

Space-time variability of phytoplankton biomass, diversity and production over the last 27 years in the Mediterranean Sea

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Abstract. Phytoplankton dynamics in the Mediterranean Sea were investigated over the period 1998–2025 using a suite of Copernicus Marine Environment Monitoring Service satellite products, jointly analysing surface phytoplankton biomass (CHL), phytoplankton size classes (PSC), and integrated primary production (PP) alongside key physical drivers such as sea surface temperature (SST), photosynthetically available radiation (PAR), and mixed layer depth (MLD). Empirical Orthogonal Function (EOF) analysis was applied independently to each variable to characterize variable-specific modes of variability, and in a multivariate configuration (MEOF) to identify coherent modes of shared physical–biological variability. The dominant univariate EOF patterns capture the [basin-scale](#) annual cycle and reveal a light–temperature-driven control: PP peaks in summer in phase with PAR and SST, while CHL and MLD peak in winter, reflecting the nutrient–light trade-off characteristic of oligotrophic systems. Secondary univariate modes highlight the [sub-basin](#) spring bloom dynamics of the northwestern Mediterranean, associated with episodic deep convection in the Gulf of Lion and the ensuing nutrient supply, with biomass accumulation as the downstream biological response. The MEOF analysis identifies two physically coherent modes of coupled variability: a dominant annual light–temperature mode and a secondary spring-bloom mode linking winter mixing, spring restratification, and enhanced biological production.

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 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. Phytoplankton biomass and size structure are recognized as Essential Ocean Variables (EOVs) by the Global Ocean Observing System (GOOS), and as Essential Biodiversity Variables (EBVs) by the Group on Earth Observations Biodiversity Observation Network (GEO BON), reflecting their relevance for ecosystem monitoring and climate studies (Muller-Karger et al., 2018). Understanding the spatiotemporal variability of phytoplankton is therefore crucial to

30 monitor 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-colour observations have revolutionized our ability to monitor phytoplankton dynamics, providing consistent, synoptic estimates of surface chlorophyll concentration over the past three decades.

35 Chlorophyll concentration (CHL) 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; Ciancia et al., 2021).

Beyond phytoplankton biomass, robust ecosystem assessments benefit from the joint analysis of complementary biological indicators, such as phytoplankton size classes (PSC) and primary production (PP), together with physical drivers that regulate upper-ocean dynamics (Halpern et al., 2012; Borja et al., 2013; Piroddi et al., 2015). Phytoplankton size structure provides insight into community organization and trophic pathways, while primary production links biomass to carbon fluxes and ecosystem functioning (Behrenfeld and Boss, 2014; Kostadinov et al., 2010). Physical variables such as sea surface temperature (SST) and mixed layer depth (MLD) describe the environmental forcing that shapes oceanic biological patterns in both space and time (Mantua and Hare, 2002; de Boyer Montégut et al., 2004). SST and MLD act as integrative proxies of surface heating, stratification and nutrient entrainment, and therefore provide a mechanistic link between atmospheric forcing and biological response. In addition, light availability, expressed in terms of photosynthetically available radiation (PAR), represents a fundamental driver of phytoplankton production and modulates the seasonal expression of biomass and productivity (Behrenfeld and Falkowski, 1997; Arteaga et al., 2020). Considering biological and physical variables together enables the identification of mechanistic links and feedbacks, helping to disentangle the natural climate variability from the anthropogenic influences (Boyce et al., 2010; Polovina et al., 2008).

50 For many years, the Mediterranean Sea has been recognized as an ideal natural laboratory for studying coupled physical–biological processes (Bethoux et al., 1999; Robinson and Golnaraghi, 1994). It is a semi-enclosed basin with strong environmental gradients, marked seasonality, 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 and Robinson, 2012). Previous satellite-based studies have documented the dominant patterns of chlorophyll variability and their relationship with physical forcing, highlighting the role of seasonal water column stratification, mesoscale dynamics, and deep convection in shaping phytoplankton variability (D'Ortenzio and Ribera d'Alcalà, 2009; Volpe et al., 2012; Mayot et al., 2016). However, most basin-scale analyses have focused primarily on CHL (e.g. Bosc et al., 2004; D'Ortenzio and Ribera d'Alcalà, 2009; Volpe et al., 2012), while none, to the best of our knowledge, have jointly examined biomass, size structure, and primary production within a unified, long-term observational framework over the Mediterranean Sea.

Over the last decade, the Copernicus Marine Environment Monitoring Service (CMEMS) has provided continuous, high-quality satellite ocean colour products (Le Traon et al., 2019, 2021). Unlike other global satellite data providers, CMEMS has progressively specialized in delivering regionally optimized products for the pan-European seas (Brando et al., 2024). In particular, recent developments include gap-free multi-sensor chlorophyll field, phytoplankton size classes and a Mediterranean-specific, wavelength-resolved primary production model integrated into the operational CMEMS processing chain (Brando et al., 2024). These advances enable, for the first time, the construction of coherent, multi-decadal time series of CHL, PSC, and PP that are mutually consistent and suitable for basin-scale variability analyses.

In this study, we explicitly build on the methodological framework introduced by Volpe et al. (2012), extending it in three main directions. First, to provide a more comprehensive description of ecosystem functioning, we include phytoplankton size classes and primary production, in addition to surface chlorophyll, extending the analysis period to 27 years. Second, we exploit improved physical proxies, replacing sea level anomaly with mixed layer depth to better represent upper-ocean dynamics controlling nutrient availability. Third, we extend the univariate EOF framework to a multivariate approach, simultaneously decomposing biological and physical variables to directly capture their coupled modes of variability. Empirical Orthogonal Function (EOF) analysis is applied both independently to each variable, to identify the dominant modes of seasonal to interannual variability, and in a joint multivariate configuration, to identify coherent patterns of co-variability across the biological–physical system. This dual approach allows us to infer the main mechanisms governing phytoplankton variability and to quantify the degree of coupling between ecosystem and physical forcing.

The objectives of this work are therefore to:

- (i) identify the dominant seasonal and interannual modes of the space–time variability of phytoplankton biomass, size structure, and primary production in the Mediterranean Sea over the period 1998–2025;
- (ii) investigate their relationship with key physical drivers, such as SST and MLD, within a coherent multivariate framework.

By focusing on variability rather than long-term trends, this study aims to provide a robust baseline for interpreting Mediterranean phytoplankton dynamics and to set the stage for future assessments of long-term ecosystem change.

2 Data and Method

2.1 Phytoplankton biomass (CHL) and phytoplankton size classes (PSC)

Phytoplankton biomass is represented by CHL (product ref. no. 1 in Table 1). CHL fields are derived from a gap-free Level-4 multi-sensor satellite product specifically developed for the Mediterranean Sea and provided by CMEMS. This product blends regionally optimized algorithms across open-ocean and coastal waters as a function of optical water types, ensuring long-term consistency over the period 1998–2025 (Volpe et al., 2019; Colella et al., 2025; Brando et al., 2024).

Phytoplankton size structure is described in terms of three PSC: pico- ($<2\ \mu\text{m}$), nano- ($2\text{--}20\ \mu\text{m}$), and microphytoplankton ($>20\ \mu\text{m}$), following the dimensional classification of Sieburth et al. (1978). PSC, expressed as fraction of total CHL, are derived from chlorophyll field using the Mediterranean-specific algorithm by Di Cicco et al. (2025), which relates total

chlorophyll concentration to the relative contribution of each size class based on diagnostic pigment relationships and regional bio-optical characteristics. 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 CHL gap-filled product.

CHL is used throughout this study as a proxy for surface phytoplankton biomass. While seasonal photoacclimation effects may modulate chlorophyll concentration independently of biomass (Bellacicco et al., 2016), CHL remains a robust indicator of phytoplankton variability at seasonal to interannual scales in the Mediterranean Sea, as demonstrated in previous studies (e.g., Volpe et al., 2012).

2.2 Sea Surface Temperature (SST) and Mixed Layer Depth (MLD)

To characterize the physical forcing to phytoplankton variability, we use SST (product ref. no. 2 in Table 1) and MLD (product ref. no. 3 in Table 1).

SST is derived from an optimally interpolated Level-4 multi-sensor satellite product providing a stable and homogeneous time series at approximately 4 km spatial resolution over the period 1998–2025. SST is used here as a proxy for surface heating and seasonal stratification, and as an indicator of the thermal environment influencing phytoplankton metabolic rates.

MLD is obtained from the Mediterranean Monitoring and Forecasting Centre (Med-MFC) physical reanalysis (199801-202305) and near-real-time (202306-202502) products. MLD is used as a proxy of upper-ocean mixing and nutrient entrainment and represents a more direct indicator of the physical processes controlling nutrient supply to the euphotic zone than surface variables alone. The use of MLD replaces the sea level anomaly variable adopted in Volpe et al. (2012), benefiting from the improved representation of vertical mixing available in recent reanalysis products.

2.3 Primary production (PP) and photosynthetically available radiation (PAR)

PP (product ref. no. 1 in Table 1) is derived from a Mediterranean-specific, wavelength-resolved bio-optical model integrated into the CMEMS operational processing chain. PP, as provided by CMEMS, represents the production throughout the full euphotic zone, including subsurface features such as the deep chlorophyll maximum.

The PP model builds on the formulation of Antoine and Morel (1996) which linked satellite 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 properties (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:

$$P=12 \int_{z=0}^{\text{Depth}} \int_{t=0}^{24} \int_{\lambda=400}^{700} \text{Chl}(z) a_{\text{chl}}^* \text{PAR}(z,t,\lambda) \varphi_{\mu}(\text{Chl},T)(z) d\lambda dz dt$$

where I_2 is the Carbon molar weight to express PP as mass of Carbon; $Chl(z)$ 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 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. The daily PP was computed as the triple integral of the production rate with respect to wavelength (over the band, 400–700 nm), time (over 24 hours), and depth.

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 between 400 and 700 nm, on a daily 4-km grid. In addition to its role in driving the primary production model, light availability was explicitly analysed using PAR derived from OASIM. PAR was considered as an independent driver of phytoplankton production variability, allowing the contribution of light-driven processes to seasonal and interannual changes in primary production to be assessed in a manner fully consistent with the modelling framework. 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.

OASIM-derived irradiance was used instead of satellite-derived PAR to ensure consistency with the wavelength-resolved PP model, which requires spectral direct and diffuse irradiance to compute light absorption, scattering and propagation through the water column. This choice also provides a homogeneous radiative forcing over the full 27-year period, avoiding potential inter-sensor discontinuities in multi-sensor satellite PAR records, and the Mediterranean implementation has been evaluated with good results against in situ radiometric observations (Lazzari et al., 2021).

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 zone 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 seven groups, each representing a trophic regime and used to associate the surface observations to the vertical distribution.

Temperature effects on phytoplankton physiology are accounted for using vertical temperature profiles from the Mediterranean Monitoring and Forecasting Centre (Med-MFC) physical reanalysis (product ref. no. 3 in Table 1). Temperature modulates the photosynthetic quantum yield, thereby influencing primary production without directly altering biomass. The PP model is primarily optimized for optically simple (Case I) open waters. In optically complex coastal waters (Case II), such as river-influenced and shallow regions, PP estimates are associated with higher uncertainty and should be interpreted with caution. Thus, areas permanently classified as Case II waters, such as the northern Adriatic coastal strip and the mouth of the Nile River (characterized by strong riverine inputs and turbid plumes (Brando et al., 2015; Masoud, 2022)), along with the Gulf of Gabès (a shallow and highly turbid system (Katlane et al., 2013)), are masked and excluded from the data analysis.

Further details on the PP calculation, including the use of OASIM, are provided in Appendix A.

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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 (2025a)	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 (2024a)	QUID: Pisano et al. (2024a) PUM: Pisano et al. (2024b)
3	MEDSEA_MULTIYEAR_PHY_006_004, numerical model	EU Copernicus Marine Service Product (2025b)	QUID: Escudier et al. (2024) PUM: Lecci et al. (2024)

2.4 Spatio-temporal harmonization and preprocessing

To ensure consistency among variables, all datasets were resampled onto a common monthly grid with 4 km spatial resolution. Spatial regridding was performed using the nearest-neighbour approach, followed by the computation of monthly averages. The monthly temporal resolution minimizes the influence of high-frequency variability, thereby emphasizing seasonal and interannual signals.

