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REVIEW

Influence of open ocean biogeochemistry on aerosol and clouds: Recent findings and perspectives

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Aerosols and clouds are key components of the marine atmosphere, impacting the Earth's radiative budget with a net cooling effect over the industrial era that counterbalances greenhouse gas warming, yet with an uncertain amplitude. Here we report recent advances in our understanding of how open ocean aerosol sources are modulated by ocean biogeochemistry and how they, in turn, shape cloud coverage and properties. We organize these findings in successive steps from ocean biogeochemical processes to particle formation by nucleation and sea spray emissions, further particle growth by condensation of gases, the potential to act as cloud condensation nuclei or ice nucleating particles, and finally, their effects on cloud formation, optical properties, and life cycle. We discuss how these processes may be impacted in a warming climate and the potential for ocean biogeochemistry—climate feedbacks through aerosols and clouds.

Keywords: Atmosphere, Ocean, Aerosol, Cloud, Biogeochemistry

1. Introduction

Clouds contribute about two-thirds of the Earth's albedo (Baker and Peter, 2008; Trenberth et al., 2009), but are still recognized as a component with a large uncertainty in future climate predictions (Bellouin et al., 2020; Zelinka et al., 2020; Ceppi and Nowack, 2021). Liquid clouds in the lower atmosphere, at the top of the marine boundary layer (MBL), are ubiquitous across the tropical and subtropical oceans. They form large marine stratocumulus decks over regions of upwelling in eastern ocean basins, which gradually evolve into trade cumulus clouds over the warmer central and western ocean basins (Wood, 2012). Liquid and mixed-phase (Danker et al., 2022) stratocumulus frequently occur in the midlatitudes as well, often in the cold sectors of midlatitude cyclones, before evolving to more broken clouds toward the equator (McCoy et al., 2017b; McCoy et al., 2023). At higher latitudes, the presence of mixed phase and ice clouds further complicates our ability to predict cloud occurrences (D'Alessandro et al., 2019). Overall, marine clouds, which stretch from over the coastline to over remote marine environments, are shaped by seasonally variable natural processes. It is essential to understand the impact that naturally emitted aerosols have on cloud formation, and the sensitivity of remote aerosol–cloud–precipitation systems to climate change if we are to reduce the uncertainty in past and future climate predictions (Carslaw et al., 2013; Carslaw et al., 2017; Belloin et al., 2020; Regayre et al., 2020; McCoy et al., 2021; Myers et al., 2021a; Christensen et al., 2022).

Aerosols are coupled tightly to all cloud processes through the microphysical, chemical, and radiative pathways, initiating a number of feedbacks that contribute to the complexity of the climate system. Aerosols can serve

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as cloud condensation nuclei (CCN) or ice nucleating particles (INPs) (Heintzenberg and Charlson, 2009; Levin and Cotton, 2009) inducing changes in the cloud microphysics by affecting condensation/evaporation rates, latent heat release, collision rates and efficiency, and droplet mobility. These changes impact cloud macroscopic properties such as reflectance (albedo), lifetime, phase (liquid or ice), size, and precipitation (Altaratz et al., 2014; Rosenfeld et al., 2014). Reciprocally, marine clouds are wet chemistry reactors that may modify aerosol size and composition (Ervens et al., 2018), and potentially their droplet condensation (Shingler et al., 2016) and ice nucleation properties.

Challenges in establishing a well-defined preindustrial baseline (hence, understanding how the "natural" climate works) for aerosols and aerosol–cloud interactions lead to fundamental uncertainties in constraining climate sensitivity (i.e., the temperature increase corresponding to doubled CO_2) and simulating past and future climate (Carslaw et al., 2013). In particular, poorly understood natural aerosol emission processes contribute substantially to uncertainties in the prediction of aerosol forcing (Carslaw et al. 2017). Consequently, although the marine atmosphere constitutes a mixture of natural, locally produced components and species transported long distances from terrestrial sources, we will focus here on the relationships and interplay between open ocean biogeochemistry, natural marine aerosol, and clouds.

Marine aerosols can be emitted at the ocean surface from breaking waves, in the form of film drops from bubble film rupture, or jet drops from seawater droplets ejected from the air–seawater interface upon bubble burst. Droplets and drops that evaporate leaving particulate residues may subsist in the atmosphere as sea spray aerosols (SSA) and are defined as primary marine aerosols. Secondary marine aerosols are formed by nucleation or condensation of gas-phase precursors in the marine atmosphere. These gas-phase precursors may either be directly transferred to the atmosphere at the air–sea interface or be the result of chemical reactions in the atmosphere. Dimethylsulfide (DMS) is a biogenic trace gas that is the main source of sulfuric acid (H_2SO_4) and methane sulfonic acid (MSA) over the oceans, where they are major contributors to secondary aerosol production (de Leeuw et al., 2014). For this reason, DMS has been extensively investigated in the last 3 decades and, to date, it is the only marine biogenic aerosol precursor implemented in Earth System Models (Séférian et al., 2019; Bock et al., 2021). Yet, large uncertainties remain in the space and time resolved estimates of DMS concentrations and fluxes (Galí et al., 2018) as well as in the sensitivity of the climate system to DMS emissions (Fiddes et al., 2018).

Large research consortia and measurement campaigns aimed to integrate marine aerosol emissions and aerosol–cloud interactions have contributed new knowledge over the last 10 years: PEGASO (Plankton-derived Emission of trace Gases and Aerosols in the Southern Ocean; Dall'Osto et al., 2017), SOAP (Surface Ocean Aerosol Production; Law et al., 2017); NETCARE (Network on Climate and Aerosols: Addressing Key Uncertainties in Remote Canadian Environments; Abbatt et al., 2019); ACE-SPACE (Antarctic Circumnavigation Expedition: Study of Preindustrial-like Aerosols and Their Climate Effects; Schmale et al., 2019); CSET (Cloud System Evolution in the Trades; Albrecht et al., 2019); MarParCloud (Marine biological production, organic aerosol Particles and marine Clouds: a process chain; van Pinxteren et al., 2020); PI-ICE (Ice–ocean–atmosphere interactions and their impacts on climate and ecosystems; Brean et al., 2021); Observations of Clouds, Aerosols, Precipitation, and Surface Radiation over the Southern Ocean (McFarquhar et al., 2021); ACE-ENA (Aerosol and Cloud Experiments in the Eastern North Atlantic; Wang et al., 2022); Sea2Cloud ("Are marine aerosols influencing clouds?"; Sellegri et al., 2023). However, these efforts also demonstrated that understanding the relationship between ocean emissions of primary and secondary aerosols and cloud properties still requires a more comprehensive knowledge of their marine sources and atmospheric interactions. One of the regions identified as particularly important for studying marine aerosol–cloud interactions is the Southern Ocean, which has received much attention during the last decade (Mallet et al., 2023). This region is little affected by anthropogenic aerosols (Hamilton et al., 2014), which allows for the study of the aerosol–cloud system under close to preindustrial conditions, that is, as natural as can be. Furthermore, it is in this region where our understanding of aerosol–cloud interactions is so poor that global models allow too much radiation to reach the surface, resulting in a large warm bias (Bodas-Salcedo et al., 2014; Cesana et al., 2022). Other regions where marine aerosol–cloud interactions are also important and that have been the focus of many recent studies are the high polar regions (see Willis et al., 2023).

In the present article, we provide a summary of the progress in the understanding of the successive steps linking ocean biogeochemistry and clouds over the last 10 years. The aim of this article is not to provide an extensive review of new knowledge but to shed light on certain key findings on critical processes and the identification of relevant unknowns. We focus on open ocean processes (and exclude coastal areas) with the aim to extract information most relevant for large-scale models and satellite retrievals. In Section 2, we address how gas-phase aerosol precursors are produced in seawater through biogeochemical processes before they are transferred to the atmosphere and involved in new particle formation (NPF), with a special focus on DMS. For more detailed chemical processes in the marine atmosphere, the reader is referred to Tinel et al. (2023). Section 3 is dedicated to SSA emission processes, and in particular to new findings about the influence of seawater biogeochemical properties on SSA fluxes. Once in the marine atmosphere, nucleated particles and SSA undergo further transformations that shape their size distribution and chemical composition. In Section 4, we address how new insights into the sources and chemical and physical transformations of marine aerosols are provided by field investigations that combine new chemical tracers with emerging analytical techniques (mass spectrometry, isotopes, etc.). In Sections 5 and 6,

we describe the latest advances in our understanding of the CCN and INP properties of marine aerosols, and of cloud properties in the remote marine atmosphere. In Section 7, we point to the impact that climate change may be having on ocean–aerosol–cloud interactions.

2. DMS and other potential precursors to particle nucleation

2.1. Nucleation and NPF occurrence in the open oceans

NPF is a chain of processes that starts with nucleation of highly condensable species into molecular clusters (approximately 1 nm in size), that grow by condensation and coagulation to a critical size which is thermodynamically stable (2–3 nm). Further rapid growth into the 10 nm size range is needed for particles to survive in the atmosphere, given their potential loss onto the preexisting particles by coagulation processes. Marine nucleation and early growth of newly formed particles have mostly been reported in coastal areas (see de Leeuw et al., 2014, Chapter 4 for a review), for understandable practical considerations, but also because of the scarcity of observed NPF by sizing instruments in the open ocean boundary layer. Here we focus on NPF events in the pristine open ocean, that is, large geographical areas that are most relevant to climate. Brean et al. (2021) reported some nucleation events over Antarctic waters, yet a very few of them were attributed to open ocean conditions. Baccarini et al. (2021) found no NPF events in marine air masses devoid of sea ice or coastal influence during 3 months of observations around Antarctica. The difficulty in elucidating the chemical mechanisms leading to nucleation and NPF in the remote open ocean atmosphere is largely due to this paucity of observations.

The paucity of NPF observations in the MBL, the lower atmosphere, led to the suggestion that most nucleation events occur in the upper troposphere, also termed free troposphere, with a subsequent reinjection into the MBL where newly formed particles would meet enough vapors to grow to a larger size (Quinn et al., 2017; Sanchez et al., 2018; Zheng et al., 2018; Sanchez et al., 2021). Williamson et al. (2019) showed that convective transport of air masses in the tropics results in NPF in the free troposphere, in line with past observations (Clarke et al., 1998). Recently, McCoy et al. (2021) added that the free troposphere of the Southern Ocean is the site of widespread and frequent NPF events driven by cyclonic uplift, which directly impact CCN concentrations in the MBL.

