrient limitation in two contrasting low arctic lakes. *Polar Biology*, 29(6), 487–494. <https://doi.org/10.1007/s00300-005-0079-0>
- Burpee, B., Saros, J. E., Northington, R. M., & Simon, K. S. (2016). Microbial nutrient limitation in Arctic lakes in a permafrost landscape of southwest Greenland. *Biogeosciences*, 13(2), 365–374. <https://doi.org/10.5194/bg-13-365-2016>
- Burpee, B. T., Anderson, D., & Saros, J. E. (2018). Assessing ecological effects of glacial meltwater on lakes fed by the Greenland Ice Sheet: The role of nutrient subsidies and turbidity. *Arctic Antarctic and Alpine Research*, 50(1), S100019. <https://doi.org/10.1080/15230430.2017.1420953>
- Cauvy-Fraunié, S., & Dangles, O. (2019). A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology & Evolution*, 3(12), 1675–1685. <https://doi.org/10.1038/s41559-019-1042-8>
- Chmiel, R. J., Kell, R. M., Rao, D., Moran, D. M., DiTullio, G. R., & Saito, M. A. (2023). Low cobalt inventories in the Amundsen and Ross seas driven by high demand for labile cobalt uptake among native phytoplankton communities. *Biogeosciences*, 20(19), 3997–4027. <https://doi.org/10.5194/bg-20-3997-2023>
- Choudhary, S., Nayak, G., Tiwari, A. K., & Khare, N. (2018). Sediment composition and its effect on the productivity in Larsemann Hills, east Antarctica. *Arabian Journal of Geosciences*, 11(15), 416. <https://doi.org/10.1007/s12517-018-3755-4>



- Choudhary, S., Tiwari, A. K., Nayak, G. N., & Bejugam, P. (2018). Sedimentological and geochemical investigations to understand source of sediments and processes of recent past in Schirmacher Oasis, East Antarctica. *Polar Science*, *15*, 87–98. <https://doi.org/10.1016/j.polar.2018.01.003>
- Colombo, M., Jackson, S. L., Cullen, J. T., & Orians, K. J. (2020). Dissolved iron and manganese in the Canadian Arctic Ocean: On the biogeochemical processes controlling their distributions. *Geochimica et Cosmochimica Acta*, *277*, 150–174. <https://doi.org/10.1016/j.gca.2020.03.012>
- Croft, M. T., Lawrence, A. D., Raux-Deery, E., Warren, M. J., & Smith, A. G. (2005). Algae acquire vitamin B12 through a symbiotic relationship with bacteria. *Nature*, *438*(7064), 90–93. <https://doi.org/10.1038/nature04056>
- Daisley, K. W. (1969). Monthly survey of vitamin B12 concentrations in some waters of the English Lake District. *Limnology & Oceanography*, *14*(2), 224–228. <https://doi.org/10.4319/lo.1969.14.2.0224>
- Davison, B. J., Hogg, A. E., Moffat, C., Meredith, M. P., & Wallis, B. J. (2024). Widespread increase in discharge from west Antarctic Peninsula glaciers since 2018. *The Cryosphere*, *18*(7), 3237–3251. <https://doi.org/10.5194/tc-18-3237-2024>
- de Paiva Magalhães, D., da Costa Marques, M. R., Baptista, D. F., & Buss, D. F. (2015). Metal bioavailability and toxicity in freshwaters. *Environmental Chemistry Letters*, *13*(1), 69–87. <https://doi.org/10.1007/s10311-015-0491-9>
- Downs, T., Schallenberg, M., & Burns, C. (2008). Responses of lake phytoplankton to micronutrient enrichment: A study in two New Zealand lakes and an analysis of published data. *Aquatic Sciences*, *70*(4), 347–360. <https://doi.org/10.1007/s00027-008-8065-6>
- Fan, X., Ding, S., Gao, S., Chen, M., Fu, Z., Gong, M., et al. (2021). A holistic understanding of cobalt cycling and limiting roles in the eutrophic Lake Taihu. *Chemosphere*, *277*, 130234. <https://doi.org/10.1016/j.chemosphere.2021.130234>
- Fransson, A., Chierici, M., Nomura, D., Granskog, M. A., Kristiansen, S., Martma, T., & Nehrke, G. (2015). Effect of glacial drainage water on the CO<sub>2</sub> system and ocean acidification state in an Arctic tidewater-glacier fjord during two contrasting years. *Journal of Geophysical Research: Oceans*, *120*(4), 2413–2429. <https://doi.org/10.1002/2014jc010320>
- Hansen, H. P., & Koroleff, F. (1999). Determination of nutrients. In *Methods of seawater analysis* (pp. 159–228).
- Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E., et al. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters*, *14*(9), 852–862. <https://doi.org/10.1111/j.1461-0248.2011.01651.x>
- Hawco, N. J., & Saito, M. A. (2018). Competitive inhibition of cobalt uptake by zinc and manganese in a pacific *Prochlorococcus* strain: Insights into metal homeostasis in a streamlined oligotrophic cyanobacterium. *Limnology & Oceanography*, *63*(5), 2229–2249. <https://doi.org/10.1002/lno.10935>
- Hawkings, J. R., Skidmore, M. L., Wadham, J. L., Priscu, J. C., Morton, P. L., Hatton, J. E., et al. (2020). Enhanced trace element mobilization by Earth's ice sheets. *Proceedings of the National Academy of Sciences*, *117*(50), 31648–31659. <https://doi.org/10.1073/pnas.2014378117>
- Krause, J., Hopwood, M. J., Höfer, J., Krisch, S., Achterberg, E. P., Alarcón, E., et al. (2021). Trace element (Fe, Co, Ni and Cu) dynamics across the salinity gradient in Arctic and Antarctic Glacier Fjords. *Front Earth Sc-Switz*, *9*. <https://doi.org/10.3389/feart.2021.725279>
- Lienemann, C.-P., Tallefert, M., Perret, D., & Gaillard, J.-F. (1997). Association of cobalt and manganese in aquatic systems: Chemical and microscopic evidence. *Geochimica et Cosmochimica Acta*, *61*(7), 1437–1446. [https://doi.org/10.1016/s0016-7037\(97\)00015-x](https://doi.org/10.1016/s0016-7037(97)00015-x)
- Mankoff, K. D., Noël, B., Fettweis, X., Ahlström, A. P., Colgan, W., Kondo, K., et al. (2020). Greenland liquid water discharge from 1958 through 2019. *Earth System Science Data*, *12*(4), 2811–2841. <https://doi.org/10.5194/essd-12-2811-2020>
- Mitchell, A., Brown, G. H., & Fuge, R. (2001). Minor and trace element export from a glacierized Alpine headwater catchment (Haut Glacier d'Arolla, Switzerland). *Hydrological Processes*, *15*(18), 3499–3524. <https://doi.org/10.1002/hyp.1041>
- Montecino, V., Pizarro, G., Cabrera, S., & Contreras, M. (1991). Spatial and temporal photosynthetic compartments during summer in Antarctic Lake Kitiash. *Polar Biology*, *11*(6), 371–377. <https://doi.org/10.1007/bf00239689>
- Moore, C. M., Mills, M. M., Arrigo, K. R., Berman-Frank, I., Bopp, L., Boyd, P. W., et al. (2013). Processes and patterns of oceanic nutrient limitation. *Nature Geoscience*, *6*(9), 701–710. <https://doi.org/10.1038/ngeo1765>
- Murray, J. W. (1975). The interaction of metal ions at the manganese dioxide-solution interface. *Geochimica et Cosmochimica Acta*, *39*(4), 505–519. [https://doi.org/10.1016/0016-7037\(75\)90103-9](https://doi.org/10.1016/0016-7037(75)90103-9)
- Norton, S. A., Perry, R. H., Saros, J. E., Jacobson, G. L., Fernandez, I. J., Kopáček, J., et al. (2011). The controls on phosphorus availability in a Boreal lake ecosystem since deglaciation. *Journal of Paleolimnology*, *46*(1), 107–122. <https://doi.org/10.1007/s10933-011-9526-9>
- Olgun, N., Tari, U., Balci, N., Altunkaynak, Ş., Gürarslan, I., Yakan, S. D., et al. (2024). Lithological controls on lake water biogeochemistry in Maritime Antarctica. *Science of the Total Environment*, *912*, 168562. <https://doi.org/10.1016/j.scitotenv.2023.168562>
- Overeem, I., Hudson, B. D., Syvitski, J. P. M., Mikkelsen, A. B., Hasholt, B., van den Broeke, M. R., et al. (2017). Substantial export of suspended sediment to the global oceans from glacial erosion in Greenland. *Nature Geoscience*, *10*(11), 859–863. <https://doi.org/10.1038/ngeo3046>
