

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

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10 **Abstract:** The Arctic physical system is changing in profound ways, with implications for the
11 transport of nutrients to and from the Arctic Ocean (AO), as well as the internal cycling of
12 material on shelves and basins. Significant increases in AO primary production (PP) have been
13 observed in the last two decades, potentially driven by a suite of mechanisms that increase
14 nutrient availability to upper ocean waters. However, the importance of these mechanisms,
15 which include increased transport from adjacent subpolar regions, enhanced within- and
16 between- season mixing, and increased mobilization of nutrients from terrestrial pools, varies
17 substantially within various AO subregions, leading to a mosaic of trajectories that vary in sign
18 and magnitude. Changes in PP are also driving regional changes in the biologically-mediated air-
19 sea exchange of CO₂, while warming, enhanced stratification, increased mobilization of carbon
20 from terrestrial pools, and changing wind patterns are also driving regionally-variable trends.

21 22 **Introduction**

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

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

but rather, a suite of complex, regional-scale trajectories. Here, I attempt to highlight key aspects of AO biogeochemical change through the lens of a foundational currency, nitrogen, which functions as the primary limiting nutrient controlling PP in the AO and as such is at the heart of many of the biogeochemical changes occurring throughout the AO. I evaluate insights that emerge from an AO-wide budget of nitrogen, as well as those that emerge from understanding regional scale dynamics underlying integrated, AO-wide net change. I will also briefly comment on some of the consequences of a changing physical system and nutrient dynamics for the air-sea exchange of CO₂ in the AO.

Changing nutrient supply in the AO

Water column nutrient distributions are a fundamental control on photosynthesis, and hence, the PP that forms the foundation of AO ecosystems. PP, and more specifically, net community production (the fraction of PP that is not respired by heterotrophs in surface waters) also facilitates the sequestration of CO₂ in the AO as the carbon contained in organic matter settles to a depth where, upon subsequent oxidation, the resulting CO₂ generated is separated from the atmosphere. The major limiting nutrient controlling primary production in the AO is nitrogen, as inorganic nitrogen (hereafter referred to as dissolved inorganic nitrogen, DIN, which includes the sum of nitrate, nitrite, and ammonium species) is typically found with phosphorus in a molar ratio much lower than the canonical Redfield stoichiometry of 16:1 (Codispoti et al., 2013; Tremblay et al., 2015). The deficiency of DIN in AO waters can be understood in the context of AO circulation and connectivity to other basins: low N:P waters from the subarctic Pacific Ocean advect into the AO (Tremblay et al., 2015; Yamamoto-Kawai et al., 2006) while additional DIN losses occur within the AO by denitrification on Arctic shelves (Figure 1; Chang & Devol, 2009). Surface waters in much of the ice-free AO exhibit depleted surface DIN inventories quickly after ice retreat, leading to nutrient limitation of PP and oligotrophic status during the rest of the open water season when light is abundant (Figure 2). Climate-related changes to the availability of DIN in surface waters therefore have special significance for primary productivity and biological pump functioning.

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

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

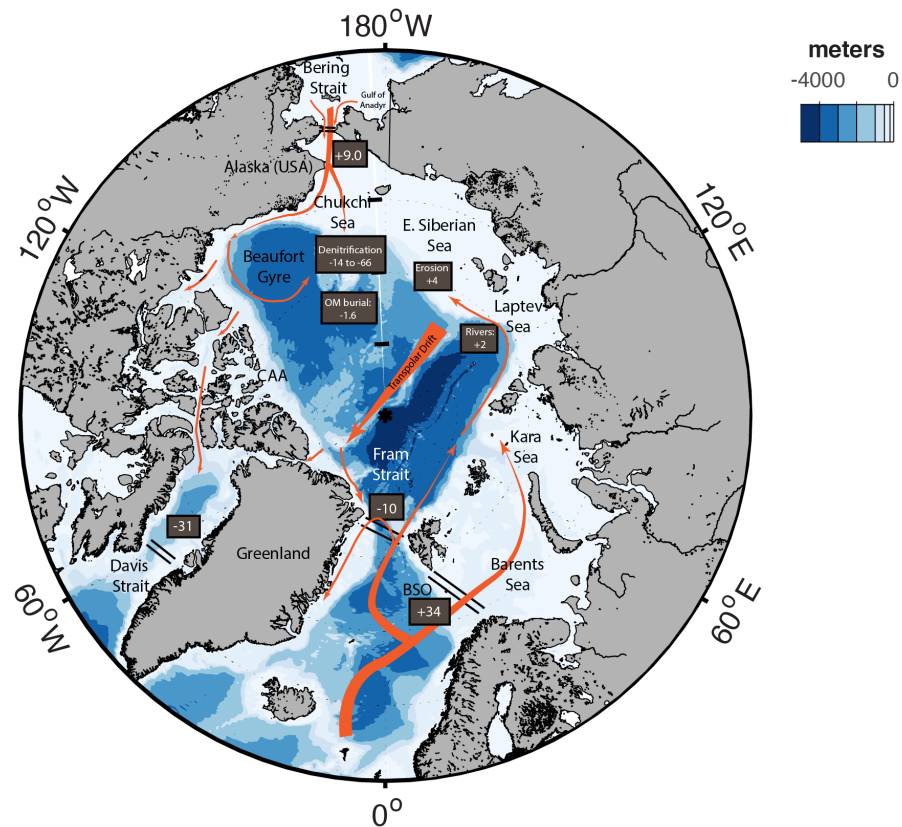


Figure 1: Map of the Arctic Ocean showing Arctic gateways at Bering Strait, Fram Strait, Davis Strait, and the Barents Sea Opening (BSO). Major regional seas characterized by inflow shelves (Chukchi and Barents Seas), interior shelves (Beaufort, Kara, Laptev, and East Siberian Seas) and outflow shelves (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 kmol N s^{-1} , for consistency with the AO gateway flux estimates.

