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Climate warming-driven changes in the flux of dissolved organic matter and its effects on bacterial communities in the Arctic Ocean: A review

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The warming of the Arctic Ocean impacts the dissolved organic matter (DOM) imports into the Arctic region, which affects the local bacterial communities. This review addressed the current status of DOM inputs and their potential influences on bacteria data (e.g., population, production, and metabolic activity of bacteria), as well as the projected changes of DOM inputs and bacterial communities as a result of climate warming. Microbial communities are likely affected by the warming climate and the transport of DOM to the Arctic Ocean. Imported DOM can alter Arctic bacterial abundance, cell size, metabolism, and composition. DOM fluxes from Arctic River runoff and adjacent oceans have been enhanced, with warming increasing the contribution of many emerging DOM sources, such as phytoplankton production, melted sea ice, thawed permafrost soil, thawed subsea permafrost, melted glaciers/ice sheets, atmospheric deposition, groundwater discharge, and sediment efflux. Imported DOM contains both allochthonous and autochthonous components; a large quantity of labile DOM comes from emerging sources. As a result, the Arctic sea water DOM composition is transformed to include a wider range of various organic constituents such as carbohydrates (i.e., glucose), proteinaceous compounds (i.e., amino acid and protein-like components) and those with terrigenous origins (i.e., humic-like components). Changes to DOM imports can alter Arctic bacterial abundance, cell size, metabolism, and composition. Under current global warming projections, increased inflow of DOM and more diverse DOM composition would eventually lead to enhanced CO₂ emissions and frequent emergence of replacement bacterial communities in the Arctic Ocean. Understanding the changes in DOM fluxes and responses of bacteria in the Arctic broadens our current knowledge of the Arctic Ocean's responses to global warming.

KEYWORDS

Arctic Ocean, sea water, dissolved organic matter (DOM), bacterial communities, climate warming

1 Introduction

The annual average Arctic temperature has risen approximately twice as fast as global temperatures in recent decades and is expected to increase by an average of $8.5 \pm 2.1^\circ\text{C}$ over the duration of the twenty-first century (Kaplan and New, 2006; Bintanja and Andry, 2017). Continued warming is likely to have profound effects on a variety of Arctic Ocean processes, including Arctic River runoff (Raymond et al., 2007; Behnke et al., 2021), Atlantic and Pacific inflow (Jones et al., 2008; Vetrov and Romankevich, 2019) to the Arctic Ocean, phytoplankton production (Kirchman et al., 2009; Osburn et al., 2019), sea ice melting (Maranger et al., 2015; Piontek et al., 2021), permafrost soil thawing (Serreze and Barry, 2011; Turetsky et al., 2020), subsea permafrost thawing (Chen et al., 2021), glacier/ice sheet melting (Hood et al., 2015), atmospheric deposition (Ruppel et al., 2015; Fang et al., 2016), groundwater discharge (Connolly et al., 2020), and efflux from sediment (Chen et al., 2016; Rossel et al., 2016; Rossel et al., 2020). These environmental processes contain and generate high quantities of dissolved organic matter (DOM). Climate change-related repercussions have led these processes to become DOM generators, accumulating substantial volumes of DOM in the Arctic Ocean, particularly in surface water (Tanaka et al., 2016; Stedmon et al., 2021). The role of DOM in marine ecosystems, notably as a substrate for bacterial communities, is highly dependent on its concentration and composition, both of which are closely related to its sources (Carlson, 2014). Therefore, it is critical to keep track of all the sources of DOM that contribute to the Arctic Ocean and to assess how climate warming is impacting and will continue to impact DOM input.

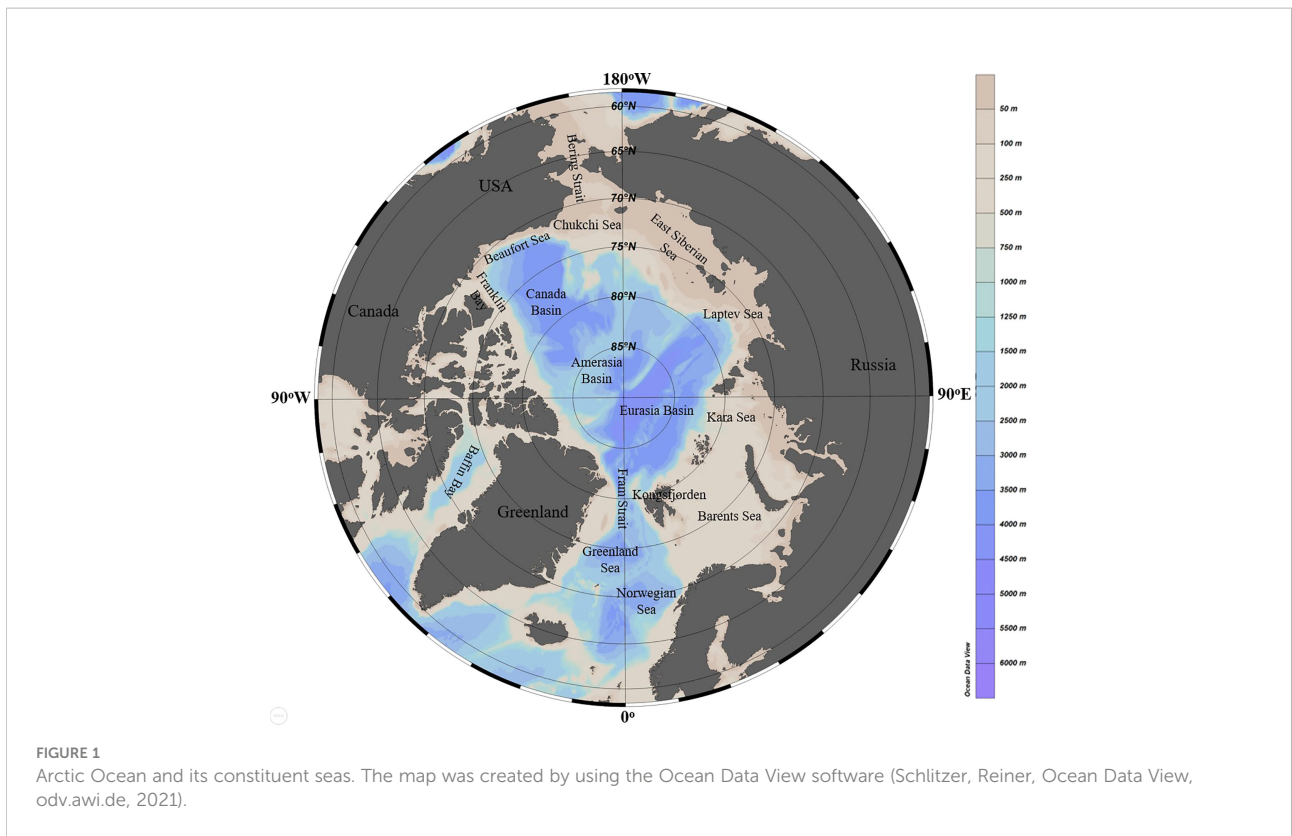
Numerous bacterial species thrive in the cold conditions of the Arctic Ocean, where *Alphaproteobacteria*, *Gammaproteobacteria*, and *Bacteroidetes* are dominant (Bano and Hollibaugh James, 2002; Alonso-Sáez et al., 2008; Comeau et al., 2011; Lee et al., 2019; Sanz-Sáez et al., 2020). Bacteria in the Arctic are evolutionarily unique compared to all other isolates, as evidenced by genetic analysis (Royo-Llonch et al., 2021). Bacterial populations in the Arctic Ocean are especially vulnerable to environmental changes caused by external factors (Fadeev et al., 2018; Carter-Gates et al., 2020; Cardozo-Mino et al., 2021; Ramachandran et al., 2021). The Arctic Ocean is known to be an oligotrophic marine environment with low levels of carbon substrates (Sala et al., 2008; Sert et al., 2022). Thus, perturbations in DOM flux caused by rising temperatures can significantly affect bacterial communities in the Arctic. DOM provides energy and carbon to bacteria, and bacteria participate in carbon cycling within aquatic environments, functioning as a sink (mineralization of DOM to CO_2) or a link (generation of biomass that may be transported through the microbial food web) (Cotner et al., 2002). Bacteria play a key role in the marine environment because they are critical components of the microbial loop; bacteria use available DOM in the surrounding water to grow, and are subsequently ingested by

grazers, which are eventually consumed by bigger organisms in the Arctic Ocean (Kirchman et al., 2009). Thus, changes in bacterial communities may have a domino effect on the entire Arctic ecosystem. The response of bacteria to DOM changes in the Arctic can be considered as the first signal of changes within the entire Arctic ecosystems caused by warming climate effects. Therefore, it is an important topic that deserves extensive research.

In this study, we collected present data regarding DOM inputs and their likely effects on bacteria, as well as projected changes as a result of the impacts of climate warming. First, we identified the possible sources of DOM discharged into the Arctic Ocean, as well as the origins and composition of DOM. In addition, updated data on bacterial abundance, metabolic activity, and composition in Arctic sea waters were compiled to gain a better understanding of the particular features that may operate as an adaptive mechanism for Arctic bacterial populations. We also summarize the consequences of DOM changes on domestic bacterial populations in the Arctic. Finally, we discuss the potential impact of warming on DOM quality and Arctic bacteria. The research region for this study covers the entire Arctic Ocean (Figure 1), with a particular emphasis on surface seawater, which receives a larger volume of DOM and varies to a greater extent as a result of environmental changes compared to Arctic deep water (Bano and Hollibaugh James, 2002; Benner et al., 2005; Tanaka et al., 2016). This study is expected to expand and deepen our knowledge of how the Arctic Ocean changes in response to global warming, in terms of DOM influx and bacterial populations.

