

1   **Changing biogeochemistry of the Arctic Ocean: insights from a nutrient and inorganic**  
2   **carbon perspective**

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7   **Abstract:** The Arctic physical system is changing in profound ways, with implications for the  
8   transport of nutrients to and from the Arctic Ocean (AO), as well as the internal cycling of  
9   material on shelves and basins. Significant increases in AO primary production (PP) have been  
10   observed in the last two decades, potentially driven by a suite of mechanisms that increase  
11   nutrient availability to upper ocean waters. However, the importance of these mechanisms,  
12   which include increased transport from adjacent subpolar regions, enhanced within- and  
13   between- season mixing, and increased mobilization of nutrients from terrestrial pools, varies  
14   substantially within various AO subregions, leading to a mosaic of trajectories that vary in sign  
15   and magnitude. Changes in PP are also driving regional changes in the biologically-mediated air-  
16   sea exchange of CO<sub>2</sub>, while warming, enhanced stratification, increased mobilization of carbon  
17   from terrestrial pools, and changing wind patterns are also driving regionally-variable trends.

18   **Introduction**

19   As a climate-sensitive region experiencing surface air temperature warming at a pace that is  
20   more than double that of the rest of the globe (Taylor et al., 2017, Jacobs et al., 2021), the Arctic  
21   is in the midst of profound change. Extensive loss of sea-ice area in all months of the year  
22   (Stroeve & Notz, 2018) is affecting regional albedo and radiative heat budgets. Decreased sea ice  
23   extent and persistence is also allowing increased communication between the upper ocean and  
24   atmosphere, with enhanced transfer of momentum from atmospheric cyclones and storms, and  
25   enhanced exchange of heat and gases in areas previously covered by ice (Crawford & Serreze,  
26   2017; Screen et al., 2011; Serreze et al., 2009). Thinning ice and increased extent and duration of  
27   seasonal open water is increasing phytoplankton primary productivity (PP) in previously light  
28   limited regions (e.g., Arrigo & van Dijken, 2015). Meanwhile, enhanced stratification from  
29   increased upper ocean freshwater content in deep basins restricts nutrient replenishment from  
30   subsurface waters and limits phytoplankton growth and the exchange of gases and heat between  
31   the atmosphere and subsurface waters of Arctic basins (Carmack et al., 2016; Haine et al., 2015;  
32   McLaughlin & Carmack, 2010).

33   These shifting baselines in the physical system are already driving changes in the  
34   biogeochemical cycling of nutrients and carbon throughout the Arctic Ocean (AO) in both  
35   predictable and less predictable (or even counterintuitive) ways. Bathymetry, stratification,  
36   seasonal vs. perennial ice coverage, exposure to storms, degree of river and terrestrial influence,  
37   and influence of advection from adjacent regions all determine regional responses.  
38   Consequently, AO subregions (i.e., shelves vs. basins, those positioned at Arctic gateways vs.  
39   those situated at interior locations on circulation pathways) are forced by a unique mélange of  
40   drivers and their responses vary in both sign and magnitude. Hence, while the long-term decrease  
41   of sea ice from the AO is a unifying trend, the AO biogeochemical responses are not singular,  
42

48 but rather, a suite of complex, regional-scale trajectories. Here, I attempt to highlight key aspects  
49 of AO biogeochemical change through the lens of a foundational currency, nitrogen, which  
50 functions as the primary limiting nutrient controlling PP in the AO and as such is at the heart of  
51 many of the biogeochemical changes occurring throughout the AO. I evaluate insights that  
52 emerge from an AO-wide budget of nitrogen, as well as those that emerge from understanding  
53 regional scale dynamics underlying integrated, AO-wide net change. I will also briefly comment  
54 on some of the consequences of a changing physical system and nutrient dynamics for the air-sea  
55 exchange of CO<sub>2</sub> in the AO.

56

## 57 **Changing nutrient supply in the AO**

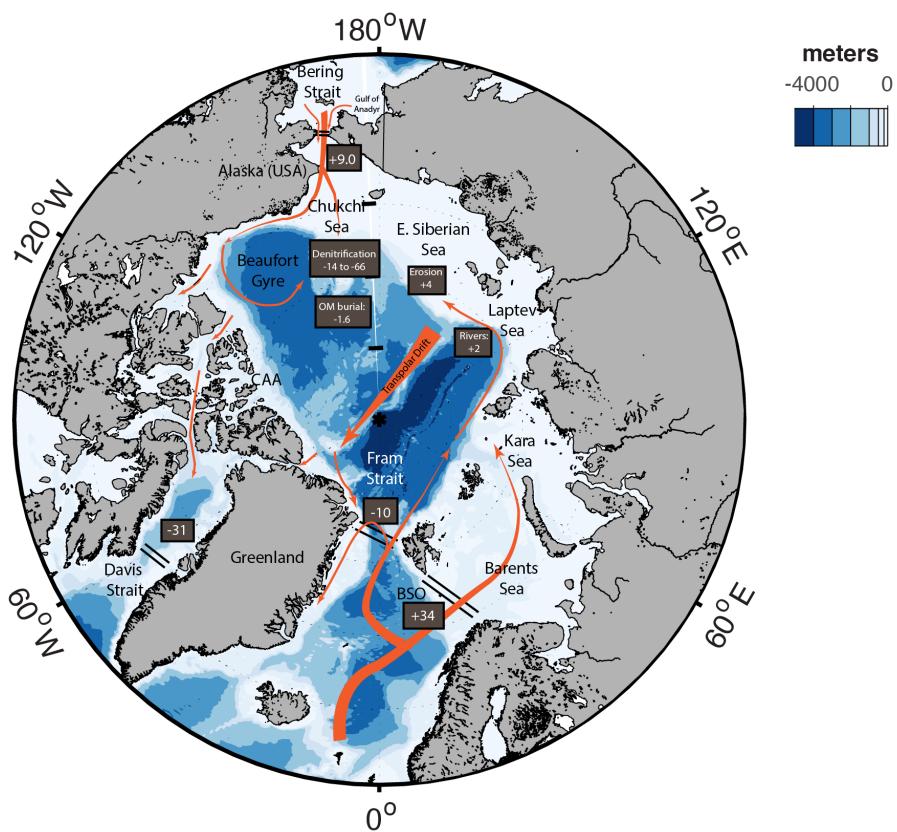
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59 Water column nutrient distributions are a fundamental control on photosynthesis, and hence, the  
60 PP that forms the foundation of AO ecosystems. PP, and more specifically, net community  
61 production (the fraction of PP that is not respired by heterotrophs in surface waters) also  
62 facilitates the sequestration of CO<sub>2</sub> in the AO as the carbon contained in organic matter settles to  
63 a depth where, upon subsequent oxidation, the resulting CO<sub>2</sub> generated is separated from the  
64 atmosphere. The major limiting nutrient controlling primary production in the AO is nitrogen, as  
65 inorganic nitrogen (hereafter referred to as dissolved inorganic nitrogen, DIN, which includes the  
66 sum of nitrate, nitrite, and ammonium species) is typically found with phosphorus in a molar  
67 ratio much lower than the canonical Redfield stoichiometry of 16:1 (Codispoti et al., 2013;  
68 Tremblay et al., 2015). The deficiency of DIN in AO waters can be understood in the context of  
69 AO circulation and connectivity to other basins: low N:P waters from the subarctic Pacific Ocean  
70 advect into the AO (Tremblay et al., 2015; Yamamoto-Kawai et al., 2006) while additional DIN  
71 losses occur within the AO by denitrification on Arctic shelves (Figure 1; Chang & Devol,  
72 2009). Surface waters in much of the ice-free AO exhibit depleted surface DIN inventories  
73 quickly after ice retreat, leading to nutrient limitation of PP and oligotrophic status during the  
74 rest of the open water season when light is abundant (Figure 2). Climate-related changes to the  
75 availability of DIN in surface waters therefore have special significance for primary productivity  
76 and biological pump functioning.

