



Space-time variability of phytoplankton biomass, diversity and production over the last 25 years in the Mediterranean Sea

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Abstract. The Mediterranean Sea, a semi-enclosed basin characterized by strong physical and biogeochemical gradients, provides a natural laboratory to study the coupling between physics and biology. Here we combine more than 25 years (1998–2025) of satellite and reanalysis products from the Copernicus Marine Environment Monitoring Service (CMEMS) to investigate the space–time variability of key biological indicators, such as chlorophyll-a concentration, phytoplankton size
10 classes and primary production, together with fundamental physical drivers including sea-surface temperature and mixed-layer depth. Gap-free satellite chlorophyll fields and a Mediterranean-specific, wavelength-resolved primary production model are used to produce consistent, high-resolution time series. Empirical Orthogonal Function analysis is applied to identify the dominant modes of variability and their links to physical forcing. This integrated approach highlights how long-term satellite and model observations can be combined to unravel the tight connections between biological productivity and
15 the physical environment across the Mediterranean basin.

1 Introduction

Marine ecosystems are undergoing rapid changes under the combined influence of natural climate variability and anthropogenic forcing (Halpern et al., 2015; IPCC, 2021). Detecting and understanding these changes requires long, continuous, and consistent observational records that span multiple decades (Doney et al., 2012). In the ocean, such records
20 allow scientists to separate short-term variability from persistent trends, attribute changes to their physical and biogeochemical drivers, and assess the resilience of ecosystems to environmental perturbations (Behrenfeld et al., 2006; Boyce et al., 2010).

Phytoplankton, the microscopic photosynthetic organisms that form the base of the marine food web, play a fundamental role in biogeochemical cycles. Understanding the spatiotemporal variability of phytoplankton is therefore crucial to monitor
25 ecosystem functioning, assess environmental status, and forecast ecological responses to climate change. In the European context, assessing primary production is also directly relevant to policy frameworks such as the Marine Strategy Framework Directive (MSFD), which requires indicators of ecosystem productivity and resilience to achieve and monitor Good Environmental Status. Satellite ocean color observations have revolutionized our ability to monitor phytoplankton dynamics,



providing consistent, synoptic estimates of surface chlorophyll-a concentration over the past three decades. Chlorophyll
30 concentration is widely used as a proxy for phytoplankton biomass, and thanks to the development of regionally-tuned
algorithms, its accuracy has significantly improved (Volpe et al., 2007; Volpe et al., 2019; Ciancea et al., 2021).

Robust long-term ecosystem assessments benefit from integrating variables describing both biological and physical aspects
of the system (Halpern et al., 2012; Borja et al., 2013; Piroddi et al. 2015). Biological indicators such as chlorophyll-a
concentration (CHL), phytoplankton size classes (PSC), and primary production (PP) provide insights into biomass,
35 community structure, and productivity (Behrenfeld and Boss, 2014; Kostadinov et al., 2010; Saba et al., 2010). Physical
variables such as sea surface temperature (SST), mixed layer depth (MLD), surface currents, and wind stress describe the
environmental forcing that shapes oceanic biological patterns (Mantua and Hare, 2002; de Boyer Montégut et al., 2004).
Considering these variables together enables the identification of mechanistic links and feedbacks, helping to separate
natural climate variability from anthropogenic influences (Boyce et al., 2010; Polovina et al., 2008). Such multi-variable
40 approaches also enhance trend detection and attribution in the context of climate change, offering a more complete picture of
how physical drivers propagate through the marine food web (e.g., Barton et al., 2016; Rykaczewski and Dunne, 2010;
Doney et al., 2012).

The Mediterranean Sea is an ideal natural laboratory for studying coupled physical–biological processes (Bethoux et al.,
1999; Robinson and Golnaraghi, 1993). It is a semi-enclosed basin with strong environmental gradients, marked seasonality,
45 and distinct trophic regimes, ranging from mesotrophic in the western waters to ultra-oligotrophic in the eastern gyres
(Siokou-Frangou et al., 2010). Its small size, high sensitivity to atmospheric forcing, and rapid response to climatic
anomalies make it an excellent testbed for climate-related ecosystem studies (Lejeusne et al., 2010; Malanotte-Rizzoli &
Robinson, 1988).

Over the past two decades, the Copernicus Marine Environment Monitoring Service (CMEMS) has provided continuous,
50 high-quality satellite ocean colour products. Unlike other global satellite data providers, CMEMS has progressively
specialized in delivering regionally optimized products for the pan-European seas, with a strong focus on the Mediterranean.
The CMEMS Ocean Colour Thematic Assembly Centre (OCTAC) has applied this approach to refine chlorophyll retrieval
algorithms, ensure temporal consistency in multi-sensor long-term datasets, and interpret variability in CHL, PSC, and PP
within the ecological context of each subregion, thus reducing biases that would arise from treating the basin as
55 homogeneous (Brando et al. 2024).

Within this multi-variable framework, primary production emerges as a pivotal rate-based indicator linking phytoplankton
biomass to carbon fluxes and overall ecosystem functioning. Its variability shapes the magnitude of the biological carbon
pump, influences atmospheric CO₂ concentrations, and supports marine food webs from microscopic grazers to apex
predators (Behrenfeld and Falkowski, 1997; Falkowski et al., 1998). Numerous studies have demonstrated marked spatial



60 gradients and temporal fluctuations in PP at both global and regional scales, largely driven by changes in light availability, nutrient supply, and hydrodynamics (Longhurst et al., 1995; Boyce et al., 2010; Bai et al., 2023; Silsbe et al., 2025).

PP can be estimated using different techniques, each with specific strengths and limitations. In situ methods, such as oxygen evolution and ^{14}C assimilation, offer accurate and direct measurements but are spatially and temporally sparse (Mattei and Scardi, 2021). Numerical models, which couple ocean circulation with biogeochemical processes, provide spatially and
 65 temporally continuous PP estimates and allow for scenario-based projections, but depend heavily on parameterizations and the accuracy of input data. Such models have been widely used for interannual and climate-scale analyses, both globally (e.g., Saba et al., 2010; Yool et al., 2013) and in the Mediterranean (e.g., Lazzari et al., 2012; Cossarini et al., 2021). Satellite-based approaches infer PP from proxies such as CHL and particle backscattering (bbp), delivering comprehensive basin-wide, multi-decadal coverage that in situ observations alone cannot provide. When regionalized, these products gain
 70 further value, as algorithms can be tuned to local optical properties, improving accuracy in optically complex environments such as the Mediterranean (Behrenfeld & Falkowski, 1997; Volpe et al., 2007; Westberry et al., 2008). Despite inherent uncertainties linked to algorithm assumptions, the integration of satellite and model-derived PP fields remains a powerful strategy for detecting and attributing variability at seasonal to interannual scales (Saba et al., 2011).

Large-scale assessments, such as those conducted by the Oregon State University Ocean Productivity group (e.g., Behrenfeld et al., 2005; Westberry et al., 2008), have provided invaluable multi-decadal datasets that reveal climate-driven anomalies and long-term trends in marine productivity (Silsbe et al. 2025). These products, derived from satellite ocean-colour observations and coupled bio-optical models, are widely used for global estimates of depth-integrated primary production. They have been instrumental in documenting basin-scale variability and in attributing productivity changes to natural climate modes such as ENSO (Behrenfeld et al., 2006), the North Atlantic Oscillation (Martinez et al., 2009), and longer-term ocean
 80 warming trends (Boyce et al., 2010). Moreover, they provide critical benchmarks for model–data intercomparisons, serving to evaluate coupled biogeochemical models (Saba et al., 2011) and to constrain carbon cycle assessments at both regional and global scales. While global initiatives have provided invaluable benchmarks, regionally focused studies are essential. In the Mediterranean, several satellite-based analyses have quantified primary production by exploiting ocean color time series and regionally tuned bio-optical models. Using SeaWiFS data, Bosc et al. (2004) produced one of the first basin-wide PP
 85 climatologies and interannual analyses, highlighting the strong west–east productivity gradient and the role of winter mixing in shaping seasonal cycles. Building on phytoplankton community structure, Uitz et al. (2012) estimated class-specific and total PP from satellite ocean color, showing how size-structured production varies across sub-basins and seasons. At the coastal scale, Salgado-Hernanz et al. (2022) documented the contribution of nearshore waters to basin-wide carbon budgets, emphasizing their marked variability. More recently, regionally parameterized Mediterranean PP models, calibrated with
 90 basin-specific bio-optical relationships and applied to long-term CHL records, have been included in the CMEMS operational processing chain (Colella et al., 2025). Taken together, these studies demonstrate that satellite-derived PP in the



Mediterranean is both quantitatively tractable and ecologically informative when algorithms and parameters are tuned to the basin's peculiar optical properties and trophic regimes.