2 Sources of DOM to the Arctic Ocean

DOM is transported to the Arctic Ocean *via* multiple sources. Arctic rivers, as well as the inflow from the Atlantic and Pacific, are the main transporters of DOM to the Arctic Ocean. The level of transported DOM can be intensified by heavier precipitation that is caused by warming climate (Raymond et al., 2007; Jones et al., 2008; Vetrov and Romankevich, 2019; Behnke et al., 2021). In addition, many other DOM sources have recently been identified as a result of the warming in the Arctic Ocean, including plankton production, melted sea ice, thawed permafrost soil, thawed subsea permafrost, melted ice sheets/glaciers, atmospheric deposition, groundwater discharge, and enhanced efflux from sediment. Ten sources of present DOM influxes to the Arctic Ocean are illustrated in Figure 2 and the corresponding DOM information (origin, concentration, and composition) are listed in Table 1. This section provides in-depth description concerning how these sources are influenced by warming climate.



2.1 Arctic River discharges

The increase in freshwater flow from rivers into the Arctic Ocean as a consequence of global warming was previously estimated to be 7% with a yearly rate of increase of $\sim 2.0 \text{ km}^3 \text{ year}^{-1}$ during 1936–1999 (Peterson Bruce et al., 2002). Recent measurements at regional and pan-Arctic scales also revealed a significant increase at a rate of $\sim 2.7 \text{ km}^3 \text{ year}^{-1}$ in the total annual river flow to the Arctic Ocean during 1936–2015 (Shiklomanov et al., 2021). The riverine DOM input to the Arctic Ocean has been estimated as approximately $25\text{--}36 \text{ Tg C yr}^{-1}$ (Raymond et al., 2007) based on the discharge from the five largest rivers (i.e., the Mackenzie, Yukon, Ob, Lena, and Yenisey Rivers) in 2004–2005. In the same vein, approximately 5–33% of the total DOC in Arctic surface waters is considered to be terrigenous in origin and is delivered *via* Arctic rivers (Opsahl et al., 1999). The DOM flux from Arctic rivers to the Arctic Ocean is expected to rise with increased water flow due to warming. A 6-year study conducted from 2012 to 2017 reported DOC concentrations in six major rivers varying from 3.2 mg L^{-1} to 11.7 mg L^{-1} (Behnke et al., 2021). The discharge of Arctic rivers is highly seasonal, with maximum fluxes in the spring and the lowest fluxes in the winter (Mann et al., 2012; Walker et al., 2013). River runoff during spring freshet is primarily affected by modern plant cover, topsoil, and surface litter (Benner et al., 2004; Walker et al., 2013); thus, the bulk of DOM exported during spring is

relatively young and includes newly fixed carbon (Benner et al., 2004; Raymond et al., 2007; Holmes et al., 2008; Wickland et al., 2012), which is considered to be relatively labile DOM. During summer and winter, water from deeper soil layers percolates to the rivers; incorporating old, relatively non-labile DOM with relatively humified structures and low content of lignin phenols (Stedmon et al., 2011; Mann et al., 2012). For organic compounds derived from Arctic rivers, terrestrial humic-like fluorophores are the most prevalent fluorescent DOM (FDOM) component (Walker et al., 2013). Enhanced river flow can lead to increases of several DOM optical indices such as the absorption coefficient at 350 nm (a_{350}), which serves as a measure of lignin content and tDOM intake, and the average specific UV absorbances at 254 nm (SUVA_{254}), which is a measure of aromaticity from allochthonous inputs (Walker et al., 2013). The biological index (BIX) values can also increase [e.g., from 0.45 to 0.68 (Birdwell and Engel, 2010)], indicating that the DOM in the Arctic rivers contains a relatively low abundance of autochthonous DOM. The core Arctic riverine fingerprint (CARF), which was proposed based on the molecular analysis of DOM from the six major rivers discharging to the Arctic Ocean over several years (2012–2017), was found to consist of 1,328 formulas (Behnke et al., 2021). The CARF contains a broad range of different substances with potential autochthonous origins, such as aliphatics and sugar-like formulas, as well as those with potential terrestrial sources, such as condensed

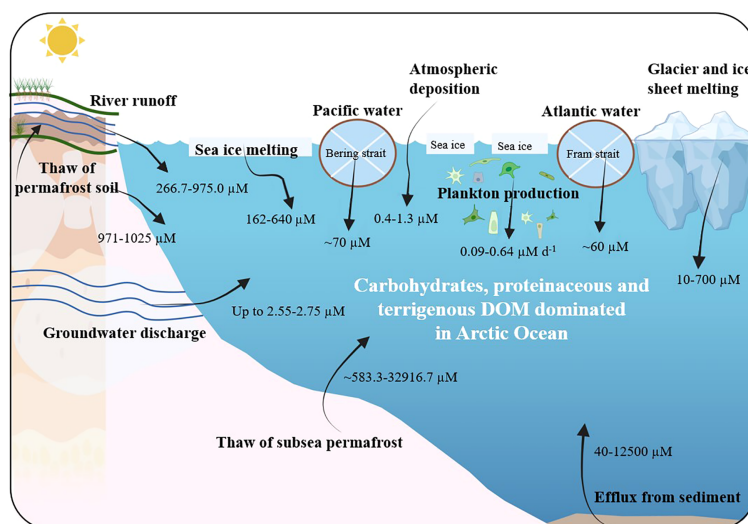


FIGURE 2
Sources of DOM imports into the Arctic Ocean. Concentration of DOM was derived the previous studies: river discharge (Behnke et al., 2021), Atlantic and Pacific water intrusion (Borsheim and Drinkwater, 2014; Jørgensen et al., 2014; Anderson and Amon, 2015), plankton production (Poulton et al., 2016), melted sea ice (Retelletti Brogi et al., 2018), thawed permafrost soil (Ward and Cory, 2015), melted ice sheets and glaciers (Bhatia et al., 2010; Bhatia et al., 2013; Kellerman et al., 2021), thawed subsea permafrost (Overduin et al., 2015; Chen et al., 2021), atmospheric deposition (Osterholz et al., 2014; Nakane et al., 2017; Fang et al., 2021), groundwater discharge (Connolly et al., 2020), efflux from Arctic sediment (Chen et al., 2016; Rossel et al., 2016; Rossel et al., 2020). Carbohydrates (i.e., glucose), proteinaceous (i.e., amino acid and protein-like components), and terrigenous characteristics (i.e., humic-like components) of DOM are predominant in surface water of Arctic Ocean as a result of increasing DOM input due to warming impacts.

aromatics and polyphenolics (Behnke et al., 2021). With continual global warming, the Arctic Ocean is thus anticipated to receive an increase in the supply of diverse organic compounds, particularly terrestrial-derived DOM compounds (humic-like and other aromatic components) along with a quantitative increase of DOM imports from the Arctic rivers.

2.2 Inflow waters from adjacent oceans

DOM is transported to the Arctic Ocean by inflows from the Pacific and Atlantic Oceans, and the inflow volume is on the rise owing to the warming effect. Long-term *in situ* Bering Strait mooring data (1990–2015) recorded nearly a doubling of the volume transport of Pacific waters into the Arctic from 2001 (0.7 Sv) to 2011 (1.1 Sv) (1 Sv = 10⁶ m³ s⁻¹) (Woodgate, 2018). The Atlantic water volume transport to the Arctic Ocean has also been expanded (Årthun et al., 2012; Wang et al., 2020), which provides not only DOM but also heat and salinity, causing the so-called “Atlantification” of the Arctic Ocean (Quadfasel et al., 1991; Lind et al., 2018). The seasonally accumulated inventory of DOC in the upper Northeast Pacific Ocean varied by a factor of ten across years (2009 to 2015), changing from 0.078 to 0.75 mol C m⁻² (Bif and Hansell, 2019). Thus, the DOC concentrations in the North Pacific and North

Atlantic waters to the Arctic Ocean tend to increase, thus increasing the likelihood of enhanced transport of DOM to the Arctic (Bif and Hansell, 2019). The fluxes of DOM into the Arctic Ocean were estimated to be 23 ± 2 Tg C yr⁻¹ and 155 ± 13 Tg C yr⁻¹ by inflow from the Pacific Ocean and the North Atlantic, respectively (Monteith et al., 2007; Bif and Hansell, 2019; Vetrov and Romankevich, 2019). Meanwhile, the concentration of DOM from the Pacific was estimated to be ~70 μM (Anderson and Amon, 2015), which is dominated by allochthonous DOM with a strong aliphatic character with very low light absorptivity (Pugach et al., 2018) and FDOM (~0.017 RU) (Stedmon et al., 2021; Cai et al., 2022). The DOC concentration in Atlantic seawater input was reported to be approximately 60 μM (Borsheim and Drinkwater, 2014; Jørgensen et al., 2014), which is characterized by a relatively low abundance of chromophoric DOM (cDOM) (Paulsen et al., 2018) and FDOM (~0.01 RU) (Stedmon et al., 2021), suggesting a lower contribution from terrestrial DOM compared to the Pacific seawater. The DOM from the surface waters of both the Atlantic and Pacific was found to be relatively bio-refractory, with only 10% of the bio-labile fraction in the total pool (Amon and Benner, 2003). Thus, it is worth noting that the influx of water from the Pacific and Atlantic is a considerable factor influencing the distribution of relatively bio-refractory DOM in the Arctic Ocean.

