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## RESEARCH LETTER

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## Relating Ocean Biogeochemistry and Low-Level Cloud Properties Over the Southern Oceans

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### Key Points:

- Nanophytoplankton biomass shows more relations to cloud occurrences than Chlorophyll-a or Particulate Organic Carbon concentrations
- Higher nanophytoplankton abundance is positively linked to warm-liquid cloud frequency of occurrence in spring in most regions of 40°S–60°S
- Higher nanophytoplankton abundance is linked to a decrease in the ice-containing cloud frequency of occurrence in most regions

### Supporting Information:

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

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**Abstract** There is growing evidence that marine microorganisms may influence cloud cover over the ocean through their impact on sea spray and trace gas emissions, further forming cloud droplets or ice crystals. However, evidence of a robust causal relationship based on observations is still pending. In this study, we use 4 years of multi-instrument satellite data to segregate low-level clouds into ice-containing and liquid-water clouds to obtain clear relationships between cloud types and ocean biological tracers, especially with nanophytoplankton cell abundances. Results suggest that microorganisms may be involved in compensating effects on cloud properties, increasing the frequency of occurrence of warm-liquid clouds, and decreasing the occurrence of ice-containing clouds in most regions during springtime. The relationships observed in most regions do not apply to the South Pacific Ocean in the 40°S–50°S latitude band. These results shed light on overlooked potential compensating effects of ocean microorganisms on cloud cover.

**Plain Language Summary** Climate is governed by interactions between the ocean and the atmosphere. While physical interactions such as exchanges of heat and water vapor are fairly well understood, the role of biology, that is, the living marine microorganisms, on atmospheric processes, is a lot more complex. For instance, marine microorganisms may influence the number and the chemical composition of sea sprays and also emit trace gasses that will form tiny particles. Sea sprays and newly formed particles can then serve as nuclei on which cloud droplets or ice crystals form, therefore influencing cloud properties and climate. These chains of processes are theoretical, and there are few clear linkages between ocean biology and cloud properties derived from observational data. This study uses new satellite retrievals to establish relationships between cloud phase occurrence (ice, warm-liquid, mixed-phase or supercooled-liquid clouds) and the biological activity of the ocean in different regions of the southern ocean. For a given month, locations of higher abundance of phytoplankton corresponds to a higher warm-liquid cloud cover but lower ice cloud cover. These results suggest compensating effects of marine microorganisms on cloud lifetime via their potential to impact the formation of particles able to become water droplets or ice crystals.

## 1. Introduction

Clouds play a major role in the Earth's radiation balance, in particular above the oceans of the southern hemisphere where their cooling effect is estimated to range from  $-15$  to  $-28$  W/m<sup>2</sup> (Matus & L'Ecuyer, 2017). However, the uncertainty of the response of clouds to climate change is still the least understood climate feedback (IPCC, 2021). Under cloudy conditions, climate and numerical weather prediction models overestimate the amount of shortwave radiation reaching the ocean surface of high-latitude regions, by up to 20 W/m<sup>2</sup> (Flato et al., 2014; Hyder et al., 2018; Schuddeboom & McDonald, 2021). One of the hypothesized reasons for this bias is the inaccurate representation of cloud ice/liquid partitioning in models that affects the surface radiative budget (Bodas-Salcedo et al., 2016; Cesana et al., 2022; Kay et al., 2016). Cloud phase and formation depend on thermodynamic conditions, and on the availability and properties of aerosol particles which can act as cloud condensation nuclei (CCN) or ice nucleating particles (INPs) (Korolev et al., 2017).

The impact of anthropogenic aerosols on clouds and climate can be accurately measured only if the impact of natural aerosols and their evolution is well quantified. Natural aerosol variability is one of the largest uncertainties in assessing climate projections (Carslaw et al., 2013, 2017). The marine aerosol variability is, among other

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factors, a function of the ocean water biogeochemical properties that are expected to evolve in a future climate. For given thermodynamic conditions, increased numbers of CCN would lead to clouds with higher numbers of smaller droplets, which in turn increases cloud albedo (Twomey effect) (Twomey, 1977) and lifetime (Albrecht effect) (Albrecht, 1989). A lack of INPs would also favor the maintenance and persistence of supercooled-liquid-containing clouds. On the other hand, increased numbers of INPs of biological origin, active at warmer temperatures, are expected to lead to a rapid glaciation of the cloud, initiate precipitation at a faster rate and therefore decrease the cloud lifetime. INPs and CCN have opposing effects on cloud lifetime, making the net impact of marine biological aerosols on cloud properties difficult to quantify. In addition to this complexity, links between ocean biogeochemical properties and marine aerosols with CCN and INP properties are driven by unraveled biological processes (Forestieri et al., 2018; Trueblood et al., 2021). Satellite and field observations point to a summertime maximum of aerosol concentrations in the Southern Ocean (SO), correlated to phytoplankton productivity (Gabric et al., 2002; Sciare et al., 2009). Recent semi-controlled experiments evidenced relationships between seawater nanophytoplankton cell abundances (Nano) and CCN fluxes produced at the ocean surface via bubble bursting (Sellegrri et al., 2021). Marine origin sea sprays are also believed to dominate the INP population over the SO (Burrows et al., 2013; Uetake et al., 2020; Vergara-Temprado et al., 2017).