The choice of a 4 km spatial resolution is consistent with the adopted monthly time scale and allows the permanent or semi-permanent mesoscale features to be retained while filtering out finer-scale variability that is incompatible with monthly sampling. All variables were analysed over the period January 1998 to February 2025.

2.5 Empirical Orthogonal Function analysis

As stated in the introduction, the objectives of this work are, on the one hand, to address the phytoplankton variability per se, in terms of biomass, size distribution, and productivity, and, on the other hand, to link this variability to key physical drivers. To this end, we perform both univariate and multivariate analyses of a consistent dataset including physical (MLD, PAR, SST) and biological (CHL, PP, PSC) variables. The univariate Empirical Orthogonal Functions (EOFs) were used to describe the dominant spatial and temporal patterns of each field independently, without imposing any a priori coupling among variables.

Comparisons among univariate EOF modes are therefore used only as an interpretative tool, based on similarities in spatial structure, temporal phasing, and lagged correlations. The multivariate EOF (MEOF) analysis (applied only to the five core variables MLD, SST, PAR, CHL, and PP, since PSC fields are diagnostically derived from CHL) was then used to identify the modes of variability that are shared by the core physical and biological variables. In contrast to the univariate EOFs, each MEOF mode is characterized by a single temporal amplitude common to all variables and therefore provides a more formal estimate of their coupled variability. Because univariate EOFs maximize the variance of each variable separately, whereas MEOF maximizes the variance of the entire standardized dataset, the ordering and spatial structure of the modes are not expected to coincide exactly between the two approaches. The two analyses should therefore be regarded as complementary: univariate EOFs diagnose variable-specific variability, while MEOFs identify basin-scale coupled modes of the physical–biological system.

Spatio-temporal variability is analysed following the methodology of Volpe et al. (2012). EOFs summarize the dominant modes of variability of a field and are interpreted as the product between the spatial pattern and the corresponding temporal amplitude. The closer to zero either of these two components is, the less relevant the associated variability of that mode will be at that specific location and time. An important aspect for interpreting the results is the sign agreement between spatial and temporal components: when they have the same sign, the mode variability follows the spatial pattern and its associated temporal amplitude as shown, whereas when their signs differ, the variability is reversed. Analogously, if the spatial pattern presents regions with positive and negative values, these regions vary in opposition of phase.

Univariate EOFs are computed independently for each variable based on the singular value decomposition of anomaly fields. No temporal filtering is applied, and the analysis therefore focuses on mean fields and dominant seasonal to interannual modes of variability. For each variable, long-term mean fields were computed and removed from the corresponding time series. The resulting anomaly fields describe deviations from the climatological mean state and constitute the input for the subsequent EOF analysis. EOF spatial patterns thus describe the characteristic structures of variability around the mean state, while the associated temporal amplitudes represent the evolution of these patterns over time.

A multivariate EOF (MEOF) analysis was then applied to the same anomaly fields, using the same spatial and temporal resolution. As in the univariate EOF analysis, the mean value of each variable was removed from the time series. In addition, each variable was divided by its standard deviation before the MEOF decomposition, so that variables with different units and variability ranges contributed comparably to the analysis.

2.6 Statistical correlation analysis

Correlation analysis is used here to support the interpretation of the dominant modes of variability; however, statistical correlation alone does not imply strict causality, and results are interpreted in the context of physical and biogeochemical processes known to occur in the Mediterranean Sea. The Pearson linear correlation was computed either between the temporal amplitudes of selected EOF modes or, where appropriate, between mean spatial fields. Moreover, to account for potential phase shifts between different phenomena, the temporal cross-correlation was computed also considering a variable time lag up to one year.

3 Results and discussion

This section presents the mean spatial fields and the dominant modes of spatio-temporal variability, explored through both univariate and multivariate EOF analyses, derived from 27 years of satellite observations of biological and physical variables.

3.1 Mean fields

The average surface mixed layer thickness (Figure 1.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 dynamic nature of the cold-water spot in the Gulf of Lion where it exceeds 125 m and represents one of the most energetic water mass formation sites in the Mediterranean (Marshall and Schott, 1999). The MLD signature in the Gulf of Lion leaves a clear imprint on phytoplankton abundance and productivity, as discussed below.

The average SST values (Figure 1.b) show 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 thermal structure is consistent with the MLD pattern described above and is likely driven by 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 insolation, only.

Figure 1.c shows the basin scale average PAR field. The southeastern basin receives approximately double the solar radiation compared to the northern part, reflecting both the expected meridional gradient and the longitudinal asymmetry visible in the image. This pattern also reflects the spatial distribution of cloudiness across the basin (Enriquez-Alonso et al., 2016).

Figure 1.d shows the average CHL concentration over the entire period, revealing the well-known west-east gradient characteristic of the Mediterranean, with higher phytoplankton biomass in the western basin. The most phytoplankton-rich areas are the bloom region of the Gulf of Lion (Marty et al., 2002; D'Ortenzio and Ribera d'Alcalà, 2009) and the African

coast, where Atlantic surface waters entering through the Gibraltar Strait drive the Algerian current (Millot, 1999; Bosc et al., 2004) and, together with Mediterranean intermediate waters, give rise to the western Alboran Gyre (Gascard and Richez, 1985), whose signature is clearly visible across all fields. Coastal areas are on average more enriched in phytoplankton than open waters, likely due to riverine nutrient inputs and coastal upwelling. The average PP (Figure 1.e) spans approximately one order of magnitude, ranging from roughly 0.25 to $1.0 \text{ g m}^{-2} \text{ d}^{-1}$. Although PP broadly mirrors the spatial patterns seen in CHL (Figure 1.d), with higher values in the western basin and along coastal areas, its basin-scale gradients are comparatively less pronounced.

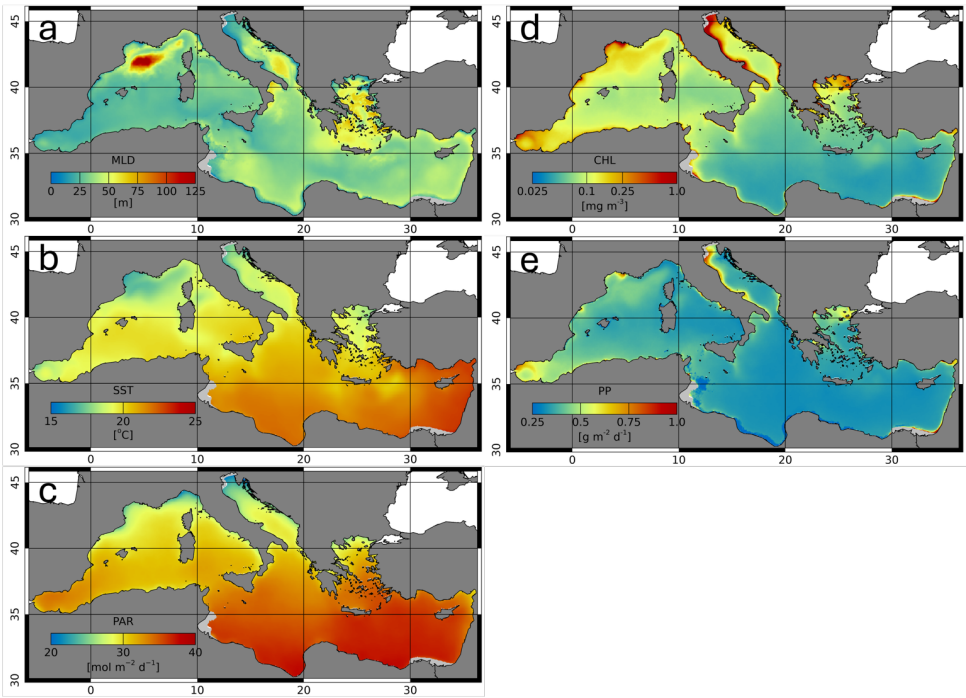


Figure 1 – Mean time averages (1998-2025) of MLD (a), SST (b), PAR (c), CHL (d), and PP (e). Light grey indicates the areas permanently masked out because of persistent or recurrent Case II water conditions.

Not surprisingly, CHL and SST mean fields (Figure 1.d-b) here computed with 27 years observations appear at 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 (Pisano et al., 2020; EU Copernicus Marine Service Product, 2024b) consistent with a basin-scale tendency toward upper-layer oligotrophication and reduced phytoplankton abundance (Colella et al., 2016; EU Copernicus Marine Service Product, 2024c). These differences can locally account for as much as 5% increase in SST and 20% decrease in CHL (Figure B 1). This SST-CHL inverse relationship 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.

Table 2 shows the outcome of the correlation analysis between the mean fields of Figure 1. High correlation is here reported for SST-PAR, SST-CHL, PAR-CHL and CHL-PP. The other spatial correlation can be considered negligible.

Table 2 – Pearson spatial correlation coefficient computed between the various variables.

	MLD	SST	PAR	CHL	PP
MLD	–	0.03	0.06	-0.29	-0.18
SST	–	–	0.71	-0.57	-0.31
PAR	–	–	–	-0.67	-0.39
CHL	–	–	–	–	0.80
PP	–	–	–	–	–

As expected from their functional forms and from being derived as a direct function of CHL (Di Cicco et al., 2017; Di Cicco et al., 2025), the mean fields of PSC (Figure B 2) spatially show patterns very close to CHL. By design and because of the known co-variability between phytoplankton accessory pigments associated with each fraction and total CHL concentration (Chisholm, 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.

To achieve the percent PSC pixel dominance (Figure 2), we counted, for each pixel, the number of months in which a given PSC showed a higher value than all the others. The resulting map was then normalized by the total number of months in the time series. Figure 2.a,d show that microphytoplankton is the most abundant class only over 1% of the basin in correspondence with coastal waters and the main river outflows. Thus, the terrigenous origin of the high nutrient levels in these areas sustains the development of larger phytoplankton cells throughout the time series, a condition otherwise rarely observed in the basin except in the deep-water formation region associated with the intense spring bloom in the northwestern 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 2.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 reflects the trophism of the areas, as clearly shown by the yellow areas in Figure 2.d where nano class is shown to be dominant. Figure 2.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

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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 smallest size class is once more the fingerprint of the oligotrophic nature of the surface Mediterranean open waters.

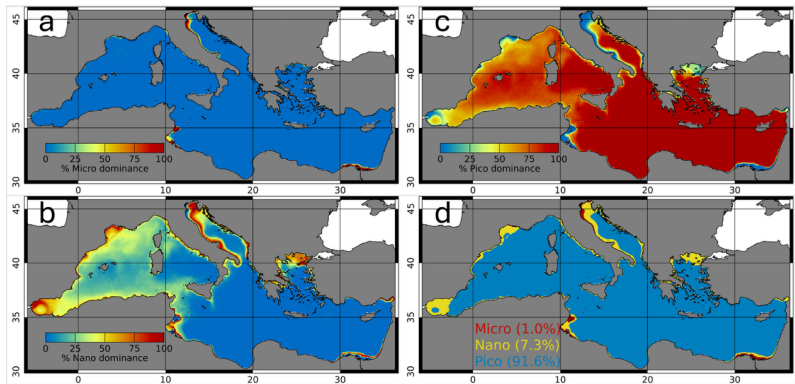


Figure 2 – Percent dominance of PSC size classes (Micro, Nano and Pico in panels a, b and c, respectively) over time. Panel d shows the overall temporal dominance of each size class in percent over the entire time series.

3.2 Variability

3.2.1 Basin-scale annual variability

Figure 3 and Figure 4 show the spatial pattern and temporal amplitudes of the first EOF modes computed over MLD, SST, CHL, PAR and PP.

