



Marine Organic Aerosols Reflect Ecosystem Variability from Phytoplankton Functional Types to Micronekton

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Abstract

Marine organic aerosols remain a major source of uncertainty in aerosol cloud–climate interactions, in part because marine ecosystem structure and biological drivers are often represented in overly simplified terms, typically reduced to bulk chlorophyll-*a*. Here, a full year of high-resolution aerosol
15 mass spectrometry measurements at Mace Head (west coast of Ireland) is combined with HYSPLIT air-masses exposure metrics and gap-free phytoplankton functional type (PFT) fields to explore influences on primary marine organic aerosol (PMOA) and methane sulphonic acid (MSA). During the spring-summer diatom climax, PMOA correlates with dominant bloom taxa ($R=0.65-0.70$) and micronekton ($R=0.55$), with rapid 1-3 day responses and secondary maxima at ~25 days, consistent
20 with early labile release and later lysis/grazing. During that same phase, MSA also showed a lagged responses to both PFT and micronekton reflecting delayed DMS production and oxidation. However, comparable phytoplankton air-mass exposure in the late summer of that same year (i.e. early depletion phase) did not reproduce such high correlations, with time-scale analyses indicating weakened coupling at warmer sea-surface temperatures despite moderately stronger winds. These results imply
25 that structured ecosystem composition and physical forcing both contribute to cross-basin seasonal differences in marine organic aerosols formation. This motivates future research vessel campaigns and mesocosm experiments to explicitly manipulate PFT interactions and air-sea physics.

Keywords: submicron organic aerosols, sea spray organics, high-resolution aerosol mass spectrometry, positive matrix factorisation, phytoplankton functional types, micronekton.



30 1 Introduction

The Earth's energy imbalance has more than doubled in recent decades, driven primarily by anthropogenic greenhouse-gas emissions, with additional contributions from declining planetary albedo linked to sea-surface temperature changes and aerosol-cloud feedback (Mauritsen *et al.*, 2025). Anthropogenic effective radiative forcing (RF) since 1750 is estimated at 2.72 W m^{-2} [1.96 to 3.48 W m^{-2}] while aerosol-radiation interactions contribute -0.22 W m^{-2} [-0.47 to 0.04 W m^{-2}] and submicron aerosol-cloud indirect interactions -0.84 W m^{-2} [-1.45 to -0.25 W m^{-2}], reflecting substantial uncertainties from aerosol-cloud interactions that remain poorly constrained in Intergovernmental Panel on Climate Change (IPCC) reports (Forster *et al.*, 2023). Beyond these anthropogenic influences, growing evidences also suggest that natural marine sources play a larger role than previously thought in modulating global RF, emphasising the urgent need for improved observational and process-level understanding (Hodshire *et al.*, 2019; Sellegri *et al.*, 2024). Concurrently, climate change increasingly modifies ocean biogenic activity and air-sea transfer physics (Hong *et al.*, 2025; Law and Miller, 2025), thereby altering the global pool of marine aerosols including sea salt, oxidised secondary organic aerosol, methane sulphonic acid (MSA), and primary marine organic aerosol (PMOA) that seed low-level marine clouds.

PMOA is produced by breaking waves as bubbles containing biogenic sea spray burst at the ocean's surface (O'Dowd *et al.*, 2004; Ovadnevaite *et al.*, 2014; Villermaux *et al.*, 2022). As a result of measurements and modelling propagating uncertainties, global PMOA fluxes are not yet fully resolved with estimates ranging from 9 to 29 Tg-year^{-1} (Burrows *et al.*, 2022; Leon-Marcos *et al.*, 2024) while global PMOA contribution to indirect RF remains highly uncertain in both magnitude and spatial variability (Burrows *et al.*, 2022; Partanen *et al.*, 2014). In contrast, total sea spray aerosol emissions, dominated by (super-micron) sea salt, are much larger ($\approx 2,000$ - $10,000 \text{ Tg yr}^{-1}$). Despite their far smaller mass, marine organic aerosols are known to exert a disproportionate influence on cloud-forming properties of marine aerosols, driven by amphiphilic biopolymers that suppress droplet surface tension, and facilitate water uptake during activation across successive phytoplankton bloom stages (Kaluvarachchi *et al.*, 2022; Kawana *et al.*, 2022; Ovadnevaite *et al.*, 2011).

Conversely, MSA arises from phytoplankton-derived dimethylsulphoniopropionate (DMSP), cleaved by algal and bacterial enzymes to yield dimethyl sulphide (DMS) which, once ventilated, is oxidised via multi-oxidant pathways (such as OH, NO_3 or halogens) to form MSA and other sulphur species (Goss and Kroll, 2024; Wang *et al.*, 2024). DMS largely dominates the global biogenic sulphur budget and accounts for most of natural sulphur emissions over oceans (Jackson and Gabric, 2022). Globally, DMS burden estimates range from 7.5 Gg S yr^{-1} (Fung *et al.*, 2021) to 40 Gg S yr^{-1} (Cala *et al.*, 2023) and $\sim 20.3 \text{ Tg C yr}^{-1}$ (Hulswar *et al.*, 2022), with estimated radiative cooling effects ranging from -1.69 W m^{-2} to -2.3 W m^{-2} (Fiddes *et al.*, 2018). Conversely, MSA contributes only weakly to radiative forcing (Hodshire *et al.*, 2019) but provides a direct tracer of marine biogenic sulphur and DMS oxidation, with



implications for particle formation and growth to cloud condensation nuclei (CCN) relevant sizes (Rosati *et al.*, 2022; Wollesen de Jonge *et al.*, 2021).

Although links between phytoplankton communities and marine aerosols have been demonstrated across multiple studies (Freney *et al.*, 2020; Schwier *et al.*, 2017; Trueblood *et al.*, 2021), the coupling remains
70 uncertain as substantial variations in ocean physics (i.e. mesoscale eddies; Becker *et al.*, 2025) and geochemical variations in epipelagic organics (Lawler *et al.*, 2024; Lowenstein *et al.*, 2025; Seidel *et al.*, 2022) exist across seasons, years and oceanic regions.

At basin scale, these heterogeneities are commonly described using the “Longhurst” biogeochemical provinces, which partition the ocean into regions defined by temperature, turbulence, salinity, nutrient
75 supply, light availability and ecosystem structure (Longhurst, 2010). These ecosystem contrasts imply large variability in the composition of the oceanic organic pool (encompassing a global marine carbon pool of ~662 Pg, comparable to the present atmospheric CO₂ burden; Seidel *et al.*, 2022) transferred to the atmosphere via sea spray. Consequently, the impact of these ecosystem contrasts on aerosol production remains potentially significant yet poorly constrained because of complex formation
80 mechanisms and limited ecosystem-level understanding (Seidel *et al.*, 2022; Selden *et al.*, 2024; Sellegri *et al.*, 2021). For example, phytoplankton bloom decline is shaped by a suite of biological interactions (Lima-Mendez *et al.*, 2015) that remain completely absent from current PMOA source frameworks.

