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

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A B S T R A C T

The phytoplankton bloom in the Liguro-Provençal deep convection region represents one of the main phytoplankton 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) increased and the Chl a-normalized photosynthetic rate (P P a

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 (Morei and
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 2mLi-Cor pyranometer. Daily incident irradiance just under the water surface (mol photons m$^{-2}$ 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 ($K_{a}$) 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 $K_d z$ or as $K_{a} z_{DCM} + K_{dp}(z - z_{DCM})$, where $z_{DCM}$ is the DCM depth, when $z > z_{DCM}$ 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 $\sigma_0(z) - \sigma_0(5) \geq 0.125$ kg m$^{-3}$, where $\sigma_0(z)$ and $\sigma_0(5)$ 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 $\sum \sigma_0^2(z+1) - \sigma_0(z)$, where $z$ is the depth in m and ranges from 5 to 79.
2.3. Nutrient analyses, nutrient fluxes and chlorophyll a determinations

Dissolved inorganic phosphorus (PO$_3^{4-}/CO_4^-$, DIP) was determined spectrophotometrically on board, using a 10 cm cuvette to increase the detection limit to 0.01 mmol m$^{-3}$, while water samples for the determination of dissolved inorganic nitrogen (NO$_3^{-}+NO_2^{-}$, DIN) and silicate (SiO$_4^{4-}$) were frozen for later analysis on land with an AA3 autoanalyzer. Methods were as described in Grasshoff et al. (1999).

Measurements of turbulent kinetic energy dissipation ($\varepsilon$) were carried out in the FAMOSO cruises by means of a microstructure turbulence profiler (Prandke and Stips, 1998) and were used to...
estimate the vertical turbulent diffusivity. On average, 7 microstructure profiles were performed in each station down to a depth of about 250–300 m, with a vertical resolution of 1 m. A single profile of the vertical diffusivity \( K_z \) was generated for each station in a 10 m grid as:
\[
K_z = \Gamma \frac{\varepsilon_{10\text{ m}}}{N^2}
\]

where \( \Gamma = 0.2 \) \cite{Osborn, 1980} is a mixing efficiency and \( N^2 \) is the squared buoyancy frequency computed by linear fitting of the slope of the density profile in 10 m bins. A detailed description of the microstructure profiler and the data processing is included in \cite{Mouriño-Carballido et al., 2011}. Nutrient (DIN or DIP) fluxes \( (F_{\text{nut}}) \) were computed as the product of the slope of the nutricline \( (d[\text{nut}]_{\text{nutricline}}/dz) \), obtained by linear fitting of the nutrient concentrations, and the averaged diffusivity for the same depth range:
\[
F_{\text{nut}} = - (K_z)_{\text{nutricline}} \frac{d[\text{nut}]_{\text{nutricline}}}{dz}
\]

Samples for Chl \( a \) determination were generally collected from 4 to 8 levels between 5 and 100 m. For Chl \( a \) analysis, between 50 and 200 ml of seawater were filtered through Whatman GF/F filters, which were stored at \(-20^\circ C\) during several hours and subsequently introduced into 90% acetone for 24 h extraction in the dark. The fluorescence of the aceton extract was determined with a Turner Designs fluorometer \cite{Yentsch and Menzel, 1963}; no phaeophytin corrections were applied because of the uncertainties of the method \cite{Welshmeyer, 1994}. In order to calculate integrated Chl \( a \) in the water column between 0 and 100 m (Chl \( a \) int, mg Chl \( a \) m \(^{-2}\)), Chl \( a \) concentration between 0 and 5 m depth was assumed to be equal to Chl \( a \) concentration at 5 m and, below this depth, when the interval between samples exceeded 10 m, Chl \( a \) concentrations at intermediate depths (typically at 10 m intervals) were interpolated according to the following procedure. First, a linear interpolation was performed, based on the closest available Chl \( a \) determinations above and below the interpolation depth. In a similar way, a linear interpolation was also carried out for the CTD in vivo fluorescence data corresponding to the same depths. Next, the interpolated Chl \( a \) concentration value calculated for the interpolation depth was multiplied by the ratio between the actually recorded fluorescence and the linearly interpolated fluorescence for this depth. This correction factor was introduced to compensate for deviations from linearity of the Chl \( a \) profile and was based on the assumption that in vivo fluorescence would be linearly proportional to Chl \( a \) concentration across subsurface depth intervals < 30 m. As different fluorescence sensors were used, to make fluorescence units roughly comparable among cruises, the fluorescence values shown in Figs. 2–3, 5 and 6 were transformed using a regression equation of measured Chl \( a \) on fluorescence for each cruise.