Despite these indications of strong biological influence on clouds, contradictory conclusions have been drawn from studies relating satellite-derived cloud properties and ocean biogeochemistry (Sato & Inoue, 2021). Most studies have focused on the Twomey effect by investigating the link between Chlorophyll-a concentration (Chl-a) products and cloud droplets size and number (Lana et al., 2012; D. T. McCoy et al., 2015; I. L. McCoy et al., 2021; Meskhidze & Nenes, 2006; Vallina et al., 2006; Wilson et al., 2015). Less attention has been given to the impact of biology on cloud cover, type, lifetime or occurrence. Yet, the cloud fraction response to increased large-scale aerosol concentrations was found to potentially double or triple the Twomey effect (Andersen et al., 2017; Christensen et al., 2017; Gryspeerd et al., 2016). Hence, the focus of our study is the effect of biologically-influenced aerosol particles on low-level cloud types and lifetimes (rather than microphysics) at the monthly and regional scales.

## 2. Materials and Methods

This study focuses on low-level (LL) clouds with altitude lower than 3000m (as in Mioche et al., 2015), that are linked to the marine boundary layer and may be influenced by ocean biogeochemistry. LL cloud-type and thermodynamic phase were extracted from DARDAR-MASK.v2.23 (for LiDAR/raDAR Ceccaldi et al., 2013; Delanoë & Hogan, 2008, 2010) products between 40°S and 82°S for the 2007–2010 period. In our study, only cloud hydrometeor type or phase classes were considered. The discrimination of cloud types is based on the synergy of observations from the CALIOP (Cloud-Aerosol Lidar with Orthogonal Polarization) lidar onboard CALIPSO (Cloud-Aerosol Lidar and Infrared Pathfinder Satellite Observations (Winker et al., 2003), and the cloud profiling radar onboard CloudSat (Stephens et al., 2002). The cloud layers (or pixels) classification mainly relies on the 532 nm lidar attenuated backscatter coefficient profiles. If the lidar signal is strongly and rapidly attenuated, the cloud layer is considered as mainly composed of liquid droplets whereas a low signal is associated with ice-only layers (Figure S1 and Text S1.1 in Supporting Information S1). Thresholds on the cloud temperature and thickness are also considered to refine the cloud layer composition (supercooled water vs. warm liquid, for instance). The 94 GHz radar reflectivity profiles are mainly used to detect the presence of ice crystals within a supercooled liquid water layer (assigned to a mixed-phase). When the lidar signal is extinguished or fully attenuated by upper cloud layers, the phase diagnostic relies only on the radar signal (estimated to 5% of the cases). Cloud layers at freezing temperature (below 0°C) are automatically diagnosed as ice, which may introduce a positive but limited bias toward ice clouds.

Southern Ocean low-level cloud occurrences (expressed in percentage, i.e. a number of cloud observation divided by the number of footprints) are investigated using dedicated Python code (DARDAR-SOCP, for Southern Ocean Cloud Phase), based on the one developed by (Mioche et al., 2015). The sampled atmospheric column is divided into 60-m “pixels,” that are all assigned to a specific class value in DARDAR-MASK products (Figure S2 in Supporting Information S1). In line with previous studies, a cloud event is counted if there are at least three vertical adjacent cloudy pixels (180 m). This threshold remains arbitrary as there is no consensus on the smallest possible thickness of a cloud (Mioche et al., 2017). In the same way, a cloud is separated from another if there are at least three vertical adjacent non-cloudy pixels. Cloud types were defined as warm-liquid clouds (with positive temperature), ice-only clouds, unglaciated supercooled-liquid clouds (USLCs) that contain only pixels of

supercooled water, and mixed-phase clouds (MPCs) composed of at least two pixels of two different phases (liquid, ice or supercooled) or one mixed-phase pixel. The cloud-type occurrences are calculated within grid-boxes of 2° latitude by 5° longitude.

DARDAR-SOCP also extracts thermodynamic variables from ECMWF analyses embedded in DARDAR-MASK files (ECMWF-AUX collocated products (Delanoë et al., 2011; Hersbach et al., 2020)). For every footprint where a cloud is detected, the air temperature, the specific humidity and the geopotential heights at 700 and 850 hPa are extracted. Sea surface temperature (SST) and surface air temperature are also stored. These parameters are used to investigate the links between meteorological conditions and cloud occurrences.

The greatest source of uncertainties in our estimation of cloud type occurrences stems from a misidentification of the retrieved cloud phase. Statistical uncertainties are very low given the large number of observations in a gridbox (standard error on the total-cloud occurrence less than a few %, Table S1 in Supporting Information S1). Based on previous intercomparison studies (Cesana et al., 2016; Jourdan, 2022; Mioche & Jourdan, 2018), cloud-type classification errors generate biases on the cloud occurrence estimated to up to: 15% for ice clouds, 20% for liquid clouds and 10% for MPCs (see Text S1.2 in Supporting Information S1 for more details).