Long-term time series, whether derived from in situ measurements, numerical models, or satellite observations, require dedicated analytical tools to extract meaningful information from their large volume and complexity. Classical techniques such as trend analysis, harmonic decomposition, and seasonal averaging have been widely applied to characterize baseline patterns and detect long-term changes in chlorophyll concentration and primary production (e.g., Bosc et al., 2004; Colella et al. 2016; Salgado-Hernandez et al. 2019; Cael et al., 2023; Silsbe et al. 2025). More advanced approaches include time-series decomposition methods (e.g., wavelet analysis, Seasonal-Trend decomposition using LOESS (STL)) to capture non-stationary signals and episodic anomalies, as well as multivariate classification techniques (e.g., Self-Organizing Maps, k-means clustering, Principal Component Analysis (PCA)) to identify coherent spatial regimes and coupled modes of variability (Ciavatta et al., 2019). More recently, machine learning frameworks have been introduced, including Bayesian networks and other data-driven models, which are increasingly integrated with numerical simulations to improve forecasting and detect potential regime shifts (Cossarini et al., 2021; Di Biagio et al., 2023). Among these, Empirical Orthogonal Function (EOF) analysis has remained a cornerstone method in marine applications, as it reduces complex spatio-temporal datasets into dominant modes of variability that can be directly related to environmental drivers (Volpe et al., 2012; Basterretxea et al., 2018).

Building on these considerations, the present study aims to: (i) investigate the space–time variability of phytoplankton biomass, size class diversity, and production over the past 25 years in the Mediterranean Sea; (ii) characterize the seasonal cycle of PP using satellite observations; (iii) explore mechanistic links between physical and biological processes. We will thus identify dominant modes of variability through EOF analysis applied to both biological and physical drivers such as SST and circulation patterns.

2 Data and Method

Here, we first describe the data that were used to achieve the goal of the work and then provide some details about the Empirical Orthogonal Function approach and the way it was applied. Phytoplankton biomass is here represented by chlorophyll concentration (Chl). We anticipate that it derives from satellite observations and specifically blending the most appropriate algorithms across the open ocean and coastal domains as function of the optical water types. Phytoplankton diversity or its size distribution in three classes (PSC, phytoplankton size classes) is expressed as the fraction of the total amount of Chl associated with each of the three size classes. The three classes are defined based on the Sieburth et al. (1978) dimensional classification as:

- micro for cell size larger than 20µm,
- nano for cell size between 2µm and 20µm and



– pico for cell size smaller than $2\mu\text{m}$

and estimated via phytoplankton diagnostic pigments considering the average size of the main taxonomic groups in the Mediterranean Sea (Di Cicco et al., 2025 and reference therein) Phytoplankton production is the Primary Production integrated over the entire euphotic layer (PP_{eu}) derived from the Mediterranean specific model recently added to the Copernicus Marine data portfolio. For comparison, we also computed and use Primary Production integrated over the first optical depth (PP_{fo}), approximately one-fifth of the euphotic depth (Morel and Berthon, 1989), which has traditionally been associated with the depth sensed by satellite remote sensors and that thus identifies the layer of both Chl and PSC.

To assess the role of the ocean dynamics onto the biological compartment as described by Chl, PSC and PP, here we use the Sea Surface Temperature (SST) and the Mixed Layer Depth (MLD) variables derived from satellite observations and from the Mediterranean component of the Copernicus Monitoring Forecasting Centre (MFC), respectively.

2.1 Data

Data used in this work are mostly directly available from the Copernicus Marine Service (CMEMS) web portal (<https://marine.copernicus.eu>) and are listed in Table 1; they include the time series of

1. the integrated primary production (PP_{eu} , product ref. no. 1),
2. phytoplankton biomass (Chl, product ref. no. 1),
3. sea surface temperature (SST, product ref. no. 2) and
4. the depth of the mixed layer (MLD, product ref. no. 3).

As previously mentioned, PP_{fo} is estimated only for the purpose of this work and is not available through the CMEMS web portal. PSC fields are distributed by CMEMS as Level-3 products, with gaps mainly due to cloud contamination. Here, PSC was instead derived directly from the chlorophyll field using the algorithm of Di Cicco et al. (2025).

Regardless of their native spatial and temporal resolution, all time series were resampled onto a common monthly grid at 4-km resolution. Monthly resolution reduces high frequency variability impact over annual and interannual signals, which constitute the topic of this work. Analogously, 4 km spatial resolution enables to spot the possible mesoscale contribution to the overall variability filtering out the finest scales of variability that are incompatible with the monthly resolution. All products derive from Mediterranean-specific processing chain and are consistent long-term gap-filled time series covering the basin from 1998-01 to 2025-02.

2.1.1 Primary Production (PP) model

In this section we provide a description of both PP_{eu} and PP_{fo} whose only difference is the integration depth. Primary production (PP) in the Mediterranean Sea is estimated with a regional, wavelength-resolved model specifically developed for this basin. This modelling framework builds on the seminal work of Antoine and Morel (1996), which linked satellite



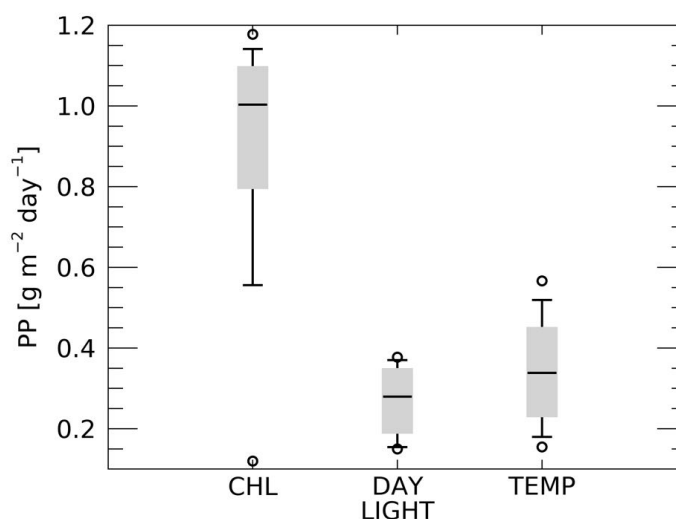
155 chlorophyll observations to PP through the coupling of an atmospheric radiative transfer model (Tanré et al., 1979) with a
 bio-optical representation of phytoplankton absorption and scattering (Morel, 1991), at global scale. Here, the Mediterranean
 implementation refines these components to account for the peculiar bio-optical properties of the basin and benefits from
 improved atmospheric and bio-optical parameterizations and the availability of recent high-resolution satellite and in situ
 datasets. In this context, daily column-integrated PP is computed as:

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$$P = 12 \text{ } Chl(z) \text{ } a_{chl}^* \text{ } PAR(z, t, \lambda) \text{ } \varphi_{\mu}(chl, T)$$

where 12 is the carbon molar weight to express the PP as mass; $Chl(z)$ is the chlorophyll concentration profile; a_{chl}^* is the
 chlorophyll-specific absorption coefficient, expressed as a function of chlorophyll concentration; $PAR(z, t, \lambda)$ is the
 165 photosynthetically available radiation at depth z , time t , and wavelength λ ; and $\varphi_{\mu}(chl, T)$ is the photosynthetic quantum
 yield, formulated as a function of chlorophyll and temperature, which expresses the efficiency of converting captured energy
 into carbon.

A major advancement of the Mediterranean configuration is the adoption of the revised Ocean Atmosphere Spectral
 Irradiance Model (OASIM; Gregg and Casey, 2009), which provides direct and diffuse irradiance at 5-nm spectral resolution
 170 between 400 and 700 nm, on a daily 4-km grid. This irradiance field, combined with the reparametrized bio-optical module,
 enables the computation of light penetration through the water column, with updated absorption (Bricaud et al., 1998) and
 scattering (Morel et al., 2002) coefficients. Since remote sensing observations provide chlorophyll information only for the
 surface layer, vertical distributions must be reconstructed to compute depth-integrated production. This follows the empirical
 approach of Morel and Berthon (1989), which relates satellite-derived surface pigment concentration to euphotic-layer
 175 chlorophyll content and profile shape. For the Mediterranean Sea, this approach has been revisited using the MedBiOp in
 situ dataset (Volpe et al., 2019). Applying k-means clustering to vertical chlorophyll profiles, the in situ dataset was
 partitioned into six groups, each representing a typical trophic regime. Mean profiles were then used to derive polynomial
 functions that reconstruct vertical chlorophyll distributions from satellite ocean-color surface concentrations. Along with
 chlorophyll vertical structure, temperature profiles are also essential to modulate phytoplankton physiology. Therefore,
 180 vertical temperature data from the regional physical reanalysis of the Mediterranean Monitoring and Forecasting Centre
 (Med-MFC), distributed through CMEMS
 (https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1), were incorporated into the model. Since
 primary production estimates rely on different input datasets, the model's response may vary depending on the specific
 parameter considered. To investigate how individual inputs affect PP variability, we performed a sensitivity analysis
 185 following the approach of Tilstone et al. (2015). First, average values and natural ranges were determined for all input
 parameters. Primary production was subsequently estimated by varying each parameter individually over its range, with all
 remaining parameters maintained at their mean values. The variability in primary production associated with each parameter
 indicates the magnitude of its influence on PP.



