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Key Points:

- Carbon burial pathways differ across NW Mediterranean Sea sites, in particular due to deep convection dynamics
- Between 2010 and 2019, biological particle and organic matter fluxes to the seafloor declined, mirroring a decrease in vertical mixing
- Contrary to the Gulf of Lion, calcareous phytoplankton increasingly dominate in the Ligurian Sea, decreasing carbon burial efficiency

Supporting Information:

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

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Contrasting Trends in Phytoplankton Diversity, Size Structure, and Carbon Burial Efficiency in the Mediterranean Sea Under Shifting Environmental Conditions

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Abstract Shifts in the phytoplankton assemblage induced by environmental changes have significant implications for carbon cycling and marine food webs, but remain poorly constrained across spatiotemporal scales. Here, we investigate the effects of rising sea surface temperatures and increased stratification on the phytoplankton composition and size in the northwestern Mediterranean Sea (2010–2019) using two sediment trap series: one in the oligotrophic Ligurian Sea and the other in the deep convection zone of the Gulf of Lion. We apply deep learning image analysis to quantify phytoplankton particle fluxes, size distributions, and relative assemblages, focusing on coccolithophores, diatoms, and silicoflagellates. Our results show a general decline of phytoplankton fluxes to the seafloor, mirroring the decrease in vertical mixing in the water column. Both sites show a shift toward phytoplankton species adapted to stratified and nutrient-depleted conditions, although with contrasting patterns. In the Ligurian Sea, deep-dwelling coccolithophore species become dominant, while in the Gulf of Lion, summer-associated siliceous species, including large diatoms and silicoflagellates, show an increase. These contrasted trends, which likely result from differences in nutrient inputs and pH changes in the surface between the two sites, have implications for the efficiency of carbon export pathways at depth. Specifically, the increasing dominance of smaller phytoplankton in the Ligurian Sea leads to a reduction in carbon burial efficiency, while in the Gulf of Lion, the enhanced contribution of larger diatoms may sustain higher export and burial rates in the future.

Plain Language Summary Phytoplankton are small marine plants that make up the base of the food web. They play a key role in regulating Earth's climate by removing carbon dioxide from the sea surface and transporting it to the deep ocean, preventing it from interacting with the atmosphere. Ongoing climate change is altering the species composition and size of phytoplankton, with potential effects on carbon cycling. We investigated the effects of rising temperatures and ocean mixing on the phytoplankton community at two sites from the northwestern Mediterranean Sea between 2010 and 2019. Using artificial intelligence to study microscope images, we found that fewer phytoplankton remains were sinking to the seafloor, an observation that could be attributed, in part, to the increasing temperatures affecting phytoplankton growth in the surface, and in part to their slower transport at depth under decreasing mixing conditions. However, in the Gulf of Lion, an area affected by faster acidification, diatom species are becoming dominant. Due to their large size, this offsets, in part, the decrease in carbon fluxes to the seafloor. As the Mediterranean continues to warm, the observed trends could weaken its role as a carbon sink, affecting regional carbon cycling and marine ecosystems.

1. Introduction

Human-induced greenhouse warming increases water column stratification (Li et al., 2020), which in turn reduces nutrient availability in surface waters. Larger phytoplankton cells, due to their smaller surface-to-volume ratio, are more prone to nutrient limitation than smaller cells, and thus tend to decline in nutrient-depleted surface waters (Falkowski & Oliver, 2007). A number of studies have pointed out an increase in the proportion of small-sized species in the phytoplankton assemblage together with warming conditions, whether on short timescales (Iriarte & González, 2004) or longer, decadal timescales (Beaugrand, 2004; Di Pane et al., 2022; Suikkanen

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et al., 2013). These shifts occur among species within a single group, or occur over different phytoplankton groups. In turn, changes in the size and taxonomic composition of phytoplankton have significant implications for food web dynamics and marine biogeochemistry (Finkel et al., 2010). For example, shifts toward dominance by smaller phytoplankton in the sea surface have been linked to a less efficient microbial loop, including a reduction in the efficiency of the biological carbon pump due to carbon being retained in the upper water column rather than exported to depth (Iriarte & González, 2004; Legendre & Rassoulzadegan, 1995). This is because large phytoplankton sink more rapidly, and because they are more likely to aggregate into large particles that are exported quickly from the surface (Thornton, 2002). In the sea, the main eukaryotic phytoplankton groups are diatoms, coccolithophores, and dinoflagellates. In situ and modeling studies confirm that diatoms, a group of silicifying phytoplankton, are more efficient for carbon export from the surface than coccolithophores, their calcifying—and smaller—counterparts (Jin et al., 2006; Mayot et al., 2017).

The Mediterranean Sea stands out as a hotspot of ongoing environmental changes, making it a key region for investigating shifts in the structure of planktonic communities. Despite a densely populated coast relying on its production, the Mediterranean Sea is a predominantly oligotrophic region, characterized by low-nutrient levels and chlorophyll concentrations. The northwestern part of the Mediterranean stands out as a more productive area (D’Ortenzio, 2009) due to Atlantic influx, riverine discharge, atmospheric deposition, and deep ocean convection (Severin et al., 2014). This last process is important for replenishing the surface in nutrients, and for storing carbon in the deep sea (Conan et al., 2018; Gogou et al., 2014; Macias et al., 2018; Touratier et al., 2016). Studies have documented that these events, caused by cold and windy winters, trigger spring blooms of higher intensity than average (Mayot et al., 2017). Recent decades have seen changes in Mediterranean ocean processes, and accompanying changes in phytoplankton productivity. The Mediterranean Sea has been warming since the 1960s (Bethoux & Gentili, 1999), with summer temperatures increasing 40% faster than the global mean (Cramer et al., 2018; Lionello & Scarascia, 2018). In parallel, deep convection episodes under the worst-case climate change scenarios are likely to collapse by the mid-21st century due to the strengthening of vertical stratification, itself caused by the warming of surface and intermediate waters (Parras-Berrocal et al., 2022; Somot et al., 2006). Margirier et al. (2020) already documented a marked reduction in deep convection events between 2010 and 2018, in conjunction with significant warming and salinization during this period.

The phytoplankton assemblage is highly sensitive to environmental changes, particularly turbulence and nutrient availability (Kiørboe, 1993; Margalef, 1978). In line with this framework, the recent increase in Mediterranean Sea surface temperatures, and the associated increase in water column stratification, have impacted the phytoplankton community structure. Between 1991 and 1997, a study on the DYFAMED sampling site in the Ligurian Sea suggested that the lengthening of the stratification period led to the increasing domination of smaller phytoplankton in surface waters relative to diatoms (Marty et al., 2002). More recently, a study from a coastal site near Marseille reported an increase in the proportion of diatoms relative to dinoflagellates as well as a decrease in pico- and nanophytoplankton size between 2005 and 2020 (Garcia et al., 2023). The authors attribute these changes to the shifting environmental conditions, in particular a relative increase in nitrate concentrations relative to phosphate and nitrite levels (Garcia et al., 2023). The implications of these community changes for biogeochemical cycling—a critical question for understanding the impacts of climate change—remain poorly constrained. For instance, the increase in smaller phytoplankton was associated with increased biomass in the study by Marty et al. (2002). Additionally, the contribution of different phytoplankton groups—and species—to carbon burial remains uncertain due to their varying efficiency in being exported from surface waters (Leblanc et al., 2018; Williams et al., 2024). Disentangling the effects of shifts in species composition and cell size on carbon export and burial therefore represents a significant scientific challenge.

The northwestern Mediterranean Sea (NW Mediterranean Sea) has benefited from extensive observation projects on particle fluxes, including the use of sediment traps (Gogou et al., 2014; Miquel et al., 2011; Stabholz et al., 2013). Despite intrinsic limitations (Buesseler et al., 2007), sediment traps remain the most efficient way to resolve both the spatial and temporal (seasonal, yearly) diversity of the phytoplankton assemblage that reaches the deeper layers of the sea. When positioned near the seafloor, they yield information on phytoplankton production in the surface waters, as well as on the biological cycling and export efficiency at the site. In this study, we investigate two sediment trap series from the NW Mediterranean Sea spanning the period between 2010 and 2019: one located in the Ligurian Sea in the oligotrophic Ligurian Current, and the other off the Gulf of Lion's plateau within the deep convection zone. We use deep learning-based approaches to detect, classify, and measure the

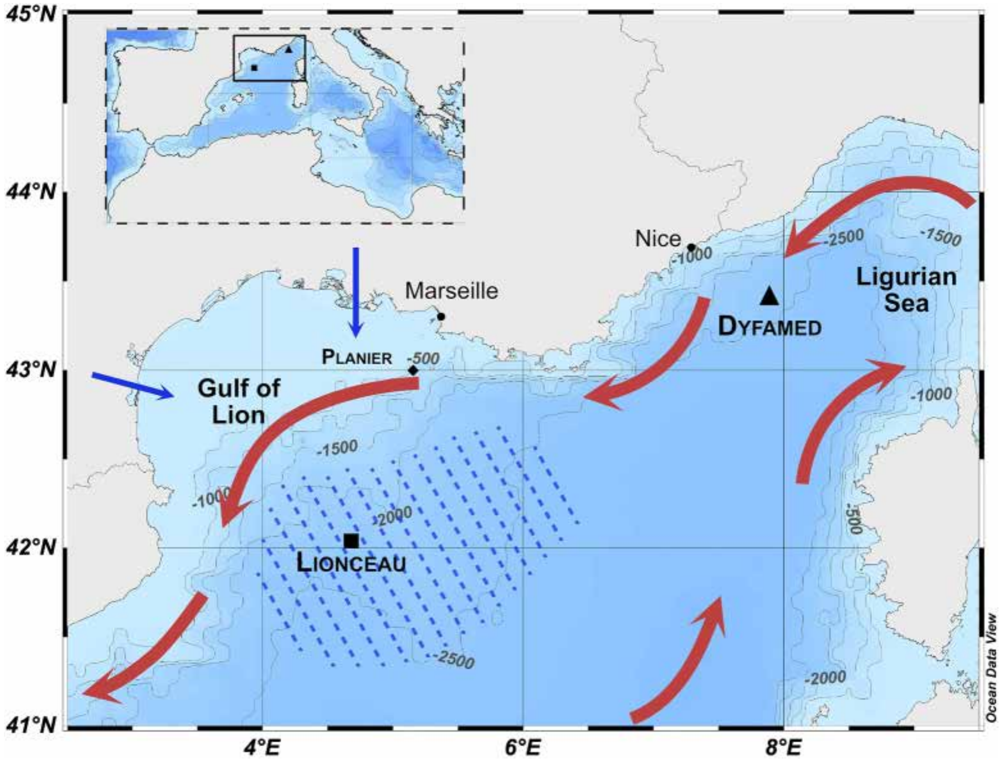


Figure 1. Oceanographic setting of the Lionceau and DYFAMED sediment traps in the NW Mediterranean Sea. The main boundary currents (Northern Current and Western Corsica Current) are represented by the red arrows, the main wind directions (Tramontane and Mistral) by the blue arrows, and the deep convection zone in dashed lines. The location of the Planier sediment trap is also indicated, as it is referenced in the Discussion for comparison with our results.

microorganisms we observe in the microscope images obtained from the sediment trap samples (Beaufort & Dollfus, 2004; Godbillot et al., 2024). Trends in phytoplankton community composition and size structure are compared to the environmental records for the sites, as well as the carbon fluxes to the trap, to improve our understanding of the relationships between environmental changes, biological community dynamics, and their implications for biogeochemical cycling in a rapidly changing Mediterranean ecosystem.