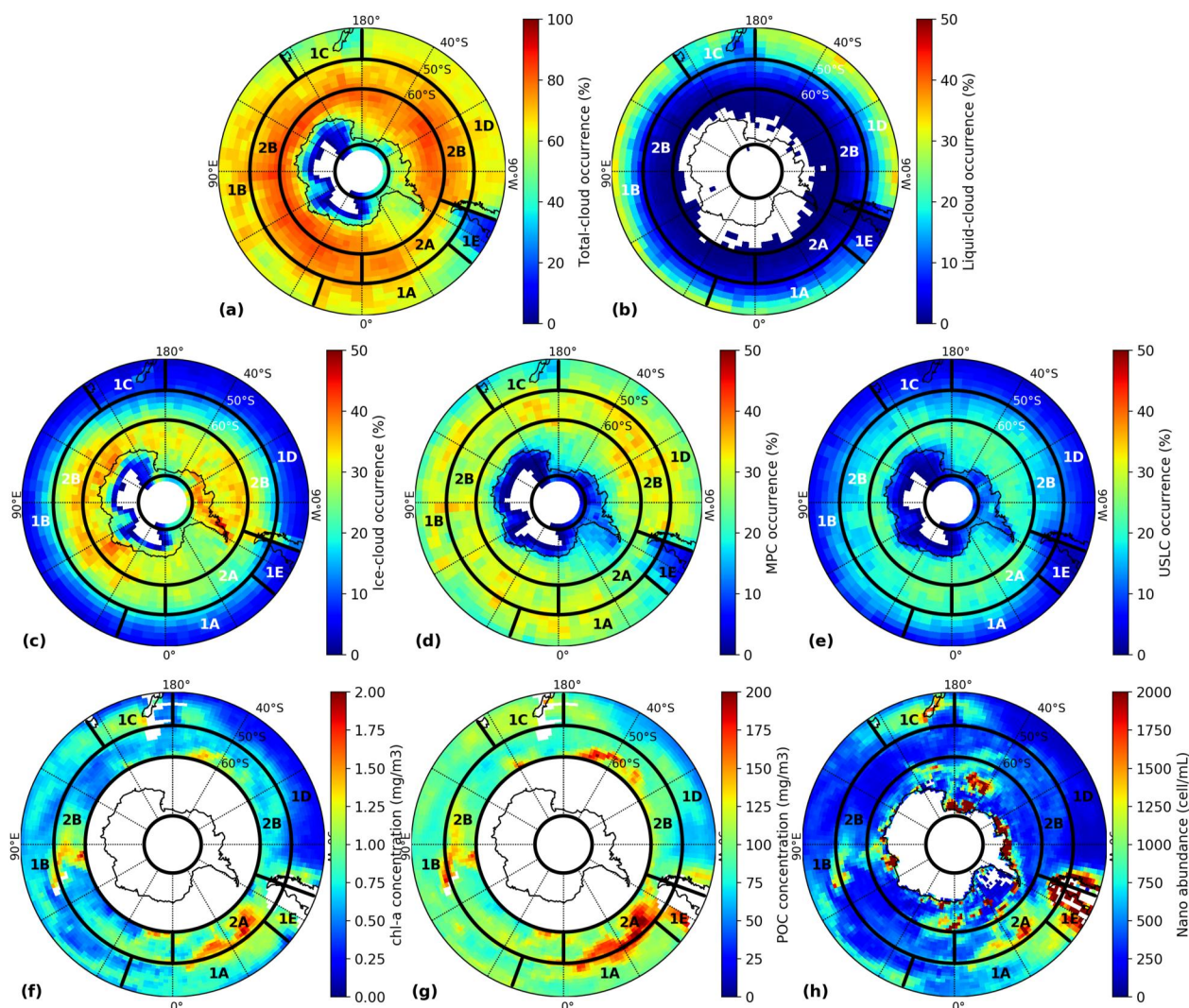
A traditional proxy of phytoplankton biomass is Chl-a. Previous studies have also examined the link between cloud forming marine aerosols and alternative biological tracers and cast doubt over the relevance of Chl-a as a tracer. In particular, the stock of Particulate Organic Carbon (POC) was found to be linked to sea spray INP emissions in oligotrophic regions (Trueblood et al., 2021), while the Nanophytoplankton cell abundance was found to be linked to sea spray emissions with CCN properties in contrasted oceanic regions (Sellegrì et al., 2021). As a result, we choose to exploit not only Chl-a products but also POC and Nano. Chl-a and POC products are inferred from an improved version of the neural network-based algorithm of (Sauzède et al., 2016). It uses as input concurrent observations of ocean color (GlobColour) and sea level anomaly satellite data and hydrological properties (ARMOR 3D fields) available from the European Copernicus Marine Service (CMEMS). The abundance of nanophytoplankton, as in (Sellegrì et al., 2021), was derived following (Uitz et al., 2006) using the MODIS-Aqua satellite surface Chl-a concentration as input. This product relies on the procedure of (de Boyer Montégut et al., 2004) to retrieve the monthly mixed layer depth data, and on a conversion from total chlorophyll-a biomass (in units of mg of chlorophyll-a per m<sup>3</sup> of water) to cellular abundance (in units of cells. mL<sup>-1</sup>), assuming that a cell of the Nanophytoplankton group contains  $2.64 \times 10^{-10}$  mg of chlorophyll-a (Stramski et al., 2001). The biological products are all based on passive (ocean color) remote sensing and are, thus, mainly limited in their seasonal coverage because of polar nights and sea-ice at high latitudes, which leads to a lack of data during winter months. The error on these products (all regions and depths together), expressed as a mean absolute percentage deviation, are 30% for POC, 40% for Chl-a (Sauzède et al., 2021) and estimated to 30%–40% for Nano (Uitz et al., 2006).