The hypothesis of the free troposphere being the main contributor of new aerosols to the lower atmosphere has been questioned using satellite-retrieved CCN concentrations (Efraim et al., 2020). Also, Zheng et al. (2021) reported regular and frequent occurrence of NPF events in the *upper* remote MBL over the North Atlantic, facilitated in broken cloud fields. Additional indication that nucleation occurs in the MBL relies on a few chamber experiments in semi-controlled ("in the field") conditions (Sellegri et al., 2016) as well as observational evidence for open ocean NPF and growth in ambient air (O'Dowd et al., 2010); these authors pointed out that the newly formed particles grew at a slow rate of the order of 1 nm per hour, therefore preventing the detection of NPF events with the same criteria as over terrestrial areas. Along these lines, Peltola et al. (2022) recently reported that sub-10 nm particle concentrations in the MBL constitute a third of the total aerosol concentration, and that this pool of nanoparticles was not necessarily observed in air masses having traveled across the free troposphere. Therefore, they conclude that NPF events in marine air masses must be sought and detected with different criteria than those classically used for fast-growing particles in continental air masses. The detection of NPF in the open ocean needs to be revisited, with specificities relative to the low concentration of gaseous precursors that result in low cluster formation rates and slow growth. The identity of the different gaseous precursors contributing to NPF in the open ocean is another big unknown (**Figure 1**).

2.2. Potential nucleating chemicals in the open ocean atmosphere

2.2.1. Sulfur-containing species

The well-established role of H_2SO_4 as a ubiquitous nucleating species in most types of environments (Lee et al., 2019), together with its proven marine source through DMS emission and oxidation, point to this species as a natural candidate for NPF should this phenomenon ever occur in the MBL. However, DMS's relatively long lifetime (around 1 day, Seinfeld and Pandis, 2006) implies that its oxidation to SO_2 and subsequently H_2SO_4 via photochemistry is unlikely to lead to atmospheric binary (H_2SO_4-H_2O) nucleation in the MBL. DMS would still take part in NPF if oxidants other than the OH radical make its oxidation

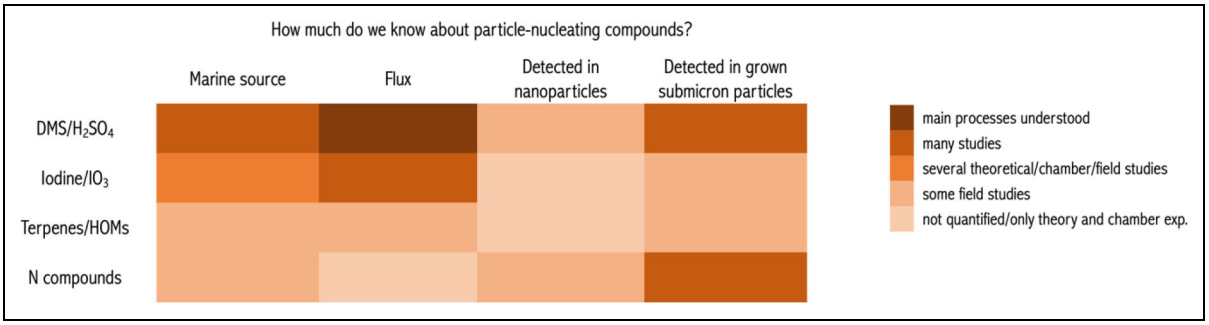

Figure 1. State of knowledge on nucleating species in the marine boundary layer of the open oceans.

significantly faster. Moreover, DMS-related nucleation is more likely to occur with the concurrent emission of volatile nitrogen compounds such as ammonia and amines. In this case, NPF may be favored through ternary nucleation of these bases with DMS-derived acids and water, as shown in experimental systems (Kirkby et al., 2011; Almeida et al., 2013). However, it is less likely to occur when multiphase chemistry dominates DMS fate, as it is expected to increase in-cloud MSA production at the expense of H_2SO_4 (Hoffmann et al., 2016). Jackson et al. (2020) suggested that DMS would contribute to the marine aerosol pool mostly via condensational growth on preexisting particles rather than through nucleation. In fact, direct measurements of sulfur acids and nitrogen bases in nucleating particles over the pristine ocean have mostly been collected in Antarctic air that is not completely free of coastal influences (Jokinen et al., 2018; Brean et al., 2021). The literature-based conclusion that DMS plays a role in NPF is mainly derived from observed covariations between chlorophyll-*a* (Chl-*a*) as a proxy for marine phytoplankton, MSA, and the number of marine aerosol particles. However, biologically rich waters can produce other chemical compounds than DMS, and MSA can condense on particles that have nucleated from other precursors, besides nucleating itself (Hodshire et al., 2019). Therefore, other chemical paths to particle nucleation precursors need further investigation. For instance, methanethiol (MeSH) is coproduced with DMS in seawater, it is more rapidly oxidized in the atmosphere than DMS and can contribute a large share of the oxidized sulfur burden in the marine atmosphere (Novak et al., 2022). MeSH fluxes have been recently reevaluated upward by a factor of 4 compared to earlier studies (Lawson et al., 2020; Kilgour et al., 2022). Hydroperoxymethyl thioformate (HPMTF, $HOOCH_2SCHO$) has also been detected as another potential DMS oxidation product (Veres et al., 2020; Novak et al., 2021), and its ability to form new particles in the natural MBL should be investigated further. The atmospheric chemistry aspects related to HPMTF are detailed in Tinel et al. (2023).

2.2.2. Iodine

Atmospheric iodine has a unique marine source and is transferred to the MBL as molecular iodine (I_2) or volatile iodocarbons (mostly as CH_3I and CH_2I_2) (see Tinel et al., 2023 for a more complete review on iodine chemistry and chemical sources). Iodine oxides (HIO, HIO_3), formed from the oxidation of I_2, are expected to be the most efficient nucleating species. Most marine nucleation studies pointing to iodine oxides have been conducted in coastal areas (Sipila et al., 2016; Beck et al., 2021) where macroalgae are the primary producers of iodine. However, a few observations indicate that plankton-derived iodine may be involved in nucleation, opening the way to open ocean NPF (Sellegri et al., 2016). Using chamber experiments, He et al. (2021) demonstrated that nucleation from iodic acid may be as efficient as that of H_2SO_4 in pristine environments. According to the flow tube experiments reported by Gómez Martín et al. (2022), iodine-containing clusters and particles are formed by aggregation of I_2O_y and HIO_3 in ambient air where water vapor is available. Prados-Roman et al. (2015) estimated that about 75% of IO comes from inorganic precursors. However, a significant biogenic source was needed to explain the gap between measurements and modeled IO over the Southern Ocean (Inamdar et al., 2020). Huang et al. (2022) suggested that a fraction of iodine associated with organics condensing on iodine oxide clusters is recycled back into the gas phase, and this may lengthen iodine lifetime and represent an efficient transport mechanism to remote regions.

2.2.3. Terpenoids and other hydrocarbons

There is a large and diverse pool of dissolved volatile organic compound (VOC) in the surface ocean, which turns over rapidly, on the scale of hours to days (see Halsey and Giovannoni, 2023 for a full review). Isoprene (C_5H_8) is the most abundant marine terpenoid and is thought to be an efficient contributor to secondary aerosol (Yu et al., 2021 and references therein). Monoterpenes ($C_{10}H_{16}$) undergo oxidation to compounds of much lower volatility, highly oxidized molecules (HOM). In terrestrial environments, HOM were shown to contribute to the growth of newly formed particles (Ehn et al., 2014) as well as to nucleate by themselves and initiate NPF (Rose et al., 2018; Yan et al., 2018), but little is known of their role in the marine atmosphere. Marine monoterpenes, dominated by α-pinene, show mixing ratios ranging 5–200 ppt over the Southern Ocean. They are generally well correlated with isoprene and tracers of marine biological activity as shown by laboratory and field studies (Colomb et al., 2008; Shaw et al., 2010; Meskhidze et al., 2015; Kim et al., 2017). Other VOCs such as aromatic hydrocarbons (e.g., benzene, toluene, and xylene), previously thought to be exclusively associated with anthropogenic sources, may be produced by phytoplankton with concentrations similar to those of DMS (Rocco et al., 2021). Estimated oceanic emission fluxes of these aromatic compounds are enough to make them a potential significant source for secondary organic aerosol (SOA) in polar atmospheres (Wohl et al., 2023). However, any involvement in NPF events has not yet been investigated.

2.2.4. Other VOCs from surface photochemical reactions

In addition to biological VOCs directly emitted from oceans, recent works have shown that photochemical processes occurring at the very surface of the ocean lead to further production of VOCs with importance as aerosol precursors (Rossignol et al., 2016; Tinel et al., 2016; Brüggemann et al., 2018). Two main requirements for surface photochemical VOC formation and release are (a) sunlight to initiate photochemical reactions and (b) the development of an organic-rich sea surface microlayer at the air–water interface. Research continues to demonstrate that photochemical and subsequent reactions that involve iron, other ions common to seawater, and organic compounds (such as phytoplankton exudates), interact to form VOCs (Ciuraru et al., 2015; Fu et al., 2015; Huang et al., 2020; Stirchak et al., 2021;

Penezić et al., 2023). Upon reaction with the common oxidants like ozone and the OH radical, these VOCs may then be precursors to SOA formation and, potentially, even to nucleation in the MBL (Bernard et al., 2016; Alpert et al., 2017). This photochemical source of nucleation precursors is a rather new research topic compared to those mentioned in previous sections; it will need confirmation in the real ambient atmosphere by identifying tracers of surface photochemistry products. There is also a need for further laboratory work to figure out when photochemical production of VOCs may or may not be important (Rapf et al., 2018; Shrestha et al., 2018), and modeling studies to evaluate the global impact on total VOC emissions and their nucleation potential.