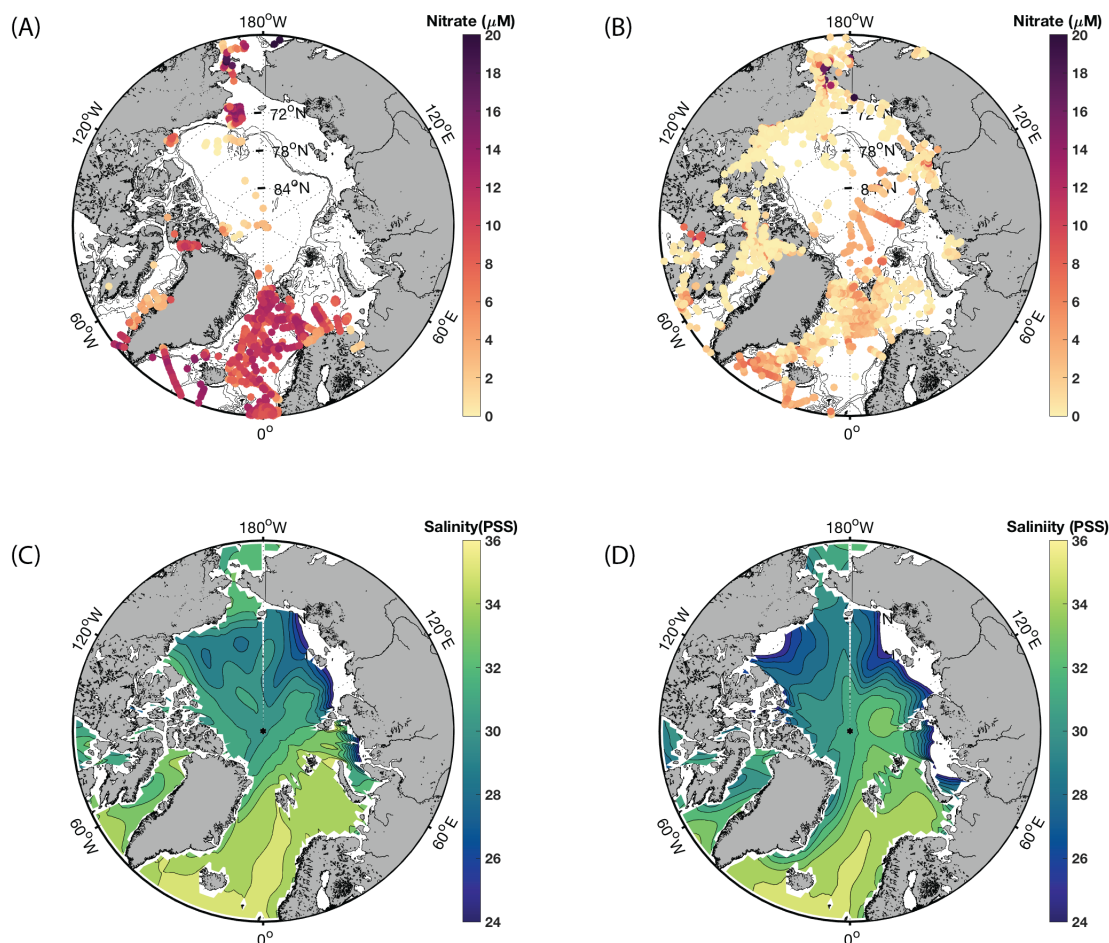


Figure 2: Seasonal patterns of nutrients and salinity in the AO. Nutrient data compiled from Codispoti et al. (2013) as well as additional sources reported in Randelhoff et al. (2020). Salinity is from a seasonal climatology based on the World Ocean Database (Boyer et al., 2014). Shown are: A) Winter (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.

A baseline DIN budget for the AO

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

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

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

Nonetheless, it is still useful to evaluate the implications of a net zero transport of DIN through AO gateways. Internal system losses of DIN are well-documented, and these could not be sustained indefinitely in the absence of additional sources if net transport of DIN was negligible. Loss of DIN by microbially-mediated denitrification (conversion of fixed and bioavailable DIN to N_2 and N_2O) is estimated to be a substantial internal sink term of 14 to 66 kmol N s^{-1} (-6 to -29 Tg N yr^{-1} ; Chang & Devol, 2009, Figure 1). Denitrification is particularly prevalent on shallow Arctic shelves receiving a high flux of organic matter (Chang & Devol, 2009; Granger et al., 2018). Additional loss of DIN is expected through sedimentary burial of organic matter. The majority of organic matter produced via PP is respired back to DIN in surface or subsurface waters, but a small fraction of organic matter escapes oxidation and is buried (primarily on shallow and adjacent continental slopes where the settling time is reduced); in the AO estimated burial is 0.7 Tg N yr^{-1} (3.7 Tg C yr^{-1} , Stein & Macdonald, 2004) which equates to $1.5 \text{ kmol N s}^{-1}$. These internal sinks are partially offset by additional DIN and dissolved organic nitrogen (DON) from terrestrial sources, mobilized by rivers and coastal erosion within the AO. These sources affect regional biogeochemical cycling but are believed to be small at the AO scale: ~ 1.5 - $1.7 \text{ kmol N s}^{-1}$ (Le Fouest et al., 2013; Torres-Valdés et al., 2013). DON flux through Arctic gateways may also represent an important source but at present it is poorly constrained (Torres-Valdés et al., 2013; Tremblay et al., 2015).

The knowledge gaps that emerge from the large scale AO nutrient budget point toward areas where there are clear research needs. Resolving nutrient inputs at Arctic gateways over a full annual cycle, and quantifying interannual variability or trends, is of utmost importance for understanding how PP and biologically mediated CO_2 uptake may change in the AO. Better constraint of DON transport/utilization and reduction in the uncertainty of the denitrification sink might also help to bring the budget toward closure. However, the budget analysis also provides

important context for understanding what is known about changing sources and sinks, as well as coupled physical and biogeochemical processes that do not act as sources or sinks on an AO scale, but do impact regional DIN availability in the upper layers where PP and CO₂ uptake occurs. The next few sections tackle what is known regarding changing nutrient supply via AO gateways, changing nutrient supply via rivers, and changing upper ocean nutrient availability from physical processes operating over a range of space and time scales.

Changing nutrient supply at Arctic inflow shelves

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

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

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

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

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

Increasing influence of terrestrial nutrient sources

Recent studies also implicate nutrients supplied by coastal erosion and rivers as having an increasingly important role in supporting observed PP increases and influencing coastal biogeochemical cycling in the AO. Increased river discharge, thawing permafrost with deepening active layers, and enhanced shoreline erosion due to a loss of buttressing ice in fall and winter all intensify the land-ocean exchange of material (Frey & McClelland, 2009; McClelland et al., 2012). One recent modeling analysis that sought to quantify the impact of terrestrial sources on the AO indicated that DIN supplied by coastal erosion and rivers (estimated as 1.6 Tg N yr^{-1} and 1.0 Tg N yr^{-1} , respectively) supports 1/3 of Arctic PP on an annual basis (rivers: 9-11%, coastal erosion 19-41%; Terhaar et al., 2021). Consistent with prior work (e.g., Frey & McClelland, 2009; Holmes et al., 2012; Peterson et al., 2002), the majority of the terrestrially-derived DIN sources were focused in the Eurasian Arctic (East Siberian, Kara, and Laptev shelves), where the Yenisey, Lena, and Ob', the 3 largest Arctic rivers by annual discharge and the 5th, 6th, and 13th 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⁻¹, while the simulated increase to productivity was 8x the biomass increase (140 Tg C yr⁻¹). 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 CO₂ because regeneration and reuse of N contained in organic matter also regenerates CO₂. 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 (²²⁸Ra and ²²⁶Ra) 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 ²²⁸Ra 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