Our study relies on monthly products, the highest frequency available for ocean products. Therefore, the spatial segregation that we will work on for extracting homogenous areas will be structured into regions of at least  $1,700 \times 1,000$  km<sup>2</sup>, influenced by meteorological conditions averaged over a month. Although cloud lifetimes are shorter than the monthly scale, this approach allows us to statistically assess an impact of ocean biogeochemical properties at larger temporal and spatial scales.

### 3. Results

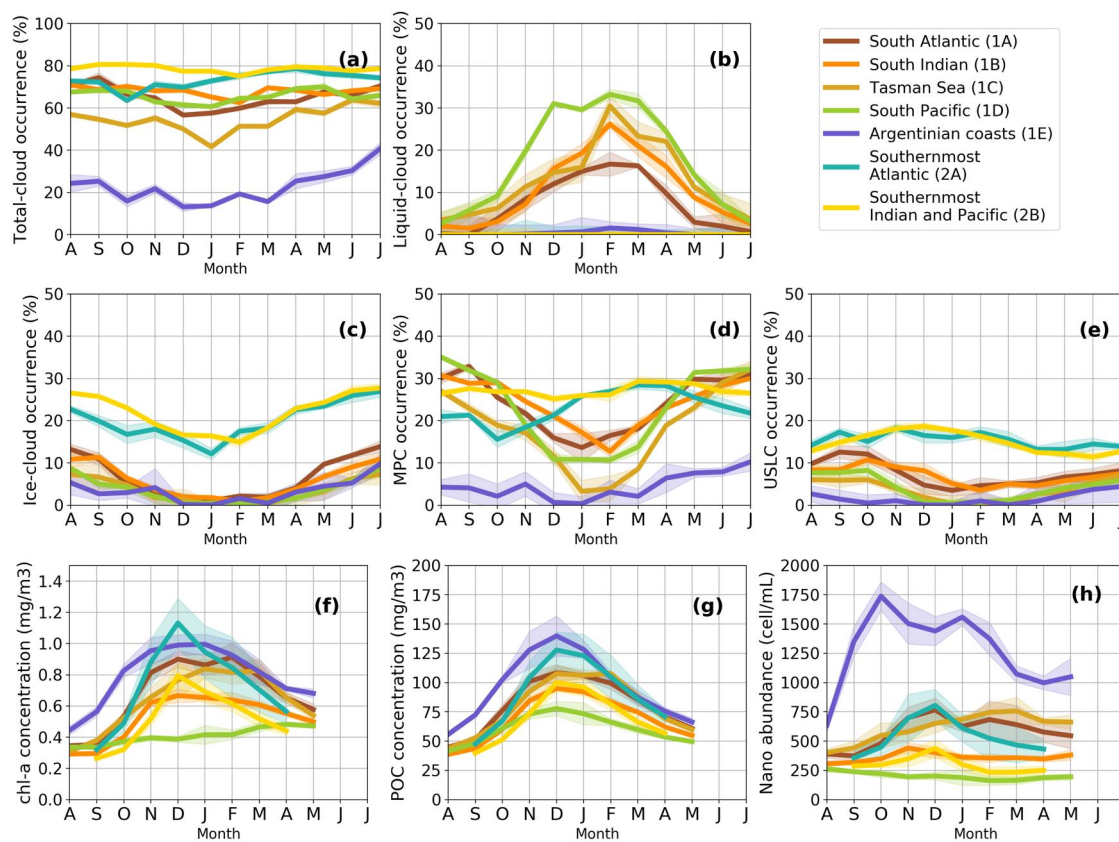
#### 3.1. Geographical and Seasonal Distributions

Low-level clouds are ubiquitous between 40°S and 82°S, occurring 67% of the time in summer and 64% of the time during winter over oceans. There are, however, some meridional differences, with larger (>75%) cloud occurrences observed between 50°S and 65°S compared to latitudes north of 50°S (<60%) (Figure 1a). Segregating LL clouds into ice-only clouds, MPCs, warm-liquid clouds and USLCs enhances the latitudinal contrasts compared to the total-cloud occurrence (Figures 1b–1e), as a consequence of the latitude-driven air temperature. Three main latitude-defined zones can be identified: Zone 1 (40°S to 50°S) where the LL warm-liquid cloud occurrence is the highest, Zone 2 (50°S to 60°S) where LL ice-containing (ice clouds and MPCs) cloud prevails over warm-liquid clouds, and the region located between 60°S and 82°S which is largely influenced by sea-ice (Frey et al., 2018; Listowski et al., 2019), and that we chose to exclude from our study, to focus on ocean-cloud interactions.