Consistent with this biological control on marine aerosols production framework, fresh phytoplankton blooms have been reported to account for over two-thirds of global PMOA mass fraction and up to
85 ~80% in the Arctic (Beaupré *et al.*, 2019; Gu *et al.*, 2023). While isotope analysis remains a benchmark for phytoplankton-aerosol coupling, this method provides limited temporal resolution and cannot resolve specific phytoplankton sources. Hence, to advance understanding of phytoplankton-aerosol coupling, there is a need to develop a more integrative framework based on online measurements (Crocker *et al.*, 2020).

90 Previous studies have revealed direct associations between atmospheric measurements and diatoms (Eickhoff *et al.*, 2023; Ickes *et al.*, 2020; Thornton *et al.*, 2023a), haptophytes (Alsante *et al.*, 2025), dinoflagellates (Wieber *et al.*, 2025), *Prochlorococcus* and other prokaryotes (Dall’Osto *et al.*, 2022; Wolf *et al.*, 2019), chlorophytes (Thornton *et al.*, 2023b) and cryptophytes (Trueblood *et al.*, 2021); yet, such studies remain scarce and some PFT (e.g. pelagophytes) or commensals still remain understudied
95 (Bar-On and Milo, 2019; Moallemi *et al.*, 2021). This work aims at responding to these challenges by using observations from the Mace Head Atmospheric Research Station, a long-term Northeast Atlantic site that frequently samples clean marine air masses influenced by regional phytoplankton activity. Here we thus combine a full year of high-resolution aerosol mass spectrometry measurements with organic aerosols source apportionment and air-mass exposure to eight phytoplankton functional types (PFTs)
100 and micronekton to define origins and properties of PMOA and MSA.



2. Materials and Methods

2.1 Site Description

The Mace Head Atmospheric Research Station is strategically located on the west coast of Ireland at 53°19'N, 9°54'W in Connemara, County Galway. Positioned approximately 100 meters from the Atlantic Ocean coastline at 5-21 meters above sea level, the station provides an exceptional vantage point for atmospheric monitoring (O'Dowd *et al.*, 2014) as the peninsula is exposed to open ocean air masses mostly devoid of anthropogenic influence. These air masses, originating from a nominal clean sector (between 190° and 300°; Grigas *et al.* 2017) are predominantly steered by westerlies (**Figure S1**) ushered by the polar jet's low-pressure systems interspersed with episodes of polar or tropical influences (Ovadnevaite *et al.*, 2014b). The station is largely representative of Northern Hemisphere background conditions and is also especially useful for improving our understanding of large scale phenomena such as phytoplankton blooms (O'Dowd *et al.*, 2015) and, more generally, sea spray dynamics over the North-East Atlantic as a whole (Ovadnevaite *et al.*, 2011b; Xu *et al.*, 2022).

2.2 *In-situ* measurements

Ambient aerosol chemical composition was quantified with an Aerodyne high-resolution time-of-flight aerosol mass spectrometer (HR-ToF-AMS) operating with a 650 °C tungsten vaporizer (DeCarlo *et al.*, 2006). Submicron ambient aerosol was drawn from the community sampling in isokinetic conditions to avoid particle losses (Brockmann, 2011). AMS data processing followed the standard Igor-based procedures (SQUIRREL v1.65B and PIKA v1.25B). Detection limit (~1 ng m⁻³ for multi-hours organic aerosols blank filters), ionisation efficiency, particle velocity, inlet flow, and composition dependent collection efficiency were determined following standard methods (Drewnick *et al.*, 2009; Middlebrook *et al.*, 2012). Standard relative ionisation efficiency values were applied (Xu *et al.*, 2018). Additionally, MSA was derived by upscaling the CH₃SO₂⁺ mesylate ion at *m/z* 78.98 as described in [Ovadnevaite *et al.* \(2014\)](#) such as:

$$MSA = CH_3SO_2 \cdot 29.12 \cdot 0.714 \quad [\mu g \ m^{-3}] \quad (1)$$

Where the numerical coefficients reflect respectively the applied HR-ToF-AMS calibration constants (including nitrate ionisation efficiency) and assumed relative ionisation efficiency for MSA.

Equivalent black carbon (eBC) mass concentrations were also measured with a multi-angle absorption photometer (MAAP, Thermo Fisher Scientific model 5012) operating at a flow rate of 10 L min⁻¹ and a 5 min time resolution with optical correction as described in (Xu *et al.*, 2020). During the first half of 2018, the MAAP was used to flag pollution events while in the second half of 2018, a dual spot aethalometer (Model 33, Magee Scientific) was used instead with optical correction as described in Fossum *et al.* (2024).



2.3 Source apportionment

135 The IGOR PRO Source Finder (SoFi v9.5.2) toolkit (Canonaco *et al.* 2013) was used to run the PMF
algorithm for the source apportionment. The HR-ToF-AMS error matrix (Corbin *et al.*, 2015) was
generated from the PIKA (Peak Integration by Key Analysis) v1.25B software package. Cell-wise
downweighing of the organic aerosol matrix was applied such that weak (signal-to-noise ratio, SNR < 2)
and poor signals (signal-to-noise ratio, SNR < 0.2, including zero and negative values) were assigned
140 proportionally larger uncertainties to limit their influence on the PMF solution. Primary marine organic
aerosol was constrained using reference mass spectra by Ovadnevaite *et al.* (2011a) with a-values
(Canonaco *et al.*, 2013) ranging from 0.1 to 0.9 with steps of 0.1 between 3 to 8 factors and refined a-
values of 0.1 to 0.5 with steps of 0.05 for the retained 6 factors final solution (These a-value controls
145 how much the model can deviate from the reference spectrum, with lower values enforcing tighter
constraints and higher values allowing more flexibility). To evaluate the stability of the PMF solution,
a bootstrap resampling approach with a total of 300 runs was applied (Crespi *et al.*, 2016; Efron, 1979).
This procedure quantifies statistical uncertainty in the PMF decomposition by evaluating the stability of
the resolved PMOA factor across resampled datasets, capturing variability in both its time series and
mass spectral profile, as well as the associated rotational ambiguity inherent to the solutions.

150 2.4 Phytoplankton Functional Types and Micronekton

PFT were taken from the AI-driven Global Daily gap-free Phytoplankton Functional Type dataset
(AIGD-PFT; Zhang *et al.*, 2024a). AIGD-PFT combines *in situ* HPLC (high performance liquid
chromatography) pigment measurements with OC-CCI v6.0 daily reflectance from SeaWiFS, MODIS,
MERIS and VIIRS, together with environmental predictors, within a deep-learning framework that
155 produces gap-free global daily surface fields at 4 km resolution spanning 1998 to 2023. In this work,
sea-surface concentrations (mg m^{-3}) of *Prochlorococcus*, other prokaryotes (i.e. excluding
Prochlorococcus), haptophytes, pelagophytes, diatoms, dinoflagellates, cryptophytes and chlorophytes
were used. All PFTs values used in this analysis were well above the approximate detection limit of the
underlying HPLC training data ($\sim 0.001 \text{ mg m}^{-3}$), and therefore uncertainty associated with low-
160 concentration oligotrophic waters was not considered a limitation here. For comparison, NOAA MSL12
multi-sensor DINEOF global 9 km gap-filled chlorophyll-*a* (chl-*a*) and suspended particulate matter
(SPM) were also retrieved from the COASTWATCH portal (Liu and Wang, 2022).

