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How do fronts affect phytoplankton communities over oceanic regions ? Contrasting responses across trophic regimes, seasons and front diagnostics

Angelina Cassianides[1], Marina Levy[1], Clément Haëck[1], Ines Mangolte[2], Roy El Hourany[3], Michela Sammartino[4], and Bruno Buongiorno Nardelli[4]

[1]LOCEAN-IPSL, Sorbonne Université, CNRS, IRD, MNHN, Paris, France
[2]ENTROPIE, IRD, CNRS, UR, UNC,Ifremer, Noumea, New Caledonia
[3]LOG, Univ. Littoral Côte d'Opale, Univ. Lille, CNRS, IRD, Wimereux, France
[4]Consiglio Nazionale delle Ricerche, Istituto di Scienze Marine (CNR-ISMAR), 80133, Naples, Italy

Correspondence: Angelina Cassianides (angelina.cassianides@locean.ipsl.fr)

Abstract.

Oceanic fronts are key features structuring marine ecosystems, yet their influence on phytoplankton communities remains difficult to quantify at regional scale. In particular, how phytoplankton responses to fronts vary across environmental conditions is still poorly understood, and may depend on the way fronts are detected. Here, we investigate how fronts affect phytoplankton biomass and community composition across the Mediterranean Sea, a region characterized by strong seasonal variability and contrasted trophic regimes. Using 23 years (1998–2021) of satellite-derived chlorophyll-a and pigment-derived phytoplankton groups data, we quantify phytoplankton responses to fronts across seasons and biogeochemical provinces, from productive northwestern regions to ultra-oligotrophic eastern basins. Fronts are identified using either the measure of an heterogeneity index (HI) or of Finite-Size Lyapunov Exponents (FSLE), applied, in both cases, to different data sources (satellite data or high-resolution fields reconstructed from machine-learning). This approach allows us to assess the sensibility of observed ecological responses to the choice of front detection method. We show that fronts are consistently associated with enhanced phytoplankton biomass by 4% to 35% and reshaped community composition across the Mediterranean Sea, with the strongest effects observed in oligotrophic regimes and during stratified periods. In particular, fronts are associated with an enrichment in diatoms by up to 20% and a relative decrease in prokaryotes, suggesting enhanced nutrient supply. However, the magnitude and consistency of these responses vary depending on the diagnostic used, with weaker to no signals detected using FSLEs. These results demonstrate that phytoplankton responses to fronts are both environmentally controlled and method-dependent. They highlight the key role of fronts in structuring ecosystems in nutrient-limited regions, and support the idea that changes in oceanic fronts should be considered when investigating ecological reorganization under future climate change scenarios, particularly in climate change hotspots such as the Mediterranean Sea.

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1 Introduction

Phytoplankton are fundamental for the functioning of the oceans, by supporting marine ecosystems and regulating biogeochemical cycles. Biogeochemical cycles and the dynamics of marine food webs are directly influenced by the diversity and composition of phytoplankton community structures. Understanding what governs phytoplankton abundance and diversity is therefore essential. Oceanic fronts are well-known to be hotspots for primary production and marine ecosystems: they can supply nutrients that stimulate phytoplankton growth (Lévy et al., 2015; Mahadevan, 2016), reorganize phytoplankton communities (d'Ovidio et al., 2004; Lévy et al., 2018; Tzortzis et al., 2021), modulate light availability and restratification (Lévy et al., 2018; McKee et al., 2023), reshape ecosystems (Lévy et al., 2018), constitute habitats to higher trophic levels including fishes, marine mammals and sea birds (Bost et al., 2009; Siegelman et al., 2019; Baudena et al., 2021) and have implications for fishing strategies (Watson et al., 2018).

Oceanic fronts are fundamentally associated with lateral density gradients, which drive along-front geostrophic currents and across-front ageostrophic secondary circulation, including vertical motions that can strongly influence phytoplankton dynamics (e.g., Lévy et al., 2018). They are ubiquitous features observed everywhere in the ocean, with quite variable characteristics. Their spatial scale spans a large range, from a few hundred meters to hundreds of kilometers in length. Some fronts are permanent features, such as the Gulf Stream (Thomas et al., 2016), while others are more seasonal (Sudre et al., 2023a) or ephemeral, persisting for only days or weeks. Some fronts are associated with large density gradients (D'Asaro et al., 2011), others with weaker ones (Haëck et al., 2023). Most fronts display signatures in both sea surface temperature (SST) and density and are also detectable through their surface physical dynamics, an along front current (Sudre et al., 2023b). Such fronts are generally associated with intense vertical velocities. However, sometimes, thermohaline compensation occurs, and SST gradients are not associated with strong density gradients, in such cases, vertical motions are much weaker or even absent (e.g., Mauzole et al., 2020). Besides, density fronts can extend from just a few meters within the mixed layer (Fox-Kemper et al., 2008) to depths, reaching up to 1000 m (Siegelman et al., 2020; Sudre et al., 2023a) thereby having different influence on oceanic vertical transport and nutrient supply (Lévy et al., 2018).

Investigating fronts has been largely facilitated by the acquisition of SST satellite images, either using thresholding of SST gradients (e.g., Belkin and O'Reilly, 2009), histogram analysis (e.g., Cayula and Cornillon, 1992), deep learning (Li et al., 2022) or SST heterogeneity (Liu and Levine, 2016; Haëck et al., 2023). Fronts can also be detected using lagrangian diagnostics from altimetric currents, such as Finite-Size Lyapunov Exponents (FSLEs) which characterize strain fields and identify regions where fluid motion undergo strong stretching (d'Ovidio et al., 2004; Hernández-Carrasco et al., 2011; Sudre et al., 2023b). Importantly, these different approaches provide different diagnostics of the same underlying physical structures, with distinct sensitivities and limitations. Typically, the SST heterogeneity method has the advantage to be applied to kilometric resolution data (such as satellite SST) which are very precise but sometimes lacking due to cloud cover. Also, it captures SST and not density fronts, and therefore might overestimate the presence of dynamically active fronts. On the other hand, the FSLE method provides a more continuous description of fronts, but based on coarser resolution satellite sea-surface high data, which can lead to potential misalignment of the actual front position by a few tens of kilometers (e.g., Lehahn et al., 2007).

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Advances in observational and detectable methods has significantly improved our ability to quantify oceanic fronts influence on phytoplankton abundance and community structure over wide ocean regions (Liu and Levine, 2016; Haëck et al., 2023; Lévy et al., 2025). These studies were focused on the tropical Pacific and North Atlantic, and used SST heterogeneities to detect fronts. Other studies have also highlighted Chl-a convergence along FSLE filaments in the Western Mediterranean Sea (Hernández-Carrasco and Orfila, 2018; Hernández-Carrasco et al., 2020; Tzortzis et al., 2021).

Our main objective is to quantify the changes in phytoplankton biomass and composition in response to fine scale fronts in the Mediterranean Sea. We aim to determine how fronts affect phytoplankton communities across seasons and trophic regimes, and to assess the robustness of these responses using different front detection diagnostics. While often considered to be an oligotrophic basin, the Mediterranean Sea is in fact characterized by a mosaic of bioregions with extremely contrasted biogeochemical conditions, from the highly productive Gulf of Lion to the ultra-oligotrophic Ionian-Levantine basin (Figure 1, Siokou-Frangou et al. (2010)). This diversity of biogeochemical conditions offers a unique opportunity to evaluate the impact of fronts across a wide range of environments. In addition, the Mediterranean Sea exhibits strong seasonal variability, making it particularly suitable to investigate how phytoplankton–front interactions evolve across seasons and trophic regimes. Fronts are ubiquituous features in the Mediterranean Sea (e.g., Hernández-Carrasco et al., 2020; Barral et al., 2021; Sudre et al., 2023b; Akpınar, 2024), detected by thermal gradients or FSLE (Sudre et al., 2023b). Several case studies have shown local phytoplankton enrichments at frontal scale (Olita et al., 2014; Ruiz et al., 2019; Hernández-Carrasco et al., 2020; Tzortzis et al., 2021), shaping of the phytoplankon landscape by frontal boundaries (d'Ovidio et al., 2004), and fronts serving as habitat for specific communities (Hernández-Carrasco et al., 2020; Tzortzis et al., 2023; Oms et al., 2026). However, these studies were generally restricted to specific events lying on ship-based observation (Hernández-Carrasco et al., 2020; Tzortzis et al., 2021; Oms et al., 2026), multiplateforms observation (Ruiz et al., 2019), or gliders (Olita et al., 2014), too scarce to provide a quantification of frontal effects on phytoplankton at the regional scale.