2. Materials and Methods

2.1. Site Locations and Material Preservation

Here, we investigate two time series from the NW Mediterranean Sea, from the Gulf of Lion and from the Ligurian Sea (Figure 1). The sediment trap series are, respectively, referred to as the Lionceau and DYFAMED moorings in this text.

The Lionceau mooring (42.01°N, 4.8°E) is located inside the winter deep convection area in the Gulf of Lion. It is equipped with a Technicap PPS-3 sediment trap (collection area of 0.125 m^2, 12 collecting cups of 260 ml) located at a depth of 2,400 m. The series comprises 80 samples collected between 2011 and 2018 with a collection period from 14 to 28 days. The sampling bottles were filled with 0.45 μm filtered seawater containing sodium borate-buffered formalin (for a final concentration of 5% formalin) to prevent microbial dissolution. After recovery, the large "swimmers" were removed by hand, and the remaining particles were either kept in the formalin solution in cold chambers, or filtered through 0.45 μm pore size membranes, rinsed and dried at 40°C. Particulate organic carbon (POC) measurements made using an elemental analyzer were available for the sediment trap samples, and described in Durrieu de Madron et al. (2017).

The sediment trap at the DYFAMED mooring site (43.25°N, 7.52°E) is a PPS-5 Technicap (collection area of 1 m^2 and 24 collecting cups) positioned at a depth of 1,000 m. We analyzed 219 samples collected between 2010 and 2020 with an average sampling period of 15 days. A detailed description of the sediment processing used at the DYFAMED sediment trap can be found in Heimbürger et al. (2013). The collecting cups are filled with a solution of 5% buffered formaldehyde in 0.22 μm-filtered seawater. After retrieval from the trap, samples were kept in the dark at 4°C. Swimmers were manually removed, and the sediments not analyzed for particular analyses were rinsed in Milli-Q water, centrifuged and lyophilized. Despite evidence for lateral inputs into the 1000-m sediment trap (Miquel et al., 2011), DYFAMED is often presented as a site of "open-sea" conditions because of the presence of a hydrological front disconnecting it from the coast, although continental inputs have been at times documented in the wintertime (Miquel et al., 2011).

2.2. Image Acquisition

We used the random settling method to obtain microscope slides from the sediment trap samples (Tetard et al., 2020): A couple of milligrams of the dried sediments were resuspended in water and lightly ultrasonicated for a minute to remove the major aggregates. Around 3 ml of the suspension was then collected and left to settle for 4 hours on 12 × 12 mm cover slips of known mass placed in a 3D-printed decanter (Tetard et al., 2020). The excess water was removed by pipetting, and the decanter was dried overnight at 50°C. The cover slips were weighed, and then fixed by sets of eight on a single microscope slide using Norland Optical Adhesive 81. The sample slides were mounted on a Leica DMR6000B automated transmitted light microscope.

Each sample was imaged twice with a Hamamatsu ORCA-Flash4.0 LT camera: once using bidirectional circular polarized light to image coccolith calcite, and a second time using bright-field microscopy to image siliceous biominerals, which are amorphous. Coccolith imaging was achieved using a HCX PL FLUOTAR 100× Leica lens. A 561 nm (green) monochromatic band-pass filter (ZET561/10X from Chroma Technology Corp.) was fitted onto the microscope to image a broad range of coccolith thicknesses (Beaufort et al., 2020). We acquired images for around 150 fields of view (FOVs, with dimensions of 125 × 125 μm) for each sample using a LabVIEW (National Instruments) interface. Hyperfocused stacks were created from 15 images obtained at different focal depths using the Helicon Focus 7 software (Helicon Soft), which enables to merge into a single image the focused parts of the image stack. Images for opal-bearing phytoplankton particles were obtained with 630× magnification using a HCX PL FLUOTAR 63× Leica lens. Fifteen images (210 μm × 210 μm) were taken and stacked for around 250 FOVs to image a depth of at least 15 μm.

2.3. Image Analysis

The image acquisition step generates two separate sets of images per sample, one under polarized light and the other using bright-field illumination, with each image containing multiple instances of biological fragments. For an approximate number of 150 focused images per sample and two steps of image acquisition, the total number of images used in this study is around 90,000. Deep learning algorithms proved to be an efficient way to analyze these images (Beaufort & Dollfus, 2004; Godbillot et al., 2024), with a detection step followed by an identification step. Coccolith detection and identification is achieved using SYRACO (Beaufort & Dollfus, 2004), a CNN-based software, which crops and then identifies specimens belonging to 33 groups of coccolithophore taxa using images taken in cross-polarized light (Beaufort et al., 2022). We used a separate pipeline for the analysis of the bright-field images. Images for siliceous biominerals were analyzed using a two-step CNN-based protocol. First, the microfossil instances were detected using a Faster R-CNN trained on a ResNet50 backbone, which achieves 0.74 recall and 0.72 precision (Godbillot et al., 2024). Then, we obtained class counts from the detected particles using a classification model built using the Particle Trieur software (Marchant et al., 2020). We tested multiple classification models using 13,675 images classified into 65 categories, including categories for debris or nonbiogenic material. Due to fragmentation and to the use of focus stacking, which produces a 2D image and masks some morphological features, most diatom classes could not be resolved to the species. As a result, the images are mostly resolved to the genus, or attributed to a morphospecies (Figure 2).

The best model outputs were obtained using a ResNet50 architecture with cyclic gain (Figure S1 in Supporting Information S1), trained over 20 ALRS epochs, using a minimum of 25 images per category and class weighing. Overall results for this model are 81.0% for precision, 83.8% for accuracy, and 82.2% for recall, including the categories that were not targeted in this study (e.g., blurry images, nonbiogenic fragments, etc.). These results are similar to those reported in comparable classification experiments on complex plankton image data sets (Adebayo et al., 2023). All relevant model files are included in the Supplement. We applied the trained model to the 1,275,709 cropped images we obtained from the bright-field microscope image data sets, using a high confidence

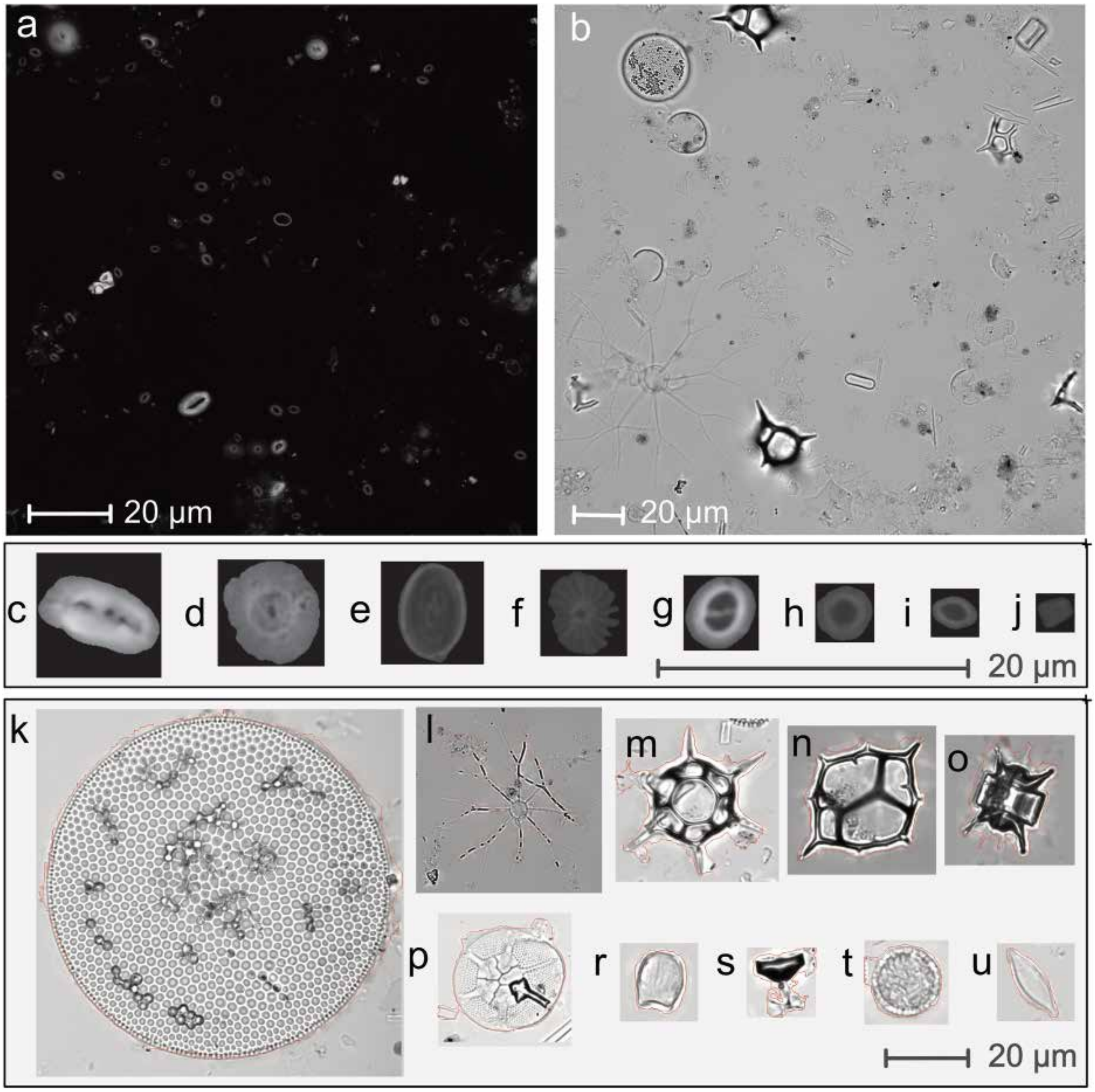


Figure 2. Image acquisition and analysis results. (a) Stacked image for sample 609 of the Lionceau sediment series in cross-polarized light. (b) Stacked for the same sample using bright-field microscopy. (c–j): Examples of segmented crops for the morphospecies counted using the SYRACO workflow. (k–u) Example crops from bright-field microscopy; segmentation results are shown in red. c. *Helicosphaera* sp. d. *Calcidiscus* sp. e. *Syracosphaera* sp. f. *Umbellosphaera* sp. g. *G. oceanica*. h. *Umbilicosphaera* sp. i. *Emiliania huxleyi*. j. *Florisphaera profunda*. k. *Thalassiosira*-like. l. *Bacteriastrum* sp. m. *Dichytocha speculum*, n. *Dichytocha* sp. o. *Odontella* sp. p. *Asteromphalus* sp. r. *Scyphosphaera* sp. s. Resting spore. t. Calcisphere. u. *Navicula*-like.

threshold of 0.9. This threshold ensured that only the most confidently classified images received a label, resulting in the automatic labeling of 917,126 cropped images (both sediment trap data sets included). For further analysis, we only considered counts for the classes that achieved over 80% for both precision and recall. Fragments were excluded due to their low detection recall (Godbillot et al., 2024). Instead, we focused on the most complete frustules, as it is common to count species that are 75% complete in diatom analyses (Kloster et al., 2023). Finally, we manually reviewed the labeled images produced by the two pipelines (coccoliths, diatoms, and silicoflagellates), with particular attention to the less frequent classes, which can be more affected by precision problems than the groups most represented in the data set.