The first MLD mode accounts for 61.7% of the total variance and is dominated by the Gulf of Lion, where values are two to three times larger than the rest of the basin (Figure 3.a), consistent with its role as the primary deep-water formation site in the Mediterranean (MEDOC group, 1970; Marshall and Schott, 1999). Large variability is also found in the south Adriatic and in the Aegean Sea, both of which are subject to recurrent deep convection events. On the other hand, reduced 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 following the Atlantic Ionian Stream (AIS) towards the Levantine Basin. The temporal evolution of this mode (Figure 4.a) 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. Unlike the temporal evolutions of the first mode of the other variables (Figure 4.b-e), the one associated with the first mode of MLD shows a pronounced interannual variability with values spanning over one order of magnitude and with lower amplitudes during the last decade. The combination of the spatial pattern and temporal evolution indicates that the first MLD mode primarily

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represents the dominant basin-scale seasonal cycle of winter mixed-layer deepening, with the largest amplitude in the Gulf of Lion.

Figure 3.b shows the SST first mode (97% of the total variance) with three main patterns of homogeneous variability. The highest pattern of variability is associated with coastal areas of the western Adriatic Sea. The lowest SST variability is found at Gibraltar, in the Gulf of Lion, in the Aegean Sea and south of Crete Island, and to a lesser extent, in the Sicily Channel. These areas are affected by distinct physical mechanisms that attenuate the amplitude of the seasonal warming and cooling cycle driven by solar shortwave radiation. At Gibraltar, the continuous inflow of cooler Atlantic waters mitigates surface warming and reduces the seasonal thermal range (Harzallah et al., 2014). In the Sicily Channel, the AIS-driven upwelling system brings colder waters to the surface preferentially during summer (Bosc et al., 2004; Bonanno et al., 2014) dampening the seasonal SST signal. In the Aegean Sea and the Gulf of Lion, the dominant seasonal wind regimes (the Meltemi and the Mistral, respectively) drive enhanced turbulent heat loss and vertical mixing that limit surface ocean warming (Ziv et al., 2004; Millot, 1999; Herrmann and Somot, 2008). The temporal evolution of the SST mode (Figure 4.b) is a smooth, nearly symmetric sinusoid with positive values in summer (August) and negative values in winter (January-February), consistent with the annual cycle of solar heating.

The first PAR mode explains 98% of its total variance (Figure 3.c). The highest variability is found in the northern and central parts of the basin, with the Aegean Sea standing out as a clear maximum. This is physically consistent with the larger seasonal swing of day length and solar zenith angle at higher latitudes, which drives a pronounced contrast between low winter PAR and high summer PAR values. The Aegean is further enhanced by the persistent clear-sky conditions maintained by the Meltemi wind regime (Tyrllis and Lelieveld, 2013), which removes clouds and aerosols and thus could maximise the amplitude of the seasonal PAR signal. Analogously, the African coast is characterized by lower variability. A band of lower variability is also visible along the northern coastlines, the Gulf of Lion, the Ligurian Sea and the northern Adriatic, where high frequency in cloud cover due to the orography of the region (Houze, 2012) could play an important role to reduce insolation and to moderate seasonal PAR variations. The temporal amplitude (Figure 4.c) is a near-perfect sinusoid with minima in December–January and maxima in June–July, similar to the SST first mode (Figure 4.b). This tight phase coherence reflects the well-established coupling between sea surface heating and incoming solar irradiance at the annual timescale, with PAR driving SST with only a slight lag (1-2 months) due to the ocean's thermal inertia.

Figure 3.d shows the CHL first mode (77.1% of the total variance). The highest CHL variability is found in the western basin, with special reference to the Balearic front area and the Algerian Current system. Variability decreases progressively eastward, reaching minima near river mouths and straits. A notable feature is the tongue of elevated variability extending from the Algerian Current toward the Tyrrhenian Sea and further into the eastern basin, closely resembling the corresponding signature in the MLD field (Figure 3.a). This spatial analogy is not coincidental: the winter reinforcement of the Algerian Current drives mesoscale instabilities that promote vertical mixing, leading to MLD deepening and the subsequent nutrient enrichment of the surface layer, which in turn enhances phytoplankton biomass and the associated chlorophyll signal. Furthermore, maximum positive values generally occur in February when cold nutrient-rich waters reach the surface through a deeper mixed layer,

stimulating phytoplankton growth. CHL minima are associated with the summer stratification period (July-August, Figure 4.d). However, photo-acclimation has been claimed to explain this CHL annual cycle which is dominated by low light conditions and nutrient enhancement during winter and the opposite during summer (Behrenfeld et al., 2005; Bellacicco et al., 2016).

The first PP mode explains 76.2% of its total variance (Figure 3.e), with areas of distinct variability. The highest variability is found in the coastal northern Adriatic Sea, where allochthonous nutrient inputs from rivers are well known to sustain elevated coastal productivity (Penna et al., 2004; Nixon, 2003, Cossarini et al. 2020). However, the PP signal in this region should be regarded with care because this area is characterized by optically complex waters and the PP model bio-optical parameterization derives from open-ocean conditions. Other coastal areas of significant variability are the straits of Gibraltar and the Dardanelles, where lateral advection of nutrient-enriched waters drives a clear seasonal signal, and with the open waters of the Ligurian Sea and the Gulf of Lion, reflecting the influence of winter convective mixing and the ensuing nutrient supply to the euphotic zone. This interpretation is consistent with Mediterranean biogeochemical studies showing that nutrient availability and primary production patterns are strongly shaped by hydrodynamic forcing, riverine inputs, and mixed-layer dynamics in key productive and convective regions of the basin (Cossarini et al., 2020; Reale et al., 2020). The remaining basin presents comparatively low annual PP 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 (Figure 4.e). This seasonal phasing perfectly matches PAR annual cycle (Figure 4.c) and SST (Figure 4.b), but in striking opposition of phase with CHL (Figure 4.d), whose maxima occur in late winter. This apparent paradox, maximum primary production when chlorophyll concentration is at its annual minimum, and vice versa, is a well-documented characteristic of the Mediterranean Sea and of oligotrophic gyres (Behrenfeld et al., 2005; Mignot et al., 2014; Bellacicco et al., 2016). The mechanistic explanation for this decoupling lies in the contrasting seasonal forcings that govern CHL and PP. In winter, deep convective mixing entrains nutrient-rich subsurface waters into the euphotic zone, stimulating phytoplankton growth and elevating bulk CHL concentrations. However, the concurrent low irradiance, as captured by the PAR minimum, limits the rate of photosynthetic carbon fixation, keeping PP suppressed despite high CHL values. Conversely, in summer, the development of strong thermal stratification reduces the vertical supply of nutrients to the euphotic layer, in agreement with Mediterranean biogeochemical studies linking nutrient availability to mixed-layer dynamics, and CHL declines to its seasonal minimum (Reale et al., 2020). Yet the high irradiance characteristic of the Mediterranean summer (PAR maximum) drives intense photosynthetic activity per unit biomass, sustaining elevated PP under otherwise oligotrophic conditions. This light-driven enhancement of summer PP is compatible with the process of cellular photo-acclimation: under high irradiance, phytoplankton reduce their cellular chlorophyll-to-carbon ratio, so that bulk CHL decreases even if photosynthetic rates remain elevated (Behrenfeld et al., 2005; Bellacicco et al., 2016). The first EOF mode of PP therefore captures a predominantly light-driven signal rather than one driven by nutrient or biomass dynamics, with PAR emerging as the primary modulator of the annual PP cycle at the Mediterranean basin scale. The alignment between the PP and PAR temporal amplitudes (Figure 4.e and c) directly reflects this dominant physical control.

It is worth mentioning that nearly the total variability of light (98%) and temperature (97%) is linked to the annual cycle while there is still a substantial part of variability to be explained for MLD, CHL and PP.

The first mode of phytoplankton CHL (Figure 4.d) presents high correlation values at lag zero with both SST (Figure 4.b, $r = -0.93$) and MLD (Figure 4.a, $r = 0.8$). Although part of this variability can surely be explained in terms of photo-acclimation (Bellacicco et al., 2016), it is likewise a clear sign of the winter cooling that deepens the MLD in turn favouring nutrients into the upper water column. This promotes biomass accumulation. Analogously, the first mode of PP (Figure 4.e) is highly correlated with the first mode of PAR (Figure 4.c, $r = 0.98$, at lag zero) which in turn also drives the SST first mode with two months lag (Figure 4.b, $r = 0.97$).

Phytoplankton size diversity (PSC) is perfectly in line with CHL (Figure 3.d and Figure 4.d), as shown in Figure B 3.a,b,c and Figure B 4.a,b,c, with maxima in winter and minima in summer. We did use the same colorbar range in Figure B 3, just to show that Micro, being the less dominant and frequent (Figure 2), 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.

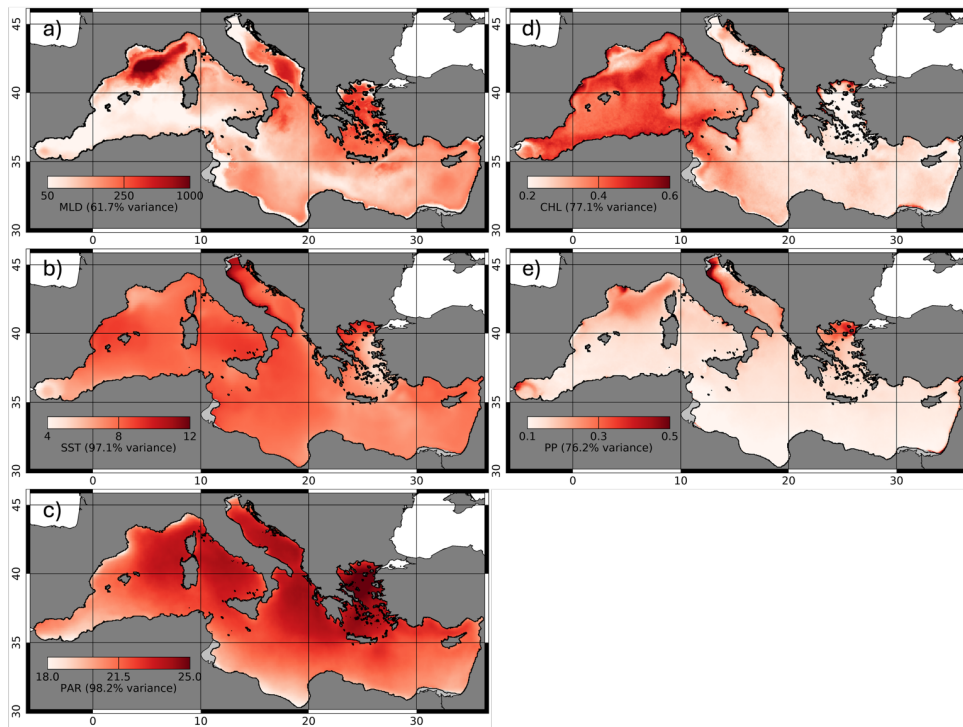
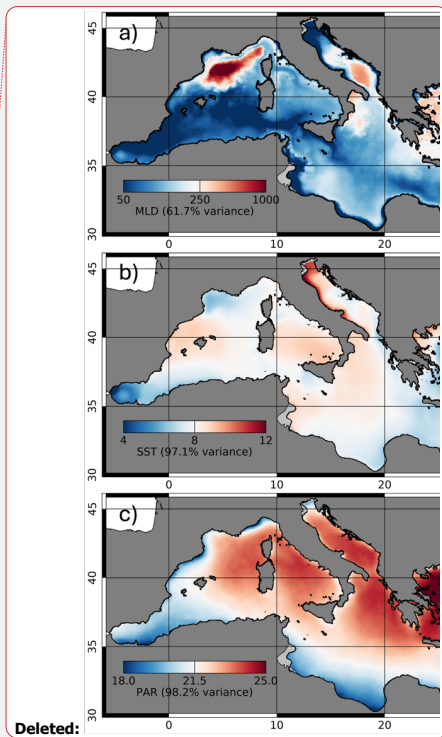


Figure 3 – Spatial patterns of the first mode of EOF for MLD (a), SST (b), PAR (c), CHL (d), and PP (e). Light grey indicates the areas permanently masked out because of persistent or recurrent Case II water conditions.



