



# Vertical Mixing Effects on Phytoplankton Dynamics and Organic Carbon Export in the Western Mediterranean Sea

Fayçal Kessouri, Caroline Ulses, Claude Estournel, Patrick Marsaleix, Fabrizio d'Ortenzio, Tatiana Severin, Vincent Taillandier, Pascal Conan

## ► To cite this version:

Fayçal Kessouri, Caroline Ulses, Claude Estournel, Patrick Marsaleix, Fabrizio d'Ortenzio, et al.. Vertical Mixing Effects on Phytoplankton Dynamics and Organic Carbon Export in the Western Mediterranean Sea. *Journal of Geophysical Research. Oceans*, 2018, 123 (3), pp.1647-1669. 10.1002/2016JC012669 . hal-02322803

**HAL Id: hal-02322803**

**<https://hal.science/hal-02322803>**

Submitted on 15 Feb 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

**Vertical mixing effects on phytoplankton dynamics and organic carbon export in the western Mediterranean Sea**

**Faycal Kessouri<sup>1</sup> †, Caroline Ulses<sup>1</sup>, Claude Estournel<sup>1</sup>, Patrick Marsaleix<sup>1</sup>, Fabrizio D’Ortenzio<sup>2</sup>, Tatiana Severin<sup>3</sup>, Vincent Taillandier<sup>2</sup>, Pascal Conan<sup>3</sup>**

<sup>1</sup>Université de Toulouse, CNRS, UPS, Laboratoire d’Aérodynamique, Toulouse, France

†Current affiliations: Department of Atmospheric and Oceanic Sciences, University of California Los Angeles. 520 Portola Plaza, 7127 Math Sciences, Los Angeles, CA 90095, USA - Southern California Coastal Water Research Project, Costa Mesa, CA, USA

<sup>2</sup>Sorbonne Universités, UPMC Université Paris 06, CNRS, Laboratoire d’océanographie de Villefranche (LOV), Observatoire Océanologique, 06230 Villefranche-sur-Mer, France.

<sup>3</sup>Laboratoire d’Océanographie Microbienne (LOMIC), Observatoire Océanologique, Sorbonne Universités, CNRS, UPMC Univ Paris 06, CNRS, 66650 Banyuls/Mer, France.

Corresponding author: Faycal Kessouri (kesf@ucla.edu)

**Key points (140)**

- Phytoplankton dynamics and organic carbon export are compared in three Mediterranean regions, differentiated by the mixed layer depth.
- Despite a subpolar regime in the north and a subtropical regime in the south, annual primary production is similar in the studied regions.
- Organic carbon export below 150 (800) m was 4–5 (3–8) times higher in convective regions than in the stratified region, in 2012/ 2013.

## **Abstract**

A 3D high-resolution coupled hydrodynamic-biogeochemical model of the western Mediterranean was used to study phytoplankton dynamics and organic carbon export in three regions with contrasting vertical regimes, ranging from deep convection to a shallow mixed layer. One month after the initial increase in surface chlorophyll (caused by the erosion of the deep chlorophyll maximum), the autumnal bloom was triggered in all three regions by the upward flux of nutrients resulting from mixed layer deepening. In contrast, at the end of winter, the end of turbulent mixing favored the onset of the spring bloom in the deep convection region. Low grazing pressure, due to convection-induced dilution in winter that reduced prey–predator interactions, allowed rapid phytoplankton growth during the bloom. Primary production in the Algerian subbasin was characterized by a long period of sustained phytoplankton development and permanent stratified conditions, unlike the deep convection region where primary production was inhibited during two months in winter. Despite seasonal variations, annual primary production in all three regions is similar. In the deep convection region, total organic carbon export below the photic layer (150m) and transfer to deep waters (800m) was 5 and 8 times, respectively, higher than in the Algerian subbasin. Up to 45% of the organic matter deeply exported has been laterally transported out of the deep convection region. The Mediterranean Sea is considered as a hotspot of climate change and understanding changes in its ecosystem in future decades could offer an insight into the evolution of the functioning of the global ocean.

## **Index Terms and Keywords**

Biogeochemical cycles, processes, and modeling, Upper ocean and mixed layer processes, Phytoplankton, Marginal and semi-enclosed seas.

Physical-biogeochemical 3D ocean modeling, western Mediterranean Sea, deep convection,

44 phytoplankton bloom, primary production, carbon deep export

## 1. Introduction

The mixed layer depth (MLD) is considered to be a major factor in controlling phytoplankton development [Sverdrup, 1953]. At large scales, gyre circulation leads to surface waters being nutrient-rich over subpolar gyres, and nutrient-poor over subtropical gyres [Williams and Follows, 2003]. The subpolar winter regime is characterized by a deepening of the mixed layer by several hundreds of meters and a large supply of inorganic nutrients in surface waters, while phytoplankton growth is limited by a lack of light when cells are transferred below the photic zone. In spring, an intense phytoplankton development occurs when the mixed layer shoals or, more generally, when turbulent mixing becomes weak [Taylor and Ferrari, 2011]. This can be compared to the subtropical regime, where the deepening of the mixed layer to ~100 m, and phytoplankton growth co-occur. Under this regime, phytoplankton development is triggered by the mixing-induced supply of nutrients.

Export of organic carbon towards the deep ocean may play a determining role in sustaining mesopelagic ecosystems [Giering *et al.*, 2017] and in sequestration of atmospheric carbon. This export exhibits large-scale variability in response to the variability of the MLD and plankton dynamics. Various authors have made satellite-based estimates of the global export, and pointed out high export under the photic zone in subpolar oceans, and low export in subtropical gyres [Henson *et al.* 2012; Laws *et al.*, 2011; Westberry *et al.*, 2012; Siegel *et al.*, 2014]. These satellite-base estimates attempt to account for export from the euphotic zone and their algorithms likely do not account for export via the mixed layer pump. Gardner *et al.* [1995] suggested that the alternation between periods of stratification, favoring phytoplankton growth, and periods of mixed layer deepening enhances the efficiency of vertical export through the “mixed layer pump” process. This consists in increasing, through mixing, the slow sinking rate of phytoplankton and particles. Dall’Olmo *et al.* [2016] estimated that, in high latitudes, the ratio of

69 mixed layer pump to biological pump (fast sinking particles) is 23% on average, and can reach  
70 over 100%.

71 The western Mediterranean Sea (Fig. 1) is characterized by the presence of subsurface water  
72 masses with high MLD gradients over several hundred kilometers in the south–north direction.  
73 Winter MLD values reach several hundred meters in the northwestern convection zone (Gulf of  
74 Lions), and only 60–80 m in the Algerian sub-basin [Houpert *et al.*, 2015]. Furthermore,  
75 D’Ortenzio and Ribera d’Alcala [2009] concluded that the western Mediterranean exhibits a  
76 bloom-like regime that is similar to the subpolar regime in its chlorophyll concentration and  
77 mixed layer seasonal evolution in the northwestern region, and a non-blooming behavior that is  
78 similar to the subtropical regime in the south.

79 Observational studies conducted in the western Mediterranean have shown that particulate  
80 organic carbon (POC) export fluxes below the euphotic layer and at mid-depth (1000 m) are  
81 maximum during (February/ March) and/ or following winter mixing events (April, May, June)  
82 (3 to 4 times higher than the rest of the year) [Miquel *et al.*, 2011; Stabholz *et al.*, 2013; Gogou *et al.*, 2014]. The authors of these studies argued that the spring peak is caused by fertilization  
83 induced by winter mixing, favoring a diatom-dominated ecosystem in the northwestern region.  
84 Moreover, Avril [2002] observed the transfer of dissolved organic carbon (DOC) at the surface  
85 to deep waters during intense vertical mixing in the northwestern region (DYFAMED station,  
86 Fig. 1) and estimated that the winter mixing flux ( $10 \text{ gC m}^{-2} \text{ year}^{-1}$ ) constituted 91% of the  
87 annual flux at 100 m. Based on modeling studies, Ulses *et al.* [2016] found that the annual  
88 amount of exported organic carbon at 100 m depth is primarily related to the intensity of the  
89 deep convection process. They found that in years with strong convection, organic carbon export  
90 was twice that of years with shallow convection. Export efficiency showed the same interannual  
91 pattern, while the transfer to deep waters ( $>1000 \text{ m}$ ) and the deposition on the seabed showed no  
92

clear trend. Bernardello et al. [2012] also used a modeling approach, and stressed the importance of the mixed layer pump in driving the interannual variability of POC export in the northwestern Mediterranean region. However, estimates of primary production and export flux remain uncertain in the western Mediterranean [Gogou et al., 2014] and, in general, for the global ocean [Henson et al., 2012 ; Siegel et al., 2014; 2016]. Uncertainties in observational methods are mainly associated with the scarcity of measurements, which cannot reflect interannual and spatial variability. Other uncertainties arise from the lack of an overview of the system; for example, limited information is available on degradation and recycling processes (such as nitrification), and the contribution of DOC to total export. Estimates from modeling approaches, which simplify the system and are poorly constrained by sparse observations, are also associated with large uncertainties.

Modifications of water masses in the Mediterranean Sea have been observed since the 1990s and are now impacting the whole basin [The MerMex Group, 2011]. Some have been partly attributed to climatic variations. For example, the Eastern Mediterranean Transient has been found to correspond to a switch in the region of deep water formation in the eastern Mediterranean, from the Adriatic to the Aegean [Roether et al., 1996], which produced a rise in the nutricline depth by 200–300 m [Klein et al., 1999]. In the western Mediterranean, an acceleration of the increasing trend in salt and heat content in deep waters was reported following an intense dense water formation event in 2004/ 2005 [Schroeder et al., 2010; Borghini et al., 2014]. It is, however, increasingly clear that climate change is already impacting water masses [Schroeder et al., 2016] and the ecosystem [Ben Rais Lasram et al., 2010]. The Mediterranean Sea, which is characterized by a small spatial extent and mild meteorological conditions that facilitate the deployment of instruments at sea, is an excellent laboratory to monitor these impacts and to prepare models to predict future changes by calibrating them based on the present transition period.

The impacts of climate change may include the frequency and/ or the intensity of convection, which could be modified as a result of increasing stratification in the upper layers [Somot *et al.*, 2006]. The weakening of convection processes could lead to a reduction in the occurrence and extent of phytoplankton blooms in the northwestern region. The consequences of climate change on the structure of the planktonic ecosystem and carbon sequestration require further examination. It is therefore a priority to better understand the functioning of the planktonic ecosystem, within both convection and stratified regions of the western Mediterranean, and assess how the ecosystem may evolve under weakened convection or in its absence.

In this context, and in the framework of the MerMex project, four cruises were carried out between July 2012 and June 2013 [Estournel *et al.*, 2016a; Waldman *et al.*, 2016]. The data that was collected made it possible to describe the spatial distribution of phytoplankton in the deep convection northwestern Mediterranean during stratified, deep convection and phytoplankton bloom periods [Mayot *et al.*, 2017a; Severin *et al.*, 2017]. This unprecedented *in situ* observation offered a great opportunity to calibrate and validate a 3D coupled physical-biogeochemical model [Estournel *et al.*, 2016b; Kessouri *et al.*, 2017]. In the present study, we used this coupled model to investigate phytoplankton dynamics and the capacity of the western Mediterranean to export organic carbon below the photic layer and to transfer it to deep waters. We focused on the comparison of regions along a trophic and vertical mixing gradient encompassing the northern and southern regions. These regions are characterized by a similar distribution of nutrients, making it easier to discriminate the role of convection on primary production and export variability from other possible influences.

The article starts with a presentation of the methods and an evaluation of the model's results. The seasonal cycle of atmospheric forcing, MLD and chlorophyll vertical profile are presented in Sections 4.1 and 4.2. The seasonal cycle of primary production and carbon export is described in



Sections 4.3 and 4.4, respectively. Finally, the conditions favoring bloom onset, export of organic carbon under the photic zone, and its transfer to deep waters are discussed in Section 5.

## **2. Methods**

### **2.1 The numerical tool**

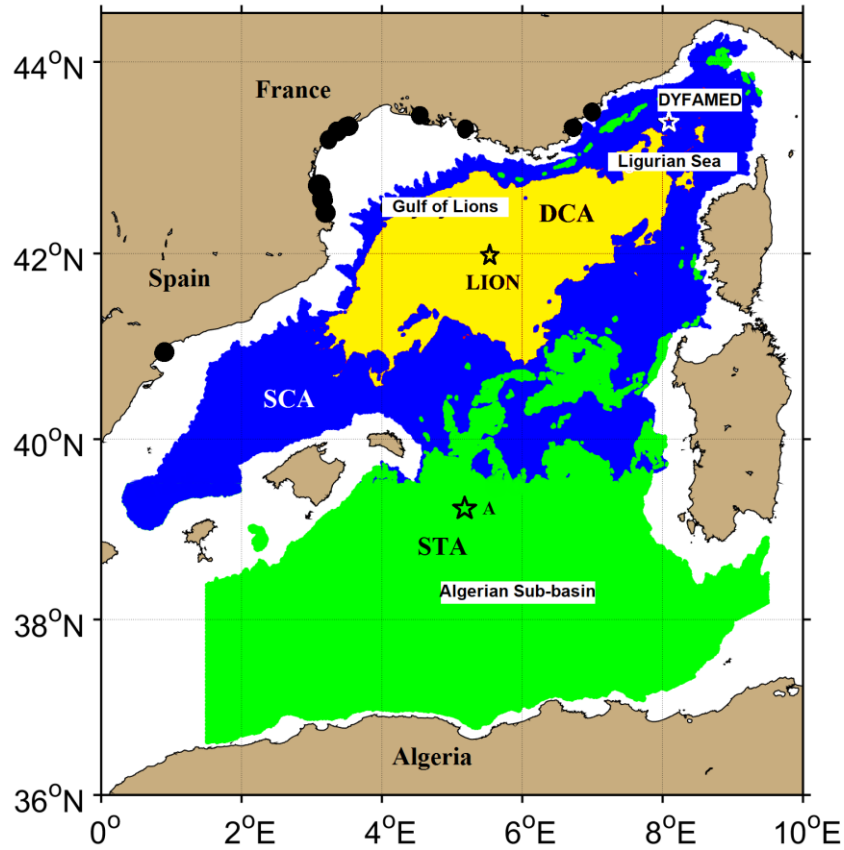
A biogeochemical model was forced offline using the daily outputs of a 3D hydrodynamic model. The models and their initial and boundary conditions are described in the following sections.

#### **2.1.1 The hydrodynamic model**

The SYMPHONIE model used in this study is a 3D primitive equation, with a free surface and generalized sigma vertical coordinate, described in Marsaleix et al. [2008, 2009, 2011 and 2012]. This model was previously used in the Mediterranean to simulate open sea convection [Estournel et al., 2016b], and ocean circulation on the slope [Rubio et al., 2009] and on the continental shelf [Petrenko et al., 2008]. The numerical domain (Figure 1) covered most of the western Mediterranean basin, using a curvilinear grid with variable horizontal resolution [Bentsen et al., 1999]. The mesh size was 1.4 km to the south and 0.8 km to the north. The southward decrease in resolution was due to a compromise between the need to cover the western Mediterranean basin at a reasonable cost, while considering the northward decrease of the Rossby radius, and the need for increased resolution in the winter convection zone [Estournel et al., 2016b]. Forty vertical levels were used with closer spacing near the surface (15 levels in the first 100 m in the center of the convection zone characterized by depths of ~2500 m).

The model was initialized and forced at its lateral boundaries with daily analyses provided by the Mercator-Ocean operational system based on the NEMO model [Maraldi et al, 2013]. The

configuration of this model was the PSY2V2R4 prototype based on the NEMO ocean modeling platform and the SAM data assimilation system [Lellouche *et al.*, 2013] at a resolution of  $1/12^\circ$  over the Atlantic and the Mediterranean from  $20^\circ$  S to  $80^\circ$  N. Following Estournel *et al.* [2016b], the initial field and open boundary conditions were corrected from stratification biases deduced from comparisons with observations taken during the MOOSE-GE cruise of August 2012. Atmospheric forcing (turbulent fluxes) was calculated using the bulk formulae of Large and Yeager [2004]. Meteorological parameters including downward radiative fluxes were taken from the ECMWF (European Centre for Medium-Range Weather Forecasts) operational forecasts at  $1/8^\circ$  horizontal resolution and 3-hour temporal resolution based on daily analyses at 00.00 UTC. River runoffs were considered based on realistic daily values for French rivers (data provided by Banque Hydro, [www.hydro.eaufrance.fr](http://www.hydro.eaufrance.fr)) and Ebro (data provided by SAIH Ebro, [www.saihebro.com](http://www.saihebro.com)) and mean annual values for the other rivers.