190 **Figure 1 – Sensitivity analysis of PP.** The grey rectangles represent the interquartile range (25th–75th percentiles) of PP estimates obtained by varying each parameter individually. The horizontal line within each box marks the median (50th percentile). Whiskers denote the 10th and 90th percentiles, while circles indicate the minimum and maximum PP values. The abscissa indicates the input parameters analyzed.

In Figure 1 we can see that the highest PP sensitivity is associated with the chlorophyll concentration, followed by the temperature and then the day light. As expected, the modelled biomass productivity is mainly driven by phytoplankton concentration and secondarily by sea temperature. This pattern highlights the dominant role of phytoplankton biomass as the main predictor of primary production, while physical factors such as temperature and light act as modulators of its variability.

2.1.2 Phytoplankton biomass (Chl) and Phytoplankton Size Classes (PSC)

200 Chl daily interpolated data are the multi-sensor field that blends the most appropriate algorithms across the open ocean and coastal domain depending on the water types (Volpe et al., 2019). The open ocean algorithm builds upon the last version of the MedBiOp dataset (Volpe et al., 2019) which is a continuously updated dataset depending on data availability; the MedBiOp dataset has been collecting bio-optical observations for the past three decades over the Mediterranean Sea. The coastal algorithm is the one by Berthon and Zibordi (2004) which mainly builds on observations acquired in the Adriatic Sea. An important update has recently been implemented to address the issue of misinterpretation by the algorithm of high productive waters as Case-2 waters (Colella et al., 2025), sediment or CDOM loaded (Brando et al., 2024).

205 PSC data for diversity estimates were derived from chlorophyll fields by applying Di Cicco et al. (2025) algorithms directly to the daily interpolated Chl field after regridding it over the PP spatial grid at 4 km resolution.



210 **2.1.3 Sea Surface Temperature**

Here we use satellite-derived sea surface temperature (SST, Table 1) to evaluate water temperature role in determining and shaping PP space-time variability. SST dataset provides a stable and consistent long-term time series over the Mediterranean Sea estimated from daily (nighttime), optimally interpolated, satellite-based estimates of the foundation temperature at roughly 4 km resolution grid covering the investigation period (January 1998 to February 2025).

215 **2.1.4 Mixed Layer Depth**

Similarly as SST, ocean mixed layer depth (MLD) data are used here to evaluate the role of upper ocean dynamics in determining phytoplankton biomass, production and diversity space-time variability. MLD field used in the analysis and presented in this work derives from the Med MFC multi-year product for the period 1998 January – 2023 May and from the near-real time product for the period 2023 June – 2025 February.

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Table 1 List of Marine Copernicus products used in this work and available from <https://marine.copernicus.eu>. Documentation column refers to relevant Quality Information Document (QUID) and Product User Manual (PUM) also available on CMEMS website.

Product ref. no.	Product ID and type	Data access	Documentation
1	OCEANCOLOUR_MED_BGC_L4_MY_009_144, satellite observations	EU Copernicus Marine Service Product (2025)	QUID: Colella et al. (2025) PUM: Colella et al. (2024)
2	SST_MED_SST_L4_REP_OBSERVATIONS_010_021, satellite observations	EU Copernicus Marine Service Product (2025)	QUID: Pisano et al. (2024a) PUM: Pisano et al. (2024b)
3	MEDSEA_MULTIYEAR_PHY_006_004, numerical model	EU Copernicus Marine	QUID: Escudier et al. (2024)



		Service Product (2025)	PUM: Lecci et al. (2024)
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2.2 Method

From all data time series, average fields were computed (Figure 2) and removed from their respective time series. The resulting anomalies constitute the input to the Singular Value Decomposition algorithm, which is equivalent to the empirical orthogonal function (EOF). The method used here is exactly the same as the one implemented in Volpe et al. (2012).

230 Since, as mentioned, the empirical orthogonal functions are computed from data anomalies, the EOF modes must be read as the variability that each field variable experiences around its average temporal field. This is the main reason why the results section includes two parts: the first about the description of the average fields and second about the main modes of variability.

3 Results and discussion

235 Here we will describe and discuss both the average features characterizing phytoplankton abundance, productivity and size class diversity in the Mediterranean Sea and the main patterns of variability that emerge from 25+ years of satellite observations. We will first define the rule emerging from the average phytoplankton abundance, productivity and diversity spatial patterns. We will then depict the main patterns of variability as outcome of the EOF analysis. Both the rule and the exceptions will be shaped in relation to the physical environment as represented by the sea surface temperature and by the

240 oceanic mixed thickness.

3.1 Mean fields

The average surface mixed layer thickness (Figure 2.a) is generally thinner than 50 meters, apart from the Aegean Sea, the south Adriatic and in particular the Gulf of Lion where it presents values twice as large as the rest of the basin. MLD pattern confirms the dynamics nature of the cold water spot in the Gulf of Lion where it exceeds 125 m, definitely marking the area

245 leaving a clear signature also in phytoplankton abundance and productivity.

The average SST values (Figure 2.b) shows a NW-SE gradient in all sub-basins, with the Alboran Sea, the Gulf of Lion, the North Adriatic and Aegean seas to be the cold end of the range of variability. This is likely induced to dynamical factors such as river outflows (Struglia et al., 2004), water mass formation (Marshall and Schott, 1999) or wind forcing (Millot 1999) rather than merely due to insulation, only.



250 Figure 2.c shows the average Chl concentration over the entire period which presents a well-known longitudinal gradient, with the west side being more abundant in phytoplankton. Coastal areas appear on average more productive than the open waters.

Regarding the average Primary Production, the basin scale variability of the euphotic depth integrated Primary Production (Figure 2.d) spans over little more than one order of magnitude, from 0.1 to 2 g m⁻² d⁻¹, roughly. PP_{eu} does present locations
 255 of higher productivity, yet it does not show relevant basin scale gradients as compared to those in the other three fields presented above. More relevant patterns with marked gradients are shown by PP_{fo} (Figure 2.e); this very closely resembles the Chl features in Figure 2.c, once more highlighting the importance of Chl role in primary production computation, consistently with the sensitivity analysis shown in section data and methods.

There are features which are evident in all the four fields and which are associated with well-known dynamical structures.
 260 Among these there is the Atlantic surface waters that enter the basin at Gibraltar Strait and together with the Mediterranean intermediate waters form the western Alboran Gyre (Gascard and Richez, 1985) whose signature is quite clearly evident in all the fields. More eastward, the low temperatures and shallow mixed layer produce higher phytoplankton biomass and productivity along the western side of the Adriatic Sea (Volpe et al., 2012; D’Ortenzio and Ribera d’Alcalà, 2009). River estuaries represent an important source to the nutrient pool of the basin, as shown by the higher productivity values in
 265 correspondence of e.g., Nile, Po, Rhone and Ebro rivers (Struglia et al., 2004; Ludwig et al., 2009). Analogously, the oceanographic dynamics of the straits (e.g., Strait of Dardanelles, Gibraltar) helps the surface water to mix with the underlying nutrient richer waters and to promote phytoplankton dynamics. The shallow waters of the Gulf of Gabes are among the permanent high productivity areas of the basin (Dowidar, 1984; Bosc et al., 2004). Apart from these coastal features, two major offshore patterns of enhanced productivity are located in the western basin. These are associated with the
 270 bloom area of the Gulf of Lion (Marty et al., 2002; D’Ortenzio and Ribera d’Alcalà, 2009) and along the African coast where the Atlantic water generates the Algerian current (Milot, 1999; Bosc et al., 2004).