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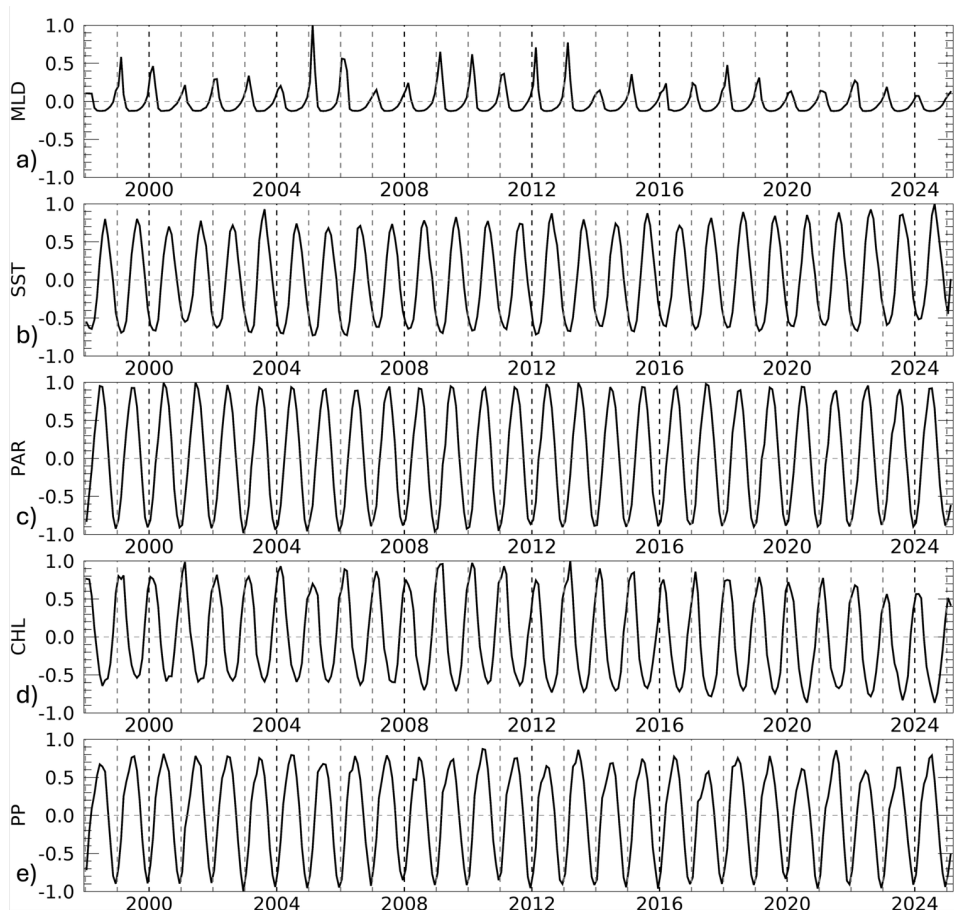


Figure 4 – First mode of EOF MLD (a), SST (b), PAR (c), CHL (d), and PP (e) temporal evolutions.

385 3.2.2 Sub-basin seasonal variability: spring bloom and deep-water formation

The second EOF mode computed over the MLD (Figure 5.a) explains 14% of its total variability and presents two spatially distinct regions in opposition of phase: the Gulf of Lion on one side and the rest of the basin on the other. This spatial opposition suggests that this mode captures localised deep convection dynamics rather than the basin-scale annual signal dominated by

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the first EOF mode. The temporal amplitude (Figure 6.a) 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 anomalous years have already been correlated with positive-to-negative North Atlantic Oscillation (NAO) transition (Basterretxea et al., 2018) which intensify northerly winds over the Gulf of Lion and favour deep-water formation events. Taken together, the spatial and temporal signals of this mode can be interpreted as representing sub-basin scale deep-water formation, with the Gulf of Lion as the primary driver, largely decoupled from the smoother seasonal pattern described by the first mode.

Figure 5.b displays the second EOF mode of SST (1.2% of the total variance) with a clear northwest–southeast gradient, with predominantly positive anomalies in the western Mediterranean and negative values over the Levantine Basin. The northern Aegean Sea constitutes an exception within the eastern sub-basin, showing positive variability. This spatial pattern closely resembles that reported by Volpe et al. (2012), despite the longer time series used here. The corresponding temporal amplitude (Figure 6.b) shows a regular seasonal cycle, with positive values typically from January to August–September and negative values during the remaining months. Nevertheless, the amplitude of both maxima and minima varies considerably from year to year, reflecting interannual modulation likely linked to large-scale atmospheric forcing such as the NAO, consistent with the variability identified in the MLD second mode.

The second EOF mode of PAR (Figure 5.c) explains only 0.6% of the total variance, confirming that PAR variability is largely dominated by the annual cycle. Its spatial pattern shows a weak dipole-like structure between the northwestern Mediterranean and the Levantine sub-basin. This residual signal may partly reflect non-seasonal modulation of cloud cover and surface shortwave radiation by atmospheric circulation patterns, but its physical interpretation remains uncertain and a contribution from noise cannot be excluded. Therefore, the second mode of PAR is not considered a robust component of the deep-water formation and spring bloom mechanism discussed in this section.

The second EOF mode of CHL (Figure 5.d) explains 5.6% of the total variance is spatially coherent with the MLD and SST second modes and aligns well with the results of Volpe et al. (2012). 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 limited variability. This pattern is clearly linked to spring bloom dynamics: the deep winter mixing captured by the MLD second mode in the Gulf of Lion supplies nutrients to the euphotic zone, and the subsequent restratification in spring, consistent with the SST second mode gradient, triggers intense phytoplankton growth. The temporal amplitude (Figure 6.d) confirms this interpretation, displaying recurring positive peaks during the spring months and negative values throughout winter and summer, with an interannual variability in bloom intensity.

The PP second EOF mode (Figure 5.e) explains 7.6% of the variance and exhibits widespread positive variability throughout the Mediterranean basin, with negative values confined to the Adriatic Sea, Aegean Sea and along African coasts of the Levantine basin. This broader spatial signature, compared to the more localised chlorophyll second mode, suggests that PP integrates the regional bloom signal of the northwestern Mediterranean with a diffuse positive response across the open basin, possibly linked to the increased light availability. The temporal amplitude (Figure 6.e) follows CHL maxima in correspondence

425 of the spring months but exhibits a faster and deeper decay during summer, with more intense negative minima than those
observed in the CHL temporal signal. This asymmetry indicates that PP is more sensitive than CHL to the combined effect of
nutrient depletion and reduced mixing in the post-bloom period.

Consistently with previous findings (Volpe et al., 2012), minima in the second mode of SST (Figure 6.b), that are likely
associated with the pre-conditioning phase to deep-water formation in the Gulf of Lion, have the potential to drive the late-
430 winter bloom in PP (Figure 6.e, $r = -0.8$ with four months lag) in turn sustaining phytoplankton CHL accumulation (Figure
6.d, $r = 0.74$) with one month lag with respect to PP peaks.

PSC second modes (Figure B 3.d,e,f and Figure B 4.d,e,f) perfectly align with the CHL second mode (Figure 5.d and Figure
6.d), exhibiting the dynamics of the spring bloom in response to the deep convection. This is consistent with the considerations
expressed for both the average fields and the annual cycle variability. As in the first mode, the spatial intensity expressed by
435 the second mode increases with the size classes, although less evidently. This indicates that during deep mixing nutrient
abundance sustains the entire phytoplankton community. This is consistent with classical and trait-based phytoplankton size
theory, according to which larger cells, particularly diatoms, are generally favoured under nutrient-rich and turbulent
conditions, whereas smaller cells are more competitive under stratified and oligotrophic conditions (Margalef, 1978; Litchman
and Klausmeier, 2008; Finkel et al., 2010). This is reflected here in the increasing extension of the blooming area with
440 phytoplankton size.

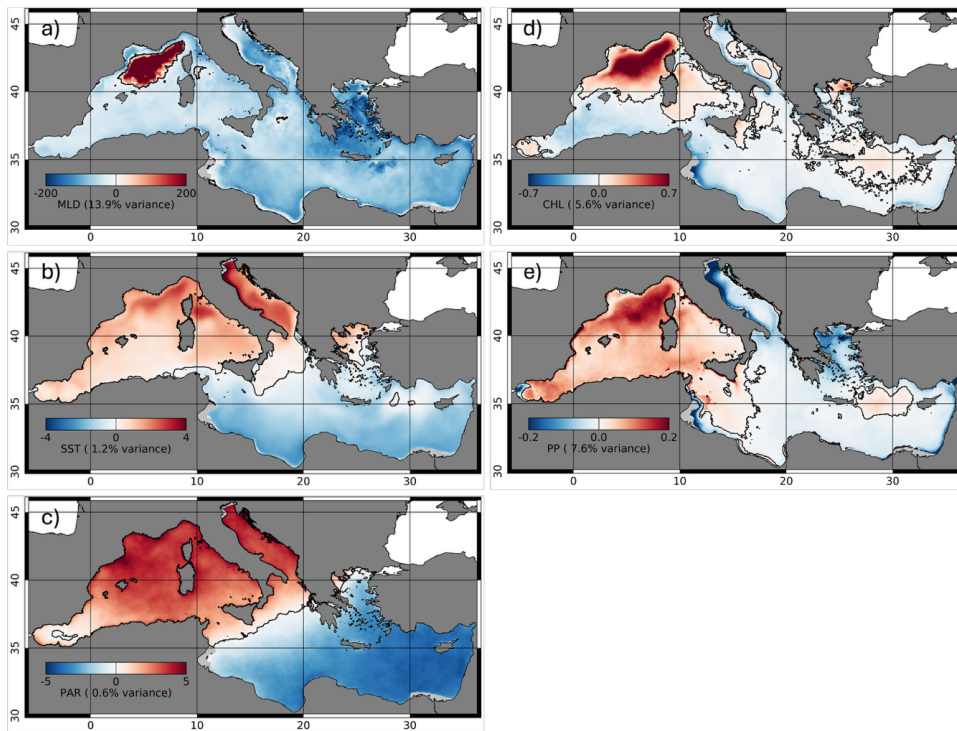
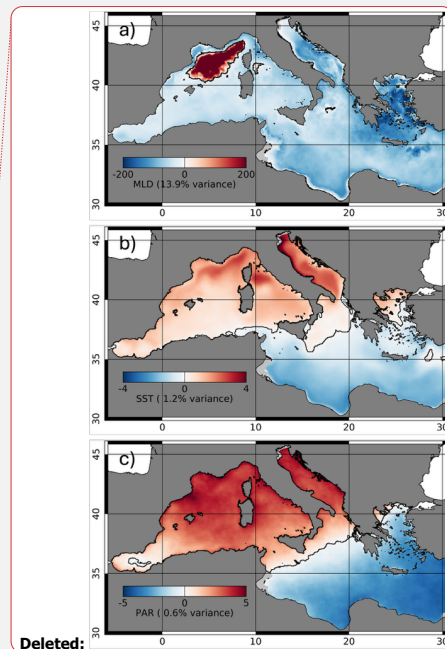


Figure 5 – Second mode of EOF variability for MLD (a), SST (b), PAR (c), CHL (d) and PP (e) spatial patterns. Light grey indicates the areas permanently masked out because of persistent or recurrent Case II water conditions.