**Figure 1.** Location of the modeled area in the western Mediterranean Sea. The colored regions correspond to the three regions considered in this study: the Deep Convection area (DCA, yellow), Shallow Convection area (SCA, blue) and Stratified area (STA, green). Black dots on the coastal band are river point-sources.

### 2.1.2 The biogeochemical model

The Eco3M-S model is a multi-nutrient and multi-plankton functional type model that simulates

the dynamics of the biogeochemical decoupled cycles of several biogenic elements (carbon, nitrogen, phosphorus and silicon), and of non-Redfieldian plankton groups. The model structure used in this study has been previously described in Ulises et al. [2016], Auger et al. [2011; 2014] and Herrmann et al. [2013]. Most parameter values are based on the study of Ulises et al. [2016], but a new calibration was carried out for some parameters using several observational datasets [Kessouri et al., 2017].

The biogeochemical model was downscaled from the Mediterranean basin scale to the regional scale described here. The biogeochemical basin scale model was forced by the temperature, current and vertical diffusivity daily fields of the NEMO model (PSY2V2R4 analyses), which was also used for the boundary conditions of our hydrodynamic model (Section 2.1.1). This basin configuration was initialized in summer 2010, with climatological fields of nutrient observations from the oligotrophic period in the Medar/ MedAtlas database [Manca et al., 2004]. Daily values of all state variables were extracted from the basin-scale run for the initial and lateral boundary conditions of the regional model. This nesting protocol ensures the coherence of the physical and biogeochemical fields at the open boundaries. The regional model was initialized in August 2012. At the Rhone River mouth, nitrate, ammonium, phosphate, silicate and DOC concentrations were prescribed using *in situ* daily data (P. Raimbault, personal communication). These data, combined with those of Moutin et al. [1998] and Sempéré et al. [2000], were used to estimate dissolved organic phosphorus and nitrogen, and particulate organic matter concentrations as described in Auger et al. [2011]. At the other river mouths, climatological values were prescribed according to Ludwig et al. [2010]. The deposition of organic and inorganic matter from the atmosphere was neglected in this study. Benthic fluxes of inorganic nutrients were considered by coupling the pelagic model with a simplified version of the meta-model described by Soetaert et al. [2001]. The parameters of the latter model were set

following the modeling study performed by Pastor et al. [2011] for the Gulf of Lions shelf.

## **2.2 MODIS satellite dataset**

Daily mean surface chlorophyll concentrations were extracted from the MODIS (Moderate Resolution Imaging Spectroradiometer) Aqua (EOS PM) satellite dataset [Ocean Biology Processing Group, 2014] for the period September 2012 to September 2013, in order to evaluate the spatial and temporal variation of the modeled surface chlorophyll concentrations in the western Mediterranean.

## **2.3 Areas of study**

Temporal variations in the MLD are considered a major forcing of phytoplankton dynamics [Williams and Follows, 2003]. In their study of the western Mediterranean, using a MLD dataset and ocean color data, Lavigne et al. [2013] concluded that MLD plays a key role in phytoplankton phenology, and can explain the coexistence of the two trophic regimes previously observed [D’Ortenzio and Ribera d’Alcala, 2009]. A first regime in the northwestern convection region is characterized by a deepening of the mixed layer in winter (reaching 1000 m for 52% of the years for which observations were available between 1980 and 2013 [Somot et al., 2016]), followed by an intense phytoplankton bloom (similar to the subpolar regime [Williams and Follows, 2003]). A second regime in the southern (Algerian) sub-basin is characterized by continuous slow phytoplankton growth, concomitant with the shallow deepening of the mixed layer (similar to the subtropical regime [Williams and Follows, 2003]). By analyzing the interannual variability of satellite-derived surface chlorophyll, Mayot et al. [2016] distinguished two sub-regimes in the northwestern convection region: bloom was found to be more pronounced and delayed in the center of the convection zone than at its periphery. Mayot et al. [2017a] showed that these two sub-regimes are distinguished by the intensity and duration of the

deepening of the mixed layer. Their study found that mean MLD exceeded 880 m for the central “high bloom” region, over a period of one month, and reached 475 m, for a couple of days, in the surrounding “bloom” region, in the winter of 2012/ 2013.

Following these earlier studies, we decided to divide the open-sea of the western Mediterranean ( $H > 1500$  m;  $H$  is the bathymetry) into three regions (Fig. 1), in order to carry out analyses of phytoplankton dynamics and estimates of primary production and export. The first was the *Deep Convection* region, defined as the area where daily average of MLD exceeded 1000 m for at least one day during the studied winter. The second was the *Shallow Convection* region, defined as the area in which daily average of MLD exceeded 150 m but did not reach 1000 m. The Shallow Convection region was located at the periphery of the first area and mostly covered the Balearic Sea. The third area, named the *Stratified* region, covered a large part of a deep pelagic zone in the southwestern Mediterranean (Algerian sub-basin) where maximum winter MLD was less than 150 m. In the present study, MLD was defined as the depth where potential density exceeded the value at a depth of 10 m by  $0.01 \text{ kg m}^{-3}$  [Coppola et al., 2017]. This density-based criterion (rather than a temperature-based criterion) avoids any overestimation of the MLD, and any consideration of surface restratification caused by a change in surface heat flux, especially in the deep convection region [Houpert et al., 2015]. The division into regions allowed us to focus our analysis on the factors underlying differences in maximum winter MLD.

The heat fluxes, and hydrodynamic and biogeochemical variables that are presented in the following sections correspond to the values of these variables averaged over all model grid points included in the three areas. Furthermore, we calculated export below the regional maximum photic zone at 150 m. Following Lazzari et al. [2012], this estimate of the depth of the photic layer was based on the regional minimum value of the diffuse attenuation coefficient of light at 490 nm derived from satellite observations (<http://marine.copernicus.eu/>), found close to

0.03 m<sup>-1</sup> over the study period, and on the Lambert-Beer formulation to evaluate photosynthetic available irradiance. Deep transfer was calculated at a depth of 800 m as, in general, temporal variability in water masses at depths > 800 m is weak [Bethoux *et al.*, 1989]. Moreover, it is possible that, in convection regions, deep waters below 800 m are mixed with overlying waters, and a fraction of exported matter and its remineralization product are imported back into surface and intermediate layers during the following winters. To discuss deep transfer on a longer period than one year (Section 5.4), we also estimated export below the maximum MLD, as recommended in Pavelsky *et al.* [2017]: this was computed at the greatest depth between 800 m and the local maximum MLD over the study period, for each model grid point.

## 2.4 Determination of bloom onset

Understanding the environmental factors that control phytoplankton bloom onset has been a key issue in a large number of studies [Siegel *et al.*, 2002; Behrenfeld, 2010; Brody and Lozier, 2015; Henson *et al.*, 2009]. Several methods have been defined to determine its date. Siegel *et al.* [2002] defined it as the first day of the year when surface chlorophyll concentration exceeds the annual median, plus 5%. Adjustments to this method have been made to capture the subtropical autumnal bloom, for instance, by considering the investigated year to start in September [Henson *et al.*, 2009], or by avoiding consideration of a small, transient concentration increase by changing the value of the threshold (10% instead of 5%, as in Bernardello *et al.* [2012]). Other studies [Behrenfeld, 2010; Brody and Lozier, 2015] used observational data to develop a method based on the net accumulation rate. The latter method is more appropriate to detect bloom onset when the phytoplankton biomass is initially low [Brody *et al.*, 2013], as is the case in convective regions. In the present study, bloom onset was considered as the day on which the net accumulation rate of carbon biomass integrated through the water column (Eq. 1) exceeded 50% of its annual maximum value.

$$r = \frac{\ln \frac{C(t+\Delta t)}{C(t)}}{\Delta t} \quad (1)$$

where  $r$  is the net accumulation phytoplankton rate,  $C(t)$  is the depth-integrated phytoplankton biomass, and  $\Delta t = 7$  days. The index  $r$  was compared to an index based on surface chlorophyll, using the method of Siegel et al. [2002], that we adapted for our study, by considering that the year began in September.

### 3. Model evaluation

A detailed validation of the coupled hydrodynamic and biogeochemical models over the study period is described in Estournel et al. [2016b] and Kessouri et al. [2017], respectively. Estournel et al. [2016b] conducted several comparisons with observations, such as the spatial distribution of water column stratification in winter at the scale of the northwestern sub-basin (their Fig. 6) or time series of the potential temperature profile in the center of the Gulf of Lions (their Fig. 11). In Kessouri et al. [2017], a comparison of the biogeochemical model results with nutrients and chlorophyll concentrations measured during the DeWEx winter and spring cruises was presented. This comparison showed that the model correctly reproduced the horizontal and vertical chlorophyll and nutrient distribution in these two seasons.

Here, the modeled seasonal evolution of surface chlorophyll in the three western Mediterranean regions (Deep Convection, Shallow Convection and Stratified) is compared with that derived from MODIS data over the period September 2012 to September 2013 (Fig. 2). Satellite data were interpolated on the model grid, then both modeled and observed chlorophyll were averaged in the three regions (model outputs corresponding to missing satellite data were not considered). Pearson correlations between surface modeled and satellite-derived chlorophyll concentrations were  $R = 0.8, 0.85$  and  $0.85$  ( $p < 0.01$ ) in the three regions, respectively (Fig. 2 upper panel). The

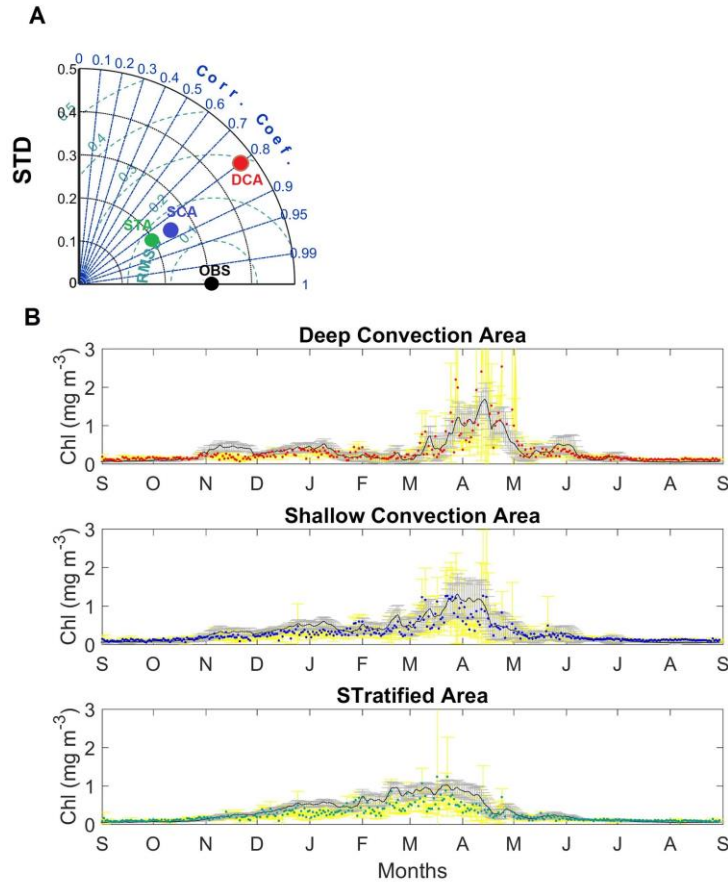


Nash-Sutcliffe efficiency (NS = 0.61, 0.55 and 0.2 respectively), indicated good-to-excellent performance of the model according to Allen et al. [2007]. Mean biases represented a percentage of the observed chlorophyll of  $-8\%$  in the Deep Convection region,  $+16\%$  in the Shallow Convection region and  $+30\%$  in the Stratified region. The temporal root mean square error was maximum ( $0.26 \text{ mg m}^{-3}$ ) in the Deep Convection area (Fig. 2 upper panel) where the signal was highly variable during bloom.

The timing of surface phytoplankton development and its magnitude were generally correctly represented by the model in the three studied regions. The observations and the model exhibited similar seasonal trends, that clearly show the contrast between the north and the south of the basin: in February, concentrations increased from north to south, while in April this trend was reversed. On the date of the maximum extent of the low chlorophyll area in the Deep Convection region (February 19 according to model outputs, cloud-free images were too scarce to confirm this), it covered the Gulf of Lions and Ligurian Sea (Fig. 1) in both model results and observations (Fig. 3A and 3B). The spatial pattern of surface chlorophyll during the period of maximum chlorophyll development (April 14) did not differ significantly between the model and observations ( $R = 0.58$  ( $p < 0.01$ )) (Fig. 3C and 3D). Spatial correlation in winter is higher ( $R=0.8$ ).

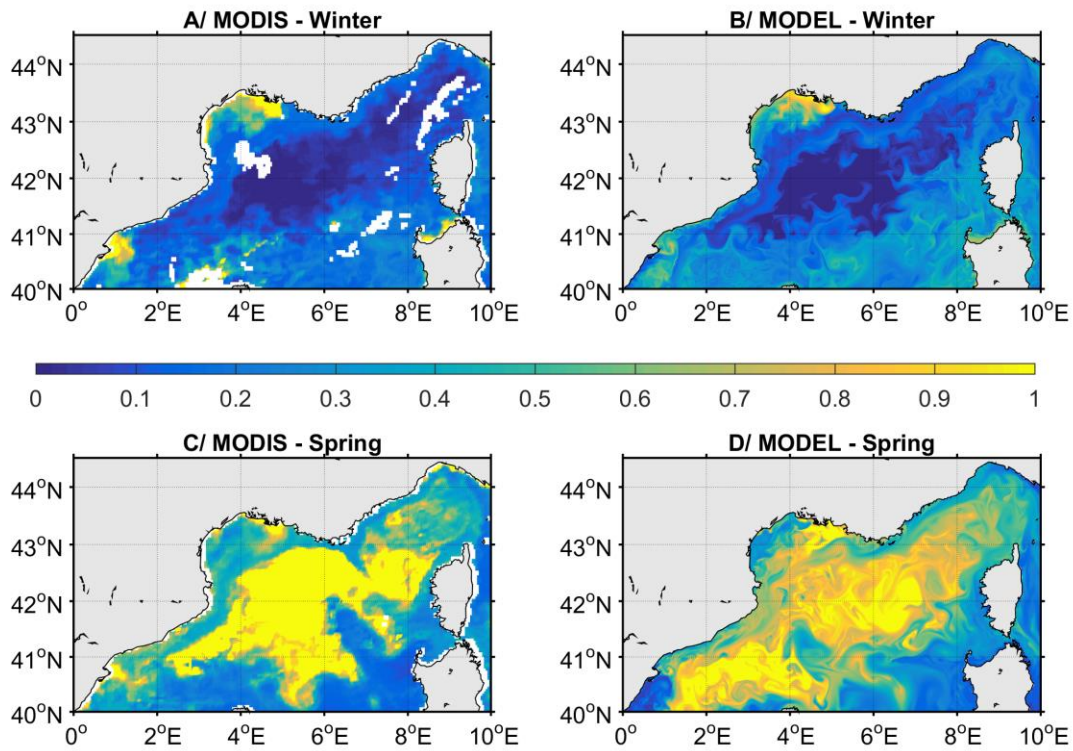
Regarding the vertical distribution of chlorophyll in convection regions, Kessouri et al. [2017] found a good agreement between model results and DeWEx cruise observations. Moreover, the time evolution of the vertical distribution of phytoplankton in the Stratified (southern) region is consistent with climatological observations reported by Lavigne et al. [2015]: the model correctly reproduces the formation of a deep chlorophyll maximum (DCM) after the winter mixing period and its deepening between 50 and 80 m in summer (presented in Section 4.2).

323 The evaluation of the model indicates that it reproduced the annual cycle of surface chlorophyll  
 324 concentration in the three studied regions. However, it underestimated  
 325 surface concentration in the Deep Convection region, and overestimated it in neighboring  
 326 regions. Furthermore, the modeled vertical distribution was consistent with observations in the  
 327 study area.