### 2.4. Phytoplankton examination

Phytoplankton samples were taken from the same depths as the primary production experiments; a volume of 150 ml was placed in glass bottles and fixed with formalin–hexamine solution. The phytoplankton was enumerated by means of the inverted microscope technique \cite{Estrada et al., 1999}, after sedimentation of 100 ml of sample in composite settling chambers. This method is not adequate for small organisms in the picophytoplankton size range; therefore, our observations concern nano and microphytoplankton, although, for simplicity, we will use the term “phytoplankton” when referring to them in the text.
The models of Platt et al. (1980) or Webb et al. (1974) were fitted to the Chl a-normalized hourly carbon fixation rates depending, respectively, on whether photoinhibition was detected or not. The derived photosynthetic parameters were \( P_{\text{int}}^a \), the light-saturated Chl a-normalized photosynthetic rate [mg C (mg Chl a)\(^{-1}\) h\(^{-1}\)], \( \alpha_B \), the initial slope of the \( P-E \) relationship [mg C (mg Chl a)\(^{-1}\) (\( \mu \)mol photons m\(^{-2}\) s\(^{-1}\))\(^{-1}\) h\(^{-1}\)] and \( \beta_B \), the photo-inhibition parameter (same units as \( \alpha_B \)). The photoacclimation parameter, \( E_B \) (\( \mu \)mol photons m\(^{-2}\) s\(^{-1}\)) was calculated as the quotient between \( P_{\text{int}}^a \) and \( \alpha_B \). For each station, the \( C \) fixation data from the \( P-E \) curves and the depth profiles of PAR and Chl a were used to estimate the daily rates of primary production at different depths of the water column. Integrated primary production values between surface and 80–100 m depth (\( PP_{\text{int}} \), mg C m\(^{-2}\) d\(^{-1}\)) were calculated by the trapezoidal method, as described in Morán and Estrada (2005). The same model was used to calculate the daily primary production values at nominal light depths coinciding with those used for the on-deck incubations (see Section 2.6). A rough estimate of the relative importance of fluctuations in irradiance due to variable cloud cover (“original” irradiance conditions) for within-cruise \( PP_{\text{int}} \) variability was obtained by recalculating the values of \( PP_{\text{int}} \). For that we used the same daily incident irradiance values (those of one of the sunny days) for all the stations of the same cruise (“sunny-day” irradiance conditions) and compared the coefficients of variation of the “original” and “sunny-day” irradiance conditions \( PP_{\text{int}} \) estimates.

### 2.6. On-deck 24 h incubations for C uptake determination

In addition to the 2 h \( P-E \) experiments, we performed \(^{14}\)C uptake experiments on-deck with natural irradiance. The incubator consisted of a rectangular container with 10 Perspex cylinders, wrapped in blue screens to provide a range of attenuation of the incident light-saturated Chl a-normalized photosynthetic rate \( \mu \)mol photons m\(^{-2}\) s\(^{-1}\). Two replicate bottles from surface and two from the DCM, plus the corresponding dark controls, were placed in each cylinder and incubated during 24 h. Care was taken to avoid the effect of ambient light on the bottles, by covering them during manipulations. The rates of carbon fixation for station E2-129 appeared to be abnormally low, relative to Chl a, when compared with those of the previous and following stations and were excluded from the regression calculations. The major axis regression lines used in the comparison between \( C \) fixation rates derived from \( P-E \) curves and from on-deck incubations were fitted using the SMATR software (Falster, et al., 2006).

### 3. Results

#### 3.1. Hydrography and phytoplankton

The two winter–early spring cruises E2 (2005) and F1 (2009) presented fairly homogeneous or weakly stratified profiles of temperature, salinity and potential density anomaly \( (\sigma_z) \), as a result of winter mixing (Figs. 2, and 3). There was considerable mesoscale and submesoscale hydrographical variability in the region, as can be observed in both the SST and Chl a distributions shown in Fig. 4A–C. During F1, the interleaving of relatively cool and high salinity waters with more stratified regions of low salinity surface water caused abrupt changes in the hydrographical structure of the upper water column (e.g., year days 77–78 in Fig. 2). The E2 series shows two different situations, with a transition towards increased...
Fig. 4. Remote-sensing derived images. (A) Sea Surface Temperature in the W Mediterranean on 22 March 2009. (B–E) Chl a on different dates during cruises E2 and F1 [region marked with a square in (A)]: 27 March 2005 (B), 15 March 2009 (C), 17 March 2009 (D) and 22 March 2009 (E). Note that the Chl a scale is logarithmic. The black circles and dates in B–E indicate the position and date of stations carried out within two days of the image observation.
stratification linked to higher temperature and lower salinity at surface after year day 86 (Fig. 3, Table 1). Average concentrations of DIN and DIP ($\pm$ SD) for surface samples (between 0 and 10 m depth) were, respectively, 4.47 $\pm$ 1.18 mmol m$^{-3}$ and 0.11 $\pm$ 0.06 mmol m$^{-3}$ for F1, and 1.41 $\pm$ 0.64 mmol m$^{-3}$ and 0.02 $\pm$ 0.01 mmol m$^{-3}$ for E2. Surface silicate concentrations during E2 averaged 0.79 $\pm$ 0.36 mmol m$^{-3}$ (silicate concentrations were not available for the FAMOSO cruises). Both F1 and E2 took place during the phytoplankton bloom period, as evidenced by surface Chl $a$ exceeding 1 mg m$^{-3}$ (Table 3). During F1, the Chl $a$ concentration was fairly homogeneous from the surface down to 20 m (as at stations F1-73 and F1-80 on 14 and 21 March 2009), and 60-80 m [as at stations F1-74, F1-77 and F1-81, on 15, 18 and 22 March respectively (Fig. 7A)]. The maximum Chl $a$ concentration reached during this cruise (about 3 mg m$^{-3}$) was measured on 19 March, (F1-78) at 5 m depth. During E2, Chl $a$ concentration at the surface reached values of 7 mg m$^{-3}$ (station E2-84), the highest value recorded during this study, and declined with the

![Fig. 5. Cruise FAMOSO 2 (F2). Temporal evolution of (A) temperature, (B) salinity, (C) potential density anomaly and (D) in vivo fluorescence. The vertical lines indicate CTD profiles. The “x” in D indicates the upper mixed layer depth.](image)