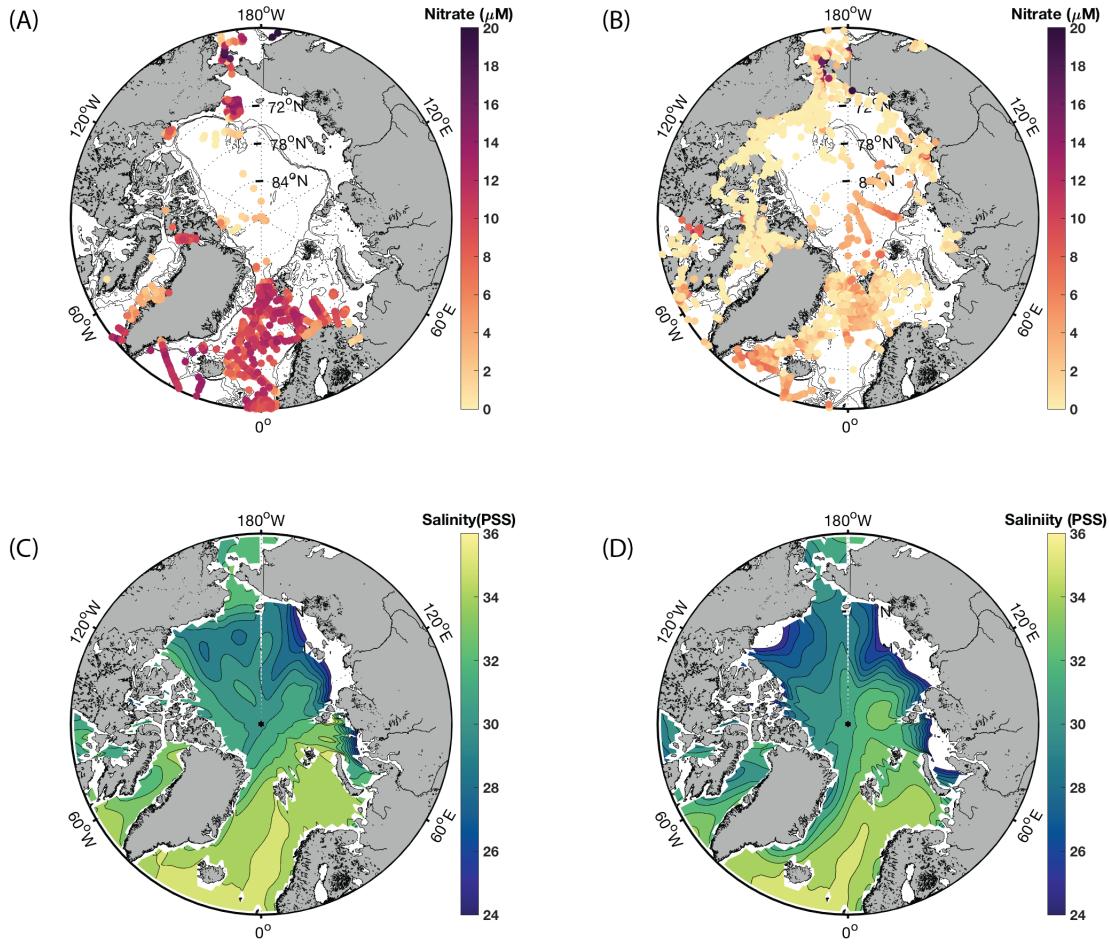
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78 Recent Pan-Arctic remote sensing studies have indicated an approximate 60% increase in Arctic  
79 PP between 1998 and 2018 in open water areas, with a recognition that reduced light limitation  
80 and increased nutrient availability are fueling this increase (Ardyna & Arrigo, 2020; Lewis et al.,  
81 2020). With regard to the former, declining ice cover, increasing open water area, and decreased  
82 sea ice persistence all clearly contribute to more light availability for photosynthesis (e.g., Pabi et  
83 al., 2008). However, with regard to the latter, nutrient concentration and flux data are generally  
84 not available at sufficient spatial and temporal resolution to quantify the importance of various  
85 mechanisms that increase nutrient supply. Consequently, hypotheses concerning PP increases  
86 fueled by changing DIN supply are largely based on inference. As an example, remote sensing  
87 indicates that some of the largest increases in PP and chlorophyll concentration occur in the  
88 Barents and Chukchi Seas (Lewis et al., 2020), regions known as AO “inflow” shelves (Carmack  
89 et al., 2006). These regions are situated at Arctic gateways where prevailing circulation advects  
90 water masses (and the nutrients contained therein) from adjacent sub-Arctic regions (Figure 1).  
91 Recent increases in water transport through Arctic gateways (Årthun et al., 2012; Polyakov et al.,  
92 2020; Woodgate, 2018) have been hypothesized to increase DIN supply and fuel observed PP  
93 and chlorophyll increases (Lewis et al., 2020).

95 In addition to these *remote* nutrient inputs from adjacent sub-Arctic seas, a suite of *local* delivery  
 96 mechanisms spurred by a changing physical environment are also likely to impact nutrient  
 97 availability in sunlit waters (Tremblay et al., 2015). These mechanisms are governed by  
 98 regionally specific physical considerations (bathymetry, relative ice cover, stratification, wind  
 99 patterns, and degree of terrestrial influence), as well as factors related to differences in the  
 100 biological community (grazing rates, community composition) and as such are regionally and  
 101 spatially variable and operate on a spectrum of inherent timescales. Together these factors  
 102 influence the degree to which nutrients are seasonally replenished in winter, as well as the degree  
 103 to which episodic nutrient fluxes occur during the ice-free season (Carmack & Chapman, 2003;  
 104 Pickart et al., 2013; Randelhoff et al., 2020; Randelhoff & Sundfjord, 2018). Mobilization of  
 105 terrestrial and shelf-derived material from increased river discharge, thawing permafrost, and  
 106 enhanced coastal erosion also plays an important role in certain regions (Frey & McClelland,  
 107 2009; Le Fouest et al., 2013; Terhaar et al., 2021).



**Figure 1:** Map of the Arctic Ocean showing Arctic gateways at Bering Strait, Fram Strait, Davis Strait, and the Barents Sea Opening (BSO). Major regional seas characterized by inflow shelves (Chukchi and Barents Seas), interior shelves (Beaufort, Kara, Laptev, and East Siberian Seas) and outflow shelves (Canadian Arctic Archipelago, CAA) are also indicated. Orange arrows indicate conceptual representation of major circulation pathways. Also shown are depth-integrated DIN transport fluxes through AO gateways as reported in Torres-Valdés et al. (2013). Estimates of internal DIN sources and sinks as discussed in the text are also indicated. All quantities are indicated in  $\text{kmol N s}^{-1}$ , for consistency with the AO gateway flux estimates.



**Figure 2:** Seasonal patterns of nutrients and salinity in the AO. Nutrient data compiled from Codispoti et al. (2013) as well as additional sources reported in Randelhoff et al. (2020). Salinity is from a seasonal climatology based on the World Ocean Database (Boyer et al., 2014). Shown are: A) Winter (November- March) surface (<10 m) nitrate concentration; B) post-bloom (August-September) surface nitrate concentration; C) winter (January-March) salinity climatology; d) summer (July-September) salinity climatology.