328  
 329 **Figure 2.** (A) Taylor diagram comparing simulated and observed surface chlorophyll  
 330 concentrations. OBS indicates MODIS data; DCA, SCA and STA indicate model outputs for the  
 331 Deep Convection, Shallow Convection and Stratified regions, respectively. (B) Time series of

simulated (black line, median; gray bar, standard deviation) and observed (colored points and colored blue bars for standard deviation) surface chlorophyll concentrations (in  $\text{mg m}^{-3}$ ) in the three regions: Deep Convection (DCA, red points), Shallow Convection (SCA, blue points) and Stratified (STA, green points) regions, from September 2012 to September 2013. Vertical dashed lines represent the dates of bloom onset (see Section 5.1 and Fig. 6).



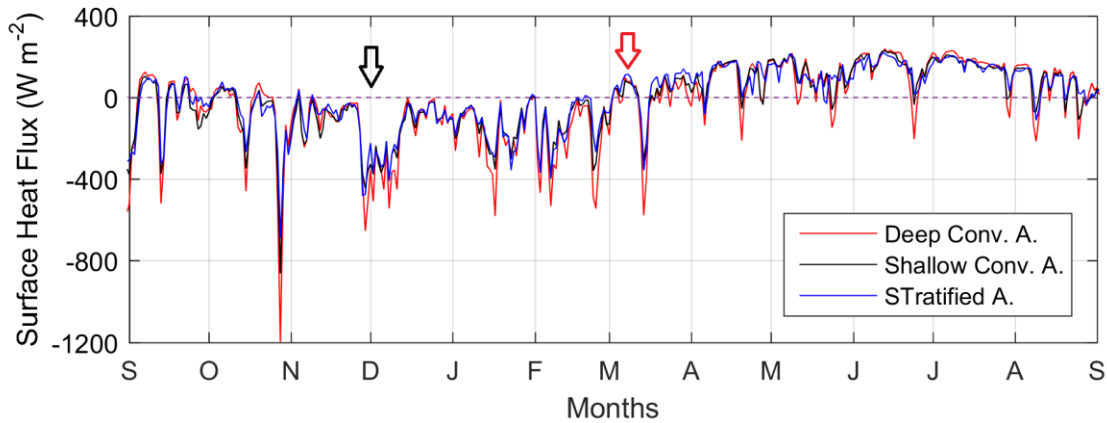
**Figure 3.** Comparison of simulated and MODIS chlorophyll concentrations ( $\text{mg m}^{-3}$ ) in winter (19 February 2013, A and B) and spring (14 April 2013, C and D).

## 4. Results

### 4.1 Atmospheric conditions

Intense cold and dry winds are an essential ingredient of deep convection. Using combined atmospheric and oceanic observations, Estournel et al. [2016a] showed restratification of the upper 500 m during periods of oceanic heat gain, generally associated with low wind conditions and, conversely, the destruction (within hours) of an ocean stratification in response to the passage of a continental air mass, associated with heat loss. Heat flux time series is therefore a relevant parameter to consider in explaining variation in the MLD, which impacts the availability of both nutrients and light for phytoplankton growth. A change in sign of surface heat fluxes can also be used to detect bloom onset, as it induces a decrease in turbulent mixing, increasing the time phytoplankton cells remain in the euphotic layer [Taylor and Ferrari, 2011].

The modeled heat flux evolution was similar in the three studied regions (Fig. 4). Temporal correlation coefficients between heat fluxes in the Shallow Convection and Deep Convection regions, and between the Stratified and Deep Convection regions, were significant at 0.96 ( $p < 0.01$ ) and 0.93 ( $p < 0.01$ ), respectively. Each region was characterized by a major heat loss between September 2012 and mid-March 2013, and a heat gain from mid-March 2013 to September 2013. However, there were clear differences in its magnitude for the three regions. Specifically, heat losses were higher in the Deep Convection region, which is directly exposed to the Mistral and Tramontane winds, than in the two other regions. In this region, average of winter heat flux was  $-180 \text{ W m}^{-2}$ , compared to  $-140 \text{ W m}^{-2}$  in the Shallow Convection region and  $-130 \text{ W m}^{-2}$  in the Stratified region. Heat loss exceeded  $400 \text{ W m}^{-2}$  eleven times in the Deep Convection region from September 2012 to March 2013, while it only exceeded this value twice in the two other regions.



**Figure 4.** Time series of spatially averaged heat flux ( $\text{W m}^{-2}$ ) calculated for the three studied regions: Deep Convection is shown in red, Shallow Convection in blue, and Stratified in green. The dates of bloom onset are indicated by arrows (in black for autumn bloom, in red for spring bloom, see Section 5.1).

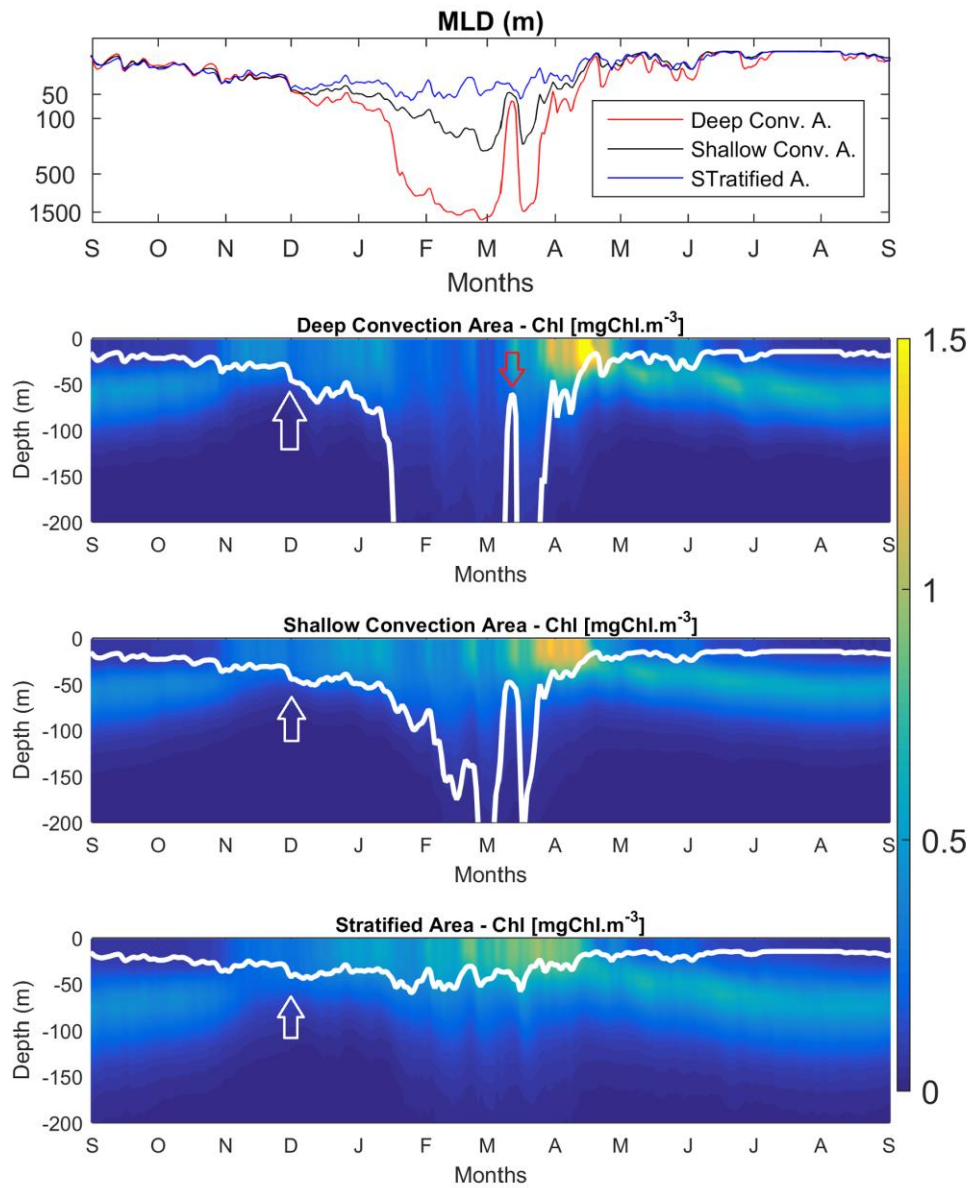
#### 4.2 Temporal variability of MLD and chlorophyll concentration

Figure 5 presents the time evolution of the modeled MLD, spatially averaged for the three regions. The mixed layer deepened progressively from October to January, and then more abruptly from January to March. Despite a few events, characterized by low surface heat loss, that interrupted this deepening, it reached maximum values of 1900 m in the Deep Convection region, 260 m in the Shallow Convection region and 60 m in the Stratified region at the end of February. During the first week of March, which was characterized by positive surface fluxes, significant restratification due to surface and intermediate waters advection was observed [Estournel *et al.*, 2016a]. This led to mixed layer shoaling in the Deep and Shallow convection regions. However, this stratification was insufficient to withstand mid-March gusty winds, which further deepened the mixed layer. After this last deep mixing event, stratification became stable,

marking the end of winter.

The three regions were broadly similar in terms of their chlorophyll dynamics, the exception being winter. A DCM was observed in spring, summer and autumn in the three regions. DCM formation was earlier in the Stratified region (mid-April) than in the Shallow Convection (end of April) and in Deep Convection (May) regions. From its formation, DCM deepened until August, when it reached 60–70 m. In autumn, it became shallower as the light intensity reduced. Chlorophyll concentrations in the DCM decreased from the time of the DCM formation in spring, until its disappearance in November. An intense wind event and heat loss at the end of October deepened the mixed layer, which reached the DCM and led to its disappearance by dilution (discussed in Section 5.1.1). During the second half of December, surface chlorophyll concentration increased considerably.

From mid-January to early March, several wind gusts interrupted surface phytoplankton development in all three regions, but the duration and frequency of these interruptions varied from one region to another. For example, in the Deep Convection region, surface chlorophyll concentrations decreased significantly in response to deep mixing, whereas in the Stratified region, the decrease was smaller and was concentrated into short periods (Fig. 5). From the end of March to mid-April, all three regions were characterized by a sustained increase in surface chlorophyll concentration. A comparison of the regions suggests that strong mixing delayed the biomass increase (discussion in Section 5.1). Moreover, surface phytoplankton development was shorter and more intense where mixing was deep. For instance, in the Deep Convection region, it lasted about 1.5 months with chlorophyll concentrations above  $1.5 \text{ mg m}^{-3}$  during the bloom. In the Stratified region, it lasted at least 2.5 months, with chlorophyll values remaining below  $1 \text{ mg m}^{-3}$ .



**Figure 5.** The top panel represents the temporal evolution of the simulated MLD (m) in the Deep Convection region (red), the Shallow Convection region (blue), and the Stratified region (green) from September 2012 to September 2013. The y-axis is logarithmic. The other panels represent average chlorophyll concentration ( $\text{mg m}^{-3}$ ) for each of the studied regions (Deep Convection, Shallow Convection and Stratified region, from upper to lower panels, respectively). The MLD is superimposed (white line). Arrows indicate bloom onset (in white for autumn bloom, in red for spring bloom, see Section 5.1).

### 4.3 Primary production

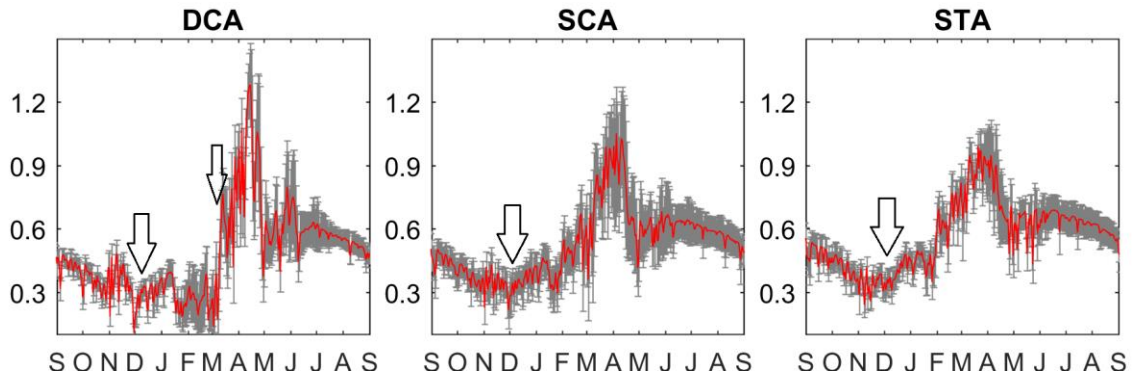
In winter (December–February), the modeled, vertically integrated net primary productivity (NPP) (Fig. 6) had a mean and standard deviation of  $0.45 \pm 0.09$  and  $0.55 \pm 0.13 \text{ gC.m}^{-2} \text{ day}^{-1}$  in the Shallow Convection and Stratified regions, respectively: both NPP means were higher than in the Deep Convection region (mean  $0.3 \text{ gC m}^{-2} \text{ day}^{-1}$ ). NPP increase began in February in the Shallow Convection and Stratified regions, and one month later in the Deep Convection region. NPP reached its maximum in all three regions in spring (mean  $\pm$  standard deviation of  $0.91 \pm 0.21$ ,  $0.86 \pm 0.13$ , and  $0.8 \pm 0.10 \text{ gC m}^{-2} \text{ day}^{-1}$  in the Deep Convection, Shallow Convection and Stratified regions, respectively). A secondary peak (higher in the Deep Convection region than in the two other regions) occurred between mid-May and early June. From early June to November, NPP slowly decreased, with average values of  $0.5 \pm 0.05 \text{ gC m}^{-2} \text{ day}^{-1}$  in the three studied regions.

This seasonal evolution of NPP is consistent with earlier results based on *in situ* observations using the  $^{14}\text{C}$  method in the Ligurian Sea [Marty and Chiavérini, 2002] and remote sensing in various regions of the Mediterranean basin [Bosc *et al.*, 2004; Uitz *et al.*, 2012]. However, summer NPP was higher in the model ( $0.6 \text{ gC m}^{-2} \text{ day}^{-1}$ ) than for observations ( $0.4 \text{ gC m}^{-2} \text{ day}^{-1}$ ),



especially in the Shallow Convection and Stratified regions. This summer overestimation has also been identified for other numerical models [Crispi *et al.*, 2002; Allen *et al.*, 2002; Lazzari *et al.*, 2012]. These differences could be nuanced by limitations in the determination of primary production based on remote sensing in the presence of a DCM, as most of the light recorded by remote sensing emanates from the upper few centimeters of the water column [Helbling and Villafane, 2009]. The impact of this limitation on the estimate of annual primary production could be all the more significant following the work of Macias *et al.* [2014], who estimated that primary production in the DCM represents 62% of the total primary production in the open-sea Mediterranean regions. The results of our model showed that 90% of primary production in spring/ summer, and 70% at the beginning of the fall occurred in the DCM layer in all three regions.

At the annual scale, we estimated a NPP of  $175 \pm 6 \text{ gC m}^{-2} \text{ year}^{-1}$  in the Deep Convection region,  $192 \pm 14 \text{ gC m}^{-2} \text{ year}^{-1}$  in the Shallow Convection region, and  $207 \pm 14 \text{ gC m}^{-2} \text{ year}^{-1}$  in the Stratified region. Because of the overestimation of surface chlorophyll in the Stratified region, and the underestimate in the Deep Convection region, we did not consider the inter-region NPP trend significant. By way of comparison, Lazzari *et al.* [2012] did not observe any clear NPP gradient between the eastern Algerian sub-basin and the northwestern region, based on a coupled physical-biogeochemical model.



**Figure 6.** Time series from September 2012 to September 2013 of simulated net primary production (NPP) ( $\text{gC m}^{-2} \text{ day}^{-1}$ ) spatially averaged (red) and standard deviation (gray) in the Deep Convection (DCA, left), Shallow Convection (SCA, middle) and Stratified (STA, right) regions. Vertical arrows indicate bloom onset (See Section 5.1).