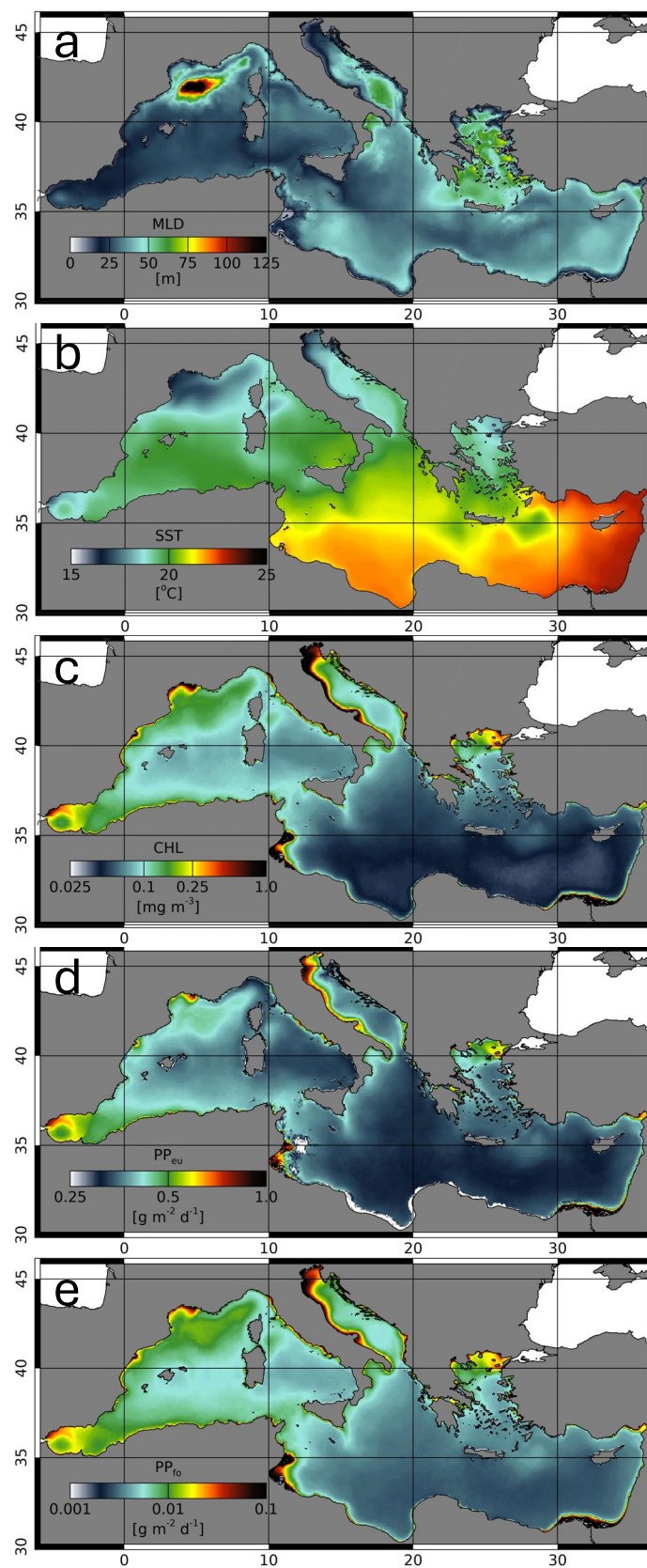




Figure 2 – Mean time averages (1998-2023) of mixed layer depth (a), sea surface temperature (b), phytoplankton chlorophyll (c), primary production integrated over the entire euphotic layer (d), primary production integrated over the first optical depth (e).

275 Not surprisingly, Chl and SST mean fields (Figure 2.b-c) here computed with 25+ years observations appear at a first sight very similar to those previously computed with only nine years observations as shown in Volpe et al (2012, Figure 3). However, a closer look at the data in the two reference periods reveals a general warming that is likely causing the observed upper layer oligotrophication that leads to the phytoplankton abundance decrease, at basin scale. These differences can locally account for as much as 5% increase in SST and 20% decrease in Chl (Figure A 1). This SST-Chl inverse relationship
 280 can be broken locally where river inputs (north Adriatic Sea), coastal dynamics (north Aegean Sea) or permanent meso-scale features (Rhodes Gyre) play a major role in regulating both the thermal and phytoplankton fields.

Correlation values between mean fields of PP_{eu} and Chl and SST highlight that Chl can explain as much as 64% of PP_{eu} average spatial pattern, whereas SST can explain only 12% of it. PP_{eu} dependence on Chl shown in Figure 2 is in line with the sensitivity analysis presented in section Data. Moreover, an important aspect that must be taken into consideration is that
 285 SST and Chl satellite observations are representative of the surface layers only (mixed layer for SST (Donlon et al. 2002) and first optical depth for Chl (Gordon and McCluney, 1975)), whereas PP_{eu} is integrated over the entire euphotic depth. This caveat will be particularly relevant when it comes to look into the various variables space-time variability (next section).

As expected by their functional forms and by their being derived as a direct function of Chl (Di Cicco et al., 2017; Di Cicco
 290 et al., 2025), main field of PSC (Figure A 2) spatially show patterns very close to Chl. Based by design on the known co-variability existing between phytoplankton accessory pigments linked to each fraction and the total Chl concentration (Chisholm et al., 1992; Hirata et al., 2011), the three size classes individually highly correlate with Chl: r^2 equals to 0.99, 0.97 and 0.99 for pico, nano and micro, respectively. The mean fields of the three PSC are characterized by different intensity, each being relevant in specific areas of the range of variability. Figure 3.a,d show that microphytoplankton is the
 295 most abundant class only over 1% of the basin in correspondence of the main river outflows in the north Adriatic (Adige, Po, Piave, Tagliamento, among others; they all cross the Po Valley before flowing into the north Adriatic), at the Nile river estuary and in the shallow waters of the Gulf of Gabes where large amounts of phosphate are known to be discharged by local chemical industry (El Kateb et al., 2018). Thus, the terrigenous origin of the high nutrient levels in these areas is the main driver of the larger cell size development and sustainment throughout the time series which is unaffordable in any
 300 other part of the basin, except in the area of deep water formation and of the strong spring bloom in the northwest Mediterranean (Marty et al., 2002; Uitz et al., 2006; D’Ortenzio & Ribera d’Alcalà, 2009; Siokou-Frangou et al., 2010; Volpe et al., 2012).

Nanophytoplankton predominance is more widespread in both space and time (Figure 3.b), significantly contributing to the size distribution of the entire western basin, in the Adriatic and in the north Aegean Sea. The relevance of its contribution
 305 reflects the trophism of the areas, as clearly shown by the yellow areas in Figure 3.d where nano class is shown to be dominant. Figure 3.c shows that the entire eastern basin along with the Tyrrhenian and the deep-bottom open waters of the



Adriatic Sea are nearly always dominated by pico phytoplankton, consistently with in situ observations (Marty et al., 2002; Siokou-Frangou et al., 2010). The occurrence of this size class remains relevant also over the western basin where it dominates the size spectrum 75% of the time. The dominance of the lowest size is once more the fingerprint of the oligotrophic nature of the surface Mediterranean open waters.

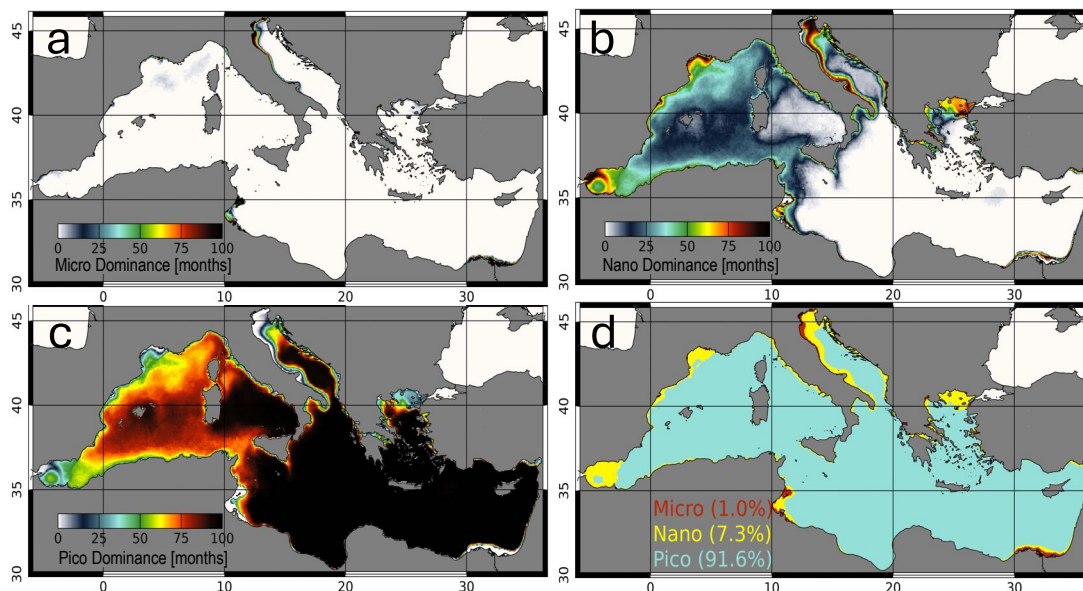


Figure 3 – spatial distribution in the Mediterranean Sea of the percent time occurrence in which each size class (Micro, Nano and Pico in panels a, b and c, respectively), dominates the phytoplankton size distribution (monthly-based, over the entire time series). Panel d shows the overall dominance over the entire time series for each group.

3.2 Variability

3.2.1 Annual variability (1st mode)

It is worth reminding that spatial patterns and relevant temporal amplitudes need to be considered at once.

Figure 4 shows the first EOF mode computed over MLD, SST, phytoplankton biomass and production. Apart from what shown in the SST field, the Gulf of Gabes and a few other coastal areas result in opposition of phase with respect to the rest of the images and were thus masked out to enhance figure readability. The variability of these areas was low as compared to the rest of the fields. Moreover, the uncertainty associated with these shallow waters are known to be much larger than open waters counterparts (Volpe et al., 2012; Volpe et al., 2019; Brando et al., 2024).

MLD variability shows maxima in the Gulf of Lion with values twice or three times as large as the rest of the basin. The Gulf of Lion is long known to be the location of the annual deep-water formation (MEDOC group, 1970; Marshall and Schott, 1999) (Figure 4.a). Large variability is also found in the south Adriatic and in the Aegean Sea. On the other hand, less pronounced variability is found in correspondence of permanent current systems such as the Algerian current in the western basin which splits into two branches: one in the Tyrrhenian and the other into the AIS towards the Levantine Basin.