- Poullton, S. W., & Raiswell, R. (2005). Chemical and physical characteristics of iron oxides in riverine and glacial meltwater sediments. *Chemical Geology*, *218*(3–4), 203–221. <https://doi.org/10.1016/j.chemgeo.2005.01.007>
- Prater, C., Bullard, J. E., Osburn, C. L., Martin, S. L., Watts, M. J., & Anderson, N. J. (2022). Landscape controls on nutrient Stoichiometry Regulate Lake Primary production at the Margin of the Greenland ice sheet. *Ecosystems*, *25*(4), 931–947. <https://doi.org/10.1007/s10021-021-00693-x>
- Préndez, M., & Adriana Carrasco, M. (2003). Elemental composition of surface waters in the Antarctic Peninsula and interactions with the environment. *Environmental Geochemistry and Health*, *25*(3), 347–363. <https://doi.org/10.1023/a:1024559809076>
- Qian, J., Xue, H. B., Sigg, L., & Albrecht, A. (1998). Complexation of cobalt by natural ligands in freshwater. *Environmental Science & Technology*, *32*(14), 2043–2050. <https://doi.org/10.1021/es971018l>
- Rapp, I., Schlosser, C., Rusiecka, D., Gledhill, M., & Achterberg, E. P. (2017). Automated preconcentration of Fe, Zn, Cu, Ni, Cd, Pb, Co, and Mn in seawater with analysis using high-resolution sector field inductively-coupled plasma mass spectrometry. *Analytica Chimica Acta*, *976*, 1–13. <https://doi.org/10.1016/j.aca.2017.05.008>
- Rudnick, R. L., & Gao, S. (2003). 3.01 - Composition of the continental crust. In H. D. Holland & K. K. Turekian (Eds.), *Treatise on geochemistry* (pp. 1–64). Pergamon.
- Schlitzer, R. (2023). Ocean data view. (Version 5.6.1) [Software]. [odv.awi.de](https://odv.awi.de)
- Schroter, A. W., Crusius, J., Hoyer, I., & Campbell, R. (2014). Estuarine removal of glacial iron and implications for iron fluxes to the ocean. *Geophysical Research Letters*, *41*(11), 3951–3958. <https://doi.org/10.1002/2014gl060199>
- van Genuchten, C. M., Hopwood, M. J., Liu, T., Krause, J., Achterberg, E. P., Rosing, M. T., & Meire, L. (2022). Solid-phase Mn speciation in suspended particles along meltwater-influenced fjords of West Greenland. *Geochimica et Cosmochimica Acta*, *326*, 180–198. <https://doi.org/10.1016/j.gca.2022.04.003>
- Wadham, J. L., Hawkings, J. R., Tarasov, L., Gregoire, L. J., Spencer, R. G. M., Gutjahr, M., et al. (2019). Ice sheets matter for the global carbon cycle. *Nature Communications*, *10*(1), 3567. <https://doi.org/10.1038/s41467-019-11394-4>

- Welschmeyer, N. (1994). Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography*, 39(8), 1985–1992. <https://doi.org/10.4319/lo.1994.39.8.1985>
- Whiteford, E. J., McGowan, S., Barry, C. D., & Anderson, N. J. (2016). Seasonal and regional controls of phytoplankton production along a climate gradient in south-west Greenland during ice-cover and ice-free conditions. *Arctic Antarctic and Alpine Research*, 48(1), 139–159. <https://doi.org/10.1657/aaar0015-003>
- Xuan, Z., & Benoit, G. (2023). Cobalt speciation and cycling in Linsley pond, Connecticut, USA. *Aquatic Sciences*, 86(1), 1. <https://doi.org/10.1007/s00027-023-01015-0>
- Zaini, N. A., Ismail, S. S., Low, V. L., Mahmud, M. H., Houssaini, J., Lee, W. Y., & Heo, C. C. (2024). Soil chemical properties associated with penguin carrion in Barton Peninsula, King George Island, Antarctica. *Polar Biology*, 47, 681–691.