![Fig. 6. Cruise FAMOSO 3 (F3). Temporal evolution of (A) temperature, (B) salinity, (C) potential density anomaly and (D) in vivo fluorescence. The vertical lines indicate CTD profiles. The “x” in D indicates the upper mixed layer depth.](image)

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stratification increase observed towards the end of the cruise, which was accompanied by the appearance of a DCM around 40 m depth (Figs. 3 and 7C). The cooler surface temperatures and the lower stratification during F1 (Table 1, Figs. 2–3), carried out in mid-March, indicate that this cruise corresponds both to an earlier calendar date and a prior phase of the seasonal stratification cycle than E2, that took place in late March. Satellite imagery of both cruises showed highly heterogeneous Chl a distributions and a Chl a-poor area, corresponding to the deep convection region, which became progressively smaller as the season advanced (Fig. 4B–E).

The F2 cruise, carried out between the end of April 2009 and mid-May (post-bloom period), revealed nearly homogeneous mixed layers of about 50 m in some of the stations (F2-120, F2-123 and F2-127) and continuous or two-step density profiles, with strong additional gradients around 12–25 m depth, at the other stations (Fig. 5, Table 1). This vertical structure of the biological casts (sampled around 8:00 GMT) was similar to that of other casts carried out on the same day before dawn, so that it could not be attributed to daily warming. A rising of the isotherms and isohalines of the upper water layer around 7–8 April (Julian days 127–128) indicated the crossing of a front (Fig. 5). Average surface DIN and DIP concentrations were, respectively, 1.77 ± 0.97 mmol m⁻³ and 0.03 ± 0.02 mmol m⁻³. Chl a increased substantially in the last stations (to a maximum value of 1.1 mg m⁻³ at station F2-133) and was fairly homogeneous down to 40–50 m depth in the first samplings and to 70–80 m depth in the last ones (Figs. 5 and 7E).

During F3 (September 2009), the water column was strongly stratified (Table 1) with a surface mixed layer of ~30 m and a salinity minimum below it, at ~35–60 m depth (Fig. 6). Just under the strong pycnocline, there was a marked DCM at 60–80 m depth (Fig. 6), and a deep oxygen maximum at slightly shallower levels (data not shown). Surface DIN and DIP concentrations were, on average, 1.48 ± 0.53 mmol m⁻³ and 0.03 ± 0.01 mmol m⁻³, and Chl a concentration fluctuated between 0.10 and 0.14 mg m⁻³ at 5 m depth and between 0.4 and 0.8 mg m⁻³ at the DCM (Figs. 6 and 7G).

Integrated Chl a between 0 and 80 m (Table 3) ranged from around 20 mg m⁻³ in some samplings of April-May and September-2009 to more than 200 mg m⁻³ in the winter cruises (up to maxima of 160 mg m⁻³ in March 2009 and 260 mg m⁻³ in March 2005). There was an overall significant linear relationship between surface and integrated Chl a (r = 0.85, p < 0.01, n = 27), but with
substantial between- and within-cruise scatter (data can be found in Table 3), in particular regarding E2.

The phytoplankton (nano–micro size range) community of the first two stations of F1 (Fig. 8A, C) was dominated by dinoflagellates and prymnesiophytes, including *Phaeocystis* sp. (with healthy-looking and senescent colonies) and coccolithophores like *Emiliania huxleyi*, *Calcidiscus leptoporus* and *Helicosphaera carteri*, but higher salinities and Chl *a* concentrations of the last stations were associated to a stronger contribution of diatoms like *Chaetoceros* spp. and *Pseudo-nitzschia* spp., accompanied by *Lauderia annulata* and *Dytilum brightwellii*, among others. During E2 (Fig. 8B, D), the phytoplankton consisted of diatom taxa like *Chaetoceros* spp. (with the presence of spores at all stations), *Pseudo-nitzschia* spp. and *Thalassiosira* spp., with a substantial contribution of dinoflagellates (mostly small gymnodinioids), and haptophytes (including colonial *Phaeocystis*, flagellate forms and coccolithophores). HPLC analyses confirmed these findings and revealed also the presence of prasinophytes, pelagophytes and cryptophytes (Gutiérrez-Rodríguez et al., 2010). The dominance of diatoms was particularly important at stations E2-84, E2-85 and E2-87 (Fig. 8B, D), while the contribution of *Phaeocystis* sp. and other haptophytes increased at the last two stations (E2-88 and E2-95). The phytoplankton community of F2 (Fig. 8E, G) was characterized by the scarcity of diatoms, the dominance of dinoflagellates and again the occurrence of both, healthy-looking and senescent colonies of...
Phaeocystis sp., in the latter case with the associated presence of numerous cryptophyte-looking heterotrophic flagellates (reaching concentrations of nearly 400 cells mL⁻¹) that appeared to be feeding on the colonies. During the stratification phase (F3, Fig. 8F, H), the phytoplankton community was dominated by dinoflagellates, but the diversity of coccolithophores was higher than in the previous cruise. However, diatoms, represented mainly by small Chaetoceros spp. could be relatively abundant at some stations. The picophytoplankton of the FAMOSO surveys (Gomes et al., under review) was dominated by Synechococcus in F1 and F2, with an important contribution of picoeukaryotes in F1. Prochlorococcus was not detected in F2 but was present in F1 and, in F3, was more abundant than Synechococcus below 25 m.