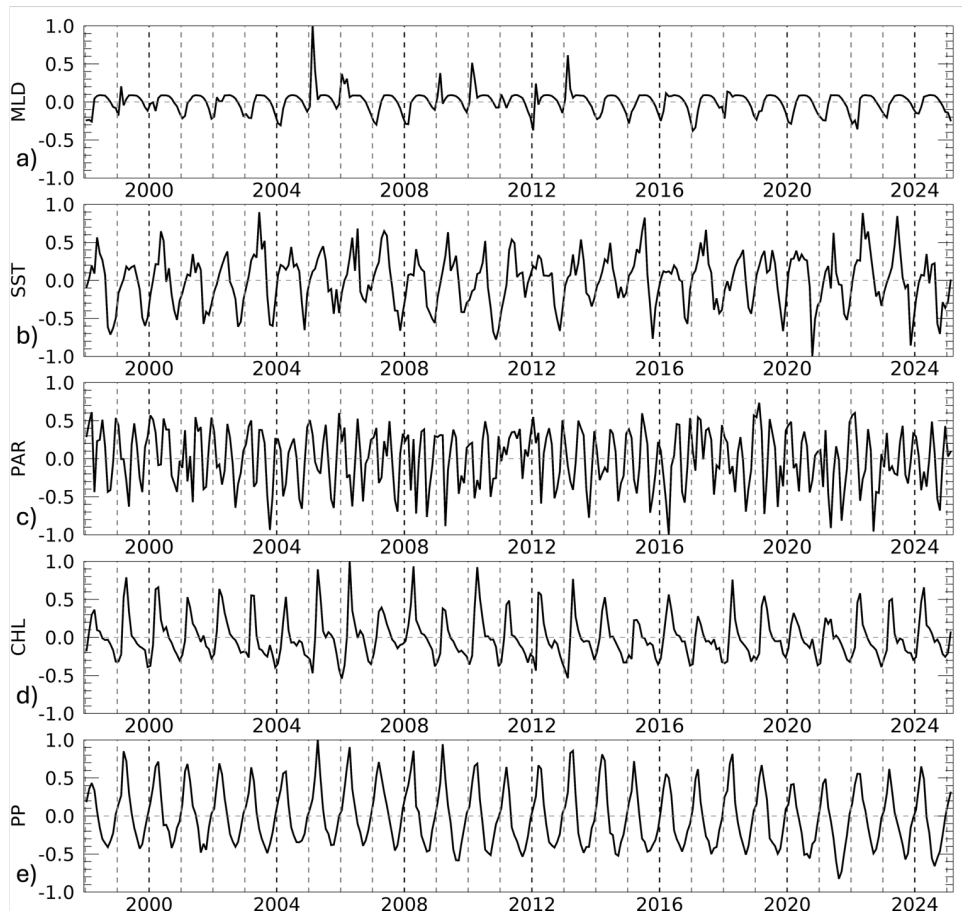


Figure 6 – Second mode of EOF MLD (a), SST (b), PAR (c), CHL (d), and PP (e) temporal evolutions.

3.2.3 Multivariate EOF (MEOF) analysis

450 The first MEOF mode (Figure 7) represents 68% of the total multivariate variance and identifies the dominant shared variability across the physical and biological variables. The temporal component (Figure 7.f) is a nearly perfect sinusoid with an annual

period (summer maxima in July), stable amplitude, and no appreciable long-term trend across the entire 1998–2025 record, confirming that the dominant mode of co-variability across all five variables is the annual cycle driven by solar radiation and surface heating. Variance of this mode is however notably lower than the variance explained by the first modes of the univariate EOFs of PAR and SST (98% and 97%, respectively), which almost entirely capture the annual cycle of their respective fields. In the multivariate framework, a single temporal amplitude must simultaneously represent all five variables, and since MLD and CHL exhibit annual cycles that differ in phase and shape from those of PAR and SST, a fraction of the total variance is necessarily redistributed to higher MEOF modes.

MLD and CHL spatial variabilities are uniformly negative across the basin, confirming that these two variables are in anti-phase with the seasonal solar-thermal forcing embedded in the temporal amplitude: MLD deepens and CHL peaks in winter, when the amplitude is negative. MLD shows the highest variability in the deep-water formation areas (Gulf of Lion and south Adriatic Sea) while CHL variability is larger in the western than in the Levantine basin. Notably, as in the univariate first EOF modes, the signature of the Algerian Current splitting into two branches is clearly recognizable here in both the MLD and CHL spatial patterns.

SST, PAR and PP variabilities are everywhere positive and in phase with temporal amplitude. Their spatial patterns are consistent with the dominant seasonal structures described by the univariate analyses, indicating that PP is organized around a physically coherent seasonal cascade: solar radiation heats the surface, stratifies the water column, suppresses deep mixing and nutrient supply, reduces phytoplankton biomass, yet sustains high photosynthetic rates per unit biomass, producing the summer PP maximum under oligotrophic conditions.

The second MEOF mode (Figure 8) accounts for 22% of the total multivariate variance and identifies the main secondary mode of shared variability across the physical–biological system. This mode is associated with the coupled spring-bloom response. Although several features are consistent with those found in the univariate second EOFs, the MEOF mode reflects shared covariance among variables rather than a direct correspondence with individual univariate EOF modes.

The temporal amplitude (Figure 8.f) displays a regular seasonal cycle with positive values in spring and negative values in late summer through winter, with clear interannual variability in peak shape and magnitude. This temporal structure is consistent with the springtime variability described by CHL and PP, indicating that this MEOF mode is mainly associated with the spring bloom signal and its interannual modulation.

The MLD (Figure 8.a) shows positive variability concentrated in the Gulf of Lion and Ligurian Sea but extends more broadly into the Aegean Sea and parts of the eastern Mediterranean. This spatial footprint suggests that, within the multivariate mode, MLD contributes through a broader mixing/preconditioning signal across multiple convection-prone areas of the basin, rather than through a signal confined to the Gulf of Lion.

The SST (Figure 8.b) is negative across the whole basin, with the largest anomalies in the western Mediterranean and northwestern coastal areas. This pattern is physically consistent with post-convection cooling and with the seasonal thermal preconditioning that precedes the spring bloom.

485 The PAR (Figure 8.c) is positive across the entire basin, with highest values in the western and central Mediterranean. The positive PAR values, in phase with the positive MLD and the negative SST, suggests that the second MEOF mode represents the transition from winter deep mixing to spring re-stratification, during which increasing irradiance acts as the trigger for phytoplankton growth.

CHL variability (Figure 8.d) shows pronounced positive anomalies in the Gulf of Lion and surrounding northwestern

490 Mediterranean regions, indicating that spring bloom dynamics strongly contribute to this multivariate mode.

The PP variability in the second MEOF mode (Figure 8.e) shows high variability mainly in the Gulf of Lion, emphasizing the productive bloom response of the northwestern Mediterranean and its tight link with CHL, in contrast with the more stable oligotrophic conditions of the eastern basin.

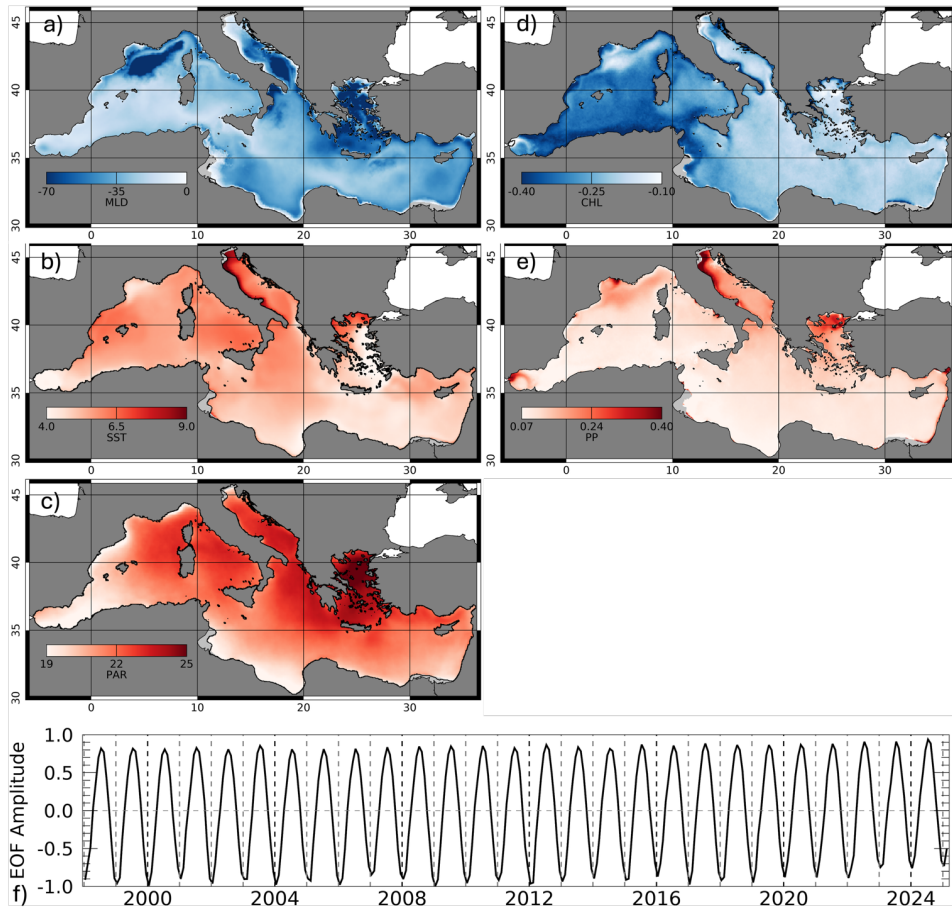
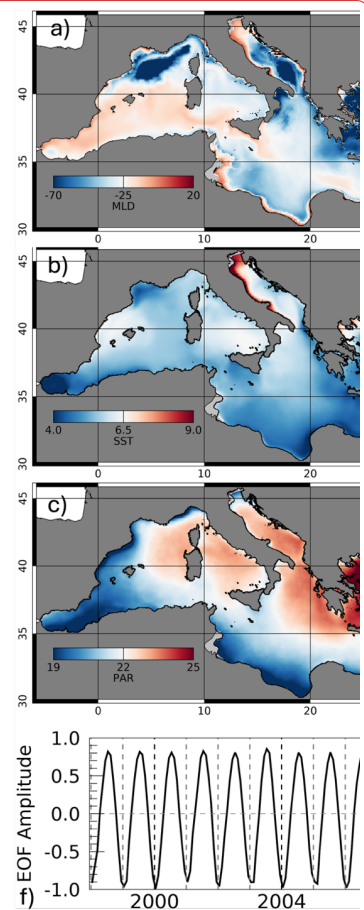


Figure 7 – First mode of MEOF of MLD (a), SST (b), PAR (c), CHL (d) and PP (e) spatial patterns and temporal evolution (f). Light grey indicates the areas permanently masked out because of persistent or recurrent Case II water conditions.