**Figure 1.** Stereographic projections of low-level cloud occurrences (500–3,000 m) over the 2007–2010 period and derived from DARDAR-MASK.v2.23: (a) total clouds, (b) warm-liquid clouds, (c) ice-only clouds, (d) mixed-phase clouds, (e) unglaciated-supercooled-liquid clouds. Maps of ocean biological variables mean concentrations/abundances for: (f) Chlorophyll-a, (g) Particulate Organic Carbon, (h) Nanophytoplankton during the same period.

Regional contrasts are also observed amongst zones 1 and 2. Based on geographical limits, on the spatial distributions of cloud occurrence (Figures 1a–1e) and ocean biogeochemical variables (Figures 1f–1h), and on the ocean circulation (Sokolov & Rintoul, 2009), Zone 1 has been subdivided into 5 contrasted sub-regions and zone 2 into two sub-regions. At this regional scale, the total cloud occurrence is lowest off the Argentinian coast (monthly medians ranging between 20% and 45%, Figure 2a). This sub-region is characterized by significantly lower MPC (5%–10%) and warm-liquid cloud (0%–5%) occurrences compared to other regions of zone 1 that otherwise experience very similar cloud types and seasonal variations (10%–35% for MPCs maxima during winter, and 5%–30% for warm-liquid clouds maxima during summer (Dec-Jan-Feb, Figures 2d and 2b). The highest total-cloud occurrence is observed over the Southernmost oceanic regions (65%–80%, 2A and 2B, Figure 2a). Unlike all other oceanic regions, the southernmost part of the Atlantic Ocean shows a higher cloud occurrence, mainly MPCs, during summer-autumn than during winter (Jun-Jul-Aug). The different subregions also display very contrasted biogeochemical properties. Figures 2f–2h show that the two regions east of the Argentinian coast (1E, 1A) and the Southernmost Atlantic region (2A) are marked by the largest concentrations of Chl-a, POC and nanophytoplankton (especially 2A). In contrast, the South Pacific (region 1D) is characterized by the lowest biological tracer concentrations of all oceanic regions. The seasonality of biogeochemical variables also differs among the different regions. Late spring maxima are frequently observed for biological tracers, as