3.2. Photosynthesis-irradiance (P-E) relationships

The values of $P_{\text{B}}^{\text{m}}$ ranged from 0.327 mg C (mg Chl a)⁻¹ h⁻¹ for the DCM sample of F3-259 to 5.89 mg C (mg Chl a)⁻¹ h⁻¹ for the 5 m one of F1-81 (Table 3). $P_{\text{B}}^{\text{m}}$ could not be calculated for station E2-84 because C uptake showed a linear relationship with PAR throughout the whole irradiance range used for the P–E curve. For E2-85, on the following day, $P_{\text{B}}^{\text{m}}$ presented the lowest values of the cruise, both for the 5 m [1.18 mg C (mg Chl a)⁻¹ h⁻¹] and the subsurface samples [0.540 mg C (mg Chl a)⁻¹ h⁻¹]. The mean values (Table 3) of $P_{\text{B}}^{\text{m}}$ at surface [3.29–3.98 mg C (mg Chl a)⁻¹ h⁻¹] were not significantly different between cruises (Kruskal–Wallis test). At each station, $P_{\text{B}}^{\text{m}}$ at the DCM depth was generally lower than at surface, although the difference was only significant for F2 and F3 (Wilcoxon test, $p < 0.05$).

At surface, the initial slope of the P–E curve, $\alpha^\#$ (Table 3), ranged from 0.002 to 0.015 mg C (mg Chl a)⁻¹ (μmol photons m⁻² s⁻¹)⁻¹ h⁻¹ in winter-spring (E2, F1 and F2) and from 0.015 to 0.020 mg C (mg Chl a)⁻¹ (μmol photons m⁻² s⁻¹)⁻¹ h⁻¹ in late summer (F3). Mean surface values (± SD) ranged from 0.006 ± 0.004 mg C (mg Chl a)⁻¹ (μmol photons m⁻² s⁻¹)⁻¹ h⁻¹ during E2 to 0.016 ± 0.004 mg C (mg Chl a)⁻¹ (μmol photons m⁻² s⁻¹)⁻¹ h⁻¹ during F3. $\alpha^\#$ values for the DCM samples were similar to those at surface for the winter cruises, and higher in spring and late summer; however, the difference was only significant for F2 (Wilcoxon test, $p < 0.01$). Substantial
photoinhibition was only observed for the deep samples of September 2009. Excluding DCM samples from E2, which formed a separate cluster, optical depth (Fig. 9) was positively correlated with $\alpha_p$ and negatively with $E_p$ (r = −0.57, p < 0.001, n = 21, after omitting an outlier corresponding to station E2-88, with $E_p = 1400$). There was no correlation between $\alpha_p$ and $P_{\text{m}}^E$, either for the whole data set or for each cruise.

### 3.3. Carbon fixation in 24 h on-deck incubations. Comparison with $P$–$E$-derived estimates

For the highest incubation irradiances (39.81–50%), the daily $C$ fixation rates of the 5 m sample estimated from the 24 h $^{14}$C incubation experiments carried out on deck and from the 2 h $P$–$E$ curve were well correlated (r = 0.97, 0 < 0.001, n = 15) (Fig. 10A). The major axis regression slope was 0.86 (0.73–1.0, 95% confidence limits). However, when the whole range of experimental light levels was considered (spanning from 0 to 39.81–50% of incident light), the relationship between the Chl $a$–normalized daily $C$ fixation rates from 24 h and $P$–$E$ incubations for equivalent light intensity conditions showed a convex shape (Fig. 10B–D). $C$ fixation rates in 24 h incubations remained relatively stable and higher than $P$–$E$-derived values from intermediate light levels down to 4–18% in F1 and F2, and to 20–30% in F3 (Fig. 10B–D).

### 3.4. Primary production and phytoplankton biomass

$P$–$E$-derived estimates of daily primary production in the water column peaked at the surface in all the cruises, but presented high variability, both between and within cruises. $C$ fixation rates at surface ranged between 124 mg C m$^{-3}$ d$^{-1}$ at the weakly stratified station F1-81 on 22 March 2009, to 2.3 mg C m$^{-3}$ d$^{-1}$ at the strongly stratified station F3-260 on 17 September 2009 (Fig. 7B, D, F, and H). In F3, the percentage of primary production occurring below 50 m was between 11 and 28% of the total integrated value down to 80 m depth. $P_{\text{int}}$ ranged from a maximum close to 2000 mg C m$^{-2}$ d$^{-1}$ in March 2009 (station F1-81) to less than 100 mg C m$^{-2}$ d$^{-1}$ in September 2009. Cruise averages (Table 3) went from 1024 mg C m$^{-2}$ d$^{-1}$ in F1 to 141 mg C m$^{-2}$ d$^{-1}$ in F3, with intermediate values for E2 (417 mg C m$^{-2}$ d$^{-1}$) and F2 (448 mg C m$^{-2}$ d$^{-1}$). There was a significant linear relationship between $P_{\text{int}}$ and surface Chl $a$ (Chl $a_s$) or integrated Chl $a$ (Chl $a_{\text{int}}$) when the E2 data were excluded (Fig. 11A, B). However, the highest $P_{\text{int}}$ values, found during F1 (late March of 2009), did not coincide with the highest surface and integrated Chl $a$ concentrations, which were measured in E2 (mid-March of 2005).