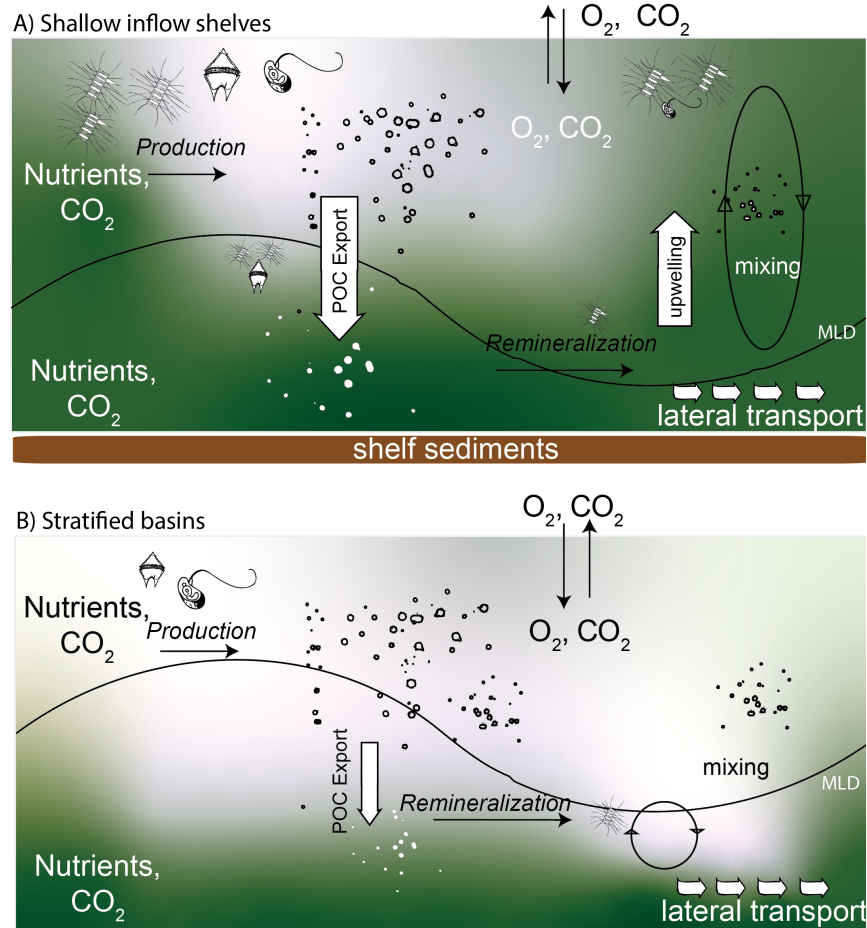


Figure 3: Conceptual realization of nutrient replenishment mechanisms on A) shallow inflow shelves and B) stratified deep basins. Green shading is meant to indicate relative nutrient availability. Inflow shelves experience advective nutrient inputs from lower latitudes, and strong replenishment within 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.

nutrient sources at AO gateways have more robust replenishment while open waters overlying deeper bathymetry and strong stratification have weakest replenishment (Figure 2 & 3). For example, the Chukchi Sea in the Pacific Arctic sector is characterized by a broad, shallow shelf (ca. 50 m), and a relatively shallow nitracline (ca. 20-40 m); in winter, storms and convective mixing completely erode the seasonal stratification and the nutrients accumulated in the near-bottom layer from remineralization of organic matter over the summer are redistributed throughout the water column (Figure 3)

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

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

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

Episodic nutrient delivery by storms and wind-events:

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

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

Analysis of long-term wind and mooring data in the vicinity of the Beaufort shelf break indicates that upwelling can be induced by moderate easterly winds (threshold of 6 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 $\sim 400 \text{ mmol C m}^{-2}$ 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).

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.

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).

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_2 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

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

Changes to AO CO₂ uptake due to changing primary productivity

Regions of the AO that have seen marked increases in PP over the last several decades, in particular the Arctic gateway inflow shelves, will also act as strong biologically-mediated sinks for CO₂ on a seasonal basis as organic matter is produced in the surface and exported to depth. As exported organic matter is respired at depth, seasonal stratification prevents mixing of accumulated respiratory CO₂ to the surface where it would otherwise outgas, much as it restricts the resupply of DIN that also accumulates (Figure 3). Input of CO₂ associated with respiration of exported organic matter at depth also contributes to seasonal undersaturation of calcium carbonate minerals (i.e., corrosivity (Bates & Mathis, 2009). Historically, this biologically-mediated organic carbon pump has helped the Chukchi and Barents Seas to maintain strongly undersaturated CO₂ at the surface, and has facilitated these areas functioning as regions of enhanced ocean uptake of CO₂ from the atmosphere, while interior shelves and deep basins with low PP rates represent much weaker sinks (Bates & Mathis, 2009; Pipko et al., 2017; Yasunaka et al., 2016). The recently reported increases in PP on Arctic shelves therefore have the potential to enhance oceanic uptake of CO₂ so long as they are associated with export of material to depth and not regenerated production, where CO₂ is alternately consumed and released by photosynthesis and respiration (Dugdale & Goering, 1967; Tremblay et al., 2015). For example, the substantial proportion of PP fueled by riverine and coastal erosion sources of DIN highlighted above (Terhaar et al., 2021) would only modestly contribute to enhanced biological CO₂ uptake since the majority of the PP in that study was determined to be regenerated. In contrast, a combination of modelling and observations suggests an increase in continental shelf PP and biological CO₂ uptake over a longer growing season on inflow shelves (Tu et al., 2021).

In AO deep basin surface waters, a reduction of an already weak biologically-mediated CO₂ sink due to enhanced stratification and associated deepening of the nutricline (McLaughlin & Carmack, 2010) has already been noted (Cai et al., 2010; Else et al., 2013). This weakening CO₂ sink has been associated with a shift phytoplankton community composition toward smaller cells (picophytoplankton) in surface waters of the Beaufort Gyre (Li et al., 2009), which is suggestive of increased regenerated production and decreased net biological CO₂ uptake potential.

Productivity associated with the previously-described shelfbreak upwelling and fall blooms warrant additional discussion with respect to new/regenerated production and biologically-mediated air-sea CO₂ exchange. The supply of DIN from depth that fuels these blooms also brings excess CO₂ leading to significant outgassing, as has been noted in several studies (Evans et al., 2015; Hauri et al., 2013; Mathis et al., 2012). Consumption of DIN at the surface during the bloom helps to mitigate this outgassing by drawing down the CO₂ of surface water; hence the timescale of DIN removal during a bloom helps to set the net source/sink status of CO₂ flux during these upwelling events. Whether or not these events represent new vs regenerated production depends on the depth from which nutrient-rich waters are sourced: DIN supplied from shallow horizons where organic matter produced earlier in the season has been respired would not in an annual budget sense be considered new production while DIN supplied from previously untapped reservoirs would be considered new production.

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 CO₂ 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 CaCO₃ shells reduces alkalinity of surface waters and increases the partial pressure of CO₂ in surface waters (pCO_{2w} , a primary determinant of air-sea CO₂ exchange) weakening the capacity for air-sea CO₂ 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 CO₂ uptake will require continued monitoring and ecosystem modelling to resolve.