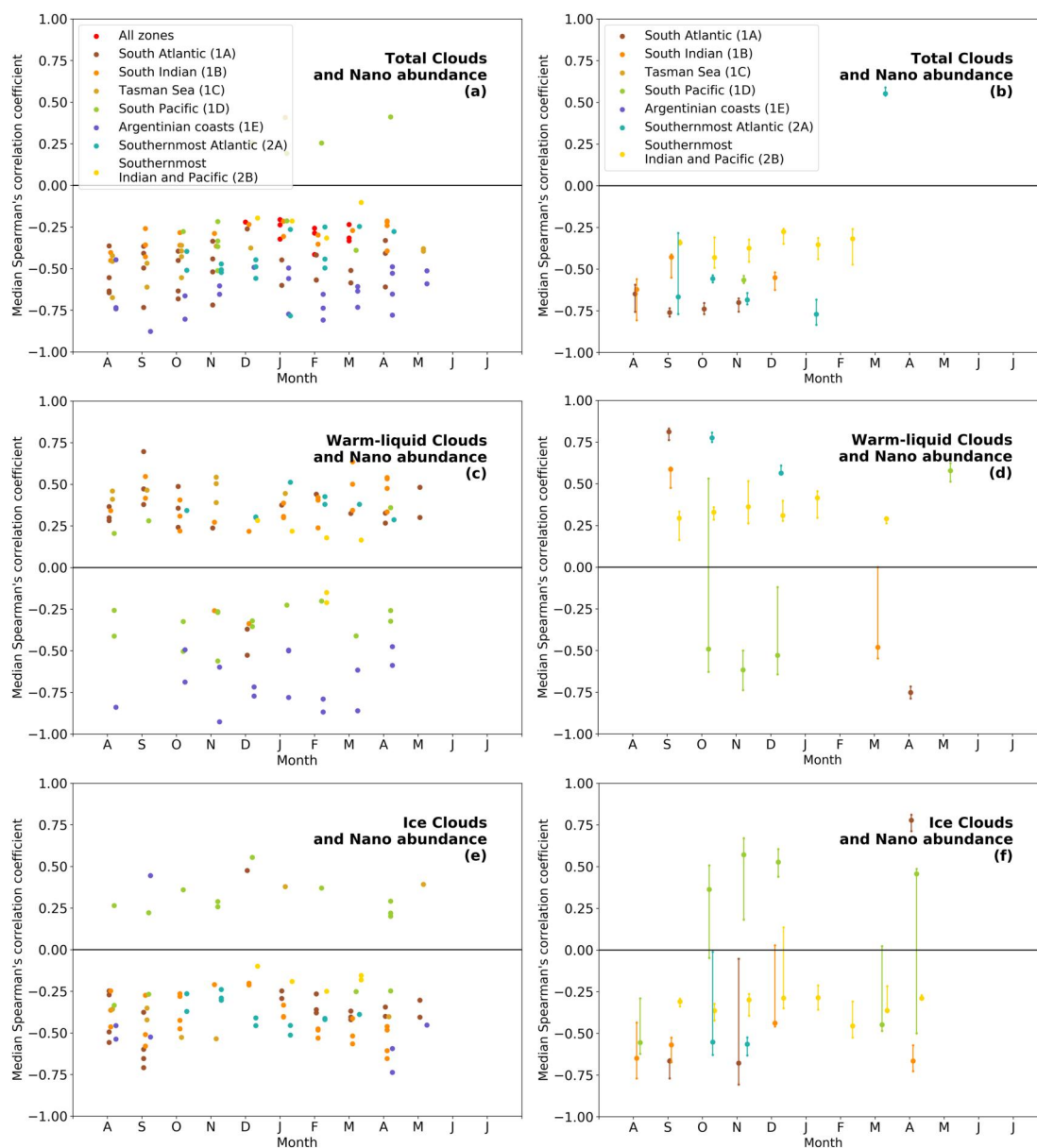


**Figure 2.** Regional annual cycles of the (a) total cloud, (b) warm-liquid cloud, (c) ice-only cloud, (d) mixed-phase cloud, and (e) unglaciated supercooled-liquid cloud 2007–2010 median occurrences. Panels (f, g, h) refer to annual cycles of Chl-a, Particulate Organic Carbon and Nanophytoplankton median concentrations/abundances between 2007 and 2010.

phytoplanktonic blooms are common during this season (Figures 2f–2h). A summer peak off the Argentinian coast and autumn peaks in the South Atlantic and Tasman Sea are also detected. Spring and autumn blooms were reported in the SO previously (Sallée et al., 2015). However, when two bloom periods appear within the same region (as it is the case for the Argentinian coast), this might result from a spatial averaging of two subregions of different seasonal behaviors as pointed in (Ardyna et al., 2017).

### 3.2. Influence of Meteorological Conditions on Cloud Occurrence

The SO cloud geographical distribution is primarily impacted by large-scale meteorological conditions (Field & Wood, 2007; Haynes et al., 2011; Wall et al., 2017). For instance, based on a combination of several satellite products and reanalysis data (Wall et al., 2017), studied the instantaneous linkages between summertime cloud properties and meteorological predictor variables. They showed that cloud properties were very sensitive to large scale subsidence/ascent conditions in the mid-troposphere. SST, low-level temperature advection and the estimated inversion strength (EIS) also influence LL-cloud properties such as cloud fraction and optical depth. Colder SST, strong cold-advections and EIS under subsidence regimes tend to result in higher horizontal LL-cloud fractions. In our study, the impact of the strength of the vertical motion on the cloud type occurrences was not investigated. Several principal component analysis were implemented to study the influence of standard thermodynamic parameters on the cloud-type occurrence. Results show that SST (or air temperature), specific humidity at 850 hPa and Lower Tropospheric Stability (LTS) are parameters that explains most of the variance of the meteorological descriptors (see Text S2 and Table S2 in Supporting Information S1). High values of these parameters are associated with large occurrences of warm-liquid clouds and low ice-only cloud occurrence (Figure S3 in Supporting Information S1). Indeed, based on the difference in specific humidity between the lifting condensation level and the cloud base as in (Wang et al., 2016), we found that 40%–70% of the LL-clouds observed over the SO are coupled with the surface (Figure S4 in Supporting Information S1). Therefore,



**Figure 3.** Monthly Spearman correlation coefficients ( $R$ ) calculated between Nano and the occurrence of (a) total cloud coverage, (c) warm-liquid clouds, (e) ice clouds. Monthly median  $R$  calculated at pseudo-constant sea surface temperature between Nano and the occurrence of (b) total clouds, (d) warm-liquid clouds, (f) ice clouds. Error bars correspond to the 25 and 75 percentiles in panels (b, d, f). An example of the correlation plot from which the Spearman correlation coefficients shown here are originating from is given on Figure S5 in Supporting Information S1 for the September months of the period in the South Atlantic sector.

surface boundary layer fluxes are expected to regulate the cloud properties and their spatial and seasonal distributions. Warmer waters (SSTs) contribute to the increase of humidity in the lower atmospheric layers and favors the initiation of the liquid water phase. For ice clouds, the opposite behavior is observed. These trends are in agreement with previous studies also showing strong correlations between liquid-phase properties (in particular relative frequency of occurrence) and SST (Huang et al., 2016) or LTS (Matsui et al., 2006). The results of this short analysis suggest that SST drives a significant part of the observed LL-cloud-type seasonal variations.