To complement this, epipelagic (i.e. down to $1.5 \times$ the local euphotic depth, typically $\sim 100\text{-}200 \text{ m}$)
micronekton biomass fields (expressed as gC. m^{-2} in seawater) were extracted from the Copernicus
165 Marine environment GLOBAL_MULTIYEAR_BGC_001_033 product (European Union-Copernicus
Marine Service, 2021). Epipelagic micronekton (e.g., fish, crustaceans and cephalopods) are active
swimmers ($\sim 1\text{-}20 \text{ cm}$) organised into depth-stratified functional groups with diel migration and explicit
behavioural dynamics. Micronekton data are available as $1/12^\circ$ ($\sim 8 \text{ km}$) daily hindcasts from 1998
onwards, generated with Spatial Ecosystem And POPulation DYnamic Model - Lower and Mid-Trophic



170 Levels (SEAPODYM-LMTL). More specifically, micronekton are simulated as low- and mid-trophic
biomass using advection-diffusion-reaction dynamics forced by ocean currents, temperature, and
satellite-derived net primary productivity, with a reported mean absolute difference of $\sim 0.44 \text{ g C m}^{-2}$
against observations (Albernhe *et al.*, 2024).

2.5 Air masses and Exposure

175 The Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPPLIT) model (Stein *et al.*, 2015)
was set up with monthly GDAS meteorological data and 72 h-long back trajectories were generated
every hour with arrival height set to 100 m above ground level. To investigate potential source
regions, the simplified Quantitative Transport Bias Analysis (SQTBA) method was used to robustly
represent Gaussian plumes transport bias along air masses (Zhou *et al.*, 2019). Building on SQTBA
180 spatial extent, meteorological and wave parameters were retrieved from the European Centre for
Medium-Range Weather Forecasts (C3S, 2018) to investigate source region conditions. Variables
included 10 m wind components (m s^{-1}), sea surface temperature (K), 2 m air temperature (K),
significant wave height (m), and peak wave period (s). Derived quantities included seawater kinematic
viscosity ($\text{m}^2 \text{s}^{-1}$) assuming a constant salinity of 35%, atmospheric stability (the air-sea temperature
185 difference), wave age and the Reynolds wave number following [Markuszewski *et al.*, \(2024\)](#) and
[Ovadnevaite *et al.*, \(2014\)](#).

The air masses exposure to surface ocean biology was adapted from the literature assuming that
submicron aerosols are well mixed within the boundary layer with diffusion and loss relating to
transport time. Exposure was set to zero for trajectories endpoint pressure falling below 850 hPa and
190 boundary layer height values below 50 m were adjusted to a minimum of 50 m (Yan *et al.*, 2024).
Values were calculated as the geometric average within a 20 km radius of each trajectory endpoint
(Liu *et al.*, 2022) since ocean biological surface activity is known to follow a log-normal distribution
(Campbell, 1995). To determine air masses origin, the retention times over land and marine boundary
layer were determined to exclude air masses with substantial terrestrial influence or weak coupling to
195 surface marine emissions (Yan *et al.*, 2024). Furthermore, to evaluate the influence of methodological
choices on the exposure estimates, sensitivity tests were performed for both the trajectory radii and
trajectory lifetime (**Figures S2-S3**). Given that fronts and eddies can move up to $50\text{-}80 \text{ km day}^{-1}$
(Gangrade and Mangolte, 2024), radii of 20-80 km were tested and yielded consistent exposure time
series, indicating limited sensitivity to buffer size. Similarly, varying the back-trajectory duration from
200 24 h to 72 h showed broad consistency in the exposure signal with inter Pearson's correlations always
exceeding 0.7.



2.6 Time series and Lags Analysis

205 Changepoints (i.e. blooms regime shifts) were identified in phytoplankton exposure time series using the *EnvCpt* R package, which compares constant, trend, and AR(1) models with and without changepoints within a unified likelihood framework using Bayesian information criterion ranking (Killick *et al.*, 2018).

210 Exposure time series contained small filtered gaps (<20% missing values) which were imputed using Kalman smoothing with *na_kalman* from the *imputeTS* package (Moritz and Bartz-Beielstein, 2017). Because conventional cross-correlation can produce spurious lag structure under non-stationary conditions (Cheng *et al.*, 2021), lag dependence was examined using cross-entropy (Giannerini and Goracci, 2023a). Cross-entropy quantifies lagged dependence by measuring the divergence between the joint distribution $f_{X_t, Y_{t+k}}(x, y)$ and marginal distribution $f_{X_t}(x)f_{Y_{t+k}}(y)$. The statistic estimates the Hellinger-type distance between these distributions, which equals zero under independence and
215 increases with nonlinear dependence, in practice the reference bandwidth and summation methods were used along with 500 bootstrap checks for p-values estimates (Giannerini and Goracci, 2023b).

220 Cross wavelet coherence was also computed using the Morlet mother wavelet in the R package *biwavelet* (Gouhier *et al.*, 2012), with significance tested against an AR1 red-noise background via 1,000 Monte Carlo surrogates; only regions within the cone of influence and exceeding the 95 % threshold were interpreted. Interpretation focused on coherent regions (black contours) with upwards arrows, reflecting phytoplankton-leading variability in marine aerosol. Arrows pointing right correspond to in-phase behaviour (concurrent increase) and left to anti-phase (i.e. phytoplankton lysis while marine aerosol increase). Coherence patches exhibiting rapidly rotating or opposing phase arrows within the same significant region were not interpreted, as illustrated in **Figure S4**, which
225 shows unstable phase relationships between PMOA and eBC. The same pairwise comparison also fails the cross-entropy test, exhibiting no statistically robust lag structure, confirming that the apparent association is spurious rather than directional.

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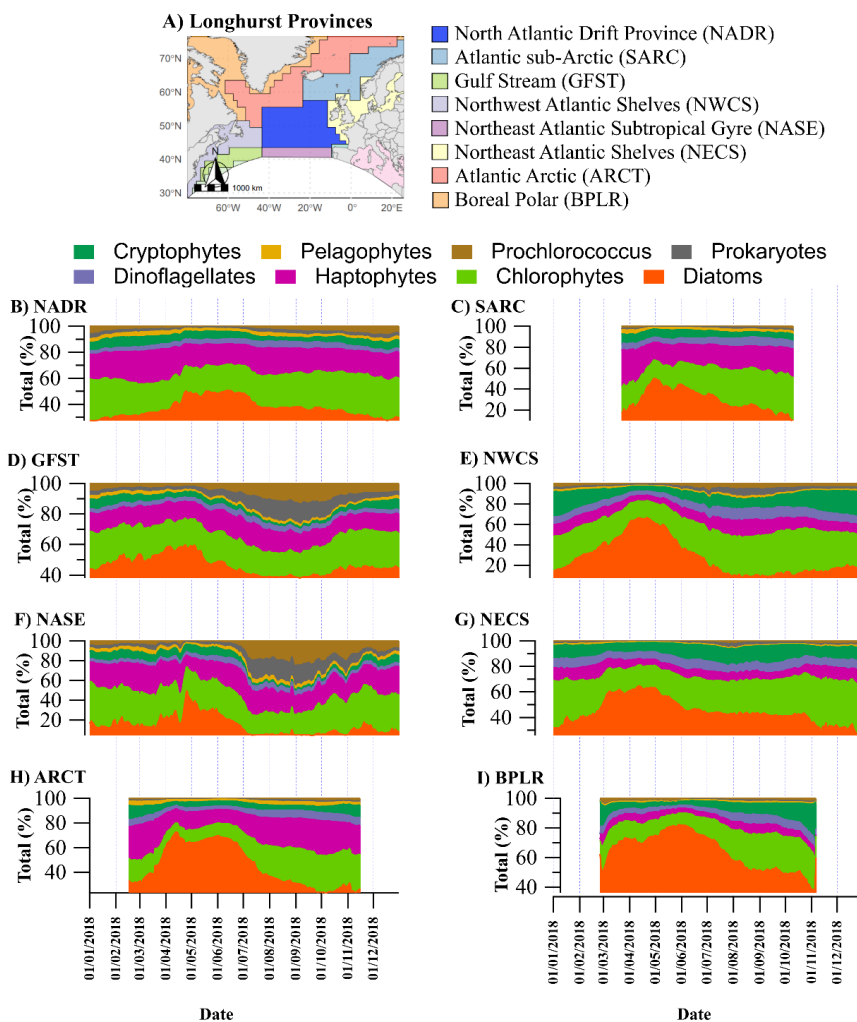
235 3. Results and Discussions