In addition to image classifications, we produced size estimates for each fossil image. For the coccolith images, we used the outputs from the SYRACO software, which uses a series of thresholding techniques to segment the coccoliths from the image background (Beaufort et al., 2022). For the opal-bearing species, for which the use of thresholding techniques was less efficient, we used a U-Net CNN, which uses a ResNet43 backbone trained for image segmentation, to generate an outline for the individual particles (Figure 2). The model files for this segmenter model can be found at https://github.com/microfossil/particle-classification (last access: April 2025). For each biological class considered, the size reported in this study corresponds to the major axis length.

2.4. Particle Fluxes to the Trap

We generated count data for the categories for which the model exhibits over 80% precision and recall. Count data for each morphospecies were converted to a flux, that is, a number of particles per day per square meter of a given species (F_i in day^{-1}.m^{-2}) as follows:

$$F_i = \frac{N_i \times A_{\text{slide}} \times m_{\text{trap}}}{N_{\text{image}} \times A_{\text{image}} \times m_{\text{sample}} \times \Delta_t \times A_{\text{trap}}}$$

where N_i is the counts per morphospecies in a sample, A_{slide} the area of the slide in m^2, m_{trap} the mass of sample collected in the trap, N_{image} the number of images kept for analysis for the sample, A_{image} the area of each image in m^2 (which depends on the lens used during image acquisition), m_{sample} the mass of the sample collected on the slide, Δ_{t} the collection period of the trap (in days), and A_{trap} the surface area of the trap in m^2.

In addition to particle fluxes to the traps, we derived coccolith-$CaCO_3$ fluxes to the trap using the methods published in Beaufort et al. (2020) and detailed in the Supplement.

2.5. Environmental Parameters

We compared the biological fluxes and the carbon fluxes measured for the two sediment traps to the different environmental variables available for the two sites. The Lionceau sediment trap is located close to the LION mooring line, located in the deep convection area. This line was equipped with 25 instruments (Houpert et al., 2016), which yielded results for temperature, salinity, and dissolved oxygen over the period considered (Bosse et al., 2023). We also retrieved data for nutrients and the carbonate system, including pH and alkalinity, from the different MOOSE and MOOSE-GE cruises which took place in the region during the period considered (Testor et al., 2010). The data set was collected from Sea Data Net (https://www.seadatanet.org/Data-Access, last access 9 July 2024). The different points sampled and the corresponding year are shown in Figure S2 of Supporting Information S1. We studied the environmental data for bottles recovered less than 50 m deep. Values for temperature at the Lionceau site are retrieved from the shallowest CTD probe, positioned at approximately 150 m depth. DYFAMED, on the other hand, has been subjected to monthly cruises performed on the *RV Téthys II* since 1991. The site has been integrated into the MOOSE network since 2010. During these cruises, CTD profiles are performed and the water column is sampled using 12 L Niskin bottles for the analysis of nutrient concentrations and carbonate system parameters (Coppola et al., 2024).

2.6. Statistical Analyses on Taxa-Specific Relative Abundances

Beyond the description of the group-specific particle fluxes to the trap, we used multivariate analyses performed on R (R Core Team, 2021) to study the seasonal and interannual changes in the compositional assemblage. Since coccolith fluxes do not directly represent coccolithophore cell fluxes, we used the species-specific average number of coccoliths per coccosphere, as reported in the literature (Yang & Wei, 2003), to calculate coccosphere fluxes (Table S1 in Supporting Information S1) in the multivariate analyses. To address the dominance of certain taxa and reduce the potential influence of skewed distributions, we applied a log transformation to the relative contributions (in %) of the taxa from both groups. This transformation helps stabilize variance and ensures a more balanced representation of all taxa. Subsequently, we standardized the data by subtracting the mean and dividing by the standard deviation for both monthly and interannual analyses.

To study the seasonal variations of the assemblage at each site, we derived a principal component analysis (PCA) from the monthly averages of the fluxes for the taxa considered. Interannual variations in the phytoplankton assemblage were studied by using the trend in the relative contributions for each species. Because seasons and years were not homogeneously represented in the sediment trap data set, we first reconstructed the missing flux values using the "stlplus" package on *R* (Hafen, 2016), which performs a season-trend decomposition using loess

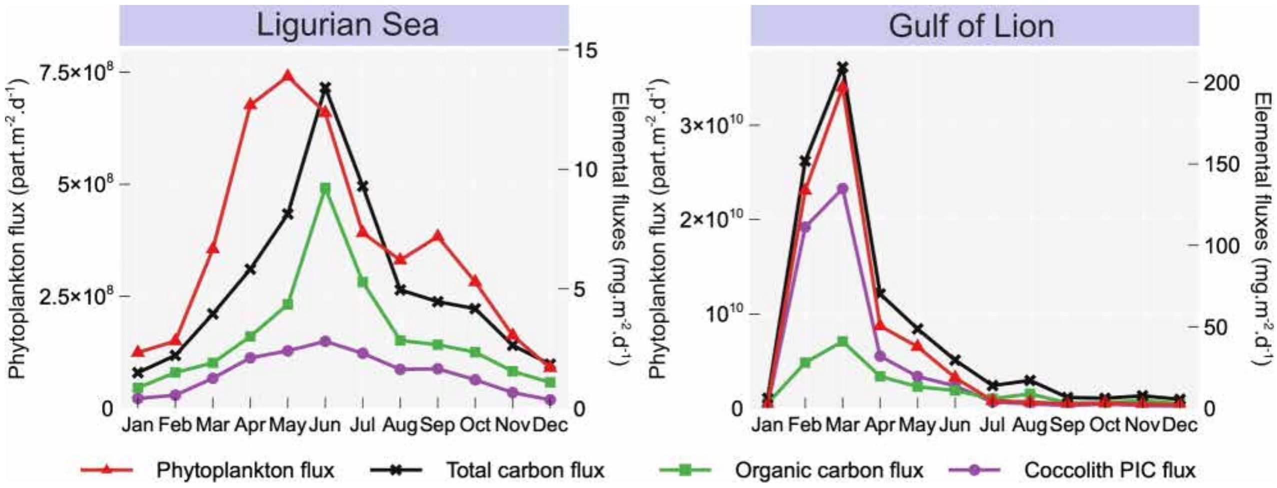


Figure 3. Average monthly fluxes recorded by the traps. The phytoplankton flux represented here is the sum of coccoliths, diatoms, calcareous dinoflagellates, and silicoflagellates, expressed in particles.m^{-2}.d^{-1}. Total carbon flux represents the sum of particulate inorganic carbon (PIC) and particulate organic carbon measured via elemental analysis. Coccolith-derived PIC is estimated from mineral birefringence.

(STL) on a time series with missing data. We used this method with the logged-transformed and scaled data of the relative abundance of each taxon to extract values for trends for each year-month pair. We used the values for trends to perform a PCA analysis. We also used this decomposition method to associate trend values for each environmental variable to the biological data set. We then used the "vegan" package (Oksanen et al., 2001) to fit environmental vectors onto the phytoplankton-derived PCA ordination.

3. Results

The study of the images obtained using both polarized light and bright-field microscopy yielded counts for a total of 13 morphospecies of coccoliths, seven morphospecies of diatoms, two dinoflagellates (one calcareous and the other siliceous), and two silicoflagellate morphospecies in the two sediment trap series. Counts for the high-relief and birefringent *Helicosphaera carteri* coccoliths were obtained using both image analysis workflows (i.e., cross-polarized and bright-field data sets). The fluxes for *H. carteri* measured for each sample using both pipelines are consistent (Figure S5 in Supporting Information S1); therefore, the counts are comparable despite the use of different imaging methods.

3.1. Total Monthly Fluxes to Trap

In the Ligurian Sea, the maximum particle fluxes of phytoplankton particles toward the DYFAMED sediment trap were recorded in May (7.41 × 10^8 part.m^{-2}.d^{-1}), with a notable secondary peak in September (3.83 × 10^8 part.m^{-2}.d^{-1}, Figure 3). Monthly phytoplankton fluxes in the Gulf of Lion were 20 times more important than in the Ligurian Sea site in average. Maximum values were measured in March (3.40 × 10^{10} part.m^{-2}.d^{-1}) in the Gulf of Lion and did not display a second peak in the fall.

When considering group-specific monthly variations in fluxes, it appears that coccolithophore fluxes were higher than diatom, dinoflagellate, and silicoflagellate fluxes at both sites, even when considering the estimates for whole coccolithophore cells (Figure 4). In the Ligurian Sea, the maximum fluxes for coccoliths to the sediment trap occurred around the month of May, with a second, smaller peak in September. The opal-forming species displayed a unimodal distribution centered in summer: Their peak export was delayed relative to coccoliths, occurring in June in the case of diatom frustules and July for silicoflagellates. Similar to coccoliths, calcareous dinoflagellates displayed a bimodal distribution, with a first peak in April and a second, more pronounced peak, in the late summer.

Maxima for all biomineral fluxes in the Gulf of Lion occurred earlier than in the Ligurian Sea. The peak for coccoliths occurred in March, along with the opal-forming species and calcareous dinoflagellates. There was a