2.3. Biogeochemical sources of nucleating precursors

2.3.1. DMS production, spatial distribution, and temporal trends

In the surface ocean, DMS is produced mostly through the enzymatic breakdown of dimethylsulfoniopropionate (DMSP), a ubiquitous cellular component that serves multiple physiological functions, such as osmolyte, cryoprotectant, antioxidant, and overflow of excess reduced sulfur (Stefels et al., 2007). DMSP is synthesized mainly by phytoplankton, with intracellular concentrations that span orders of magnitude across taxa (McParland and Levine, 2019; Moran and Durham, 2019). It is also synthesized by bacteria (Curson et al., 2017), yet the quantitative significance of the bacterial production in the DMSP budget has not been evaluated. DMS can also be produced through enzymatic reduction of the other ubiquitous organosulfur compound, dimethylsulfoxide (DMSO; Spiese et al., 2009; Dixon et al., 2020), but the contribution of this process to pelagic gross DMS production remains uncertain due to the scarcity of measurements (Dixon et al., 2020; Herr et al., 2020). Recent advances in genetic approaches to understand the processes of DMSP metabolism and DMS production are making it possible to study how they evolved in marine microorganisms (Bullock et al., 2017), how they distribute in the ocean (Teng et al., 2021), and how they are part of the biogeochemistry of ocean sulfur (Moran and Durham, 2019).

The distribution patterns of DMS result from the interplay between the abundance and taxonomic patterns of DMSP-producing phytoplankton, their physiological status, and a complex network of DMS production and removal processes (Lizotte et al., 2012; Galí and Simó, 2015). On average, most of the produced DMS is consumed by biological (approximately 70%) and photochemical (approximately 20%) processes, allowing only approximately 10% to be vented to the atmosphere (Galí and Simó, 2015). Yet, these proportions may vary largely depending on irradiation, stratification, wind speed and mixing, and hence across regions, seasons, and even the diel cycle (Royer et al., 2016). Therefore, predicting the distribution of the DMS concentration and sea-to-air emission across space and time represents a formidable challenge. DMS concentration fields in the surface ocean can be derived by producing climatologies from databases (Lana et al., 2011; Hulswar et al., 2022) or can be diagnosed semiempirically (statistically) from a set of environmental variables (Belviso et al., 2004). Pioneering statistical models included just a few diagnostic variables chosen from hypothetical phenomenological relationships to DMS (Belviso et al., 2004) and captured a limited share of the DMS variance (Halloran et al., 2010). Recently, more sophisticated machine-learning methods (like neural networks) with an increasing number of diagnostic environmental variables have notably improved DMS predictability at both regional and global scales (Wang et al., 2020; McNabb and Tortell, 2022; Mansour et al., 2023; McNabb and Tortell, 2023). However, a limitation of both the simple and the machine-learning diagnostic methods is that they rely on variables that cannot be synoptically diagnosed in near-real time, like the mixed layer depth or nitrate concentration. Consequently, they provide climatological maps but can hardly provide snapshots of the current DMS distribution, or interannual patterns to address the response of ocean DMS to global environmental change. Galí et al. (2018) proposed an algorithm to derive surface ocean DMSP and DMS concentrations from satellite-based variables such as Chl-*a* and solar radiation. Even though this algorithm does not work equally well everywhere over the global ocean, it represents an invaluable tool to produce regional synoptic maps and temporal trends of DMS (Galí et al., 2019). Remote sensing, however, still has the limitation of the incapacity to project into the future.

Alternatively, DMS fields can be predicted by prognostic modeling. Hitherto, the representation of DMS in prognostic biogeochemical models has barely paralleled advances in the knowledge of the processes in the DMS cycle. DMSP production and content in phytoplankton has been revealed to be less dependent on nutrients than thought as the DMSP quota of the strongest DMSP producers is less prone to regulation by nitrogen availability (McParland and Levine, 2019). Phytoplankton do not only act as the main source of DMSP, many also take up DMSP for unknown reasons (Vila-Costa et al., 2006; Spielmeyer et al., 2011). Consequently, they can represent a major sink that competes with bacterial degradation and has yet to be incorporated in DMS models. More than a decade ago, the first global prognostic model that included a sulfur module only represented 2 or 3 types of phytoplankton, each with its intracellular DMSP quota and mortality and exudation rates (see review in Bock et al., 2021). There was the appreciation that a better representation of phytoplankton composition and succession, bacterial processes, and solar radiation effects was required to improve DMS simulations (Le Clainche et al., 2010; Vogt et al., 2010). As an example, explicit incorporation of some of the strongest DMSP producers, *Phaeocystis*, in the Community Earth System Model attributed as much as 13% of global DMS emission to this phytoplankton genus (Wang et al., 2015). A process-based study using ship-borne mesocosm experiments found a positive relationship between the DMS flux and the nanophytoplankton cell abundance

(Rocco et al., 2023). On the other hand, the relative contributions of bacterial and algal DMSP-lysis enzymes to DMS production have not yet been fully assessed, nor has DMS production from DMSO, so that these processes are not yet represented in global prognostic models.

2.3.2. Biogenic production of other potential nucleation precursors

Seawater iodide originates from biological activity of microalgae and bacteria (Hepach et al., 2019; Hughes et al., 2021). Several phytoplanktonic groups consume iodate and produce iodide, with no functional-type specificity but with a larger yield for cultures that had reached a later senescent stage (Hepach et al., 2019). Like DMS, some other VOCs are produced as a regulated response to environmental stressors such as light, temperature, acidification, nutrient limitation, grazing, and viral-induced mortality (Halsey and Giovannoni, 2023). VOC production is commonly light dependent indicating a link to photosynthetic metabolism, but the diel cycles of reactive non-DMS VOCs are not described in the literature. Moore et al. (2020) suggest that VOCs are not only stress-induced metabolic end products but also intermediates in carbon metabolic pathways, which can diffuse out of cells. Furthermore, VOCs also serve as signal molecules in large aquatic organisms (Saha and Fink, 2022), but the same role in phytoplankton has been challenging to prove. Although phytoplankton are thought to be the primary source of most VOCs, other processes such as the degradation of dissolved organic matter (DOM) by heterotrophic bacteria also release VOCs. However, monoterpenes and other highly reactive VOC production by direct phytoplankton or bacterial production are poorly characterized.

Another suite of marine volatiles of great interest are ammonia (NH_3) and methylamines. The air–sea flux of NH_3 is sensitive to temperature, pH, and salinity (in decreasing order of importance) (Altieri et al., 2021). An interlink between the NH_3 and the DMS fluxes has been suggested (Johnson and Bell, 2008). This would arise from the complementation of the processes that give rise to DMS (and its precursor DMSP) and those that produce NH_3/NH_4^+ in the surface ocean. Recent work on NH_3 fluxes in the Southern Ocean suggests that the biogeochemistry that drives the seasonality in surface ocean NH_4^+ concentrations determines when the Southern Ocean becomes a source of NH_3 to the atmosphere (Altieri et al., 2021). Regarding methylamines, concentrations of trimethylamine in the surface ocean are in the nM range and its sources are not well characterized. It's mainly attributed to the bacterial degradation of phytoplanktonic N-osmolytes such as glycine betaine, trimethylamine oxide, and choline (Carpenter et al., 2012; Mausz and Chen, 2019), which serve similar physiological functions as DMSP. Phytoplankton can be both a direct and indirect source of trimethylamine (Mausz and Chen, 2019), which can subsequently be transformed to dimethylamine and further to monomethylamine by marine bacteria (Sun et al., 2019).

With regard to VOCs produced through photochemical reactions at the sea surface microlayer, a dependence of fluxes on the concentration and composition of organic matter is to be expected. Therefore, biological processes that produce surfactants with the potential to accumulate in the surface microlayer will play a regulating role. For instance, lipids are released during the lysis of, or the predation on, phytoplankton cells, and subsequent enzymatic digestion leads to the formation of fatty acids (Budge et al., 2014; Cochran et al., 2016). In summary, **Figure 1** illustrates the recent investigations and the state of knowledge on the source, flux, and detection of particle nucleating species as discussed above.

3. Biogenic impact on SSA properties and emission flux

Despite the abundance of SSA flux parameterizations in the literature (see Russell et al., 2023 for a complete review), SSA flux estimations still suffer from large uncertainties. In recent global modeling exercises, the default sea spray emissions needed to be increased by around a factor of 3 to be consistent with measurements (Regayre et al., 2020), pointing to a lack of understanding of the processes involved in sea spray emissions. Using observational constraints, Bian et al. (2019) concluded that the negative bias in the aerosol optical depth simulated by a global model could partially be explained by missing sub-micron sea spray sources. A largely studied source of SSA is bubble bursting. When bubbles burst on the ocean surface, 2 types of droplets are formed, jet droplets leading to super-micron particles upon evaporation, and film droplets leading to sub-micron particles. **Figure 2** summarizes the recent investigations and the state of

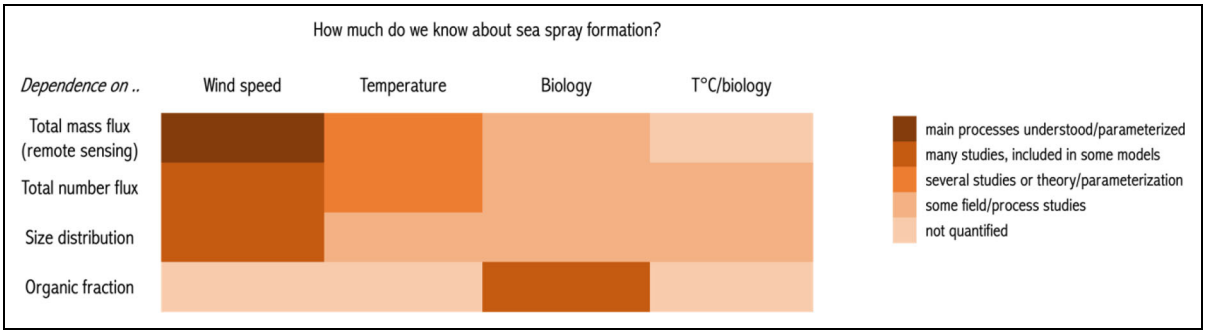

Figure 2. State of knowledge on the dependence of sea spray sources on environmental variables.

knowledge on the dependence of sea spray properties and flux on environmental and biological variables which will be discussed as follows.

3.1. Factors influencing the SSA emission flux and parameterizations

Sea spray production is not only dependent on wind speed—surface temperature, salinity, and seawater composition have also been identified as important properties controlling the SSA emission flux (Fuentes et al., 2011; Hultin et al., 2011; Salter et al., 2015). The complexity of processes controlling SSA production via bubble bursting has resulted in many different formulations of the SSA source function that span over an order of magnitude for a given wind speed, especially in the smallest (<20 nm) and largest (>500 nm) size ranges (Ovadnevaite et al., 2014). This large spread may be due to different methods used to derive the size segregated sea spray flux. The SSA flux may be directly measured in ambient air using eddy correlation or gradient methods (Method A). A second method is the combination of transport models and observations of aerosol concentrations in a source–receptor approach (Method B). The last approach is laboratory-generated sea spray from seawater samples using bubble bursting devices that mimic the wave-breaking process (Method C). However, a large spread is also observed among sea spray flux formulations obtained with the same method. For Method A, wind speed, wave-state, or air entrainment in the SSA flux parameterizations reported in the literature are not always harmonized for a given seawater temperature, biological content, atmospheric washout state. For instance, since the SSA flux depends on both wind speed and temperature, the dependence of each variable should be investigated with the other variable kept constant. This is usually not done and for example regions of higher wind speed may correspond to regions of lower temperature implying a bias in the parameterizations relating SSA fluxes with wind speed.