### 3.5. Relationships between primary production and physico-chemical forcing

When the whole data set was considered, $P_{\text{int}}$ decreased with increasing vertical stratification index (VSI) from winter to late summer, but the relationship could be negative (F1), positive (E2 and F2) or non-existent (F3) for the individual cruises (Fig. 12A). The $P_{\text{int}}$ to Chl $a$ ratio ($P_{\text{int}}$/Chl $a_{\text{int}}$) was not correlated with total incident irradiance for values of this variable above approximately 35 mol photons m$^{-2}$ d$^{-1}$, which included the samples from F1 and F2. However, the correlation between $P_{\text{int}}$/Chl $a_{\text{int}}$ and surface incident irradiance was significantly positive during the cruises E2 and F3 (Fig. 12B), for which incident irradiance was generally lower than the 35 mol photons m$^{-2}$ d$^{-1}$ threshold (Fig. 12B). $P_{\text{int}}$ and surface incident irradiance were significantly correlated only for F3 (r = 0.91, p < 0.01, n = 5; data not shown).

Cruise-averaged DIN and DIP fluxes to the euphotic layer declined strongly, due to the reduction of the diffusion coefficients through the
thermocline, from a mean (± SD) of 23.13 ± 34.77 mmol m⁻² d⁻¹ for DIN and 1.40 ± 2.68 mmol m⁻² d⁻¹ for DIP in F1, to respective values of 0.385 ± 0.190 mmol m⁻² d⁻¹ and 0.016 ± 0.011 mmol m⁻² d⁻¹ in F2, and 0.089 ± 0.088 mmol m⁻² d⁻¹ and 0.003 ± 0.004 mmol m⁻² d⁻¹ in F3. There was a globally significant positive correlation between the logarithm of the upward DIN and DIP fluxes across the nutrient line and the logarithm of PPint (Fig. 12C, D). However, these relationships were not significant within cruises. As expected, the logarithms of the DIN and DIP fluxes of the whole data set were significantly correlated between themselves and with the logarithm of VSI (data not shown).

The ratio between DIN and DIP fluxes was lower than the classical Redfield value of 16 only at stations F1-73, F1-74 and F2-132, while it ranged from 18 (F2-123) to 110 (F2-129) in the rest. The C equivalents (according to the classic C, N, P Redfield ratios of 106, 16, 1) of the DIN and DIP upward fluxes were in general lower than the measured PPint (the exceptions were stations F1-74 and F1-81 for DIN and station F1-74 for DIP). The molar ratios between PPint and the C equivalents derived from the DIN fluxes were (mean ± SD) 2.9 ± 2.2, 18.6 ± 13.8 and 28.0 ± 17.8 for F1, F2 and F3, respectively. The corresponding values for DIP were 5.7 ± 6.2, 32.7 ± 27.1 and 73.8 ± 60.3.

The relationships among the within-cruise coefficients of variation of PPint calculated with the “original” daily incident irradiance corresponding to each station (52%, 50%, 46% and 30%, respectively for F1, E2, F2 and F3) and with the same “sunny-day” incident irradiance for all the stations (54%, 29%, 48% and 11%, respectively), indicate that changes in incident irradiance played a

Fig. 10. Relationships between C fixation rates obtained from on-deck, 24 h incubations (Ext), and derived from the P–E curves (P–E). (A) Relationship between the daily C fixation rates corresponding to the highest irradiances (39.81–50%) used in the on-deck incubations, and the corresponding C fixation rates in the P–E experiments; the dashed line is the major axis regression line. (B-D) Relationship between Chl a-normalized daily C fixation rates for different stations (indicated in the legend) of cruises F1 (B), F2 (C) and F3 (D); the gray dotted line indicates the relationship 1:1.

Fig. 11. Relationships between (A) surface (5 m) Chl a (Chl aₙₑₒ) and integrated primary production (PPₚₑₑ), (B) integrated Chl a (Chl aₐₑₑ) and PPₚₑₑ.
and an increment of stratification at the end of F1 (stations F1-80 and F1-81 on year days 80–81, Fig. 2) were accompanied by a three to four-fold rise of PP\text{int}. This increase was a consequence of increments in both phytoplankton biomass and surface irradiances in E-84 and E-85) and for about 63% of it in F3. During winter, hydrographic heterogeneity at the sampling point was important, as suggested by the remote sensing images (Fig. 4). The salinity increase, the deepening of the mixed layer (down to more than 200 m, Table 3) and the decrease of vertical stratification at the end of F1 (stations F1-80 and F1-81 on year days 80–81, Fig. 2) were accompanied by a three to four-fold rise of PP\text{int}. This increase was a consequence of increments in both phytoplankton biomass and surface irradiance (Table 3), a parameter which showed a significant positive correlation with surface salinity ($r^2=0.94$, $p<0.001$; data not shown). In this context, salinity could be considered as a proxy of the intensity of previous water column mixing (stronger mixing originates higher salinity in the upper layers). However, the relatively high salinities of the two first stations in E2, which had unusually high Chl a concentration (Fig. 3), were associated with shallow mixed layers. A connection between hydrographical and biological variability could also be made for the last three stations of F2, in which the Chl a and PP\text{int} increases (Fig. 7E, F) were linked to a shallowing of the mixed layer and an increment of stratification (Tables 1 and 3).