#### 4.4 POC and DOC export

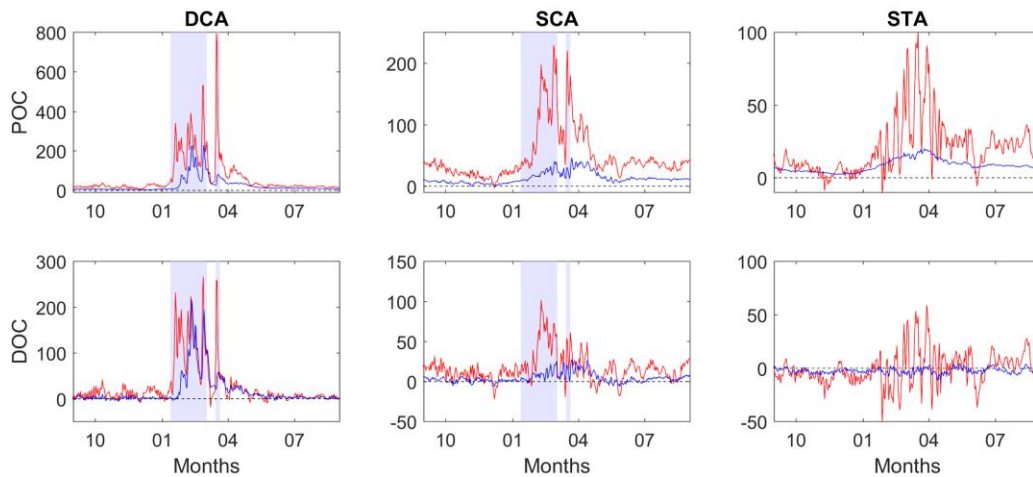
Figure 7 presents the time evolution of the modeled export of DOC and POC at 150 and 800 m depths. This was calculated as the net downward flux induced by turbulent mixing, advection and sedimentation (for particulate matter). In summer and autumn, vertical export was low in all three regions. In the Deep Convection region, where the MLD reached at least 500 m between mid-January and the first week of March (Fig. 5), POC and DOC fluxes were strong and variable, with peaks coinciding with strong mixing events (mid-January, beginning and end of February, and mid-March, see Fig. 4). During the main convection event, the export at 150 (800) m reached  $0.6$  ( $0.2$ )  $\text{gC m}^{-2} \text{ day}^{-1}$  for POC, and  $0.25$  ( $0.2$ )  $\text{gC m}^{-2} \text{ day}^{-1}$  for DOC. During the secondary convection event (the third week of March), simulated export is characterized by a high peak at 150 m ( $0.95$   $\text{gC m}^{-2} \text{ day}^{-1}$  for POC, and  $0.30$   $\text{gC m}^{-2} \text{ day}^{-1}$  for DOC), with another moderate peak at 800 m ( $0.06$  and  $0.05$   $\text{gC m}^{-2} \text{ day}^{-1}$  for POC and DOC, respectively). Similarly,

in the Shallow Convection region, POC and DOC export was maximum during mixing events, exceeding  $0.15 \text{ gC m}^{-2} \text{ day}^{-1}$  and  $0.05 \text{ gC m}^{-2} \text{ day}^{-1}$ , respectively, at 150 m (compared to  $0.02 \text{ gC m}^{-2} \text{ day}^{-1}$  and  $0.02 \text{ gC m}^{-2} \text{ day}^{-1}$ , respectively, at 800 m). In both convection regions, an increase of POC and DOC export was simulated at 150 m in April during bloom. In the Stratified region, POC export at both depths was maximum during mixing periods, notably the period coinciding with maximum phytoplankton development (when it reached  $0.10$  and  $0.02 \text{ gC m}^{-2} \text{ day}^{-1}$ ). DOC export at 150 m was highly variable (positive and negative peaks reaching  $0.05 \text{ gC m}^{-2} \text{ day}^{-1}$ ), especially in winter; it was much lower at a depth of 800 m for the whole year.

At the annual scale (Table 1), modeled POC and DOC export at both depths followed the same increasing trend: it was higher in regions where vertical mixing was deeper. The spatial mean and standard deviation of export at 150 (800) m were estimated at  $25 \pm 34$  ( $8 \pm 9$ ),  $15 \pm 14$  ( $4 \pm 6$ ) and  $8 \pm 6$  ( $3 \pm 4$ )  $\text{gC m}^{-2} \text{ year}^{-1}$  for POC, and  $10 \pm 17$  ( $5 \pm 7$ ),  $5 \pm 6$  ( $1 \pm 1.5$ ) and  $-1 \pm 5$  ( $-2 \pm 3$ )  $\text{gC m}^{-2} \text{ year}^{-1}$  for DOC, in the Deep Convection, Shallow Convection and Stratified regions, respectively. It is noteworthy that spatial variability was high within each region. The influence of convection on annual export will be discussed in Section 5.2. and the efficiency of export and transfer to deep waters in Section 5.3. The deep transfer of organic carbon and the comparison of the three regions on a decadal timescale will be discussed in Section 5.4.

The simulated seasonal evolution of POC export below the photic zone agrees with sediment trap measurements from the DYFAMED station in the Ligurian Sea (Fig. 1) [Miquel *et al.*, 2011] and the LION site in the Gulf of Lions (Fig. 1) [Stabholz *et al.*, 2013]. Both indicated: (1) rapid exports of particulate and dissolved matter during convection; (2) a bloom-induced export in spring; and (3) low export rates during the stratified period. From a quantitative point of view, Gogou *et al.* [2014] estimated an annual flux of  $23 \text{ gC m}^{-2} \text{ year}^{-1}$  at 100 m at the LION site (Fig.1); Miquel *et al.* [2011] found an annual flux of  $2.5 \text{ gC m}^{-2} \text{ y}^{-1}$  at 200 m at DYFAMED; and

Zúñiga et al. [2007] reported an annual flux of  $\sim 6 \text{ gC m}^{-2} \text{ year}^{-1}$  at 250 m in the Algerian sub-basin (Point A on Fig 1). At the same locations and depths, our model estimated annual POC fluxes of 52, 19 and  $11 \text{ gC m}^{-2} \text{ year}^{-1}$ , respectively. The higher POC fluxes obtained in the convection regions in the model may be partly explained by an underestimation of POC export from sediment trap measurements during intense mixing periods [Buesseler et al., 2007]. Regarding DOC export, our estimate of  $18 \text{ gC m}^{-2} \text{ year}^{-1}$  is similar to measurements carried out by Copin-Montégut and Avril [1993] and Avril [2002] of 18 and  $12 \pm 6 \text{ gC m}^{-2} \text{ year}^{-1}$ , respectively, at 100 m in the Ligurian Sea. The annual POC flux at mid-depth has been estimated in observational studies at the LION site as 2.4 and  $1.9 \text{ gC m}^{-2} \text{ year}^{-1}$  at 1000 m [Stabholz et al., 2013; Gogou et al., 2014]. This can be compared to  $1.6 \text{ gC m}^{-2} \text{ year}^{-1}$  at 1000 m at DYFAMED [Miquel et al., 2011], and  $4.8 \text{ gC m}^{-2} \text{ year}^{-1}$  at 845 m in the Algerian sub-basin [Zúñiga et al., 2007]. At the same locations and depths, the model computed sedimentation export of 2.8, 2.6 and  $3.1 \text{ gC m}^{-2} \text{ year}^{-1}$ , respectively, which is close to observations.



**Figure 7.** Time series from September 2012 to September 2013 of modeled particulate (upper panel) and dissolved (lower panel) organic carbon export ( $\text{mgC m}^{-2} \text{ day}^{-1}$ ) at 150 m depth (in red)

and 800 m (in blue), in the Deep Convection Area (DCA, left), Shallow Convection Area (SCA, middle) and Stratified Area (STA, right). The first blue bar corresponds to the main convection event, and the second blue bar represents the short deep mixing event of the third week of March.

## **5. Discussion**

### **5.1. Conditions favoring bloom onset**

#### ***5.1.1. Autumnal bloom***

As described in Section 2.4, we determined bloom onset based on the net accumulation rate of phytoplankton biomass. The autumnal bloom onset occurred at the beginning of December in the two convective regions, and a few days later in the Stratified region (red vertical dashed lines in Fig. 8). This difference is not significant, as it is sensitive to the choice of the threshold for the rate of accumulation (especially in the Stratified region). The following analysis concerns the early December period for the three regions.

Atmospheric forcing, biotic and abiotic conditions at the onset of the autumnal bloom were similar in the three regions: (1) bloom was triggered during a period of high heat losses (Fig. 8b, 8h, 8n); (2) the mixed layer suddenly deepened (40–50 m in the three regions, Fig. 8c, 8i, 8o); (3) turbulent diffusivity suddenly increased in all regions (Fig. 8d, 8j, 8p); (4) zooplankton integrated biomass constantly decreased after September (Fig. 8e, 8k, 8q); and (5) nitrate and phosphate concentrations at the surface began to increase in all regions: concentrations reached 2 mmol m<sup>-3</sup> and > 0.1 mmol m<sup>-3</sup>, respectively, in the Deep Convection region, about two times lower in the Shallow Convection region, and four times lower in the Stratified region, while they had been close to 0 prior to the bloom triggering (Fig. 8f, 8l, 8r).

An estimate of bloom onset based on surface chlorophyll, rather than vertically integrated organic carbon would have brought it forward by one month (Fig 8, dashed black lines). The increase of surface chlorophyll at the end of October was caused by the erosion of the DCM, at a time when the mixed layer deepened, without reaching the nutricline. This purely physical process was not accompanied by an increase in integrated carbon (red solid line in Fig 8a, 8g, 8m) and was therefore not considered as bloom within the meaning of integrated biomass increase. It should be noted that the corollary of this process is a potential bias in remote sensing detection of post-DCM bloom. The period between the two estimates (based on surface chlorophyll and vertically integrated biomass) corresponds to the increase in the MLD from the DCM to the nutricline. In our case, this period lasted one month, which appears long if we consider the proximity of the DCM to the nutricline (about 20 m, see Kessouri et al. [2017]). However, in the present case, it corresponded to the period between two strong wind and heat loss events at the end of October and the end of November (Fig. 4), each of which coincided with a sudden deepening of the mixed layer (see Estournel et al. [2016b] their Fig. 11 for the temperature evolution in the 150-m upper layer). The first event deepened the mixed layer down to the DCM, and the second brought it below the nutricline. This sequence of events, which began with the mixing of the DCM, followed by an increase of primary production caused by the nutrient supply from deeper layers, induced by increased wind stress, has been previously described by Chiswell et al. [2013]. Lavigne et al. [2015] indicated that DCM erosion could explain 60% of chlorophyll profiles observed in the Ionian region in December and January.

The triggering of the autumn bloom corresponds to the description by Williams and Follows [2003] of the subtropical bloom onset, which occurs when the deepening mixed layer provides new nutrients (Fig. 9). However, we noted that the integrated zooplankton biomass was low in all three regions at autumn bloom onset (reaching a minimum in the Shallow Convection and

Stratified regions). Therefore, it is likely that the low magnitude of grazing pressure participated to trigger the autumn bloom [Behrenfeld *et al.*, 2010; Behrenfeld and Boss, 2014]. Moreover, we noted that the ongoing mixed layer deepening following the autumn bloom induced dilution, which prevented the zooplankton biomass taking advantage of the autumn bloom to grow in the Deep Convection region.

### **5.1.2. Winter/ early spring bloom in the Deep Convection area**

In the Deep Convection region, the autumnal bloom was interrupted for a period of two months (from mid-January to mid-March) due to a lack of light that was, in turn, due to deep mixing. In February, the patch of chlorophyll was vertically homogeneous with a surface chlorophyll concentration below  $0.1 \text{ mg Chl m}^{-3}$  (Fig. 3a and 5a) and high nutrient concentrations ( $> 7 \text{ mmol N m}^{-3}$  and  $> 0.3 \text{ mmol P m}^{-3}$ ) [Kessouri *et al.*, 2017]. The vertically integrated phytoplanktonic biomass was almost constant (Fig. 8a). Winter/ early spring bloom onset was identified in the Deep Convection region on March 8. The conditions that triggered it differed from those that triggered autumnal bloom. Specifically, the former started after a few days of positive heat flux (Fig. 8b), when vertical turbulence decreased significantly (Fig. 8d) and the mixed layer became abruptly shallower (100 m, Fig. 8c). Nitrate and phosphate surface concentrations were high, with values  $> 6.5 \text{ mmol m}^{-3}$  and  $> 0.25 \text{ mmol m}^{-3}$ , respectively (Fig. 8f), while zooplankton biomass and grazing rate reached their annual minimum (Fig. 8e).

These results (summarized in Fig. 9) are consistent with the analysis of the triggering of the North Atlantic subpolar bloom by Williams and Follows [2003], and the results of Taylor and Ferrari [2011] obtained from analytical theory and high-resolution numerical simulations. Both studies emphasized the role of positive (or the reduction of negative) surface heat fluxes. The

simultaneous breakdown of turbulence and a decrease in MLD means that our results also support the discussion of Brody et al. [2013], who argued that a change in sign of heat flux is not the only factor that could restratify the mixed layer, horizontal advection being another. For example, restratification could occur in response to horizontal advection by mixed layer eddies, as shown by Mahadevan et al. [2012], based on observations in the North Atlantic.

The work of Estournel et al. [2016b] showed that, based on a heat and salt budget in the convection zone, from December, horizontal advection acted to stratify the surface layer, with a sustained warming trend that opposed the effect of surface heat fluxes. They reported that during a period of light winds (the beginning of March), the heat budget became positive in surface and intermediate layers. This was argued to be due to the fact that the front between the convective dense layer and adjacent light water became baroclinically unstable, producing restratification by advection of warm water inside the mixed patch.

Following these authors, it is clear that restratification is intrinsically linked to the change in sign of surface fluxes (or the fall of negative fluxes) as baroclinic instability develops when surface heat losses decrease and no longer maintain the verticality of isopycnals. This suggests that the bloom was indirectly triggered by the decline in surface heat losses, which induced a conjunction of closely-related effects: the breakdown of turbulence and water column restratification. However, it should be noted that these arguments were based on a spatial average over a relatively wide, and very heterogeneous area. It is probable that if each point of the model is examined, processes would be more differentiated. For example, the main impact of restratification induced by frontal instabilities should have been at the perimeter of the domain, whereas the 1D turbulence breakdown process was probably more effective in the center of the convective patch. Although a study of these coupled, submesoscale processes is beyond the scope of this paper, it deserves dedicated examination.



Our results also illustrate that the decoupling of phytoplankton and grazers during the winter period was another factor that favored phytoplankton growth after bloom onset. It is of note that small positive and negative changes in the integrated phytoplankton biomass in winter (from December to the spring bloom onset) were associated with the beginning and end of windy conditions and induced heat flux, and uncorrelated with variations in grazing pressure. This indicates that prey–predator decoupling was strong throughout the winter (phytoplankton development being mostly related to mixing-induced nutrient supply). As Behrenfeld and Boss [2014] describe, recoupling is slow, as phytoplanktonic concentration must increase to stimulate grazing and encourage a subsequent increase in herbivores. This recoupling condition was not met during winter, and this explains the continuous decrease of zooplanktonic biomass, which only recovered when phytoplankton rapidly accumulated during the spring bloom as a result of the hydrodynamic factors discussed above.