2 Data and Methods

To detect fronts, we applied two methods : the Heterogeneity Index (HI) algorithm and FSLEs diagnostics. We first applied these methods to 23 years (1998-2021) of satellite data (SST for HI and SSH for FSLEs). Then we applied them to high-resolution density (for HI) and velocity fields (for FSLEs), reconstructed over 6 years (2016-2021, 4DMed-Sea project, Sammartino et al., 2025). We also used satellite data of Chl-a and pigment-derived phytoplankton groups, over 23 years, to quantify the impact of fronts on phytoplankton based on the Chl-a excess and the anomaly of phytoplankton groups over fronts. This quantification is conducted seasonally, to capture the pronounced seasonality in Chl-a (Siokou-Frangou et al., 2010) and in fine scale front dynamics (Hernández-Carrasco and Orfila, 2018; Akpınar, 2024) of the Mediterranean Sea. It is also conducted regionally to contextualize interactions under regionally coherent physical and biogeochemical conditions. Our methodological choices allow us to quantify phytoplankton responses to fronts across contrasting environmental conditions, and to assess how these responses depend on both environmental variability and the diagnostic used to detect fronts.

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2.1 Data

For SST, we used the European Space Agency Sea Surface Temperature Climate Change Initiative (ESA SST CCI) and Copernicus Climate Change Service (C3S) level 4 analysis product. The SST field is created with Operational SST and Sea Ice Analysis (OSTIA, Good et al., 2020) combining data from different infrared sensors ((A)ATSR, SLSTR, and AVHRR sensors, Merchant et al., 2019). The SST CCI covers the period from 1st September 1981 to 31st December 2016, and the C3S data from 1st January 2017 onwards. To coincide with the period of availability of Chl-a data, we use SST data between 1998 to 2021, daily, with a resolution of 1/20°. In order to generate a cloud-free product, a spatial interpolation is applied where SST are unavailable. While this approach ensures comprehensive coverage across the studied area, the interpolation leads to an underestimation of front detection due to the smoother SST field over regions covered by clouds. Nevertheless, using multiple sensors serves to minimise the extent of these areas.

Density fields are available for the entire Mediterranean basin, on a regular grid with a spatial resolution of 1/24°, and a time interval of 1 day from 1st January 2016 to 1st August 2022. These data take part of the 4DMed-Sea project, which aims to use Machine Learning algorithm to reconstruct vertically several parameters such as density, from the surface across 148 verticals levels from 3m to 150 m depth, with a step interval of 1m (4DMed-Sea project, Sammartino et al., 2025). In our case study, we focused solely on surface data obtained through a multivariate optimal interpolation algorithm, that combines satellite UHR SST data and sea surface salinity images from various satellites sources and in situ measurements (Sammartino et al., 2022). These density fields provide a more direct representation of frontal density gradients and allow us to identify dynamically relevant fronts.

We used the daily FSLE product distributed by AVISO, derived from the SSALTO/Duacs delayed-time global ocean absolute geostrophic currents a resolution of 1/4°. FSLE are computed backward-in-time, in order to measure the separation rate of initially contiguous particles, with the initial separation fixed as 0.02°and the final separation as 0.6°. They are available over the period 1998-2021, with a spatial resolution of 1/25°(d'Ovidio et al., 2004). We also used the FSLE data developed in the 4DMED-SEA project, derived from velocity fields with a finer grid in order to investigate whether the spatial resolution of products can influence our quantification (Cortés-Morales and Hernández-Carrasco, 2024). These FSLEs are derived from reconstructed geostrophic currents, using the 4DVARNET algorithm (Fablet et al., 2021), at a resolution of 1/24°. The initial distance δ_0 separating the particles is set at 1/24°, the final separation is set to $\delta_f = \delta_0 * \alpha$ with α = 30 (Hernández-Carrasco et al., 2011). The 4DMED-FSLE are daily from April 2016 to July 2022, with a horizontal resolution of 1/24°.

For Chl-a data, we used the L3 product provided by ACRI-ST over the period 1998–2021, based on the Copernicus-GlobColour processor. It is obtained by merging and reprocessing data from different sensors (SeaWIFS, MODIS Aqua & Terra, MERIS, VIIRS-SNPP & JPSS1, OLCI-S3A & S3B). Data are daily and available at 4 km resolution (Garnesson et al., 2019).

To retrieve phytoplanktonic taxonomic groups we used the algorithm developed by Hourany et al. (2019), which estimates nine secondary phytoplankton pigments from satellite remote sensing reflectances at different wavelengths, along with SST and Chl-a, using a neural network classifier. It provides the relative abundances of six distinct eukaryotic groups (diatoms,

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dinoflagellates, haptophytes, green algae, cryptophytes, and pelagophytes) and one prokaryotic group, available daily at a 4 km resolution from 1998 to 2021.We merged the five non-diatom eukaryotic groups (dinoflagellates, haptophytes, green algae, cryptophytes, and pelagophytes) into a single category, as their share common variabilities and distributions. We then focused our analysis on three primary categories: diatoms, other eukaryotes, and prokaryotes.

2.2 Method

2.2.1 Regionalisation

The Mediterranean Sea is characterized by complex biogeochemical conditions featuring both highly productive region, such as the intense spring bloom in the Gulf of Lion, and oligotrophic areas, particularly in the Ionian and Levantine basins. Besides, several studies have highlighted the complex submesoscale and mesoscale circulation within the basin. These include the propagation of numerous eddies (Millot, 1991; Hernández-Carrasco et al., 2011; Pegliasco et al., 2021), the formation of jets in specific sub-basins (Renault et al., 2012; Sala et al., 2022) and the development of filaments and frontal areas (Hernández-Carrasco et al., 2020; Barral et al., 2021; Sudre et al., 2023b).

To recontextualize the effect of fronts to phytoplankton considering the biogeochemical and physical complexity of the Mediterranean Sea, we divided the basin into four regions (Figure 1b) using a semi-automatic regionalization method. Initially, we used the regionalization of Hourany et al. (2021), based on a self-organizing classification, combining SST, mixed layer depth and Chl-a data to identify seven regions, each characterized by distinct physical and biogeochemical characteristics. Then, we simplified this clustering to delineate four large and homogeneous regions, identified as: the Alboran basin (light blue), the Gulf of Lion (green), the Algerian and Tyrrhenian basins (yellow) and the Ionian and Levantine basins (orange). In contrast to Hourany et al. (2021), we excluded the Adriatic and Aegean basins as well as the coastal regions where phytoplankton biomass is predominantly influenced by river runoff and continental shelf dynamics, thereby pixels where water depth is less than 100m are excluded.