3.1 Temporal Dynamics and Biogeographic Patterns of Phytoplankton Functional Types

Daily biomass fields for major PFTs are first assessed against known established ecological seasonal and regional patterns to ensure model qualitative consistency with literature. **Figure S5** shows the North Atlantic weighted averages time series of seasonal dynamics of PFT biomass over a full year (2018) overlaid with changepoint analysis structural breaks. The weighted average is made from every grid cell retrieval from region bounded by 20°-66°N and 72°W-0° longitude (**Figure S6**), similar to [Mansour *et al.* \(2024\)](#).

Changepoint analysis shows a temporally ordered succession consistent with canonical bloom dynamics as diatoms enter the spring-summer climax phase on March 16th, followed by dinoflagellates on April 6th, haptophytes on April 17th, and chlorophytes on April 30th, consistently with typical PFT succession (Needham and Fuhrman, 2016). The diatoms climax phase persists until July 17th, after which their relative biomass declines steadily as diatoms are expected to progress into the stratified nutrients-limited depletion phase (Behrenfeld *et al.*, 2019). Further autumn to winter restructuring is also observed with *Prochlorococcus* and other prokaryotes increasing on September 22nd, and subsequent prokaryotic reorganisations on December 6th and 20th as the winter transition to deep mixing conditions sets in (Behrenfeld *et al.*, 2019). This increase is also consistent with the well-known rise in prokaryotes following seasonal entrainment of thermocline material and deep-ocean taxa into surface waters (Wenley *et al.*, 2021) whereas their strongly fluctuating standard deviation reflects patchy mesoscale filaments and eddy structures typical of prokaryotic mesoscale filaments (Gray *et al.*, 2024).

To further explore spatial variability in surface concentrations, AIGD-PFT data are split into bioregions following Longhurst biomes delineation (Longhurst, 2010) (**Figure 1**) with respective contributions (%) to PFT chl-*a* biomass shown in **Table S1**. Overall, throughout the year and all Longhurst provinces, diatoms biomass is prevailing (19.4%-65.5%), only closely followed by chlorophytes (15.7%-32.3%), haptophytes (4.7%-23.7%) and cryptophytes (5.2%-8.7%). Dinoflagellates remain relatively constant across basins (~5%), consistently with the ~5% relative abundance reported in previous field studies in the Western North Atlantic (Wang *et al.*, 2021) and in the subtropical North Atlantic (Duhamel *et al.*, 2019a). In contrast to this, *Prochlorococcus* (0.9-7.6%) and other prokaryotes (0.6-6.7%) display a clear south-north concentrations gradient, with higher contributions at lower latitudes (consistent with observations of increasing cyanobacterial dominance toward subtropical regions; Bolaños *et al.*, 2021) whereas pelagophytes remain minor (0.9-3.1%). In addition, haptophytes visibly decline in the boreal polar region (4.7%), where diatoms are known to outcompete them (Krisch *et al.*, 2020; Pierella Karlusich *et al.*, 2025). Overall, the relative ordering of total surface phytoplankton biomass across Longhurst provinces is consistent with *in-situ* Atlantic transect observations, with lowest biomass in oligotrophic gyres and enhanced biomass in subpolar and shelf regions (Brotas *et al.*, 2022).



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Figure 1. Weighted averages of Phytoplankton functional types by Longhurst regions. BPLR: Boreal Polar, NADR: North Atlantic Drift, GFST: Gulf Stream, ARCT: Atlantic Arctic, SARC: Atlantic Subarctic, NASW: Northwest Atlantic subtropical gyre, NASE: Northeast Atlantic subtropical gyre, NECS: Northeast Atlantic shelf, NWCS: Northwest Atlantic shelf.

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3.2 Primary marine organic aerosol constraining