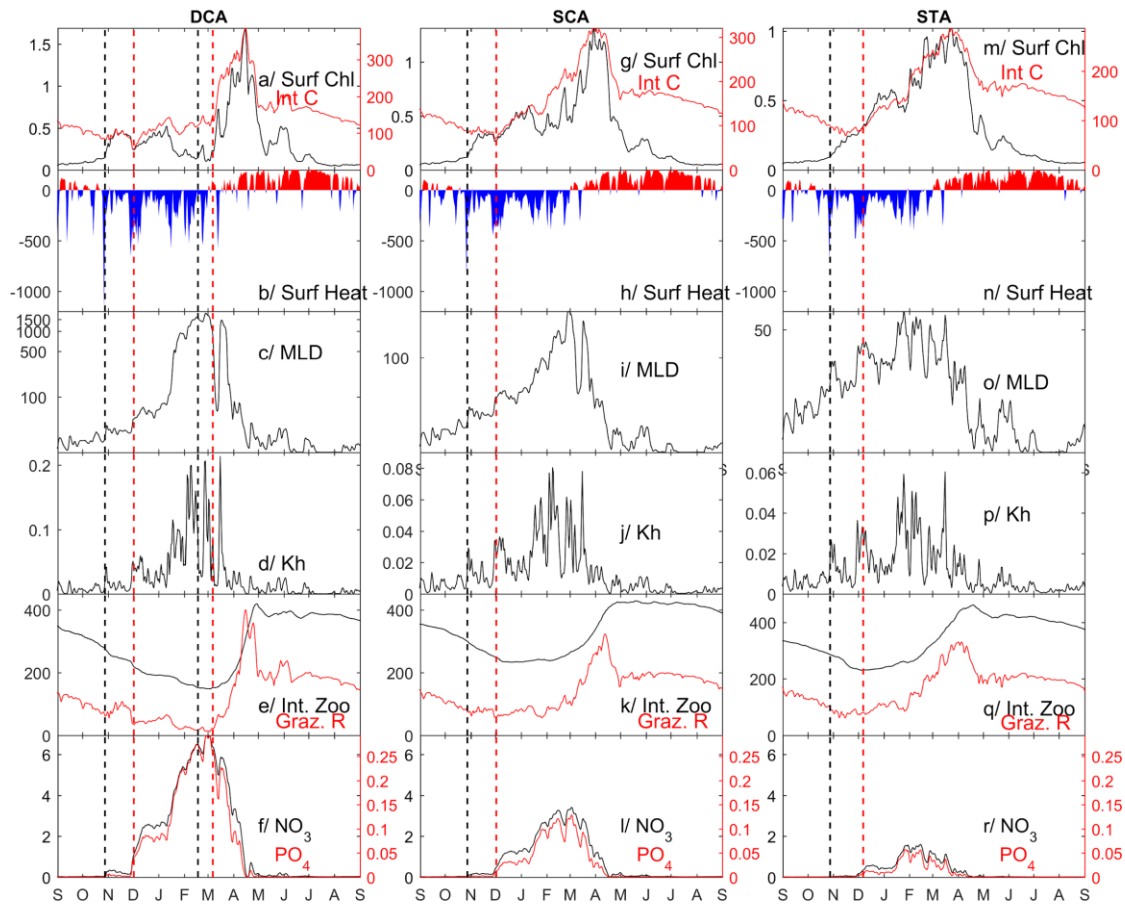
Our results for the northwestern Mediterranean are consistent with those of Bernardello et al. [2012], who found that bloom started as vertical mixing decreased, generally in mid-March. They are also consistent with an observational study by D’Ortenzio et al. [2014] who reported that, in the deep convection region, the triggering of the bloom was unrelated to a change in the nutrient stocks of the euphotic layer since this stock was already available three months before onset. Finally, Auger et al. [2014] found a negative correlation between convection intensity and winter zooplankton biomass; this finding confirms the hypothesis that phytoplankton zooplankton decoupling induced by convection favors the explosion of the phytoplankton biomass.

### ***5.1.3. Phytoplankton growth in the Shallow Convection and Stratified regions***

In the Stratified region, no new bloom onset was identified during the months that followed the

618 autumn bloom, while the vertically integrated biomass progressively increased. This is a  
619 characteristic of the subtropical region. In our results, after the autumn bloom, sustained winter  
620 mixing supplied nutrients almost continuously, producing a moderate accumulation of  
621 phytoplankton that was controlled by herbivores whose biomass was low, but which remained at  
622 a higher level than in the Deep Convection region.

623 The method based on accumulation rates identified several blooms in the Shallow Convection  
624 region in winter (not shown). Biomass increases corresponded to short, calm periods (heat gain  
625 or low heat loss), and were followed by long periods of slow growth that resembled those of the  
626 Stratified region. It is likely that this behavior was specific to the particular year studied. Indeed,  
627 during the study period, the mixed layer remained relatively undeveloped for a long time, not  
628 exceeding 150 m in depth until the end of February (Fig. 8i). Finally, findings for the Shallow  
629 Convection region lay between the other two regions (Fig. 9). Like the Stratified region, the  
630 increase in integrated biomass was progressive but, like the Deep Convection region, surface  
631 chlorophyll increased rapidly in March/ April. The grazing time series was more similar to that  
632 of the Stratified region than the Deep Convection region.



**Figure 8.** Time series from September 2012 to September 2013 of (a, g, m) modeled depth-integrated phytoplankton biomass ( $\text{mgC m}^{-2}$ ) in red and surface chlorophyll concentration ( $\text{mmol.m}^{-3}$ ) in black, (b, h, n) net heat flux ( $\text{W m}^{-2}$ ) with heat losses in blue and heat gains in red, (c, i, o) MLD (m), (d, j, p) the 0–75 m averaged turbulent diffusivity ( $\text{m}^2 \text{s}^{-1}$ ), (e, k, q) depth-integrated zooplankton biomass in black ( $\text{mgC m}^{-2}$ ) and grazing rate in red ( $\text{mgC m}^{-2} \text{day}^{-1}$ ), and (f, l, r) nitrate (in black) and phosphate (in red) surface concentrations ( $\text{mmol.m}^{-3}$ ), in the Deep Convection area (DCA, left), the Shallow Convection area (SCA, middle) and the Stratified area

(STA, right). Vertical dashed lines indicate the dates of bloom onset (black = using surface chlorophyll concentrations; red = using the vertically integrated biomass, see Section 2.4).

## 5.2 Influence of convective mixing on organic carbon export

Organic carbon is exported under the productive layer through two main mechanisms: (1) sedimentation, which only involves individual or aggregated particles with a sufficiently high settling velocity compared to their rate of decomposition and remineralization; and (2) vertical mixing and advection that affect all organic carbon. Observations of the DeWEx Leg1 campaign in February 2013 showed the presence of phytoplankton at depths  $> 2000$  m, at concentrations of  $0.16 \text{ mg m}^{-3}$  [Kessouri *et al.*, 2017]. These observations suggest that vertical mixing and advection are responsible for the presence of organic carbon, including light cells and detritus, in deep layers, as observed by Giering *et al.* [2016] in the Iceland Basin, and modeled by Ulses *et al.* [2016] in the northwestern Mediterranean. It is likely that a fraction of the exported matter observed in deep waters during the winter of 2012/ 2013 was permanently trapped when mixing stopped.

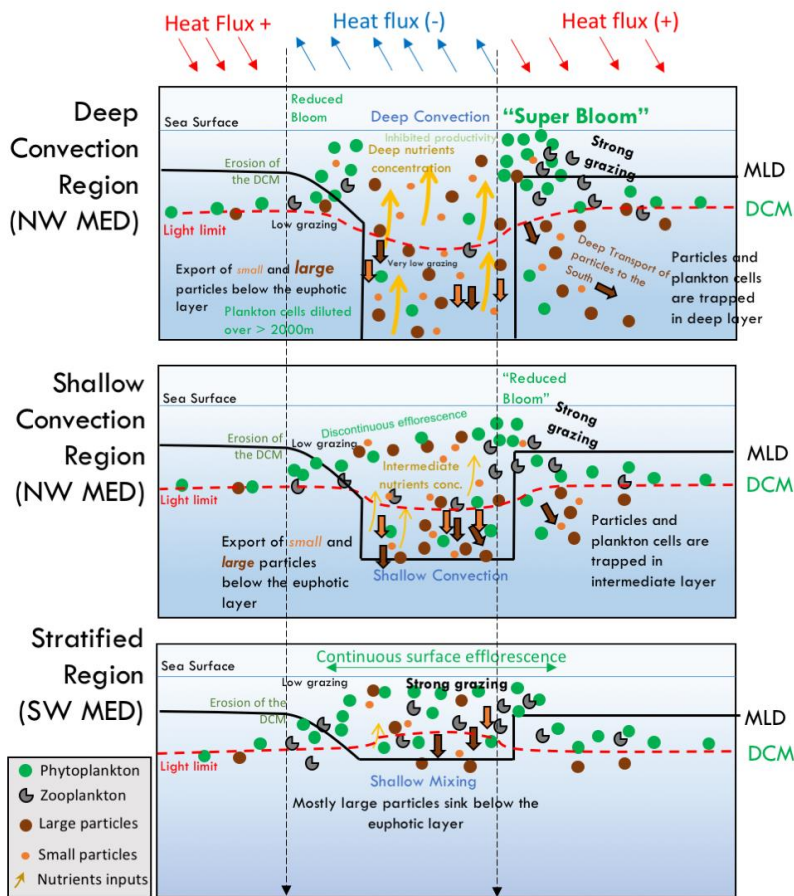
Our model reproduces the homogenization of chlorophyll throughout the mixed layer during convective events, shown by a comparison of the model's results with DeWEx cruise observations performed by Kessouri *et al.* [2017] (see their Fig. 3). Our findings show that the net export fluxes of POC and DOC at 150 m are more than six times higher during these events than during the rest of the year (Fig. 7). The first convection event (15 January to 7 March) took place after the autumnal bloom (Section 5.1). In the Deep Convection region, POC and DOC exports during this event constituted 48 and 61%, respectively, at 150 m, and 50 and 66%, respectively, at 800 m, of the annual amount. The percentages were lower in the Shallow Convection region: 32% and 39% for the export of POC and DOC, respectively, at 150 m (21 and 24%, respectively, at 800 m).

The secondary convection episode lasted 9 days, from 15 to 23 March 2013, and followed a period of weak stratification during which the winter/ early spring bloom began (Section 5.1). In the Deep Convection region, the export of POC and DOC integrated on this secondary event represented 12 and 9% at 150 m (6 and 7% at 800 m) of the respective annual export. This can be compared to the Shallow Convection region, with 8% and 6% at 150 m (6 and 11% at 800 m).

Intermittent convection was observed by Houpert et al. [2016] based on mooring data in the center of the Gulf of Lions, with a secondary deep convection event occurring in March, each year from 2009 to 2013. The model revealed the importance of this recurrent characteristic on the annual export of organic matter. It appears an alternation of periods of restratification, that favors phytoplankton growth, and vertical mixing, that entrains a fraction of new biomass under the euphotic layer. This phenomenon could explain the different peaks in POC and DOC export modeled in mid-January, the beginning and end of February, and the third week of March in convection regions. These peaks corresponded to peaks in heat loss at the ocean surface (Fig. 4) that triggered convection.

The importance of this “mixed layer pump” mechanism [*Gardner et al.*, 1995], which is very clear in the present study period, has been reported in other studies. Bernardello et al. [2012] showed that the frequency of gales during the bloom period was a determining factor in the interannual variability of export in the deep convection region of the northwestern Mediterranean. In other regions, Bishop et al. [1986] estimated that 67% of primary produced carbon was removed by convective mixing during a transient stratification period in a warm-core ring in the northwest Atlantic. Similarly, Ho and Marra [1994] found that a large amount of newly produced organic carbon was exported by mixing during a transient stratification period in the northeast Atlantic. In their study of a shallow convection region in the North Atlantic and equatorial Pacific, Gardner et al. [1995] reported the importance of the deepening of the mixed

layer at night, which favored the new production during the day and export of organic carbon produced. Koeve et al. [2002] estimated that vertical mixing associated with storms, which interrupted the beginning of the early spring bloom, contributed to the export of a large fraction of seasonal new production (between 56% and 65% in 1992, and about 36% in 1989) in the northeast Atlantic.



**Figure 9:** Conceptual model representing plankton and particles behavior for three different

regimes in the western Mediterranean Sea. This conceptual model resumes the various sequences from the destruction of the DCM, the injection of nutrients to the euphotic layer, the deep mixing of the living cells (in the 1<sup>st</sup> region), the triggering of the blooms and the new setting up of the DCM affected by different strength mixing. These sequences are shown simultaneously with different ways of small and large organic particles export and trapping below the euphotic layer via the mixing layer pump.

### **5.3 Efficiency of the export of organic carbon and transfer to the deep layer**

Table 1 presents the annual efficiency of the export of organic carbon produced in the surface layer, and its transfer to deep layers in the three study regions. We calculated the efficiency of organic carbon export as the ratio of the net export at 150 m to the depth-integrated NPP. The efficiency of organic carbon transfer to deep waters was defined as the ratio of net export at 800 m to net export at 150 m.

Since the modeled annual NPP showed no significant differences between the three regions (Section 4.3), the overall efficiency of organic carbon export followed the same trend as exports at 150 m: it was higher in deep mixing regions (Table 1). Furthermore, a similar spatial pattern was found for the ratio of the net export of organic carbon at 800 m to the depth-integrated NPP. No clear trend was found for the fraction of organic carbon exported below 150 m that was also exported below 800 m; the only notable observation was that the highest value was found in the Stratified region.

Henson et al. [2012] estimated that the large-scale efficiency of organic carbon transfer to the deep ocean is opposite to the export efficiency; specifically, export efficiency is high (and transfer efficiency low) at high latitudes, while the opposite is found at low latitudes. The authors suggest that spatial variability in transfer efficiency can be explained by the structure of the

ecosystem. At high latitudes a diatom-dominated ecosystem favors export efficiency; material that is exported below the euphotic is labile and substantially degraded in the mesopelagic zone, leading to a poor deep transfer efficiency. At low latitudes, due to extensive recycling in the euphotic layer, more refractory organic matter is exported under the euphotic layer, favoring deep transfer efficiency. In our simulation, in the Stratified region, export at 150 m was dominated by the sedimentation of large organic particles (78%), a large proportion of which eventually reached deep waters. In convection regions, organic carbon was mainly exported by vertical motion, meaning that it was mostly composed of small particles (heavy particles represented 27% of the POC export at 150 m in the Deep Convection region). Higher transfer efficiency in the Deep Convection region compared to the Shallow Convection region could then be explained by the deeper mixed layer. On the one hand, intensified vertical mechanical mixing supported deep transfer. On the other hand, in the Shallow Convection region, a fraction of small particles that were exported at intermediate depths were remineralized before reaching 800 m, as Henson et al. [2012] suggest for low latitude regions.

Our analysis of the DOC and POC contribution to the export at 150 and 800 m depths showed that the POC export dominated total organic carbon export in the three regions (Fig. 7, Table 1). Our estimation of the DOC contribution to total export in convection regions (28.7% in the Deep Convection region, 22.5% in the Shallow Convection region) is close to the estimate of 20% by Hansell and Carlson [1998] for the global ocean. The DOC net flux at 150 m increased the efficiency of organic carbon export in convective regions (by more than 25%), while its contribution was negative (−30%) in the Stratified region. The increasing contribution of DOC to total export in stronger mixing regions was consistent with the fact that DOC was only exported towards the bottom by turbulent mixing and vertical advection in the model, while POC was also exported by sedimentation. The export of POC by sedimentation occurred throughout the year. Ulses et al. [2016] used the same coupled model in the northwestern Mediterranean deep



convection region, and found the contribution of sedimentation export to total export ranged from 20 to 34%, with a maximum linked to the spring bloom in April/ May. In contrast, we found that DOC export under the euphotic layer was very low outside the winter mixing period, and in downwelling zones (continental slope, meso-scale vortices). As a consequence, DOC accumulated in the surface layer during the stratified period, as observed by Avril [2002] and modeled by Guyennon et al. [2016].

Consistent with the study of Giering et al. [2017] and Dall’Olmo et al. [2016], our results suggest that regions characterized by a clear deepening of the mixed layer may be characterized by a high export of organic carbon towards deep waters. The supply of organic carbon under the photic zone could constitute an important food source for organisms that inhabit the mesopelagic zone.

**Table 1:** Annual organic carbon export ( $\text{gC m}^{-2} \text{ year}^{-1}$ ), and export and transfer efficiency in % from September 2012 to September 2013 at 150 and 800 m depths. The max (800 m, MLD) export reflects the export at depths corresponding to the maximum between 800 m and the local, annual maximum MLD.