Hartery et al. (2020) have provided a parameterization of a large SSA source function specific for the Southern Ocean that takes into account wet scavenging. Their results are substantially different from the traditionally used parameterizations such as in Jaeglé et al. (2011). The parameterization proposed by Hartery et al. improved the representation of the SSA flux in global climate models (Revell et al., 2019) as well as the correspondence of modeled CCN with Southern Ocean cloud observations (Kang et al., 2022). The different methods for providing a temperature dependance of the SSA flux seem to lead to different conclusions depending on the method used. Using Method B, Ovadnevaite et al. (2014), Grythe et al. (2014), and Liu et al. (2021) report a monotonic, positive relationship between the sea spray mass flux and the sea surface temperature (SST) over the whole temperature range investigated. Conversely, the temperature dependences of laboratory-generated sub-micron sea spray number flux (Method C) show opposite trends. For temperatures colder than 10°C, all studies report a strong increase of the sea spray number flux with decreasing temperature (Mårtensson et al., 2003; Salter et al., 2014). This apparent contradiction in temperature dependences between Method B and Method C may be due to the size of SSA investigated. Salter et al. (2014) indeed reported different behaviors for sub- and super-micron SSA. Opposite behaviors between sub- and super-micron SSA are likely due to different production mechanisms as pointed out by Crocker et al. (2022).

Different temperature dependences of the SSA flux may also result from different influences from the biogeochemical properties of different seawater types (Forestieri et al., 2018; Christiansen et al., 2019). This area of research is largely understudied due to the difficulty in decoupling the chemical and biological effects from the temperature effect in studies of ambient-air SSA. Both types of variables (temperature and those derived from ocean biogeochemistry) have been shown to largely impact the SSA emission flux individually under controlled experimental conditions. Using seawater collected from 3 contrasting locations (Mediterranean Sea, Arctic coastal waters, and New Zealand), Sellegri et al. (2021) reported that the artificially generated sea spray flux of particles larger than 100 nm, assimilated to CCN at 0.2% supersaturation, is linearly correlated to the seawater nanophytoplankton cell abundance for a given SST. They suggest that this effect results from biogenic surface-active components that modulate bubble lifetime and therefore the number SSA flux. A similar feature was found for SSA generated from sea ice samples, with a larger SSA number flux for the highest nanophytoplankton cell abundances (Dall'Osto et al., 2022). This feature was associated with the presence of humic-like substances. In Sellegri et al. (2023), the SSA flux to SST relationship is quantified as a function of the seawater biogeochemical properties, with 30% decrease in the cyanobacterium *Synechococcus* leading to an average 4-fold increase in the SSA flux at 2°C SST compared to 8°C–12°C SST. This impact may be related to *Synechococcus*-derived DOM of specific properties, released via secretion, natural cell death, viral lysis, and predation (Fiore et al., 2015; Zhang et al., 2022).

3.2. Nascent SSA size distribution

SSA size distribution is important for atmospheric processing as it determines the surface area for condensation and reaction of nitrogen, sulfur, and organic species. It also determines the distances that particles can travel and transport the chemical species they are composed of (Neumann et al., 2016). Nascent SSA artificially generated during bubble bursting experiments consistently show a number size distribution with a sub-micron Aitken mode (i.e., around 40 nm) and small accumulation mode (i.e., around 100 nm) dominating the total size distribution, and frequently even a large nucleation mode contribution to the SSA number concentration (Schwier et al., 2015; Schwier et al., 2017 and references therein; Sellegri et al., 2021). Due to the difficulty in segregating SSA from secondary aerosols in the ambient marine atmosphere, some models use the assumption that SSA size distribution can be approximated by a single broad mode encompassing particles from 100 nm to super-micron sizes, scaled from larger than 500 nm particles assimilated as

pure SSA (Modini et al., 2015). Using this methodology, the contribution of SSA number concentration to total aerosol concentrations in marine air masses may therefore be highly underestimated. This was recently shown by Xu et al. (2022), who used an hygroscopicity-derived ambient aerosol mixing state to confirm the large contribution of SSA to the Aitken and accumulation modes of natural marine ambient air. The effect of seawater biology on the SSA size distribution shape is not very clear and the organic content of nascent SSA has shown little impact on its size distribution shape (Sellegri et al., 2021). Therefore, the stability of the ratio of super-micron to submicron aerosol generated in the laboratory could also be a valid method to infer a number concentration of submicron SSA from ambient air marine aerosol.

The detection of a nucleation mode in the ambient aerosol size distribution over remote areas does not necessarily point to secondary aerosol formation, as it was also detected during nascent sea spray experiments (Schwier et al., 2015; Schwier et al., 2017), especially in low SST conditions (Sellegri et al., 2023). Conditions when these ultrafine SSA are produced are unclear. Surface-active compounds of the sea surface microlayer play a major role in the number of SSA emitted to the atmosphere (Modini et al., 2013), yet we don't know what biogeochemical or photochemical processes are at the origin of these surface-active components and their dependence on SST. Surface tension should be a measure to deploy in parallel to other seawater biogeochemical variables in the future and lab studies are needed to tackle this.

3.3. Nascent SSA chemical composition

Nascent SSA is a complex mixture of sea salt and organic matter, with organic matter comprising a substantial fraction of the total particle mass under certain conditions, especially for particles with diameters less than 1 μm (de Leeuw et al., 2014). The chemical composition of jet droplets is believed to reflect the composition of the bulk surface ocean (Burrows et al., 2014; Wang et al., 2017). The chemical composition of the film droplets is believed to reflect the composition of the film cap from which the droplets were born (Burrows et al., 2014). Given this, the chemical composition of these droplets is often assumed to be similar to that of the air–water interfaces present on bubble surfaces or at the ocean surface, that is, the sea surface microlayer. As such, these droplets are believed to be enriched in surface-active organic matter when the sea surface microlayer has a different composition than the underlying bulk seawater. It is therefore important to understand the factors driving sea surface microlayer enrichment in organic matter, which has received attention in the past decade but still lacks understanding both from the physical and chemical points of view (Tinnel et al., 2023).

The role that biological activity plays in determining the quantity and composition of organic matter present in nascent SSA has been an active area of research over the last 20 years and remains a large area of research (O'Dowd et al., 2015; Quinn et al., 2015; Ceburnis et al., 2016; Gerard et al., 2016; Jayarathne et al., 2016; van Pinxteren et al., 2017; Beaupré et al., 2019; Frossard et al., 2019; Crocker et al., 2020; Radoman et al., 2022; Santander et al., 2022). The conclusions from the recent review by Bertram et al. (2018) can generally be characterized as falling into 2 groups. First, a series of studies have observed that the organic mass/Na^+ ratios of nascent SSA (Facchini et al., 2008; O'Dowd et al., 2015) are highly dependent on the level of biological activity (e.g., the abundance of phytoplankton). Lower organic mass/Na^+ ratios correspond to periods of low biological activity compared to periods of high biological activity, resulting in primary marine organic content being parameterized as a function of Chl-*a* in many modeling exercises (de Leeuw et al., 2014). In contrast, a second group of studies has observed little difference in the organic mass/Na^+ ratio of nascent SSA when comparing oligotrophic and productive oceanic regions (Quinn et al., 2015) or during mesocosm phytoplankton experiments (Jayarathne et al., 2016; Schwier et al., 2017). Instead, some of these studies argue that a ubiquitous reservoir of organic mass in surface seawater is responsible for the organic mass enrichment of nascent SSA, overpowering any influence of local biological activity. These studies conclude that the organic mass fraction of nascent SSA can be approximated as constant across different ocean basins and seasons (Quinn et al., 2015; Saliba et al., 2019; Bates et al., 2020), a conclusion that is questioned in observation–modeling comparison exercises (Burrows et al., 2014).

Numerous studies have investigated the impact of ocean biology on the composition of the organic fraction of nascent SSA. For example, Gerard et al. (2016) observed a correlation between Chl-*a* and the concentration of anionic and cationic surfactants in ambient aerosol sampled over the Baltic Sea, and Frossard et al. (2019) found that surfactant concentrations in laboratory-generated SSA were correlated with the level of biological activity in seawater samples. However, transport of organic species to the atmosphere through SSA was not directly related to measures of primary productivity and was more likely related to more complex processes such as bacterial transformation and degradation of the primary products of plankton (Santander et al., 2022) and further linked to polysaccharides and fatty acids likely of bacterial origin (Glicker et al., 2022). Interestingly, Radoman et al. (2022) observed measurable changes in the composition of the organic mass present in laboratory-generated SSA during a phytoplankton bloom using high-resolution mass spectrometry, despite the organic mass fraction of the aerosol remaining unchanged during the sampling period, suggesting that the 2 parameters may be decoupled or have different dependency of the bloom stage (rise or demise). Overall, the transfer of organic carbon from seawater to aerosol appears to result from complex biological processes and finding direct universal relationships between a biological tracer (such as Chl-*a*) and the fraction of organic matter in nascent sea spray seems illusory.

A reconciliation between observations and modeling of the organic content of primary aerosol particles is proposed in the conceptual model OCEANFILMS (Organic

Compounds from Ecosystems to Aerosols: Natural Films and Interfaces via Langmuir Molecular Surfactants), which links sea spray chemistry with ocean biogeochemistry. This is done by mapping groups of organic compounds to the output of an ocean biogeochemistry model, and partitioning these organic groups into SSA on the basis of physico-chemical properties (absorptivity at the air–water interface, molecular weight, etc.) that are assigned to biological macromolecule types (proteins, polysaccharides, lipids, processed compounds, and humics) (Burrows et al., 2014; Burrows et al., 2022). The nature of the organic compounds determines the efficiency with which they are transferred to the atmosphere, resulting in a model where correlations between organics and Chl-*a* exist but are highly region- and season-dependent. These regional specific relationships further match recent seagoing campaigns (Bates et al., 2020) and seasonality observed at coastal stations such as Mace Head, Ireland.