108

109 *A baseline DIN budget for the AO*

110

111 To provide important context for how DIN supply and availability may be changing in various  
 112 subregions of the AO, it is helpful to first start with a zoomed out, pan-Arctic scale view of how  
 113 known DIN sources and sinks contribute to the AO baseline budget. The budget approach, a  
 114 tried-and-true tool in the biogeochemistry playbook, identifies important knowledge gaps and  
 115 helps provide important context regarding potential sensitivities to perturbations. Multiple  
 116 attempts to construct DIN budgets for the AO have been undertaken in the last 50 years, often  
 117 with spatially and temporally sparse data (see Torres-Valdés et al., 2013 and references therein).  
 118 The most recent and comprehensive effort to date used a model of depth-resolved circulation and  
 119 measured nutrient profiles from Arctic gateway regions in summer to constrain the DIN inputs  
 120 and outputs via transport (Torres-Valdés et al., 2013). This analysis found that the major net  
 121 sources of DIN to the AO were via inflow gateways at Bering Strait ( $9.0 \text{ kmol s}^{-1}$ ) and the

122 Barents Sea Opening (34 kmol s<sup>-1</sup>, Figure 2). The Fram and Davis Strait gateways also had  
123 substantial DIN inputs, but these were offset by large nutrient outputs in equatorward currents.  
124 Fram Strait was a net exporter of DIN (-10 kmol s<sup>-1</sup>), a balance of inputs (53 kmol s<sup>-1</sup>), primarily  
125 via the West Spitsbergen Current, and outputs (-63 kmol s<sup>-1</sup>) from the East Greenland Current.  
126 The net DIN transport in Davis Strait (-31 kmol s<sup>-1</sup>) was dominated by the outflow on the  
127 western side (-38 kmol s<sup>-1</sup>), with a weak inflow on the shallow waters of the eastern side (6 kmol  
128 s<sup>-1</sup>). Perhaps more importantly, the sum of all DIN inputs and outputs at AO gateways was 1  
129 kmol s<sup>-1</sup>, indistinguishable from zero given the methodological uncertainties.  
130

131 A near-zero net DIN transport is an intriguing result because it suggests that the nutrient budget  
132 is balanced with respect to transport, which indicates that there cannot be additional, internal  
133 DIN losses within the AO without additional sources. Otherwise, DIN inventories would deplete  
134 over time. However, there are a few important caveats. The aforementioned analysis (Torres-  
135 Valdés et al., 2013) relied solely on summer transport and nutrient profiles (primarily from a  
136 single season in 2005, with some sensitivity studies); thus seasonal and interannual variability in  
137 nutrient fluxes was not captured. As will be discussed in the following section, the advection of  
138 nutrients through Arctic gateways in winter months, and interannual variability in DIN  
139 transports, are likely critical for setting the inventory of nutrients within the AO. To fully close  
140 the nutrient budget requires that coupled transport and nutrient fluxes be resolved over  
141 timescales relevant to AO circulation. These required observations are not yet available.  
142

143 Nonetheless, it is still useful to evaluate the implications of a net zero transport of DIN through  
144 AO gateways. Internal system losses of DIN are well-documented, and these could not be  
145 sustained indefinitely in the absence of additional sources if net transport of DIN was negligible.  
146 Loss of DIN by microbially-mediated denitrification (conversion of fixed and bioavailable DIN  
147 to N<sub>2</sub> and N<sub>2</sub>O) is estimated to be a substantial internal sink term of 14 to 66 kmol N s<sup>-1</sup> (-6 to -29  
148 Tg N yr<sup>-1</sup>; Chang & Devol, 2009, Figure 1). Denitrification is particularly prevalent on shallow  
149 Arctic shelves receiving a high flux of organic matter (Chang & Devol, 2009; Granger et al.,  
150 2018). Additional loss of DIN is expected through sedimentary burial of organic matter. The  
151 majority of organic matter produced via PP is respired back to DIN in surface or subsurface  
152 waters, but a small fraction of organic matter escapes oxidation and is buried (primarily on  
153 shallow and adjacent continental slopes where the settling time is reduced); in the AO estimated  
154 burial is 0.7 Tg N yr<sup>-1</sup> (3.7 Tg C yr<sup>-1</sup>, Stein & Macdonald, 2004) which equates to 1.5 kmol N s<sup>-1</sup>.  
155 These internal sinks are partially offset by additional DIN and dissolved organic nitrogen  
156 (DON) from terrestrial sources, mobilized by rivers and coastal erosion within the AO. These  
157 sources affect regional biogeochemical cycling but are believed to be small at the AO scale:  
158 ~1.5-1.7 kmol N s<sup>-1</sup> (Le Fouest et al., 2013; Torres-Valdés et al., 2013). DON flux through  
159 Arctic gateways may also represent an important source but at present it is poorly constrained  
160 (Torres-Valdés et al., 2013; Tremblay et al., 2015).  
161

162 The knowledge gaps that emerge from the large scale AO nutrient budget point toward areas  
163 where there are clear research needs. Resolving nutrient inputs at Arctic gateways over a full  
164 annual cycle, and quantifying interannual variability or trends, is of utmost importance for  
165 understanding how PP and biologically mediated CO<sub>2</sub> uptake may change in the AO. Better  
166 constraint of DON transport/utilization and reduction in the uncertainty of the denitrification sink  
167 might also help to bring the budget toward closure. However, the budget analysis also provides

168 important context for understanding what is known about changing sources and sinks, as well as  
169 coupled physical and biogeochemical processes that do not act as sources or sinks on an AO  
170 scale, but do impact regional DIN availability in the upper layers where PP and CO<sub>2</sub> uptake  
171 occurs. The next few sections tackle what is known regarding changing nutrient supply via AO  
172 gateways, changing nutrient supply via rivers, and changing upper ocean nutrient availability  
173 from physical processes operating over a range of space and time scales.  
174

175 *Changing nutrient supply at Arctic inflow shelves*

176 The AO gateway nutrient fluxes calculated by Torres-Valdés et al., 2013 relied on data from  
177 summer 2005, but observations from Arctic inflow shelves suggest that transport is changing  
178 significantly in these regions. At the Bering Strait gateway, a ~50% increase in the volume  
179 transport has been observed from the 1990s through 2014 (i.e., 0.7 to 1.1 Sv; Woodgate, 2018),  
180 leading some to hypothesize that this corresponds to increased DIN input to the areas  
181 immediately downstream (e.g., Ardyna & Arrigo, 2020; Lewis et al., 2020). However, the DIN  
182 flux (mass/time) is a product of both the volume transport (volume/time) and DIN content of  
183 various water masses (mass/volume) entering Bering Strait. Higher nutrient water is derived  
184 from outer slope waters of the Bering, and in particular waters that circulate in the Gulf of  
185 Anadyr to the southwest of Bering Strait (see sidebar by Frey et al., 2022 this issue). Terrestrial-  
186 origin fresh waters conveyed north by the Alaska Coastal Current on the eastern side of Bering  
187 Strait tend to be low-nutrient (Codispoti et al., 2013). Long-term trends in salinity monitored at  
188 Bering Strait have indicated that the transport has freshened significantly, particularly in winter  
189 (Woodgate & Peralta-Ferriz, 2021), which suggests that a direct correlation between transport  
190 and DIN flux cannot be presumed.  
191