	Deep convection	Shallow convection	Stratified
NPP 0–150m	174	190	206
POC export at 150 m	24.8	15.4	8.1
DOC export at 150 m	10.0	4.5	−1.1
POC export at 800 m	7.8	4.2	3.4
DOC export at 800 m	5.4	1.5	−1.7
POC export at max (800 m, MLD)	1.4	4.2	3.4
DOC export at max (800 m, MLD)	0.1	1.5	−1.7

POC export 150m / NPP	14.3	8.1	3.9
POC export 800m / NPP	4.5	2.2	1.6
POC export max (800m, MLD) / NPP	0.8	2.2	1.6
OC 150 m / NPP	20.0	12.4	3.0
OC 800 m / NPP	7.6	3.0	0.8
OC max (800 m, MLD) / NPP	0.9	3.0	0.8
POC export 800m / POC export 150m	31.6	27.1	41.8
POC export max (800m, MLD) / POC export 150m	5.6	27.1	41.8
OC export 800m / OC export 150 m	38.1	28.7	23.6
OC export max (800m, MLD) / OC export 150 m	4.3	28.7	23.6

#### 5.4 Potential implications on carbon sequestration

The role of convection regions in terms of carbon sequestration efficiency is unclear, due to the counteracting effects of convective mixing. These effects are characterized by, on the one hand, an increased export of organic carbon under the euphotic layer and, on the other hand, the supply in the surface layer of dissolved inorganic carbon, which is produced in deep layers by remineralization of exported organic carbon. The latter effect was suggested by Copin-Montégut and Bégovic [2002], who reported high values of  $\text{CO}_2$  fugacity, and episodes of over-saturation of  $\text{CO}_2$  with respect to atmospheric equilibrium during winter wind gusts at the DYFAMED deep station (Fig. 1). Our coupled simulation does not represent the dynamics of dissolved inorganic carbon, and therefore only shows the initial effect of increasing OC export. According to Körtzinger et al. [2008] in the North Atlantic, the physical supply of dissolved inorganic carbon could have a significant effect on carbon drawdown: between 40–45% of the organic carbon

produced during the stratified period could be respired and reinjected into the surface layer during winter mixing. Pavelsky et al. [2017] estimated this physical supply to be 40% and 90% of exported organic carbon at two sites in the North Pacific. By including this mixing-induced carbon supply in their budget, Pavelsky et al. [2017] found that carbon sequestration efficiency was lower in regions where the mixed layer was deeper.

The results of our model show that if calculated below the mixed layer, deep transfer (export at depths corresponding to the maximum between 800 m and the local annual maximum MLD, see Section 2.3) and its efficiency were poorer in the Deep Convection region than in the two other regions, in 2012/ 2013 (Table 1). Indeed, in the Deep Convection region, deep transfer was much lower below the MLD than at 800 m (5 and 45 times for POC and DOC, respectively). Efficiency of deep export and transfer under the annual maximum MLD falls to 11 and 17% respectively compared to the flux below 800 m. In an area corresponding to one sixth of the region surface, the mixed layer reached the seabed, and OC export only corresponded to the deposition of POC. Moreover, the proportion of POC and DOC exported below the MLD during the main convection event falls to 17 and 5% (vs. 50 and 66% at 800 m), respectively. We are also showing weaker POC and DOC exports in the deep convection region compared to the other regions if we interpret the result at the base of the annual maximum (800 m, MLD) rather than an estimation below 150m or 800m.

However, two key characteristics of the hydrodynamics in this area suggest that this latter assessment underestimates the amount of carbon exported under the euphotic layer and isolated from the atmosphere on a decadal timescale. First, the depth of the mixed layer and the extension of the convection zone show a high interannual variability in this region [Houpert et al., 2016] (for instance, they reported that the area of low surface chlorophyll ( $<0.25 \text{ mg m}^{-3}$ ), considered as a proxy of the deep convection zone, ranged between 1.5 and 56.3 km<sup>2</sup> between 2007/ 2008

and 2012/ 2013). Notably, according to Somot et al. [2016], the year 2012/ 2013 was one of the strongest convective years in the period 1980–2013. Conversely, convection was probably low in 2013/ 2014 (owing to the especially low heat losses in ECMWF fields), suggesting that most of the material exported below 800 m in 2012/ 2013 would not have been transferred back in the surface (at least in 2014), and indicating an additional vertical deep transfer through POC sedimentation. Second, the results of our model show a loss of organic carbon in the intermediate (150–800 m) and deep layers (800 m–seabed) by lateral transport during and after convection periods (an amount corresponding to 20 and 45% of the OC exported during convective periods was laterally exported from the Deep Convection area into intermediate and deep layers, respectively, between February and May 2013). Concomitant with this loss in the Deep Convection region, a gain of OC in the Stratified region suggests that the OC that is transferred to deep waters by convective events in the northern region could be transported to the southern region. This is consistent with the results of Ulses et al. [2016] who calculated a north-south transfer corresponding to 53% of the OC exported below 100 m, based on the same coupled model. Moreover, this north–south transfer of OC in deep waters was suggested by Zúñiga et al. [2007] who reported higher POC fluxes at 2145 m than at 1440 m, based on sediment trap measurements. Our results are also consistent with the study of Schroeder et al. [2016] who demonstrated that deep dense waters formed during convective events in the northwestern region propagate throughout the western Mediterranean Sea and towards the Atlantic Ocean. It is likely that these deep waters contain carbon that was exported during convection episode, which then escapes from a transfer back to the surface layer in the following convective winters.

Finally, these findings suggest that multi-annual simulations that include the dynamics of dissolved inorganic carbon are necessary to more accurately estimate the impact of convection processes on the uptake of atmospheric CO<sub>2</sub>, and to compare the net efficiency of the three studied regions regarding this uptake.

## 6. Conclusion

A 3D high-resolution coupled hydrodynamic-biogeochemical model was used to study phytoplankton dynamics and biogeochemical and physical carbon fluxes in three distinct regions of the western Mediterranean Sea. These three regions were characterized by deep convection, shallow convection, and shallow mixing during winter. Comparisons of the results of the model with ocean color satellite observations presented here, and with *in situ* data presented in Kessouri et al. [2017], showed that the model correctly represented the evolution over time of chlorophyll in the three investigated regions.

The model confirms that regimes similar to subpolar and subtropical regimes coexist in the western Mediterranean Sea, within a distance of several hundreds of kilometers, in response to contrasting winter mixing conditions (Fig. 9). Although this has already been established from the annual surface chlorophyll cycle, here we confirm it, based on a broader description of the functioning of the planktonic ecosystem.

The conditions of bloom onset do not significantly differ from those already described in other regions. However, in the case of the autumn bloom, we found that an increase in surface chlorophyll did not correspond to bloom onset, but rather to the erosion of the DCM. In the case of the specific period studied here, the “real” bloom (corresponding to an increase in integrated biomass) occurred one month later, when the mixed layer reached the nutricline. The winter/early spring bloom, as it is known in the North Atlantic, was only identified in the Deep Convection region. The processes triggering this bloom correspond to earlier descriptions of subpolar regions, with the first condition being the breakdown of turbulence. In the northwestern convection region, we identified the importance of restratification, due to baroclinic instabilities that developed rapidly after the change in sign of surface heat fluxes. This process thinned the

844 mixed layer. This indicates that the difference between the active mixed layer (corresponding to  
845 a period of surface heat losses) and the passive mixed layer (after the change in sign of heat  
846 fluxes) is not relevant in explaining the breakdown of turbulence. This is at least true at the  
847 periphery of the convective zone, which was rapidly affected by frontal instabilities. As  
848 expected, the low grazing pressure brought about by convection through dilution allowed the  
849 explosion of the bloom.

850 NPP differences between the stratified and convective regions were considered insignificant  
851 because of opposing biases in the simulated surface chlorophyll in these regions. In deep  
852 convection regions, the inhibition of winter productivity during the two-month period of the deep  
853 mixed layer contributed to reduce primary production. In contrast to annual primary production,  
854 annual export of organic carbon and its deep transfer were very different in convective and  
855 stratified regions in 2012/ 2013. Deep convection produced an export of particulate organic  
856 matter that was 3.5 (2.3) times higher than in the stratified region below 150 (800) m, while for  
857 total (particulate + dissolved) organic carbon, this ratio reached 5.0 (8.0) below 150 (800) m. The  
858 consequence of the two points described above is that export efficiency (export/ primary  
859 production) was much higher in convective regions than in the stratified region. This is largely  
860 the result of the mixed layer pump process described by Dall’Olmo et al. [2016], which  
861 transports POC and DOC to great depths. The results of the model showed that in the deep  
862 convection region, export at 150 m during the convection period represented 60% (70%) of the  
863 annual export of POC (DOC). These results suggest that the higher amount of organic matter  
864 transferred to deep waters, and representing a food source for marine organisms, may make the  
865 northwestern Mediterranean convection areas a favorable habitat for the mesopelagic ecosystem.  
866 Furthermore, they highlight the importance of monitoring convective regions, as they may be  
867 modified in response to climate warming, supporting the development of a regime similar to the

subtropical regime with a lower deep transfer rate. Our estimation of the POC and DOC exports as well as their transfer and efficiency rates below the annual maximum (MLD, 800 m) are lower in the deep convection region compared to the two other regions. These low rates are due to the lateral transfer of the exported matter from the deep convection region to the adjacent regions.

Our analysis, which relied mainly on vertical mixing, did not investigate the coupling between different regions of the Mediterranean that, in the long term, governs the spatial distribution of nutrients. Thermohaline circulation produces a rather complex circulation of the different water masses. In the context of the present paper, Atlantic waters flow into the Algerian sub-basin, and a part of them reaches then the Gulf of Lions convection zone taking a cyclonic path through the western basin. The deep waters formed in the Gulf of Lions are dispersed towards the Algerian sub-basin and feed the deep waters of the western basin. Finally, the Levantine intermediate waters link the eastern and western basins. Formed in the Rhodes gyre in the Levantine basin, they collect organic matter sinking from the surface, which is recycled into nutrients [Crise *et al.*, 1999], part of which is ultimately exported to the Atlantic. During convection in the Gulf of Lions, the nutrients transported in intermediate waters are mixed over the water column and fuel the nutrient pool of surface and deep waters. We have seen that convection exports organic matter. A consequence of deep circulation is horizontal transport of this organic matter towards the Algerian basin. In this context, we refer to the quantification of Ulses *et al.* [2016], who found the transfer to the Algerian sub-basin deep waters (100 m–seabed) was equivalent to 53% of the OC exported below 100 m in the convective region ( $337 \cdot 10^4 \text{ tC y}^{-1}$ ). An additional  $165 \cdot 10^4 \text{ tC y}^{-1}$  was conveyed in the first 100 m. These advective processes are thought to create a coupling between the three regions, and their consequences, notably on carbon sequestration deserve more attention.

To conclude, it is worth restating that the results presented in the present study relate to one year,

characterized by strong convection in the northwestern Mediterranean. This is supported by the work of Somot et al. [2016] (from a model), Mayot et al. [2017b] (from satellite chlorophyll), and Herrmann et al. [2017] (from an analysis of altimetry and surface chlorophyll). These results should be revisited on an interannual basis, when convection is variable. Ulses et al. [2016] found that during mild winters, surface chlorophyll in the deep convection area increases almost constantly from January to mid-March. The authors also found low interannual variability in primary production (~ 4%), and a POC and DOC export at 100 m of about two times higher for years with strong convection than with weak convection. The differences found in our study between the Deep Convection region and the two other regions are generally consistent with these results, and support the argument that the depth of the mixed layer plays a major role in the control of phytoplankton dynamics.



## Acknowledgements

This study has been funded by the PERSEUS project (European Union FP7 Grant Agreement 287600). It is a contribution to the MerMex (Marine Ecosystem Response in the Mediterranean Experiment) project of the MISTRALS international program. Numerical simulations were performed using the computing cluster of Laboratoire d'Aérodynamique and HPC resources from CALMIP (grants P1325, P09115 and P1331). We thank two anonymous reviewers for constructive comments. We thank NASA for providing surface chlorophyll data (10.5067/NIMBUS-7/CZCS/L3B/CHL/2014).

## Table caption

**Table 1:** Annual organic carbon export ( $\text{gC m}^{-2} \text{ year}^{-1}$ ), and export and transfer efficiency in % from September 2012 to September 2013 at 150 and 800 m depths. The max (800 m, MLD) export reflects the export at depths corresponding to the maximum between 800 m and the local, annual maximum MLD.

## Figure captions

**Figure 1.** Location of the modeled area in the Western Mediterranean Sea. The colored regions correspond to the three regions considered in this study: the Deep Convection area (DCA, red), Shallow Convection area (SCA, blue) and Stratified area (STA, green).

**Figure 2.** (Upper panel) Taylor diagram comparing the simulated and observed surface chlorophyll concentrations, where OBS indicates MODIS data and DCA, SCA and STA indicate the model outputs in the Deep Convection region, Shallow Convection region, and Stratified

region, respectively. (Lower panel) Time series of the simulated (black line, median; gray bar, standard deviation) and observed (colored points and colored blue bars for standard deviation) surface chlorophyll concentrations (in  $\text{mg m}^{-3}$ ) in three western Mediterranean regions: the Deep Convection region (DCA, red points), Shallow Convection region (SCA, blue points) and Stratified region (STA, green points) from September 2012 to September 2013. The vertical dashed lines represent the dates of the blooms onset (see Section 5.1 and Fig. 6).

**Figure 3.** Comparison between the simulated and MODIS chlorophyll concentration ( $\text{mg m}^{-3}$ ) in winter (19 February 2013, A and B) and spring (14 April 2013, C and D).

**Figure 4.** Time series of the spatially averaged heat flux ( $\text{W m}^{-2}$ ) calculated for the three studied regions: Deep Convection area in red, Shallow Convection area in blue and stratified area in green. The dates of the blooms onsets are indicated with arrows (see Section 5.1).

**Figure 5.** Top panel represents the temporal evolution of the simulated MLD (m) in the Deep Convection region (black), the Shallow Convection region (blue) and the Stratified region (green) from September 2012 to September 2013. The y-axis is logarithmic. The other panels represent the chlorophyll concentration ( $\text{mg m}^{-3}$ ) averaged in each of the studied regions (Deep Convection region, Shallow Convection region and Stratified region, from upper to lower panel, respectively). The MLD is superimposed (white line). Arrows indicate the bloom onsets (see Section 5.1).

**Figure 6.** Time series from September 2012 to September 2013 of the simulated net primary production (NPP) ( $\text{gC m}^{-2} \text{ day}^{-1}$ ) spatially averaged (red) and standard deviation (grey) in the Deep Convection (DCA, left), Shallow Convection (SCA, middle) and Stratified (STA, right) regions. Vertical arrows indicate the blooms onset (See Section 5.1).

**Figure 7.** Time series from September 2012 to September 2013 of the modeled particulate (upper panel) and dissolved (lower panel) organic carbon export ( $\text{mgC m}^{-2} \text{ day}^{-1}$ ) at 150 m depth in red and 800m in blue, in the Deep Convection Area (DCA, left), Shallow Convection Area (SCA, middle) and Stratified Area (STA, right). The first blue bar corresponds to the main convection event and the second blue bar represents the short deep mixing event of the third week of March.

**Figure 8.** Time series from September 2012 to September 2013 of (a, g, m) modeled depth-integrated phytoplankton biomass ( $\text{mgC m}^{-2}$ ) in red and surface chlorophyll concentration ( $\text{mmol m}^{-3}$ ) in black, (b, h, n) net heat flux ( $\text{W m}^{-2}$ ) with heat losses in blue and heat gains in red, (c, i, o) MLD (m), (d, j, p) the 0-75 m averaged turbulent diffusivity ( $\text{m}^2 \text{ s}^{-1}$ ), (e, k, q) depth-integrated zooplankton biomass in black ( $\text{mgC m}^{-2}$ ) and grazing rate in red ( $\text{mgC m}^{-2} \text{ day}^{-1}$ ), and (f, l, r) nitrate (in black) and phosphate (in red) surface concentrations ( $\text{mmol.m}^{-3}$ ), in the Deep Convection area (DCA, left), the Shallow Convection area (SCA, middle) and the Stratified area (STA, right). Vertical dashed lines indicate the dates of the bloom onsets (black=using surface chlorophyll, red=using the vertically integrated biomass).

**Figure 9.** Conceptual model representing plankton and particles behavior for three different regimes in the western Mediterranean Sea. This conceptual model resumes the various sequences from the destruction of the DCM, the injection of nutrients to the euphotic layer, the deep mixing of the living cells (in the 1<sup>st</sup> region), the triggering of the blooms and the new setting up of the DCM affected by different strength mixing. These sequences are shown simultaneously with different ways of small and large organic particles export and trapping below the euphotic layer via the mixing layer pump.