4. Developments in the identification of marine aerosol sources from observations and modeling

Most marine aerosols are composed of salts (mainly sodium chloride) and sulfates, and a mixture of organic compounds. While sodium chloride is clearly primary, that is, a tracer for SSA, sulfates and organics may be primary or secondary. Source apportionment of marine aerosols depends strongly on our ability to chemically characterize particles across all sizes and independently of their primary or secondary nature. Several modeling studies (Gantt et al., 2011; Burrows et al., 2022) have used the water-insoluble organic carbon content of marine aerosol as a proxy for the primary organic source, based on observational studies (O'Dowd et al., 2004; van Pinxteren et al., 2017). However, the ratio of insoluble to soluble organic carbon in nascent SSA is variable (cf. Section 3; Freney et al., 2021) and therefore a potential source of uncertainty. The source apportionment between primary and secondary marine aerosol is further complicated by the fact that some of the molecular products of atmospheric photochemistry that contribute to marine SOA formation can also be produced within the seawater via either photochemical processes at the ocean surface or biological processing. For instance, Beaupré et al. (2019) observed that 19%–40% of the organic carbon present in nascent laboratory-generated SSA (less than 2 min of age) was chemically indistinguishable from highly aged SOA, and Freney et al. (2021) found that signatures of SOA, such as MSA, were already present in nascent sea spray. Enami et al. (2019) suggested that the oxidation of marine biogenic VOCs is facilitated by the presence of iodide in the surface microlayer, and their oxidation products are left in seawater or found in the marine primary organic aerosol.

A detailed concomitant analysis of the same chemical organic tracers in the atmosphere and ocean would be very valuable. For instance, a study by van Pinxteren et al. (2020) shows highly surface-active lipids being enriched in the sea surface microlayer. Looking for (and quantifying) these compounds in the aerosol phase would be helpful to assess their transfer function to the atmosphere. Using X-ray spectro-microscopy, the organic matter associated with relatively freshly formed SSA particles was revealed to be dominated by acid and alcohol functionalities (Ault et al., 2013; Prather et al., 2013). Again, it would be valuable to apply a similar approach to seawater and surface microlayer samples. Recent advances in the measurement of carbon isotopes have also provided insight into marine organic matter sources. In the ocean, photosynthesizing plankton produce organic matter with lighter isotopes, indicated by a lower $^{13}C/^{12}C$ ratio. This particulate organic matter undergoes isotopic fractionation over the course of weeks to years as it is broken down and decomposed through trophic-level interactions, ultimately transitioning into isotopically heavier DOM, characterized by a higher $^{13}C/^{12}C$ ratio. Ejected SSA contain the C isotopic ratio of the associated marine DOM, which subsequently undergoes kinetic fractionation through SOA formation via photochemical and cloud-processing mechanisms. Consequently, the aerosol organic matter becomes isotopically heavier on a timescale of approximately 1 week. In this way, C isotopes are instrumental to trace the pathway of organic matter from the surface ocean to SSA and SOAs. For example, Ceburnis et al. (2016) found that most of the organic enrichment in marine aerosol over the southern Indian Ocean was attributable to fresh marine particulate organic matter. Consistent with these findings, Crocker et al. (2020) observed that the C isotopic composition of laboratory-generated SSA reflected changes in seawater composition during mesocosm phytoplankton blooms.

There is a severe lack of information on the sources and chemistry of marine Aitken mode particles (20–80 nm) due to measurement limitations. The Aitken mode is a persistent feature over the global oceans (Hoppel and Frick, 1990) and is critical because these particles are on their way to growing into the CCN size range, where they will influence cloud properties. Two main sources of Aiken mode particles are (i) primary sea spray emissions (see Section 3) and (ii) growth of nucleation mode particles by condensation of secondary compounds (e.g., Burkart et al., 2017; Zheng et al., 2020). The relative importance of the two sources remains unclear and is expected to vary by region. Significant advances have been made in the knowledge of sea spray sources of Aitken mode particles by analyzing laboratory-generated nascent SSA using single particle microscopic analyses (Prather et al., 2013) or hygroscopicity-derived chemical composition (Schwier et al., 2015; Schwier et al., 2017). These studies have clearly established that most small SSA contain organics at the point of emission. An early study by Oppo et al. (1999) proposed a theoretical model that explains this phenomenon as caused by adsorption of organic components on the surface of small saline droplets. In this model, small SSA have larger fractions of surface-adsorbed organic compounds due to the large surface-to-volume ratio of particles, while large SSA are composed primarily of salt.

Although the presence of high organic mass fractions in nascent SSA is well-established, it is more difficult to quantify the relative contributions of primary and secondary organic matter in the ambient Aitken mode particles.

The reason is that the small size and mass of Aiken particles makes it difficult to analyze their chemical composition. Traditional filter-based approaches require long sampling times which may introduce artifacts for the semi-volatile species and do not allow fine size discrimination. Online mass-spectrometric methods exist for the analysis of sub-50 nm particles (Lawler et al., 2021), but these systems are rare since they are custom-built, and difficult to operate. Therefore, the nature of the condensable gases responsible for the growth of nucleation mode particles into Aitken mode particles remains unclear. Instrumental development in several directions is needed: (a) a high-volume collection technique specific for Aitken mode particles, which can then be characterized by traditional filter-based chemical analyses; (b) offline organic and inorganic chemical analysis techniques with extremely low detection limits that can be applied with short sample collection times; and (c) making existing online mass spectrometry or Fourier Transform InfraRed spectroscopy techniques to target the sub-50 nm size range.

The processes that cause growth of particles from the Aitken to the accumulation mode are also still poorly understood. Growth can happen either through direct condensation of semi- or low-volatile gases issued from oxidation processes, through surface heterogenous chemistry, or through aqueous phase processing. Indirect evidence of the contribution of oxygenic volatiles to dry formation of SOA can be derived from their detection in the gas phase. Organic acids, known precursors of SOA, have been detected in the Arctic MBL as well as in aerosol formed from photochemistry or DOM at the sea surface microlayer (Mungall et al., 2017). Once in the atmosphere, there is also the difficulty in segregating dry and wet formation of SOA. Cloud processing is often more efficient than the dry oxidation pathways, particularly in the case of MSA formation (Chen et al., 2018; Baccarini et al., 2021). To constrain the reaction pathways, isotopic analyses are again a powerful tool (e.g., Harris et al., 2014; Ishino et al., 2021; AuYang et al., 2022). Atmospheric aging hence poses a challenge to source attribution and the community needs to think of new tracers to be targeted. New developments, such as the Extractive Electrospray Ionization time-of-flight (EESI-TOF; Wang et al., 2021) for near-molecular aerosol speciation, the EESI-Ultrahigh-Resolution Mass Spectrometry (EESI-Orbitrap; Lee et al., 2020) allowing insights into compound structure, and the High-Resolution Time-of-Flight Chemical Ionization Mass Spectrometer with a Filter Inlet for Gases and AEROsols (FIGAERO-HRToF-CIMS; Siegel et al., 2021), providing molecular composition information, open up new routes to understand chemical reaction mechanisms, kinetics, and sources. So far, these emerging mass spectrometric techniques have only rarely been used in marine aerosol research, thereby representing a great underexplored potential.

An advantage of applying high-resolution spectrometric techniques on Aitken and accumulation mode particle (roughly 100–1,000 nm) characterization is that it allows the consolidation of results by statistical methods such as positive matrix factorization, which are established methods for source apportionment. Based on the spectrometric spectra, fingerprints of recurring composition can be extracted and related to potential sources using chemical markers. Recent works in the Arctic (Moschos et al., 2022a, 2022b) and Atlantic oceans (Lawler et al., 2020; Huang et al., 2022), and the Sea of Japan (Loh et al., 2023) demonstrate the ability to distinguish among natural-terrestrial, natural-marine, and anthropogenic aerosol sources.

5. Marine CCN and INPs

5.1. Marine-related CCN

The properties of a CCN at a given water vapor supersaturation are reasonably well described by the Koehler theory that includes size and chemical components of the aerosol, as shown by several successful closures between modeled and measured CCN (Asmi et al., 2012 and references therein). A good estimation of the number of CCN at a given supersaturation could be obtained from the number of particles above a certain size (activation size), knowing the large chemical classes (organics, ammonium sulfate, sodium chloride) present in particles at this size. Fresh SSA CCN concentration could adequately be approximated from the number concentration of SSA larger than about 100 nm at 0.2% supersaturation (typical of marine low level clouds) (Sellegri et al., 2021). However, ambient SSA and marine secondary particles with high organic fractions tend to deviate from the theory due to the disconnection between the organic component hygroscopicity at subsaturated and supersaturated conditions and the organic surface tension effect (Ovadnevaite et al., 2011; Ovadnevaite et al., 2017). The global importance of this effect and deviation from the classical theory is still under debate, but Lowe et al. (2019) demonstrate that accounting for the surface phase becomes essential in clean environments such as the remote MBL under certain circumstances.

Many studies on marine CCN concentrations do not investigate what makes a marine particle a CCN, but rather what the contributions from different sources are (i.e., primary or secondary sources). At wind speed greater than 16 m s^{-1}, Fossum et al. (2018) estimated that SSA may contribute up to 100% of marine CCN-relevant aerosol particles present in the MBL in the Southern Ocean. On the other hand, non-sea-salt sulfate was argued to dominate CCN concentrations, either based on correlation with Aitken mode particles (Tatzelt et al., 2022) or from measurements of nonrefractory chemical composition in marine aerosol (by up to 60% during summer; Zheng et al., 2018; Zawadowicz et al., 2021). Sanchez et al. (2018) estimated "new sulfate" contributes about one-third of North Atlantic CCN during spring and autumn while sea spray dominates during winter. Biogenic organics were also found responsible for the growth of preexisting particles to CCN sizes, alone or by co-condensing with sulfates (Zheng et al., 2020). Secondary particles from DMS oxidation were also predicted to contribute to the MBL CCN burden in modeling exercises mostly during summer (Revell et al., 2019). McCoy et al. (2015) used top-down constraints from satellite observations of cloud droplet number

concentration to infer the relative contributions of DMS-derived sulfate aerosol, sea spray, and marine organic matter to the regional-scale seasonal variations in CCN. They found that DMS-related sources drive variations in the cloud droplet number concentration across the entire Southern Ocean, *via* sulfate aerosol at lower Southern Ocean latitudes (35°S–45°S) and impacts on SSA at higher latitudes (45°S–55°S). However, as discussed above, SSA can significantly contribute to the sub-micron particle mode, including Aitken mode particles (Lawler et al., 2021; Xu et al., 2022) and, thus, can potentially add more significantly to the CCN population than previously thought (Lauvset et al., 2017; Quinn et al., 2017).