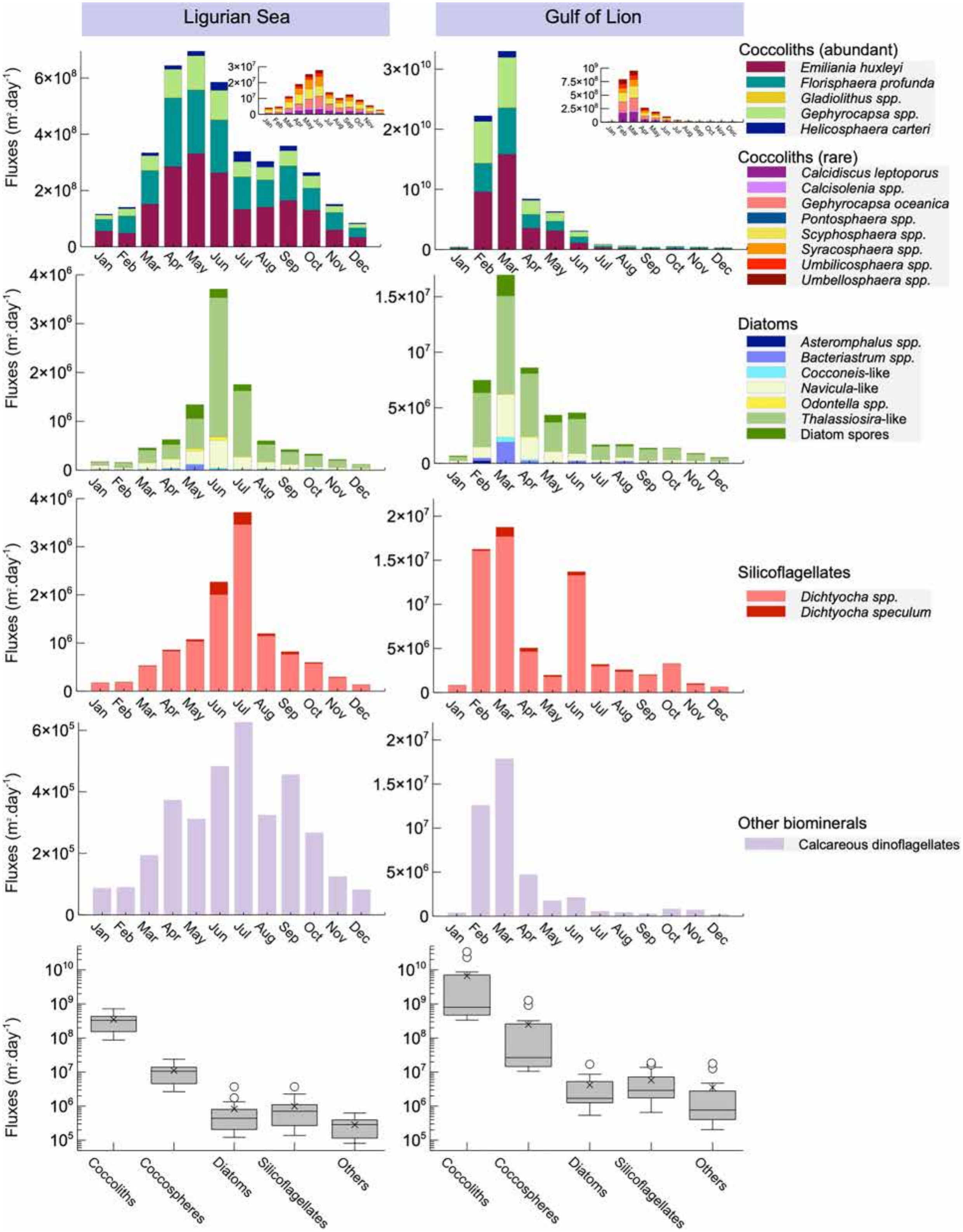


Figure 4. Monthly fluxes to the trap averaged over the study period for all phytoplankton classes considered in this study. Bottom panels are whisker plots built using the sum of the average monthly values of the morphospecies in each group (e.g., 12 values for each boxplot). Values for coccolithophores in the bottom panels are expressed both in coccoliths and coccospheres for comparison.

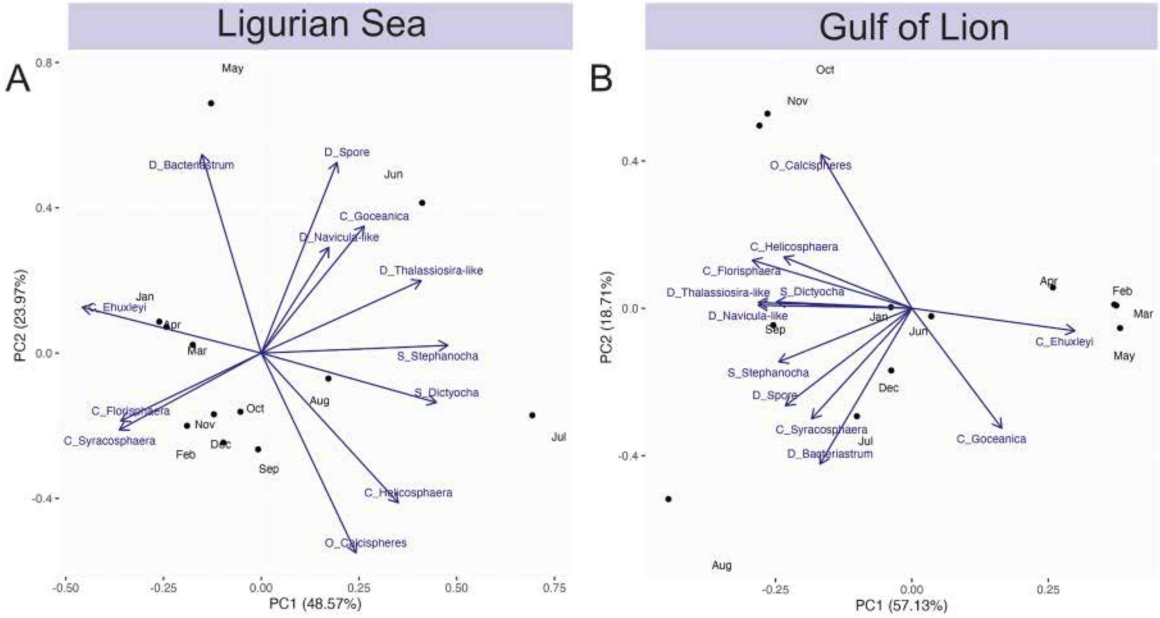


Figure 5. Monthly variations in the biological particle fluxes to the trap. Principal component analysis of the monthly relative assemblage for (a) the DYFAMED series and (b) the Lionceau series.

small increase in diatom, silicoflagellate, and calcareous dinoflagellate fluxes in June at the site, which did not appear in the coccolith group (Figure 4).

3.2. Monthly Phytoplankton Assemblages in the NW Mediterranean Sea

Species within a given phytoplankton group exhibited distinct monthly variation patterns, highlighting differences in phenology among taxa (Figure 4). The phytoplankton space was investigated using only species that constituted more than 0.5% of the coccolith assemblage. For the remaining categories (diatoms, silicoflagellates, and others), only species present as more than 0.02% of the assemblage were included. Thus, the analysis for species-specific variations was achieved considering the following 12 morphospecies: for coccoliths, *Emiliania huxleyi*, *Florisphaera profunda*, *Gephyrocapsa oceanica, Helicosphaera carteri,* and *Syracosphaera* sp., and for diatoms, *Navicula*-like*, Bacteriastrum* sp., resting spores, and *Thalassiosira*-like cells. We also considered the silicoflagellates *Dichtyocha fibula* and *Dictyocha speculum*, as well calcareous dinoflagellates (both the genii *Thoracosphaera* and *Calciodinellum* have been described in the area).

Emiliania huxleyi dominated the coccolith assemblage at both sites, along with *Florisphaera profunda* and, to a lesser extent, *Gephyrocapsa* sp. The relative contribution of *Emiliania huxleyi* to the total microfossil assemblage was high throughout the year in the Ligurian Sea (Figure S11 in Supporting Information S1), and dominated the assemblage in the winter and early spring (Figure 5). The diatom genus *Bacteriastrum* sp. peaked in May. The assemblage then moved to being dominated by diatom spores (mostly from the *Chaetoceros* genus), when the other morphospecies described in the sedimentary assemblage seemed to generally decrease (Figure S11 in Supporting Information S1). June was marked by an increase in the small but rather calcified *Gephyrocapsa oceanica*, along with the large centric diatoms grouped under "*Thalassiosira*-like" that dominated the diatom assemblage, and smaller pennate diatoms grouped under "*Navicula*-like" (Figure 5, Figure S11 in Supporting Information S1). These morphospecies were followed by an increase in both silicoflagellate categories and the heavily calcified *Helicosphaera carteri* and calcareous dinoflagellates. Finally, fall conditions were mostly dominated by coccolithophores from the *Florisphaera profunda* species and *Syracosphaera* sp.

Samples from the Gulf of Lion displayed a similar ecological succession although the corresponding months can precede those observed in the Ligurian Sea by 2–3 months. *Emiliania huxleyi* dominated the assemblage in the midwinter and spring. These were periods where other Noelaerhabdaceae species were also abundant in the assemblage, including *Gephyrocapsa oceanica* and *Gephyrocapsa* sp. (Figure 5, Figure S13 in Supporting

Information S1). In July, the assemblage was dominated by the diatom *Bacteriastrum*, although this was rather due to a decrease in the numbers of Noelaerhabdaceae coccoliths reaching the seafloor than because of an increase in this diatom's fluxes to the trap (Figure S8 in Supporting Information S1). The succession in diatoms was then similar to the one observed in the Ligurian Sea: diatom spores dominated in late August, and *Thalassiosira*-like and *Navicula*-like in September, together with silicoflagellates. The heavily calcified *Helicosphaera carteri* and calcareous dinoflagellates were last to appear in this succession in October to November. *Florisphaera profunda* occurred simultaneously to these species, dominating the assemblage in the fall (Figure 5, Figure S13 in Supporting Information S1).

3.3. Interannual Variations in Fluxes, Relative Assemblages, and Size

In the Ligurian Sea, the maximum fluxes and the minimum fluxes were recorded, respectively, in May 2013 (3.02×10^9 part. $m^{-2}.d^{-1}$) and January 2018 (6.45×10^6 part. $m^{-2}.d^{-1}$). Maximum and minimum phytoplankton fluxes toward the sediment trap were recorded, respectively, in February 2012 (1.82×10^{11} part. $m^{-2}.d^{-1}$) and January 2017 (1.48×10^8 part. $m^{-2}.d^{-1}$) in the Gulf of Lion.

In general, total biological fluxes to the seabed decreased in the NW Mediterranean Sea over the period of study (Figure S10 in Supporting Information S1), as did most species-specific fluxes (Figure 6, Figures S15–S17 in Supporting Information S1). The decrease in total particle fluxes was more marked in the Gulf of Lion than in the Ligurian Sea (Figure S10 in Supporting Information S1). In the Ligurian Sea, the decrease in fluxes was more apparent for opal-forming species than for calcareous phytoplankton: *Navicula*-like and *Thalassiosira*-like are the classes where fluxes decreased the most (Figure S15 in Supporting Information S1), while most coccolithophore species were preserved. In the Gulf of Lion on the other hand, calcifying species were most affected by the decrease in fluxes: *Helicosphaera carteri* displayed the steepest decline, and calcareous dinoflagellates also displayed a sharp decrease. Opal biominerals were comparatively less impacted by the general decline, or displayed, in the case of *Bacteriastrum* sp. and *Navicula*-like, increased fluxes to the sediment trap during the period of study (Figure 6, Figure S16 in Supporting Information S1).

The composition of the phytoplankton assemblage also varied during the period of study. In the Ligurian Sea, the two PCA axes represented 60% of the changes in relative assemblages across the period of study (Figure 7). The first PCA loading increased throughout the interval, which was due, in particular, to an increase in the number of the species *Florisphaera profunda* and *Syracosphaera* sp. in the relative assemblage, while opal-bearing species such as *Bacteriastrum* sp., *Navicula*-like and *Dichtyocha speculum* decreased. In the Gulf of Lion, the first two axes gathered 70% of the changes in the relative assemblage. The changes are mainly explained by a decrease in coccoliths from the Noelaerhabdaceae family in the assemblage, whereas most opal-forming species (including *Thalassiosira*- and *Navicula*-like, the two silicoflagellate categories, etc.) increased (Figure 7). At both sites, these changes were most correlated to an increase in temperature and a decrease in pH. A second source of variation in the Gulf of Lion, shown by the decrease along the second axis of the PCA during the study period, is related to a general increase in *Florisphaera profunda* and *Syracosphaera* sp. in the assemblage between 2011 and 2018.

Finally, our study yielded results for the evolution of coccolith, frustule, and silicoflagellate sizes across the period of study. It appears that size variations were quite restricted during the period of study at both sites (Figures S18–S20 in Supporting Information S1). The largest size changes in the Ligurian Sea maybe attributed to *Thalassiosira*-like diatoms and the silicoflagellates *Dichytocha* sp., which both increased slightly over the period of study. In the Gulf of Lion *Florisphaera profunda* and *Dichtyocha speculum* both increased during the period of study, while both *Emiliania huxleyi* and *Navicula*-like decreased over the interval, with a steep decline occurring after 2015 in both cases.