The Alboran Sea (in light blue on Figure 1b) is one of the most productive regions within the Mediterranean Sea (Lazzari et al., 2011), sustained by an upwelling forced by the wind (Mercado et al., 2012) and the Atlantic Jet (Macías et al., 2008). The dynamical circulation consists of two coherent anticyclonic gyres and is characterized by strong density gradients resulting from the contrast between the saltier warmer waters of the Mediterranean Sea and the incoming fresher, cold inflows from the Atlantic Ocean. In the northwestern Mediterranean Sea (green region on Figure 1b), phytoplankton seasonality is similar to temperate regions characterized by a pronounced spring bloom, summer oligotrophy, and a secondary autumn bloom (Siokou-Frangou et al., 2010; Mayot et al., 2017). The spring bloom is primarily driven by winter deep convection, which is induced by atmospheric forcing (Lévy et al., 1998; Heimbürger et al., 2013; Severin et al., 2017). The Algerian-Tyrrhenian basins and the Ionian-Levantine basins are the largest regions with ultra-oligotrophic conditions persisting throughout the year (Uitz et al., 2012). Numerous eddies propagate in the Algerian-Tyrrhenian area, which coexist with quasi-permanent structures such as a wind-driven gyre in the North Tyrrhenian Sea and the Rhodes gyre. The Ionian-Levantine basin is characterized by elevated SST with a circulation pattern marked by the Ierapetra Gyre, located southeast of Crete. Figure 1c shows that other

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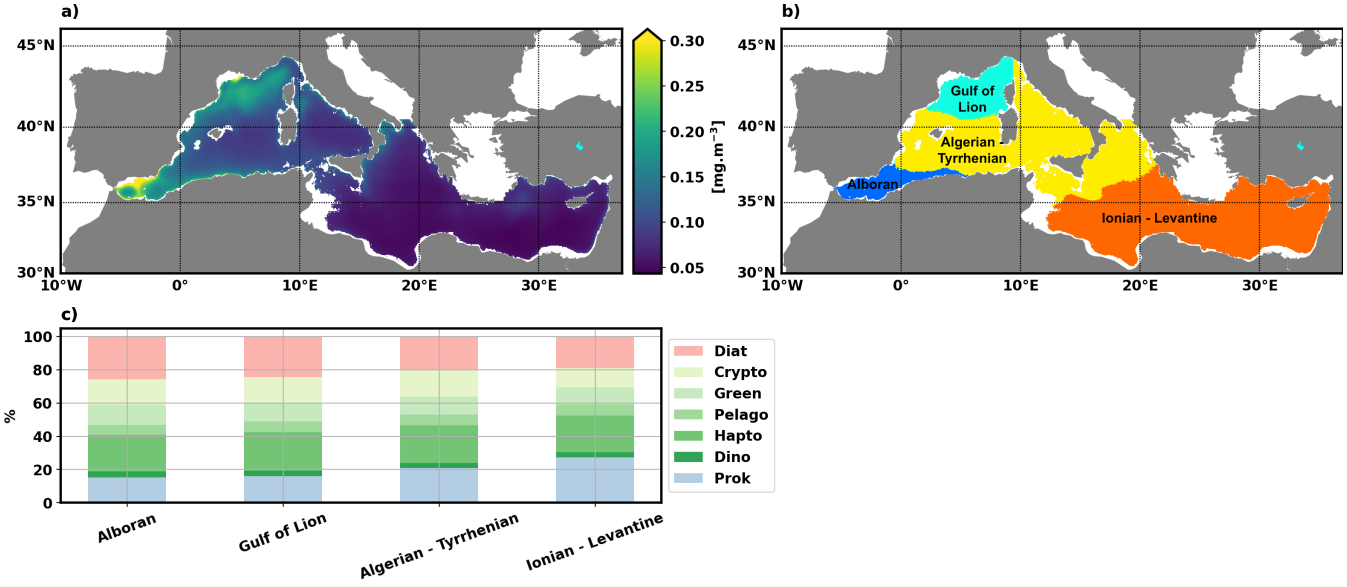

Figure 1. Overview of the study domain. (a) Time-mean of Chl-a from remote sensing over 1998-2021. (b) Regionalisation of the Mediterranean sea into four bio-regions. (c) Time-mean of phytoplankton assemblages from pigment-derived phytoplankton groups data.

eukaryotes are the dominant group basin-wide, reflecting the oligotrophic conditions, while studies highlighted the emergence of a phytoplanktonic groups mosaic at finer spatial and temporal scales (Siokou-Frangou et al., 2010).

2.2.2 Front detection

We detected fronts using two diagnostics (HI and FSLE) in order to compare how each method captures frontal structures associated with phytoplankton variability. To enable comparison between diagnostics, all fronts are projected onto a common grid and analyzed using a consistent statistical framework. Differences in data sources, spatial resolution and temporal coverage are taken into account when interpreting phytoplankton responses.

Fronts detected using HI

We used the method described by Haëck et al. (2023), inspired by Liu and Levine (2016). This method implies to compute the heterogeneity of SST (or density), and to assume that larger heterogeneities are associated with the presence of fronts. The heterogeneity can be described by three statistical metrics the bimodality, the standard deviation and the skewness. These three metrics are then combined into a single index named Heterogeneity Index (HI). This method identifies fronts as regions of enhanced horizontal gradients and spatial heterogeneity in SST (or density) fields.

The process started by sorting the domain into pixels. A moving window was then applied, of 7 × 7 pixels, centered on a pixel. This limited the computation of the three components and HI to a 28 km square window in order to quantify the heterogeneity for structures smaller than 28 km, and larger than 10 km. In the Mediterranean Sea, the Rossby deformation radius ranges from 10 to 15 km (Capó et al., 2019). Thus, this window size captured the signature of fine scale fronts and eddy

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edges. We conducted sensitivity tests by varying the window size (3 × 3 pixels and 5 × 5 pixels) to confirm that the 7 × 7 pixels window was the most optimized choice for our study.

HI is the weighted sum of the skewness γ, the standard deviation σ, and bimodality B of SST density, defined as : $\mathrm{HI} = a\,(b\gamma + c\sigma + dB)$, with a, b, c, d constant normalization coefficients. b, c, d are defined as the inverse of the standard deviation of each component, calculated over one year. The bimodality B is defined as the L2 norm of the difference between the SST histogram and a Gaussian fit of the histogram. Each component is normalized by its variance. Then, HI is normalized by the coefficient a, so that 95% of the values are below an arbitrary value of 9.5.

We finally defined pixels with small heterogeneity referred to as background circulation ($\mathrm{HI} < 10$) and pixels with large heterogeneity as fronts ($\mathrm{HI} > 10$).

Fronts detected using FSLE

FSLEs identify regions of strong horizontal stretching in the flow and are widely used to detect frontal structures and transport barriers. We defined pixels with small FSLE intensity as the background circulation $\mathrm{FSLE} < 0.17$ and pixels with large FSLE intensity as fronts $\mathrm{FSLE} > 0.17$. Our choice of the threshold is based on a comparison with previous studies (d'Ovidio et al., 2004; García-Olivares et al., 2007; Sudre et al., 2023b) and sensitivity tests we conducted, which guided us toward this optimal value. Because standard (AVISO-based) FSLE fields are derived from altimetric currents, their effective spatial resolution may limit their ability to accurately localize fine scale frontal structures. To assess whether the coarse resolution of AVISO currents to compute FSLEs influences our quantification, we compared our results using AVISO-FSLEs with FSLEs computed with higher resolution velocities (4DMED-FSLEs) .

2.2.3 Quantification of the impact of fronts on phytoplankton

Our main objective is to quantify the effect of fronts on phytoplankton biomass for each region and for each season. Thus, we want to compare the value of Chl-a over fronts to the regional value. For each day, we colocated Chl-a data with front positions (identified as pixels belonging to fronts). Then we computed the median of Chl-a over these frontal pixels. Note that our quantification depends on the data availability.

We also computed the local excess of Chl-a, E, express in percent, defined as the median value over fronts minus the median value of total Chl-a, divided by the median value of total Chl-a:

$$E = \frac{Chl_{front} - Chl_{tot}}{Chl_{tot}} \tag{1}$$

This metric quantifies the relative enrichment of Chl-a at frontal zones compared to the background.

Haëck et al. (2023) make a difference between weak fronts ($5 < \mathrm{HI} < 10$) and strong fronts ($\mathrm{HI} > 10$) since Chl-a increased with front intensity. In our study, we also started by distinguishing two groups of front according to their intensity. Nevertheless, when we analyzed the distribution of Chl-a over the different groups, Chl-a over weak fronts were close to Chl-a ouside fronts ($5 < \mathrm{HI}$). This aligned with the results of Tzortzis et al. (2021), which showed that moderate energetic fronts in the

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Mediterranean Sea are mostly dynamical barriers between phytoplankton communities. Thus, we focused exclusively on strong fronts for both HI and FSLE analysis.