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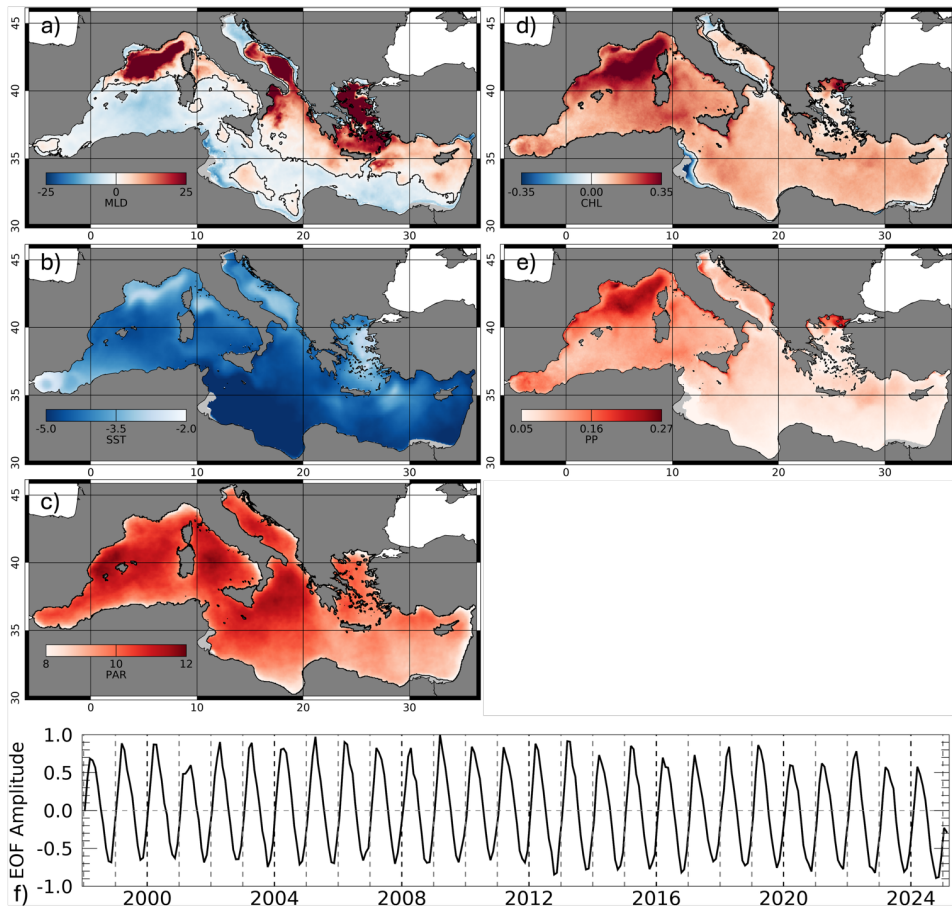
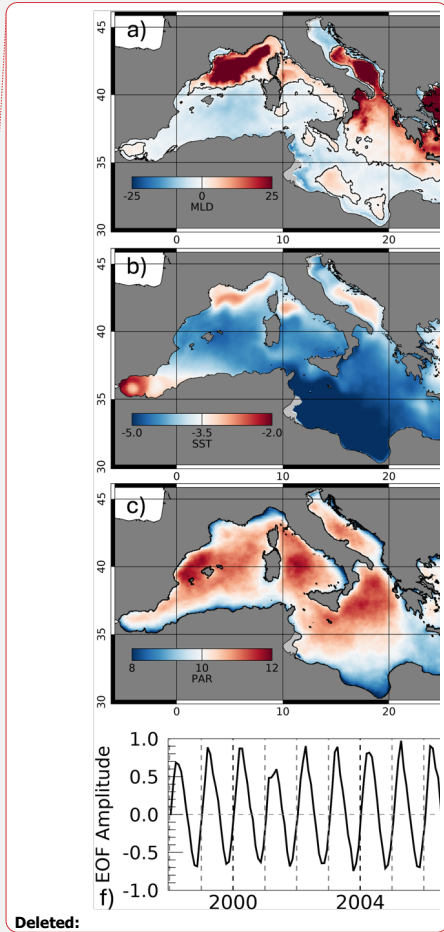


Figure 8 – Second mode of MEOF of MLD (a), SST (b), PAR (c), CHL (d) and PP (e) spatial patterns and temporal evolution (f). Light grey indicates the areas permanently masked out because of persistent or recurrent Case II water conditions.

4 Summary and Conclusions

505 This study presented a comprehensive analysis of the physical–biological coupling in the Mediterranean Sea over the period 1998-2025, characterising the space-time variability of phytoplankton biomass, size structure, and primary production and



their relationships with sea surface temperature, photosynthetically available radiation, and mixed layer depth. Building on the methodological framework of Volpe et al. (2012), the analysis was extended in several main directions: the extension of the time series until 2025, the inclusion of PP and PSC alongside CHL, the replacement of sea level anomaly with mixed layer depth as a proxy for upper-ocean dynamics, and the addition of a multivariate EOF approach to simultaneously decompose the coupled biological-physical system. The combined univariate and multivariate framework enabled a robust characterisation of the dominant modes of seasonal and interannual variability and of the mechanistic links between physical forcing and ecosystem response.

The mean fields computed over the full 27-year record confirm the well-established physical-biological structure of the Mediterranean basin. A pronounced west-east gradient characterises CHL and PP, with higher values in the western basin driven by enhanced vertical mixing and nutrient supply, and progressively oligotrophic conditions toward the Levantine basin. MLD confirmed the Gulf of Lion as the dominant deep-water formation site of the basin, whose mixing signal leaves a clear imprint on phytoplankton abundance and productivity. Phytoplankton size structure is consistent with regional trophic conditions: microphytoplankton dominance is confined to river-influenced coastal areas and the deep-mixing zone of the northwestern Mediterranean, nanophytoplankton is widespread in the western basin and semi-enclosed seas, while picophytoplankton dominates the oligotrophic open waters of the eastern Mediterranean more than 75% of the time. A direct comparison with Volpe et al. (2012), whose climatology spanned only nine years, reveals a detectable basin-scale warming of up to 5% in SST (with possible links to the higher frequency of the marine heatwaves) accompanied by a corresponding decrease in CHL of up to 20%, consistent with a long-term oligotrophication driven by intensified thermal stratification.

The EOF and MEOF analyses consistently identified two dominant modes of variability in the Mediterranean physical-biological system. The first mode represents the basin-scale annual cycle and explains most of the total variance. It reflects the seasonal interplay between solar radiation, surface heating, stratification, mixed-layer dynamics, and biological response, highlighting the contrasting seasonal behaviour of phytoplankton biomass and primary production. In particular, primary production follows light availability more closely than chlorophyll concentration, consistent with the role of photoacclimation in shaping the seasonal chlorophyll cycle in oligotrophic environments.

The second mode captures the sub-basin spring-bloom dynamics of the northwestern Mediterranean and its interannual modulation. This mode links winter deep convection, nutrient replenishment, spring restratification, and the subsequent enhancement of phytoplankton biomass and primary production. While chlorophyll and primary production exhibit different relationships at the annual scale, they become more closely coupled during bloom conditions, when biological variability is more directly associated with biomass accumulation.

The multivariate EOF analysis further demonstrates that these annual-cycle and spring-bloom regimes are coherent coupled modes emerging from the covariance between physical forcing and biological response, thereby providing an integrated description of Mediterranean ecosystem variability.

Despite the robustness of the framework adopted, several limitations should be acknowledged. The present analysis is deliberately centred on the abiotic forcing of phytoplankton variability, and biotic processes, such as top-down grazing control

Deleted: The first EOF modes of all variables are dominated by the annual cycle and collectively explain the large majority of total variance. CHL and MLD peak in winter and are in anti-phase with SST and PAR, which attain their maxima in summer. This seasonal opposition reflects the nutrient-light trade-off that governs Mediterranean phytoplankton dynamics: winter deep convection supplies nutrients to the euphotic zone and drives biomass accumulation (CHL maximum), while summer stratification depletes nutrient availability despite maximum irradiance. Remarkably, the first EOF mode of PP is in phase with PAR and SST and in anti-phase with CHL, demonstrating that annual primary production variability at the basin scale is primarily light-driven rather than biomass-driven, a decoupling attributable to cellular photo-acclimation and well-documented in oligotrophic systems. The tight correlation between the PP and PAR temporal amplitudes ($r = 0.98$ at zero lag) confirms PAR as the dominant physical modulator of the annual PP cycle.[‡]

The second EOF modes capture localised, sub-basin-scale variability superimposed on the annual cycle. The second MLD mode isolates the interannual modulation of Gulf of Lion deep-water formation, driven by NAO-controlled Mistral variability. This convective signal propagates sequentially through the biological system, from anomalous SST pre-conditioning to late-winter nutrient enrichment, spring bloom onset, and lagged biomass accumulation, as confirmed by the cross-correlations between SST, CHL, and PP temporal amplitudes. The second PP mode exhibits a broader spatial signature, integrating the northwestern bloom with a diffuse basin-scale response to increased spring irradiance.[‡] PP and CHL are uncoupled at the scale of the annual cycle but result to be closely linked at the scale of the bloom. This lack of consistency in the PP-CHL relationship across the two modes of variability should be attributed to photoacclimation dominating CHL annual cycle whose signal only partly represents a biomass oscillation. On the other hand, CHL variability associated with the spring bloom dynamics appears less affected by this phenomenon thus resulting in a stronger coupling with PP.[‡]

The multivariate EOF analysis adds value to the univariate decomposition by identifying the dominant modes of variability shared by all variables, rather than analysing each field independently. It therefore confirms that the annual light-temperature forcing and the spring bloom response are not isolated features of individual variables, but coherent coupled modes of the Mediterranean physical-biological system. The first MEOF mode captures the dominant annual cycle driven by solar radiation and surface heating. Its temporal amplitude is a near-perfect sinusoid with stable interannual amplitude, indicating no detectable long-term trend in the dominant seasonal forcing over the study period. MLD and CHL show negative variability pattern, confirming their winter maxima, while SST, PAR, and PP positive variability values are in phase with the summer maximum. The second MEOF mode represents a coupled spring-bloom response and its interannual variability, mainly expressed by CHL and PP, while MLD and SST describe the associated physical preconditioning. In this multivariate framework, the MLD variability highlights the contribution of several convection-prone regions, including the Gulf of Lion and the Aegean Sea, while the PP signal emphasizes the productive response of the northwestern Mediterranean, supporting the tight link between convective productivity and phytoplankton biomass accumulation in this dynamically active region.[‡]

by zooplankton, inter-specific competition among phytoplankton functional types, and nutrient recycling mediated by the microbial loop, are not explicitly represented. This is an inherent constraint of the adopted method. As a consequence, a fraction of the residual variability, particularly at sub-seasonal timescales and at the local scale, may reflect biological processes that remain hidden in higher modes and outside the explanatory reach of the variables considered.

605 Taken together, the results establish a robust observational baseline for the interpretation of Mediterranean phytoplankton dynamics at seasonal to interannual scales. The analysis reveals a clear separation in the dominant controls of variability: the first mode, accounting for the bulk of the seasonal signal, is primarily driven by the light-temperature cascade (solar irradiance heating the surface, suppressing vertical mixing, and modulating photosynthetic rates) whereas the second mode, linked to the spring bloom dynamics of the northwestern Mediterranean, is driven by nutrient supply through episodic deep convection, 610 with biomass accumulation as the downstream biological response. The consistency between the univariate and multivariate frameworks, and the agreement with previous satellite-based studies, reinforce the reliability of the CMEMS multi-decadal products for ecosystem monitoring. At the same time, the emerging signals of warming-driven oligotrophication in the long-term mean fields underscore the need for continued observation and dedicated trend analyses. Future work should extend the present variability-focused approach to explicitly quantify long-term trends in CHL, PP, and PSC and their attributable physical 615 drivers, while also exploring the role of interannually varying atmospheric modes such as the NAO and East Atlantic Pattern in modulating the spring bloom intensity. Beyond these scientific directions, the results also point to potential improvements to the operational CMEMS processing chain. In particular, it would be valuable to incorporate phytoplankton size class information directly into the PP model parameterisation, given that larger and smaller cells differ substantially in their chlorophyll-specific absorption properties and photosynthetic quantum yields, a refinement that could improve the accuracy 620 of satellite-derived PP estimates across the trophic gradients of the Mediterranean basin.

5 Appendix A

The primary production (PP) model adopted in this study is based on the formulation originally developed by Antoine and Morel (1996), which links satellite-derived chlorophyll concentration to phytoplankton primary production through the coupling of an atmospheric radiative transfer model (Tanré et al., 1979) with a bio-optical representation of phytoplankton absorption and scattering processes (Morel, 1991).

Primary production is computed on a daily basis as a column-integrated quantity through the explicit resolution of spectral, temporal, and vertical variability of photosynthesis. Daily PP is expressed as:

$$P = 12 \int_{z=0}^{\text{Depth}} \int_{t=0}^{24} \int_{\lambda=400}^{700} \text{Chl}(z) a_{\text{Chl}}^* \text{PAR}(z, t, \lambda) \phi_{\mu}(\text{Chl}, T)(z) d\lambda dz dt \quad \text{Eq. 1}$$

where the factor 12 represents the Carbon molar mass, allowing PP to be expressed as mass of Carbon per square meter per day; $\text{Chl}(z)$ is the vertical chlorophyll concentration profile; a_{Chl}^* is the chlorophyll-specific absorption coefficient, parameterized as a function of chlorophyll concentration; $\text{PAR}(z, t, \lambda)$ is the photosynthetically available radiation at depth z , time t , and wavelength λ ; and $\phi_{\mu}(\text{Chl}, T)$ is the photosynthetic quantum yield, formulated as a function of chlorophyll concentration and temperature and expressing the efficiency of conversion of absorbed light into fixed carbon.