5.2. Ice formation on marine-related particles

Atmospheric INP concentrations measured at marine observatories are often used to infer the ice nucleating abilities of marine aerosol particles (McCluskey et al., 2018a; Knopf et al., 2022). However, it is important to note that not all particles found over oceans or in the marine atmosphere are derived from marine sources. Ice nucleation studies on the natural atmospheric aerosol must deal with the complexity of measuring low INP concentration and determining INP composition from diverse sources. In general, great care is needed when implementing parameterizations of INP concentration for atmospheric ice production as INP overestimation can bias estimates of radiative balance, shown especially for the Southern Ocean (Vergara-Temprado, 2018). Using a combination of global modeling and observations, Burrows et al. (2013) suggested that the biogenic marine INP concentration dominated the total INP concentration in the Southern Ocean, but also pointed to a lack of observations in this area to confirm their conclusion. Zhao et al. (2021) showed that marine organic INP concentrations can be up to 1,000 times higher than dust INPs at 40°S. However, sources of INPs in models are still not well constrained as some parameterizations tend to underestimate the observed INP concentrations except for at temperatures representative of cirrus clouds (parameterization from McCluskey et al., 2018b) or tend to overestimate them except for temperatures representative of supercooled clouds (source functions from Wilson et al., 2015; Trueblood et al., 2021). It is therefore important to better constrain SSA INP sources, in particular their biogenic components.

5.2.1. Evidence of a biogenic source of marine INPs

A strong biogenic contribution to marine INP concentrations is suggested from the evidenced relationships between seawater and sea surface microlayer water particulate organic carbon and atmospheric INPs concentrations at warm temperatures representative of supercooled clouds (>20°C) (Wilson et al., 2015; Trueblood et al., 2021). In the North Atlantic, ice nucleation due to SSA at the warmest freezing temperatures always coincided with observed total phytoplankton cell concentrations in water on the order of 10^8 L^{-1} and when dominated by picoeukaryotes (Wilbourne et al., 2020). It was shown that INPs were relatively stable over the Southern Ocean and increased due to coastal (either marine or additional terrestrial) sources with concentrations generally coinciding with fluorescent, hence potentially biogenic, particles (Landwehr et al., 2021; Moallemi et al., 2021). In the laboratory, early research showed that phytoplankton cultures contain INPs capable of forming ice as warm as −4°C (Schnell, 1975) through the liquid-to-ice phase transition known as immersion freezing. The first marine derived INPs were unambiguously identified no more than 4 decades later as the fragmented and intact phytoplankton cells of *Thalassiosira pseudonana*, *Nanochloris atomus*, and *Emiliana huxleyi* (Alpert et al., 2011a, 2011b). Uniquely, ice formation from both immersion freezing and deposition ice nucleation (the vapor-to-ice phase transition) was quantified. Ice nucleation experiments using cultures of diatoms, *Melosira arctica*, *Skeletonema marinoi*, and *T. pseudonana* as well as other phytoplankton and aerosolized sea surface microlayer water all show ice nucleation ability (Wilson et al., 2015; Ickes et al., 2020). Even after filtering cultures of marine phytoplankton and bacteria (0.1 μm filter), biogenic materials in the water retain freezing ability (Wilson et al., 2015; Ladino et al., 2016). This indicates that not only cell or cell fragments of phytoplankton are INPs, but also their exudates generated through their metabolism or lysis. SSA particles produced from cultures of *Prochlorococcus* from 3 different strains were INPs via deposition ice nucleation, with a link to polysaccharide, lipopolysaccharide, and protein content (Wolf et al., 2019).

Understanding of SSA particle production, composition, and ice nucleation was greatly enhanced through a series of laboratory breaking wave channel studies with actively growing mixed microorganism communities (Prather et al., 2013; DeMott et al., 2016). Through careful examination of seawater conditions that influence SSA production, the authors determined that SSA particles were INPs. However, they found higher INP concentrations prior to microbial growth and when most SSA particles were internal mixtures of sea salt and organic matter (Prather et al., 2013). This was contrary to expectations that increasing microbial growth would increase biogenic matter in aerosol particles and thereby, ice nucleation efficiency or INP concentrations. It was later confirmed that ice nucleation tended not to be enhanced as a function of microbial growth or biological markers, such as chlorophyll concentration, heterotrophic bacterial counts, and enzyme activity (DeMott et al., 2016; McCluskey et al., 2017). The complex balance between the numbers and efficiency of INPs produced, released, and consumed in water due to phytoplankton and bacteria metabolism prior to aerosolization has yet to be understood.

Single particle analysis of sub- and super-micron-sized SSA has aided their chemical and morphological identification, giving a unique look into the origin of why SSA nucleated ice at all. Recently, single SSA that formed ice was identified using X-ray spectro-microscopy and their chemical characteristics was compared against those SSA that did not form ice attempting to identify the chemical agents, peculiarities, or unique features responsible for ice nucleation (Alpert et al., 2022). It was directly found that

all SSA particles, INPs and non-INPs alike, were practically identical, and that the organic matter associated with them was entirely derived from phytoplankton and bacterial exudates (Alpert et al., 2022). Therefore, current analytical techniques failed to provide the relevant information on the feature that makes SSA a good INP at the temperatures considered. Further research with comprehensive techniques is needed to reveal the unique features of INPs, especially regarding warmer temperatures relevant for biological aerosol. Continuing to quantify marine INP concentrations is just as important to using that data for shaping theoretically based parameterizations. This may involve identifying water properties suspected to be important for ice nucleation, such as hydrogen bonding interaction between water and ice nucleating biogenic/organic surfaces with ions commonly present in seawater.

5.2.2. Parameterizing the sources of marine INPs

As a result of the recent wealth of research on ambient marine INPs, parameterizations of their emissions and ice nucleation efficacy have been proposed, some of which are suitable for application in atmospheric models. As previously mentioned, organic carbon has been shown to be a predictor for marine INPs in some studies and has been used to parameterize marine INP concentrations in the sea surface microlayer (Wilson et al., 2015) and in generated SSA (Trueblood et al., 2021). Other parameterizations include those based on the sea salt abundance in air as a reference to predict marine INP concentrations (Irish et al., 2019). INP concentrations normalized to the total sea spray surface area, n_s, measured either in the clean marine sector of ambient air or as laboratory generated SSA were parameterized as a function of air temperature (i.e., independently of biology) for use in modeling exercises (McCluskey et al., 2018b; Knopf et al., 2022). Nearly 2 years of ship-based measurements of INP concentrations were made from the Arctic to the Antarctic and showed that n_s has a similar slope as a function of temperature compared to over land but are typically less by about 2 orders of magnitude (Welti et al., 2020).

Ice nucleation rate coefficients, J_{het}, have also been parameterized from various field and laboratory studies, and they can be derived from nucleation theory and calculated from observations as INP numbers normalized to surface area and time (Cornwell et al., 2021; Alpert et al., 2022; Knopf et al., 2022). A reliable link between thermodynamic control and heterogeneous ice nucleation kinetics is quantified only with knowledge of temperature and relative humidity (Knopf and Alpert, 2013). Alpert et al. (2022) developed a model that allows accurate prediction (within a factor of 10) of marine INPs using J_{het} from SSA size distributions, temperature, and relative humidity (i.e., a thermodynamic control) despite their various inorganic and biogenic components or microbial sources. Other studies previously mentioned (Ickes et al., 2020; Wagner et al., 2021) have been even more conservative, claiming the low level of understanding is insufficient for developing a generalized parameterization for ice nucleation due to SSA particles. This is partly due to the variations in ice nucleation abilities of phytoplankton cells, particle sources (i.e., sea surface microlayer or bulk water), aerosolization methods, INP measurement techniques, and the relative humidity particles are exposed to in experiments prior to ice formation which may promote the formation of solid salts. Much more research is needed to identify, quantify, and understand the fundamental processes for ice nucleation by marine aerosol particles due to various ice formation pathways and particle complexity.

We add that the degree of chemical or photochemical aging of SSA and any influence on ice nucleation ability apart from fresh SSA is far understudied by comparison. Some evidence suggests that ambient atmosphere aged SSA are as good INPs as nascent SSA particles (China et al., 2017; Lata et al., 2021; Knopf et al., 2022), but to the best of our knowledge, this has not been the subject of a targeted study. Furthermore, the degree of SSA aging due to condensation of secondary organic or inorganic material from the gas phase on the ice nucleation ability of ambient particles (whether of marine or terrestrial origin) is absent from scientific literature. **Figure 3** summarizes the recent investigations and the current understanding on properties of marine aerosols serving as CCN and INPs as discussed above.

6. Marine aerosol—cloud interactions, cloud properties, and radiative impact

Aerosol, cloud, and precipitation interactions develop through complex relationships between microphysical

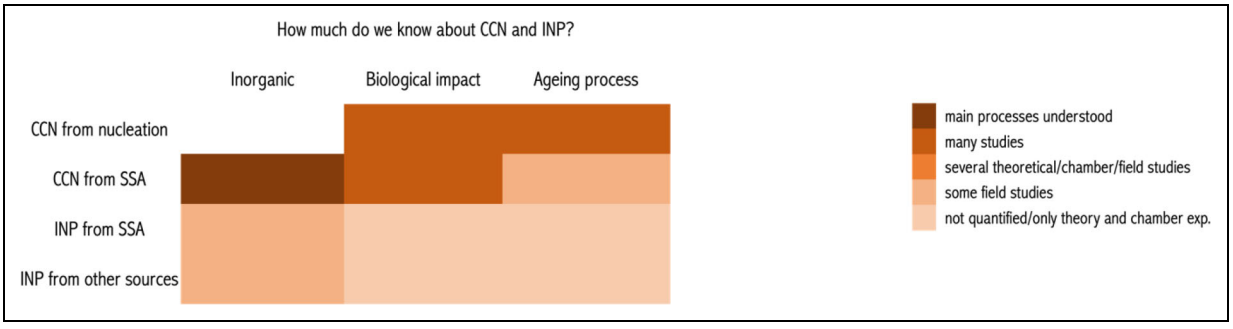

Figure 3. State of knowledge on the cloud condensation nuclei (CCN) and ice nucleating particle (INP) properties of marine aerosol components.