192 Several lines of evidence suggest that delivery of DIN through Bering Strait may in fact be  
193 decreasing in the past decade. Moored sensor-based observations of near-bottom nitrate  
194 concentrations in the northern Bering Sea in late summer/early fall indicate an overall 50%  
195 decline over the 2005-2017 period (from ~20  $\mu$ M to ~10  $\mu$ M) with a rebound in 2018-2019  
196 (Mordy et al., 2020). These late summer/early fall nitrate concentrations in the northern Bering  
197 were also found to be highly correlated with those on the northern Chukchi shelf in mid-May,  
198 which roughly corresponds to the timing of sea-ice retreat and associated spring phytoplankton  
199 bloom in this region. In a separate analysis reported in this special issue, Frey et al. (2022) found  
200 a decline in remotely sensed- PP in western Bering Strait waters typically influenced by high-  
201 nutrient Anadyr water. Anomalously high PP in May in the Gulf of Anadyr, hypothesized to be  
202 driven by earlier ice retreat, mirrored a decrease in PP in downstream waters of the western  
203 Bering Strait in June (34% over 2004-2010), suggesting that nutrients were being consumed in  
204 the northern Bering and depleting nutrients that would normally allow PP to occur downstream  
205 in the Chukchi (Frey et al. 2022).  
206

207 On the other side of the AO in the Atlantic gateway region, the temporal trend in DIN flux is  
208 similarly unclear. Observations suggest a doubling of warm, Atlantic-origin water in the Barents  
209 Sea – a phenomenon termed the “Atlantification” of the European Arctic sector (Årthun et al.,  
210 2012). The heat content of this water mass has been implicated in the northward migration of the  
211 seasonal ice zone (Oziel et al., 2017), and, as a major source of nutrients to the region, might be  
212 presumed to support higher rates of primary production in the Barents Sea inflow shelf (Henley  
213 et al., 2020). However, the degree to which the high preformed nutrient content of Atlantic water

214 can be utilized by phytoplankton is influenced by stratification and ice-cover, which interact with  
215 local wind forcing to set seasonal nutrient replenishment in winter as well as intermittent pulses  
216 of nutrients into the system during the open water season (Figure 2; Henley et al., 2020; Slagstad  
217 et al., 2015; Wiedmann et al., 2017). The depth of mixing controls the inventory of DIN  
218 available for PP in the stratified surface layer; thus, even though Atlantic water may convey a  
219 reservoir of nutrients into the AO it has little influence on Arctic biogeochemical cycling unless  
220 it reaches surface waters. An ocean biogeochemical model run under a future warming scenario  
221 found a decrease in productivity in the southern Barents Sea inflow region over the next century  
222 due to enhanced thermal stratification, which reduces nutrient replenishment in winter (Slagstad  
223 et al., 2015). In addition, a decline in the nitrate concentration of inflowing Atlantic water in the  
224 Barents Sea has been observed over the 1990-2010 period; variations in the source region of  
225 waters feeding into the Barents Sea (due to climate-ocean responses to the North Atlantic  
226 Oscillation) may play a role in this trend (Oziel et al., 2017; Rey, 2012).  
227

228 In addition to nutrient-based controls on PP on inflow shelves, the importance of other processes  
229 that regulate biomass, including advection of phytoplankton and grazers from adjacent regions  
230 (Vernet et al., 2019; Wassmann et al., 2019), should be considered. Recent biogeochemical  
231 modeling in the Barents Sea and Fram Strait regions suggest that a substantial proportion of  
232 biomass and resulting PP is supported by advection of phytoplankton from south to north along  
233 major currents (Vernet et al., 2019). The importance of advected vs. in situ production is  
234 seasonally and spatially variable but the upshot is that this advection allows more northerly  
235 regions to maintain much higher rates of PP than they otherwise would with no advective inputs.  
236 This advected biomass ultimately amounts to a  $0.76 \text{ Tg C yr}^{-1}$  supplement of organic carbon (and  
237 its stoichiometric equivalent of organic N) to the AO north of Svalbard, with internal subregions  
238 within the Barents Sea receiving higher subsidies (Vernet et al., 2019). Advection of grazers  
239 (e.g., copepods and microzooplankton) northward also regulates existing biomass and is an  
240 important control on PP in inflow shelf regions (Wassmann et al., 2019, 2021). Thus, physical  
241 and ecological factors that influence grazer communities (surface warming, changes in advective  
242 transport, changing spatial patterns of phytoplankton biomass) will ultimately influence AO PP  
243 trends as well.  
244

#### 245 *Increasing influence of terrestrial nutrient sources*

246  
247 Recent studies also implicate nutrients supplied by coastal erosion and rivers as having an  
248 increasingly important role in supporting observed PP increases and influencing coastal  
249 biogeochemical cycling in the AO. Increased river discharge, thawing permafrost with deepening  
250 active layers, and enhanced shoreline erosion due to a loss of buttressing ice in fall and winter all  
251 intensify the land-ocean exchange of material (Frey & McClelland, 2009; McClelland et al.,  
252 2012). One recent modeling analysis that sought to quantify the impact of terrestrial sources on  
253 the AO indicated that DIN supplied by coastal erosion and rivers (estimated as  $1.6 \text{ Tg N yr}^{-1}$  and  
254  $1.0 \text{ Tg N yr}^{-1}$ , respectively) supports 1/3 of Arctic PP on an annual basis (rivers: 9-11%, coastal  
255 erosion 19-41%; Terhaar et al., 2021). Consistent with prior work (e.g., Frey & McClelland,  
256 2009; Holmes et al., 2012; Peterson et al., 2002), the majority of the terrestrially-derived DIN  
257 sources were focused in the Eurasian Arctic (East Siberian, Kara, and Laptev shelves), where the  
258 Yenisey, Lena, and Ob', the 3 largest Arctic rivers by annual discharge and the 5<sup>th</sup>, 6<sup>th</sup>, and 13<sup>th</sup>  
259 largest rivers globally, respectively, are located. However, the N supply was only estimated to

support a biomass increase (new production) of 17 Tg C yr<sup>-1</sup>, while the simulated increase to productivity was 8x the biomass increase (140 Tg C yr<sup>-1</sup>). Hence, the large modeled PP response is mostly from continued recycling of the initial (modest) DIN input (i.e., regenerated production, (Dugdale & Goering, 1967). This finding is consistent with prior analyses that also found modest contributions of river-derived nutrients to new production (Le Fouest et al., 2013; Tank et al., 2012) due to the carbon-rich and nitrogen poor nature of Arctic rivers (Holmes et al., 2012). The distinction between new vs. regenerated PP is important because these types of PP influence carbon and nutrient cycling differentially. Regenerated production is a zero sum process and does not involve a net biological uptake of CO<sub>2</sub> because regeneration and reuse of N contained in organic matter also regenerates CO<sub>2</sub>. New production is not zero sum, and can support biomass transfer to higher trophic levels, thus fueling Arctic ecosystems. Alternatively, organic matter produced during new production can sink to subsurface water masses that are out of reach of seasonal mixing horizons; in so doing the carbon and nutrient contained becomes isolated from further biogeochemical cycling in the surface environment.

Observations from the recent Arctic GEOTRACES mission provide additional evidence of an increasing signature of terrestrial and shelf inputs into AO waters. An increase in radiotracer activities (<sup>228</sup>Ra and <sup>226</sup>Ra) in the Transpolar Drift of the central AO (Figure 1) in 2015 relative to 2007 is indicative of increased shelf-based inputs from East Siberian and Laptev Sea shelves (Kipp et al., 2018). Kipp et al hypothesized that disturbance of a large <sup>228</sup>Ra reservoir in shelf sediments by enhanced wind-driven mixing over a longer open water season was the primary driver of these changes. These findings are broadly consistent with those of the coastal erosion modeling study (Terhaar et al., 2021), which found largest modeled increases in PP from terrestrial sources were on the East Siberian, Laptev, and Kara shelves.