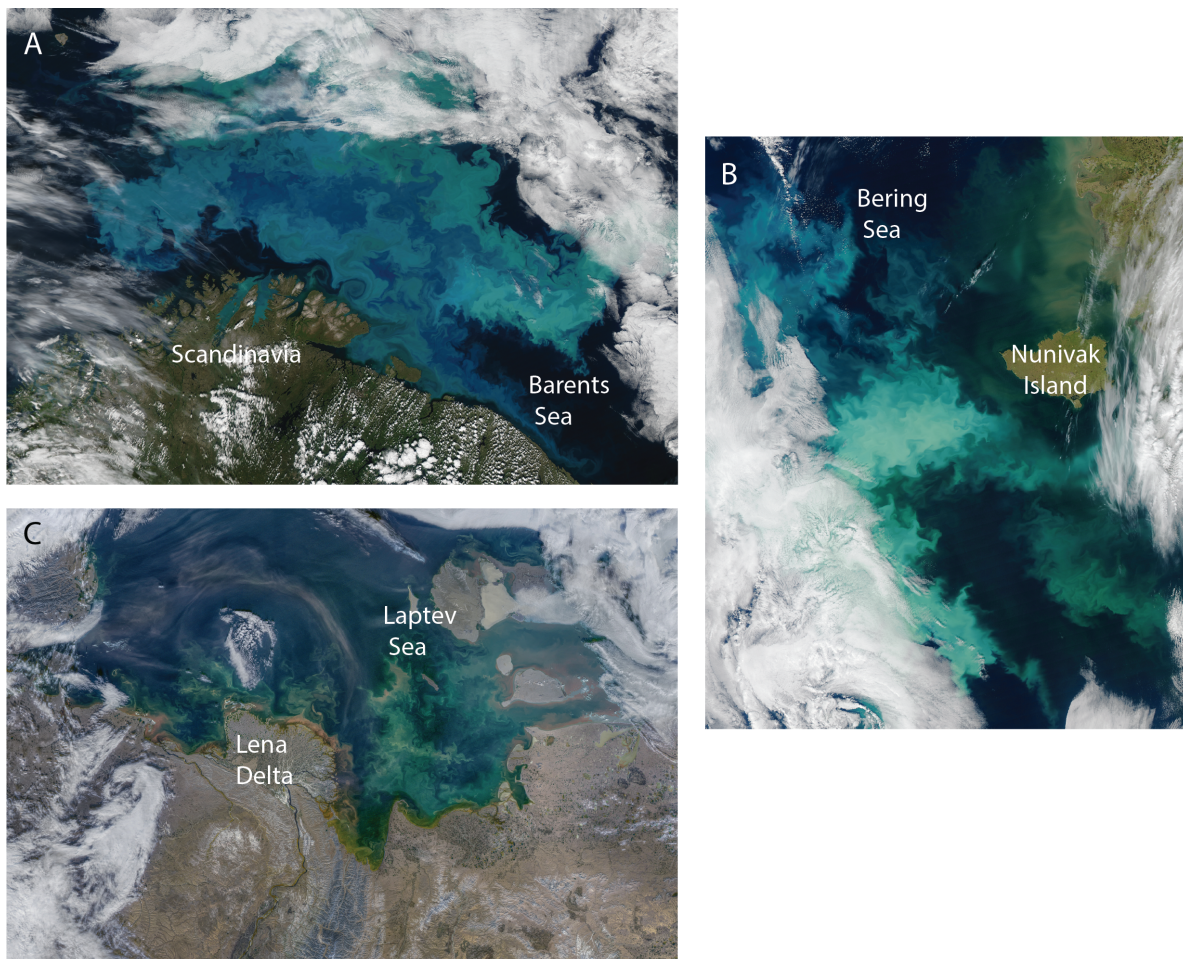


Figure 4: Remotely-sensed visible images from MODIS Aqua showing coccolithophore blooms in the A) Barents Sea B) Bering Sea. Also shown is C) turbidity in the Laptev Sea associated with terrestrial material delivered by the Lena delta. All images courtesy NASA Earth Observatory (<http://earthobservatory.nasa.gov>).

Changes in abiotic drivers of AO CO₂ uptake

Warming and freshening of AO surface waters will also impact the source/sink status of some AO regions, particularly AO deep basins and some interior shelves where biologically-mediated rates of CO₂ uptake are low. The expansion of the seasonal ice zone and reduction in sea ice extent in theory presents an opportunity for enhanced ocean uptake of CO₂ as cold high latitude surface waters can now more readily communicate with the atmosphere (Olsen et al., 2015) but pronounced warming and freshening of Arctic basins counter this potential. Increasing surface pCO_{2w} in the Beaufort Sea over the last few decades, an expected outcome of warming, has already been noted in a number of studies (Cai et al., 2010; Else et al., 2013; Ouyang et al., 2020). This increased pCO_{2w} reduces the gradient between atmosphere and ocean, i.e. $\Delta pCO_2 = pCO_{2w} - pCO_{2a}$ (where subscript a denotes atmosphere), an important determinant of the rate of air-sea CO₂ exchange:

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

where k_{CO_2} is the air-sea gas transfer velocity, typically parameterized by a relationship with wind speed (Wanninkhof, 2014), and K_o is solubility of CO₂, calculated as a function of temperature and salinity (Weiss, 1974). Seasonal freshwater input from sea ice melt or river discharge (Carmack et al., 2016) additionally reduces the capacity of these waters to buffer against additions/removals of CO₂ (by biological or abiotic processes), leading to reduced uptake capacity with additions of CO₂ (Rysgaard et al., 2011; Takahashi et al., 2014). Meanwhile, increased wind speeds (from more frequent storm activity) will tend to increase the rate of air-sea CO₂ exchange for a given air-sea gradient by increasing k_{CO_2} .

Increasing thermal stratification in the Barents Sea is also expected to reduce the CO₂ sink in this region in the future. Indeed, observations already indicate increasing pCO_{2w} and decreasing CO₂ uptake in the southern Barents Sea (Yasunaka et al., 2016). This stands in contrast to the other inflow shelf in the Chukchi, where biotic factors appear to be dominating over warming-related reductions (Tu et al., 2021).

Intensified land-ocean carbon exchange on Eurasian/Siberian shelves

Generally, discharge of AO Rivers is organic carbon rich and DIN poor (Holmes et al., 2012; McClelland et al., 2012). Thus, while the impact of PP supported by riverine nutrients may be slight, the impact of the organic carbon supplied by rivers on ocean-atmosphere CO₂ fluxes can be quite prominent, particularly on interior shelves in the Eurasian Arctic sector where a significant fraction of AO riverine discharge is focused (Anderson et al., 2009; Frey & McClelland, 2009; Pipko et al., 2017). Thawing of peat-rich permafrost in the Siberian Arctic, coupled with increasing river discharge, has the potential to increase loading of allochthonous carbon to the coastal ocean. Loss of buttressing sea ice and enhanced wave energy from wind events also appears to be contributing to enhanced erosion of coastlines and resuspension of shelf sediments, with increased lithogenic and organic matter particle loading (McClelland et al., 2012). Subsequent remineralization of allochthonous organic matter increases pCO_{2w} while turbidity associated with increased particle load lowers light penetration and dampens primary productivity (Carmack et al., 2006).

These processes are reflected in a gradient toward increasing pCO_{2w} from west to east across the Eurasian shelves, with low pCO_{2w} in the Barents Sea driven by cooling of Atlantic Water and high productivity rates and increasingly high pCO_{2w} toward the eastern Siberian Seas where stratification-induced warming of surface waters, high pCO_{2w} in river discharge, and high rates of terrestrial organic matter remineralization dominate (Anderson et al., 2009; Pipko et al., 2017). The East Siberian Seas still represent a sink for CO_2 but are prone to periods of outgassing; one might expect that with increased mobilization of permafrost and continued warming these areas might become a more reliable source in the future (Anderson et al., 2009). More generally enhanced stratification from increased surface temperatures and increased river discharge may reduce CO_2 uptake capacity on Eurasian interior shelves, although this stratification increase may be countered by increased storm-induced-mixing (Pipko et al., 2017)..