(e.g., aerosol growth, droplet or ice crystal nucleation, time-evolution of droplet size distributions, and precipitation processes), dynamical and thermodynamical (e.g., system motions, mesoscale organization, phase changes and internal energy exchanges on the local scale), and large-scale, environmental processes (e.g., radiation, wind-driven surface fluxes and advection, and other meteorological controlling factors) (e.g., Wood, 2012; Boucher et al., 2013; Rosenfeld et al., 2014; Klein et al., 2017; Bellouin et al., 2020; Wall et al., 2022). These processes are further modulated by a network of positive and negative feedbacks spanning a range of scales (e.g., Stevens and Feingold, 2009; Wood, 2012; Boucher et al., 2013; Altaratz et al., 2014; Rosenfeld et al., 2014; Fan et al., 2016; Bellouin et al., 2020; Scott et al., 2020; Christensen et al., 2022).

Aerosols interact with cloud systems in 2 general ways. For a fixed liquid amount, clouds with increased CCN have more, smaller droplets and thus a higher albedo, proportional to the increased scattering surface area due to this aerosol perturbation (Twomey, 1977). Another response to this aerosol-driven microphysical change can also occur at the macrophysics scale, further modifying the cloud albedo (Bellouin et al., 2020). These adjustments encompass a broad range of mechanisms for liquid, mixed phase, and ice clouds, and their influence on the radiative properties of the cloud system varies by their cloud dynamics and environmental conditions (e.g., Bellouin et al., 2020; Wall et al., 2022; Zhang et al., 2022; Zhang and Feingold, 2023). Precipitation suppression (i.e., resulting in longer cloud lifetimes; Albrecht, 1989) and entrainment enhancement (i.e., reducing cloud liquid and thus brightness, e.g., Xue and Feingold, 2006; Bretherton et al., 2007) are 2 key adjustments to aerosol increases in liquid marine clouds.

Bubble bursting generates small concentrations of relatively large SSA (giant CCN with $r \geq 0.5$ μm) that are activated at the lowest supersaturations, modulate the maximum cloud supersaturation, and speed up drizzle formation (Jensen and Nugent, 2017; Prank et al., 2022). However, fine SSA and secondary aerosols (e.g., associated with marine biology) increase the number of potential CCN, delaying the onset of drizzle (e.g., Albrecht, 1989; Prank et al., 2022). Droplet growth consumes supersaturation by diffusion. The collective droplet surface area will thus determine the diffusion efficiency and latent heat release. Latent heat serves as a (cloud) internal fuel driving their dynamics and influencing their mesoscale organization (e.g., Bretherton and Blossey, 2017; Narenpitak et al., 2021; Janssens et al., 2023). Smaller droplets can be lifted higher up because of their higher mobility (Koren et al., 2015). Simultaneously, at the cloud's edges a larger number of small droplets imply more efficient evaporation and enhanced mixing. The competition between the cloud enhancing processes in the core and cloud suppressing processes in the margins implies that the final impact of larger aerosol number concentrations (for instance due to biologically richer conditions) on cloud properties and lifetime depends on the initial cloud size. Larger clouds with lower surface to volume ratio may benefit from the cloud enhancing processes while smaller clouds that exhibit a relatively larger entrainment zone will experience suppression (Dagan et al., 2017).

In parallel, precipitation processes also depend heavily on the droplet size distribution, a function of total condensed mass, and aerosol number concentrations itself (Pruppacher and Klett, 1997). Clouds formed from higher aerosol concentrations tend to have smaller droplets with a narrower size distribution. This implies delay of the onset of efficient precipitation processes in biologically active cases, impacting cloud lifetime (Albrecht, 1989). This marine biology driven aerosol–cloud–precipitation interaction can occur in a complex, multistep process. For example, precipitating clouds reduce CCN and remove sub-cloud surface area available for condensation upon updraft, increasing peak supersaturation. In a biologically active case with large Aitken number concentrations, this increase in peak supersaturation increases activation and growth of Aitken mode particles into CCN, helping the cloud system to resist precipitation depletion and cloud break up (McCoy et al., 2021; Wyant et al., 2022). In contrast, in an aerosol-poor (low biology) case rain droplets can efficiently clean clouds and generate rain evaporation below cloud base. This can further influence cloud field organization, particularly through cold pool formation (e.g., Zuidema et al., 2018), which may further modulate the sensitivity of cloud systems to aerosol perturbations (e.g., Wall et al., 2022; Zhou and Feingold, 2023). This implies that aerosol has an important role in cloud field organization which can strongly affect the cloud amount, size, and lifetime and therefore their overall radiative effect (e.g., Eastman et al., 2022; Wall et al., 2022; Zhang et al., 2022; McCoy et al., 2023; Zhang and Feingold, 2023). The strong nonlinearities of these interactions are difficult to predict and warrant further examination.

Marine organic particles are an important consideration in modeling exercises on cloud impact (i.e., either added to the CCN and INP number concentrations or modulating the size and hygroscopicity of existing marine aerosols). Ignoring the fine SSA mode could largely diminish the indirect climate effect of SSA (Quinn et al., 2017). However, ambient measurements (Fossum et al., 2020) and modeling studies (Partanen et al., 2014) showed a positive (0.3 W m^{-2}) rather than negative indirect radiative forcing effect by SSA if sufficiently detailed aerosol microphysics and physics-based parameterizations of cloud activation are considered. This positive effect is ascribed to the tendency of SSA to suppress both the in-cloud supersaturation and the formation of CCN from non-sea-salt sulfate. On the other hand, addition of primary marine organics results in a small negative indirect effect (−0.07 W m^{-2}), showing the importance of knowing the sea spray composition (Partanen et al., 2014). Prank et al. (2022) noted that the sensitivity of clouds to variations in organic fraction of sea spray and hygroscopicity was relatively limited compared to differences between sea spray emission flux parameterizations. Another sensitivity study on marine organic particles, however, shows that a strong effect is observed in terms of significant changes in CCN and cloud droplet number only in the Southern Hemisphere over 40°S–60°S, while the effect in terms of

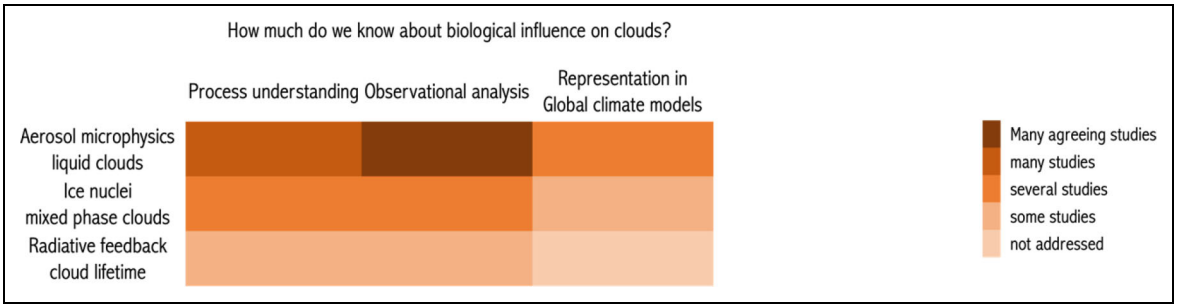

Figure 4. State of knowledge on the biological influence impacting cloud properties.

significant changes in cloud ice mass and number concentrations is notable over 50°–70° in both hemispheres (Zhao et al., 2021). None of these studies includes the effect that biogenic organics present in the sea water have on the SSA number emission flux, nor the potential impact of organics on the sea spray flux temperature dependence (Section 3.1). Including these processes could increase the sensitivity of cloud properties to marine biology in models.

Observational Southern Ocean cloud comparisons were successful when the OCEANFILMS model (cf. Section 3.2; McCoy et al., 2015) and improved sulfur chemistry and DMS oxidation parameterizations were implemented (Revell et al., 2019), resulting in a more realistic radiative impact (Mulcahy et al., 2018). Other global climate model simulations (i.e., in CAM6) corresponding to flight sampling were less successful as CCN and droplet number concentration were biased low, potentially due to underproduction of Aitken aerosols (McCoy et al., 2021). Neglecting biogenic NPF (cf. Section 2.2) in global climate models critically impacts the cloud-related radiative effect (Gordon et al., 2016), which is consistent with the difficulty of capturing remote marine environments in other recent climate models (McCoy et al., 2021). This further highlights the importance of global climate models incorporating more nuances of aerosol pathways and their interactions with the cloud-climate system (cf. Sections 2–5, 7, **Figure 2**).

There are also many uncertainties remaining on the impact of INPs and secondary ice formation processes on marine cloud properties (Bellouin et al., 2020). In the Southern Ocean, the underestimation of ice formation in CAM6 (D'Alessandro et al., 2019) results in too much cloud liquid and too little cloud ice in mixed-phase clouds. One reason could be that the cloud lifetime is reduced in models because their CCN/INP ratios are too low, because of either too low marine CCN or too high marine INPs concentrations (Vergara-Temprado et al., 2018). As noted by Field et al. (2017), another reason could be that most models misrepresent several important secondary ice formation mechanisms (e.g., rime splintering, ice–ice collision fragmentation, droplet shattering during freezing, and fragmentation during sublimation of ice bridges) which were found of major importance in the summertime Southern Ocean (Järvinen et al., 2022).

As for cloud measurements, which are rarely accessible in situ, a breakthrough is expected to come from satellite remote sensing observations, which, in the last 5 years, have progressed significantly by increasing their spatial and temporal resolutions (e.g., TropOMI, GEMS), providing more detailed spectral information and developing new approaches for cloud inversion (Tzabari et al., 2021). Combining multiple satellite datasets resulted in better insights into complex processes such as detection and quantification of mixed-phase clouds in subpolar regions (Listowski et al., 2020), areas notoriously difficult to survey with a single sensor. Without being able to replace the ground-based evidence, the continued support and development of satellite observations, particularly of the aerosol, cloud, and climate system, is critical (National Academies of Sciences, Engineering, Medicine, 2018). Such satellite observing systems (e.g., ACCP, the Aerosol and Cloud, Convection and Precipitation Designated Observable, https://science.nasa.gov/earth-science/decadal-surveys/decadal-accp/) open new opportunities for marine science and complement the complex, expensive, and difficult to achieve in situ measurements in remote regions. **Figure 4** summarizes the recent investigations and the current understanding on the biological influence impacting cloud properties as discussed above.