The north Adriatic also displays weak variability. The temporal evolution of this mode shows a pulsed sinusoidal signal with sharp maxima during winter mixing, much more pronounced than the low background value characteristic of the rest of the stratified period (Figure 4.e). Differently than the other temporal evolutions, the one associated with the first mode of MLD shows a remarkable interannual variability with values spanning one order of magnitude and with the last ten years showing a reduced intensity. This is in line with deep water formation interannual variability in the Gulf of Lion (Herrmann et al., 2010), that governs the pattern associated with this mode and where the largest intensity is observed. The interannual variability is only evident for the maximum values as the minima are stable over the entire period.

Figure 4.b shows the SST field with three main patterns of homogeneous variability. The highest is associated with coastal areas of the western Adriatic Sea, the Gulf of Gabes and the Nile River Delta. The lowest SST variability is found at Gibraltar, in the Aegean Sea, in the Gulf of Lion and to a lesser extent also in the Sicily Channel. In these areas there are seasonal phenomena that prevent the surface ocean heating and cooling associated with solar shortwave radiation. Indeed, at Gibraltar, the Atlantic inflow to the Mediterranean mitigates the seasonal surface warming (Harzallah et al., 2014). Analogously, the Sicily upwelling system, mostly driven by the Atlantic Ionian Stream (AIS), is a permanent feature with maximum strength during summer (Bosc et al., 2004; Buonanno et al., 2014) resulting in the deeper colder waters to reduce the surface warming and variability on annual time scale. The Aegean Sea and the Gulf of Lion are areas where the seasonal regimes of dominant winds (Meltemi and Mistral, respectively) play a clear role in reducing the surface ocean heating (Ziv et al., 2004; Millot 199; Herrmann and Somot, 2008). The rest of the basin presents an intermediate level of variability which, as expected, is amplified by the temporal amplitude showing summer maxima and winter minima.

The highest phytoplankton biomass variability is in the western basin with special reference to the Balearic front area and the Algerian current system (Figure 4.c). Biomass variability reduces in the rest of the basin exhibiting minima in correspondence of river mouths and straits. It is interesting to note that the Algerian Current has its signature in the bifurcation tongue towards the Tyrrhenian and Levantine basin. This feature very close resembles that in the MLD field variability; still, the winter reinforcing of the Algerian current gives ground to instabilities that promote vertical mixing, traceable through the deepening of the MLD and resulting in this very clear signal in the Chl variability pattern. Observing relevant temporal amplitude, we find maximum positive values to generally occur in February while minima are mostly associated with the period July-August. Winter is the season of cold nutrient rich waters that through a deeper mixed layer reach the surface enhancing phytoplankton chlorophyll. As demonstrated by several works, part of this phytoplankton chlorophyll enhancement can be associated with the phytoplankton response to seasonal low light levels, namely photo-acclimation (among others Behrenfeld et al., 2005; Bellacicco et al., 2016).

Four main areas of homogeneous variability stand out from the first mode computed on PP_{eu} (Figure 4.d): in decreasing order of importance there are i) the areas facing the river mouths (Po in the Adriatic Sea, the Nile in the Levantine Basin and the Rhones River in the Gulf of Lion), ii) the straits of Gibraltar and Dardanelles, iii) the Gulf of Lion along with the open waters of the Ligurian Sea and iv) the rest of the basin that present a very low annual variability. This pattern is modulated by a marked temporal amplitude, oscillating sinusoidally with positive values during summer, reaching maxima generally in



July, and minima in winter, typically in December or January (red line in Figure 4.e). Thus, at annual time scale (Figure 4.e) PP_{eu} variability seems to be more sensitive to the water temperature that promotes metabolic activity, the maxima being closer in time to SST's. This is counterintuitive as on average PP_{eu} showed higher correlation with Chl (see section Mean fields). At the latitude and climate of the Mediterranean Sea, SST can be used as a proxy for the upper layer dynamics in which lower temperatures correspond to the intrusion of deeper waters to the surface, with their nutrient load. Thus, generally, we expect phytoplankton biomass and production to positively respond to temperature decreases which are therefore symptoms of new nutrient entrainment into the upper mixed layer. On the other side, water temperature increases do favor biological production by enhancing cellular metabolic rates (Eppley, 1972; Bissinger et al., 2008; Regaudie-de Gioux and Duarte, 2012). As such, water temperature has in theory a dual role in shaping and modulating phytoplankton biomass and production. PP_{eu} and SST are in phase (with PP_{eu} anticipating SST by one month, $r=0.95$). This can be explained by the fact that PP_{eu} , accounting for the deep chlorophyll maximum (DCM), is more resilient than it would be if it was computed over the first optical depth (PP_{fo}), as is the case for Chl. DCM is a consistent and widespread phytoplankton feature of the Mediterranean Sea (Marty et al., 2002; Siokou-Frangou et al., 2010; Mignot et al., 2014; Lavigne et al., 2015), whose depth varies according to location and season but generally deeper than the first optical depth. The first optical depth is the depth at which the phytoplankton mostly contributes to the satellite signal and hence all features out of this depth range result out of the satellite field of view. Indeed, to assure a tighter coupling with the other surface variables, we computed the first EOF mode on the PP_{fo} (Figure 6). The main outcome is that the temporal amplitude resembles that of Chl with maxima in winter and lows during summer. Analogously, the spatial pattern is in line with that of Chl with the western basin showing larger variability along with the specific dynamical features such as those associated with the Algerian current and the Balearic frontal areas. However, the spatial pattern also suggests that there are areas where the temperature field drives PP_{fo} variability such as the Adriatic current along the Italian shores or the Gulf of Gabes. In these areas the spatial pattern presents highly negative values that together with the temporal amplitude give an overall signal very close to first mode computed over PP_{eu} , with maxima during summer. The first modes of the two PPs (eu and fo) explain 73% and 60% of total variability, respectively. This difference once more highlights that the PP_{eu} is more resilient as it takes into account processes characterized by slower variability.

Phytoplankton biomass presents high correlation values at lag zero with both SST ($r = -0.93$) and MLD ($r = 0.8$). Although part of this variability can surely be explained in terms of photoacclimation (Bellacicco et al., 2016), it is likewise a clear sign of the winter cooling that deepens the MLD in turn favoring nutrients into the upper water column. This promotes biomass accumulation. It takes four months for PP_{eu} to reach its maximum under warmer ($r = -0.98$) stratified conditions with phytoplankton biomass in declining conditions ($r = 0.94$). The subsequent lack of a biomass pick during summer PP_{eu} maxima is likely due to top-down control by zooplankton resident stocks. Moreover, size-differential cell sinking also contribute to the water column phytoplankton dynamics. In summary, at the annual time scale, the sea water temperature late winter minima along with the maximum phytoplankton biomass accumulation dictate the summer phytoplankton production



maxima. As expected, when the correlation is computed with PP_{fo} the consistency with the other surface fields emerges more clearly, with high correlation values at zero lag ($r = -0.93$ with SST, $r = 0.95$ with Chl and $r = 0.71$ with MLD).