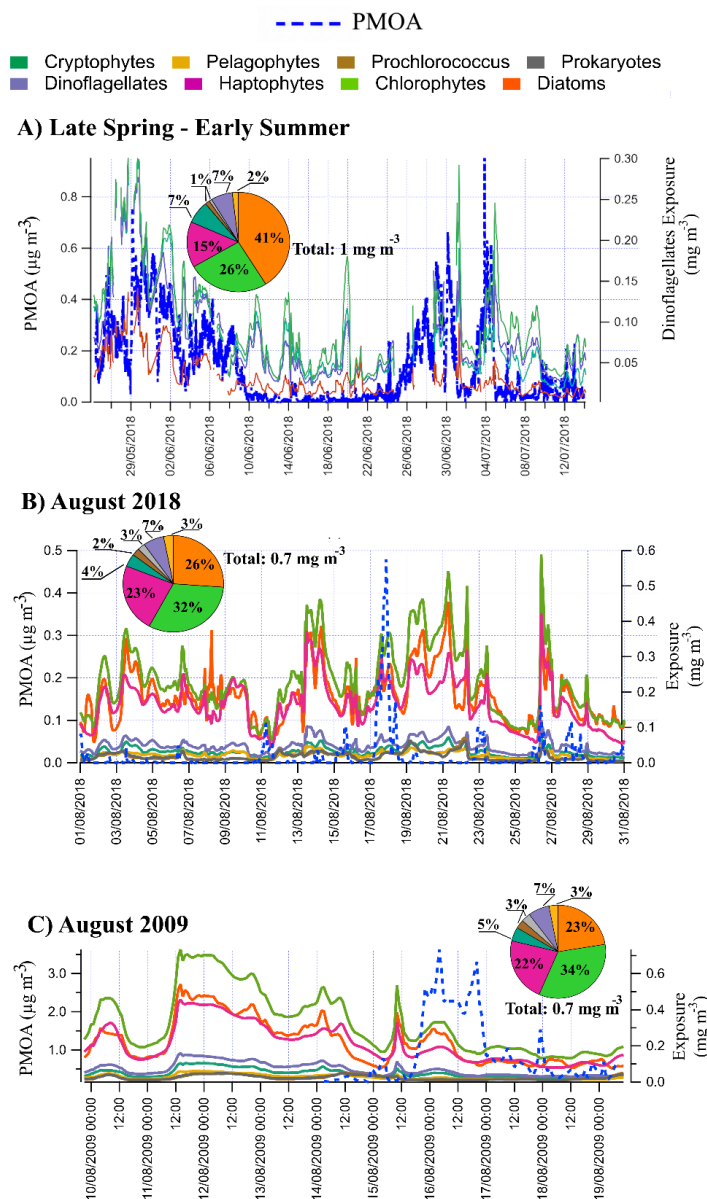
280 To robustly estimate PMOA time series, PMOA was constrained using its characteristic mass spectral fingerprint previously established at Mace Head (Ovadnevaite *et al.*, 2011a) and shown in **Figure S7**. PMOA mass spectra comprise oxygenated carbons (CHO-type fragments) that dominate the mass spectra intensity (55%), followed by aliphatic fragments (C_xH_y) contributing 39%. Representative ion series include C_xH_{2y-3} (i.e. m/z 39.02, 53.03, 67.05, 81) for alkynes, dienes and cycloalkenes, $C_xH_{2y-1}CO$ (i.e. m/z 55.02, 69.03, 83.05) related to alkenyl groups, diunsaturates, cyclic alcohols, and ethers as well as C_xH_{2y+1} (i.e. m/z 15.02, 29.03, 37.00) reflecting alkyls fragments. Further descriptions and implications of PMOA fingerprint are provided in earlier Mace Head studies (Chevassus *et al.*, 2025; Ovadnevaite *et al.*, 2011b). For low factor solutions (3-5 factors; **Figure S7**), the retrieved PMOA time series across all a -values show unrealistic behaviour, with large spikes and artificial co-variability with eBC ($R=0.35-0.62$, **Figure S8**). Also, the six-factor solution provides a physically consistent representation, minimising correlation with eBC ($R = 0.16$, **Figure S9**). Seven or eight-factor solutions were not retained, as they showed the same PMOA correlations with external tracers than six factors, and furthermore, recent work also indicates that Mace Head submicron aerosols are best represented by six factors (Moschos *et al.*, 2026). Bootstrap diagnostics further support the selection of the six-factor solution (**Figure S10**). The reconstructed PMOA time series is stable across resamples, with uncertainty remaining small relative to peak amplitudes (**Figure S10A**). The Q/Q_{exp} ratio decreases from 1.24 ± 0.02 (3 factors) to 1.03 ± 0.02 (4 factors), 0.88 ± 0.02 (5 factors), and 0.71 ± 0.02 for the six-factor solution (**Figure S10B**). The relative Q/Q_{exp} variability stabilises beyond five factors (**Figure S10C**), and the incremental improvement in Q/Q_{exp} becomes marginal after seven factors (**Figure S10D**). Residuals for the six-factor solution remain randomly distributed without systematic structure (**Figure S10E**) and finally, the bootstrap-derived uncertainty distribution is moderately skewed but well constrained (**Figure S10F**). The PMOA series from six-factor solution is presented in **Figure 2** as a dashed blue line. PMOA concentrations peaked in late spring-early summer, with a sharp maximum in early July, reflecting the PFT bloom climax, concentrations then declined through late summer (August) and remained low during autumn-winter with only minor fluctuations (**Figure S10**). Two contrasting cases were then retained: The Northeast Atlantic shelves (NECS) during phytoplankton bloom climax (May 25th to July 13th 2018) and the North Atlantic drift province (NADR) during late summer early depletion (Both August 2018 and August 2009, with the latter featuring PMOA concentrations one order of magnitude higher than August 2018)

310 3.3 Exposure to phytoplankton functional types, micronekton and aerosol seasonal source regions

Since AIGD-PFT can capture real world phytoplankton growth dynamics, with coherent ecological succession across space and time, the atmospheric consequences of these dynamics are examined next. During the spring-summer climax bloom, PMOA closely tracks recent biological activity (**Figure 2A**,



315 S9), with strong correlations for dinoflagellates ($R = 0.70$), cryptophytes ($R = 0.68$), diatoms ($R = 0.65$), and chlorophytes ($R = 0.62$). Conversely, haptophytes ($R = 0.30$), prokaryotes ($R = 0.32$), and pelagophytes ($R = 0.21$) exhibit weaker values, while *Prochlorococcus* shows no measurable relationship ($R = -0.02$).





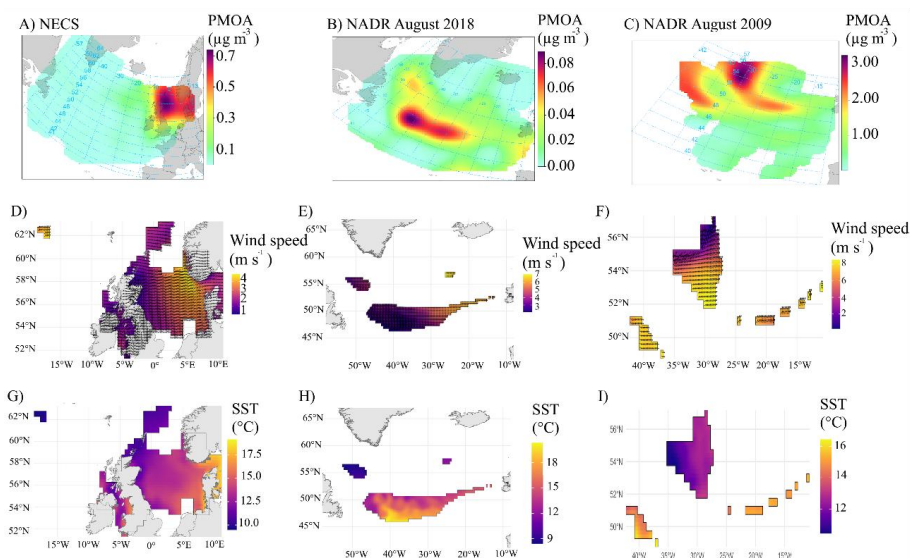
320 **Figure 2. Primary marine organic aerosol (PMOA) time series and associated phytoplankton**
functional type (PFT) air masses exposure for A) Climax phase - May 25th to July 13th 2018, B)
Depletion phase - August 2018, and C) August 2009. PMOA concentrations (left y-axis; dashed
blue lines) are shown together with the cumulative PFT exposure along the 72-h back
325 **trajectories (right y-axis). Insets report the relative PFT composition (percentage contribution**
and total exposure) for each period.