While initially conceived for global-scale applications, this framework has been specifically adapted to the Mediterranean Sea to account for the basin's distinctive bio-optical characteristics.

The computation of primary production relies on an accurate description of the spectral, spatial, and temporal variability of solar radiation reaching the ocean surface. In the Mediterranean configuration adopted here, atmospheric forcing is provided by the revised Ocean Atmosphere Spectral Irradiance Model (OASIM; Gregg and Casey, 2009), which represents the atmospheric radiative transfer component of the bio-optical framework.

OASIM is a physically based radiative transfer model that simulates the propagation of solar radiation through the atmosphere by accounting for absorption and scattering by atmospheric gases, aerosols, and clouds. The model resolves both direct and diffuse downwelling irradiance and provides spectrally resolved fluxes over the PAR range. In the CMEMS Mediterranean processing chain, OASIM delivers daily fields of downwelling spectral irradiance at 5 nm resolution between 400 and 700 nm, on a 4 km spatial grid, ensuring full consistency with satellite ocean-colour products and allowing an explicit coupling with wavelength-dependent bio-optical properties.

The Mediterranean implementation of OASIM has been specifically validated against independent in situ radiometric observations from the BOUSSOLE mooring and Biogeochemical Argo floats, demonstrating good skill in reproducing surface and subsurface irradiance across the PAR spectrum and supporting its suitability for regional applications (Lazzari et al., 2021).

The model is forced with ancillary atmospheric data including cloud properties (cloud cover, liquid water path and optical thickness), surface meteorological variables (sea-level pressure, wind speed and humidity), atmospheric absorbing gases (notably ozone and water vapour), and aerosol optical properties. These inputs are derived from a combination of operational

atmospheric reanalyses (e.g. ECMWF products) and satellite-based climatologies, ensuring temporally resolved (daily) forcing consistent with the ocean-colour and bio-optical datasets used in the primary production model.

655 The marine bio-optical component of the primary production model describes how solar radiation, once transmitted through the atmosphere, is attenuated and spectrally transformed within the water column and made available to phytoplankton photosynthesis. It follows the spectral light–photosynthesis framework originally developed by Antoine and Morel (1996), which provides a mechanistic coupling between underwater light fields, phytoplankton biomass distribution, and photosynthetic response.

660 In this framework, PAR is explicitly resolved as a function of wavelength, depth, and time. Light propagation within the water column is governed by absorption and scattering by water itself and by optically active constituents, primarily phytoplankton pigments and associated particles. As a result, the vertical chlorophyll concentration profile plays a dual role: it quantifies phytoplankton biomass and simultaneously controls the attenuation and spectral composition of light with depth.

The interaction between the underwater spectral irradiance field and phytoplankton biomass is mediated by the chlorophyll-specific absorption coefficient, a_{chl}^* , which determines the chlorophyll efficiency in absorbing photons at each wavelength. 665 The absorbed radiant energy is then converted into fixed carbon through photosynthesis, with an efficiency described by the photosynthetic quantum yield, ϕ_μ . Together, a_{chl}^* and ϕ_μ link light availability to local photosynthetic rates, ensuring consistency between optical conditions and phytoplankton physiological response.

Following the original formulation, the realized quantum yield is expressed as a fraction of its maximum value, $\phi_{\mu,\text{max}}$, through a dimensionless light-response function:

$$\phi_\mu = \phi_{\mu,\text{max}} f(x), \quad \text{Eq. 2}$$

670 where $x = \text{PUR}/K_{\text{PUR}}$, PUR is the photosynthetically usable radiation, and K_{PUR} is a scaling irradiance controlling the transition between light-limited and light-saturated photosynthesis. The function $f(x)$ follows the formulation of Platt et al. (1980), accounting for saturation and photoinhibition effects. Temperature influences photosynthesis indirectly through its effect on K_{PUR} , which is parameterized using an Eppley-type formulation:

$$K_{\text{PUR}}(T) = K_{\text{PUR}}(20^\circ\text{C}) 1.065^{(T-20)}. \quad \text{Eq. 3}$$

Through this mechanism, temperature modulates the photosynthesis–irradiance response without altering either the functional 675 form of $f(x)$ nor the definition of $\phi_{\mu,\text{max}}$.

In the original model, the $\phi_{\mu,\text{max}}$ and the maximum chlorophyll-specific absorption coefficient a_{max} was assumed constant under the hypothesis that opposite variations of the two quantities compensate each other. Consistently with this assumption, the spectral shape and magnitude of the chlorophyll-specific absorption coefficient were also treated as invariant. In the present

study, following Bricaud et al. (1998), chlorophyll-specific absorption spectra are instead allowed to vary in both magnitude and spectral shape as a function of chlorophyll concentration, thereby breaking the assumption of a constant $\phi_{\mu, \max} a_{\max}$ product and requiring an explicit representation of their variability. Following Morel et al. (1996), the maximum quantum yield is therefore expressed as a function of chlorophyll concentration:

$$\phi_{\mu, \max} = 0.05 \frac{\text{Chl}^{0.66}}{0.44 + \text{Chl}^{0.66}}. \quad \text{Eq. 4}$$

This formulation accounts for observed photo-physiological adaptations across trophic regimes while preserving the original representation of light and temperature effects on photosynthesis. By explicitly introducing chlorophyll dependencies in both $a_{\max}$ and $\phi_{\mu, \max}$, the present model makes explicit the physiological variability that was implicitly embedded in their constant product in the original formulation.

Since remote sensing observations provide chlorophyll information only for the surface layer, vertical chlorophyll distributions must be reconstructed in order to compute depth-integrated primary production. This reconstruction follows the empirical approach of Morel and Bérthon (1989), which relates satellite-derived surface pigment concentration to both the total chlorophyll content within the euphotic zone and the shape of the vertical chlorophyll profile.

For the Mediterranean Sea, the empirical reconstruction of vertical chlorophyll structure has been revisited using the MedBiOp in situ dataset (Volpe et al., 2019). Each measured vertical chlorophyll profile is first normalized by dividing chlorophyll concentration at each depth by the mean chlorophyll concentration within the euphotic zone, while depth is normalized by the euphotic depth. This normalization places all profiles on a common, dimensionless vertical coordinate, allowing structures with different magnitudes and depth ranges to be directly compared.

The normalized profiles are then classified using a k-means clustering technique, resulting in seven groups representative of distinct Mediterranean trophic regimes. For each cluster, a mean normalized vertical chlorophyll profile is computed (Figure A 1) and subsequently parameterized using the analytical function:

$$\text{CHL}(\zeta) = A - B\zeta + C \cdot \exp\left[-\frac{(\zeta - D)^2}{2E^2}\right], \quad \text{Eq. 5}$$

where $\text{CHL}(\zeta)$ is chlorophyll normalized by the euphotic zone mean and ζ is normalized depth (depth divided by euphotic depth). This formulation captures both monotonic decay and the possible occurrence of a subsurface chlorophyll maximum.

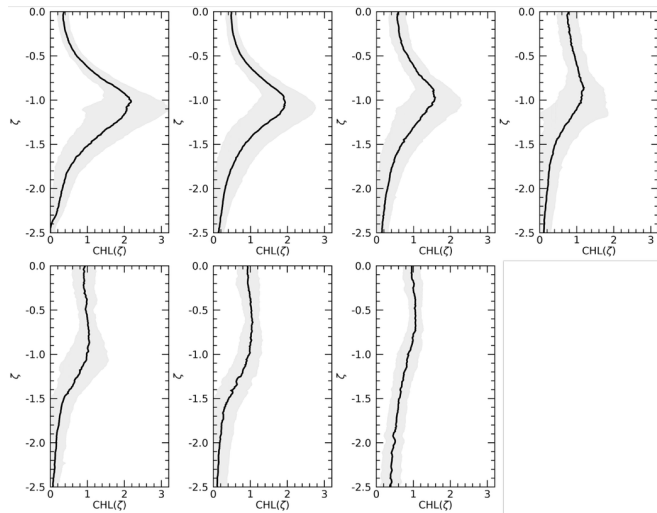


Figure A 1 – normalized mean chlorophyll profiles for each cluster and their standard deviation (grey shadow)

To enable application to satellite data, the parameters A , B , C , D , and E are expressed as fourth-degree polynomial functions of the logarithm of surface chlorophyll concentration. The polynomial relationships are derived during the calibration phase using the mean surface chlorophyll concentration associated with each trophic class identified through clustering:

$$Param = a + b \log Chl + c \log Chl^2 + d \log Chl^3 + e \log Chl^4 \quad \text{Eq. 6}$$

where $Param$ represents each of the five parameters A - E and a - e are polynomial regression coefficients (Table A 1). Once the polynomial coefficients are determined, the relationships are applied operationally using satellite-derived surface chlorophyll concentration to estimate the corresponding set of parameters A - E for each pixel. Through this two-step parameterization, functional representation of mean normalized profiles and polynomial linkage to surface chlorophyll, a continuous vertical chlorophyll profile can be reconstructed on a pixel-by-pixel basis. The method therefore provides pixel-specific estimates of vertical chlorophyll structure consistent with observed Mediterranean trophic regimes.

Table A 1 - coefficients (a-e) as derived by the polynomial regression (Eq. 6) to estimate the five parameters (A-E) to be used in Eq. 5 to obtain the chlorophyll vertical profile from satellite observation

	A	B	C	D	E
a	0.8755	0.3540	0.4556	0.8229	0.3827

b	-0.0544	-0.1707	0.0235	-0.1910	0.1297
c	-0.1769	-0.5926	-0.1879	-0.3334	-0.0333
d	0.4562	-0.1325	-1.812	-0.5699	-0.1379
e	0.2654	0.0744	-0.8461	-0.2413	-0.0474

715 Figure A 2 compares the Mediterranean reconstructed vertical chlorophyll profiles with the global parameterizations of Morel and Berthon (1989) and Uitz et al. (2006), highlighting systematic regional differences in profile shape and vertical structure. The Mediterranean profiles exhibit subsurface chlorophyll maxima that are generally shallower and less pronounced than those predicted by the Morel and Berthon formulation, while remaining deeper and more intense than those derived from the Uitz et al. (2006). The normalized depth of the maximum tends to occupy an intermediate position between the two global parameterizations.

720 In oligotrophic conditions (low surface chlorophyll), the near-surface structure of the Mediterranean profiles is broadly consistent with global reconstructions. However, as surface chlorophyll increases toward mesotrophic and eutrophic regimes, Mediterranean profiles display comparatively lower chlorophyll concentrations in the upper layer and a reduced vertical

725 contrast between surface waters and the deep chlorophyll maximum, suggesting a more vertically distributed biomass structure.

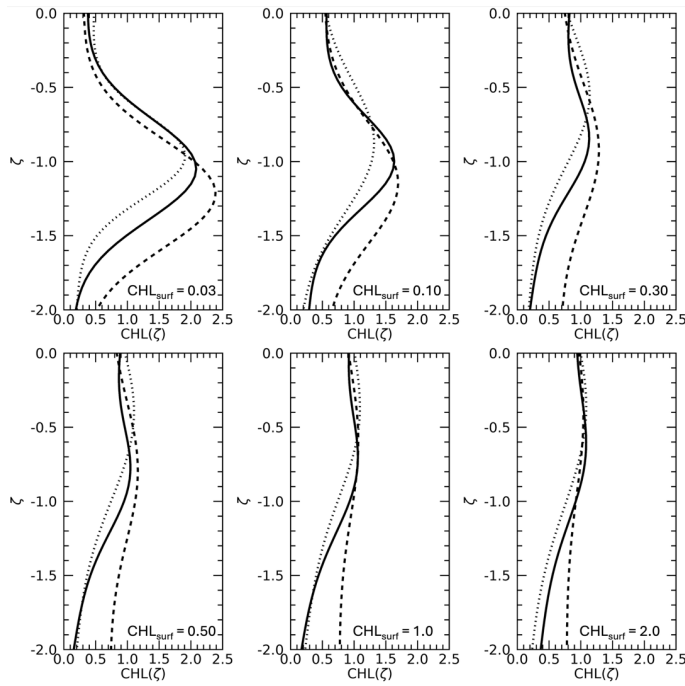


Figure A 2 – reconstructed vertical chlorophyll profiles from the Mediterranean model (solid lines), Morel and Berton (1989) (dashed lines) and Uitz et al. (2006) (dotted lines). The surface chlorophyll concentration (CHLsurf) is indicated in the bottom-right corner of each panel.