TABLE 1 Origin, concentration, and composition of DOM sources imported into the Arctic Ocean.

DOM source	DOM origin	DOM quantity	DOM composition
Arctic River discharge	Allochthonous	266.7–975 μM (Behnke et al., 2021)	-Newly fixed carbon and semi-labile carbon molecules in the spring to older and refractory carbon compounds in the summer and winter (Benner et al., 2004; Raymond et al., 2007; Holmes et al., 2008; Stedmon et al., 2011; Mann et al., 2012; Wickland et al., 2012); -High humic-like fluorescent and aromatic compounds (Mann et al., 2012);
Atlantic and Pacific water intrusion	Allochthonous Autochthonous	$\sim 60\text{--}70$ μM (Borsheim and Drinkwater, 2014; Jørgensen et al., 2014; Anderson and Amon, 2015)	-Strong aliphatic character in Pacific water (Pugach et al., 2018); -Small quantity of chromophoric DOM and fluorescent DOM in Atlantic water (Paulsen et al., 2018);
Plankton production	Autochthonous	0.09–0.64 $\mu\text{M d}^{-1}$ (Poulton et al., 2016)	-Carbohydrates, nitrogenous compounds, lipids, and organic acids (Lancelot, 1984; Emerson and Hedges, 2008); -High protein-like components (Chen et al., 2017);
Melted sea ice	Autochthonous	162–640 μM (Retelletti Brogi et al., 2018)	-LMW compounds (<350 Da) (e.g., amino acids and glucose) and protein-like substances (Muller et al., 2013; Jørgensen et al., 2015; Retelletti Brogi et al., 2018; Retelletti Brogi et al., 2019; Piontek et al., 2021);
Thawed permafrost soil	Allochthonous Autochthonous	998 \pm 27 μM (Ward and Cory, 2015)	-Amino acids, protein, peptides, aliphatic components, and carbohydrates (Ward and Cory, 2015; Heslop et al., 2019; Bruhn et al., 2021; MacDonald et al., 2021);
Melted ice sheets and glaciers	Allochthonous Autochthonous	10.0–700.0 μM (Bhatia et al., 2010; Bhatia et al., 2013; Kellerman et al., 2021)	-High protein-like components, LMW (<350 Da), and nitrogen-rich compounds (Hood et al., 2009; Bhatia et al., 2010; Lawson et al., 2014; Lawson et al., 2014); -Lignin-like and previously overridden soil and plant-derived compounds during the late melt season (Bhatia et al., 2010);
Thawed subsea permafrost	Allochthonous Autochthonous	$\sim 583.3\text{--}32916.7$ μM (Overduin et al., 2015; Chen et al., 2021)	-LMW compounds (<350 Da) (Overduin et al., 2015; Chen et al., 2021); -Humic-like and protein-like components (Chen et al., 2021);
Atmospheric deposition	Allochthonous	0.4–1.3 μM (Osterholz et al., 2014; Nakane et al., 2017; Fang et al., 2021)	-Condensed hydrocarbons, which are compounds deficient in oxygen and hydrogen and typically contain aromatic ring structures in DOM molecules (Kim et al., 2004; Bhatia et al., 2010);
Groundwater discharge	Allochthonous Autochthonous	Up to 2.75 \pm 0.2 μM (Connolly et al., 2020)	-Radiocarbon age shifts toward an older signal, high aromatic compounds, and hydrophobic acids (O'Donnell et al., 2012);
Efflux from Arctic sediment	Allochthonous Autochthonous	40–12500 μM (Chen et al., 2016; Rossel et al., 2016; Rossel et al., 2020)	-Abundance of peptide and aliphatic molecular formulas in productive ice edges and shallower sediments, but relatively more aromatic structures in multiyear ice-covered stations and deep sediments (Rossel et al., 2016; Rossel et al., 2020)

2.3 Plankton production

Plankton is a significant source of DOM production in the Arctic Ocean (Wheeler et al., 1997; Osburn et al., 2019). The annual DOM input from fresh phytoplankton is estimated to be approximately 66 Tg C y^{-1} over the entire Arctic Ocean (Stein et al., 2004). Phytoplankton photosynthesizes inorganic carbon (i.e., CO_2) and transforms it into organic carbon, which releases 2–50% of the total fixed carbon as DOM to seawater *via* passive diffusion and active exudation (Thornton, 2014). The physical breaking of phytoplanktonic cells by predators and virus lysis also contributes to DOM production (Urban-Rich et al., 2006; Saba et al., 2011). Phytoplankton development is on the rise as a result of the accelerating loss of sea ice cover in the Arctic Ocean, which is experiencing a warming climate (Dadaglio et al., 2018; Lewis et al., 2020). Spring was formerly thought to be the only season for phytoplankton blooms; however, autumn blooms have also been reported in Arctic seas (Uchimiya et al., 2016; Chen et al., 2017). Integrated primary production in the Arctic Ocean increased by 56.5% from 1998 to 2018, with an average annual increase of 6.79 Tg C

(Lewis et al., 2020). In particular, sea ice and under-ice algae play substantial roles in primary production in the Arctic Ocean, accounting for 3–60% of the total production in the Arctic Ocean (Legendre et al., 1992; Gosselin et al., 1997; Ambrose et al., 2005; Mundy et al., 2009). It was previously reported that the amount of DOC generated by phytoplankton was 0.09–0.64 $\text{mmol C m}^{-3} \text{ day}^{-1}$ in Nordic waters of the Arctic Ocean during the summer of 2012 (Poulton et al., 2016). Carbohydrates, nitrogenous substances, lipids, and organic acids constitute phytoplankton-derived DOM, which is highly labile (Lancelot, 1984; Emerson and Hedges, 2008). Protein-like fluorescent DOM (FDOM) has been suggested to be closely linked to the fall phytoplankton bloom in the Chukchi Sea and East Siberian Sea (Chen et al., 2017). Tyrosine- and tryptophan-like fluorophores are recognized as FDOM components in the polar ocean, which represent proteins (Chen et al., 2018; Retelletti Brogi et al., 2019; Jung et al., 2021). Additionally, phytoplankton blooms are significant producers of particulate and extracellular carbon in the Barents Sea (Vernet et al., 1998), which may serve as a major source of labile organic carbon for pelagic bacterioplankton (Poulton et al., 2016). In other words,

marine phytoplankton is also thought to be the source of the Chukchi Sea's marine humic-like fluorescence (Chen et al., 2018). Taken together, the enhanced primary production in the Arctic Ocean seems to result in increased distributions of diverse labile organic components with a predominance of carbohydrates, amino acids, and protein-like molecules in Arctic sea water.

2.4 Melted sea ice

When sea ice melts, it releases a large quantity of DOM into the surface waters of Arctic seas (Niemi et al., 2014; Retelletti Brogi et al., 2018; Retelletti Brogi et al., 2019; Piontek et al., 2021). Since 1980, both the permanent and annual central Arctic sea ice zones have diminished by approximately 13–15% every decade (Vaughan et al., 2013). The DOM content in sea ice is affected by allochthonous DOM, such as that trapped in brine channels and pores within the ice matrix (Petrich and Eicken, 2010), as well as autochthonous DOM, which is generated by bacteria and algae in the sea ice (Stedmon et al., 2007; Underwood et al., 2013). DOM is more enriched in the sea-ice matrix than in the surrounding seawater (Giannelli et al., 2001; Muller et al., 2013; Retelletti Brogi et al., 2018). For example, in Cambridge Bay, Canada, the concentration of DOM in sea ice (162–640 μM) was ~ 6.2 times higher than that in the surrounding seawater (Retelletti Brogi et al., 2018). The DOM extracted from sea ice was found to be labile, mostly comprising low molecular weight (LMW) molecules (<350 Da), such as amino acids and glucose (Muller et al., 2013; Jorgensen et al., 2015; Retelletti Brogi et al., 2018; Retelletti Brogi et al., 2019; Piontek et al., 2021). Protein-like compounds have been reported to be the most abundant constituents of DOM in sea ice cores (Retelletti Brogi et al., 2018; Zablocka et al., 2020). The mean humification index (HIX) and SUVA_{254} values of sea ice were in low levels, ranging from 0.454 to 0.629 and 1.137 to 1.390 $\text{m}^2 \text{g}^{-1} \text{C}$, respectively, indicating mostly autochthonous origin for CDOM (Zablocka et al., 2020). Thus, the melting of Arctic sea ice caused by rising temperatures is likely to supply a large quantity of labile DOM to Arctic seawater.