4. Discussion

4.1. Impact of Depositional Processes on the Particle Export to Trap

The average monthly flux for coccoliths in the Ligurian Sea during the study period was 3.47×10^8 part.$m^{-2}.d^{-1}$, which is comparable to the fluxes recorded at the nearby Planier sediment trap (6.1×10^8 coccoliths.$m^{-2}.d^{-1}$; Rigual-Hernández et al., 2013) located off the coast of Marseille at a depth of ∼500 m (Figure 1). This value is also similar to the maximum fluxes reported for a sediment trap located in the central eastern Mediterranean Sea

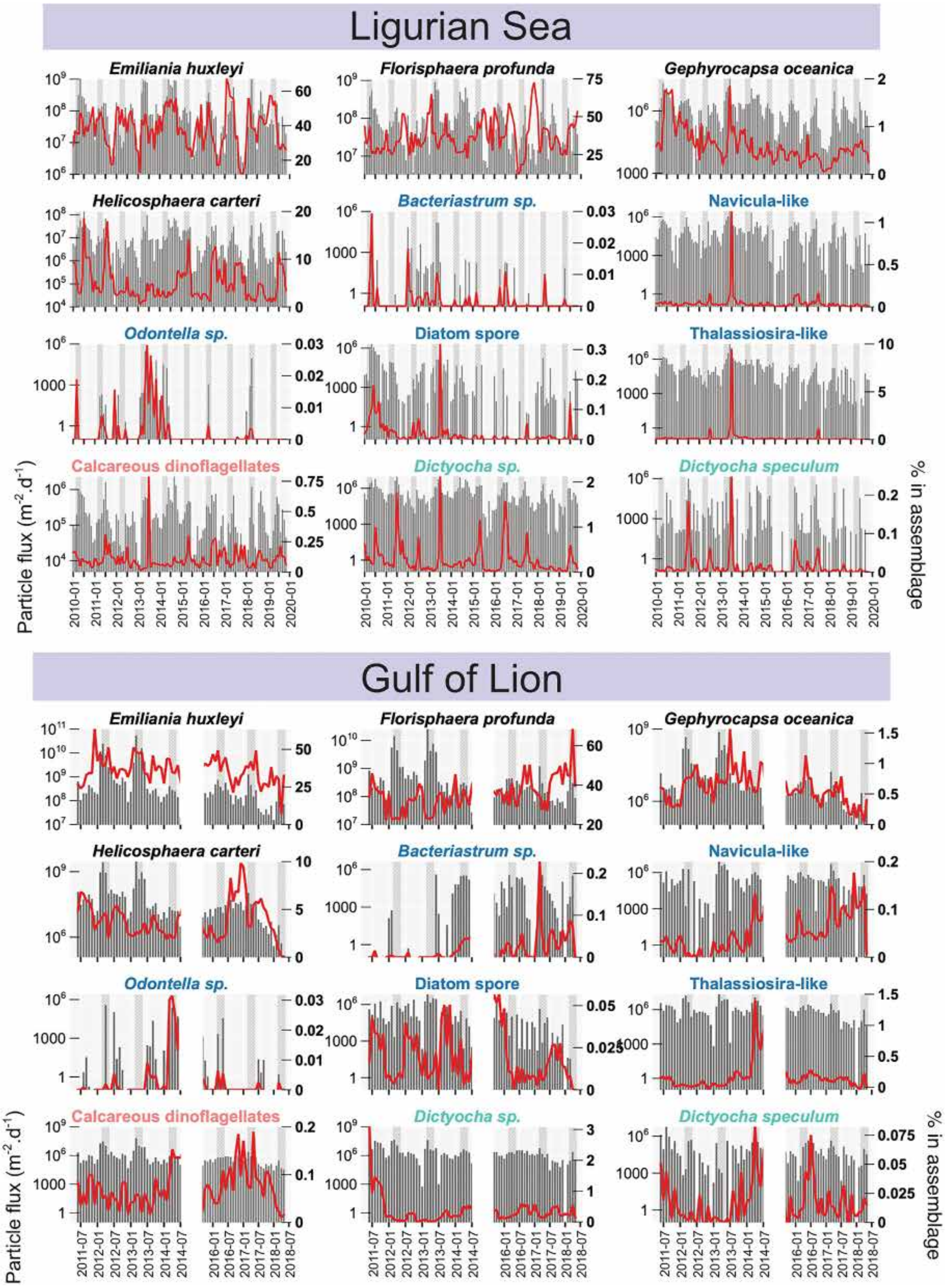
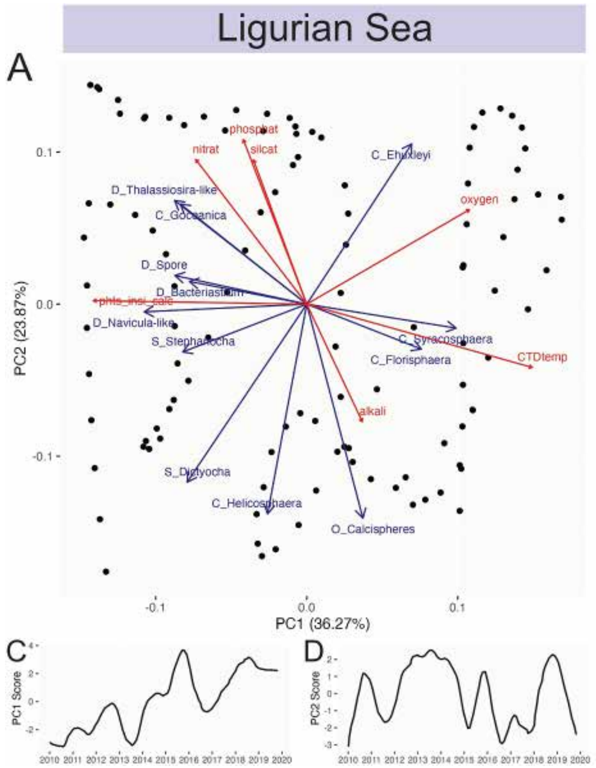


Figure 6. Interannual variations in species-specific monthly fluxes and relative contribution to the assemblage. The relative presence of the species in the assemblage is represented by the red line, and the fluxes by black bars. Overall fluxes for all species considered here decrease over the period of study. Missing monthly values were reconstructed using a seasonal-trend decomposition method; for fluxes, this was applied to the log-transformed data on coccolith data. Note the interruption in the Gulf of Lion series in 2015.



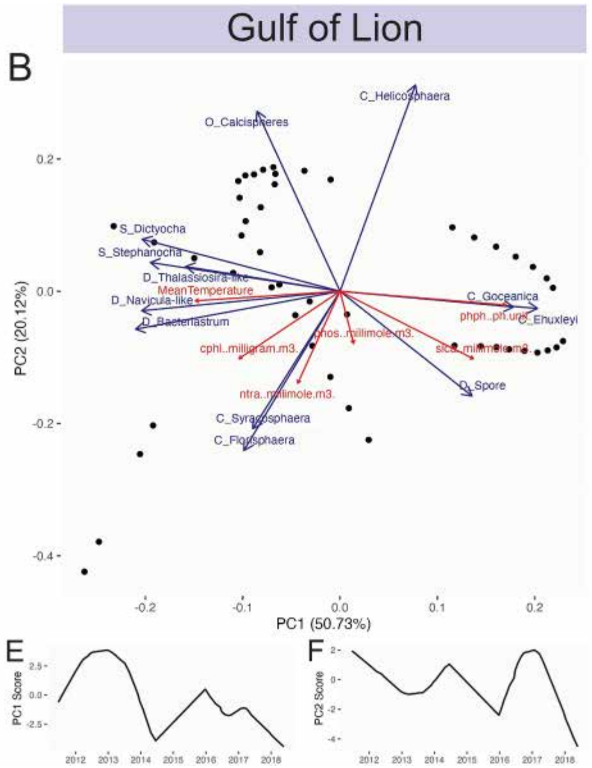


Figure 7. Interannual variations in the phytoplankton assemblage. Principal component analysis (PCA) of the relative assemblage trends over the study period for (a) the DYFAMED (Ligurian Sea) time series and (b) the Lionceau (Gulf of Lion) time series. Environmental variables are projected as supplementary elements. (c and d) Monthly PCA scores for DYFAMED along axes 1 and 2. (e and f) Same for Lionceau. Panels (c – f) reflect monthly variability projected along the main trend axes.

(Ziveri et al., 2000) at 3,000 m depth (3×10^8 coccoliths.m^{-2}.d^{-1}). By comparison, the sediment trap from the Gulf of Lion recorded significantly higher coccolith monthly fluxes, averaging 6.61×10^9 coccoliths.m^{-2}.d^{-1}. The order-of-magnitude difference between the Ligurian Sea and the Gulf of Lion exceeds the depth-related variability in particle fluxes observed between 200 and 1,000 m in the Ligurian Sea (Miquel et al., 2011), highlighting a strong spatial variability in coccolith export.

Calcareous dinoflagellates also made up an important component of the calcareous particles identified in the sediment trap series. Average monthly fluxes were 3.53×10^6 part. m^{-2}.d^{-1} in the Gulf of Lion and 2.84×10^5 part. m^{-2}.d^{-1} in the Ligurian Sea, representing, respectively, 54 and four times the fluxes reported for the central eastern Mediterranean Sea.

Diatom valve fluxes were markedly lower in this study than at the coastal Planier site. The Planier sediment trap recorded average diatom fluxes (3×10^7 valves.m^{-2}.d^{-1}) that were seven times higher than in the Gulf of Lion (5.8×10^6 valves.m^{-2}.d^{-1} in average) and 36 times the average flux measured in the Ligurian Sea (9.9×10^5 valves.m^{-2}.d^{-1}). By comparison, fluxes at the Planier sediment trap for the other silicifying group studied here, namely silicoflagellates, were half those recorded in the Gulf of Lion and three times the fluxes measured in the Ligurian Sea (Rigual-Hernández et al., 2010).

Thus, diatom fluxes appear depressed relative to the other phytoplankton particles identified in the traps, in comparison to similar existing studies. This could reflect either nutrient-depleted conditions in the Gulf of Lion and Ligurian Sea, or differences in their preservation during their transfer to the sediment traps. Coccolithophores are nutrient stress-tolerant species (S-strategists), which thrive in open sea environments and under nutrient-poor conditions (Brun et al., 2015). Satellite observations, which provide insight into surface processes during the study period, suggest that haptophytes, of which coccolithophores are a major group, dominate the assemblage across most of the year at both sites (Figure S5 in Supporting Information S1). The persistent nutrient-depleted conditions of the Mediterranean Sea likely contribute to their overwhelming presence in the sediment trap record (Nikolopoulou et al., 2024). Similarly, the higher fluxes of silicoflagellates than diatoms may be linked to the oligotrophic nature of the region. Silicoflagellates are known to be mixotrophic, capable of both photosynthesis and phagocytosis, which allows them to exploit low-nutrient environments more effectively than strictly autotrophic diatoms (Nikolopoulou et al., 2024).