Another important trend in this region is a significant 3.5 decade increase in alkalinity exported to the AO from the Yenisei and Ob' Rivers; between 1974 and 2015 alkalinity export by these two rivers more than doubled (i.e. from 225 to 642 $Geq\ yr^{-1}$ and from 201 to 470 $Geq\ yr^{-1}$ for the Yenisei and Ob', respectively, Drake et al., 2018). Proposed drivers of this increase include increased temperature, deepening of the permafrost active layer, and longer contact time with unweathered mineral surfaces. If similar increases in alkalinity export apply for the two other large Eurasian rivers (Lena and Kolyma) the increase in AO alkalinity has the potential to enhance CO_2 sequestration by 3.4 $Tg\ yr^{-1}$ (120 $Tg\ C$ over the 3.5 decades, Drake et al., 2018). This increase is of the same magnitude as the currently compiled estimates of regional uptake in the Kara, Laptev, and East Siberian Sea (Bates & Mathis, 2009); hence, increased buffering capacity will be an important determinant of this region's future CO_2 uptake trajectory.

Conclusions

Changes to the biogeochemical cycling of nutrients through AO sub-regions are inevitable as aspects of the physical system change. DIN availability might increase due to advected inputs at inflow regions, increase due to reduced ice conditions coupled with enhanced storm activity (shelf break upwelling or storm-induced mixing), or decrease as source waters change or stratification limits seasonal replenishment. Hence, there is no single, unified trajectory of AO biogeochemical change – rather, profound regional differences shape a mosaic of trends and outcomes. Changes to nutrient availability already seem to be driving changes in AO PP (Lewis et al., 2020; Terhaar et al., 2021), but what is less clear is the extent to which these trends are driven by new or regenerated production. This new/regenerated distinction has important implications for understanding future changes to Arctic ecosystems, trophic transfers, pelagic-benthic coupling, and capacity for biologically-mediated air-sea CO_2 exchange.

Given the mosaic of individual regional responses, observations and modeling are both critical needs for tracking the shifting baselines of AO change, the mechanisms driving them, and implications for the future. Observations must be collected at appropriate spatiotemporal resolution to resolve processes of interest; however, this is challenging given the importance of event-driven features (storms) and the need for measurements outside of the easily accessible open water period (to assess seasonal nutrient replenishment trends). Models will also need to adequately resolve mixing processes and their responses in shallow coastal environments and 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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599 **References:**

- 600 Anderson, L. G., Jutterström, S., Hjalmarsson, S., Wåhlström, I., & Semiletov, I. P. (2009). Out-
 601 gassing of CO₂ from Siberian Shelf seas by terrestrial organic matter decomposition.
 602 *Geophysical Research Letters*, 36(20), L20601. <https://doi.org/10.1029/2009GL040046>
- 603 Ardyna, M., & Arrigo, K. R. (2020). Phytoplankton dynamics in a changing Arctic Ocean. *Nature*
 604 *Climate Change*, 10(10), 892–903. <https://doi.org/10.1038/s41558-020-0905-y>
- 605 Ardyna, M., Babin, M., Gosselin, M., Devred, E., Rainville, L., & Tremblay, J.-É. (2014). Recent
 606 Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms. *Geophysical Research*
 607 *Letters*, 41(17), 6207–6212. <https://doi.org/10.1002/2014GL061047>
- 608 Arrigo, K. R., & van Dijken, G. L. (2015). Continued increases in Arctic Ocean primary production.
 609 *Progress in Oceanography*, 136, 60–70. <https://doi.org/10.1016/j.pocean.2015.05.002>
- 610 Årthun, M., Eldevik, T., Smedsrud, L. H., Skagseth, Ø., & Ingvaldsen, R. B. (2012). Quantifying the
 611 Influence of Atlantic Heat on Barents Sea Ice Variability and Retreat*. *Journal of Climate*,
 612 25(13), 4736–4743. <https://doi.org/10.1175/JCLI-D-11-00466.1>
- 613 Bates, N. R., & Mathis, J. T. (2009). The Arctic Ocean marine carbon cycle: evaluation of air-sea
 614 CO₂ exchanges, ocean acidification impacts and potential feedbacks. *Biogeosciences*,
 615 6(11), 2433–2459.
- 616 Beaird, N. L., Shroyer, E. L., Juranek, L. W., Hales, B., & Goñi, M. A. (2020). Nutrient-Rich Gravity
 617 Current Formed by Upwelling in Barrow Canyon: High-Resolution Observations. *Journal*
 618 *of Geophysical Research: Oceans*, 125(7). <https://doi.org/10.1029/2020JC016160>
- 619 Cai, W.-J., Chen, L., Chen, B., Gao, Z., Lee, S. H., Chen, J., et al. (2010). Decrease in the CO₂
 620 Uptake Capacity in an Ice-Free Arctic Ocean Basin. *Science*, 329(5991), 556–559.
 621 <https://doi.org/10.1126/science.1189338>
- 622 Carmack, E., & Chapman, D. C. (2003). Wind-driven shelf/basin exchange on an Arctic shelf: The
 623 joint roles of ice cover extent and shelf-break bathymetry: WIND-DRIVEN SHELF/BASIN
 624 EXCHANGE. *Geophysical Research Letters*, 30(14).
 625 <https://doi.org/10.1029/2003GL017526>
- 626 Carmack, E., Barber, D., Christensen, J., Macdonald, R., Rudels, B., & Sakshaug, E. (2006).
 627 Climate variability and physical forcing of the food webs and the carbon budget on
 628 panarctic shelves. *Progress in Oceanography*, 71(2–4), 145–181.
 629 <https://doi.org/10.1016/j.pocean.2006.10.005>
- 630 Carmack, E. C., Yamamoto-Kawai, M., Haine, T. W. N., Bacon, S., Bluhm, B. A., Lique, C., et al.
 631 (2016). Freshwater and its role in the Arctic Marine System: Sources, disposition,

632 storage, export, and physical and biogeochemical consequences in the Arctic and global
633 oceans. *Journal of Geophysical Research: Biogeosciences*, 121(3), 675–717.
634 <https://doi.org/10.1002/2015JG003140>

635 Castro de la Guardia, L., Garcia-Quintana, Y., Claret, M., Hu, X., Galbraith, E. D., & Myers, P. G.
636 (2019). Assessing the Role of High-Frequency Winds and Sea Ice Loss on Arctic
637 Phytoplankton Blooms in an Ice-Ocean-Biogeochemical Model. *Journal of Geophysical*
638 *Research: Biogeosciences*, 124(9), 2728–2750. <https://doi.org/10.1029/2018JG004869>

639 Chang, B. X., & Devol, A. H. (2009). Seasonal and spatial patterns of sedimentary denitrification
640 rates in the Chukchi sea. *Deep Sea Research Part II: Topical Studies in Oceanography*,
641 56(17), 1339–1350. <https://doi.org/10.1016/j.dsr2.2008.10.024>

642 Codispoti, L. A., Kelly, V., Thessen, A., Matrai, P., Suttles, S., Hill, V., et al. (2013). Synthesis of
643 primary production in the Arctic Ocean: III. Nitrate and phosphate based estimates of
644 net community production. *Progress in Oceanography*, 110, 126–150.
645 <https://doi.org/10.1016/j.pocean.2012.11.006>

646 Crawford, A. D., & Serreze, M. C. (2017). Projected Changes in the Arctic Frontal Zone and
647 Summer Arctic Cyclone Activity in the CESM Large Ensemble. *Journal of Climate*, 30(24),
648 9847–9869. <https://doi.org/10.1175/JCLI-D-17-0296.1>