2.5 Thawed permafrost soil

Under the climate warming effects, a substantial quantity of ancient frozen carbon from the permafrost soil may be mobilized and transferred to the Arctic seas (Schuur et al., 2015; O'Donnell et al., 2016; Turetsky et al., 2020; Behnke et al., 2021). It was projected that without noticeable reductions in human greenhouse gas emissions, up to 80% of near-surface permafrost is expected to disintegrate by 2100 (Slater and Lawrence, 2013). The remnants of plants and animals that have accumulated over thousands of years in permanently

frozen soil are known as permafrost carbon (Zimov et al., 2006; Tarnocai et al., 2009). Permafrost is found across the Northern Hemisphere, especially on terrain surrounding the Arctic Ocean (Pugach et al., 2018; Obu et al., 2019). Permafrost covers approximately 1300–1700 Pg of soil organic carbon in the Northern Hemisphere, almost half of the total belowground organic carbon stock (Tarnocai et al., 2009; Schuur et al., 2015; Turetsky et al., 2020). The amount of DOC leached from permafrost soil has been estimated at 13.3 ± 0.4 $\text{mmol-DOC g-soil}^{-1} \text{day}^{-1}$, according to a study based on the present permafrost at 95–105 cm depth on the North Slope of Alaska's Innnavit Creek watershed (Ward and Cory, 2015). The DOM leached from the permafrost soil is expected to increase under a warming scenario because of deeper permafrost soil layer thawed (Slater and Lawrence, 2013). Permafrost DOM is labile to bacteria. For example, DOM in Yedoma permafrost, which is widespread in Siberia, Alaska, and Yukon, Canada (Strauss et al., 2017), contains a substantial proportion (34–62%) of highly biodegradable organic carbon (Vonk et al., 2013; Anthony et al., 2014; Spencer et al., 2015). The labile DOM comprises highly saturated and aliphatic structures (i.e., amino acids, proteins, and peptides) as well as carbohydrates (Ward and Cory, 2015; Heslop et al., 2019; Bruhn et al., 2021; MacDonald et al., 2021). Research on Canadian permafrost soil revealed that the LMW proteinaceous molecules with low aromaticity (i.e., tyrosine- and tryptophan-like components) were abundant in the permafrost leachates (Fouché et al., 2020). According to Fouché et al. (2020), permafrost stores more protein-derived DOM with a low molecular weight than the active soil layer. This was confirmed by the fluorescence index (FI) and the ratio of spectral slopes (S_R), which both increased with soil core depth (upper 3 m). The Arctic sea water is likely to contain more labile organic substances (such as amino acids, polysaccharides, and protein-like components) as a result of increasing breakdown of the permafrost soil in the region.

2.6 Melted glaciers and ice sheets

Glaciers and ice sheets constitute the world's second largest water storage area, and changes in the glacier volume driven by global warming may significantly affect the amount of DOM entering the Arctic Ocean. By 2050, the loss of global glacier mass is anticipated to result in a reduction of 15 Tg in glacial carbon reserves owing to climate change (Hood et al., 2015). Each year, the Greenlandic glacier releases DOC at a range of 0.2–0.5 Tg (Lawson et al., 2014; Pain et al., 2020). The DOC of supraglacial water and glacially fed river samples usually varies from 10 μM to 700 μM (Bhatia et al., 2010; Bhatia et al., 2013; Kellerman et al., 2021). DOM origins include aerosol and wind-blown organic material deposition on glacier surfaces, ancient terrestrial sources, inputs carried from the surface into glacier beds, and products of *in situ* microbial synthesis (Bhatia et al.,

2010; Lawson et al., 2014; Wadham et al., 2019). 26–53% of glacial DOM is bioavailable (Lawson et al., 2014; Musilova et al., 2017). The vast majority of DOM produced by glaciers consists of protein-like, nitrogen-rich compounds with low molecular weights (Hood et al., 2009; Bhatia et al., 2010; Lawson et al., 2014; Lawson et al., 2014). Simultaneously, lignin-like and previously overridden soil and plant-derived compounds can be liberated from glacier meltwater during the late melt season (Bhatia et al., 2010). Compared to other aquatic systems (such as the Greenland and Svalbard rivers), glacial DOM is notably richer in aliphatic and peptide-like organic materials (Kellerman et al., 2021). Increased contribution of bioavailable DOM to the Arctic sea water is anticipated as a consequence of continued mass loss of the glaciers and ice sheets by the rising temperature.

2.7 Thawed subsea permafrost

Permafrost in Arctic shelf areas stores 1400 Pg C of carbon (Shakhova et al., 2010; Vonk et al., 2012). If thawed, the subsea permafrost could be an important carbon source for the Arctic Ocean. Arctic subsea permafrost consists of frozen sediment interlayered with inundated peatland that has developed in the Arctic shelf area since the Holocene transgression of 7–15 kyrs BP, which was submerged due to glacier melting and is primarily located in the Beaufort, Chukchi, Laptev, and East Siberian Seas (Romanovskii et al., 2005; Shakhova et al., 2010; Overduin et al., 2015). Recently, numerous studies have reported the possibility of the rapid thawing of subsea permafrost in the Arctic Ocean (Vonk et al., 2012; Shakhova et al., 2017; Angelopoulos et al., 2019; Semenov et al., 2020; Steinbach et al., 2021). A study conducted in the East Siberian Arctic reported 9–2240 g C m⁻² yr⁻¹ of DOM flux from the Arctic shelf underlain by undersea permafrost, with the most pronounced DOM release occurring at the continuous-discontinuous transition zone of the subsea permafrost. (Chen et al., 2021). Also, the entire Arctic shelf with offshore permafrost was projected to supply DOM discharge at rates of ~0.7–1.0 Pg C yr⁻¹ (Chen et al., 2021). DOC concentrations in sediment pore fluids in a shelf with subsea permafrost vary from ~7 mg L⁻¹ to 395 mg L⁻¹, with LMW (<350 Da) compounds being dominant (Overduin et al., 2015; Chen et al., 2021). Humic-like and protein-like fluorescent components have also been found in pore water collected from subsea permafrost (Chen et al., 2021). As a result, the Arctic sea water may receive a benthic outflow of various organic components from thawed subsea permafrost.

2.8 Atmospheric deposition

Melted sea ice creates an extended open sea in the Arctic Ocean, which is projected to increase DOM intake in ice-free waters through atmospheric deposition. Atmospheric particulate

organic carbon of terrigenous origin, such as particulate black carbon (BC), generated from biomass and fossil fuel combustion, is a possible source of DOM in the Arctic Ocean (Khan et al., 2017; Mori et al., 2020). Globally, biomass burning produces 40–250 Tg C yr⁻¹ of BC (Jaffé et al., 2013; Jones et al., 2020), which can be transported to the Arctic from mid- and high latitudes. This is the reason why the Arctic is recognized as a pollution receptor zone (Shindell et al., 2008; Hall and Loboda, 2017; Backman et al., 2021). Increased BC deposition has been observed in parts of the European Arctic over the last few decades (Ruppel et al., 2015). In the central Arctic Ocean, BC concentrations of 0.021 ± 0.016 μmol L⁻¹ have been detected in seawater (Fang et al., 2016). In such an aquatic environment, BC may be oxidized by microbial or photochemical pathways, releasing DOM into the surrounding environment (Kim et al., 2004). In addition, BC is deposited on Arctic snow and sea ice (Doherty et al., 2010; Wang et al., 2011), where it is then imported into seawater when snow and sea ice melt. Recent research has shown that the concentration of dissolved BC in the Arctic Ocean ranges between 4.8 μg C L⁻¹ and 15.5 μg C L⁻¹ (Osterholz et al., 2014; Nakane et al., 2017; Fang et al., 2021). A fraction of condensed hydrocarbons, which are compounds deficient in oxygen and hydrogen and typically contain aromatic ring structures in DOM molecules, can be sourced from black carbon-like compounds (Kim et al., 2004; Bhatia et al., 2010). Atmospheric deposition has been established as the primary route by which terrigenous POM is directly transported to the open parts of the North Atlantic Ocean (Hernes and Benner, 2006). Thus, if the melting of sea ice in the Arctic Ocean accelerates in response to climate change scenarios, the flux of terrestrial DOM (tDOM) imported *via* atmospheric deposition is expected to become more significant.

2.9 Groundwater discharge

Groundwater may serve as an important source of DOM to Arctic coastal waters as permafrost thaws. A previous study reported that suprapermafrost groundwater (SPGW) can directly enter nearshore coastal waters in the Arctic (Connolly et al., 2020). DOC concentrations in the SPGW near the land-sea interface along the Alaska Beaufort Sea were up to two orders of magnitude greater than those in nearby rivers during the sampling periods in August 2011 and 2012, reaching 33 ± 2 mg C L⁻¹. Approximately 14–71 kg of DOC can be supplied by the SPGW to the coastal ocean per kilometer of coastline every day in late summer (Connolly et al., 2020). This DOM originates from easily leachable organic matter in surface soils, as well as deeper centuries-to-millennia-old soils that extend into melting permafrost (Connolly et al., 2020). It was reported that DOC leached from permafrost zones like suprapermafrost aquifer consisted of old radiocarbon, high aromatic compounds, and hydrophobic acids (O'Donnell et al., 2012). In addition, the

groundwater level has been on the rise in the Arctic region, implying an increased input of groundwater to the streamflow (Smith et al., 2007; Walvoord and Striegl, 2007; O'Donnell et al., 2012), which eventually flows into the Arctic seas. The long-term streamflow record (>30 years) in the Yukon River Basin indicates a general increasing trend in the groundwater contribution to streamflow at 0.7–0.9% yr⁻¹ (Walvoord and Striegl, 2007). In general, it is presumed that the increase in groundwater discharge in the warming Arctic could result in a greater fraction of DOM being exported to the Arctic Ocean. Groundwater is a source of “island of stability” (IOS), which denotes the last products of DOM disintegration and includes chemically stable molecular formulas formed following DOM processing by biological and physical pathways (Lechtenfeld et al., 2014; Kellerman et al., 2018; Behnke et al., 2021). Therefore, if groundwater flow increased, the export of stable DOM/IOS to the Arctic Ocean could also rise, which adds the oceanic carbon sink the stable DOM pool (Jiao et al., 2010; Behnke et al., 2021).