- Zhang, R., John, S. G., Zhang, J., Ren, J., Wu, Y., Zhu, Z., et al. (2015). Transport and reaction of iron and iron stable isotopes in glacial meltwaters on Svalbard near Kongsfjorden: From rivers to estuary to ocean. *Earth and Planetary Science Letters*, 424, 201–211. <https://doi.org/10.1016/j.epsl.2015.05.031>
- Zhu, K., Krause, J., Marín-Arias, C., Mestre, M., Höfer, J., Browning, T. J., et al. (2024). Raw data for the analysis of cobalt impacts on freshwater phytoplankton in warming polar regions [Dataset]. *Mendeley Data*, V1. <https://data.mendeley.com/datasets/97n2vvg6tx/1>

## References From the Supporting Information

- Bertrand, E., Saito, M., Lee, P., Dunbar, R., Sedwick, P., & DiTullio, G. (2011). Iron limitation of a springtime bacterial and phytoplankton community in the Ross Sea: Implications for vitamin B12 nutrition. *Frontiers in Microbiology*, 2. <https://doi.org/10.3389/fmicb.2011.00160>
- Bertrand, E. M., McCrow, J. P., Moustafa, A., Zheng, H., McQuaid, J. B., Delmont, T. O., et al. (2015). Phytoplankton–bacterial interactions mediate micronutrient colimitation at the coastal Antarctic sea ice edge. *Proceedings of the National Academy of Sciences*, 112(32), 9938–9943. <https://doi.org/10.1073/pnas.1501615112>
- Blaen, P. J., Milner, A. M., Hannah, D. M., Brittain, J. E., & Brown, L. E. (2014). Impact of changing hydrology on nutrient uptake in high Arctic rivers. *River Research and Applications*, 30(9), 1073–1083. <https://doi.org/10.1002/rra.2706>
- Browning, T. J., Achterberg, E. P., Rapp, I., Engel, A., Bertrand, E. M., Tagliabue, A., & Moore, C. M. (2017). Nutrient co-limitation at the boundary of an oceanic gyre. *Nature*, 551(7679), 242–246. <https://doi.org/10.1038/nature24063>
- Docherty, C. L., Riis, T., Hannah, D. M., Rosenhøj Leth, S., & Milner, A. M. (2018). Nutrient uptake controls and limitation dynamics in north-east Greenland streams. *Polar Research*, 37(1), 1440107. <https://doi.org/10.1080/17518369.2018.1440107>
- Fork, M. L., Karlsson, J., & Sponseller, R. A. (2020). Dissolved organic matter regulates nutrient limitation and growth of benthic algae in northern lakes through interacting effects on nutrient and light availability. *Limnology and Oceanography Letters*, 5(6), 417–424. <https://doi.org/10.1002/lol2.10166>
- Granéli, W., Bertilsson, S., & Philibert, A. (2004). Phosphorus limitation of bacterial growth in high Arctic lakes and ponds. *Aquatic Sciences*, 66(4), 430–439. <https://doi.org/10.1007/s00027-004-0732-7>
- Havig, J. R., & Hamilton, T. L. (2019). Snow algae drive productivity and weathering at volcanic rock-hosted glaciers. *Geochimica et Cosmochimica Acta*, 247, 220–242. <https://doi.org/10.1016/j.gca.2018.12.024>
- Heal, K. R., Qin, W., Ribalet, F., Bertagnoli, A. D., Coyote-Maestas, W., Hmelo, L. R., et al. (2016). Two distinct pools of B12analogs reveal community interdependencies in the ocean. *Proceedings of the National Academy of Sciences*, 114(2), 364–369. <https://doi.org/10.1073/pnas.1608462114>
- Hogan, E. J., McGowan, S., & Anderson, N. J. (2014). Nutrient limitation of periphyton growth in arctic lakes in south-west Greenland. *Polar Biology*, 37(9), 1331–1342. <https://doi.org/10.1007/s00300-014-1524-8>
- Keenan, J. D., & Auer, M. T. (1974). The influence of phosphorus luxury uptake on algal bioassays. *Journal (Water Pollution Control Federation)*, 46(3), 532–542.