The Kipp et al (2018) study as well as aforementioned river and coastal erosion studies all paint a picture of Eurasian shelves that are “interior” in AO circulation pathways (Figure 1, Carmack et al., 2006)) and heavily influenced by large Arctic rivers as sites of intensified land-ocean biogeochemical cycling and sediment mobilization. This unique regional character is important to note because, as described above, these regions exhibit a different suite of responses to AO change than are seen in other regions.

### *Changes to seasonal nutrient replenishment*

In addition to nutrient sources from Arctic rivers and transport through Arctic gateways, processes that affect the depth distribution of nutrients over an annual cycle are also critical for influencing biogeochemical nutrient and carbon cycling in the AO. In seasonally and perennially ice-free waters, pre-bloom nutrient inventories at the surface are well correlated with patterns of annual primary production throughout the AO (Figure 2, Randelhoff et al., 2020; Tremblay et al., 2015; Tremblay & Gagnon, 2009). The association is somewhat intuitive since DIN inventory amassed during winter mixing determines the reservoir available to phytoplankton when sea-ice seasonally thins and retreats and light levels become sufficient for growth (Codispoti et al., 2013; Randelhoff & Sundfjord, 2018; Tremblay et al., 2015). However, the degree of winter replenishment varies across Arctic shelves and deep basins, governed by the regional stratification, the depth of winter mixing, and depth of the nitracline (Randelhoff et al., 2020; Tremblay et al., 2015; Wassmann & Reigstad, 2011). Typically, shallow shelves nearest to

306 nutrient sources at  
 307 AO gateways have  
 308 more robust  
 309 replenishment while  
 310 open waters  
 311 overlying deeper  
 312 bathymetry and  
 313 strong stratification  
 314 have weakest  
 315 replenishment  
 316 (Figure 2 &3). For  
 317 example, the  
 318 Chukchi Sea in the  
 319 Pacific Arctic sector  
 320 is characterized by a  
 321 broad, shallow shelf  
 322 (ca. 50 m), and a  
 323 relatively shallow  
 324 nitracline (ca. 20-40  
 325 m); in winter, storms  
 326 and convective  
 327 mixing completely  
 328 erode the seasonal  
 329 stratification and the  
 330 nutrients  
 331 accumulated in the  
 332 near-bottom layer  
 333 from  
 334 remineralization of  
 335 organic matter over  
 336 the summer are  
 337 redistributed  
 338 throughout the water  
 339 column (Figure 3)

340 (Mordy et al., 2020; Pacini et al., 2019). The Barents Sea shelf is deeper (ca. 200 m), but this  
 341 region has also historically been characterized by extensive replenishment of DIN by convective  
 342 and storm-driven mixing in fall/winter (Randelhoff et al., 2020; Slagstad et al., 2015). The strong  
 343 replenishment contributes to the very high rates of PP in these locales during ice retreat in spring  
 344 (V. Hill & Cota, 2005; Matrai et al., 2013). In contrast, the depth of the nitracline in the deep  
 345 Canada Basin of the Central AO exceeds that of typical winter mixing depths (Carmack et al.,  
 346 2016; McLaughlin & Carmack, 2010; Randelhoff et al., 2020). In regions of the high latitude  
 347 central AO that have transitioned from perennial to seasonal ice-cover, nutrient replenishment is  
 348 also likely weak but a lack of complete DIN drawdown during the vegetative season in these  
 349 regions indicates that light limitation still plays an important role in limiting PP (Figure 2,  
 350 Randelhoff et al., 2020); hence, at present, the role of seasonal nutrient replenishment is not as

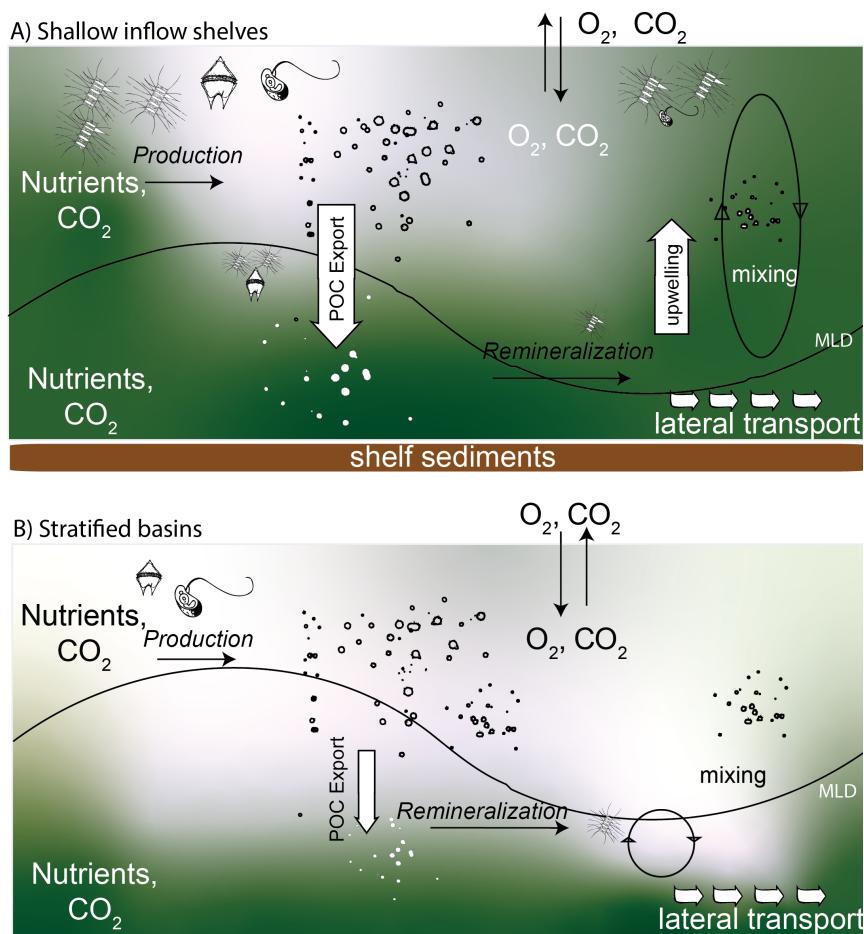


Figure 3: Conceptual realization of nutrient replenishment mechanisms on A) shallow inflow shelves and B) stratified deep basins. Green shading is meant to indicate relative nutrient availability. Inflow shelves experience advective nutrient inputs from lower latitudes, and strong replenishment within and between seasons, supporting high rates of biological productivity and organic matter export. Stratified interior shelves and basins have weaker within and between season nutrient replenishment, with consequent lower productivity rates.

351 important here but with continued declines in ice cover this pattern is expected to change  
352 (Slagstad et al., 2015).

353  
354 However, the degree of winter nutrient replenishment is certainly a process that is sensitive to  
355 future climate forcing. For example in the Barents Sea, biogeochemical modeling indicates that  
356 future warming and enhanced thermal stratification will restrict winter nutrient replenishment in  
357 the southern Barents Sea, limiting PP (Slagstad et al., 2015). Observations suggest that enhanced  
358 stratification in the Beaufort gyre has already depressed the nitracline, limiting the resupply of  
359 DIN to surface waters (McLaughlin & Carmack, 2010), consistent with the low PP rates  
360 typically observed in this region as well as an observed shift to smaller picoplankton that are  
361 better equipped for nutrient-limited conditions (Li et al., 2009). Biogeochemical modeling also  
362 predicts further decreases in PP in the Beaufort gyre in the future (Slagstad et al., 2015). The  
363 fundamentally different trajectories of inflow shelves and deep basins with respect to declining  
364 ice cover and seasonal nutrient replenishment typify the mosaic of responses experienced by AO  
365 subregions to warming-induced physical system change. In the former, decrease in ice coverage  
366 over winter months facilitates mixing and momentum transfer whereas in the latter enhanced  
367 haline stratification limits seasonal replenishment. Again, these differences demonstrate that  
368 understanding the unique character of AO subregions is critical to understanding biogeochemical  
369 responses to climate-driven changes.