2.10 Efflux from Arctic sediments

DOM flux from Arctic sediment can be another DOM input source to Arctic seawater. A previous study has shown that the heating of near-surface marine sediment causes the bulk generation and release of reactive DOM (Lin et al., 2017). Advective fluid flow (i.e., cold seeps) from the seabed may facilitate the efflux of DOM from the sediment to the overlying water (Pohlman et al., 2011; Lin et al., 2017). In addition, several studies observed DOM efflux from the Arctic sediment to the overlying water column (Chen et al., 2016; Rossel et al., 2016; Rossel et al., 2020); all suggested that the release of DOM from sediment might increase as the Arctic warms. When the Arctic is subjected to a warming climate, the release of DOM from sediment could be considerable, which is supported by several studies that mention DOM efflux from the Arctic sediment to the overlying water column (Chen et al., 2016; Rossel et al., 2016; Rossel et al., 2020). DOM in Arctic sediment originates mainly from sedimented materials of primary production and terrigenous deposits (Boucsein and Stein, 2000; Belicka et al., 2004; Chen et al., 2016; Grosse et al., 2016). The deposited DOM is further reworked in the sediment *via* a complex combination of physical, chemical, and biological processes (Burdige and Komada, 2015; Chen et al., 2016). It was reported that DOC concentrations in the porewater of surficial sediment (0–10 cm) exhibited a wide range of spatial variations, ranging from 0.04 mM to 1.0 mM in the Eurasian Basin and HAUSGARTEN (Fram Strait) (Rossel et al., 2016; Rossel et al., 2020) and from 1.0 mM to 12.5 mM in the Chukchi-East Siberian Seas (Chen et al., 2016). The porewater DOM extracted from surficial sediment in the Eurasian Basin was characterized by an abundance of peptide and aliphatic molecular formulas in productive ice edges, but relatively more

aromatic structures in multiyear ice-covered stations (Rossel et al., 2016). In addition, the properties of the porewater DOM changed with depth in the Fram Strait. For example, surface porewaters at shallower stations (1500 m water depth) exhibited a signal of a higher and more recent OM input, which was associated with higher abundances of unsaturated aliphatic and N-containing formulas, whereas those from deeper stations presented a molecular signature of a lower and older OM input, which was linked with higher abundances of aromatic and oxygen-deficient compounds (Rossel et al., 2016; Rossel et al., 2020). With the spatial variation in porewater DOM taken into account, the warming effect can generate a benthic flux of DOM containing diverse chemical compositions to the Arctic sea water.

Overall, DOM from various sources enters the Arctic Ocean, and DOM concentrations are expected to rise owing to global warming. Imported DOM consists of both allochthonous and autochthonous components. A significant amount of labile DOM, such as amino acids, carbohydrates, glucose, LMW compounds (<350 Da), protein-like fluorescent components, and aliphatic and peptide components, are imported from the emerging sources highlighted in this article (i.e., phytoplankton, melted sea ice, melted ice sheets/glaciers, and thawed permafrost) (Table 1). Additionally, bio-refractory DOM, which includes humic-like fluorescent and aromatic compounds, is also supplied from river runoff, adjacent seas, thawed subsea permafrost, atmospheric deposition, groundwater discharge, and Arctic sediment efflux (Table 1). As bacteria and DOM have close interactions with each other, the increased DOM imports can affect the Arctic bacterial community in seawater. Before assessing potential DOM-induced alterations in bacteria caused by the impacts of a warming climate, fundamental information on the Arctic microbial population will be provided in Section 3.

3 Bacterial communities in the sea water of the Arctic Ocean

3.1 Bacterial abundance

The bacterial abundance of many Arctic Ocean sites has been studied; the majority of these studies were conducted in the summer and spring at varying depths (Table 2). In general, the number of bacteria in the Arctic Ocean has been reported to be in the 0.1–41.0 × 10⁵ cells mL⁻¹ range. Bacterial abundance generally peaks near the surface (euphotic zone: 30–80 m) and tends to decrease exponentially with increasing depth (Garneau et al., 2008). Bacterial distribution also varies spatially and seasonally. For example, the bacterial numbers are relatively high (~10⁶ cells mL⁻¹) in coastal seas (Børsheim, 2000; Howard-Jones et al., 2002; Benedikt and Rainer, 2004; Bezzubova et al.,

TABLE 2 Summary of bacterial abundance in sea waters of the Arctic Ocean.

Location	Sampling depth,m	Sampling period	Bacterial abundance, (10 ⁵)cells mL ⁻¹	Reference
Central Arctic Ocean	≤4080–120	June–Sept 1998	3.2 (1.9–6.7)1.1 (0.7–1.8)	(Sherr et al., 2003, Sherr and Sherr, 2003)
	≤4080–120	Nov 1997/Feb–May 1998	1.8 (1.3–2.9)1.3 (0.7–2.1)	(Sherr et al., 2003, Sherr and Sherr, 2003)
Eurasian Basin	≤4041–150	2 Aug–8 Oct 2012	2.1–17.90.9–8.5	(Piontek et al., 2021)
Western Canada Basin	≤200	11 Aug–4 Sept 2008	1.7 (0.2–8.4)	(He et al., 2012)
Beaufort and Chukchi Seas	2	July 2007 and Aug 2008 Jan 2008 Jan 2009	14 (9.3–20.9)4.0 (2.2–7.5)	(Nikrad et al., 2012)
Chukchi Sea	≤10	18 Aug–14 Sept 1992	2.1–21.0	(Steward et al., 1996)
Laptev Sea	≤5050–70	Sept–Oct 2015	3.5–4.35.1–8.6	(Savvichev et al., 2018)
Kara Sea	1–2	Aug–Sept 2001	3.5 (2.3–4.7)	(Benedikt and Rainer, 2004)
	≤527	17–29 Sept 2011	0.2–22.2	(Kopylov et al., 2015)
Barents Sea	2	June/July 1999	4.1–41	(Howard-Jones et al., 2002)
	<200	8–22 July 2003 20 July– 4 Aug 2004 18 May–5 June 2005	3.6 (0.8–9.1)	(Sturluson et al., 2008)
Greenland Sea	≤5051–100101–200201–500	End of July 1995	11 (0.97–28.0)5.9 (2.8–11.0)3.6 (2.4–4.7)1.9 (1.0–3.5)	(Børsheim, 2000)
Greenland Sea and Norwegian Sea	0–1	Sept 2000	0.22–6.0	(Naganuma et al., 2006)
Chukchi Sea Shelf	<20	10–26 Sept 2013	4.2–6.0	(Uchimiya et al., 2016)
Coastal Beaufort Sea	≤32	26 July–2 Aug 2004	6.7	(Vallières et al., 2008)
East Siberian Sea Shelf	≤47	5–7 Sept 2017	5.9–20.9	(Kopylov et al., 2021)
Laptev and East Siberian Sea Shelf	≤855	5 Aug–20 Sep 2017	0.8–16.0	(Bezzubova et al., 2020)
Franklin Bay	≤10	4 Nov 2003–6 Aug 2004	3.2 (0.87–11.0)	(Garneau et al., 2008)
	≤200		2.6 (1.0–6.8)	
	≤40	10 Dec 2003–28 May 2004	2.1 (1.4–7.3)	(Belzile et al., 2008)
Fram Strait	≤ 60	22 April–27 May 2008	1.3–3.09	(Seuthe et al., 2011)
	≤100	16–23 July 2018 16 Sept–4 Oct 2018	3.0–22.02.0–15.0	(von Jackowski et al., 2020)
Baffin Bay	< 5	17–30 Sept 1999	1.1–2.7	(Fouilland et al., 2007)
Kongsfjorden	0.5	May 2016	10	(Caruso et al., 2020)
	40	29 June 2015	8.13	(Müller et al., 2018)
	5–80	June–Oct 2012	0.14–5.0	(Sinha et al., 2017)

2020) and Atlantic-influenced waters (Børsheim, 2000; Caruso et al., 2020; von Jackowski et al., 2020). Bacterial abundance tends to decrease from the coast to the central Arctic Ocean (Garneau et al., 2006; He et al., 2012; Bezzubova et al., 2020; Piontek et al., 2021); it is greater in ice-free water (10⁶ cells mL⁻¹) than in ice-covered sections (10⁵ cells mL⁻¹) (Cardozo-Mino et al., 2021). In addition, from winter to summer, the heterotrophic bacterial abundance in central Arctic sea waters (0–40 m) almost doubles, while it remains relatively constant at a depth of 80–120 m (Sherr et al., 2003).

3.2 Bacterial cell size and activity

Bacteria in the Arctic Ocean are often assumed to have small cell sizes and low levels of activity. Throughout the spring and

summer, bacteria have an average cell volume of approximately 0.05–0.09 μm³ in the Chukchi Sea and the Canada Basin (Kirchman et al., 2007). The bacterial growth rates in the top 50 m of seawater were 0.004 ± 0.003 d⁻¹ in winter and 0.019 ± 0.009 d⁻¹ in summer, with an average doubling period of 300 and 46 days, respectively (Sherr and Sherr, 2003). The ratios of bacterial production (BP) to primary production (PP) vary from 0.03 to 0.32 (Sturluson et al., 2008; Uchimiya et al., 2016; Piontek et al., 2021); in several sites of the Arctic Ocean, these ratios were higher than 0.11, a common value in other oceans (Kirchman et al., 1993; Ducklow et al., 1995), which indicates that the fraction of PP that passes through DOM-bacteria coupling is not low under cold conditions, signifying an important role of bacteria in the carbon dynamics within the Arctic Ocean. Bacterial assemblages in marine oligotrophic settings, such as the Arctic Ocean, exhibit a high degree of metabolic adaptability to be able

to access scarce carbon sources for growth (Sala et al., 2008). In addition, bacterial communities in the Arctic can adjust their metabolism to the high-latitude cycles of PP (Hop and Wiencke, 2019). It has been observed that organic matter breakdown by extracellular enzyme activity occurs in cold Arctic seas at rates comparable to those recorded in warmer lower-latitude seas (Huston and Deming, 2002). Furthermore, a previous study reported that microbial communities in (near-) Arctic climates functioning similarly to those in warmer climates, with algal carbon processed at similar rates and *via* similar paths (Oakes et al., 2016).