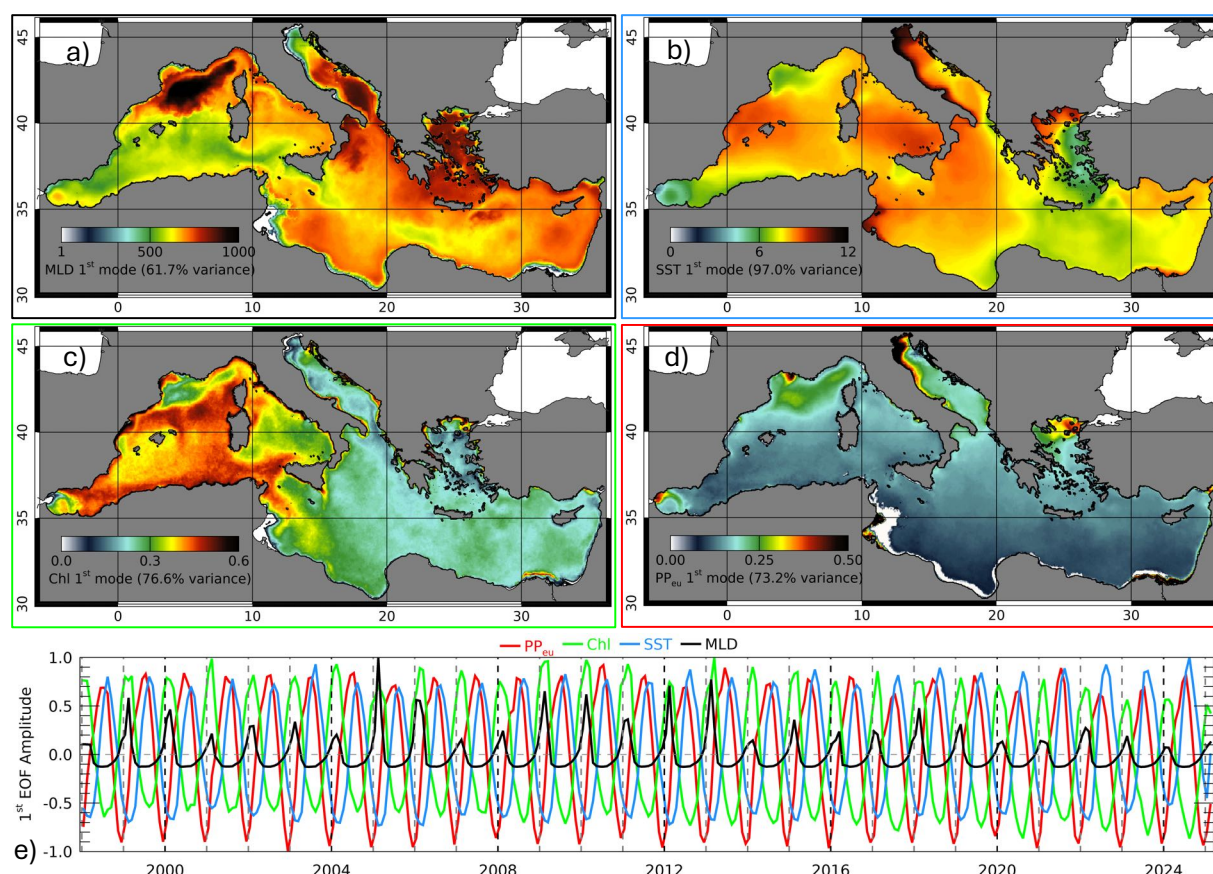


Figure 4 – first mode of EOF variability for MLD (a), SST (b), Chl (c) and PPeu (d) spatial patterns. Temporal evolutions are colour-coded in panel e. Relatively small areas in opposition of phase with respect to the rest of the images were masked out in white to enhance figure readability.

3.3 Deep convection and phytoplankton bloom variability (2nd mode)

The second EOF mode computed over the MLD (Figure 5.a) explains 14% of its total variability and presents two major areas of interest: the Gulf of Lion and the rest of the basin. These two are in opposition of phase with the Gulf of Lion reaching values as high as five times those associated with the Aegean or the Adriatic Sea. These values are modulated by the black line in Figure 5.e, which shows recurrent negative pulses during winter and positive values throughout the rest of the year, although occasional winter maxima can be observed in 2005, 2006, 2009, 2010, 2012, and 2013. These years' winter maxima have already been correlated with positive-to-negative North Atlantic Oscillation transition (Basterretxea et al., 2018). Since, apart from the Gulf of Lion, on one side, and the Adriatic and Aegean seas, on the other, the rest of the



410 basin presents negligible variability, it is reasonable to assume that this mode represents the process of deep-water formation at sub-basin scale in general with particular emphasis on the Gulf of Lion.

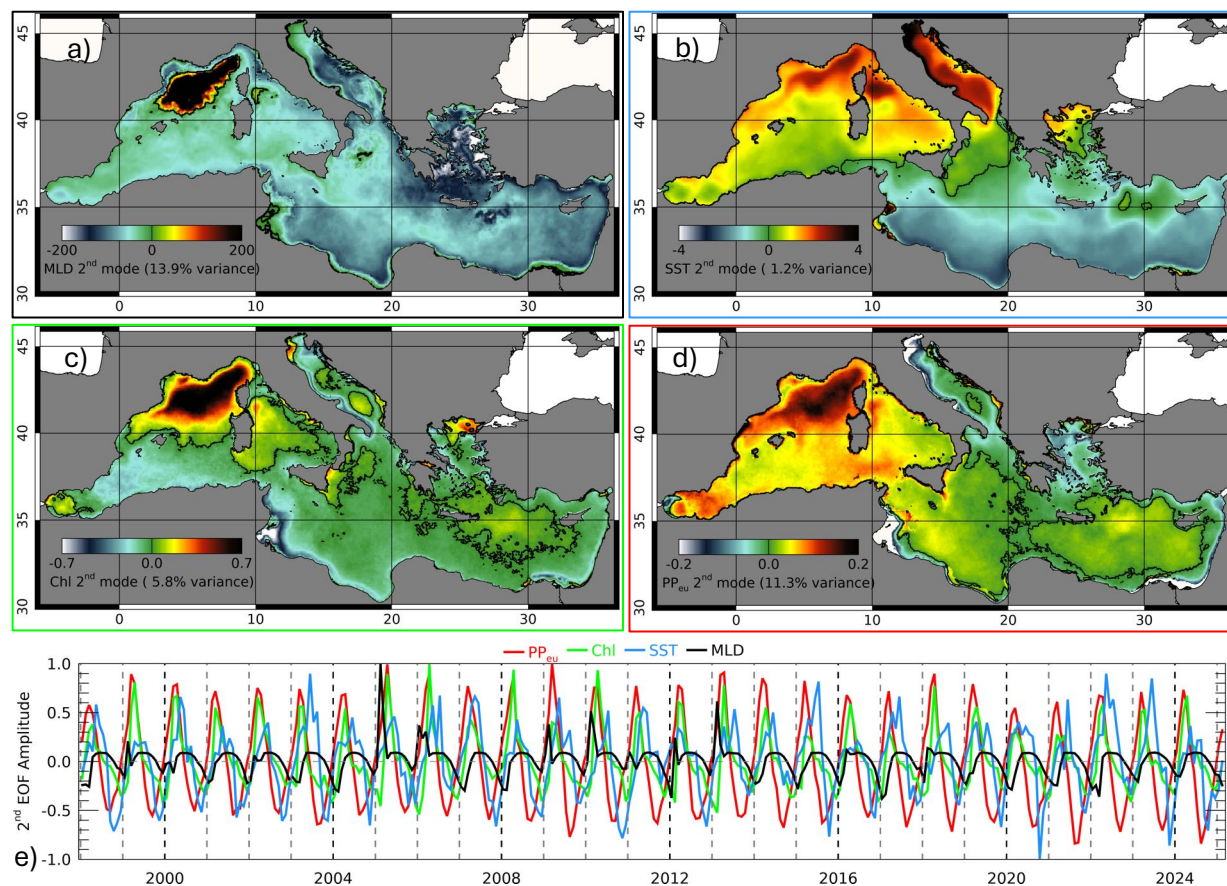
Figure 5.b displays the second EOF mode of SST. The spatial pattern closely resembles that reported by Volpe et al. (2012), despite the longer time series used here. A clear northwest–southeast gradient emerges, with predominantly positive values in the western Mediterranean and negative values over the Levantine Basin. Within the eastern sub-basin, only the northern
 415 Aegean Sea exhibits positive anomalies. The corresponding temporal amplitude shows a regular seasonal cycle, with positive values typically from January to August–September and negative values during the remaining months. However, the strength of both maxima and minima varies considerably from year to year. The second EOF mode of phytoplankton biomass (Figure 5.c) in this study also aligns well with the results of Volpe et al. (2012). Although the explained variance is slightly lower here (6% compared to 8%), the spatial pattern remains consistent and is clearly linked to spring bloom events.

420 Pronounced positive anomalies are found in the northwestern Mediterranean, particularly in the Gulf of Lion, the Ligurian Sea, and to a lesser extent around the Bonifacio Gyre, while the rest of the basin shows more limited variability. The temporal amplitude further supports the connection with seasonal bloom dynamics, displaying recurring positive peaks during the spring months and negative values throughout winter and summer.

The PP_{eu} second EOF mode (Figure 5.d) exhibits widespread positive variability throughout the Mediterranean basin.
 425 Negative values are displayed in the Adriatic Sea, Aegean Sea and along African coasts of the Levantine basin. As for the phytoplankton biomass this pattern is linked with the seasonal bloom dynamics of the northwest Mediterranean Sea and with the spring bloom, less evident but still observable, in the Rhodes Gyre. The temporal amplitude of the PP_{eu} (Figure 5.e) follows phytoplankton biomass maxima in correspondence of the spring months while, in the summer months, PP_{eu} decays faster and deeper than Chl with more intense minima. Apart from the Adriatic and Aegean Sea, this space-time pattern is
 430 mirrored also in the PP_{fo} second EOF field. This is somehow counterintuitive as one would expect the PP_{eu} and PP_{fo} to match in absence of deep important features such as the DCM or in shallow water conditions. Moreover, the PP_{fo} signals of the spring blooms last longer than the PP_{eu} counterpart, probably due to surface heating that enhances the phytoplankton metabolic capability and helps maintaining phytoplankton production. This second annual pick finds expression during 2021; the causes are still unclear but certainly merit further investigation. Finally, we show that, in accordance with previous
 435 works, deep convection in the NW Mediterranean (Macias et al., 2018) is the major driver of both phytoplankton production (with an explained variance of 11%) and biomass accumulation (with an explained variance of 6%).

As for the average and the first EOF mode, PSC second modes of variability perfectly align with the total phytoplankton abundance (Chl, Figure 5.c and green line in Figure 5.e), as shown in Figure A 3, exhibiting the dynamics of the spring bloom in response to the deep-convection.