Furthermore, these PFT correlation values are partly in line with PMOA-related measurements literature correlation values (**Table S2**) although values are highly specific to sampling location and are generally lacking for the North Atlantic. For instance, the HR-ToF-AMS correlations with the main PFT obtained here ($R = 0.60-0.70$) are comparable to those reported for sea spray fluorescence (SSF) and chlorophytes in the Southern Ocean (Moallemi *et al.*, 2021), similar to those found for haptophytes in the Mediterranean (Sellegrì *et al.*, 2021) but lower than the strong correlations with diatoms observed in the Amundsen Sea (Jung *et al.*, 2020). Conversely, diatoms and dinoflagellates relationships fall within the same range as CCN-based correlations (Schwier *et al.*, 2017) reported for the Mediterranean ($R \approx 0.60$), except for *Prochlorococcus* (Schwier *et al.*, 2015) which shows
330 negligible association here while the link with cryptophytes is substantially stronger in this study than the weak or absent relationships found between PMOA and cryptophytes in the Mediterranean (Freney *et al.*, 2020; Trueblood *et al.*, 2021). In contrast to this spring-summer climax, the early depletion phase North Atlantic open-ocean (NADR) PMOA source in August 2018 (**Figure 2B**) or August 2009 (**Figure 2C**) are characterised by PFT spikes preceding PMOA variability which weakens the apparent contemporaneous correlations (**Figure S11**) and instead suggests a more lagged response, investigated
340 in section 3.4 below.

In addition, air-masses exposure to micronekton concentrations (**Figure S12**) span $3.3 \pm 2.1 \text{ gC m}^{-2}$ (August 2018), $5.6 \pm 2.3 \text{ gC m}^{-2}$ (spring-summer 2018), and $11.2 \pm 1.6 \text{ gC m}^{-2}$ (August 2009), with PMOA-micronekton correlations ($R \approx 0.55, -0.20, \text{ and } -0.11$, respectively) following the same
345 structure as PFT, with micronekton spikes also preceding PMOA (**Figure S13**). PMOA-micronekton variations align in a first-order sense with previous Arctic measurements reporting substantial enrichment of humic-like organic material in PMOA (40-280% relative to seawater) associated with delayed zooplankton grazing and excretion processes (Dall'Osto *et al.*, 2025). Micronekton concentrations were nearly 3 times higher in August 2009 (**Figure 2C**) than in August 2018 (**Figure S13**), coinciding with an almost one order of magnitude elevation in PMOA concentrations, although
350 this also reflected more efficient air-sea transfer conditions as detailed below.



To further investigate potential drivers, PMOA source regions are identified using simplified quantitative transport bias analysis. Two dominant source regions are resolved: The North Atlantic Drift (NADR) region and the Northeast European Continental Shelf (NECS) region (**Figure 3**).



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Figure 3. Simplified quantitative transport bias analysis (SQTBA) for primary marine organic aerosol during A) May 25th to July 13th 2018, B) August 2018, and C) August 2009. Panels D-F) show the corresponding 10-m wind speed fields from ERA5 for the same periods, and panels G-I) show the associated sea-surface temperatures (SST). Each map displays only the grid cells contributing to the top 10 % of the PMOA back-trajectory mass concentrations footprint for each event.

360

Wind speed explains the enhanced PMOA concentrations observed in August 2009. Winds during May-July 2018 (climax phase) were weak (median 1.66 m s^{-1} ; inter quartile: $0.57\text{-}3.77 \text{ m s}^{-1}$), increasing in August 2018 (median 3.45 m s^{-1} ; $2.48\text{-}6.00 \text{ m s}^{-1}$), but still not reaching substantially higher values that were observed in August 2009 (median 6.83 m s^{-1} ; $2.40\text{-}8.13 \text{ m s}^{-1}$). These stronger winds in August 2009 sustained wave breaking and bubble plume formation, promoting shallow bubble-layer renewal and deeper plume penetration, thereby increasing the probability that bubbles resurface and burst (Czerski *et al.*, 2022). At the same time, winds $>4\text{-}6 \text{ m s}^{-1}$ also disrupt bacterioneuston (Rahlff *et al.*, 2017), mixing surface organics and bacteria into the upper water column where they become more readily accessible to bubbles. This progression in wind forcing was accompanied by a coherent shift in wave-state parameters (**Figure S14**). Significant wave height increased from 1.14 m ($0.50\text{-}1.72 \text{ m}$) in spring-summer 2018, to 1.76 m ($1.60\text{-}2.06 \text{ m}$) in August 2018, and 2.50 m ($2.17\text{-}2.73 \text{ m}$) in August 2009, while the wave Reynolds number rose from 1.86×10^5 ($7.41 \times 10^4\text{-}2.96 \times 10^5$) to 3.24×10^5 ($2.76 \times 10^5\text{-}4.63 \times 10^5$) and 5.88×10^5 ($4.18 \times 10^5\text{-}7.47 \times 10^5$).

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375 The Reynolds number integrates wind stress, wave height, and water viscosity and therefore directly reflects more efficient bubble-mediated aerosol production (Ovadnevaite *et al.*, 2014a) as can be seen in August 2009 here.

Atmospheric stability also strengthened from 0.18 °C (-0.65-0.48 °C) in spring-summer 2018 to 0.21 °C (-0.28-0.85 °C) in August 2018 and 0.49 °C (0.05-1.18 °C) in August 2009, implying a shift
380 toward conditions where whitecaps could be sustained (Markuszewski *et al.*, 2024), while SST ranged from 10.9-15.7 °C (median 13.3 °C) in spring-summer 2018, 9.6-17.8 °C (14.9 °C) in August 2018, and 10.4-16.1 °C (12.6 °C) in August 2009. These values sit well above the <8 °C regime in which [Sellegrì *et al.*, \(2023\)](#) observed a strong, four-fold enhancement of sea spray flux. Yet, the 1.7-5.3 °C cooling in August 2009 relative to 2018 led to increased viscosity (**Figure S14**), which is known to
385 slow down microbial degradation rates (Guadayol *et al.*, 2021), leading to stabilised gel-like particles and colloids, all of which can increase the persistence of surface-active material available for bubble scavenging at the sea-air interface as cooler, thicker, bubble films are formed (Hu *et al.*, 2024). In addition, colder SST systematically increase the degree of lipid unsaturation in planktonic membranes as part of a homeoviscous adaptation that preserves membrane fluidity and enzymatic activity (Holm
390 *et al.*, 2022; Liu *et al.*, 2025a) which in principle increases the pool of surface-active organic precursors available for bubble scavenging. Similarly, cooler conditions are also known to favour viral production and viral lysis efficiency thereby further concurring to PMOA formation (Anesio and Bellas, 2011; Demory *et al.*, 2021). Taken together, the contrasting wind, waves, and temperatures help clarify why PMOA amplitudes differ across periods with similar phytoplankton exposure and hint
395 at PMOA plumes spiking after PFT increase with more or less delay, as such, temporally resolved approaches (Ali *et al.*, 2024) are next explored to disentangle genuine source-receptor dynamics.