3.3 Bacterial composition

Bacteria in the Arctic Ocean mostly include newly identified bacterial taxa. Several recent studies have shown that the phylogenetic composition of Arctic bacteria is dominated by *Alphaproteobacteria*, *Gammaproteobacteria*, and *Bacteroidetes* (Table 3). At the sub-level, *Pelagibacter* (the SAR11 clade) accounts for the majority of *Alphaproteobacteria* (Bano and Hollibaugh James, 2002). The majority of *Bacteroidetes* sequences belong to *Polaribacter* (Comeau et al., 2011). Although the same predominant classes of bacteria are found in other ocean systems, including the Antarctic (Murray and Grzymalski, 2007), the bacteria in the Arctic are evolutionarily distinct from all other isolates (Bano and Hollibaugh James, 2002). It was revealed that 441 of the 530 metagenome-assembled microbial genomes from 41 Arctic seawater samples belonged to previously unknown species, while 299 genomes exhibited an exclusively polar distribution (Royo-Llonch et al., 2021).

There are indications that bacterial populations in the Arctic are shifting as a consequence of global warming effects. Ramachandran et al. (2021) uncovered a previously unknown freshwater-originated *Methylophilaceae* clade (BS01) in the surface seawater of the Canada Basin. As freshwater bacteria transported by rivers rarely survive in the Arctic Ocean for long (Elifantz et al., 2007), this finding suggests the possibility of a bacterial evolutionary transition from freshwater to marine water in the Arctic Ocean, which receives increased water inputs from Arctic rivers as a result of climate warming effects (Ramachandran et al., 2021). In addition, *Gammaproteobacteria* and *Flavobacteriia* have been reported to be abundant in Atlantic-influenced waters (i.e., the Fram Strait, Svalbard archipelago, and the Norwegian Sea) (Fadeev et al., 2018; Carter-Gates et al., 2020; Thomas et al., 2020), which may reflect “Atlantification” in the Arctic Ocean. Notably, the *Rhodobacteraceae* and SAR11 clades (both members of the class *Alphaproteobacteria*) have been found in open ocean regions, such as Chukchi Borderland (Zeng et al., 2013; Lee et al., 2019) and the Fram Strait (Cardozo-Mino et al., 2021). Both *Rhodobacteraceae* and SAR11 abundances showed substantially

positive correlations with water temperature (Pearson’s correlation coefficient > 0.5, p-value < 0.05) (Cardozo-Mino et al., 2021), suggesting a close linkage between cell prevalence and the warm Atlantic and Pacific input waters. Photoheterotrophic bacteria have recently been discovered in the Arctic Ocean (Cottrell Matthew and Kirchman David, 2009; Boeuf et al., 2013; Nguyen et al., 2015). This bacterial type can depart from completely heterotrophic living by receiving energy through nontraditional methods associated with increased sunlight penetration into surface waters caused by the melting of Arctic sea ice (Boeuf et al., 2014).

Overall, the bacteria in the Arctic are distinct from previously known taxa. According to the current understanding, they can be susceptible to environmental changes. This sensitivity raises more concerns about changes that may occur in bacterial populations as a result of increasing DOM influx into the Arctic Ocean.

4 Effects of DOM changes on bacterial communities in the Arctic Ocean

4.1 Bacterial abundance, cell size, and activity

Increased DOM can stimulate bacterial growth in the Arctic Ocean. The addition of glucose to western Arctic seawater resulted in the increase of leucine incorporation that was almost three times higher than that of the control at the same low temperature (Kirchman et al., 2005). Leucine is required to create new cellular proteins, and its incorporation rate can be applied to predict the produced amount of bacterial biomass (Piontek et al., 2021). Similarly, the addition of DOM produced from diatoms or permafrost results in an increase in the number and production of bacteria in the Arctic (Dadaglio et al., 2018; Müller et al., 2018). The yields of bacterial growth were found to range between 0.35 d⁻¹ and 0.67 d⁻¹ when the DOM obtained from sea ice was added naturally (Niemi et al., 2014). Based on these experiments, it was deduced that the addition of DOM may be more effective in stimulating the development of bacterial communities in cold waters than in warm seas (Wiebe et al., 1992; Wiebe et al., 1993). In addition, the lability of DOC is a critical factor in determining the quantity and activity of bacteria under polar conditions (Arnosti et al., 2011; Caruso et al., 2020; von Jackowski et al., 2020; Piontek et al., 2021). Numerous studies have shown a high degree of bacterial consumption in the Arctic Ocean, which is favorably correlated with amino acids, carbohydrates (i.e., glucose), and protein-like fluorescent DOM (Rich et al., 1997; Lønborg et al., 2010; Tisserand et al., 2020; Bruhn et al., 2021).

TABLE 3 Composition of bacteria in sea waters summarized from previous studies in the Arctic Ocean.

Location	Sampling period	Sampling depth	Analysis method	Major bacteria	Reference
Central Arctic	Winter-spring 1995, Summer 1996, Summer-fall 1997	55 m and 131 m	Denaturing gradient gel electrophoresis (DGGE)	<i>Alphaproteobacteria</i> 36% <i>Gammaproteobacteria</i> 32% <i>Deltaproteobacteria</i> 14% <i>Cytophaga-Flexibacter-Bacteroides</i> spp. 9% <i>Verrucomicrobium</i> spp. 6% <i>Epsilonproteobacteria</i> 1% Green nonsulfur bacteria 2%	(Bano and Hollibaugh James, 2002)
Bering Strait to Chukchi Borderland	Summer of 2017	0–2 m	Illumina Miseq	<i>Alphaproteobacteria</i> 35% <i>Bacteroidia</i> 34% <i>Gammaproteobacteria</i> 19% <i>Actinobacteria</i> 5% <i>Verrucomicrobiae</i> 3%	(Lee et al., 2019)
Chukchi Borderland	July 2010	10–1800 m depth	454 GS-FLX Titanium Sequencing System	<i>Alphaproteobacteria</i> 43.2% <i>Gammaproteobacteria</i> 16.7% <i>Flavobacteria</i> 13.7% <i>Deltaproteobacteria</i> 12%	(Han et al., 2015)
Chukchi Sea	Spring and summer of 2002 and 2004	5–30 m	Fluorescence <i>in situ</i> hybridization (FISH)	<i>Gammaproteobacteria</i> 53% <i>Bacteroidetes</i> 29% <i>Alphaproteobacteria</i> 17%	(Rex et al., 2007)
Beaufort Sea	October 2003–October 2010	Subsurface chlorophyll maximum (SCM) layer	Roche 454 GS-FLX Titanium platform	<i>Alphaproteobacteria</i> 55% ^{a)} <i>Gammaproteobacteria</i> 15% ^{a)} <i>Bacteroidetes</i> 13% ^{a)} <i>Verrucomicrobia</i> 2% ^{a)}	(Comeau et al., 2011)
Beaufort and Chukchi Seas	July 2007 August 2008 January 2008 January 2009	2 m	MAR-FISH	<i>Gammaproteobacteria</i> 33% <i>Cytophaga-Flavobacteria</i> 20% <i>Alphaproteobacteria</i> 33%	(Nikrad et al., 2012)
Franklin Bay	Several dates from December 2003 to August 2004	3 m under the ice	MAR-FISH	<i>Alphaproteobacteria</i> 34% ^{b)} <i>Bacteroidetes</i> 14% ^{b)} <i>Gammaproteobacteria</i> 8% ^{b)} <i>Betaproteobacteria</i> 3% ^{b)}	(Alonso-Sáez et al., 2008)
Svalbard archipelago	August–September 2017	Chlorophyll maxima (10–50 m)	HiSeq platform 2500	<i>Proteobacteria</i> 97% (<i>Gammaproteobacteria</i> 87.6%) <i>Actinobacteria</i> 2% <i>Bacteroidetes</i> 0.6%	(Thomas et al., 2020)
Laptev Sea	October 2018	From the pycnocline (25 m) and the horizon above the pycnocline (16 m)	MiSeq platform	<i>Proteobacteria</i> (75.6–81.5%) <i>Bacteroidetes</i> (9.9–	(Samylnina et al., 2021)

(Continued)

TABLE 3 Continued

Location	Sampling period	Sampling depth	Analysis method	Major bacteria	Reference
				11.5%) <i>Actinobacteria</i> (0.5–1.8%) <i>Verrucomicrobia</i> (0.6–2.2%)	

^{a)}Relative abundance of bacteria derived from Figure 4A; ^{b)}Relative abundance of bacteria derived from Figure 2B.