649 Drake, T. W., Tank, S. E., Zhulidov, A. V., Holmes, R. M., Gurtovaya, T., & Spencer, R. G. M.
650 (2018). Increasing Alkalinity Export from Large Russian Arctic Rivers. *Environmental*
651 *Science & Technology*, 52(15), 8302–8308. <https://doi.org/10.1021/acs.est.8b01051>

652 Dugdale, R. C., & Goering, J. J. (1967). UPTAKE OF NEW AND REGENERATED FORMS OF
653 NITROGEN IN PRIMARY PRODUCTIVITY1. *Limnology and Oceanography*, 12(2), 196–206.
654 <https://doi.org/10.4319/lo.1967.12.2.0196>

655 Else, B. G. T., Galley, R. J., Lansard, B., Barber, D. G., Brown, K., Miller, L. A., et al. (2013). Further
656 observations of a decreasing atmospheric CO₂ uptake capacity in the Canada Basin
657 (Arctic Ocean) due to sea ice loss. *Geophysical Research Letters*, 40(6), 1132–1137.
658 <https://doi.org/10.1002/grl.50268>

659 Evans, W., Mathis, J. T., Cross, J. N., Bates, N. R., Frey, K. E., Else, B. G. T., et al. (2015). Sea-air
660 CO₂ exchange in the western Arctic coastal ocean. *Global Biogeochemical Cycles*, 29(8),
661 1190–1209. <https://doi.org/10.1002/2015GB005153>

662 Frey, K. E., & McClelland, J. W. (2009). Impacts of permafrost degradation on arctic river
663 biogeochemistry. *Hydrological Processes*, 23(1), 169–182.
664 <https://doi.org/10.1002/hyp.7196>

- 665 Granger, J., Sigman, D. M., Gagnon, J., Tremblay, J., & Mucci, A. (2018). On the Properties of the
666 Arctic Halocline and Deep Water Masses of the Canada Basin from Nitrate Isotope
667 Ratios. *Journal of Geophysical Research: Oceans*, 123(8), 5443–5458.
668 <https://doi.org/10.1029/2018JC014110>
- 669 Haine, T. W. N., Curry, B., Gerdes, R., Hansen, E., Karcher, M., Lee, C., et al. (2015). Arctic
670 freshwater export: Status, mechanisms, and prospects. *Global and Planetary Change*,
671 125, 13–35. <https://doi.org/10.1016/j.gloplacha.2014.11.013>
- 672 Hauri, C., Winsor, P., Juranek, L. W., McDonnell, A. M. P., Takahashi, T., & Mathis, J. T. (2013).
673 Wind-driven mixing causes a reduction in the strength of the continental shelf carbon
674 pump in the Chukchi Sea: CO₂ OUTGASSING IN THE CHUKCHI SEA. *Geophysical Research*
675 *Letters*, 40(22), 5932–5936. <https://doi.org/10.1002/2013GL058267>
- 676 Henley, S. F., Porter, M., Hobbs, L., Braun, J., Guillaume-Castel, R., Venables, E. J., et al. (2020).
677 Nitrate supply and uptake in the Atlantic Arctic sea ice zone: seasonal cycle, mechanisms
678 and drivers. *Philosophical Transactions of the Royal Society A: Mathematical, Physical*
679 *and Engineering Sciences*, 378(2181), 20190361.
680 <https://doi.org/10.1098/rsta.2019.0361>
- 681 Hill, V., & Cota, G. (2005). Spatial patterns of primary production on the shelf, slope and basin
682 of the Western Arctic in 2002. *Deep Sea Research Part II: Topical Studies in*
683 *Oceanography*, 52(24–26), 3344–3354. <https://doi.org/10.1016/j.dsr2.2005.10.001>
- 684 Holmes, R. M., McClelland, J. W., Peterson, B. J., Tank, S. E., Bulygina, E., Eglinton, T. I., et al.
685 (2012). Seasonal and Annual Fluxes of Nutrients and Organic Matter from Large Rivers
686 to the Arctic Ocean and Surrounding Seas. *Estuaries and Coasts*, 35(2), 369–382.
687 <https://doi.org/10.1007/s12237-011-9386-6>
- 688 Juranek, L., Takahashi, T., Mathis, J., & Pickart, R. (2019). Significant Biologically Mediated CO₂
689 Uptake in the Pacific Arctic During the Late Open Water Season. *Journal of Geophysical*
690 *Research: Oceans*. <https://doi.org/10.1029/2018JC014568>
- 691 Kahru, M., Brotas, V., Manzano-Sarabia, M., & Mitchell, B. G. (2011). Are phytoplankton blooms
692 occurring earlier in the Arctic? *Global Change Biology*, 17(4), 1733–1739.
693 <https://doi.org/10.1111/j.1365-2486.2010.02312.x>
- 694 Kipp, L. E., Charette, M. A., Moore, W. S., Henderson, P. B., & Rigor, I. G. (2018). Increased
695 fluxes of shelf-derived materials to the central Arctic Ocean. *Science Advances*, 4(1),
696 eaao1302. <https://doi.org/10.1126/sciadv.aao1302>
- 697 Le Fouest, V., Babin, M., & Tremblay, J.-É. (2013). The fate of riverine nutrients on Arctic
698 shelves. *Biogeosciences*, 10(6), 3661–3677. <https://doi.org/10.5194/bg-10-3661-2013>

699 Lewis, K. M., van Dijken, G. L., & Arrigo, K. R. (2020). Changes in phytoplankton concentration
700 now drive increased Arctic Ocean primary production. *Science*, 369(6500), 198–202.
701 <https://doi.org/10.1126/science.aay8380>

702 Li, W. K. W., McLaughlin, F. A., Lovejoy, C., & Carmack, E. C. (2009). Smallest Algae Thrive As the
703 Arctic Ocean Freshens. *Science*, 326(5952), 539–539.
704 <https://doi.org/10.1126/science.1179798>

705 Manizza, M. (n.d.). Modeling the carbon cycle in the polar oceans : Present and Future
706 Challenges, 43.

707 Mathis, J. T., Pickart, R. S., Byrne, R. H., McNeil, C. L., Moore, G. W. K., Juranek, L. W., et al.
708 (2012). Storm-induced upwelling of high p CO₂ waters onto the continental shelf of the
709 western Arctic Ocean and implications for carbonate mineral saturation states.
710 *Geophysical Research Letters*, 39(7), n/a-n/a. <https://doi.org/10.1029/2012GL051574>

711 Matrai, P. A., Olson, E., Suttles, S., Hill, V., Codispoti, L. A., Light, B., & Steele, M. (2013).
712 Synthesis of primary production in the Arctic Ocean: I. Surface waters, 1954–2007.
713 *Progress in Oceanography*, 110, 93–106. <https://doi.org/10.1016/j.pocean.2012.11.004>

714 McClelland, J. W., Holmes, R. M., Dunton, K. H., & Macdonald, R. W. (2012). The Arctic Ocean
715 Estuary. *Estuaries and Coasts*, 35(2), 353–368. [https://doi.org/10.1007/s12237-010-](https://doi.org/10.1007/s12237-010-9357-3)
716 9357-3

