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Seasonal and mesoscale variability of primary production in the deep winter-mixing region of the NW Mediterranean

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ABSTRACT

The phytoplankton bloom in the Liguro-Provençal deep convection region represents one of the main fertilization mechanisms in the Mediterranean. This communication examines nano- and microphytoplankton observations, and measurements of primary production and chlorophyll *a* concentration (Chl *a*) in the southwestern part of the deep convection region, where such information is scarce. Data were obtained from four cruises, carried out in 2005 (EFLUBIO project) and 2009 (FAMOSO project), covering the seasonality between mid-March and September in the region. Our aims were to constrain primary production estimates and to ascertain the importance of short-term variability on the photosynthetic response of phytoplankton assemblages during bloom, post-bloom and late-summer stratification periods in the area. Overall, the initial slope of the *P–E* relationship (α^B) increased and the Chl *a*-normalized photosynthetic rate (P^B_m) decreased with increasing optical depth of sample origin, but there were exceptions. In general, there were marked seasonal trends, with stratification increasing and Chl *a* concentration, primary production and dissolved inorganic nitrogen and phosphate fluxes decreasing from winter to late summer. Chl *a* at 5 m depth reached a maximum of 7 mg m^{-3} on 25 March 2005, one of the highest values measured in the region. Average surface values (±SD) ranged from respectively 2.4 ± 2.3 mg m^{-3} and 2 ± 0.7 mg m^{-3} in the March 2005 and March 2009 cruises to 0.12 ± 0.01 mg m^{-3} in the September 2009 cruise. Vertically integrated (0–80 m) primary production (PP_{int}) attained 1800 mg C m^{-2} d^{-1} in March 2009, with an average of 1024 ± 523 mg C m^{-2} d^{-1}, and decreased to a mean of 141 ± 0.43 mg C m^{-2} d^{-1} in September 2009. Superimposed to the seasonal trends, there was a considerable within-cruise variability of biomass and primary production, especially during the spring-winter bloom and post-bloom periods, when PP_{int} could change more than threefold within a few days. These differences were mainly associated with the intense hydrographic mesoscale and sub-mesoscale heterogeneity in the region and with the differences in the physiological and ecological history of the phytoplankton communities inhabiting the different water bodies. In late summer, most PP_{int} variability could be explained by fluctuations in surface incident irradiance.

1. Introduction

Winter mixing is one of the main mechanisms bringing nutrients to the euphotic zone throughout the Mediterranean. However, its intensity and subsequent biological effects present a marked variability. D'Ortenzio and Ribera d'Alcalà (2009) used SeaWIFS imagery to conclude that, in the open sea, a marked late winter–early spring bloom, typical of a temperate regime, was only observed regularly in the Liguro-Provençal basin of the NW Mediterranean. The cyclonic circulation in this region, together with wind and temperature forcing, favor intense winter convection, which in some years spans all the way to depths exceeding 2000 m and originates the Western Mediterranean Deep Water (MEDOC-Group, 1970; Siokou-Frangou et al., 2010). The development of the phytoplankton bloom in the Ligurian Sea has been described by a number of remote sensing studies (Morel and

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André, 1991; Antoine et al., 1995; Bosc et al., 2004; Morales, 2006), which typically show a period of blue water followed by the appearance of chlorophyll patches in late winter early spring. Years with more intense convection tend to present more phytoplankton biomass due to factors like increased surface nutrient concentrations derived from deeper mixing and the greater spatial extension, duration and recurrence of the mixing events (Volpe et al., 2012; Marty and Chiavérini, 2010). The surface concentration of phytoplankton is reduced by deep mixing, but phytoplankton proliferation may take place as soon as conditions allow growth to exceed losses. The interplay between vertical mixing and phytoplankton bloom development has been modeled by Lévy et al. (1998), who showed the importance of mesoscale features in shaping phytoplankton production.

Although the phytoplankton bloom in the Liguro-Provençal deep convection region (the so-called MEDOC area, between 3° 30′ to 6° E and 41° to 43°N, Gascard, 1978) represents one of the main fertilization mechanisms in the Mediterranean (Bosc et al., 2004), most *in situ* measurements of phytoplankton biomass and primary production, based on some oceanographic cruises and the visits to the DYFAMED time series station, have been concentrated on the Ligurian side of the basin (Jacques et al., 1973, 1976; Vidussi et al., 2000; Marty and Chiavérini, 2002; Marty et al., 2008). Primary production data are scarce in the southwestern part of the MEDOC area and there is little information on the characteristics of the photosynthesis-irradiance relationships of the phytoplankton in the region, a knowledge that would enhance our understanding of basic phytoplankton ecophysiology and could help to improve primary production modeling from remote sensing studies. In addition, there are few *in situ* data of the effects of this phytoplankton bloom on the other trophic levels and on the fluxes of carbon through the water column and the atmosphere. Answering this question was the main objective of the FAMOSO project, which included repeated cruises to the southwestern part of the deep convection zone during three periods of 2009 covering winter-spring bloom, post-bloom and late-summer stratification situations. In this paper, we examine primary production data from these surveys and from a previous one carried out in March–April 2005 in the same region. Our aims were to ascertain the importance of seasonal and short-term variability (including both temporal changes in the biological populations and the effects of mesoscale or sub-mesoscale spatial processes) on primary production estimates in the area and on the photosynthetic response of the phytoplankton assemblages. Given the importance of the winter-spring bloom of the NW Mediterranean, knowledge of the C fluxes during this period is a prerequisite to learn whether this region acts as a source or a sink of atmospheric C. In addition, because the NW Mediterranean has been identified as a sensitive region to global change (Somot et al., 2006), information on its biogeochemical and ecological processes is needed for establishing baseline conditions and allowing a reliable assessment of the potential effects of climate change in this marine ecosystem.