370  
371 *Episodic nutrient delivery by storms and wind-events:*  
372

373 While changes in transport and winter replenishment set total nutrient inventories in the upper  
374 water column that are available to phytoplankton for early season growth, episodic pulses of  
375 nutrients facilitated by regional wind-forcing and/or current-bathymetry interactions can be  
376 important for maintaining productivity throughout the post-bloom, summer open water season  
377 when nutrients are scarce (Ardyna et al., 2014; Nishino et al., 2015; Pickart et al., 2013;  
378 Wiedmann et al., 2017). Because these mechanisms help to relieve nutrient limitation and  
379 support continued lower trophic level production over an expanding growing season duration  
380 (i.e., due to lengthening open water duration) they may be increasingly important in a warming  
381 Arctic.

382  
383 Enhancement of shelf break upwelling by the expansion of the seasonal melt zone has long been  
384 recognized as an important mode by which PP might be enhanced in a warming Arctic (Carmack  
385 & Chapman, 2003). Reduced or minimal ice cover at continental shelf breaks facilitates the  
386 transfer of wind momentum; when prevailing high and low atmospheric pressure centers  
387 facilitate directional, upwelling-favorable winds and shelf break depths are shallow enough to  
388 constrict flow and allow horizontal divergence (Randelhoff & Sundfjord, 2018), nutrient-rich  
389 waters are brought to the surface. This is particularly true along the Beaufort Sea shelf break and  
390 in the vicinity of Barrow Canyon in the NE Chukchi Sea (Pickart et al., 2013). While much of  
391 the Eurasian Arctic sector is characterized by relatively deep shelves, conditions for upwelling  
392 may be favorable at the comparatively shallow Laptev Sea shelf break (Randelhoff & Sundfjord,  
393 2018).

394  
395 Analysis of long-term wind and mooring data in the vicinity of the Beaufort shelf break indicates  
396 that upwelling can be induced by moderate easterly winds (threshold of  $6 \text{ m s}^{-1}$ ) and that the

frequency of upwelling-favorable events has likely increased in recent decades (Pickart et al., 2013). The estimated upward DIN flux associated with these events could support significant rates of new production (average of ~400 mmol C m<sup>-2</sup> per storm) if all supplied DIN is converted to biomass, but it is presently unknown the extent to which this occurs. Remotely-sensed and ship-based observations do indicate clear PP response to coastal upwelling events (Pickart et al., 2013) and the long-term satellite chlorophyll record notably indicates increased concentrations at both the Beaufort and Laptev Sea shelf breaks (Lewis et al., 2020).

404

The duration of upwelling events likely plays a role in their overall impact – longer events will allow more time for phytoplankton communities to respond and draw down available DIN inventories. Retentive circulation features facilitated by current-bathymetry interactions, such as those which facilitate aggregation of krill to the east of Pt. Barrow following upwelling (Okkonen et al., 2011) may extend PP responses beyond the lifetime of the initial wind-forcing. Recent work also suggests that shear and instabilities related to frequent changes in wind forcing can induce higher rates of cross-isopycnal nutrient flux in the Chukchi (Beaird et al., 2020). In contrast to the ‘reversible’ nutrient fluxes facilitated by temporary upwelling events these ‘non-reversible’ turbulent nutrient fluxes facilitate transfer of N from nutrient-rich bottom waters to shallower mid-water column depths where light is sufficient to fuel photosynthesis.

415

More generally, there is a growing recognition that turbulent and storm-induced nutrient fluxes away from shelf breaks may play an increasingly important role in supporting higher PP in the AO as the seasonal ice-zone and open water growing season expand. An analysis of satellite chlorophyll from 1998 to 2012 found an increased prevalence of fall blooms throughout the AO attributed to increased frequency of high-wind events during open water conditions in September and October (Ardyna et al., 2014). The most significant increases in fall bloom occurrence were on inflow shelves (Chukchi, Barents), Eurasian interior shelves (Siberian, Laptev, Kara), and ice-free portions of the Central Arctic. More recently, a biogeochemical modeling study found that high-frequency winds facilitate higher AO primary productivity by two main nutrient-delivery mechanisms: first, and most significant, was the enhanced and earlier deepening of mixed layer and nutrient entrainment in fall when light was still sufficient to allow blooms to occur, but a secondary effect was attributed to a prolonged mixing period in winter which enhanced nutrient inventories that fuel spring productivity (Castro de la Guardia et al., 2019). Thus, an increase in mixing associated with high wind events is likely to manifest both within and between seasons. In addition earlier ice retreat has been noted to facilitate earlier spring blooms in some areas, including the Canadian Arctic Archipelago, Baffin Bay, and the Kara Seas (Kahru et al., 2011).

432

433

### 434 **Implications for Carbon Cycling**

The coupling of carbon, nitrogen, and phosphorus in biologically mediated processes (Redfield et al., 1963) means that changing patterns of nutrient supply and consequent PP are inextricably linked to carbon cycling as well. However, changes to the physical system (warming, freshwater inputs, sea-ice loss, changing wind speeds) also exert strong control on carbon exchange at the atmosphere-ocean and the terrestrial-ocean boundaries. Here, I briefly touch on ways that Arctic CO<sub>2</sub> is responding to the physical and biological system changes mentioned in previous sections. Here, the intention is not to provide a comprehensive review of AO carbon cycle dynamics (as is found in other comprehensive sources: e.g., (Bates & Mathis, 2009; Olsen et al., 2015) but

443 rather, to highlight key notable trends occurring at ocean-atmosphere and ocean-lithosphere  
444 boundaries.

445

446 *Changes to AO CO<sub>2</sub> uptake due to changing primary productivity*

447

448 Regions of the AO that have seen marked increases in PP over the last several decades, in  
449 particular the Arctic gateway inflow shelves, will also act as strong biologically-mediated sinks  
450 for CO<sub>2</sub> on a seasonal basis as organic matter is produced in the surface and exported to depth.  
451 As exported organic matter is respiration at depth, seasonal stratification prevents mixing of  
452 accumulated respiratory CO<sub>2</sub> to the surface where it would otherwise outgas, much as it restricts  
453 the resupply of DIN that also accumulates (Figure 3). Input of CO<sub>2</sub> associated with respiration of  
454 exported organic matter at depth also contributes to seasonal undersaturation of calcium  
455 carbonate minerals (i.e., corrosivity (Bates & Mathis, 2009). Historically, this biologically-  
456 mediated organic carbon pump has helped the Chukchi and Barents Seas to maintain strongly  
457 undersaturated CO<sub>2</sub> at the surface, and has facilitated these areas functioning as regions of  
458 enhanced ocean uptake of CO<sub>2</sub> from the atmosphere, while interior shelves and deep basins with  
459 low PP rates represent much weaker sinks (Bates & Mathis, 2009; Pipko et al., 2017; Yasunaka  
460 et al., 2016). The recently reported increases in PP on Arctic shelves therefore have the potential  
461 to enhance oceanic uptake of CO<sub>2</sub> so long as they are associated with export of material to depth  
462 and not regenerated production, where CO<sub>2</sub> is alternately consumed and released by  
463 photosynthesis and respiration (Dugdale & Goering, 1967; Tremblay et al., 2015). For example,  
464 the substantial proportion of PP fueled by riverine and coastal erosion sources of DIN  
465 highlighted above (Terhaar et al., 2021) would only modestly contribute to enhanced biological  
466 CO<sub>2</sub> uptake since the majority of the PP in that study was determined to be regenerated. In  
467 contrast, a combination of modelling and observations suggests an increase in continental shelf  
468 PP and biological CO<sub>2</sub> uptake over a longer growing season on inflow shelves (Tu et al., 2021).  
469