4. Discussion

4.1. Hydrography and phytoplankton

The marked stratification increase between winter and late summer and the hydrographical characteristics of the cruises studied here are typical of the seasonal variation in the NW Mediterranean. In addition, the physico-chemical variables showed substantial short-term variability, as can be seen in Figs. 2–6. In F1 and E2, the variability shown in the mesoscale heterogeneity of the surface fields (Fig. 4) and the interleaving of high and low salinity waters in the upper layer waters (Figs. 2 and 3) may be a result of the combination of several processes, including baroclinic instabilities associated with deep water formation, various restratification mechanisms and destratification events due to wind bursts (Lévy et al., 1999, 2000; Madec et al., 1991). During F2, the relatively high and homogeneous salinity of the upper water layer after day 128 (Fig. 5, Table 1) might reflect the crossing of a hydrographic structure comparable to the cyclonic eddy reported by Salat et al. (2013) based on satellite imagery.

The relatively high nutrient concentrations in the winter cruises are the result of deep convection and mixing, which are a characteristic of the study area (Siokou-Frangou et al., 2010) and were particularly intense in the cold and windy winters of 2004–2005 (Salat et al., 2007) and 2008–2009 (Salat et al., 2010). DIN concentrations at surface continued to be relatively high (> 1 mmol m$^{-3}$) through spring (F2) and also exceeded 1 mmol m$^{-3}$ in the late summer cruise (F3). This is a rather high value for this time of the year, as compared with the DYFAMED data (Marty et al., 2002), but we lack sufficient additional information to provide an explanation. The surface concentration of DIP only reached 0.1 mmol m$^{-3}$ in the early March cruise (F1); in the others, surface DIP concentrations did not exceed 0.05 mmol m$^{-3}$.

The winter cruises, F1 and E2, present a well-developed diatom-dominated phytoplankton bloom. In these cruises, the dynamism and patterns of variability of the Chl a (Fig. 4B–E) reflect a strong hydrodynamic signal, which can be associated to meanders and eddies of the untransformed Atlantic Waters recently penetrated from the South, and the Liguro-Provençal-Catalan Current flowing from the NW to the SE (Fig. 4A).
highest surface and integrated Chl a values recorded in our study were measured in March, in agreement with in situ measurements at the DYFAMED station (43° 25′ N, 07° 52′ E), situated in the central Ligurian Sea (Marty and Chiavérini, 2002), and satellite-based reports that locate the Chl a peak of the NW Mediterranean in late winter–early spring (Bosc et al., 2004; D’Ortizeno and Ribera d’Alcâia, 2009). During E2, Chl a concentrations at 5 m depth reached 7 mg m⁻³ at station E2-84, on 25 March 2005 (Table 3). This is one of the highest values measured in the open sea region throughout the Mediterranean, the occurrence of diatom prolif-eration during the winter-spring bloom has been documented in coastal zones, respectively, an early and a late winter-spring bloom situation (seawards of the shelf slope) of the NW Mediterranean, where Chl a concentrations beyond 3 mg m⁻³ have rarely been reported (Siokou-Frangou et al., 2010). The high Chl a concentration found in March 2005 is probably related to the unusually cold 2004–2005 winter, in which the convection process that produces the Western Mediterranean Deep Water was particularly intense and affected not only the Gulf of Lion area, but also the Catalan and the western Ligurian sub-basins (Salat et al., 2007; Smith et al., 2008). This intense deep convection event induced an extraordinary nutrient enrichment of the surface waters and subsequent phytoplankton biomass build-up in the NW Mediterranean region (Volpe et al., 2012; Arin et al., 2013). On 25 March 2005, the integrated Chl a concentration reached 260 mg m⁻², a value similar to the maxima (230 and 250 mg C m⁻²) registered by Marty and Chiavérini (2002) and by Morán and Estrada (2005), respectively.

The composition of the nano-microphytoplankton communities during the E2 and FAMOSO cruises followed a typical seasonal pattern for the region (Siokou-Frangou et al., 2010, Estrada and Vaqué, 2013). F1 and E2 appeared to present, respectively, an early and a late winter-spring bloom situation with strong contributions of the diatoms Chaetoceros spp, Pseudo-nitzchia spp. and Thalassiossira spp., and the haptophyte Phaeocystis spp. During F2 (post-bloom) and F3 (late summer conditions), the phytoplankton was dominated by dinoflagellates and cocco- lithophores. It must be noted that, although a diatom-dominated winter-spring bloom has been documented in coastal zones throughout the Mediterranean, the occurrence of diatom prolif-erations in the open sea seems to be limited to areas where processes like deep convection, fronts or gyres sufficiently enrich the surface waters (Siokou-Frangou et al., 2010). Phaeocystis sp. is an important contributor to the winter-spring blooms in the NW Mediterranean and may be the dominant taxon in regions where diatoms do not proliferate (Estrada, 1991). Its higher abundances appear to be associated with Recent Atlantic Waters of relatively low salinity. For example, in March 1985, high Chl a concentrations offshore of the Catalan Front were due to a proliferation of Phaeocystis sp. (Estrada, 1991) and, in February-March 1999, an anticyclonic eddy of Recent Atlantic Waters at the northern boundary of the Balearic Sea (Pascual et al., 2002) was characterized by a community of Phaeocystis and other haptophytes (Estrada et al., 2003). The association of Phaeocystis sp. with Recent Atlantic Waters would explain the opposite population density changes of diatoms (increasing) and Phaeocystis sp.+ haptophyte flagellates (decreasing) with increasing salinity in the last three stations of F1 and E2 (Figs. 2B, 3B, 9A and B).