## 969    **References**

- 970 Allen, J. I., P. J. Somerfield, and J. Siddorn (2002), Primary and bacterial production in the  
 971        Mediterranean Sea: A modelling study, *J. Mar. Syst.*, 33-34, 473–495, doi:10.1016/S0924-  
 972        7963(02)00072-6.
- 973 Anderson, T. R., and P. Pondaven (2003), Non-redfield carbon and nitrogen cycling in the Sargasso  
 974        Sea: Pelagic imbalances and export flux, *Deep Sea Res., Part I*, 50, 573–591.
- 975 Auger, P. A., F. Diaz, C. Ulses, C. Estournel, J. Neveux, F. Joux, M. Pujo-Pay, and J.J. Naudin  
 976        (2011), Functioning of the planktonic ecosystem on the Gulf of Lions shelf (NW  
 977        Mediterranean) during spring and its impact on the carbon deposition: A field data and 3-D  
 978        modelling combined approach, *Biogeosciences*, 8(11), 3231–3261, doi:10.5194/bg-8-3231-  
 979        2011.
- 980 Auger, P. A., C. Ulses, C. Estournel, L. Stemann, S. Somot, and F. Diaz (2014), Interannual  
 981        control of plankton communities by deep winter mixing and prey/predator interactions in the  
 982        NW Mediterranean: Results from a 30-year 3D modeling study, *Prog. Oceanogr.*, 124, 12–  
 983        27, doi:10.1016/j.pocean.2014.04.004.
- 984 Avril, B. (2002), DOC dynamics in the Northwestern Mediterranean Sea (DyFaMed site), *Deep-Sea*  
 985        *Res. II*, 49, 2163–2182.
- 986 Baklouti, M., V. Faure, L. Pawlowski, and A. Sciandra (2006), Investigation and sensitivity analysis  
 987        of a mechanistic phytoplankton model implemented in a new modular *numerical tool*  
 988        (*Eco3M*) dedicated to biogeochemical modelling, *Prog. Oceanogr.*, 71(1), 34–58,  
 989        doi:10.1016/j.pocean.2006.05.003.

- 990 Behrenfeld, M.J. (2010), Abandoning Sverdrup's critical depth hypothesis on phytoplankton  
991 blooms. *Ecology*, 91: 977–989.
- 992 Behrenfeld, M.J. and E.S. Boss (2014), Resurrecting the ecological underpinnings of ocean plankton  
993 blooms. *Annu. Rev. Mar. Sci.*, 6:167–94.
- 994 Ben Rais Lasram, F., F. Guilhaumon, C.Albouy, S. Somot, W. Thuillier, and D. Mouillot (2010),  
995 The Mediterranean Sea as a 'cul-de-sac' for endemic fishes facing climate change. *Global*  
996 *Change Biology*, 16: 3233–3245. doi:10.1111/j.1365-2486.2010.02224.x
- 997 Bentsen, M., G. Evensen , H. Drange, and A.D. Jenkins (1999), Coordinate Transformation on a  
998 Sphere Using Conformal Mapping, *Mon. Wea. Rev.*, 127, 2733-2740
- 999 Bernardello, R., J. G. Cardoso, N. Bahamon, D. Donis, I. Marinov,. and A. Cruzado (2012), Factors  
1000 controlling interannual variability of vertical organic matter export and phytoplankton bloom  
1001 dynamics-a numerical case-study for the NW Mediterranean Sea, *Biogeosciences*, 9, 4233-  
1002 4245, doi:10.5194/bg-9-4233-2012.
- 1003 Bethoux J.P, (1989), Oxygen consumption, new production, vertical advection and environmental  
1004 evolution in the Mediterranean Sea. Deep Sea Research Part A. Oceanographic Research  
1005 Papers. Volume 36, Issue 5, May 1989, Pages 769-781. [https://doi.org/10.1016/0198-](https://doi.org/10.1016/0198-0149(89)90150-7)  
1006 [0149\(89\)90150-7](https://doi.org/10.1016/0198-0149(89)90150-7)
- 1007 Bishop, J. K. B., M. H. Conte., P. H. Wiebe, M. R.Roman and C. Langdon (1986), Particulate  
1008 matter production and consumption in deep mixed layers—observations in a warm-core ring.  
1009 *Deep-Sea Res. A*, 33, 1813–1841.
- 1010 Bosc, E., A.. Bricaud, and D. Antoine (2004), Seasonal and interannual variability in algal biomass

- 1011 and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS  
 1012 observations, *Global Biogeochem. Cycles*, 18(1), 1–17, doi:10.1029/2003GB002034.
- 1013 Brody, S. R., M. S. Lozier, and J. P. Dunne (2013), A comparison of methods to determine  
 1014 phytoplankton bloom initiation, *J. Geophys. Res. Oceans*, 118, 2345–2357,  
 1015 doi:10.1002/jgrc.20167.
- 1016 Brody, S. R., and M. S. Lozier. (2015), Characterizing upper-ocean mixing and its effect on the  
 1017 spring phytoplankton bloom with in situ data. *ICES Journal of Marine Science*;  
 1018 doi:10.1093/icesjms/fsv006
- 1019 Buesseler, K. O., (2007), An assessment of the use of sediment traps for estimating upper ocean  
 1020 particle fluxes. *Journal of Marine Research*, 65, 345–416, 2007
- 1021 Chiswell, S. M., J. Bradford-Grieve, M. G. Hadfield, and S. C. Kennan (2013), Climatology of  
 1022 surface chlorophyll a, autumn-winter and spring blooms in the southwest Pacific Ocean, *J.*  
 1023 *Geophys. Res. Oceans* , 118, 1003–1018, doi:10.1002/jgrc.20088.
- 1024 Copin-Montégut, G., and B. Avril (1993), Vertical distribution and temporal variation of dissolved  
 1025 organic carbon in the North-Western Mediterranean Sea, *Deep-Sea Res. I*, 40(10), 1963-  
 1026 1972.
- 1027 Copin-Montégut, C. and M. Bégovic (2002), Distributions of carbonate properties and oxygen along  
 1028 the water column (0–2000 m) in the central part of the NW Mediterranean Sea (Dyfamed  
 1029 site): influence of winter vertical mixing on air–sea CO<sub>2</sub> and O<sub>2</sub> exchanges. *Deep Sea*  
 1030 *Research Part II: Topical Studies in Oceanography*, 49, 11, 2049–2066. doi:[10.1016/S0967-](https://doi.org/10.1016/S0967-0645(02)00027-9)  
 1031 [0645\(02\)00027-9](https://doi.org/10.1016/S0967-0645(02)00027-9)

- 1032 Coppola, L., L. Prieur, I. Taupier-Letage, C. Estournel, P. Testor, D. Lefevre, S. Belamari, S.  
1033 LeReste, and V. Taillandier (2017), Observation of oxygen ventilation into deep waters  
1034 through targeted deployment of multiple Argo-O<sub>2</sub> floats in the north-western Mediterranean  
1035 Sea in 2013, *J. Geophys. Res. Oceans*, 122, 6325–6341, doi:10.1002/2016JC012594.
- 1036 Crise, A., J. I Allen, J. Baretta , G. Crispi, R. Mosetti, C. Solidoro (1999), The Mediterranean  
1037 pelagic ecosystem to physical forcing. *Progress in Oceanography*, 44 (1999) 219–243.
- 1038 Crispi, G., A. Crise, and C. Solidoro (2002), Coupled Mediterranean ecomodel of the phosphorus  
1039 and nitrogen cycles. *Journal of Marine Systems* 33– 34 p497– 521.
- 1040 Dall’Olmo, G. J., Dingle, L. Polimene, R. J. W. Brewinn and H. Claustre (2016), Substantial energy  
1041 input to the mesopelagic ecosystem from the seasonal mixed-layer pump. *Nature*  
1042 *Geoscience*, 9, 820–823, doi:10.1038/ngeo2818
- 1043 D’Ortenzio, F., and M. Ribera d’Alcalà (2009), On the trophic regimes of the Mediterranean Sea: a  
1044 satellite analysis, *Biogeosciences*, 6, 139-148, doi:10.5194/bg-6-139-2009.
- 1045 D’Ortenzio, F., H. Lavigne, F. Besson, H. Claustre, L. Coppola, N. Garcia, A. Laës-Huon, S. Le  
1046 Reste, D. Malardé, C. Migon, P. Morin, L. Mortier, A. Poteau, L. Prieur, P. Raimbault, and  
1047 P. Testor (2014), Observing mixed layer depth, nitrate and chlorophyll concentrations in the  
1048 northwestern Mediterranean: A combined satellite and NO<sub>3</sub> profiling floats experiment,  
1049 *Geophys. Res. Lett.*, 41, 6443–6451, doi:10.1002/2014GL061020.
- 1050 Durrieu de Madron, X. and Mermex Group (2011), Marine ecosystems’ responses to climatic and  
1051 anthropogenic forcings in the Mediterranean. *Prog. Oceanogr.*, 91(2), 97–166.  
1052 doi:10.1016/j.pocean.2011.02.003.

- 1053 Estournel C., P. Testor, I. Taupier-Letage, M.N. Bouin, L. Coppola, P. Durand, P. Conan, A.  
 1054 Bosse, P.E. Brilouet, L. Beguery, S. Belamari, K. Béranger, J. Beuvier, D. Bourras, G.  
 1055 Canut, A. Doerenbecher, X. Durrieu de Madron, F. D'Ortenzio, P. Drobinski, V. Ducrocq, N.  
 1056 Fourrié, H. Giordani, L. Houpert, L. Labatut, C. Lebeaupin Brossier, M. Nuret, L. Prieur, O.  
 1057 Roussot, L. Seyfried, and S. Somot (2016a), HyMeX-SOP2, the field campaign dedicated to  
 1058 dense water formation in the north-western Mediterranean, *Oceanography*, 29,4.
- 1059 Estournel C., P. Testor, P. Damien, F. D'Ortenzio, P. Marsaleix, P. Conan, F. Kessouri, X.  
 1060 Durrieu de Madron, L. Coppola, J.M. Lellouche, S. Belamari, L. Mortier, C. Ulses, M.N.  
 1061 Bouin, and L. Prieur (2016b), High resolution modeling of dense water formation in the  
 1062 north-western Mediterranean during winter 2012-2013: Processes and budget, *J. Geophys.*  
 1063 *Res. Oceans*, 121, 5367–5392, doi:[10.1002/2016JC011935](https://doi.org/10.1002/2016JC011935).
- 1064 Gardner, W. D., S. P. Chung, M. J. Richardson, and I. D. Walsh (1995), The oceanic mixed-layer  
 1065 pump. *Deep-Sea Res. II*, 42, 757–775.
- 1066 Giering, S. L. C., R. Sanders, A. P. Martin, S. A. Henson, J. S. Riley, C. M. Marsay, and D. G.  
 1067 Johns (2017), Particle flux in the oceans: Challenging the steady state assumption, *Global*  
 1068 *Biogeochem. Cycles*, 31, 159–171, doi:[10.1002/2016GB005424](https://doi.org/10.1002/2016GB005424).
- 1069 Gogou, A., A. Sanchez-Vidal, X. Durrieu de Madron, S. Stavrakakis, A.M. Calafat, M. Stabholz, S.  
 1070 Psarra, M. Canals, S. Heussner, I. Stavrakaki, and E. Papathanassiou (2014), Carbon flux  
 1071 to the deep in three open sites of the Southern European Seas (SES), *J. Mar. Syst.*, 135, 170–  
 1072 179, doi:[10.1016/j.jmarsys.2014.04.012](https://doi.org/10.1016/j.jmarsys.2014.04.012).
- 1073 Guyennon, A., M. Baklouti, F. Diaz, J. Palmieri, J. Beuvier, C. Lebaupin-Brossier, T. Arsouze, K.  
 1074 Béranger, J.-C. Dutay, and T. Moutin (2015), New insights into the organic carbon export in



- 1075 the Mediterranean Sea from 3-D modeling, *Biogeosciences*, 12, 7025-7046, doi:10.5194/bg-  
1076 12-7025-2015, 2015.
- 1077 Hansell, D. A., and C. A. Carlson (1998), Net community production of dissolved organic carbon,  
1078 *Global Biogeochem. Cycles*, 12(3), 443–453, doi:10.1029/98GB01928.
- 1079 Helbling E. W. and V. E. Villafane (2009), Phytoplankton and Primary Production in Fisheries and  
1080 Aquaculture - Volume 5. No. of Pages:458. ISBN:978-1-84826-112-9 (eBook), ISBN: 978-  
1081 1-84826-562-2 (Print Volume).
- 1082 Henson, S., J. Dunne, and J. Sarmiento (2009), Decadal variability in North Atlantic phytoplankton  
1083 blooms. *J. Geophys. Res.*, 114, C04013, doi:[10.1029/2008JC005139](https://doi.org/10.1029/2008JC005139).
- 1084 Henson, S. A., R. Sanders, and E. Madsen (2012), Global patterns in efficiency of particulate  
1085 organic carbon export and transfer to the deep ocean, *Global Biogeochem. Cycles*, 26,  
1086 GB1028, doi:[10.1029/2011GB004099](https://doi.org/10.1029/2011GB004099).
- 1087 Herrmann, M., F. Diaz, C. Estournel, P. Marsaleix and C. Ulses (2013), Impact of atmospheric and  
1088 oceanic interannual variability on the Northwestern Mediterranean Sea pelagic planktonic  
1089 ecosystem and associated carbon cycle, *J. Geophys. Res. Oceans*, 118, 5792–5813,  
1090 doi:[10.1002/jgrc.20405](https://doi.org/10.1002/jgrc.20405).
- 1091 Herrmann, M., P.-A. Auger, C. Ulses, and C. Estournel (2017), Long-term monitoring of ocean  
1092 deep convection using multisensors altimetry and ocean color satellite data, *J. Geophys. Res.*  
1093 *Oceans*, 122, 1457–1475, doi:[10.1002/2016JC011833](https://doi.org/10.1002/2016JC011833).
- 1094 Ho, C. and J. Marra, (1994) Early-spring export of phytoplankton production in the northeast  
1095 Atlantic-ocean. *Mar. Ecol. Prog. Ser.* 114, 197–202.
- 1096 Houpert, L., P. Testor, X. Durrieu de Madron, S. Somot, F. D'Ortenzio, C. Estournel and H.