### 3.3. Relating Cloud Occurrence and Marine Biological Tracers

The spatial relationships between cloud occurrences and biological variables were investigated for each month using a Spearman analysis on all grid-boxes included in each region (Figure 3 and Figures S5 and S6 in

Supporting Information S1). When considering all regions merged together, the total cloud coverage is unrelated to Chl-a (Figure S7a in Supporting Information S1) and POC (Figure S8a in Supporting Information S1), but is anticorrelated to Nano (Figure 3a) during summertime when biological activity is the highest. In general, stronger relationships are found between cloud-type occurrences and Nano (Figure 3) than with Chl-a or POC (Figures S7 and S8 in Supporting Information S1). Chl-a is a tracer for the total photosynthetic biomass and Chl-a satellite products are widely used, for instance in modeling exercises. However Chl-a seems unsuitable as an “universal” predictor of air-sea exchanges processes (Burrows et al., 2013). Satellite Nano products are emerging and may be more relevant for air-sea interaction processes (Sellegrri et al., 2021). In the following, we will focus our analysis on the cloud-Nano relationships, keeping in mind that Chl-a and POC show similar, but weaker correlations to cloud occurrences (Figures S7 and S8 in Supporting Information S1).

The anti-correlation between total cloud coverage and Nano is also found at the regional scale for most regions, not only during summer when Nano is highest but also during other seasons. To further investigate the causes of these trends, cloud occurrences-Nano relationships are studied for different cloud-types. Contrary to total cloud coverage, the warm-liquid cloud occurrence is positively correlated to Nano in most regions, with the strongest relationships observed in the South Atlantic (1A) and South Indian Oceans (1B), especially in Spring (Figure 3c) and weaker but significant in summer for the Southernmost Indian and Pacific Oceans. Only off the Argentinian coast, where warm-liquid cloud occurrences are always lower than 5% (Figure 2b), and in the South Pacific (1D), where the Nano is the lowest of all regions (Figure 2h), this positive correlation between the warm-liquid cloud coverage and Nano is not observed. Anticorrelations are found instead. This may be due to the low statistics in one or the other variable, however this feature is quite constantly found from 1 month or year to the other.

Contrary to the general behavior of warm-liquid clouds occurrences, the ice-containing clouds (ice-only and MPC) occurrence is anticorrelated to biological variables and Nano in particular, for most regions (Figure 3c and Figure S6a in Supporting Information S1). The strongest anticorrelations between Nano and ice-containing clouds are found over the South Atlantic in September and over the South Indian ocean in April. South of 50°S, the negative correlations between ice-containing cloud occurrence and Nano are statistically reliable from late spring to early autumn. An opposite behavior is again observed in the South Pacific region where positive correlations are observed for several months. The relationship with USLCs (Figure S6c in Supporting Information S1) is following the same pattern as the one for ice-containing clouds, with Nano negatively influencing the occurrence for most regions except over the South Pacific Ocean.

The observed relationships may be driven by geographical contrasts of SST that impact both biological variables and cloud-type frequencies. Indeed, at the regional scale, areas of higher SSTs may favor the abundance of Chl-a and Nano. They also correspond to locations where the maintenance of the liquid clouds is promoted. Therefore, we next investigate if relationships between ocean biogeochemical properties and cloud occurrence exist independently of their potential mutual relationship to SST. Pseudo-constant SST ranges narrower than 2K width are selected for each region and month within which the cloud and ocean biology relationships are further investigated.

Several positive correlations between warm-liquid cloud occurrence and Nano observed across all SST ranges (Figures 3a–3c and 3e) are lost when selecting pseudo-constant SST periods (Figures 3b–3d and 3f), indicating that they may have resulted from similar dependencies to the SST. However, we observe that the positive relationships between Nano and warm-liquid cloud occurrences are preserved at near-constant SST in Spring in the South/southernmost Atlantic and Indian regions (1A, 2A, 1B) and during all investigated seasons in the high latitudes of the Indian and Pacific Oceans (2B). This indicates that under these conditions the ocean biology may have an impact on the liquid phase, with more biological activity inducing higher warm-liquid cloud occurrence. In the South Pacific region (1D), the anticorrelation between warm-liquid clouds and Nano is still observed at near-constant SST in Spring.

Cloud type occurrences in relations to biology in the South Pacific may be very specific, as in almost all the other regions, negative correlations between ice-containing cloud occurrence and Nano are observed across all temperature ranges and preserved at pseudo-constant SSTs. This is especially true during springtime for the South and southernmost Atlantic regions (1A, 2A) and across all seasons for the southernmost Indian and Pacific Oceans (2B). Similarly to ice-containing clouds, the occurrence of USLCs is inversely related to Nano also at pseudo-constant SST but mostly during summer in regions where it exceeds 15% (regions 2A and 2B).



From these results, we conclude that, in many given regions and mainly during spring when ocean microorganisms are blooming after the winter season, warm-liquid clouds and ice-containing clouds are related to ocean biogeochemical variables, with a regional specificity for the South Pacific Ocean. We also observe less intense Nano-to-cloud relationships in other seasons, with more significant trends found during late winter than in summer. During the cold season, clouds are more often coupled to the ocean surface thereby promoting stronger relationships.