470 In AO deep basin surface waters, a reduction of an already weak biologically-mediated CO<sub>2</sub> sink  
471 due to enhanced stratification and associated deepening of the nutricline (McLaughlin &  
472 Carmack, 2010) has already been noted (Cai et al., 2010; Else et al., 2013). This weakening CO<sub>2</sub>  
473 sink has been associated with a shift phytoplankton community composition toward smaller cells  
474 (picophytoplankton) in surface waters of the Beaufort Gyre (Li et al., 2009), which is suggestive  
475 of increased regenerated production and decreased net biological CO<sub>2</sub> uptake potential.  
476

477 Productivity associated with the previously-described shelfbreak upwelling and fall blooms  
478 warrant additional discussion with respect to new/regenerated production and biologically-  
479 mediated air-sea CO<sub>2</sub> exchange. The supply of DIN from depth that fuels these blooms also  
480 brings excess CO<sub>2</sub> leading to significant outgassing, as has been noted in several studies (Evans  
481 et al., 2015; Hauri et al., 2013; Mathis et al., 2012). Consumption of DIN at the surface during  
482 the bloom helps to mitigate this outgassing by drawing down the CO<sub>2</sub> of surface water; hence the  
483 timescale of DIN removal during a bloom helps to set the net source/sink status of CO<sub>2</sub> flux  
484 during these upwelling events. Whether or not these events represent new vs regenerated  
485 production depends on the depth from which nutrient-rich waters are sourced: DIN supplied  
486 from shallow horizons where organic matter produced earlier in the season has been respired  
487 would not in an annual budget sense be considered new production while DIN supplied from  
488 previously untapped reservoirs would be considered new production.

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Additional potential shifts in phytoplankton community composition in response to warming and other physical system change also stand to reduce the efficiency of biologically-mediated CO<sub>2</sub> uptake in the AO. Already, the Atlantification of the southern Barents Sea and the northward migration of the polar front has been implicated in the proliferation and northward expansion of coccolithophore blooms in this region (Neukermans et al., 2018)(Figure 4). Formation of CaCO<sub>3</sub> shells reduces alkalinity of surface waters and increases the partial pressure of CO<sub>2</sub> in surface waters ( $pCO_2 w$ , a primary determinant of air-sea CO<sub>2</sub> exchange) weakening the capacity for air-sea CO<sub>2</sub> uptake. Coccolithophores tend to proliferate under conditions expected in this region in the future -- i.e., warm waters with low to moderate nutrients and shallow mixed layers (Neukermans et al., 2018). While coccolithophore blooms have not been a noted occurrence in the Chukchi Sea, they have been noted in the adjacent Bering Sea (Figure 4). The overall consequences of these ecological shifts for net regional CO<sub>2</sub> uptake will require continued monitoring and ecosystem modelling to resolve.

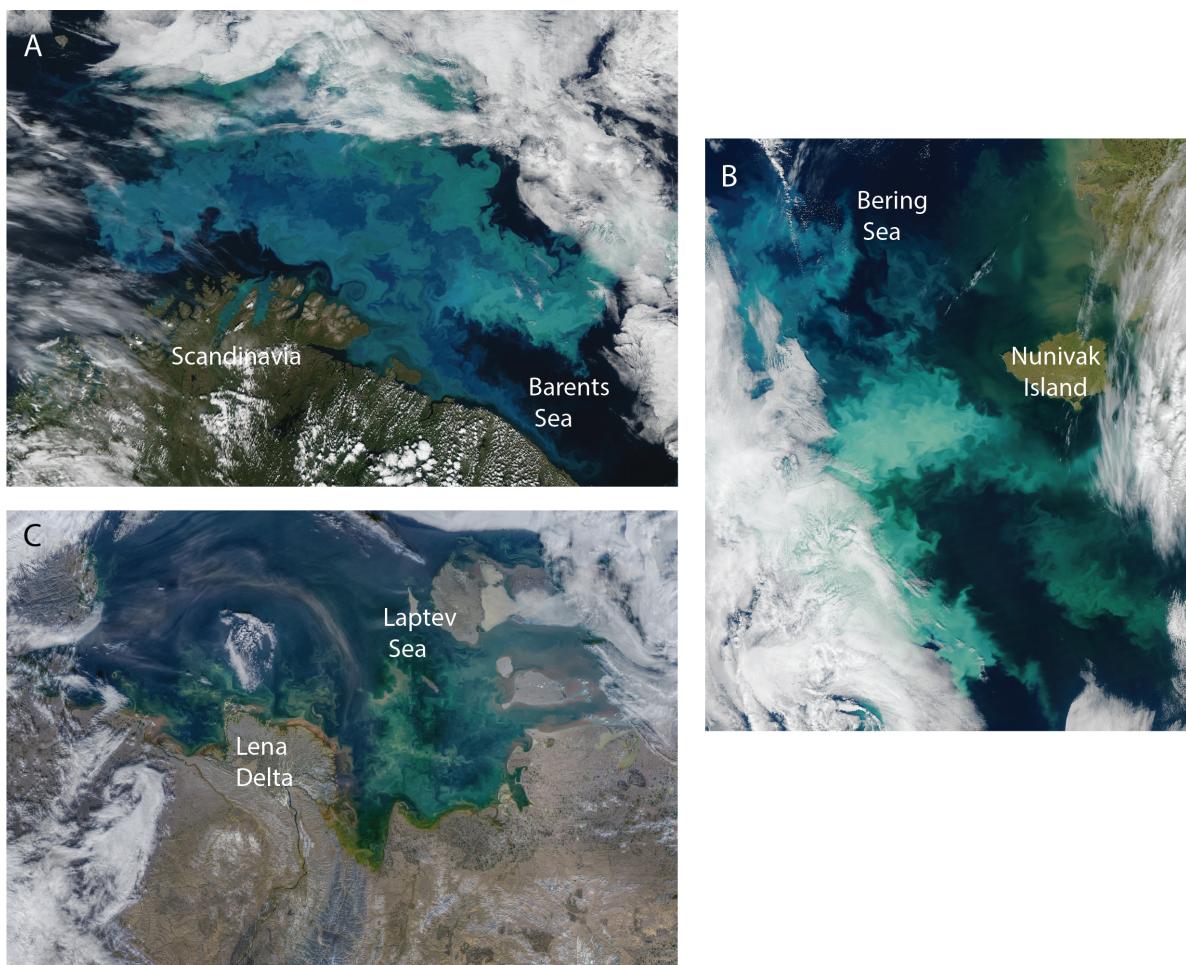


Figure 4: Remotely-sensed visible images from MODIS Aqua showing coccolithophore blooms in the A) Barents Sea B) Bering Sea. Also shown is C) turbidity in the Laptev Sea associated with terrestrial material delivered by the Lena delta. All images courtesy NASA Earth Observatory (<http://earthobservatory.nasa.gov>).