440 As in the first mode, the spatial intensity expressed by the second mode increases with the size classes, although less evidently. This is a clear sign of the fact that during deep mixing nutrient abundance is such that the entire phytoplankton community benefits from it. As one would expect, larger cells are more competitive during these circumstances of nutrient abundance, and this is reflected in the increasing extension of the blooming area from Pico to Nano and Micro.



445 **Figure 5 – second mode of EOF variability for MLD (a), SST (b), Chl (c) and PP (d) spatial patterns. Temporal evolutions are colour-coded in panel e.**

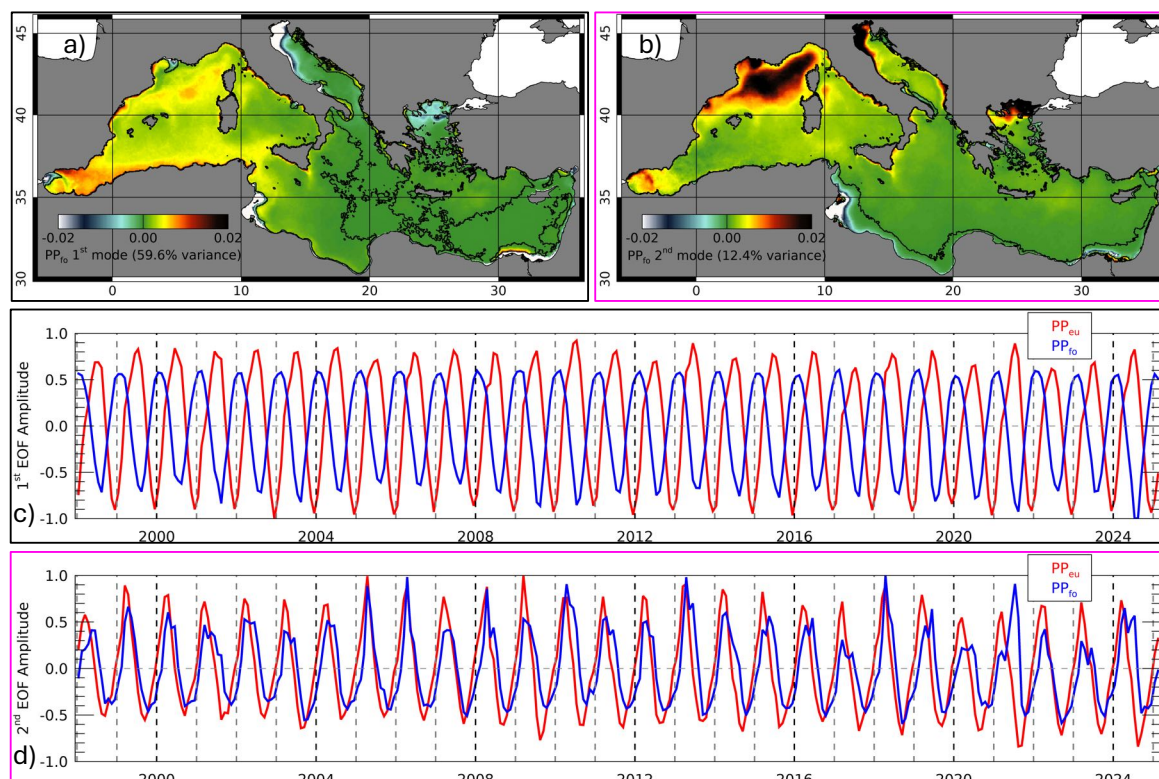


Figure 6 – spatial patterns of the first two EOF modes computed over PPfo (a and b). Temporal evolutions are shown in panel c and d (blue lines). To ease comparison, the two PPeu amplitudes are also reported (red lines).

450 Phytoplankton size diversity (PSC) is perfectly in line with the total phytoplankton abundance (Chl, Figure 4.c and green line in Figure 4.e), as shown in Figure A 3, with maxima in winter and minima in summer. We did use the same colorbar range in Figure A 3, just to show that Micro, being the less dominant and frequent (Figure 3) it shows the most pronounced variability. Variability reduces with the dominance of the cell size with Pico being the most stable, still with the very same space-time pattern as the others, including total Chl.

455 4 Summary and Conclusions

The analysis of long-term mean fields, annual variability, and deep-convection modes collectively illustrates the strong coupling between physical forcing and phytoplankton dynamics in the Mediterranean Sea.

460 The analysis performed over mean fields points towards the central importance of chlorophyll concentration in determining primary production patterns, while also revealing how regional hydrodynamics and nutrient inputs create spatial heterogeneity that modulates ecosystem productivity. The mixed layer depth and sea surface temperature distributions confirm the prominent role of regional circulation, winter mixing, and riverine inputs in shaping phytoplankton dynamics. A clear longitudinal gradient in chlorophyll and phytoplankton biomass persists, with higher values in the western basin and in



coastal and river-influenced areas, while open waters of the eastern Mediterranean remain largely oligotrophic. Primary production integrated over the euphotic zone exhibits less pronounced gradients than chlorophyll or SST, but the similarity
 465 between PP_{fo} and Chl fields reinforces the dominant role of phytoplankton biomass as the main driver of production, in line with the sensitivity analysis. Productive hotspots, such as the Gulf of Lion, the western Adriatic, and the Gulf of Gabes, stand out as areas where local dynamics and nutrient inputs sustain higher biomass and production.

Long-term comparisons also suggest a basin-wide warming trend accompanied by a decline in surface chlorophyll, indicating progressive oligotrophication. Nevertheless, regional processes, such as river discharges, coastal upwelling, and
 470 mesoscale gyres can locally counteract this trend and maintain productive conditions. The distribution of phytoplankton size classes further emphasizes the oligotrophic character of the basin, with pico-phytoplankton dominating most of the open Mediterranean and larger cells confined to nutrient-enriched coastal and riverine regions.

At seasonal scales, the first EOF mode reveals the dominant annual cycle linking physical forcing and phytoplankton dynamics across the Mediterranean. Variability in the mixed layer depth, particularly in the Gulf of Lion, the south Adriatic
 475 and the Aegean Sea, reflects the role of winter deep-water formation and interannual changes in convective intensity. Sea surface temperature patterns confirm the influence of regional circulation features and wind regimes in modulating seasonal heating and cooling, while coastal regions such as the western Adriatic, the Nile delta, and the Gulf of Gabes show enhanced variability due to local dynamics. Phytoplankton biomass exhibits strongest annual variability in the western basin, especially along the Balearic front and the Algerian current, consistent with the reinforcement of vertical mixing during
 480 winter. The seasonal cycle, with biomass maxima in late winter and minima in summer, is consistent with nutrient replenishment during mixing and subsequent photoacclimation under low light. Primary production displays a distinct phase relationship: PP_{eu} and SST are largely in phase, with PP_{eu} anticipating SST by about one month, reflecting both the metabolic effects of temperature and the resilience introduced by the deep chlorophyll maximum. Conversely, PP_{fo} tracks the surface chlorophyll cycle more closely, with higher variability and stronger winter peaks. The coherence between phytoplankton size
 485 classes and total biomass further indicates that the seasonal cycle is expressed consistently across community structure, with microphytoplankton showing the largest amplitude of variability and picophytoplankton the most stable.

The second EOF mode further underscores the pivotal role of deep convection in the northwestern Mediterranean. The marked opposition of phase between the Gulf of Lion and the rest of the basin confirms the dominant role of convection in shaping mixed-layer dynamics, with interannual pulses reflecting years of stronger or weaker winter mixing. The associated
 490 SST pattern reinforces this interpretation, with a robust northwest–southeast gradient and strong seasonal modulation that mirrors the intensity of convective activity. Biological responses are clearly linked to these physical drivers. Phytoplankton biomass variability shows its strongest expression in the northwestern Mediterranean, where recurrent spring blooms coincide with deep mixing and nutrient entrainment. The corresponding PP_{eu} mode displays widespread positive anomalies across the basin, with negative values confined to semi-enclosed seas such as the Adriatic and Aegean. The temporal
 495 amplitude highlights pronounced spring peaks and strong summer minima, indicating that production decays more rapidly than biomass once stratification is established. Interestingly, apart from semi-enclosed regions such as the Adriatic and



Aegean, this space–time pattern is also reproduced in the PP_{fo} field, though differences emerge: PP_{fo} maintains bloom signatures for longer, likely reflecting the influence of surface warming on phytoplankton metabolism. The phytoplankton size-class analysis further confirms the link between deep convection and community structure. Although all size classes benefit from enhanced nutrient supply, larger cells gain a competitive advantage, expanding their spatial dominance during bloom periods. This pattern underlines the critical role of nutrient abundance in regulating both productivity and size structure.