4.2. Photosynthetic parameters

The average values of March surface Chl a-normalized maximum photosynthetic rates, $P_{\text{max}}^B$ (Table 3) were somewhat higher than those reported by Morán and Estrada (2005) for March 1999 [mean ± SD, 2.32 ± 0.76 mg C (mg Chl a)⁻¹ h⁻¹]. $P_{\text{max}}^B$ (mean ± SD) increased slightly from winter [3.34 ± 1.42 mg C (mg Chl a)⁻¹ h⁻¹ for E2 and 3.98 ± 1.32 mg C (mg Chl a)⁻¹ h⁻¹ for F1] to spring [3.47 ± 1.04 mg C (mg Chl a)⁻¹ h⁻¹], to remain within the same range through late summer [3.29 ± 0.82 mg C (mg Chl a)⁻¹ h⁻¹], a pattern that agrees with the findings of Morán and Estrada (2005) and Marty and Chiavérini (2002). Assuming a Q₉₀ value of 1.88 (Eppley, 1972, Bissinger et al., 2008), the variation of temperature between winter and late summer (13–24 °C) should theoretically double $P_{\text{max}}^B$. However, the between-cruise differences in the $P_{\text{max}}^B$ averages are smaller than two-fold, indicating that other factors, such as irradiance conditions, nutrient availability, and phytoplankton composition and physiological state override temperature effects. Significant differences between $P_{\text{max}}^B$ in surface and DCM of the same station could be found even in relatively well-mixed winter waters (E2), indicating that the time scale for photoaclimiation was faster than for mixing. In contrast to $P_{\text{max}}^B$, surface and DCM $\alpha_B$ were practically the same at all stations of the two winter cruises, suggesting a slower response of this parameter (Morán and Estrada, 2005). When all the data were considered, the lowest $P_{\text{max}}^B$ corresponded to optical depths (OD) > 3 (Fig. 9A). This observation and the overall positive correlation of $\alpha_B$ (and negative of $E_R$) with OD (Fig. 9) (the exception were the deep samples from E2) agree with previous work associating $\alpha_B$ increase (and $P_{\text{max}}^B$ and $E_R$ decrease) with photoaclimiation to lower irradiances (Falkowski, 1981; Moore et al., 2006). There was no relationship between $P_{\text{max}}^B$ and MLD (data not shown), suggesting that phytoplankton communities had at least partially photoaclimiated to in situ irradiance. In this sense, stations F1-80 and F1-81 with MLDs exceeding 200 m, and hence with phytoplankton communities presumably exposed to low average light levels, presented $P_{\text{max}}^B$ values that were among the highest of our data set (Tables 1 and 3). The coexistence of high $P_{\text{max}}^B$ (and $E_R$) with deep MLDs at these stations agrees with the results of Moore et al. (2006), who found that populations of mixed water columns were aclimiated to relatively high irradiances, and proposed that this response could represent a strategy to avoid excessive photoinhibition damage. In contrast to the high $P_{\text{max}}^B$ of the last stations of F1, it was not possible to define a saturated C fixation rate for the P-E curves of station E2-84, carried out about the same time of the year (but in 2005), while the $P_{\text{max}}^B$ for both surface and 20 m deep samples of the next day station, E2-85, were among the lowest recorded in this study. Physiological parameters derived from fast repetition rate fluorometer (FRRF) measurements in these stations were coherent with these peculiar characteristics of their phytoplankton communities (Gutiérrez-Rodríguez, unpublished results).

Thus, a maximum of in situ electron transport rates (ETR$_{\text{max}}$) could not be assessed for E2-84 while the ETR$_{\text{max}}$ attained in surface waters of E2-85 was again among the lowest values recorded in this data set (data not shown). Moreover, the corresponding $\alpha_B$ and $E_R$ values (Table 3) were also outliers in the overall relationship between these parameters and OD (Fig. 9). E2-84, E2-85 and in general all E2 stations presented a diatom-dominated phytoplankton community with substantial presence of Chaetoceros spores, suggesting that the bloom was in a decay phase. Given the high phytoplankton biomass accumulated at E2-84, E2-85 and although to a lower degree at other E2 stations, it seems feasible that rapidly growing diatoms had consumed a large portion of the available nutrients, leading to nutrient starvation. This view is supported by FRRF observations during E2, which showed a marked decrease of Photosystem II maximum quantum yield ($F_{v}/F_{m}$) and an increase of effective absorption cross-section (sPSII) in the upper part of the water column, both during the day and at night (Gutiérrez-Rodríguez, unpublished results). As there were no substantial changes in the phytoplankton community composition of the surface and deep samples of E2, an observation that is consistent with the relatively well-mixed water column, these vertical patterns of $F_{v}/F_{m}$ and sPSII can be taken as an indicator of nutrient starvation and unbalanced growth (Parkhill et al., 2001; Suggett et al., 2009). However, narrow MLDs (26–22 m) and high vertical attenuation with shallow euphotic layers (19–26 m) at
both E-84 and E-85, which coincided with surface incident irradiance about half that of the following days (Tables 1 and 3) due to covered skies, suggest that light-limitation could also contribute to the distinctive photosynthetic parameters assessed at these stations. The above examples indicate that different photoacclimation strategies may be very important in determining phytoplankton growth in oligotrophic ecosystems and must be taken into account in model parameterizations (Ayata et al., 2013), emphasizing the need for in situ measurements.