- 1097 Lavigne (2015). Seasonal cycle of the mixed layer, the seasonal thermocline and the upper-  
1098 ocean heat storage rate in the Mediterranean Sea derived from observations. *Progress in*  
1099 *Oceanography*, 132, 333-352
- 1100 Houpert, L., X. Durrieu de Madron, P. Testor, A. Bosse, F. D'Ortenzio, et al.. (2016). Observations  
1101 of open-ocean deep convection in the northwestern Mediterranean Sea: Seasonal and  
1102 interannual variability of mixing and deep water masses for the 2007-2013 Period. *Journal*  
1103 *of Geophysical Research. Oceans*, 121, pp.8139-8171 <10.1002/2016JC011857>.
- 1104 Kessouri, F., C. Ulses, C. Estournel, P. Marsaleix, T. Severin, M. Pujo-Pay, J. Caparros, P.  
1105 Raimbault, O. Pasqueron de Fommervault, F. D'Ortenzio, V. Taillandier, P. Testor, P.  
1106 Conan. Nitrogen and phosphorus budgets in the Northwestern Mediterranean deep  
1107 convection region. (2017). DOI: 10.1002/2016JC012665 *Journal of Geophysical Research*  
1108 *Oceans*.
- 1109 Klein B., Roether W., Manca B.B., Bregant D., Beitzel V., Kovacevic V., and A. Luchetta, (1999)  
1110 The large deep water transient in the Eastern Mediterranean, *Deep Sea Research Part I*, 46,  
1111 3, 371-414
- 1112 Koeve, W. (2001), Wintertime nutrients in the North Atlantic—New approaches and implications  
1113 for new production estimates. *Mar. Chem.*, 74, 245–260.
- 1114 Körtzinger, A. U. Send, R. S. Lampitt, S. Hartman, D. W. R. Wallace, J. Karstensen, M. G.  
1115 Villagarcia, O. Llina, and M. D. DeGrandpre (2008), The seasonal pCO<sub>2</sub> cycle at 49 degrees  
1116 N/16.5 degrees W in the northeastern Atlantic Ocean and what it tells us about biological  
1117 productivity. *J. Geophys. Res.*, 113, 1–15 (2008).
- 1118 Large, W. G. and S. Yeager (2009), The global climatology of an interannually varying air-sea flux

- 1119 data set. *Clim. Dyn.*, *33*, 341–364, doi:10.1007/s00382-008-0441-3.
- 1120 Lavigne, H., F. D'Ortenzio, C. Migon, H. Claustre, P. Testor, M. Ribera d'Alcalà, R. Lavezza, L.  
 1121 Houpert, and L. Prieur (2013), Enhancing the comprehension of mixed layer depth control  
 1122 on the Mediterranean phytoplankton phenology, *J. Geophys. Res. Oceans*, *118*, 3416–3430,  
 1123 doi:10.1002/jgrc.20251.
- 1124 Lavigne, H., F. D'Ortenzio, M. Ribera D'Alcalà, H. Claustre, R. Sauzède, and M. Gacic (2015), On  
 1125 the vertical distribution of the chlorophyll a concentration in the Mediterranean Sea: a basin  
 1126 scale and seasonal approach, *Biogeosciences*, *12*, 5021-5039, doi:10.5194/bg-12-5021-2015
- 1127 Laws, E. A., E. D'Sa, and P. Naik (2011), Simple equations to estimate ratios of new or export  
 1128 production to total production from satellite-derived estimates of sea surface temperature and  
 1129 primary production, *Limnol. Ocean. Methods*, *9*, 593–601, doi:10.4319/lom.2011.9.593.
- 1130 Lazzari, P., C. Solidoro, V. Ibello, S. Salon, A. Teruzzi, K. Béranger, S. Colella, and A. Crise  
 1131 (2012), Seasonal and inter-annual variability of plankton chlorophyll and primary production  
 1132 in the Mediterranean Sea: A modelling approach, *Biogeosciences*, *9*, 217-233,  
 1133 doi:10.5194/bg-9-217-2012
- 1134 Lellouche, J.-M., O. Le Galloudec, M. Drévillon, C. Régnier, E. Greiner, G. Garric, N. Ferry, C.  
 1135 Desportes, C.E. Testut, C. Bricaud, R. Bourdallé-Badie, B. Tranchant, M. Benkiran, Y.  
 1136 Drillet, A. Daudin, and C. De Nicola (2013), Evaluation of global monitoring and  
 1137 forecasting systems at Mercator Océan, *Ocean Sci.*, *9*, 57-81, doi:10.5194/os-9-57-2013.
- 1138 Ludwig, W., A. F. Bouwman, E. Dumont, and F. Lespinas (2010), Water and nutrient fluxes from  
 1139 major Mediterranean and Black Sea rivers: Past and future trends and their implications for  
 1140 the basin-scale budgets, *Global Biogeochem. Cycles*, *24*, GB0A13,

1141 doi:[10.1029/2009GB003594](https://doi.org/10.1029/2009GB003594).

1142 Macias, D., E. Garcia-Gorriz, C. Piroddi, and A. Stips (2014), Biogeochemical control of marine  
1143 productivity in the Mediterranean Sea during the last 50 years, *Global Biogeochem. Cycles*,  
1144 28, doi:10.1002/2014GB004846.

1145 Mahadevan, A., E. D'Asaro, C. Lee, M-J. Perry (2112). Eddy-Driven Stratification Initiates North  
1146 Atlantic Spring Phytoplankton Blooms. *Science*, 337, 6090, 54-58, DOI:  
1147 10.1126/science.1218740

1148 Manca, M., M. Burca, A. Giorgetti, C. Coatanoan, M.J. Garcia, and A. Iona (2004), Physical and  
1149 biochemical averaged vertical profiles in the Mediterranean regions: an important tool to  
1150 trace the climatology of water masses and to validate incoming data from operational  
1151 oceanography, *J. Mar. Syst.*, 48, 1–4, 83-116.

1152 Maraldi, C., J. Chanut, B. Levier, N. Ayoub, P. De Mey, G. Reffray, F. Lyard, S. Cailleau, M.  
1153 Drevillon, E.A. Fanjul, M.G. Sotillo, P. Marsaleix, and the Mercator Research and  
1154 Development Team (2013), NEMO on the shelf: assessment of the Iberia–Biscay–Ireland  
1155 configuration. *Ocean Sci.*, 9, 745–771. <http://dx.doi.org/10.5194/os-9-745-2013>.

1156 Marsaleix, P., F. Auclair, J. W. Floor, M. J. Herrmann, C. Estournel, I. Pairaud, and C. Ulses  
1157 (2008), Energy conservation issues in sigma-coordinate free-surface ocean models, *Ocean*  
1158 *Modell.*, 20, 61–89.

1159 Marsaleix, P., F. Auclair, and C. Estournel (2009), Low-order pressure gradient schemes in sigma  
1160 coordinate models: The seamount test revisited, *Ocean Modell.*, 30, 169–177,  
1161 doi:10.1016/j.ocemod.2009.06.011.

- 1162 Marsaleix, P., F. Auclair, C. Estournel, C. Nguyen, and C. Ulses (2011), An accurate  
 1163 implementation of the compressibility terms in the equation of state in a low order pressure  
 1164 gradient scheme for sigma coordinate ocean models, *Ocean Modell.*, *40*, 1-13  
 1165 doi:10.1016/j.ocemod.2011.07.004
- 1166 Marsaleix, P., F. Auclair, T. Duhaut, C. Estournel, C. Nguyen, and C. Ulses (2012), Alternatives to  
 1167 the Robert-Asselin filter, *Ocean Modell.*, *41*, 53–66, doi:10.1016/j.ocemod.2011.11.002.
- 1168 Marty, J.C, and J. Chiaverini (2002). Seasonal and interannual variations in phytoplankton  
 1169 production at DYFAMED time-series station, northwestern Mediterranean Sea, *Deep-Sea*  
 1170 *Res. II*, *49(11)*, 2017-20130.
- 1171 Mayot, N., F. D’Ortenzio, M. Ribera d’Alcalà, H. Lavigne, and H. Claustre (2016), Interannual  
 1172 variability of the Mediterranean trophic regimes from ocean color satellites, *Biogeosciences*,  
 1173 *13*, 1901–1917
- 1174 Mayot, N., F. D’Ortenzio, V. Taillandier, L. Prieur, O. Pasqueron de Fommervault, H. Claustre, A.  
 1175 Bosse, P. Testor and P. Conan (2017a), Physical and biogeochemical controls of the  
 1176 phytoplankton blooms in North Western Mediterranean Sea: a multiplatform approach over  
 1177 a complete annual cycle (2012-2013 DEWEX experiment), In press, *Journal of Geophysical*  
 1178 *Research: Oceans*, doi:10.1002/2016JC012668.
- 1179 Mayot N., F. D’Ortenzio, J. Uitz, B. Gentili, J. Ras, V. Vellucci, M. Golbol, D. Antoine and H.  
 1180 Claustre (2017b) Influence of the phytoplankton community structure on the spring and  
 1181 annual primary production in the North-Western Mediterranean Sea. In press, *Journal of*  
 1182 *Geophysical Research: Oceans*, DOI: 10.1002/2016JC012668

- 1183 MERMEX Group, 2011. Marine ecosystems responses to climatic and anthropogenic forcings in the  
1184 Mediterranean. *Prog. Oceanogr.* 91:97–166. <http://dx.doi.org/10.1016/j.pocean.2011.02.003>
- 1185 Miquel, J. C., J. Martín, B. Gasser, A. Rodriguez-y-Baena, T. Toubal, and S.W. Fowler (2011),  
1186 Dynamics of particle flux and carbon export in the northwestern Mediterranean Sea: A two  
1187 decade time-series study at the DYFAMED site, *Prog. Oceanogr.*, 91(4), 461–481,  
1188 doi:10.1016/j.pocean.2011.07.018
- 1189 Moutin, T., P. Raimbault, H.L. Golterman, and B. Coste (1998), The input of nutrients by the Rhône  
1190 river into the Mediterranean Sea: recent observations and comparison with earlier data,  
1191 *Hydrobiologia*, 373: 237. doi:10.1023/A:1017020818701
- 1192 Pastor, L., B. Deflandre, E. Viollier, C. Cathalot, E Metzger, C. Rabouille, K. Escoubeyrou, E.  
1193 Lloret, A.M. Pruski, G. Vétion, M. Desmalades, R. Buscail, and A. Grémare (2011),  
1194 Influence of the organic matter composition on benthic oxygen demand in the Rhône River  
1195 prodelta (NW Mediterranean Sea), *Cont. Shelf Res.*, 31(9), 1008–1019,  
1196 doi:10.1016/j.csr.2011.03.007
- 1197 Palevsky, H. I., and P. D. Quay (2017), Influence of biological carbon export on ocean carbon  
1198 uptake over the annual cycle across the North Pacific Ocean, *Global Biogeochem.*  
1199 *Cycles*, 31, 81–95, doi:10.1002/2016GB005527.
- 1200 Petrenko, A., C. Dufau, and C. Estournel (2008), Barotropic eastward currents in the western Gulf  
1201 of Lion, north-western Mediterranean Sea, during stratified conditions, *J. Mar. Syst.*, 74,  
1202 406–428 doi:10.1016/j.jmarsys.2008.03.004
- 1203 Roether, W., Manca, B.B., Klein, B., Bregant, D., Georgopoulos, D., Beitzel, V., Kovacevic, V.,  
1204 and A. Luchetta (1996), Recent changes in Eastern Mediterranean deep waters. *Science* 271,

1205 333–335.

1206 Rubio, A., B. Barnier, G. Jorda, M. Espino, and P. Marsaleix (2009), Origin and dynamics of  
 1207 mesoscale eddies in the Catalan Sea (NW Mediterranean): Insight from a numerical model  
 1208 study, *J. Geophys. Res.*, *114*, C06009, [doi:10.1029/2007JC004245](https://doi.org/10.1029/2007JC004245)

1209 Santinelli, C., L. Nannicini, and A. Seritti (2010), DOC dynamics in the meso and bathypelagic  
 1210 layers of the Mediterranean Sea. *Deep-Sea Res. II*, *57*, 1446–1459.

1211 Schroeder, K., Ribotti, A., Borghini, M., Sorgente, R., Perilli, A., and Gasparini, G.P.: An extensive  
 1212 Mediterranean deep water renewal between 2004 and 2006, (2016), *Geophysical Research*  
 1213 *Letters*, *35*, L18605, [doi: 10.1029/2008GL035146](https://doi.org/10.1029/2008GL035146), 2008. Schroeder, K., Chiggiato, J.,  
 1214 Bryden, H.L., Borghini, M., and Ben Ismail, S.: Abrupt climate shift in the Western  
 1215 Mediterranean Sea. *Scientific Reports*, *6*:23009, [doi: 10.1038/srep23009](https://doi.org/10.1038/srep23009).

1216 Sempéré, R., B. Charrière, F. Van Wambeke, and G. Cauwet (2000), Carbon Inputs of the Rhône  
 1217 River to the Mediterranean Sea: Biogeochemical Implications, *Global Biogeochem. Cycles*,  
 1218 *14*, 2, 669–681.

1219 Severin, T., Kessouri .F, Rembauville, M., et al. (2017), Open-ocean convection process: A driver  
 1220 of the winter nutrient supply and the spring phytoplankton distribution in the Northwestern  
 1221 Mediterranean Sea, *J. Geophys. Res. Oceans*, *122*, [doi:10.1002/2016JC012664](https://doi.org/10.1002/2016JC012664).

1222 Siegel, D.A., S.C. Doney, and J.A. Yoder (2002), The North Atlantic spring phytoplankton bloom  
 1223 and Sverdrup's critical depth hypothesis, *Science*, *296*, 730–733, DOI:  
 1224 [10.1126/science.1069174](https://doi.org/10.1126/science.1069174)

- 1225 Siegel, D. A., K. O. Buesseler, S. C. Doney, S. F. Sailley, M. J. Behrenfeld, and P. W. Boyd (2014),  
1226 Global assessment of ocean carbon export by combining satellite observations and food-web  
1227 models, *Global Biogeochem. Cycles*, 28, 181–196, doi:10.1002/2013GB004743.
- 1228 Soetaert, K., P.M.J. Herman, J.J. Middelburg, C. Heip, C.L. Smith, P. Tett, and K. Wild-Allen  
1229 (2001), Numerical modelling of the shelf break ecosystem: Reproducing benthic and pelagic  
1230 measurements, *Deep-Sea Res. II*, 48(14-15), 3141–3177, doi:10.1016/S0967-  
1231 0645(01)00035-2
- 1232 Somot S, Sevault F, Déqué M (2006) Transient climate change scenario simulation of the  
1233 Mediterranean Sea for the twenty-first century using a high-resolution ocean circulation  
1234 model. *Clim Dyn* 27(7–8):851–879.
- 1235 Somot, S., Houpert, L., Sevault, F. et al. (2016), Characterizing, modelling and understanding the  
1236 climate variability of the deep water formation in the North-Western Mediterranean Sea.  
1237 *Clim Dyn*, doi:10.1007/s00382-016-3295-0
- 1238 Stabholz M., X. Durrieu de Madron, A. Khripounoff, M. Canals, I. Taupier-Letage, P. Testor, S.  
1239 Heussner, P. Kerhervé, L. Houpert, and N. Delsaut (2013), Impact of open-sea convection  
1240 on particulate fluxes and sediment dynamics in the deep basin of the Gulf of Lions.  
1241 *Biogeosciences*, 10, 1097-1116.
- 1242 Sverdrup H.U. (1953), On conditions for the vernal blooming of phytoplankton. *ICES J Mar Sci*  
1243 (1953) 18 (3): 287-295. DOI:10.1093/icesjms/18.3.287.
- 1244 Taylor J. R. and R. Ferrari (2011), Shutdown of turbulent convection as a new criterion for the  
1245 onset of spring phytoplankton blooms, *Limnology and Oceanography*, 56, doi:  
1246 10.4319/lo.2011.56.6.2293.



- 1247 Uitz, J., D. Stramski, B. Gentili, F. D’Ortenzio, and H. Claustre (2012), Estimates of phytoplankton  
 1248 class-specific and total primary production in the Mediterranean Sea from satellite ocean  
 1249 color observations, *Global Biogeochem. Cycles*, 26, GB2024, doi:[10.1029/2011GB004055](https://doi.org/10.1029/2011GB004055).
- 1250 Ulses, C., P.-A. Auger, K. Soetaert, P. Marsaleix, F. Diaz, L. Coppola, M.Herrmann, F. Kessouri,  
 1251 and C. Estournel (2016), Budget of organic carbon in the North-Western Mediterranean  
 1252 Open Sea over the period 2004-2008 using 3D coupled physical biogeochemical modeling,  
 1253 *J. Geophys. Res. Oceans*, 121, 7026–7055, doi:[10.1002/2016JC011818](https://doi.org/10.1002/2016JC011818).
- 1254 Waldman R., S. Somot, M. Herrmann, P. Testor, C. Estournel, F. Sevault, L. Prieur, L. Mortier, L.  
 1255 Coppola, V. Taillandier, P. Conan and D. Dausse (2016) Estimating dense water volume  
 1256 and its evolution for the year 2012-2013 in the North-western Mediterranean Sea: an  
 1257 Observing System Simulation Experiment approach, *J. Geophys. Res. Oceans*, 121, 6696–  
 1258 6716, doi:[10.1002/2016JC011694](https://doi.org/10.1002/2016JC011694).
- 1259 Westberry, T. K., P. J. I. B. Williams, and M. J. Behrenfeld (2012), Global net community  
 1260 production and the putative net heterotrophy of the oligotrophic oceans, *Global Biogeochem.*  
 1261 *Cycles*, 26, GB4019, doi:[10.1029/2011GB004094](https://doi.org/10.1029/2011GB004094).
- 1262 Williams, R.G. and · M. J. Follows (2003), Physical transport of nutrients and the maintenance of  
 1263 biological production. in Ocean Biogeochemistry. Part of the series Global Change — The  
 1264 IGBP Series (closed) pp 19-51. Springer Berlin Heidelberg. doi:[10.1007/978-3-642-55844-](https://doi.org/10.1007/978-3-642-55844-3_3)  
 1265 [3\\_3](https://doi.org/10.1007/978-3-642-55844-3_3)
- 1266 Zúñiga, D., A. Calafat, A. Sanchez-Vidal, M. Canals, B. Price, S. Heussner, and S. Miserocchi  
 1267 (2007), Particulate organic carbon budget in the open Algero-Balearic Basin (Western  
 1268 Mediterranean): Assessment from a one-year sediment trap experiment. *Deep-Sea Res. I*, 54

1269 (9),1530-1548.