717 McLaughlin, F. A., & Carmack, E. C. (2010). Deepening of the nutricline and chlorophyll
718 maximum in the Canada Basin interior, 2003-2009: DEEPENING OF THE CANADA BASIN
719 NUTRICLINE. *Geophysical Research Letters*, 37(24), n/a-n/a.
720 <https://doi.org/10.1029/2010GL045459>

721 Mordy, C. W., Bell, S., Cokelet, E. D., Ladd, C., Lebon, G., Proctor, P., et al. (2020). Seasonal and
722 interannual variability of nitrate in the eastern Chukchi Sea: Transport and winter
723 replenishment. *Deep Sea Research Part II: Topical Studies in Oceanography*, 177,
724 104807. <https://doi.org/10.1016/j.dsr2.2020.104807>

725 Neukermans, G., Oziel, L., & Babin, M. (2018). Increased intrusion of warming Atlantic water
726 leads to rapid expansion of temperate phytoplankton in the Arctic. *Global Change*
727 *Biology*, 24(6), 2545–2553. <https://doi.org/10.1111/gcb.14075>

728 Nishino, S., Kawaguchi, Y., Inoue, J., Hirawake, T., Fujiwara, A., Futsuki, R., et al. (2015). Nutrient
729 supply and biological response to wind-induced mixing, inertial motion, internal waves,
730 and currents in the northern Chukchi Sea. *Journal of Geophysical Research: Oceans*,
731 120(3), 1975–1992. <https://doi.org/10.1002/2014JC010407>

- Okkonen, S. R., Ashjian, C. J., Campbell, R. G., Clarke, J. T., Moore, S. E., & Taylor, K. D. (2011). Satellite observations of circulation features associated with a bowhead whale feeding 'hotspot' near Barrow, Alaska. *Remote Sensing of Environment*, 115(8), 2168–2174. <https://doi.org/10.1016/j.rse.2011.04.024>
- Olsen, A., Anderson, L. G., & Heinze, C. (2015). Arctic Carbon Cycle: Patterns, Impacts and Possible Changes. In B. Evengård, J. Nymand Larsen, & Ø. Paasche (Eds.), *The New Arctic* (pp. 95–115). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-17602-4_8
- Ouyang, Z., Qi, D., Chen, L., Takahashi, T., Zhong, W., DeGrandpre, M. D., et al. (2020). Sea-ice loss amplifies summertime decadal CO₂ increase in the western Arctic Ocean. *Nature Climate Change*, 10(7), 678–684. <https://doi.org/10.1038/s41558-020-0784-2>
- Oziel, L., Neukermans, G., Ardyna, M., Lancelot, C., Tison, J.-L., Wassmann, P., et al. (2017). Role for Atlantic inflows and sea ice loss on shifting phytoplankton blooms in the Barents Sea: SHIFTING BLOOMS IN THE BARENTS SEA. *Journal of Geophysical Research: Oceans*, 122(6), 5121–5139. <https://doi.org/10.1002/2016JC012582>
- Pabi, S., van Dijken, G. L., & Arrigo, K. R. (2008). Primary production in the Arctic Ocean, 1998–2006. *Journal of Geophysical Research*, 113(C8). <https://doi.org/10.1029/2007JC004578>
- Pacini, A., Moore, G. W. K., Pickart, R. S., Nobre, C., Bahr, F., Våge, K., & Arrigo, K. R. (2019). Characteristics and Transformation of Pacific Winter Water on the Chukchi Sea Shelf in Late Spring. *Journal of Geophysical Research: Oceans*, 124(10), 7153–7177. <https://doi.org/10.1029/2019JC015261>
- Peterson, B. J., Holmes, R. M., McClelland, J. W., Vörösmarty, C. J., Lammers, R. B., Shiklomanov, A. I., et al. (2002). Increasing River Discharge to the Arctic Ocean. *Science*, 298(5601), 2171–2173. <https://doi.org/10.1126/science.1077445>
- Pickart, R. S., Schulze, L. M., Moore, G. W. K., Charette, M. A., Arrigo, K. R., van Dijken, G., & Danielson, S. L. (2013). Long-term trends of upwelling and impacts on primary productivity in the Alaskan Beaufort Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 79, 106–121. <https://doi.org/10.1016/j.dsr.2013.05.003>
- Pipko, I. I., Pugach, S. P., Semiletov, I. P., Anderson, L. G., Shakhova, N. E., Gustafsson, Ö., et al. (2017). The spatial and interannual dynamics of the surface water carbonate system and air–sea CO₂ fluxes in the outer shelf and slope of the Eurasian Arctic Ocean. *Ocean Science*, 13(6), 997–1016. <https://doi.org/10.5194/os-13-997-2017>
- Polyakov, I. V., Alkire, M. B., Bluhm, B. A., Brown, K. A., Carmack, E. C., Chierici, M., et al. (2020). Borealization of the Arctic Ocean in Response to Anomalous Advection From Sub-Arctic Seas. *Frontiers in Marine Science*, 7, 491. <https://doi.org/10.3389/fmars.2020.00491>

- 767 Randelhoff, A., & Sundfjord, A. (2018). Short commentary on marine productivity at Arctic shelf
768 breaks: upwelling, advection and vertical mixing. *Ocean Science*, 14(2), 293–300.
769 <https://doi.org/10.5194/os-14-293-2018>
- 770 Randelhoff, A., Holding, J., Janout, M., Sejr, M. K., Babin, M., Tremblay, J.-É., & Alkire, M. B.
771 (2020). Pan-Arctic Ocean Primary Production Constrained by Turbulent Nitrate Fluxes.
772 *Frontiers in Marine Science*, 7, 150. <https://doi.org/10.3389/fmars.2020.00150>
- 773 Redfield, A. C., Ketchum, B. H., & Richards, F. A. (1963). The Influence of Organisms on the
774 Composition of the Sea Water. In M. N. Hill (Ed.), *The Sea* (Vol. 2, pp. 26–77). New York:
775 Interscience Publishers.
- 776 Rey, F. (2012). Declining silicate concentrations in the Norwegian and Barents Seas. *ICES Journal*
777 *of Marine Science*, 69(2), 208–212. <https://doi.org/10.1093/icesjms/fss007>
- 778 Rysgaard, S., Bendtsen, J., Delille, B., Dieckmann, G. S., Glud, R. N., Kennedy, H., et al. (2011).
779 Sea ice contribution to the air–sea CO₂ exchange in the Arctic and Southern Oceans.
780 *Tellus B: Chemical and Physical Meteorology*, 63(5), 823–830.
781 <https://doi.org/10.1111/j.1600-0889.2011.00571.x>
- 782 Screen, J. A., Simmonds, I., & Keay, K. (2011). Dramatic interannual changes of perennial Arctic
783 sea ice linked to abnormal summer storm activity. *Journal of Geophysical Research*,
784 116(D15). <https://doi.org/10.1029/2011JD015847>
- 785 Serreze, M. C., Barrett, A. P., Stroeve, J. C., Kindig, D. N., & Holland, M. M. (2009). The
786 emergence of surface-based Arctic amplification. *The Cryosphere*, 9.
- 787 Slagstad, D., Wassmann, P. F. J., & Ellingsen, I. (2015). Physical constrains and productivity in
788 the future Arctic Ocean. *Frontiers in Marine Science*, 2.
789 <https://doi.org/10.3389/fmars.2015.00085>
- 790 Stein, R., & Macdonald, R. W. (2004). The organic carbon cycle in the Arctic Ocean.
- 791 Stroeve, J., & Notz, D. (2018). Changing state of Arctic sea ice across all seasons. *Environmental*
792 *Research Letters*, 13(10), 103001. <https://doi.org/10.1088/1748-9326/aade56>
- 793 Takahashi, T., Sutherland, S. C., Chipman, D. W., Goddard, J. G., Ho, C., Newberger, T., et al.
794 (2014). Climatological distributions of pH, pCO₂, total CO₂, alkalinity, and CaCO₃
795 saturation in the global surface ocean, and temporal changes at selected locations.
796 *Marine Chemistry*, 164, 95–125. <https://doi.org/10.1016/j.marchem.2014.06.004>
- 797 Tank, S. E., Manizza, M., Holmes, R. M., McClelland, J. W., & Peterson, B. J. (2012). The
798 Processing and Impact of Dissolved Riverine Nitrogen in the Arctic Ocean. *Estuaries and*
799 *Coasts*, 35(2), 401–415. <https://doi.org/10.1007/s12237-011-9417-3>