To evaluate the statistical significance of Chl-a differences over and outside frontal regions, we computed the probability density functions of Chl-a over and outside fronts, from 1998 to 2021 and from 2016 to 2021. From these distributions, we randomly selected 300 samples from each pool and compared them with the Brunner-Munzel statistical test. This nonparametric test assessed the null hypothesis that, for random samples X and Y from two distributions, the probabililty of X being higher than Y is equal to the probability of X being lower than Y. We selected the Brunner-Munzel test due to its robustness in scenarios where distributions showed unequal variances, unlike the Mann–Whitney U test. This comparison was conducted regionally and seasonally across 23 years of data.

We also investigated the local impact of fronts on phytoplankton community structure. For each day, we calculated the mean proportion of each pigment-derived phytoplankton groups over and outside fronts. We then computed the anomaly for each phytoplankton groups to highlight their response to fronts. This analysis is performed for each region and over the 23-years and 6-years periods, allowing us to characterize the mean seasonal variability in phytoplankton groups proportions associated with frontal presence.

3 Results

3.1 Characterization of fine scale fronts distribution

We start by characterizing the distribution of fronts detected by SST, density and FSLE data, by computing the occurrence (Figure 2).

Our results reveal a similar distribution between fronts detected by SST and density but pronounced disparities with the distribution of fronts detected by FSLE, consistent with Sudre et al. (2023b). Fronts with SST outline persistent oceanographic structures, including the Alboran Gyre, the Liguro-Provençal Current within the Gulf of Lion, and the Rhodes and Ierapetra gyres in the Levantine region (Figure 2a). Fronts identified by density highlight the same structures but with higher occurrence values (Figure 2c). Fronts derived both from AVISO and 4DMED data exhibit a homogeneous distribution across the Alboran region, much of the Algerian-Tyrrhenian basin, and the Ionian-Levantine region, where fronts delineate the boundaries of numerous eddies passing by (Figure 2b). However, marked differences emerge between these two distributions. Occurrences from AVISO-FSLE are weaker throughout the bassin and even absent in the smaller regions like the Gulf of Lion. In contrast, fronts from 4DMED-FSLE are characterized by higher occurrences everywhere, even in the Gulf of Lion (Figure 2d). We suggest that because AVISO-FSLE are derived from SSALTO/DUACS geostrophic currents at a resolution of 1/4°, fronts associated to finer currents might be missed in the Gulf of Lion.

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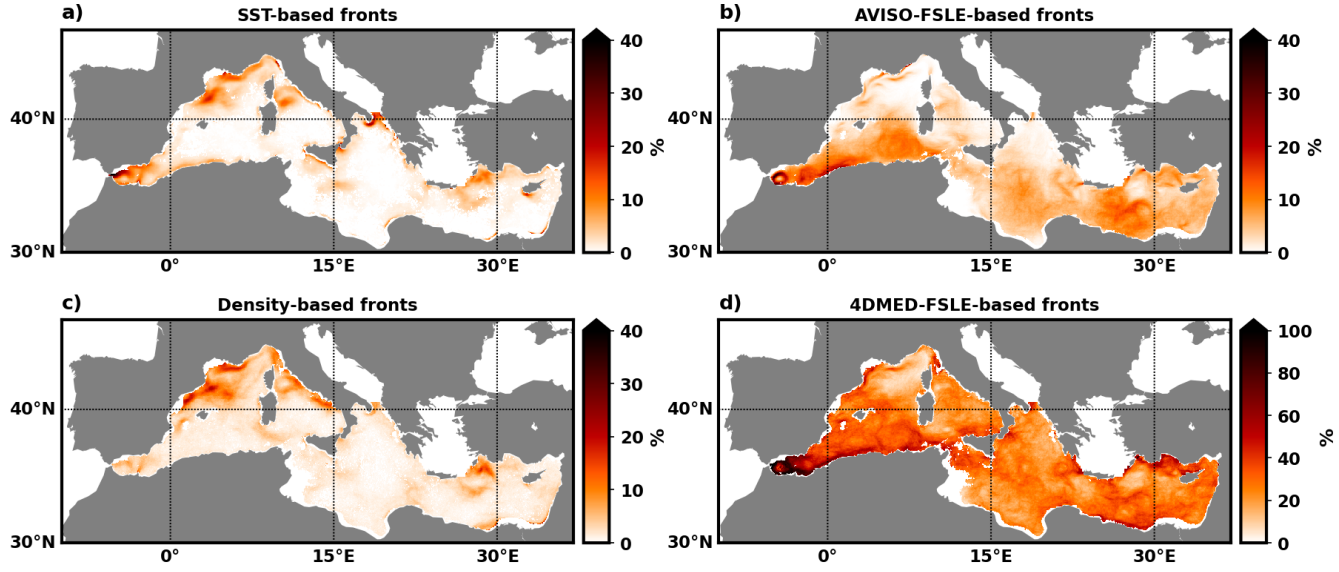

Figure 2. Occurrence of (a) fronts from SST fields and (b) fronts from AVISO-FSLE data over the period 1998-2021, and (c) fronts from density fields and (d) fronts from 4DMED-FSLE data over the period of 2016-2021. The occurrence is expressed as the percentage of time for which a pixel is occupied by a front. Note that the colorbar scale for panel (d) is adjusted to prevent saturation and improve map visibility.

3.2 Front effect on phytoplankton biomass

3.2.1 SST-based fronts

We found that fronts detected from SST diagnostics systematically enhance Chl-a, especially in summers low-productivity regimes or in oligotrophic conditions.

In the Alboran basin, a large enhancement in fronts is observable in spring, with a Chl-a average of 0.43 mg.m^{-3} (Figure 3a), representing an excess of 35.1% compared to the total Chl-a (Figures 3a, c and 5a). The Chl-a excess remains above 20% for the rest of the year, and falls sharply to 4% in winter. In the Gulf of Lion, fronts have a favorable effect in winter by sustaining a Chl-a excess of 17.8% (not significant in Figure 5), associated to a Chl-a mean of 0.36 mg.m^{-3}. In spring, this excess sharply decreases to 4.6% (Figure 3f and Figure 5a), coinciding with the large-scale spring bloom event (Figure 3d). Summer and autumn are characterized by larger Chl-a excess in fronts of 15% and 13.5%, respectively. In the Algerian-Tyrrhenian and Ionian-Levantine basins, fronts induces similar Chl-a seasonal variability and excess values (Figures 3o and r and Figure 5a). Their influence is larger in summer than in winter, despite lower Chl-a values during summer. For instance, in the Algerian-Tyrrhenian basin, Chl-a are approximately 0.28 mg.m^{-3} in winter and 0.12 mg.m^{-3} in summer. However, the Chl-a excess associated with fronts is less than 10% in winter but reaches 22.2% in summer.