7. Climate change impact and potential feedback loops

We presented recent knowledge on how marine biogeochemistry could impact climate via gas and aerosol emissions and their impact on clouds. Here we discuss how future climate may affect biogeochemical changes, closing feedback loops. The key feedback loop in which climate influences ocean biogeochemistry and in turn influences climate via DMS emissions and cloud formation is known as the CLAW hypothesis (Charlson et al., 1987). Even for DMS—the most studied aerosol-relevant biogenic compound—little progress has been made on its overall impact on climate due to uncertainties on fundamental mechanisms in its production and oxidation pathways (Ghahreman et al., 2017; Yu et al., 2021). While significant efforts have been undertaken to understand the effects of ocean biogenic emissions on climate, the opposite is less frequently investigated. If a changing climate (e.g., changes in temperature, ocean acidity and radiation via cloud cover) affects aerosol sources, there will likely be an additional aerosol-mediated cloud feedback (Gettelman and Sherwood, 2016; Gettelman et al., 2016). Climate controls on aerosol and cloud activation processes must be better

understood (Gordon et al., 2017; Tegen and Schepanski, 2018; Twohy et al., 2021).

Temperature—The average ocean surface temperature is expected to increase by 2.5°C by 2100, with consequences for marine biology (Bindoff et al., 2019). Increases in SST may have different impacts on SSA emissions. Struthers et al. (2013) predicted a general increase in sea salt aerosol number emissions due to both increasing surface wind speed (with nonuniform effects for different size ranges) and SST. However, taking into account the impact of biogeochemistry on sub-micron SSA emission may lead to different conclusions; for instance, ocean warming is expected to expand the distribution range and cell abundances of *Synechococcus* (Flombaum et al., 2013). Also, in a changing climate, the strong temperature and humidity dependance of ice nucleation rates may lead to less ice crystal formation (all other parameters equal). Due to the lack of understanding of the biological processes leading to more or less INPs, the impact of a redistribution of different phytoplankton assemblages on future INP concentrations is unknown.

CO_2—The oceanic uptake of anthropogenic CO_2 is leading to surface ocean acidification (Findlay and Turley, 2021). This acidification may result in climate feedbacks via changes to the net production and emission flux of short-lived climate-active gases, including DMS (Hopkins et al., 2020). The response of DMS to ocean acidification has been explored primarily by means of large-scale in situ mesocosm experiments, typically performed by exposing nutrient-induced blooms of phytoplankton to varying levels of CO_2 over a period of 4–6 weeks. In general, net DMS production decreases with increasing CO_2 concentrations (Hopkins et al., 2020). Inclusion of these results in Earth System Models has suggested a potential positive climate feedback driven by major reductions of DMS production in high-productivity areas, and consequent changes to aerosol and cloud properties that lead to surface warming (Six et al., 2013; Schwinger et al., 2017). In a first attempt to model the entire CLAW cycle, from ocean to clouds and back to ocean, Wang et al. (2018) concluded that truly coupled and dynamic marine ecosystem and sulfur models are needed if we are to assess the occurrence and strength of DMS-mediated climate feedback as presented in the CLAW hypothesis. Due to these limitations in model configuration, Earth System models diverge even in the sign of the simulated future trends of ocean DMS emission under global warming scenarios (Bock et al., 2021). Moreover, the effects of other stressors that act in concert with ocean acidification, such as warming, deoxygenation, and especially solar radiation, remain poorly explored although there has been some advances (Boyd et al., 2016; Hussherr et al., 2017). Moving forward requires improved mechanistic representation of DMS-related processes in climate models, and the integration of experimental data which considers the influence of multiple climate stressors on DMS production.

Cloud coverage—Satellite records show that boundary layer cloud cover has decreased between the 1980s and the 2000s across the subtropics (Norris et al., 2016). This resulted in a positive shortwave subtropical cloud feedback due to increasing SST (Myers and Norris, 2016; McCoy et al., 2017a). Positive subtropical feedback is expected under future climate warming while other regions and cloud types experience more varied, uncertain shortwave feedback (e.g., Myers et al., 2021b; Scott et al., 2020; Sherwood et al., 2020; Zelinka et al., 2020; Ceppi and Nowack, 2021; McCoy et al., 2023). Additional to this uncertainty on the current and future evolution of the cloud cover, there are large unknowns on how associated changes in solar radiation, and in particular ultraviolet light, influence the distribution and activity of phytoplankton assemblages, their grazers and the concurrent bacterioplankton across oceanic regions (Gao et al., 2007; Ruiz-González et al., 2013; Häder et al., 2015). These unknowns hamper our ability to anticipate how changes in exposure to solar radiation will result in changes in the planktonic release of cloud-forming substances, and what will be the climate feedbacks, although some progress has been made with a few trace gases (Galí et al., 2011; McLeod et al., 2021).

Future climate effects are foreseen to be most prominent at the poles, with many studies showing effects of reducing sea ice cover in the Arctic. Among other effects, the increase in open water surfaces would cause an increase in SSA production as well as changes in its composition (Kirpes et al., 2019; Burrows et al., 2022; Willis et al., 2023). In addition, an increase in open water in the polar oceans (in both hemispheres) allows for more marine gas-phase organic emissions, which can either contribute to NPF or to existing particle growth.

Finally, future studies should take advantage of increasing modeling capacities to run Earth system models at higher spatial resolution and/or with inclusion of more processes believed important such as those highlighted above. The main processes included in recent regional/global models are summarized in **Figure 5a** with an attempt to identify how are they expected to be impacted under climate change. To these, **Figure 5b** adds processes identified as phenomenologically important, but not yet well enough characterized to be included in regional/global models.

Overall, the recent observations mentioned across the sections of this article show the importance of conducting coordinated ocean–atmosphere studies embracing the diversity of the aerosol sources and understanding their biogeochemical drivers. The long-term measurements in remote locations should be co-localized in both the atmosphere and ocean, which is technically challenging but also missing due to a historical relative impermeability between the 2 research communities. Laboratory studies are essential for disentangling complexity and understanding processes. While results must be carefully considered, process-based studies linking ocean biogeochemistry and the atmospheric composition should be (i) exportable to the modeling community, hence guided by the processes identified as missing in the models, (ii) designed to include model-compatible variables, and (iii) quantitative. Lastly, utilization of long-term aerosol records to interpret past aerosol changes in terms of climate

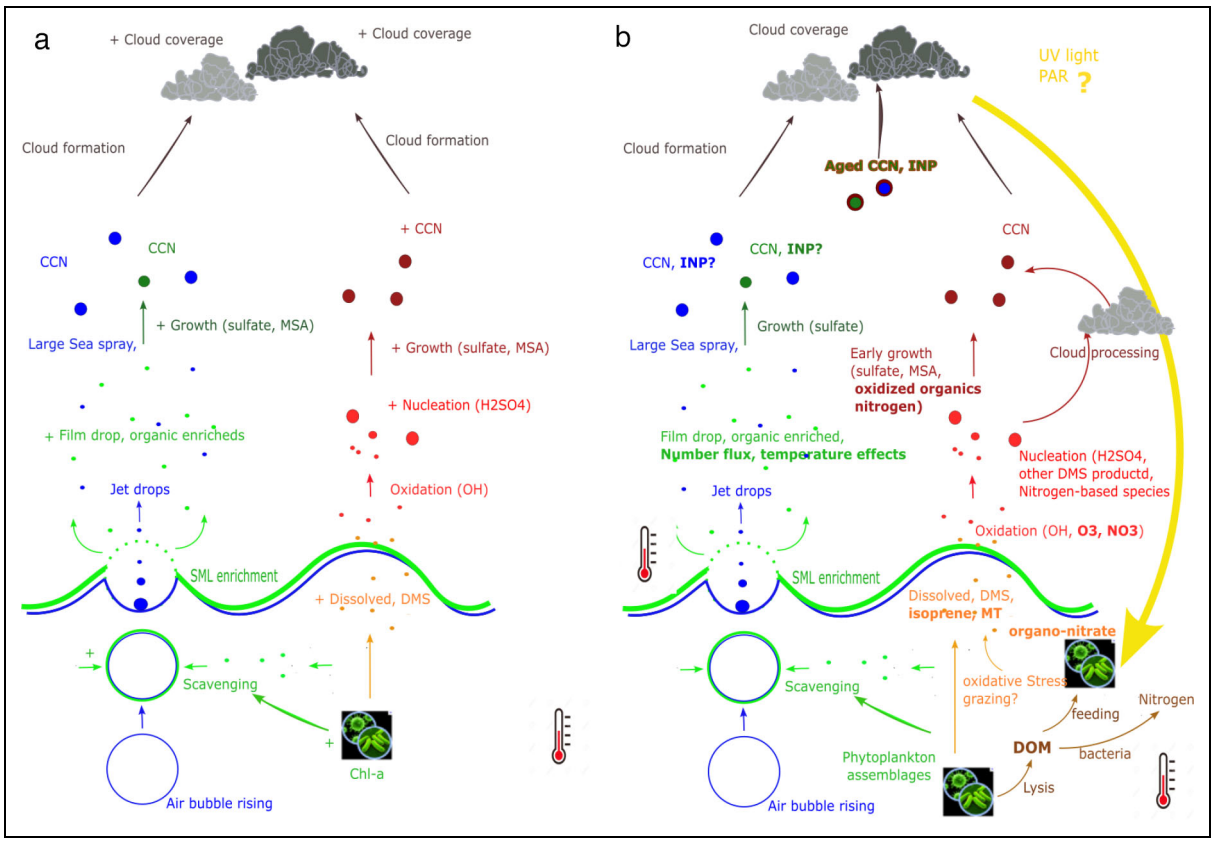

Figure 5. The evolving view of marine ecosystem impacts on aerosols and climate. (a) Traditional view of the interconnections between marine ecosystems, aerosols, and clouds, and main processes that have been considered in regional/global model studies (but may not be included in all models), "+" signs indicate how future warming is expected to change total oceanic biomass, and how the resulting processes would be impacted under this high versus low biological activity. (b) Processes identified as important but not yet well characterized enough to be included in regional/global models (bold). The impact of climate change is not shown since different factors may result in opposing effects.

variability remains essential for robust future projections of aerosol distributions and feedbacks (Tegen and Schepanski, 2018).

Data accessibility statement

All data that were considered in this work are available in the cited literature.

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Author contributions

Contributed to conception and design: KS, RS, BW.

Drafted and revised the article: All authors.

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