800 Taylor, P. C., Maslowski, W., Perlwitz, J., Wuebbles, D. J., Wuebbles, D. J., Fahey, D. W., et al.
801 (2017). *Ch. 11: Arctic Changes and their Effects on Alaska and the Rest of the United*
802 *States. Climate Science Special Report: Fourth National Climate Assessment, Volume I.*
803 U.S. Global Change Research Program. <https://doi.org/10.7930/J00863GK>

804 Terhaar, J., Lauerwald, R., Regnier, P., Gruber, N., & Bopp, L. (2021). Around one third of
805 current Arctic Ocean primary production sustained by rivers and coastal erosion. *Nature*
806 *Communications*, 12(1), 169. <https://doi.org/10.1038/s41467-020-20470-z>

807 Torres-Valdés, S., Tsubouchi, T., Bacon, S., Naveira-Garabato, A. C., Sanders, R., McLaughlin, F.
808 A., et al. (2013). Export of nutrients from the Arctic Ocean: ARCTIC OCEAN NUTRIENT
809 EXPORTS. *Journal of Geophysical Research: Oceans*, 118(4), 1625–1644.
810 <https://doi.org/10.1002/jgrc.20063>

811 Tremblay, J.-É., & Gagnon, J. (2009). The effects of irradiance and nutrient supply on the
812 productivity of Arctic waters: a perspective on climate change. In J. C. J. Nihoul & A. G.
813 Kostianoy (Eds.), *Influence of Climate Change on the Changing Arctic and Sub-Arctic*
814 *Conditions* (pp. 73–93). Dordrecht: Springer Netherlands. [https://doi.org/10.1007/978-](https://doi.org/10.1007/978-1-4020-9460-6_7)
815 [1-4020-9460-6_7](https://doi.org/10.1007/978-1-4020-9460-6_7)

816 Tremblay, J.-É., Anderson, L. G., Matrai, P., Coupel, P., Bélanger, S., Michel, C., & Reigstad, M.
817 (2015). Global and regional drivers of nutrient supply, primary production and CO₂
818 drawdown in the changing Arctic Ocean. *Progress in Oceanography*, 139, 171–196.
819 <https://doi.org/10.1016/j.pocean.2015.08.009>

820 Tu, Z., Le, C., Bai, Y., Jiang, Z., Wu, Y., Ouyang, Z., et al. (2021). Increase in CO₂ Uptake Capacity
821 in the Arctic Chukchi Sea During Summer Revealed by Satellite-Based Estimation.
822 *Geophysical Research Letters*, 48(15). <https://doi.org/10.1029/2021GL093844>

823 Vernet, M., Ellingsen, I. H., Seuthe, L., Slagstad, D., Cape, M. R., & Matrai, P. A. (2019). Influence
824 of Phytoplankton Advection on the Productivity Along the Atlantic Water Inflow to the
825 Arctic Ocean. *Frontiers in Marine Science*, 6, 583.
826 <https://doi.org/10.3389/fmars.2019.00583>

827 Wanninkhof, R. (2014). Relationship between wind speed and gas exchange over the ocean
828 revisited: Gas exchange and wind speed over the ocean. *Limnology and Oceanography:*
829 *Methods*, 12(6), 351–362. <https://doi.org/10.4319/lom.2014.12.351>

830 Wassmann, P., & Reigstad, M. (2011). Future Arctic Ocean Seasonal Ice Zones and Implications
831 for Pelagic-Benthic Coupling. *Oceanography*, 24(3), 220–231.
832 <https://doi.org/10.5670/oceanog.2011.74>

- 833 Wassmann, P., Slagstad, D., & Ellingsen, I. (2019). Advection of Mesozooplankton Into the
834 Northern Svalbard Shelf Region. *Frontiers in Marine Science*, 6, 458.
835 <https://doi.org/10.3389/fmars.2019.00458>
- 836 Wassmann, P., Krause-Jensen, D., Bluhm, B. A., & Janout, M. (2021). Editorial: Towards a
837 Unifying Pan-Arctic Perspective of the Contemporary and Future Arctic Ocean. *Frontiers*
838 *in Marine Science*, 8, 678420. <https://doi.org/10.3389/fmars.2021.678420>
- 839 Weiss, R. F. (1974). Carbon dioxide in water and seawater: the solubility of a non-ideal gas.
840 *Marine Chemistry*, 2(3), 203–215. [https://doi.org/10.1016/0304-4203\(74\)90015-2](https://doi.org/10.1016/0304-4203(74)90015-2)
- 841 Wiedmann, I., Tremblay, J.-É., Sundfjord, A., & Reigstad, M. (2017). Upward nitrate flux and
842 downward particulate organic carbon flux under contrasting situations of stratification
843 and turbulent mixing in an Arctic shelf sea. *Elementa: Science of the Anthropocene*, 5,
844 43. <https://doi.org/10.1525/elementa.235>
- 845 Woodgate, R., & Peralta-Ferriz, C. (2021). Warming and Freshening of the Pacific Inflow to the
846 Arctic From 1990-2019 Implying Dramatic Shoaling in Pacific Winter Water Ventilation
847 of the Arctic Water Column. *Geophysical Research Letters*, 48(9).
848 <https://doi.org/10.1029/2021GL092528>
- 849 Woodgate, R. A. (2018). Increases in the Pacific inflow to the Arctic from 1990 to 2015, and
850 insights into seasonal trends and driving mechanisms from year-round Bering Strait
851 mooring data. *Progress in Oceanography*, 160, 124–154.
852 <https://doi.org/10.1016/j.pocean.2017.12.007>
- 853 Yamamoto-Kawai, M., Carmack, E., & McLaughlin, F. (2006). Nitrogen balance and Arctic
854 throughflow. *Nature*, 443(7107), 43–43. <https://doi.org/10.1038/443043a>
- 855 Yasunaka, S., Murata, A., Watanabe, E., Chierici, M., Fransson, A., van Heuven, S., et al. (2016).
856 Mapping of the air–sea CO₂ flux in the Arctic Ocean and its adjacent seas: Basin-wide
857 distribution and seasonal to interannual variability. *Polar Science*, 10(3), 323–334.
858 <https://doi.org/10.1016/j.polar.2016.03.006>

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