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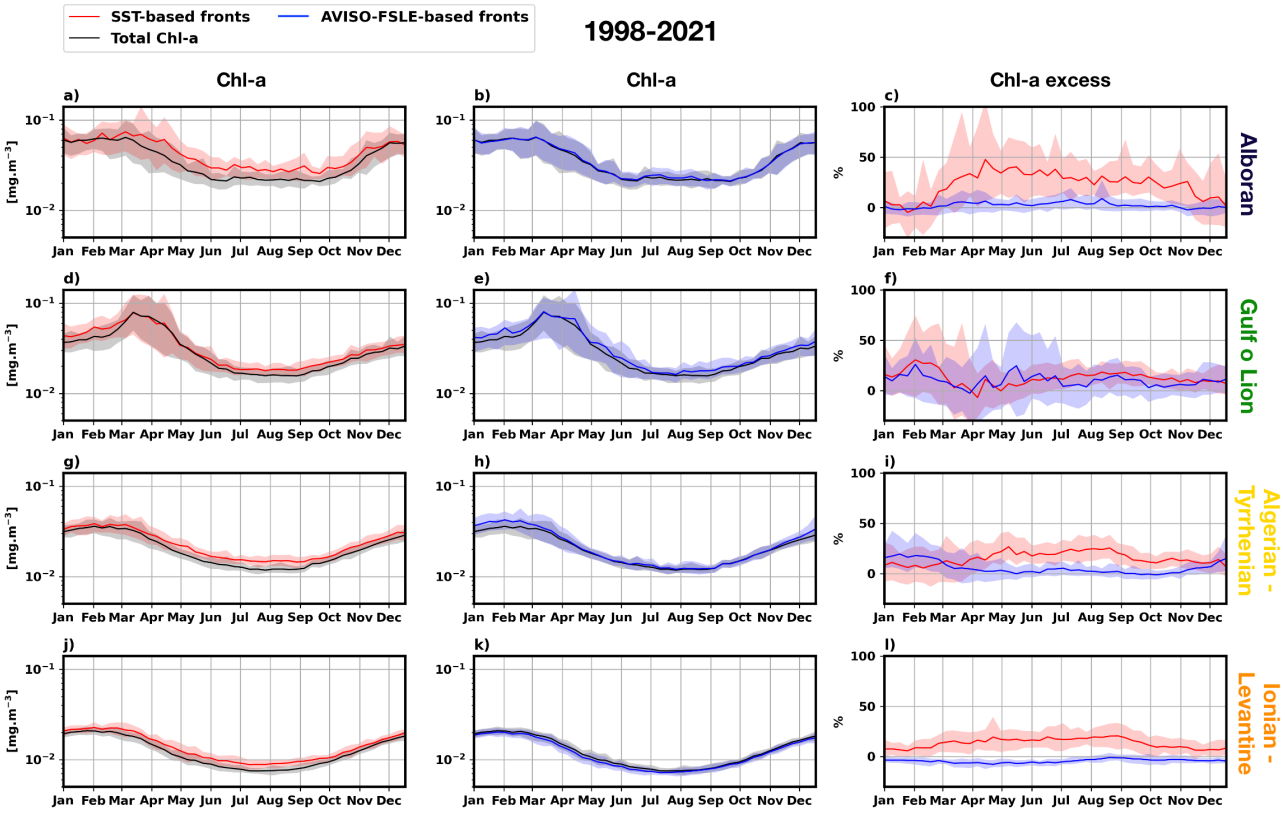

Figure 3. Seasonal variability of Chl-a median values and excess of Chl-a averaged over the period 1998–2021, for each region (per row) described on Figure 1. Total Chl-a are shown in black, values computed over fronts detected from SST fields in red and fronts from AVISO-FLSE data in blue. The plain lines represent the climatological mean of 8-day distributions, and the envelopes mark the 10% ans 90% percentile across the entire time series.

3.2.2 Density-based fronts

Our analysis of fronts detected from HI over density fields highlights the consistent enhancement of Chl-a at front-scale, still larger in low-productivity conditions, while the front effect is negligible in eutrophic conditions such as the spring bloom event in the Gulf of Lion (Figures 4d and 5c). The seasonal variability of fronts effect still aligns with the regional seasonal variability (Figure 4a, d, g and j). In the Alboran and Ionian-Levantine basins, the effect of fronts is more pronounced in summer, during low-productivity regimes, rather than in winter during the large-scale bloom event (Figures 4a, j and 5c). In contrast, in the Gulf of Lion and Algerian-Tyrrhenian basins, fronts have a stronger influence in winter-autumn than in summer (Figures 4d, g). The larger phytoplankton enhancement remains in the Alboran region in summer, reaching up to 35.6% of Chl-a excess (Figure 5c).

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3.2.3 FSLE-based fronts

Fronts detected using FSLE diagnostics do not show a consistent enhancement of phytoplankton biomass (Figures 3b, e, h, k and 4b, e, h, k). Most of the Chl-a excess results are non-significant or negative. We supposed that this likely reflects limitations in the effective resolution and front localization of FSLE diagnostics, rather than the absence of a biological response to frontal dynamics.

In the Alboran region, although fronts are prominent features (Figure 2b, d), there is no phytoplankton enrichment related (Figures 3b, c and 4b, c). Chl-a excess are non-significative with fronts from AVISO-FSLE data, and mostly negative with fronts from 4DMED-FSLE data (Figure 5b, d).

In the Gulf of Lion, fronts sustain a Chl-a enhancement in summer, with an excess from 5.7% to 10.3% (Figures 5b, d), while this effect disappeared for the rest of the year (Figures 3e, f and 4e, f).

In the Algerian-Tyrrhenian region, fronts from AVISO-FSLE have a positive effect in winter with a Chl-a excess reaching up to 15.1%, which declines sharply to 2.8% in summer. The Ionian-Levantine region is characterized by negative values of Chl-a excess (Figures 3k, l and 4k, l), ranging from -3% to -6% (Figures 5b, d). In both regions, Chl-a excess associated with 4DMED-FSLE fronts are not statistically significant.

3.3 Shift in phytoplankton community structure

Our previous results indicate that fronts detected from SST and density have a stronger effect on phytoplankton growth, with Chl-a excess reaching up to 35%, than FSLE-based fronts. To investigate further how this influence shapes phytoplankton composition, we quantify the impact of fronts on phytoplankton community structures using pigment-derived phytoplankton groups data. Here we present only the analyses for fronts detected from SST and density fields, as results for FSLE-based fronts were not significant. The seasonal average proportions of phytoplankton groups for each region are presented in Supplementary Figure A1, revealing a Mediterranean-wide dominance of the other eukaryotes group. Diatoms and prokaryotes seasonally alternate as the second-most abundant phytoplankton group. In Figures 6 and 7, we present front-scale anomalies of phytoplankton groups proportions, showing how fronts influence the contribution of a group within the phytoplankton community. This allows us to investigate whether fronts drive shifts in phytoplankton community composition.

A consistent pattern across the regions is the systematic increase in diatom proportions and the concomitant decrease in prokaryotes within fronts (Figures 6 and 7). For example, SST-derived fronts induce a large shift in summer in the Alboran region, with an increase of 3.57% of diatom proportion while the proportion of prokaryotes decreases of -2.88% (Figure 6). When assessing relative changes, meaning the proportional change within each group itself, we find that diatom proportions increase by 20%, while prokaryote proportions decrease by -13%. This highlights both how fronts reshape community structure and how they independently enhance or reduce the proportion of each phytoplankton group. Besides, the seasonal variability of diatoms anomaly mirrors the seasonal cycle of Chl-a excess, reinforcing that diatoms are a key contributor to the Chl-a enhancement over fronts (Figures 3c, f, i, l and 4c, f, i, l).