The addition of DOC to Arctic bacteria can also result in an increase in cell size and activation. For example, the release of DOM from Arctic sea ice (at 840 $\mu\text{mol L}^{-1}$) resulted in a 2.1–3.2-fold increase in the apparent cell size of Arctic surface seawater bacteria (Niemi et al., 2014). Müller et al. (2018) noticed an increase in cell size in the coastal Arctic due to the input of tDOM. In addition, after sea-ice DOM enrichment, Niemi et al. (2014) found that the entire prokaryotic population was characterized by cells with a high nucleic acid (HNA) content (on average 97% of the total prokaryotic abundance). The quantity of HNA bacteria in the surface waters of Franklin Bay increased 5–6 weeks after phytoplankton development began in spring, growing from 1×10^5 to 3×10^5 cells mL^{-1} during an 8-week period at a net growth rate of 0.018 d^{-1} (Belzile et al., 2008). The presence of HNA suggests that prokaryotes develop metabolic activity and enter the exponential growth phase (Niemi et al., 2014). Müller et al. (2018) demonstrated that the addition of aged tDOM extracted from the active layer of permafrost soil increased the number of HNA cells. Consistently, bacteria of larger size (microbial size < 3.0 μm) are capable of metabolizing a broader spectrum of DOM, including aromatic terrestrial material from river

discharge, than those with smaller cells (microbial size < 0.2 μm and < 0.7 μm) (Grunert et al., 2021). In summary, the reviewed literature reveals that the increase in the DOM fluxes to the Arctic Ocean can impact several features of bacterial community (Figure 3). Increased DOM can significantly increase the bacterial population, cell size, and metabolic activity, thereby releasing a substantial quantity of CO_2 into the atmosphere.

4.2 Bacterial enzymatic system

The bacterioplankton populations in the Arctic are capable of enzymatic adaptations to DOM components. The genetic capability of bacterial strains to generate extracellular enzymes (e.g., leucine aminopeptidase, peptidase, glucosidase, polysaccharide hydrolase, etc.) is related to the degradability of DOM (Arnosti, 2010; Balmonte et al., 2020; Tisserand et al., 2020). The majority of Arctic microbial communities have large genomes and the capacity for rapid generation rates, which may facilitate adaptation to a copiotrophic lifestyle in nutrient-dense environments, particularly those rich in carbon (Royo-Llonch et

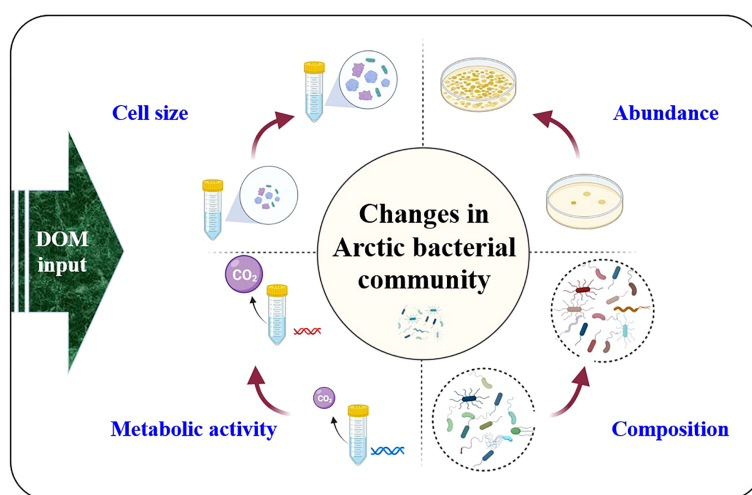


FIGURE 3
Elevation in population, size, metabolic activity, and structure of the bacterial communities in the Arctic Ocean as a result of the increased DOM in seawater.

al., 2021). Several recent studies have documented alterations in the metabolism of bacterioplankton populations through enzymatic modifications in response to the diverse chemical composition of DOM in the Arctic Ocean. For example, bacterioplankton in the Fram Strait, Greenland Sea, and Kongsfjorden of the Arctic Ocean exhibited accelerated enzymatic hydrolysis of dissolved mixed carbohydrates that were produced in substantial amounts as a result of phytoplankton blooms and melted sea ice (Sala et al., 2010; Piontek et al., 2014; Jain and Krishnan, 2017). In addition, a metagenomic analysis of the Canada Basin of the western Arctic Ocean found that the pelagic phylum *Chloroflexi* was enriched with aromatic chemical degradation genes, which were acquired mostly by lateral exchange from terrestrial bacteria (Colatriano et al., 2018). Overall, changes in DOM have impacts on bacterial enzymatic activity in the Arctic seawater. Furthermore, alteration of the bacterial enzymatic system can eventually result in a shift in the taxonomic composition of the Arctic Ocean subpopulation community (Figure 3).

4.3 Structure of the bacterial community

Different types of DOM input can promote unique bacterial taxonomic groups. By choosing the most sensitive species with the proper genetic material to break down DOM at their disposal in their unique habitat, newly input DOM can change the bacterial community makeup in the Arctic Ocean (Tisserand et al., 2020). For example, *Alphaproteobacteria* have been shown to utilize DOM with an LMW (Nikrad et al., 2012; Amaral et al., 2016). Labile DOM from phytoplankton and sea ice is likely to be released more in open water areas than in other environments, thereby facilitating the growth of *Alphaproteobacteria* in open waters far from coastal areas in the Arctic Ocean (Bano and Hollibaugh James, 2002; Galand et al., 2008; Han et al., 2014). In contrast, *Gammaproteobacteria* are well-known for their ability to break down a diverse spectrum of carbon sources (Alonso-Sáez et al., 2008; Wilson et al., 2017; Lund Paulsen et al., 2019), which allows them to be widely distributed in coastal areas (Rex et al., 2007; Kellogg and Deming, 2009) that receive high tDOM from the river discharge.

The labile DOM input derived from phytoplankton blooms and melted sea ice facilitates the establishment of particular bacterial species. These are *Roseobacter* and operational taxonomic units close to *Pseudoalteromonas* of the *Alphaproteobacteria* class, *Oceanospirillaceae* and *Alteromonadaceae* of the *Gammaproteobacteria* class, and *Flavobacteriaceae*, *Polaribacter*, *Formosa*, and *Tenacibaculum* of the *Flavobacteriia* class in the *Bacteroidetes* phylum

(Alonso-Sáez et al., 2008; Wilson et al., 2017; Dadaglio et al., 2018; Underwood et al., 2019; Piontek et al., 2021). The metabolic features of these bacteria allow them to respond rapidly to phytoplankton blooms linked with organic substances (Buchan et al., 2014). In particular, there are specific relationships among phytoplankton, roseobacteria, and flavobacteria in oceans (Buchan et al., 2014). *Roseobacter* possess a variety of metabolic characteristics that likely favor interactions with DOM derived from seawater phytoplankton (Buchan et al., 2014). *Roseobacter* isolates also have larger genomes (~4.5 Mb) and greater gene content (Newton et al., 2010) than other abundant marine lineages that are geographically restricted to marine planktonic settings (Rocap et al., 2003; Giovannoni Stephen et al., 2005). Both these features may be critical for the abundance succession of *Roseobacter* over phytoplankton blooms in the Arctic Ocean. *Flavobacteriia* genomes contain several physiological mechanisms that are likely involved in their interaction with phytoplankton-derived DOM (Buchan et al., 2014).

The addition of DOM from terrestrial sources may promote the formation of new bacterial groups in the Arctic Ocean. For example, *Rhodobacteraceae* (Sipler et al., 2017) and *Sulfitobacter* (Dyda et al., 2009) of the *Alphaproteobacteria* class, *Colwellia* (Sipler et al., 2017), *Glaciecola*, and *Marinomonas* (Müller et al., 2018), *Balneatrix* and SAR92 clade (Lund Paulsen et al., 2019) within *Gammaproteobacteria*, *Arcobacter* sp (Sipler et al., 2017), of the *Epsilonproteobacteria* class, and *Polaribacter* (Sipler et al., 2017) of *Bacteroidetes* increase their relative abundance with increasing tDOM concentration. These bacteria can decompose a wide range of complex organic substances. *Marinomonas* sp. includes several genes encoding enzymes involved in the breakdown of aromatic hydrocarbons (Liao et al., 2015). *Arcobacter*-affiliated sequences comprise genes encoding proteases, peptidases, and oligopeptidases, as well as enzymes required for the oxidative tricarboxylic acid cycle (He et al., 2020). In particular, *Polaribacter* and *Colwellia* can use a variety of organic substrates. *Polaribacter* are psychrophilic bacteria found in seawater and ice (Sipler et al., 2017; Yergeau et al., 2017), that are capable of decomposing polymeric organic molecules (Sipler et al., 2017). The genus *Colwellia* is a polar taxonomic species that produces well-adapted extracellular enzymes for the degradation of organic molecules (Méthé et al., 2005). In general, future changes in the delivery of DOM to the Arctic Ocean may result in substantial alterations in the composition of the bacterial population.

Taken together, the critical changes in DOM influxes to the Arctic seas under climate warming effects have numerous implications on bacterial community, which was simplistic shown in Figure 4. Increased DOM input levels tend to modify the entire bacterial community in terms of quantity, cell size, metabolism, and composition.