730 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 primary production (PP) variability, we performed a sensitivity analysis following the approach of Tilstone et al. (2015). Mean values and natural variability ranges were first defined for all model input parameters based on the observational and climatological datasets used in the primary production computation. PP was then estimated by varying each parameter independently across its range while maintaining all other variables fixed at their mean values. This one-at-a-time (OAT) approach allows the relative contribution of each driver to PP variability to be isolated and quantified.

735 The resulting spread in modelled PP provides a measure of the sensitivity of primary production to each parameter. As shown in Figure A 3, the largest variability in PP is associated with chlorophyll concentration, followed by temperature and, to a lesser extent, daylight duration (photoperiod).

740 The strong sensitivity to chlorophyll reflects the central role of phytoplankton biomass in determining primary production, as chlorophyll directly controls both light absorption and the magnitude of photosynthetic carbon fixation. Temperature exerts a secondary influence by modulating the photosynthesis–irradiance response through its effect on physiological rates, while variations in daylight primarily affect the temporal integration of photosynthesis rather than its instantaneous efficiency.

Overall, this ranking highlights phytoplankton biomass as the dominant predictor of primary production variability in the

745 model, with physical drivers such as temperature and light acting mainly as modulators that regulate the efficiency and seasonal expression of photosynthetic activity.

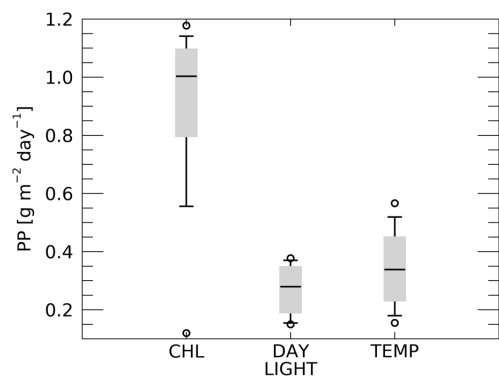
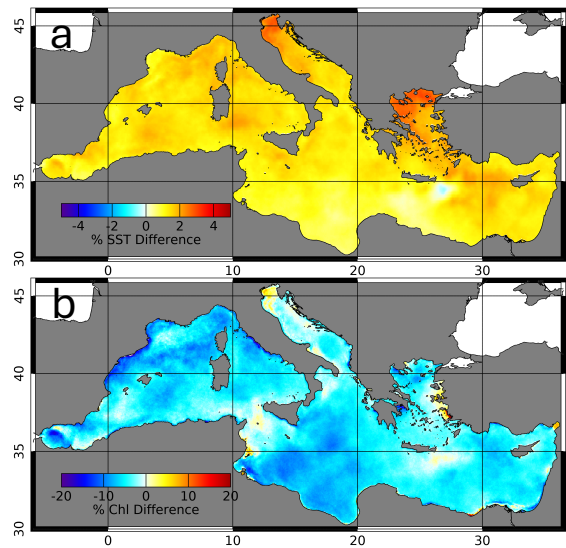


Figure A 3 – Sensitivity analysis of PP. The grey rectangles represent the interquartile range (25th–75th percentiles) of PP estimates obtained by varying each parameter individually. The horizontal line within each box marks the median (50th percentile). Whiskers denote the 10th and 90th percentiles, while circles indicate the minimum and maximum PP values. The abscissa indicates the input parameters analyzed.

750



755 Figure B 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).

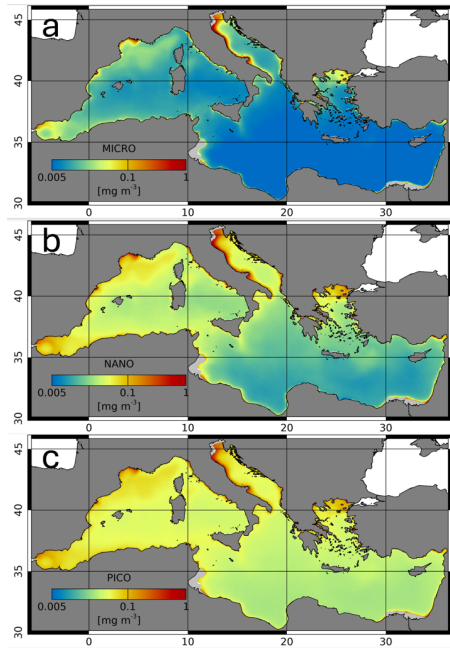


Figure B 2 – Mean time averages (1998-2025) of Microphytoplankton chlorophyll (a), Nanophytoplankton chlorophyll (b) and Picophytoplankton chlorophyll (c). Light grey indicates the areas permanently masked out because of persistent or recurrent Case II water conditions.

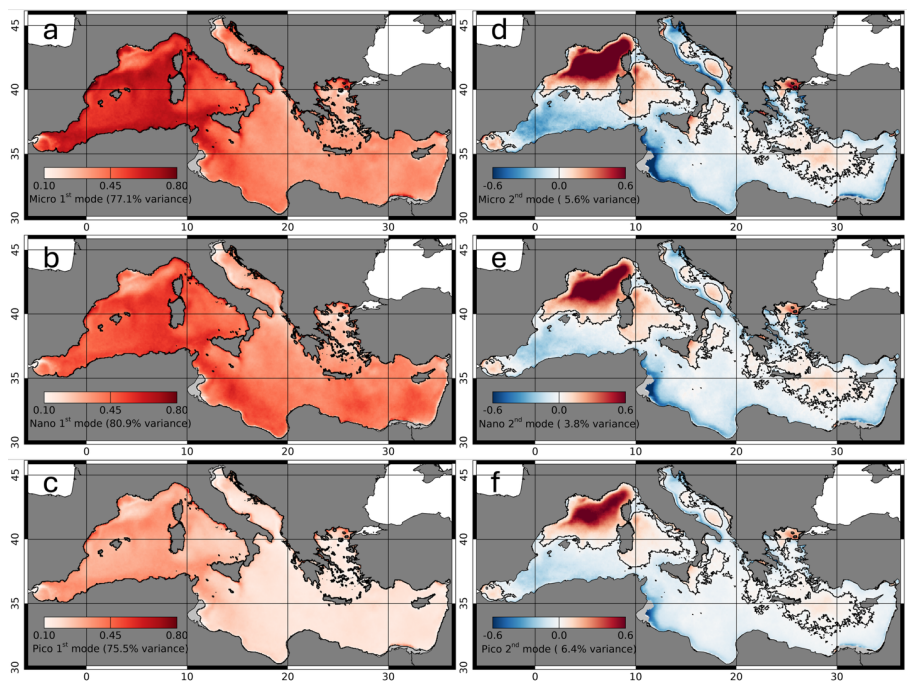
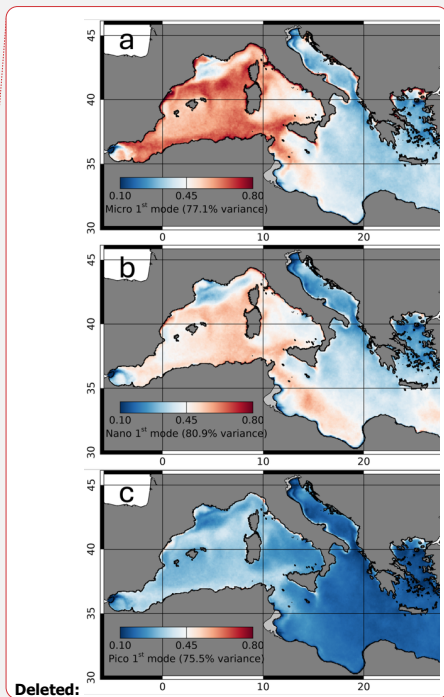


Figure B 3 – First two EOF spatial patterns computed over Micro- (a-d), Nano- (b-e) and Pico-phytoplankton (c-f). Light grey indicates the areas permanently masked out because of persistent or recurrent Case II water conditions.



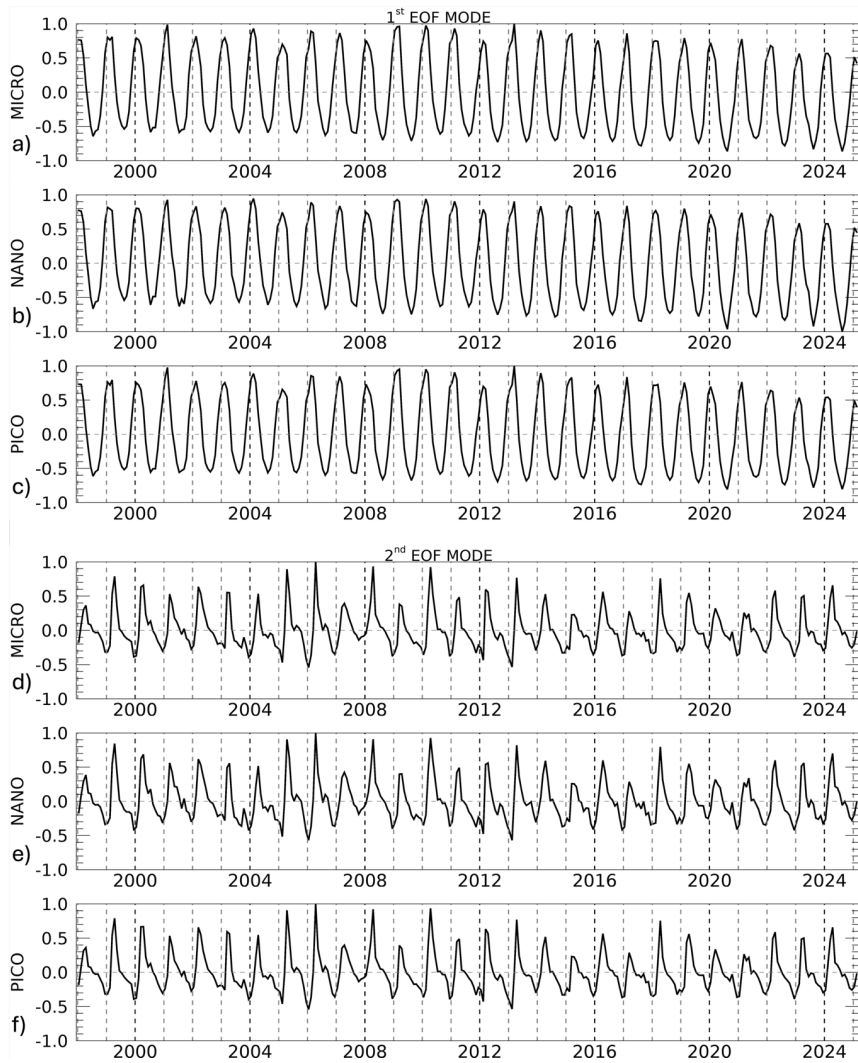


Figure B 4 – First two EOF temporal evolutions computed over Micro- (a-d), Nano- (b-e) and Pico-phytoplankton (c-f).

770 **7 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.

8 Author Contribution

- 775
- 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.
- 780
- VB: Writing – review & editing, Investigation, Validation, Supervision.

9 Competing interests

The authors declare that they have no conflict of interest.

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