Beyond the environmental factors, preservation can also explain the smaller fluxes of diatoms recorded at both sediment traps than the other groups considered in this study. Some lightly silicified diatom species have been shown to experience selective dissolution during their transfer from the surface to the sediment (Rigual-Hernández et al., 2013; Sancetta, 1992). At our sites, this potentially contributes to increasing both the relative proportion of coccoliths in the samples and the presence of heavily silicified species, including silicoflagellates. In detail, the most abundant diatom taxa identified at the Planier sediment trap—located closer to the surface and nearer to the coast—were *Thalassionema frauenfeldii* and *Skeletonema* sp., the latter making up more than 43% of the assemblage. In contrast, *Skeletonema* was nearly absent in our sediment samples. It was also absent from the superficial sediment samples collected at the Planier site, which was attributed to state of undersaturation of the surface in silica (Rigual-Hernández et al., 2013). *Thalassionema* sp. exists in our data set but almost exclusively as fragments, for which counts were not used in this study. In contrast to these degraded taxa, resting spores, which made up the third most observed group at the Planier site, were observed in our samples. The high export efficiency of resting spores has been noted before (Rembauville et al., 2015; Riaux-Gobin, 1996; Rynearson et al., 2013), in part due to their robustness. Heavily silicified diatoms thus appear to be overrepresented in the diatom assemblage in our study, a result which has been documented before for core-top and trap sediments (Abrantes, 1999; Zúñiga et al., 2021).

4.2. Drivers of Total Biological Export to the Trap and Link With Carbon Export

4.2.1. Ligurian Sea

The collection of sinking particles in sediment traps can be affected by the sinking particle concentrations and velocities (Buesseler et al., 2007). Previous studies on the DYFAMED sediment trap in the Ligurian Sea have shown that stable and weak hydrodynamic conditions ensure the trap's efficiency. Under the conditions prevailing at the site, the particles produced in the surface typically reach the 1,000 m-trap in approximately 2 weeks (Miquel et al., 2011).

Phytoplankton fluxes to the sediment trap in the Ligurian Sea exhibit a bimodal distribution, reflecting the presence of a spring and an autumn bloom at the site, a documented feature in the NW Mediterranean Sea (Mayot et al., 2020; Rigual-Hernández et al., 2013). The spring bloom is generally triggered between March and May, when increasing stratification in the surface concentrates the nutrients replenished by winter mixing in the photic zone. The autumn bloom, on the other hand, occurs between September and November, when the breakdown of summer stratification enables some nutrients to reach the surface.

Our study highlights that the maximum fluxes of organic matter to the trap in June occur approximately 1 month after the maximum flux of biological particles. A similar lag had been observed between total mass fluxes and organic carbon fluxes at this trap series before, and had been attributed to the production of material with higher organic carbon content in the late spring (Miquel et al., 2011). Our results suggest that this lag is caused by the export of different particles at depth. In the sedimentary assemblage, coccolithophores are an important component of the spring peak in fluxes, with coccoliths making up more than 90% of what reaches the seafloor in the spring, a number that remains generally above 80% if we consider, for example, that a single coccosphere is made up of 50 coccoliths. Coccolith production does not appear to be responsible for burying organic carbon at the site; instead, peak organic carbon fluxes at the site are reached in the late spring, when opal-bearing species from the diatom and silicoflagellate groups dominate the assemblage. Similarly, the increase in coccoliths in the sediment trap samples in the autumn is not accompanied by an increase in POC. This may provide an explanation as to why the autumn bloom does not contribute significantly to the annual export of organic carbon from the surface, as noted by Miquel et al. (2011).

Interestingly, the peak in total coccolithophore fluxes to Ligurian Sea trap are not correlated to the Particulate inorganic carbon (PIC) fluxes represented by coccoliths calculated using our workflow (Beaufort et al., 2020). The maximum coccolithophore fluxes are found during the spring, with *Emiliania huxleyi* dominating the assemblage. PIC fluxes, on the other hand, are maximum during the summer, at a time when *Helicosphaera* *carteri*, a larger and very calcified species, increases both in total and relative abundance in the sedimentary assemblage. Thus, this species seems to drive PIC burial in this region of the Mediterranean Sea.

4.2.2. Gulf of Lion

In the Gulf of Lion, the biological fluxes to the trap display a unimodal distribution that matches the one observed at the coastal Planier sediment trap (Rigual-Hernández et al., 2013). However, the average coccolith fluxes at the site (1.0×10^{10} coccoliths.m^{-2}.d^{-1}) are an order of magnitude higher than reported at this coastal site, and seven times the average flux reported in the Canaries in an area affected by coastal upwelling episodes (Sprengel et al., 2000). In the Gulf of Lion, the maximum fluxes coincide with episodes of winter convection. Similar to regions such as the Greenland Sea, the NW Mediterranean Sea is a known region of dense water formation. In the winter, cold and dry winds trigger the formation of dense water in the surface, leading to convection events that, on certain years, affect the entire water column (Durrieu De Madron et al., 2013; Houpert et al., 2016; Margirier et al., 2020). Increased biological activity due to deep winter mixing is a general feature in the NW Mediterranean, supplying the surface in nutrients: the 2012 deep convection episode is associated with positive chlorophyll a anomalies in both the Gulf of Lion and the Ligurian Sea in March 2012 (Ciancia et al., 2021), coinciding with the maximum fluxes in biological particles to the Lionceau sediment trap in the Gulf of Lion. Beyond the direct effect on biological production, convection episodes have consequences on particle deposition at depth that may explain why the fluxes exceed those recorded in other series (Stabholz et al., 2013). In 2011, the convection episode was detected between January and March, while the phytoplankton bloom developed at the beginning of March (Severin et al., 2014), as reflected in the satellite-derived total chlorophyll a (Figure S6 in Supporting Information S1). In situ sampling suggests the 2011 bloom continued to develop in April after the end of the convection episode (Severin et al., 2014), a feature that is absent from our record, where instead biological fluxes to the trap drop after March. At least part of the biological fluxes recorded at the Gulf of Lion sediment trap could thus be attributed to physical processes, such as resuspension episodes. Such events occurred in the winters of 2010–2013 during episodes of bottom-reaching convection and the subsequent dispersion phase of the newly formed dense bottom waters (Durrieu de Madron et al., 2017; Severin et al., 2017). They may also be derived from concurrent dense shelf water cascading input, which that has been shown to concentrate biological material (Canals et al., 2006; Pusceddu et al., 2013; Yoder & Ishimaru, 1989). These processes can explain why fluxes at the Lionceau site exceed those observed in the Ligurian Sea and the Canaries.

Contrary to the Ligurian Sea, maximum PIC and POC fluxes to the trap in the Gulf of Lion coincide with the total fluxes of biological particles, which are dominated by coccoliths. While deep convection reduces the organic content of the sediments collected in the trap by burying nonorganic material (Stabholz et al., 2013), it constitutes an important means of sequestering carbon at depth (Kessouri et al., 2018). Increased burial of POC during deep convection episodes has been linked to increased export efficiency (i.e., export/primary production) rather than to increased biological activity in the surface layer (Kessouri et al., 2018).

4.3. Monthly Phytoplankton Assemblages Reflect Sea Surface Conditions

There is a clear monthly succession in the microfossils found in the sediment traps. Similar to the results found at the Planier site (Rigual-Hernández et al., 2013), colder conditions seem to favor coccolithophores from the Noelaerhabdaceae family, with *Emiliania huxleyi* dominating the assemblage in the winter and early spring at both sites. This species is also the most abundant in the assemblage in high-nutrient conditions, which prevail in the winter in the Gulf of Lion when convection events occur, and around the month of April in the Ligurian Sea. The ability of *E. huxleyi* to outcompete other coccolithophore species in high light and eutrophic environments has been documented before (Tyrrell & Merico, 2004). However, the phytoplankton blooms in the region are usually dominated by diatoms rather than coccolithophores (Marty et al., 2002). Our observations do not correspond either to the group succession classically described in midlatitude oceans (Margalef, 1978), which posits that diatoms typically dominate during periods of high nutrient availability and turbulence, such as in early spring. We explain this apparent paradox by the absence in our data set of most of the diatom species traditionally associated with the turbulent and nutrient-rich waters that develop in the spring: *Chaetoceros* sp., *Odontella* sp., and *Skeletonema* sp. These weakly silicified species were likely not preserved in the samples collected from the two trap series we studied, which are located deeper than the one at the Planier site where they were observed (Rigual-Hernández et al., 2013). The secondary peak exhibited by *E. huxleyi* in the late summer (September) in the Ligurian Sea was also noted at the Planier site off the coast of Marseille, whereas it is absent in the Gulf of

Lion. This later bloom develops when decreasing temperatures break the pycnocline, enabling nutrient input to the surface. Rigual-Hernández et al. (2013) attribute the absence of diatoms in the assemblage during this period to the weaker mixing and nutrient concentrations, which distinguish this second bloom from the spring bloom.

Contrary to diatoms, silicoflagellates appear overrepresented in sediment trap samples compared to sea surface records, probably due to their robustness. Our record shows that their presence in the assemblage is most associated to warm and nutrient-depleted conditions, similar to *Helicosphaera carteri*, which has been associated to oligotrophic conditions (Keuter et al., 2022; Ziveri et al., 2000). Silicoflagellates peak in the total assemblage in the summer at other Mediterranean sites with similar environmental conditions (Nikolopoulou et al., 2024). We observe no seasonal difference between the different silicoflagellate morphospecies identified in the sediment trap, an observation previously made in other Mediterranean sediment trap studies (Rigual-Hernández et al., 2010). The summer is also marked by a greater diversity in the phytoplankton community, which is typical for oligotrophic regimes (Keuter et al., 2022). The summer assemblage at both sites includes large centric diatoms, grouped under *Thalassiosira*-like, which are also most present in the summer assemblage at the coastal Planier site (Rigual-Hernández et al., 2013), as was *Nitzschia bicapitata*, which in our data set is included in the *Navicula*-like group. Calcareous dinoflagellates also peak in the summer. A study by Vink (2004) showed that these species were mostly associated with a stratified upper water column and a well-established thermo/pycnocline.

Finally, autumn (October–November) conditions at the sites display contrasting assemblages: In the Ligurian Sea, the assemblage is composed of *F. profunda*, a species known for developing in the lower photic zone under oligotrophic conditions. Similarly, *Syracosphaera* sp., which tends to cooccur in the assemblage, has been associated to the lower photic zone, although this genus is less well documented and diverse (Bown et al., 2009). An increase in *F. profunda*'s relative presence in an assemblage could suggest the presence of very nutrient-depleted conditions in the surface in the Ligurian Sea, a feature that is absent from the record in the Gulf of Lion. Overall, the phytoplankton monthly averages reflect the more oligotrophic conditions present in the Ligurian Sea compared to the deep convection area. The coccolithophore phenology described here aligns with observations from the Gulf of Biscay (Beaufort & Heussner, 2001), which similarly documented *F. profunda* in late fall, *H. carteri* in summer, and *Syracosphaera pulchra* in early fall.

4.4. A Decrease in Phytoplankton Fluxes in the NW Mediterranean

Total phytoplankton fluxes generally decreased at the two sites investigated between 2010 and 2018 (Figure S10 in Supporting Information S1). In the Gulf of Lion, it appears that contrary to some very robust coccoliths, some fragile elements such as *Bacteriastrum* experience an increase in fluxes across the period of study. This indicates that the state of preservation probably did not vary during the period of study and suggests that the decrease in fluxes instead reflects changes in primary production in the surface.