3.4 Lag estimates and synergistic-unique-redundant decomposition

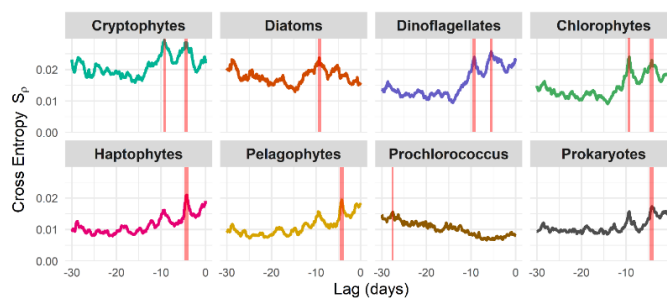
For primary marine organic aerosol (PMOA) during the spring-summer climax phase, PMOA-PFT cross entropy shows significant lags between PMOA and several PFT. Significant lags are observed
400 for cryptophytes from 2 to 25 days, dinoflagellates from 2 to 28 days, diatoms from 2 to 25 days, and chlorophytes from 3 to 25 days. Longer-lag contributions are detected for haptophytes at 25 days, *Prochlorococcus* at 15 and 28 days, and other prokaryotes at 25 days while pelagophytes show no significant lagged association with PMOA (**Figure 4**). Overall, cross-entropy scores from haptophytes, *Prochlorococcus* and other prokaryotes were half those of cryptophytes, diatoms, dinoflagellates and
405 chlorophytes that form a clear upper tier. This might be explained by *Prochlorococcus* and other prokaryotes being comparatively less intense lipid emitters (Becker *et al.*, 2025) whereas pelagophyte biomass is extremely small over the North Atlantic (2.7%). In addition, diatoms, dinoflagellates, cryptophytes and chlorophytes all have similar PMOA lag patterns, with a first early-bloom-stage (~2-3 days) followed by a lysis-stage after 25 days (also seen in haptophytes and prokaryotes), hinting at
410 both lysis and/or late stage prokaryote-diatoms interactions sustaining exopolymers production



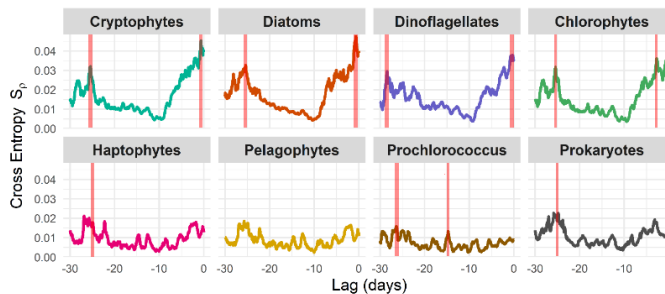
(Zamanillo *et al.*, 2019). Furthermore, micronekton ranks alongside the upper-tier PFTs with peaks at 2 days and additional contributions near 10 and 30 days, indicating that trophic-level processes contribute to PMOA at magnitudes comparable to direct phytoplankton emissions, plausibly through bubble-mediated enrichment of lipid-rich faecal pellets and excretion products.

- 415 For MSA, cross entropy during the same climax phase further shows a significant maximum information transfer between MSA and cryptophytes at lags of 4 and 9 days, dinoflagellates at 5 days and 9 days, diatoms at 9 days, chlorophytes at 4 and 9 days, haptophytes, pelagophytes, *Prochlorococcus* at 30 days and other prokaryotes at 4 days. These lags span over nascent blooms (~4 days) to intermediate lags (~9 days) hinting at delayed bloom senescence, and a long lag (~30 days)
- 420 phase specifically showing for *Prochlorococcus*. This long lag likely reflects *Prochlorococcus* having limited DMSP-cleaving enzyme activity, shifting late-stage DMS production to bacteria, viruses, or enzymes species decoupled from the initial bloom phase (Malfatti *et al.*, 2019).

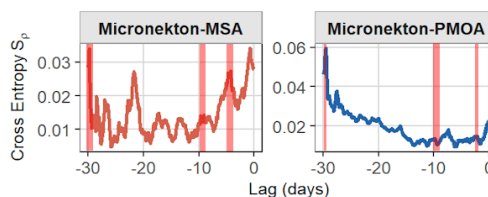
A) Lagged cross entropy MSA ~ Phytoplankton



B) Lagged cross entropy PMOA ~ Phytoplankton



C) Lagged cross entropy {MSA, PMOA} ~ micronekton





425 **Figure 4. Lagged cross-entropy during the spring-summer climax between A) PMOA and PFT, B) Lagged cross-entropy between MSA and PFT, C) Lagged cross-entropy between PMOA, MSA and micronekton. Significant lags obtained with bootstrapping are highlighted with a small red star (n = 1189, 1 h resolution).**

Micronekton cross-entropy with MSA also peaks at 4 days with secondary contributions near 10 and 30 days which is consistent with grazing-driven DMS release followed by atmospheric oxidation, 430 though it does not exclude behavioural aggregation of higher trophic levels along DMS gradients acting as chemosensory cues (Owen *et al.*, 2021) or substantial DMS release from planktivory micronekton or lower-trophic level grazing (e.g. copepods grazing on dinoflagellates; Dacey and Wakeham, 1986). Overall, the PFT-micronekton contributions ranking for MSA is markedly diffuse as MSA is the product of a multi-step pathway (DMSP → DMS → multi-oxidant atmospheric chemistry) 435 where atmospheric oxidation results in homogenised source-specific signatures.

More subtle and transient lagged coupling patterns were also investigated to explain the differences between the spring-summer climax phase and the august depletion phase from April to August 2018 using bivariate wavelet analysis. This metric quantifies the local correlation between two non-stationary signals as a function of time and period, with values approaching 1 denoting strong co-variability. In **Figure S15**, arrows pointing right correspond to in-phase behaviour, left to anti-phase 440 (i.e. phytoplankton lysis concurrent with increases in PMOA), upward to phytoplankton leading PMOA, and downward to PMOA leading phytoplankton. Coherence between PMOA and diatoms, dinoflagellates, haptophytes and cryptophytes is largely confined to spring and early summer, with no significant coupling for these species persisting into August. Conversely, chlorophytes, 445 *Prochlorococcus* and other prokaryotes displayed a distinct 9-11 day period coherence patch, significant against an AR(1) red-noise background (black contour), with anti-phase orientation (arrows pointing left) typical of phytoplankton lysis concomitant with lagged PMOA increase. This phase coherence points towards a (weaker) persistence of the phytoplankton-PMOA senescent coupling even during the depletion phase. In other words, PMOA sources shift away from diatoms, dinoflagellates, 450 haptophytes and cryptophytes during the spring-summer climax to only chlorophytes, *Prochlorococcus* and other prokaryotes during the late summer depletion stage.

Finally, raw chl-*a* time series exhibited weaker correlations with PMOA ($R = 0.43$ and 0.28) than PFTs but improved substantially after Hampel outliers filtering ($R = 0.59$ and 0.60) while still showing weakly significant paired cross-entropy at 2-4 days and missing out on longer lysis related lags 455 (**Figure S16**). This likely reflects the confounding influence of optical and biogeochemical artefacts, such as photoacclimation, lysis by-products (phaeophytin, chlorophyllide), and radiative interferences from post-bloom organic matter (Prochaska and Frouin, 2024; Simis *et al.*, 2007), which obscure true biomass signals. In oligotrophic regions, chl-*a* increases may even arise from light-driven physiological adjustments rather than nutrient-fueled growth (Liu *et al.*, 2025b). While lag-adjusted 460 chl-*a* generally correlates moderately well with sea spray organics (O'Dowd *et al.*, 2015), its



reliability as a productivity proxy is known to degrade over senescent blooms or oligotrophic waters (Collins *et al.*, 2016). PFTs and micronekton, however, manage to capture more plausible early bloom emissions and late-stage lysis lags. This advantage is rooted in AIGD-PFT's combination of input pigment data (for which degradation products are carefully treated; [Roesler *et al.*, 2017](#); [Swan *et al.*, 2016](#)) and multi-source environmental inputs which allow here for ecologically coherent marine organic aerosol lag resolution (Zhang *et al.*, 2024).