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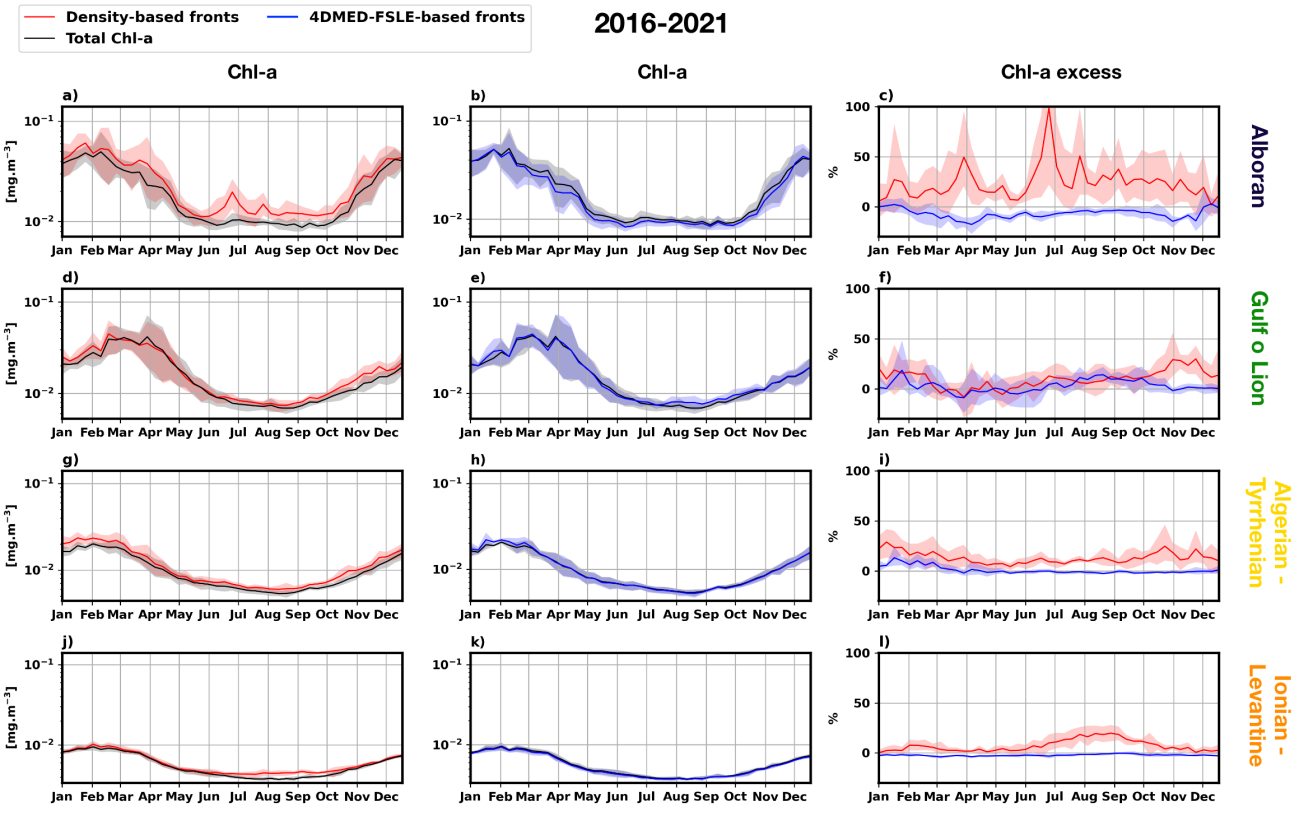

Figure 4. Seasonal variability of Chl-a median values and excess of Chl-a averaged over the period 2016–2021, for each region (per row) described on Figure 1. Total Chl-a are shown in black, values computed over fronts from density fields in red and fronts from 4DMED-FSLE in blue. The plain lines represent the climatological mean of 8-day distributions, and the envelopes mark the 10% ans 90% percentile across the entire time series.

285 The response of the other eukaryotes group is not consistent. Relative to the total community, their proportion decreases at front-scale throughout the year in the Alboran Sea. But this response differs in the rest of the Mediterranean Sea and some co-enrichment with diatoms can occur regarding the context. In Algerian-Tyrrhenian and Ionian-Levantine regions, for example, seasonal increases in Chl-a excess over SST-detected fronts (from spring to autumn) coincide with proportional increases in both diatoms and other eukaryotes. A similar co-enrichment pattern occurs in fronts detected from density during spring and
290 summer in the Algerian-Tyrrhenian basin.

4 Discussion

Our results provide both new insights into phytoplankton-front interactions in the Mediterranean Sea and a comparative assessment of how different detection methods capture these relationships. They highlight the pronounced effect of fronts on

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a) SST-based fronts

	Winter	Spring	Summer	Autumn
Alboran	3.9±23.3	33.8±32.2	29.9±21.4	21.9±20.9
Gulf of Lion	-	4.5±28.0	14.2±11.2	12.2±9.6
Alg-Tyr	9.0±13.0	16.6±14.1	21.8±9.7	13.0±7.4
Ion-Lev	8.2±7.8	15.8±9.6	18.3±8.9	-

b) AVISO-FSLE-based fronts

	Winter	Spring	Summer	Autumn
Alboran	-0.5±6.5	-	-	-
Gulf of Lion	-	-	10.3±20.8	-
Alg-Tyr	15.1±13.1	-	2.8±5.7	-
Ion-Lev	-3.8±3.1	-6.4±3.3	-3.9±3.3	-

c) Density-based fronts

	Winter	Spring	Summer	Autumn
Alboran	13.4±23.0	19.9±22.3	35.6±41.2	23.9±21.2
Gulf of Lion	13.9±15.7	-1.1±12.4	8.1±10.8	18.4±14.0
Alg-Tyr	18.6±12.2	9.1±7.8	10.2±4.9	15.0±11.7
Ion-Lev	3.8±4.8	-	13.1±8.7	8.5±7.0

d) 4DMED-FSLE-based fronts

	Winter	Spring	Summer	Autumn
Alboran	-1.7±-1.7	-	-6.2±-6.2	-8.1±-8.1
Gulf of Lion	-	-	5.7±5.7	-
Alg-Tyr	-	-0.2±-0.2	-	-
Ion-Lev	-	-3.0±-3.0	-	-

Figure 5. Table of average seasonal of Chl-a excess values with the standard deviation sustained by fronts from SST fields (a), fronts from AVISO-FSLE fields (b), fronts from density fields (c) and fronts from 4DMED-FSLE fields (d) for each region. Positive values are shown in green and negative values in pink. Excess values are shown when the differences between distributions within and outside the fronts are statistically significant.

both phytoplankton biomass and community structure, with the strongest effects observed during low-productivity regimes. However, the observed ecological responses vary to the choice of front detection method used.

Local enhancements of Chl-a at fronts detected from SST and density diagnostics are systematic, by 4% to 35%, with stronger effects in oligotrophic regions and during stratified periods. Our findings aligns with those of Liu and Levine (2016) which found a local increase of 38% in fronts detected from SST within the North Pacific subtropical gyre, and Haëck et al. (2023) which measured an increase of more than 60% at front scale in the vicinity of the the Gulf Stream. This result is consistent with the fact that strong density gradients are associated with ageostrophic secondary circulation and vertical nutrient fluxes, which are key mechanisms controlling phytoplankton growth at fronts.

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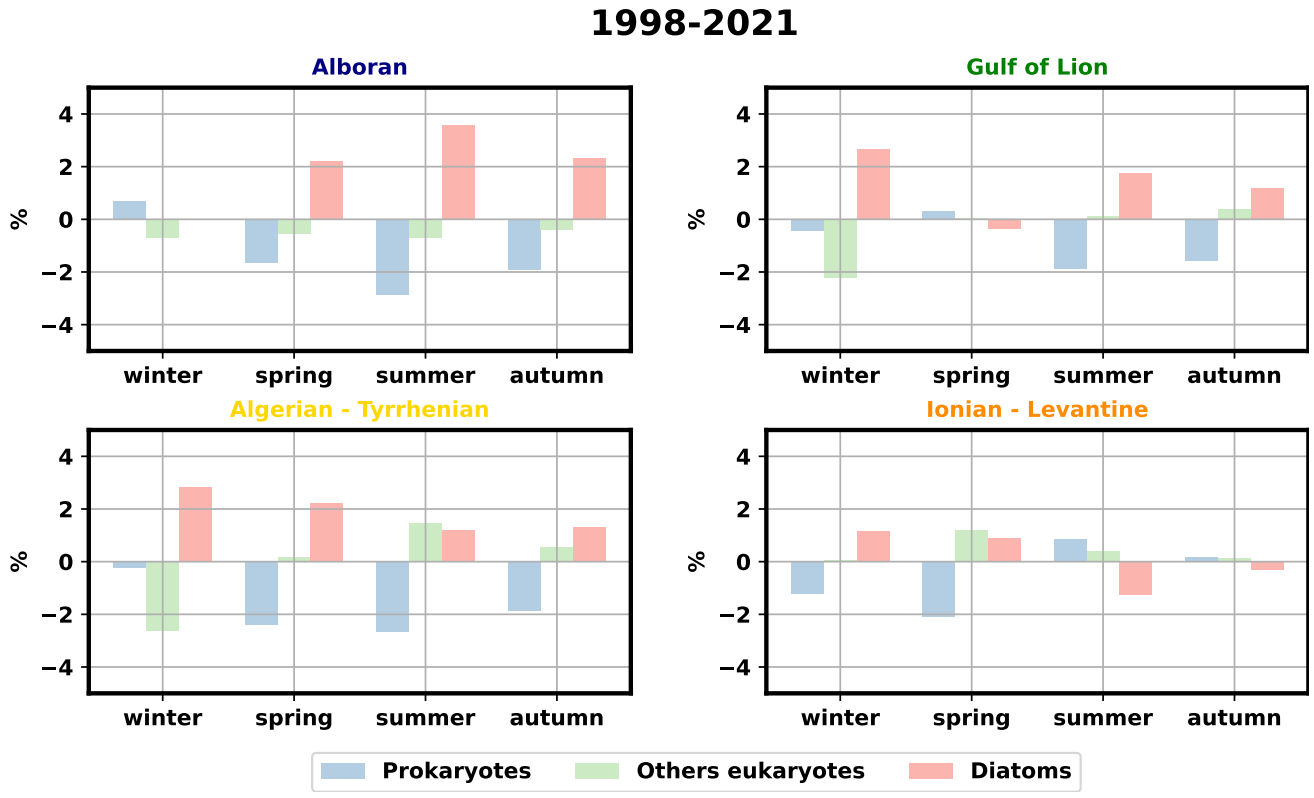