The total phytoplankton fluxes in the Gulf of Lion decrease abruptly in 2014 (Figure S10 in Supporting Information S1). In the Ligurian Sea, the overall decrease in phytoplankton and carbon fluxes is less pronounced. An exception to the decreasing trend occurs between 2013 and 2014 (Figure S10 in Supporting Information S1), with trends in phytoplankton and carbon fluxes instead displaying an increase. The decrease in phytoplankton total abundance since 2010 has been documented for the NW Mediterranean Sea before, and attributed to the decrease in nutrient concentrations in the sea surface (Garcia et al., 2023).

Under present-day conditions, concentrations in chlorophyll a in the NW Mediterranean Sea are correlated to the mixed-layer depth (Macias et al., 2018). Therefore, we suggest that the decrease in phytoplankton fluxes to the sediment traps is linked to the reduction in vertical mixing that affects the region, through its impact on nutrient concentrations. Decreasing phytoplankton fluxes in the Gulf of Lion indeed mirror the environmental changes that affected the water column during the period of study: Studies show that unlike the period between 2009 and 2013, where the intensification of winds in the winter triggered a deep convection episode, the years between 2014 and 2018 were not affected by a similar phenomenon (Margirier et al., 2020). This absence of deep convection was attributed to reduced winter heat loss in 2014, which led the region to transition into a warmer and more saline state lasting until 2018—a phenomenon that is likely to occur more frequently in the NW Mediterranean Sea, as the air warms more rapidly than the sea surface (Josey & Schroeder, 2023; Parras-Berrocal et al., 2022). In contrast to the Gulf of Lion, deep convection episodes are less frequent in the Ligurian Sea (Macias et al., 2018), although the region experiences vertical mixing in the upper part of the water column. In the period between 2008 and 2018, the winter convection was most intense in 2013 and 2014 (Bosse et al., 2017;

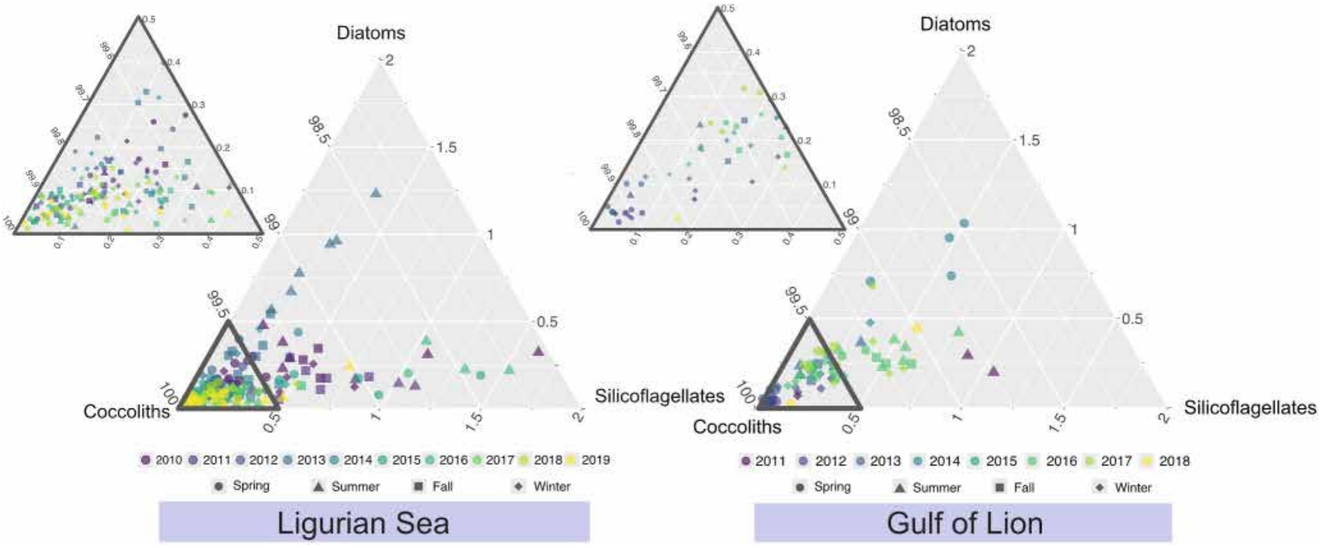


Figure 8. Ternary plots for the relative contributions of all coccolith, diatom, and silicoflagellate particles to the trap. Points are colored by year. The sites show contrasting trends over the period of the study, with coccoliths increasing relative to both diatoms and silicoflagellates in the Ligurian Sea, while the Gulf of Lion displays the opposite trend.

Margirier et al., 2020). The decrease in phytoplankton fluxes observed in both sediment trap series thus appear to be closely linked to the decreased mixing conditions in the water column, which reduce the upward flux of nutrients to the surface, and lead to warmer temperatures in the upper water column (Margirier et al., 2020).

4.5. Contrasting Trends in Diatoms and Coccolithophores at Both Sites

While both sites exhibit reduced biological fluxes to the sediment traps between 2010 and 2018, the study of the phytoplankton assemblages reveals distinct trends. In the Ligurian Sea, coccoliths show an increased relative to diatoms and silicoflagellates in the assemblage (Figure 8). This relative increase of coccoliths in the assemblage is driven mainly by a relative increase in the *Florisphaera profunda* and *Syracosphaera* sp., two groups associated with very nutrient-depleted conditions in the sea surface. A comparison with environmental parameters (Figure 7) suggests that these changes are most correlated to a temperature increase and a pH decrease in the Ligurian Sea. An increase in *F. profunda* abundances relative to other coccoliths has been linked to increased temperatures for latitudes above 30°N (Hernández-Almeida et al., 2019), although the mechanisms for this relationship remain elusive. At DYFAMED in the Ligurian Sea, the increase in *F. profunda* % at the site is the result of a larger decrease in both diatom and Noelaerhabdaceae fluxes across the interval (Figure 6). Fluxes for opal-bearing species, especially large centric diatoms, indeed seem to decline faster than those of this carbonate producer (Figure S15 in Supporting Information S1).

While the occurrence of the deep-dwelling *F. profunda* and *Syracosphaera* sp. also increases slightly in the phytoplankton assemblage of the Gulf of Lion (Figure 7), the largest trend observed at this site of deep convection is an increase in diatom and silicoflagellate percentages in the assemblage (Figures 7 and 8). This result converges with the observation that PIC fluxes are decreasing faster than total carbon fluxes at the site (Figure S10 in Supporting Information S1), a feature that is less evident in the Ligurian Sea. While part of this decrease can be attributed to a larger decline in the fluxes of carbonate producers, it appears that some opal-bearing classes, namely *Bacteriastrum* sp. and *Navicula*-like, display increasing fluxes to the trap. Similar to the Ligurian Sea, these assemblage changes are most correlated to an increase in subsurface temperatures and to a decrease in pH (Figure 7). However, an increase in silicate concentrations is also correlated to the change, which could explain why the opal-bearing classes appear to increase in the assemblage. There is a general lack of data for nutrient trends in the open sea, making it difficult to highlight a causal influence of nutrient changes on the assemblage changes observed. The Gulf of Lion is the only site in the NW Mediterranean Sea where an increase in nutrients has been documented for intermediate waters, although this observation holds for nitrates only (Fourrier et al., 2022) and has not been reported for the surface. Alternatively, the decrease in coccoliths relative to other

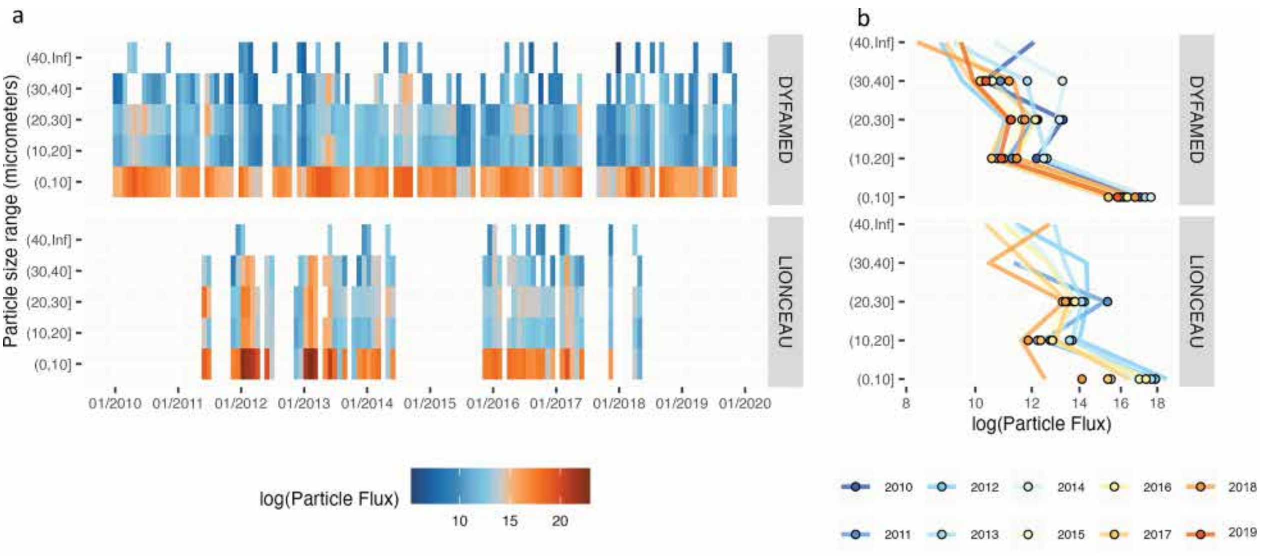


Figure 9. Size-specific changes in phytoplankton fluxes between 2010 and 2017. Panel (a): Color chart for the biological particle fluxes to the trap per size category over time. Small particles (coccoliths) overwhelmingly dominate both assemblages. Panel (b): Yearly averages for the fluxes of particles of each size category, per year. Yearly averages were measured using the unmodified data from panel (a) (lines) and a second time using uninterrupted reconstructed values when the seasonal decomposition method was possible (points). This second method accounts for seasonal biases in fluxes that maybe present in the unmodified data. Both methods suggest that while average fluxes are decreasing throughout the size categories, in the Gulf of Lion, this decrease is more evident for smaller size classes, effectively increasing the proportion of large biological particles in the assemblage.

biological particles at Lionceau could be related to a decrease in surface pH. The data from the MOOSE cruises suggest that a mean pH drop of 0.2 points (from 8.3 to 8.1) occurred in the Gulf of Lion between 2012 and 2014 (Figure S3 in Supporting Information S1), whereas the pH decrease in the Ligurian Sea remained rather limited. Additional data are needed in the region to corroborate such an abrupt decrease. Nevertheless, other studies have documented that while the entire Mediterranean Sea is subjected to decreasing pH, the Gulf of Lion is acidifying at a rate twice as important as the rest of the region (Tsiaras et al., 2024), including the Ligurian Sea (Fourrier et al., 2022). Acidification has been shown to hinder calcification for most coccolithophore species in *in vivo* experiments (Meyer & Riebesell, 2015), and has been shown to impair the bloom-forming abilities of *Emiliania huxleyi* (Riebesell et al., 2017).