#### 4. Discussion and Outlooks

One hypothesis for the increase of warm-liquid cloud occurrence with Nano abundance during spring in several regions is the role of nanophytoplankton increasing the number emission flux of sea spray that can serve as CCN (Sellegrì et al., 2021). We note that, according to (Sellegrì et al., 2021), Chl-a is not the best tracer for CCN, but nanophytoplankton abundance is. Higher numbers of nanophytoplankton-driven CCN would increase the number of droplets, decrease their size and therefore increase the cloud lifetime and occurrence. This hypothesis is in line with studies highlighting larger number concentrations of smaller droplets in liquid clouds above biologically rich areas, especially in the South Atlantic compared to other regions (Huang et al., 2016). The formation of a larger number of cloud droplets will limit the formation of ice also at sub-zero temperatures, as reported in (Borys et al., 2003), and explain the spatial inverse correlation between Nano and ice-containing clouds. An additional effect could be the role of some (a few compared to CCN precursors) microorganisms that can serve as efficient ice nuclei particles (Trueblood et al., 2021; Wilson et al., 2015). The decrease in ice-containing cloud occurrence with higher biology in most regions during spring, and during all investigated seasons for the South Indian and Pacific Oceans in the 50°S–60°S latitude range could be enhanced by the presence of these marine microorganisms. They could be efficient ice-nucleating particles, later triggering precipitation and further reducing the lifetime of ice clouds and their resulting frequency of occurrence. In line with this hypothesis, we find mostly positive correlations between Nano and precipitation at pseudo-constant SST (Figure S6f in Supporting Information S1) especially for the South Indian and Pacific Oceans in the 50°S–60°S latitude range.

Our results also show that Nano seems to be inversely linked to the persistence of USLCs at moderately cold temperatures in the southernmost Indian and Pacific Ocean. It has been suggested that more supercooled clouds exist in the Southern Ocean due to the very low INP concentrations in this region (McCluskey et al., 2018; Tan et al., 2016). Our result would confirm this hypothesis during the summer time in the Southernmost Indian and Pacific Ocean where microorganisms could serve as INP at warm, sub-zero temperatures and lower the frequency of occurrence of USLCs.

At this stage, it is unclear why the relationships found between Nano and the different cloud type occurrences in the 40°S–50°S latitude range South Pacific are consistently opposite to those found for the other regions. In this region, it may be that the total cloud occurrence, dominated by liquid clouds and MPC, has a negative impact on the biological activity, by lowering the availability of PAR (Photosynthetically Active Radiation) on which photosynthetic microorganisms depend. However, a positive relationship between Nano and ice-containing clouds is also observed during Spring at pseudo-constant SST (Figure 3f and Figure S6b in Supporting Information S1). We may speculate that in the warmer and more oligotrophic South Pacific, dominated by cyanobacteria of the pico-size, nanophytoplankton encompasses phytoplankton taxa that are different from those of the other regions. Further research is needed at the process scale in this region to test this hypothesis.

In this study we address the potential influence of ocean biogeochemistry on cloud occurrence by isolating an overall negative relationship between ocean biological tracers and LL ice-containing cloud occurrences on one hand, and a positive relationship between these tracers and warm-liquid clouds on the other hand, except in the 40°S–50°S Pacific Ocean. We show that these relationships are preserved at pseudo-constant SST mostly during the springtime, when clouds are most often coupled to the ocean surface. Our study includes, for statistical reasons, not only cases when clouds are dynamically coupled to the ocean, but all LL-clouds. Therefore we suspect that a study performed on a longer time period only on cases of boundary layer clouds would highlight stronger (and maybe additional) relationships. Our observations show complex interactions that are difficult to interpret because of the interplays and unbalanced, contradictory effects of marine microorganisms on cloud properties and lifetimes. To confirm these observations using modeling tools, and evaluate the impact of biological marine aerosols on cloud occurrence in a future climate, we stress the need to include process-based relationships between ocean biology and CCN on one hand, and freezing properties of marine biological

aerosols on the other hand in future modeling exercises. Our study highlights the specificities of ocean-clouds interactions for each oceanic region, and calls for more process studies in contrasted regions, as these processes would be solely representative of the oceanic region where they have been performed.

### Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

### Data Availability Statement

- “DARDAR-MASK.v2.23” products used for cloud phase retrieval in the study are available with free registered access (<https://www.icare.univ-lille.fr/dardar/overview-dardar-mask/>).
- “Global Ocean 3D Chlorophyll-a concentration, Particulate Backscattering coefficient and POC” products used for Chl-a and POC concentration retrieval in this study are available with free registered access (European Union-Copernicus Marine Service, 2020).
- Data for Nanophytoplankton abundance over the studied area was generated by Julia UITZ using her own peer-reviewed tool (Uitz et al., 2006). The data products are available with free registered access at <https://sea2cloud.data-terra.org/en/catalogue/>, by looking for the “Sea2Cloud–Satellite-based products–Nanophytoplankton abundance” folder. This data is not considered as new data but was only generated over the area of interest of this study.
- DARDAR-SOCP program (written in Python 2.7) is available with free registered access at <https://sea2cloud.data-terra.org/en/catalogue/>, by looking at the “DARDAR-SOCP” folder (Bazantay & Mioche, 2024).

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