Figure 6. Anomaly of phytoplankton community composition over fronts detected from SST fields within each bioregions. The averages are computed over the full period 1998-2021. Diatoms are in red, other eukaryotes in green and prokaryotes in blue.

In contrast, fronts detected using FSLE diagnostics show a weaker relationship with changes in phytoplankton biomass. This result is likely due to a limitation of the FSLE diagnostic in resolving and localizing fronts accurately enough to co-localize them with the fine-scale biological signal seen in satellite ocean color data. Because FSLE fields are derived from altimetric currents, their effective spatial resolution may not be sufficient to capture the exact localization of fronts associated to finer currents that drive vertical exchanges. The differences observed between HI and FSLE diagnostics suggest that the detection method is key in evaluating the magnitude of the observed phytoplankton response. Our results raise questions about the suitability of FSLE data for studying the impact of density-driven vertical exchanges at fronts on phytoplankton at the scale of fronts. The results from the Gulf of Lion region are surprising: while we expected the phytoplankton-front interaction to be influenced by the improved representation of fronts from the 4DMED-FSLE data, this was not the case. Minor discrepancies between the two analyses can be attributed to differences in their respective study periods and the higher spatial resolution of the 4DMED-FSLE dataset.

Beyond methodological aspects, our results provide new insights into the spatial and seasonal variability of phytoplankton responses to fronts in the Mediterranean Sea. The stronger response observed in oligotrophic regions and during summer

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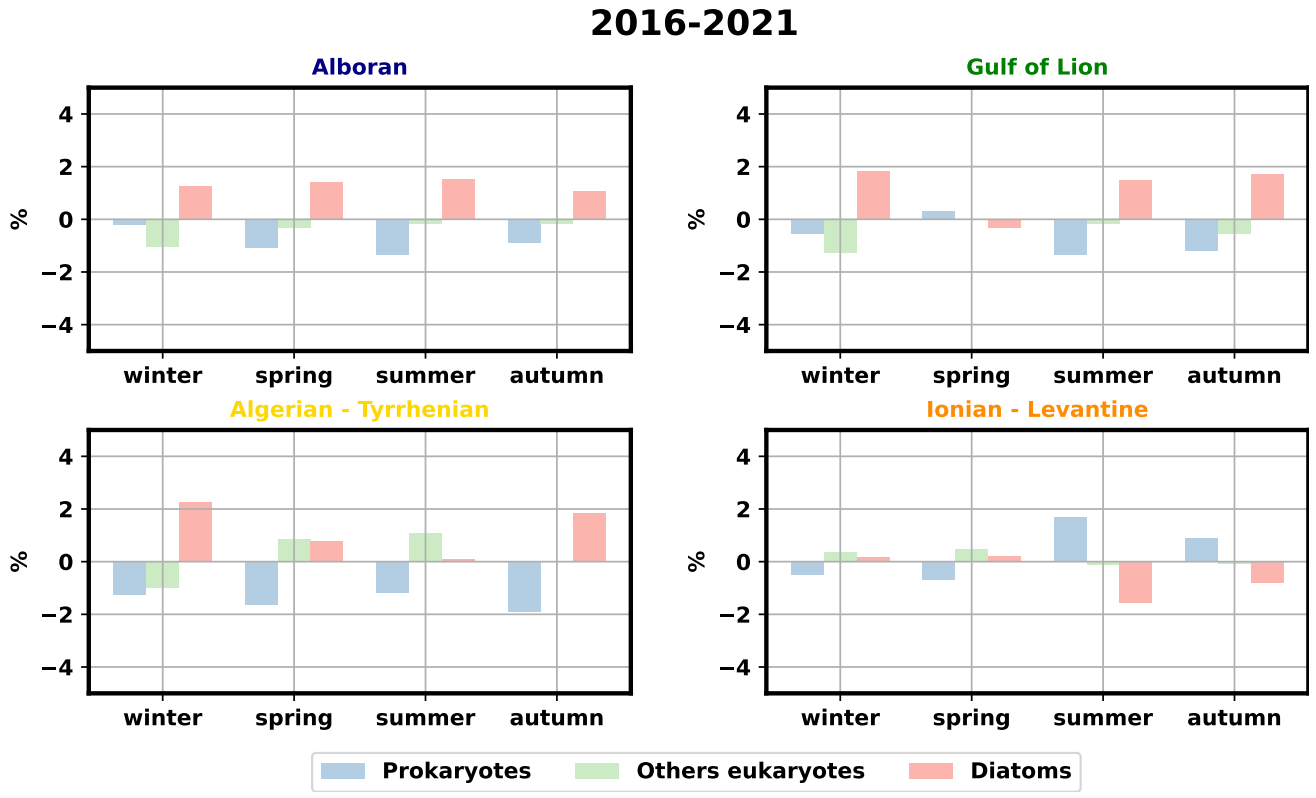

Figure 7. Excess of phytoplankton community composition over fronts detected from density fields within each bioregions. The averages are computed over the full period 2016-2021. Diatoms are in red, other eukaryotes in green and prokaryotes in blue.

suggests that fronts play a particularly important role in nutrient-limited environments. During summer, enhanced vertical stratification leads to the formation of a shallow mixed layer, promoting oligotrophic conditions and reduced surface Chl-a. In such oligotrophic environments where phytoplankton growth is nutrient-limited, frontal processes can sustain localized nutrient supply through vertical transport (Mahadevan, 2016; Lévy et al., 2018) or horizontal stirring (Fadida et al., 2026). This influence is weaker during winter and spring, when deepening of the mixed layer supplies nutrients that drive large-scale bloom. Although fronts may still enhance local nutrient fluxes to the surface, it does not influence phytoplankton growth due to the basin-wide contribution of mixed-layer deepening. We suggest that regional differences may also arise from regional variations in stratification structure, nutricline depth, or the efficiency of vertical velocities in reaching the nutricline.

The observed shifts in phytoplankton community composition, including diatom enrichment and prokaryotes depletion at fronts, further support the role of frontal processes in structuring marine ecosystems in this region. Our findings reveal a consistent increase of diatoms at frontal scales, up to 20%, whenever phytoplankton biomass is enhanced over fronts. These results are consistent with previous studies showing that frontal dynamics can enhance nutrient supply and favor larger phytoplank-

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ton, related to their adaptability to the rapidly changing conditions (Lévy et al., 2015; Liu and Levine, 2021; Mangolte et al., 2022, 2023; Lévy et al., 2025), while reducing the relative contribution of smaller oligotrophic-adapted organisms.