2. Material and methods

Several oceanographic cruises were conducted in the southwestern part of the Liguro-Provençal Basin, within the region delimited approximately by coordinates 41°30′ to 42°N and 4° to 5°E, an area with depths exceeding 2000 m and typically subjected to deep convection in winter (Fig. 1, Table 1). The cruises were carried out on board the R.V. Cornide de Saavedra, in March to early April 2005 [EFLUBIO 2, (E2)], and on board the R. V. Sarmiento de Gamboa in mid-March, late April–May and September 2009 [cruises FAMOSO 1 (F1), FAMOSO 2 (F2) and FAMOSO 3 (F3)], respectively. The sampling strategy intended a Lagrangian approach by following the track of an array of free drifting Particle Interference Traps deployed during 24 h (EFLUBIO) or 72 h (FAMOSO). Thus, the within-cruise spatial variability observed in our time series reflects both changes in the position of the stations and in the hydrographical fields.

2.1. Satellite imagery

Sea Surface Temperature (SST) was obtained from nighttime measurements done by the AVHRR sensor on board the NOAA-18 platform and provided by the SAIDIN facility at the Institut de Ciències del Mar (http://coo.icm.csic.es/content/saidin-and-thredds). Brightness Temperature (BT) from channel 4 was used to derive a new SST field instead of using the original SST, with the objective of reducing the noise (*e.g.* Isern-Fontanet and Hascoët, 2014). The bias associated with the lack of atmospheric correction in the BT field was addressed through linear filtering between the BT and the SST fields and, then, both fields were compared to verify that no spurious structures were introduced by this procedure. The Chl *a* field was derived from measurements done by the MODIS sensor on board the Aqua platform using the OC3M-547 algorithm. The data were downloaded from the NASA's Ocean Color server (http://oceancolor.gsfc.nasa.gov/). We used Level 1B (AVHRR) and Level 2 (AVHRR and MODIS) products with the objective to keep the full spatial resolution of the original measurements.

2.2. Hydrography

Several CTD casts were carried out each day (except for some gaps due to bad weather) within the same area, at varying positions following the track of the free drifting traps. Vertical profiles of temperature, salinity, oxygen concentration and *in vivo* fluorescence were obtained from all the casts with a CTD SBE 911plus equipped with additional sensors of dissolved oxygen concentration, turbidity, fluorescence, light transmission, irradiance (PAR), surface irradiance (SPAR) and bottom proximity (altimeter). Water from selected depths was collected from a daily “biological” cast (or “station”) starting around 8 GMT, by means of 12 L Niskin bottles mounted on a rosette, and samples were taken for determination of major nutrient and chlorophyll *a* (Chl *a*) concentrations, phytoplankton examination and primary production measurements. On one occasion (station F1-74, see Table 1 for station codes), water for the 24 h on-deck incubations was collected from an additional cast carried out three hours later. Incident irradiance was measured continuously with a LI-200 2πLi-Cor pyranometer. Daily incident irradiance just under the water surface (mol photons $\mathrm{m}^{-2}\,\mathrm{d}^{-1}$) was estimated from the pyranometer records using an empirical conversion expression (obtained comparing pyranometer readings with a cosine PAR sensor deployed overboard). Water-column downward PAR (400–700 nm) was measured around noon at each station with a spherical quantum sensor mounted on a FRRF instrument. The vertical light extinction coefficients (K_d) were obtained from the regression of log (PAR) *versus* depth (z) for the whole upper water column, or for adjoining layers above (K_ds) and below (K_dp) the deep chlorophyll maximum (DCM) when changes in the slope of the plots were detected. Optical depths (OD) for a depth z were calculated as the product of $K_\mathrm{d}z$ or as $K_\mathrm{ds}z_\mathrm{DCM}+K_\mathrm{dp}(z-z_\mathrm{DCM})$, where z_DCM is the DCM depth, when $z>z_\mathrm{DCM}$ and different light extinction coefficients had been determined for layers above and below the DCM. The mixed layer depth was estimated as the first depth (z) for which $\sigma_\theta(z)-\sigma_\theta(5)\geq 0.125\ \mathrm{kg\ m}^{-3}$, where $\sigma_\theta(z)$ and $\sigma_\theta(5)$ are, respectively, the potential density anomalies at depths z and 5 m. A vertical stratification index (VSI), between 5 and 80 m depth, was calculated as $\Sigma|\sigma_\theta(z+1)-\sigma_\theta(z)|$, where z is the depth in m and ranges from 5 to 79.