504

505 *Changes in abiotic drivers of AO CO<sub>2</sub> uptake*

506

507 Warming and freshening of AO surface waters will also impact the source/sink status of some  
508 AO regions, particularly AO deep basins and some interior shelves where biologically-mediated  
509 rates of CO<sub>2</sub> uptake are low. The expansion of the seasonal ice zone and reduction in sea ice  
510 extent in theory presents an opportunity for enhanced ocean uptake of CO<sub>2</sub> as cold high latitude  
511 surface waters can now more readily communicate with the atmosphere (Olsen et al., 2015) but  
512 pronounced warming and freshening of Arctic basins counter this potential. Increasing surface  
513  $pCO_{2w}$  in the Beaufort Sea over the last few decades, an expected outcome of warming, has  
514 already been noted in a number of studies (Cai et al., 2010; Else et al., 2013; Ouyang et al.,  
515 2020). This increased  $pCO_{2w}$  reduces the gradient between atmosphere and ocean, i.e.  $\Delta pCO_2 =$   
516  $pCO_{2w} - pCO_{2a}$  (where subscript *a* denotes atmosphere), an important determinant of the rate  
517 of air-sea CO<sub>2</sub> exchange:

518 
$$F_{CO_2} = k_{CO_2} K_o (pCO_{2w} - pCO_{2a}),$$

519 where  $k_{CO_2}$  is the air-sea gas transfer velocity, typically parameterized by a relationship with  
520 wind speed (Wanninkhof, 2014), and  $K_o$  is solubility of CO<sub>2</sub>, calculated as a function of  
521 temperature and salinity (Weiss, 1974). Seasonal freshwater input from sea ice melt or river  
522 discharge (Carmack et al., 2016) additionally reduces the capacity of these waters to buffer  
523 against additions/removals of CO<sub>2</sub> (by biological or abiotic processes), leading to reduced uptake  
524 capacity with additions of CO<sub>2</sub> (Rysgaard et al., 2011; Takahashi et al., 2014). Meanwhile,  
525 increased wind speeds (from more frequent storm activity) will tend to increase the rate of air-  
526 sea CO<sub>2</sub> exchange for a given air-sea gradient by increasing  $k_{CO_2}$ .

527

528 Increasing thermal stratification in the Barents Sea is also expected to reduce the CO<sub>2</sub> sink in this  
529 region in the future. Indeed, observations already indicate increasing  $pCO_{2w}$  and decreasing  
530 CO<sub>2</sub> uptake in the southern Barents Sea (Yasunaka et al., 2016). This stands in contrast to the  
531 other inflow shelf in the Chukchi, where biotic factors appear to be dominating over warming-  
532 related reductions (Tu et al., 2021).

533

534 *Intensified land-ocean carbon exchange on Eurasian/Siberian shelves*

535

536 Generally, discharge of AO Rivers is organic carbon rich and DIN poor (Holmes et al., 2012;  
537 McClelland et al., 2012) Thus, while the impact of PP supported by riverine nutrients may be  
538 slight, the impact of the organic carbon supplied by rivers on ocean-atmosphere CO<sub>2</sub> fluxes can  
539 be quite prominent, particularly on interior shelves in the Eurasian Arctic sector where a  
540 significant fraction of AO riverine discharge is focused (Anderson et al., 2009; Frey &  
541 McClelland, 2009; Pipko et al., 2017). Thawing of peat-rich permafrost in the Siberian Arctic,  
542 coupled with increasing river discharge, has the potential to increase loading of allochthonous  
543 carbon to the coastal ocean. Loss of buttressing sea ice and enhanced wave energy from wind  
544 events also appears to be contributing to enhanced erosion of coastlines and resuspension of shelf  
545 sediments, with increased lithogenic and organic matter particle loading (McClelland et al.,  
546 2012). Subsequent remineralization of allochthonous organic matter increases  $pCO_{2w}$  while  
547 turbidity associated with increased particle load lowers light penetration and dampens primary  
548 productivity (Carmack et al., 2006).

549

550 These processes are reflected in a gradient toward increasing  $pCO_{2w}$  from west to east across the  
551 Eurasian shelves, with low  $pCO_{2w}$  in the Barents Sea driven by cooling of Atlantic Water and  
552 high productivity rates and increasingly high  $pCO_{2w}$  toward the eastern Siberian Seas where  
553 stratification-induced warming of surface waters, high  $pCO_{2w}$  in river discharge, and high rates  
554 of terrestrial organic matter remineralization dominate (Anderson et al., 2009; Pipko et al.,  
555 2017). The East Siberian Seas still represent a sink for CO<sub>2</sub> but are prone to periods of  
556 outgassing; one might expect that with increased mobilization of permafrost and continued  
557 warming these areas might become a more reliable source in the future (Anderson et al., 2009).  
558 More generally enhanced stratification from increased surface temperatures and increased river  
559 discharge may reduce CO<sub>2</sub> uptake capacity on Eurasian interior shelves, although this  
560 stratification increase may be countered by increased storm-induced-mixing (Pipko et al., 2017)..  
561

562 Another important trend in this region is a significant 3.5 decade increase in alkalinity exported  
563 to the AO from the Yenisei and Ob' Rivers; between 1974 and 2015 alkalinity export by these  
564 two rivers more than doubled (i.e. from 225 to 642 Geq yr<sup>-1</sup> and from 201 to 470 Geq yr<sup>-1</sup> for the  
565 Yenisei and Ob', respectively, Drake et al., 2018). Proposed drivers of this increase include  
566 increased temperature, deepening of the permafrost active layer, and longer contact time with  
567 unweathered mineral surfaces. If similar increases in alkalinity export apply for the two other  
568 large Eurasian rivers (Lena and Kolyma) the increase in AO alkalinity has the potential to  
569 enhance CO<sub>2</sub> sequestration by 3.4 Tg yr<sup>-1</sup> (120 Tg C over the 3.5 decades, Drake et al., 2018).  
570 This increase is of the same magnitude as the currently compiled estimates of regional uptake in  
571 the Kara, Laptev, and East Siberian Sea (Bates & Mathis, 2009); hence, increased buffering  
572 capacity will be an important determinant of this region's future CO<sub>2</sub> uptake trajectory.  
573

## 574 **Conclusions**

575 Changes to the biogeochemical cycling of nutrients through AO sub-regions are inevitable as  
576 aspects of the physical system change. DIN availability might increase due to advected inputs at  
577 inflow regions, increase due to reduced ice conditions coupled with enhanced storm activity  
578 (shelf break upwelling or storm-induced mixing), or decrease as source waters change or  
579 stratification limits seasonal replenishment. Hence, there is no single, unified trajectory of AO  
580 biogeochemical change – rather, profound regional differences shape a mosaic of trends and  
581 outcomes. Changes to nutrient availability already seem to be driving changes in AO PP (Lewis  
582 et al., 2020; Terhaar et al., 2021), but what is less clear is the extent to which these trends are  
583 driven by new or regenerated production. This new/regenerated distinction has important  
584 implications for understanding future changes to Arctic ecosystems, trophic transfers, pelagic-  
585 benthic coupling, and capacity for biologically-mediated air-sea CO<sub>2</sub> exchange.  
586

587 Given the mosaic of individual regional responses, observations and modeling are both critical  
588 needs for tracking the shifting baselines of AO change, the mechanisms driving them, and  
589 implications for the future. Observations must be collected at appropriate spatiotemporal  
590 resolution to resolve processes of interest; however, this is challenging given the importance of  
591 event-driven features (storms) and the need for measurements outside of the easily accessible  
592 open water period (to assess seasonal nutrient replenishment trends). Models will also need to  
593 adequately resolve mixing processes and their responses in shallow coastal environments and  
594 deep basins alike. Finally, given the interwoven functioning of AO physical, biogeochemical,

595 and ecological systems, our ability to understand and predict future change hinges on  
596 interdisciplinary coordination from measurement to synthesis.

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