Our results also reveal a complex response within the other eukaryotes group, which occasionally benefits from frontal dynamics, especially in the two larger basins. Unlike the diatom-specific enrichment observed in the Alboran region, our results suggest that both diatoms and other eukaryotes groups benefit from frontal conditions (Figures 6 and 7). In certain cases, fronts are not associated with a single, uniform plankton community, rather some plankton types may be more or less favored, or even disadvantaged, depending on the specific environmental context (e.g., d'Ovidio et al., 2004; Tzortzis et al., 2021; Mangolte et al., 2022, 2023). While nutrient inputs at fronts primarily drive the dominance of fast-growing species, other processes can also play a large role in phytoplankton diversity such as abiotic processes (horizontal advection, Gangrade and Franks, 2023) and reactive processes (light competition, shared predation pressure, Lévy et al., 2018; Mangolte et al., 2022). In the western Mediterranean Sea, Oms et al. (2024) used an NPZ model to explain the coexistence of picophytoplankton and microphytoplankton groups near fine-scale fronts observed by Tzortzis et al. (2021). Their analysis show that pulsed nutrient inputs affect the system by combining bottom-up and top-down controls through zooplankton, leading to complex seascape of phytoplankton communities.

Several limitations should be considered when interpreting our results. Differences in spatial resolution, temporal coverage, and physical meaning between diagnostics may affect the comparison. In particular, FSLE diagnostics may fail at precisely locating fronts, while SST may fail to capture density-compensated fronts. Indeed, the comparison between SST and density fronts (occurrence, distribution and Chl-a excess) also highlights the role of thermohaline compensation, which can lead to strong temperature gradients without significant density gradients and therefore without enhanced vertical exchanges. It reinforces the idea that fronts detected from density fields provide a direct representation of the physical structure of fronts and show consistent biological responses, supporting the central role of density gradients in controlling phytoplankton dynamics. Finally, phytoplankton responses to frontal dynamics may not be instantaneous (Gangrade and Franks, 2023; Gangrade and Mangolte, 2024), and therefore the systematic co-localisation of fronts and of their biological response, as assumed here and in previous studies (e.g., Haëck et al., 2023; Lévy et al., 2025), may underestimate the impact of fronts when the biological signal is advected away from the front.

Overall, our results demonstrate that the quantification of the apparent ecological impact of fronts depends strongly on both the detection method and the nature of the underlying dataset. While the enhancement of phytoplankton biomass at fronts detected from SST and density appears robust, the weaker signal observed for FSLE highlights the importance of carefully selecting diagnostics when studying front–biogeochemistry interactions.

5 Conclusions

This study provides a comprehensive assessment of phytoplankton responses to oceanic fronts across the Mediterranean Sea, combining long-term satellite observations with high-resolution fields reconstructed using in-situ data. Our results show that fronts consistently enhance phytoplankton biomass and influence community composition, with stronger effects in oligotrophic

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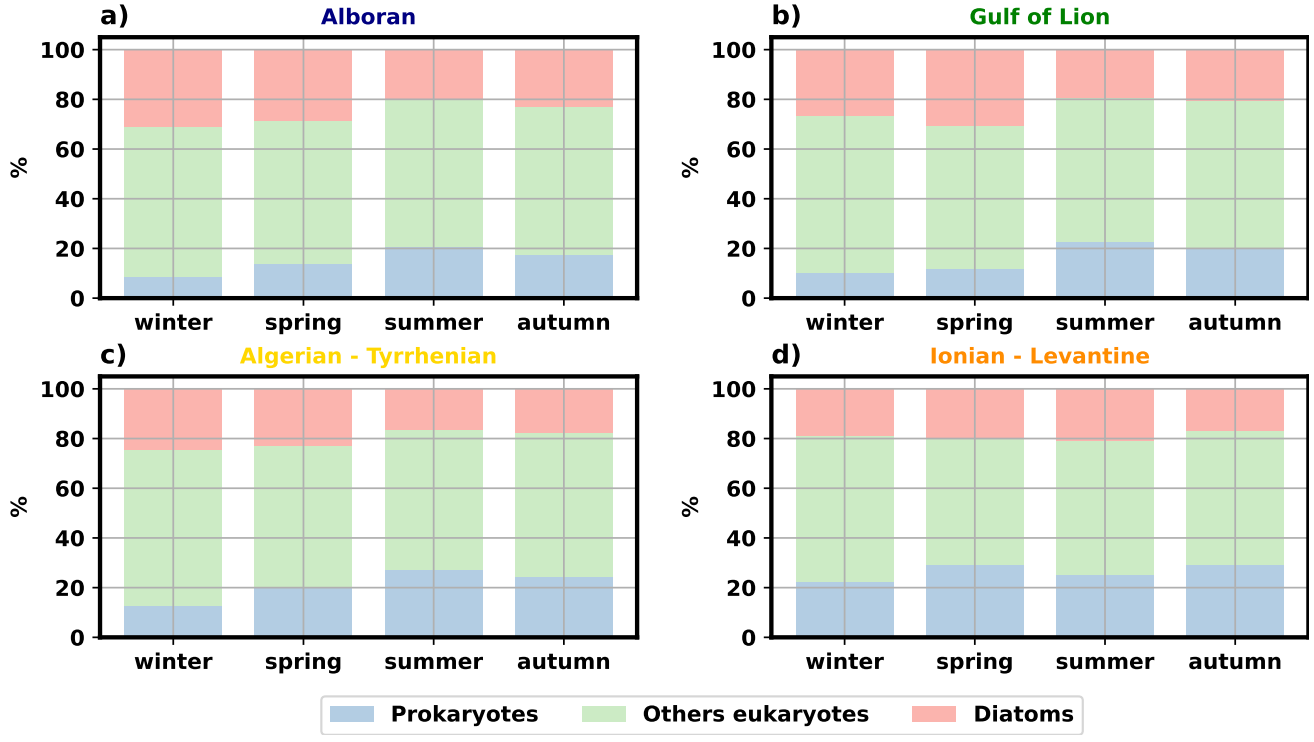

Figure A1. Seasonal time-mean of phytoplankton community composition for each region.

regions and during stratified periods. These findings highlight the important role of fronts in structuring marine ecosystems in nutrient-limited environments such as the Mediterranean Sea. By computing the sensitivity of our results to the front detection method and data sets used, we found that SST heterogeneity is the synoptic diagnostics most capable of capturing the spatio-temporal scale of an associated biological response.

More broadly, by highlighting the crucial role of fronts in shaping phytoplankton biomass and phenology, our study sustains the idea that changes in oceanic fronts should be considered when investigating ecological reorganization under future climate change. Studies evidence undergoing shifts in front intensity and frequency under climate change with profound regional variability (Xing et al., 2024). While Yang et al. (2023) began documenting trends in fronts and Chl-a, they noted that, despite significant trends in ocean warming hotspots, some regions, such as the Mediterranean Sea, do not exhibit statistically significant changes. This underscores the need for longer time series to achieve conclusive insights.

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Appendix A

Data availability. Chl-a GlobColour data were downloaded from the E.U. Copernicus Marine Service (https://doi.org/10.48670/moi-00280, Garnesson et al., 2019)). These data have been developed, validated, and distributed by ACRI ST, France. SST data were also downloaded from the E.U. Copernicus Marine Service (https://doi.org/10.48670/moi-00169, Good et al., 2020). Surface density fields from the 4DMED-SEA project (Sammartino et al., 2022, 2025) data are available from this repository: https://opensciencedata.esa.int/products/4dmed-t-s-geo-a-150/collection. FSLE data from AVISO were downloaded from the AVISO service (10.24400/527896/a01-2022.002, d'Ovidio et al., 2004). The altimeter products were produced by Ssalto/Duacs in collaboration with LOCEAN and CTOH and distributed by Aviso+, with support from CNES (https://www.aviso.altimetry.fr/). The FSLE data from 4DMED-SEA project were downloaded from Zenodo repository (https://zenodo.org/records/11610512, Cortés-Morales and Hernández-Carrasco, 2024).

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Competing interests. The contact author has declared that none of the authors has any competing interests.

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