4. Conclusion

By combining a full year of high-resolution aerosol mass spectrometry at Mace Head with HYSPLIT-derived air-mass exposure to gap-free phytoplankton functional type (PFT) and micronekton fields, this study delivers four main contributions to the understanding of marine organic aerosols.

First, the PMOA-PFT connections shift throughout the year, from diatoms, dinoflagellates, haptophytes and cryptophytes during the spring-summer climax, to only chlorophytes, *Prochlorococcus* and other prokaryotes during the late summer depletion stage. During the spring-summer climax, diatoms, dinoflagellates, chlorophytes, and cryptophytes all covaried along with PMOA. This is expected since diatoms are the main PFT biomass contributors as well as one of the main producers of organic carbon (Hansell *et al.*, 2024; Lu *et al.*, 2025), cryptophytes have significant lipids content (Taipale *et al.*, 2020), chlorophytes are abundant in the North-East Atlantic and known to be strong aliphatic and alcohol emitters (Duhamel *et al.*, 2019b) whereas dinoflagellates are also known to be active emitters of various fatty acids (Bi *et al.*, 2019). Conversely, haptophytes are less significant despite their ability to also emit aliphatic and alcohol during viral lysis or open ocean oligotrophic starvation (Fulton *et al.*, 2014; Malitsky *et al.*, 2016; Rosenwasser *et al.*, 2014). Nevertheless, this taxonomic framing remains context-dependent, as plankton lipidomes broadly vary across regions and species assemblages (Liu *et al.*, 2025a)

Second, MSA showed a broader and less taxonomically concentrated PFT signature than PMOA. While several diatom taxa are known to exceed haptophytes in cellular DMSP (Bullock *et al.*, 2017; Shemi *et al.*, 2023) and despite their overwhelming biomass in polar and subarctic blooms where they tend to dominate system-level DMSP production and associated sulphur emissions (Dani and Loreto, 2017; Jang *et al.*, 2019), no such prevalence can be ascertained here. Conversely, haptophytes and pelagophytes distinctively contributed as early-stage DMS sources, whereas *Prochlorococcus* were rather associated with a delayed lysis-stage. Overall, these results are consistent with recent DMS literature reporting that diatoms, cryptophytes and chlorophytes once thought to lack DMSP lipase enzyme, may in fact all be new emerging players in the marine sulphur cycle (Shemi *et al.*, 2023; Wang *et al.*, 2024).

Third, this study provides observational evidence that higher trophic levels contribute directly to PMOA with cross-entropy placing micronekton contributions alongside the upper-tier PFTs. While the



contribution of micronekton (or that of zooplankton; [Dall'Osto *et al.*, 2025](#)) to epipelagic organic carbon is well established, with pellets and dead bodies accounting for a substantial fraction of their total carbon production (Thibault *et al.*, 2025), their contributions to marine organic aerosols are still globally underexplored.

500 Fourth, the phytoplankton-aerosol coupling was found to be modulated by both ecosystem succession and air-sea physics. The spring-summer 2018 shelf climax, under calm winds and moderate wave breaking, rapidly produced PMOA whereas August 2018, despite comparable phytoplankton exposure, gave a weak and more lagged PMOA response, as warmer SST and low wave Reynolds numbers limited bubble plume penetration and film drops. August 2009 instead produced a strong but lagged PMOA
505 response: cooler SST raised viscosity and stabilised gel-like surfactants, higher significant wave heights and a markedly larger wave Reynolds number sustained breaking waves and film drops so the same PFT pool was transferred to the atmosphere far more efficiently.

Several mechanisms may also account for the temporal and spatial variability observed in phytoplankton-aerosol coupling. First, changes in the concentration and composition of surface-active
510 compounds can alter bubble film thickness and lifetime, thereby modulating the organic enrichment of sea spray aerosol (Ovadnevaite *et al.*, 2017; Sellegri *et al.*, 2021). Second, seasonal shifts in microbial processing may influence the availability of organic precursors, with enhanced microbial recycling during summer compared to spring and spatial variability in viral lysis rates across oceanic regions (Eigemann *et al.*, 2024; Mojica *et al.*, 2016). Third, not all biological activity is represented (e.g. viruses,
515 archaea, fungi), nor is the significant functional diversity within taxa or synergistic effects. Fourth, switches to mixo-/heterotrophy over time within groups as well as differences in PFT cells sizes can in principle strongly change marine organic aerosols emission. Fifth, microbial communities can eventually transition to act as a net DMS sink rather than source (Le Gland *et al.*, 2024). Lastly, recent evidence suggests that temperature effects also propagate through delayed biological responses in
520 productivity with thermal history shaping phytoplankton performance (Anderson *et al.*, 2025) and community-level responses being modulated by a sequences of prior warm and cool phases (Wolf *et al.*, 2024).

In conclusion, these results motivate future research vessel campaigns and mesocosm experiments to explicitly manipulate PFT interactions and air-sea physics. Such experiments still remain scarce, often
525 focusing on single species (i.e. pseudo-axenic cultures) such as the coccolithophore *Emiliana huxleyi* (O'Dowd *et al.*, 2015) or diatoms like *Thalassiosira pseudonana* or *Nitzschia closterium* (Alpert *et al.*, 2015; Sellegri *et al.*, 2021). Accordingly, mesocosm studies have yet to completely capture the role of fully resolved PFT assemblages and neuston interactome (Martínez-Pérez *et al.*, 2024) in marine organic aerosols formation, and to explicitly resolve non-linear temperature-biology interactions and
530 realistic wave breaking conditions (Anderson *et al.*, 2025; Liu *et al.*, 2024; Sellegri *et al.*, 2024)



Author contributions. JO, CO'D, and DC designed the research. DC, JO, VM and KNF operated the instruments and verified the raw data processing. EC, VM and JO produced the postprocessed data and figures. JO, CO'D, DC, WX, LC, VM, DS, LL and VP reedited the manuscript. EC wrote the paper with support from all authors, who commented on the paper.

535 *Competing interests.* The authors declare that they have no conflict of interest.

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540 *Data availability.* The codes supporting the analyses presented in this study will be made openly available on <https://zenodo.org/records/20155093>. The observational time series from the Mace Head Atmospheric Research Station are available from the corresponding author upon request, with a later release planned on EBAS. Phytoplankton functional type fields are available from the AIGD-PFT dataset (<https://doi.org/10.5194/essd-16-4793-2024>) while global 9 km gap-filled chl-*a* and suspended particulate matter (SPM) were retrieved from

545 <ftp://ftp.star.nesdis.noaa.gov/pub/socd1/mecb/coastwatch/viirs/science/L3/global>. Micronekton and zooplankton can be accessed online from the Copernicus Marine Service GLOBAL_MULTIYEAR_BGC_001_033 dataset (<https://doi.org/10.48670/moi-00020>), while meteorological data are available from ERA5 services (<https://doi.org/10.24381/cds.adbb2d47>).

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