4.6. Implications on Phytoplankton Size Structure and Carbon Burial

The size of the phytoplankton community influences carbon cycling in the water column (Jin et al., 2006). In the Ligurian Sea, the phytoplankton assemblage shows a marked decrease in larger size categories between 2010 and 2019, while smaller particles experience a slower decline (Figure 9). The Gulf of Lion displays the opposite trend, with fluxes of small particles decreasing more rapidly than those of larger ones, leading to an overall increase in the proportion of larger particles in the assemblage. This observed shift in size structure is not due to species-specific changes in size, as no individual species shows a consistent size trend over the study period (Figure S19 in Supporting Information S1). Instead, we attribute these changes to variations in the dominant phytoplankton groups. In the Gulf of Lion, the increase in diatoms, generally larger than coccolithophores, contributes to the relative increase in larger particles. Meanwhile, in the Ligurian Sea, the small-sized *F. profunda* coccoliths become more prominent in the assemblage, contributing to the overall decrease in particle size (Figure 9). Water column stratification and the resulting nutrient-depleted conditions have been shown to favor small coccolithophores over large diatoms in the Humboldt Current system, inhibiting carbon burial (Iriarte & González, 2004). Similarly, in the NW Mediterranean Sea, diatoms appear more efficient at burying carbon at the sites studied: in the Ligurian Sea, monthly organic carbon fluxes are decorrelated from phytoplankton fluxes. While the maximum biological fluxes to the trap are in the spring, the organic carbon flux is maximum in the summer. At this site, the diatom peak is delayed relative to the peak fluxes in coccoliths, suggesting that diatoms could be responsible for more carbon burial in the sediments.

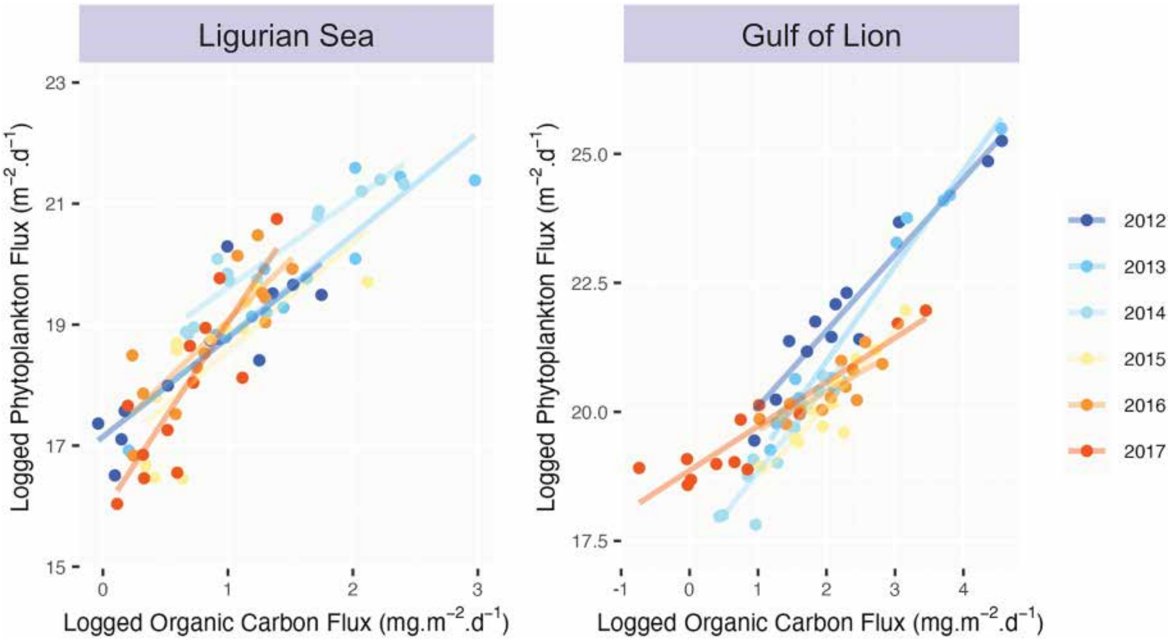


Figure 10. Evolution of particulate organic carbon (POC) burial across the period of study. Points and best fit are colored by years. Maximum POC and phytoplankton fluxes decrease at both sites over the period 2012–2017. However, in the Ligurian Sea, organic carbon burial is decreasing faster than the biological fluxes to the trap (i.e., the slope is increasing), suggesting decreasing carbon burial efficiency, while the Ligurian Sea displays the opposite trend. We link these trends to the opposing trends in phytoplankton size structure observed at the sites.

Previous studies have shown that carbon export from the surface increases when diatoms dominate, while smaller phytoplankton, such as coccolithophores, are thought to contribute less to carbon export toward the deep sea because of their slower sinking rates and recycling in the microbial loop (Jin et al., 2006). This principle has been refined, with small nanoplankton blooms now acknowledged for their role in carbon burial (Leblanc et al., 2018; Richardson & Jackson, 2007), in particular as phytoplankton aggregates can counterbalance this effect by increasing the sinking rate of small particles. Nevertheless, our results suggest it remains applicable in the NW Mediterranean Sea: Plotting the particle flux against the organic carbon flux shows that in recent years in the Gulf of Lion, a smaller biological particle input to the sediment trap buries more carbon than at the beginning of the studied period (Figure 10). Such a trend is not evident in the Ligurian Sea, where instead carbon burial becomes less sensitive to the phytoplankton flux to the trap between 2012 and 2017. The larger input of organic carbon to the sediment per particle to the seafloor in the Gulf of Lion can be related to the increasing occurrence of opal-bearing species in the assemblage (Figure 11). Diatom-dominated assemblages are indeed the ones that display the highest POC export rates from the surface ocean (Henson et al., 2012). However, the efficiency with which this material reaches and is buried in sediments remains debated, as geological records show nonlinear relationships between carbon burial and diatom productivity (Lopes et al., 2015). Despite uncertainties as to the mechanisms governing production, export, and remineralization, the central role of diatoms in mediating carbon burial and the efficiency of the biological pump has long been recognized and remains a key focus of current research (Cabrera-Brufau et al., 2021; Tréguer et al., 2018).

5. Conclusions

In this study, we explored the biological record of two sediment trap series in the northwestern Mediterranean Sea: the Ligurian Sea and the Gulf of Lion. Our findings document the seasonal and interannual variations in both the fluxes of biological particles collected in the sediment traps over approximately 10 years, and in the composition of the assemblage. The export of biological particles to the traps decreases in both locations during the ~10-year duration of the record. We show that the biological fluxes to the seafloor are adversely affected by a reduction in vertical mixing, which reduces the nutrient input to the surface—a trend increasingly observed in the NW Mediterranean Sea. In the Gulf of Lion, halts in the deep convection episodes that occur regularly in the winter lead to a significant reduction in particle fluxes, which likely reflects both the absence of resuspension

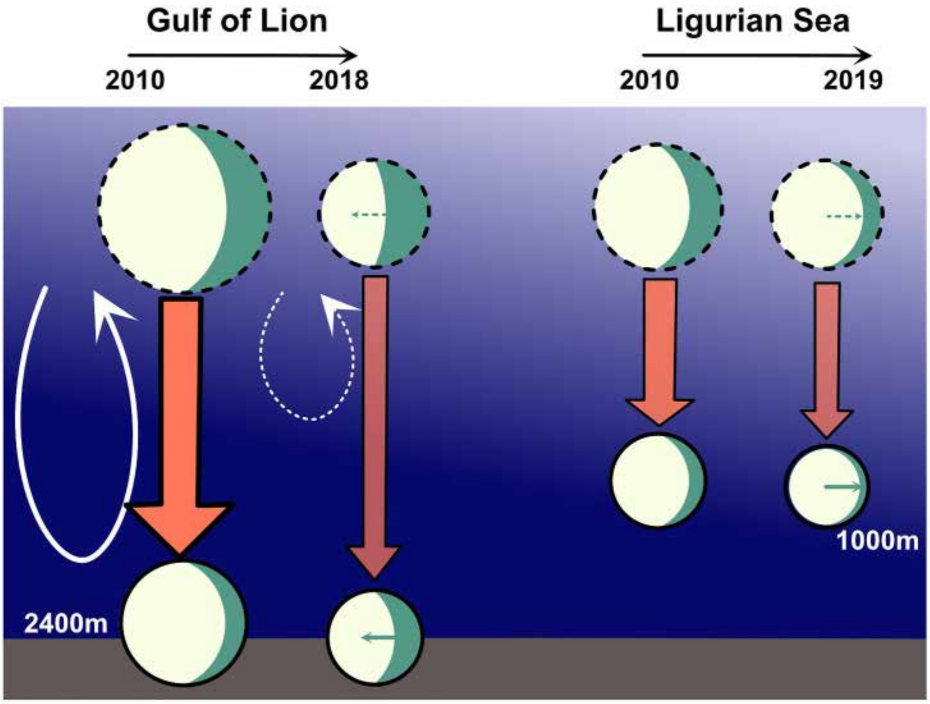


Figure 11. Schematic representation of carbon burial evolutions in the NW Mediterranean Sea between 2010 and 2019. Particulate organic carbon (POC) concentrations are shown in the circles, with POC originating from siliceous material, including diatoms, in green, and from coccolithophores in yellow. The respective depths of the sediment traps are indicated. The orange arrows represent the particle fluxes. Convection dynamics are shown with the white arrow. The POC content in the surface layer was not constrained in this study, and thus is essentially hypothesized. Diatoms are probably more present in the surface POC than at depth, being more exposed to fragmentation and/or dissolution in the water column. At the beginning of the interval, the diatom/coccosphere ratio in the particle flux to the sediment trap is about the same at both sites. Deep convection episodes enhance particle fluxes and POC burial, either through enhanced biological activity in the surface, or faster transport through the water column. They boost primary production in the Ligurian Sea as well. At the end of the interval, the interruption of deep convection episodes decreases POC production at both sites, and leads to a decrease in particle fluxes to the seafloor. The relative increase of large siliceous particles in the total assemblage at depth in the Gulf of Lion probably reflects, in part, enhanced diatom production in the surface due to increasing nutrient input, as some siliceous taxa show increasing flux trends over the study period (e.g., *Bacteriastrum* sp. and *Navicula*-like). Coccolithophores might also be decreasing at this site due to faster acidification trends than in the Ligurian Sea. The particle fluxes at Lionceau toward the end of the interval are around the same than at DYFAMED, but siliceous particles are more efficient at exporting POC; therefore, POC burial remains higher in the sediment trap located in the Gulf of Lion than in the Ligurian Sea.

episodes and decreased ventilation and nutrient input to the surface. At both sites, there is a shift toward assemblages dominated by the biological particles most associated with summer and autumn conditions, correlating most with the increasing temperatures at the site. However, while the Ligurian Sea record is increasingly dominated by small coccoliths produced by deep-dwelling species, the Gulf of Lion displays a shift toward opal-bearing species, including large centric diatoms and silicoflagellates. We attribute these differences to site-specific environmental trends, including nutrient inputs and pH, although these exploratory results would require more comprehensive environmental data to identify the drivers. Finally, we show that these trends in relative assemblages lead to contrasted evolutions of the phytoplankton size structure between the two sites, with consequences on the carbon export at depth. Specifically, we show that a transition toward large and robust siliceous species in the Gulf of Lion increases the burial efficiency of carbon at depth, whereas in the Ligurian Sea, the shift toward smaller phytoplankton reduces it. These findings highlight the complex relationship between environmental changes and biological responses, offering new insights into how climate-driven ocean changes influence carbon cycling in the Mediterranean Sea.

Conflict of Interest

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

Data Availability Statement

Data for phytoplankton counts, fluxes, and sizes have been uploaded to the SEANOE repository (https://doi.org/10.17882/106844). All object detection and classification model output files and metrics are available at https://doi.org/10.5281/zenodo.15473229.

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