- Levine, M. A., & Whalen, S. C. (2001). Nutrient limitation of phytoplankton production in Alaskan Arctic foothill lakes. *Hydrobiologia*, 455(1/3), 189–201. <https://doi.org/10.1023/a:1011954221491>
- McCutcheon, J., Lutz, S., Williamson, C., Cook, J. M., Tedstone, A. J., Vanderstraeten, A., et al. (2021). Mineral phosphorus drives glacier algal blooms on the Greenland Ice Sheet. *Nature Communications*, 12(1), 570. <https://doi.org/10.1038/s41467-020-20627-w>
- Myrstener, M., Fork, M. L., Bergström, A.-K., Puts, I. C., Hauptmann, D., Isles, P. D. F., et al. (2022). Resolving the drivers of algal nutrient limitation from boreal to Arctic lakes and streams. *Ecosystems*, 25(8), 1682–1699. <https://doi.org/10.1007/s10021-022-00759-4>
- Panzeca, C., Beck, A. J., Leblanc, K., Taylor, G. T., Hutchins, D. A., & Sañudo-Wilhelmy, S. A. (2008). Potential cobalt limitation of vitamin B12 synthesis in the North Atlantic Ocean. *Global Biogeochemical Cycles*, 22(2), GB2029. <https://doi.org/10.1029/2007gb003124>
- Saito, M. A., Moffett, J. W., & DiTullio, G. R. (2004). Cobalt and nickel in the Peru upwelling region: A major flux of labile cobalt utilized as a micronutrient. *Global Biogeochemical Cycles*, 18(4), GB4030. <https://doi.org/10.1029/2003gb002216>
- Saito, M. A., Rocap, G., & Moffett, J. W. (2005). Production of cobalt binding ligands in a *Synechococcus* feature at the Costa Rica upwelling dome. *Limnology & Oceanography*, 50(1), 279–290. <https://doi.org/10.4319/lo.2005.50.1.0279>
- Schade, J. D., Seybold, E. C., Drake, T., Spawn, S., Sobczak, W. V., Frey, K. E., et al. (2016). Variation in summer nitrogen and phosphorus uptake among Siberian headwater streams. *Polar Research*, 35(1), 24571. <https://doi.org/10.3402/polar.v35.24571>
- Tanabe, Y., Kudoh, S., Imura, S., & Fukuchi, M. (2008). Phytoplankton blooms under dim and cold conditions in freshwater lakes of East Antarctica. *Polar Biology*, 31(2), 199–208. <https://doi.org/10.1007/s00300-007-0347-2>
- Tanabe, Y., Ohtani, S., Kasamatsu, N., Fukuchi, M., & Kudoh, S. (2010). Photophysiological responses of phyto-benthic communities to the strong light and UV in Antarctic shallow lakes. *Polar Biology*, 33(1), 85–100. <https://doi.org/10.1007/s00300-009-0687-1>
- Tanabe, Y., Hori, M., Mizuno, A. N., Osono, T., Uchida, M., Kudoh, S., & Yamamoto, M. (2019). Light quality determines primary production in nutrient-poor small lakes. *Sci Rep-Uk*, 9(1), 4639. <https://doi.org/10.1038/s41598-019-41003-9>
- Vadeboncoeur, Y., Jeppesen, E., Zanden, M. J. V., Schierup, H. H., Christoffersen, K., & Lodge, D. M. (2003). From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology & Oceanography*, 48(4), 1408–1418. <https://doi.org/10.4319/lo.2003.48.4.1408>
- Xing, P., Tao, Y., Jeppesen, E., & Wu, Q. L. (2021). Comparing microbial composition and diversity in freshwater lakes between Greenland and the Tibetan Plateau. *Limnology & Oceanography*, 66(S1), S142–S156. <https://doi.org/10.1002/lno.11686>