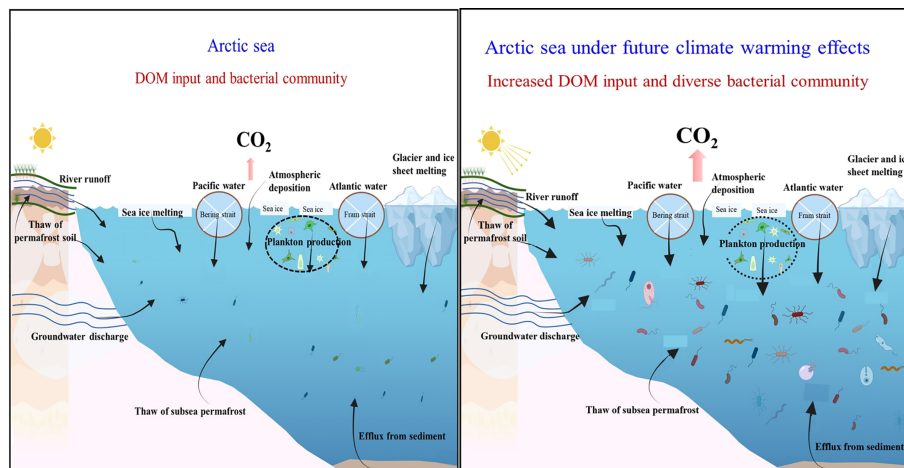


FIGURE 4 Changes in DOM input and its consequence on the bacterial community in the Arctic Ocean under the effects of climate warming. The arrows represent DOM input.

5 Changes of DOM quality in the Arctic Ocean and their consequences on bacteria under warming effects

5.1 Variations in DOM quality in the Arctic Ocean

It is well recognized that the Arctic Ocean is an oligotrophic marine ecosystem with insufficient carbon substrates (Sala et al., 2008; Sert et al., 2022). The chemical makeup of DOM in the Arctic sea water varies with changing dominant input sources (or different regions) with dissimilar compositions of different organic components (Table 1). In the central Arctic Ocean, carbohydrates (i.e., glucose) and five distinctive fluorescent components, including tryptophan-like, tyrosine-like, terrestrial humic-like and two humic-like components, were detected (Piontek et al., 2021; Williford et al., 2021), and intensity of *in-situ* DOM fluorescence (water depths <25 m) reached >0.030 RU (up to 0.089 RU) (Stedmon et al., 2021). The Canadian Basin surface waters were characterized by high percentage of autochthonous CDOM ($a_{375} = 0.21 \text{ m}^{-1}$), and the surface waters of the Eurasian Basin (100 m depth) showed a riverine feature ($a_{375} = 0.41 \text{ m}^{-1}$) (Rossel et al., 2020). Seawater samples taken along a transect over the Chukchi shelf and Arctic fjords exhibited the higher values of CDOM and FDOM intensities than those of the central Arctic Ocean (Chen et al., 2018; Retelletti Brogi et al., 2019; Chen et al., 2021; Cai et al., 2022). Temporal and vertical changes in DOM quality in the Arctic Ocean are also observed. In the central Canada Basin of the Arctic Ocean, a long-term research for DOM composition

(from 2007 to 2017) found a substantial upward trend of protein-like component with the yearly increase from 0.0021 to 0.0046 RU (DeFrancesco and Guéguen, 2021). Furthermore, microbial humic-like and terrestrial humic-like components were all significantly higher in the lower polar mixed layer (LPML) at a depth of 31 m in the Canada Basin than in the upper water layer (average depth of 12 m) ($p < 0.05$) (DeFrancesco and Guéguen, 2021). The authors indicated that as sea ice cover diminished in the warming Arctic Ocean, photodegradation increased, leading to a more terrigenous DOM in the LPML. Overall, the current data suggested that carbohydrates (i.e., glucose), proteinaceous (i.e., amino acid and protein-like components), and terrigenous characteristics (i.e., humic-like components) in DOM are all expected to rise in their abundances in surface Arctic sea water as a result of increasing DOM input sources caused by warming.

5.2 Impacts of DOM quality on bacterial communities in the Arctic Ocean

Changes in DOM quality in Arctic waters (i.e., increased prevalence of various organic compounds) have impacts on the growth of microbial communities in Arctic waters. Many previous studies have reported that bacterial utilization positively correlates to the succession patterns of various organic components such as amino acids, carbohydrates, and proteinaceous compounds (Rich et al., 1997; Jørgensen et al., 2014; Lund Paulsen et al., 2019; Tisserand et al., 2020; von Jackowski et al., 2020; Bruhn et al., 2021). Amino acids are a molecular indicator of DOM bioavailability (Benner, 2003; Lund Paulsen et al., 2019). Aromatic amino acids (tryptophan,

tyrosine, and phenylalanine) are connected to protein-like fluorescent DOM, which has been proposed as a feasible tracer for bio-labile DOM (Yamashita and Tanoue, 2003; Lønborg et al., 2010). These labile organic components are subject to rapid (hours-weeks) microbial utilization and transformation (Hansell and Carlson, 2014). A previous study investigated utilization of the prokaryotic community in western Arctic Ocean surface water of different classes of labile organic compounds, including amino acids, diatom-derived extracellular polymers, protein, and glucose and reported that amino acids were the most readily assimilated by the bacteria (50–60%), followed by protein (20–30%), glucose (10–20%), and the extracellular polymeric substances (EPS) produced from diatoms (30–40%) (Elifantz et al., 2007). The study also found that *Alphaproteobacteria* contributed more to the degradation of amino acids and glucose, while *Cytophaga*-like bacteria (*Bacteroides-Cytophaga-Flexibacter* group) were more involved in the assimilation of proteins and EPS and *Gammaproteobacteria* contributed equally to the assimilation of both DOM subgroups (i.e., amino acids plus glucose and proteins plus EPS) (Elifantz et al., 2007).

Bacteria in Arctic sea water tend to degrade humic-like fluorescent components at slow rates. For example, bacterial communities from the Chukchi Sea water consumed ~7% of “humic-like” terrestrial-derived DOM within 4–6 d (Sipler et al., 2017). Another experimental study using microbial communities in Fram Strait seawater revealed only 11% consumption of humic substances over 400 h of incubation (Ingeborg, 1999). Humic-like fluorescent DOM is considered to be an indicator for recalcitrant DOM (Jørgensen et al., 2014). A very long period is usually required for the complete biodegradation of refractory compounds, up to 16,000 years or longer (Hansell, 2013). Lund Paulsen et al. (2019) observed that a reduction in visible FDOM, which is often associated with humic-like components in subsurface waters, corresponded with an increase in bacterial population and activity, suggesting an active bacterial uptake or modification of the DOM fraction in Arctic fjord water. The breakdown of visible FDOM seems to be linked to certain bacterial taxa in the class *Gammaproteobacteria* (Lund Paulsen et al., 2019). In general, different microbial groups are likely to be stimulated by various DOM inputs, all resulting in the enhanced diversity in the microbial community in the Arctic waters. In summary, enhanced DOM import fluxes into Arctic seas as a consequence of climate change are expected to result in increased CO₂ emissions and heighten the likelihood that resident bacterial communities in the Arctic Ocean will eventually be replaced.

6 Conclusions and perspectives

The Arctic Ocean plays a critical role in global climate control, and is a particularly vulnerable system that has

already undergone significant disturbances owing to climate change (Peterson Bruce et al., 2002; Camill, 2005). One of the most significant disturbances in Arctic waters is likely to be the increase in the concentration of DOM originating from multiple sources. Bacterial communities in the Arctic are highly specialized and highly susceptible to environmental stresses, thereby being able to respond rapidly to changes in DOM concentrations. As was detailed in this review, increased DOM levels may increase the population, production, and metabolic activity of bacteria in the seawater of the Arctic Ocean, thereby releasing a significant amount of CO₂ into the atmosphere. In addition, the Arctic sea water is transitioning from a narrow range of organic substrates to a diverse spectrum of DOM constituents composed of carbohydrates (i.e., glucose), proteinaceous (i.e., amino acid and protein-like components), and terrigenous characteristics (i.e., humic-like components). By selecting the most sensitive species with the appropriate genetic material to degrade the extra DOM, the DOM input may change bacterial communities, perhaps resulting in the emergence of replacement resident populations. In summary, global warming-induced changes in the DOM input to the Arctic Ocean have massive consequences for entire bacterial communities in the Arctic (Figure 4). This finding emphasizes the importance of determining the rate of DOM entry into the Arctic and provides new aspects for estimating the influence of climate change on the Arctic Ocean from various perspectives.

An increase in DOM can further alter the dynamics of marine food webs and DOM cycling in the Arctic Ocean. As a higher DOM intake boosts bacterial development, the consumption of bacteria by protist grazers increases accordingly; then, the material and energy consumed by the grazers can be transferred to larger species in the Arctic Ocean (Kirchman et al., 2009). Grazers and larger creatures can also generate and mineralize DOM. A proportion of labile DOM can be rapidly utilized in microbial processes, while refractory DOM can persist for a long time in the ocean (Jiao et al., 2010; Hansell, 2013). In addition, approximately 2.9–10.3 Tg C yr⁻¹ of tDOM discharged by rivers to the Arctic Ocean is exported to the North Atlantic through the East Greenland Current's surface waters (Opsahl et al., 1999). This reveals a significant effect of increased DOM input in the Arctic on carbon fluxes in the oceans (Boeuf et al., 2014). Therefore, further research may focus on the impacts of DOM input to the Arctic on the carbon cycling of the whole Arctic Ocean. Investigations of changes in DOM flow patterns in oceans as a result of DOM sources entering Arctic waters are also a crucial topic for future studies.

Author contributions

HN was responsible for the conceptualization, investigation, visualization, and writing the original draft. YL made her contribution to reviewing the draft and validation. JKH made

a contribution to funding acquisition. SH contributed to reviewing the original draft. MC made a contribution to the conceptualization and reviewing the original manuscript. JH was responsible for the project administration, conceptualization, and also writing the original manuscript. All authors contributed to the article and approved the submitted version.

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