Our results demonstrate the tight coupling between physical forcing and phytoplankton dynamics in the Mediterranean Sea. Chlorophyll remains the main driver of primary production, while circulation, mixing, and nutrient inputs modulate its spatial and temporal variability. Despite a long-term trend toward basin-wide warming and oligotrophication, local processes such as deep convection, river discharges, and mesoscale structures sustain recurrent productivity events and influence phytoplankton community structure. This balance between climatic pressure and episodic drivers ultimately shapes the resilience of Mediterranean primary production.



5 Appendix A

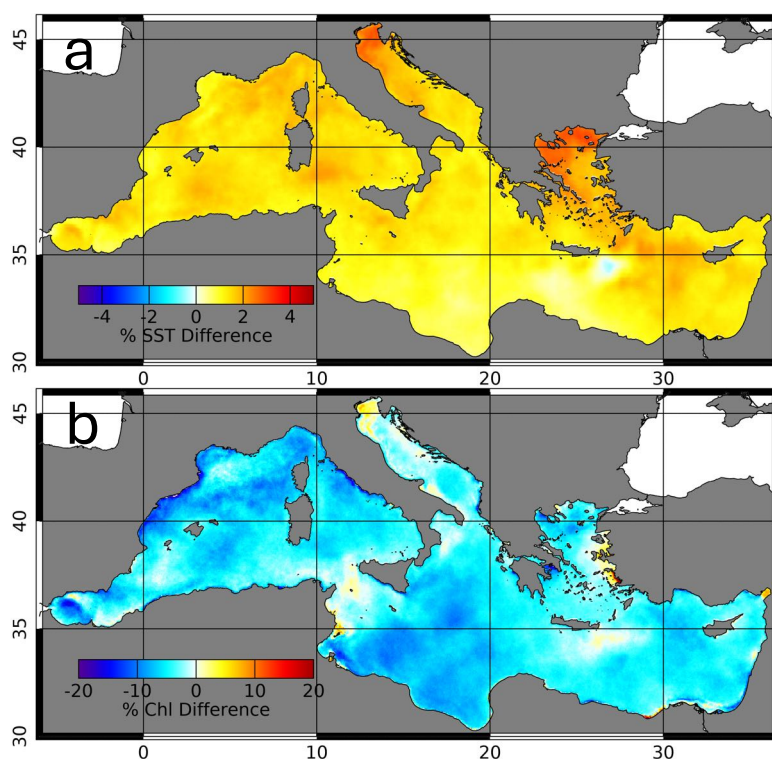
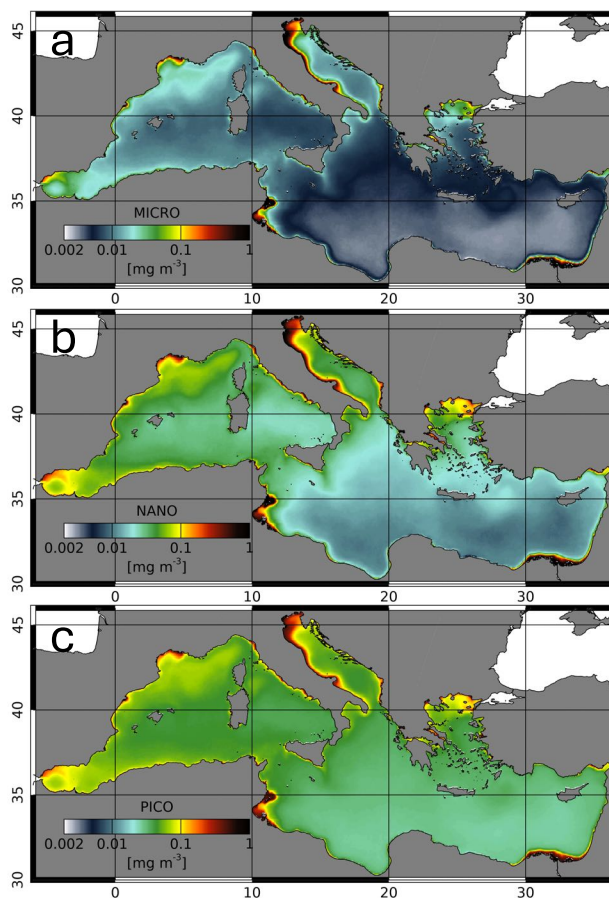


Figure A 1 – Relative percent difference $RPD = 100 \frac{X-Y}{Y}$, with Y being the mean time average (1998-2006) of SST and Chl for the same period as Volpe et al. (2012). X is the mean time average of SST (panel a) or Chl (panel b) computed over the full time range (1998-2025).



515 **Figure A 2 – Mean time averages (1998-2025) of Microphytoplankton chlorophyll (a), Nanophytoplankton chlorophyll (b) and Picophytoplankton chlorophyll (c).**

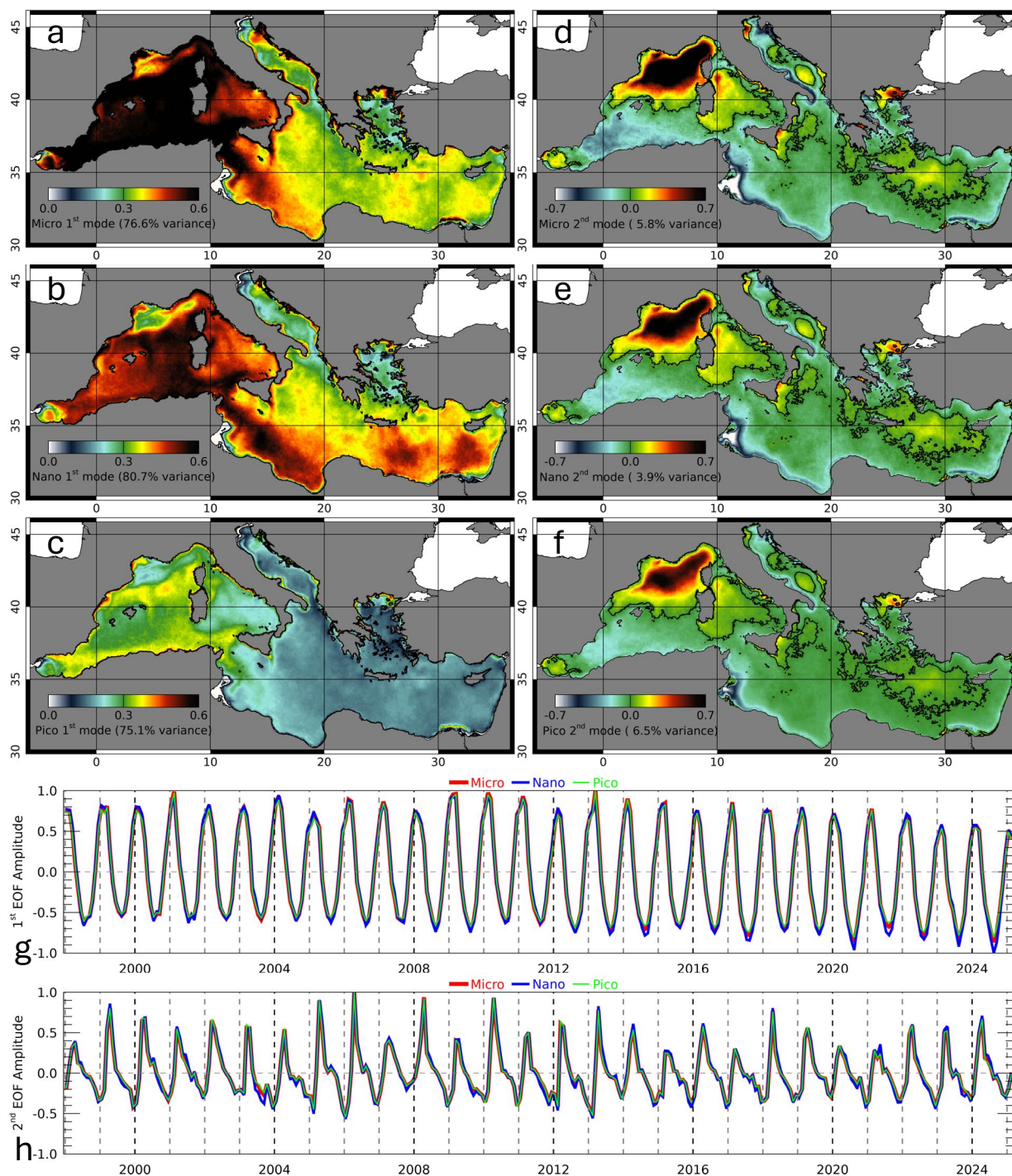


Figure A 3 – first two EOF spatial patterns computed over Micro- (a-d), Nano- (b-e) and Pico-phytoplankton (c-f). Temporal evolutions are colour-coded in panel g for the first modes and h for the second



520

6 Data availability

All the datasets used for this work that are not available on the Copernicus Marine Service can be provided by the corresponding authors upon request.

7 Author Contribution

525 SC: Writing – original draft, Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization.

GV: Writing – original draft, Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization.

ADC: Writing – review & editing, Investigation, Validation.

530 VB: Writing – review & editing, Investigation, Validation, Supervision.

8 Competing interests

The authors declare that they have no conflict of interest.

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