4.3. Comparison between P–E curves and on-deck incubations

As can be seen in Fig. 10A, for the highest incubation irradiance the relationship between daily C fixation rates derived from P–E experiments and from on-deck incubations is linear. However, when Chl a-normalized daily C fixation values for the whole range of incubation irradiances are considered (Fig. 10B–D), the relationship between measurements from P–E experiments and from 24 h on-deck incubations presents generally higher values for the external than for the P–E incubations and tends to be more convex in F1 and F2 than in F3. It must be noted that light attenuation was obtained with blue filters in the on-deck incubators and with neutral (levels of gray) screens in the P–E ones. However, the observation that stations with less convex curves were the most stratified of the data set (F3) suggest that the differences between incubation methods could be related to a photoacclimation response to the experimental intensity (rather than quality) of light exposure. In fact, photoacclimation was evidenced by flow cytometrically detected changes in fluorescence per cell in 24 h dilution experiments carried out during E2 (Gutiérrez-Rodríguez et al., 2010). The bias introduced by photoacclimation into estimates of PPint is generally limited by the fact that the highest concentrations, which were seldom lower than 1 mmol m$^{-3}$, suggest that light limitation could also enter a stage of decay.

Much of the between-cruise variability of PPint appears to be controlled, directly or indirectly, by the stratification of the water column, as reflected in the overall relationships of PPint with VSI and with the nutrient fluxes across the nutricline (Fig. 12A, C and D). As VSI increases from winter to late summer, the nutrient and the Chl a maxima deepen, the diffusion coefficient and the nutrient fluxes across the nutricline decrease and PPint becomes limited by nutrient exhaustion in the upper layers and low light at the nutricline level. Under these conditions, as found for F3, there is no correlation between PPint and VSI (Tables 1–3, the data are not shown in Fig. 12A). In contrast, in the winter and spring cruises, the positive (E2, F2) or negative (F1) relationship between PPint and VSI (Fig. 12A) could be linked to hydrographical heterogeneity of the water bodies and differences in the composition and history of the associated phytoplankton community and planktonic food web (see Section 4.1). The increase of the average ratio between PPint and C equivalent corresponding to the nutrient fluxes (Section 3.5) agrees with the general picture of an increasing contribution of nutrient recycling to phytoplankton growth expected under increasing stratification. However, neither nutrient concentrations in the euphotic zone nor nutrient fluxes across the nutrient showed any meaningful within-cruise relationships with PPint or with the photosynthetic parameters. In addition to the methodological errors and limitations that affect the calculation of these variables, one should be aware that nutrient concentrations, nutrient fluxes across the nutrient and C fixation rates in short-term experiments are controlled by processes acting at different time scales. Phytoplankton cells integrate environmental and ecological (zooplankton grazing, for example) influences over variable periods of time, and C uptake in primary production experiments may be modulated by factors such as taxonomical affinity, optical history of the cells, nutrient fluxes across the cell membrane or internal nutrient quotas (Falkowski and Raven, 2007). These constraints make it difficult to relate environmental nutrient variables with the short-term physiological response of the cells. This difficulty is particularly important for fast-recycling nutrients such as phosphorus (Benitez-Nelson and Bueseler, 1999). Assuming half saturation constants of approximately 0.5–1 mmol m$^{-3}$ (Laws, 2013), DIN concentrations, which were seldom lower than 1 mmol m$^{-3}$ at surface (Section 3.1), could have been non-limiting in all the cruises. Given that there are reports of almost fully saturated growth rates for phosphate concentrations below the limit of detection of usual colorimetric techniques (Laws, 2013), phosphorus could have been non-limiting in F1, but the situation for the other cruises is
uncertain. There are no silicate data for the FAMOSO cruises; the mean concentration of this nutrient in E2 was lower than that of DIN. Assuming a half saturation concentrations around 1 mmol m\(^{-3}\) (Aumont et al. 2003), and considering the very scarce presence of diatoms in surface waters of the post-bloom phase (Fig. 8E), it is likely that silicate could have limited or co-limited diatom growth at the end of the bloom. In this context, there is a relevant distinction between nutrient limitation, which refers to balanced growth at a rate acclimated to nutrient supply, and nutrient starvation, which refers to unbalanced growth when cellular demand exceeds nutrient supply rate (Parkhill et al., 2001). As discussed below, it is likely that in situations of high biomass like those found in the first stations of E2, relatively low availability of DIN, DIP or both could have caused nutrient starvation.

Superimposed to the seasonal trends, the Chl a concentration and primary production measured during this study revealed a high day-to-day spatio-temporal variability, which was particularly important during the winter-spring bloom period and was only in a minor part associated to fluctuations in daily irradiance (see Section 3.5). The intricate satellite-based winter distributions of surface Chl a (Fig. 4) suggest an important role of hydrographical mesoscale and submesoscale forcing in the short-term spatio-temporal fluctuations of phytoplankton standing stock and primary production. A detailed comparison of the stations within each of the winter cruises covering the phytoplankton bloom period may provide valuable insight on the links between environmental forcing and phytoplankton response. The particularities of some of the E2 samples have been discussed in Section 4.2 and in the first paragraph of this section. In the case of F1, the last two biological stations (F1-80 and F1-81, on 21 and 22 March 2009, respectively), which showed the highest P\(_{\text{pp}}\), values recorded in this study, presented upper mixed layers deeper than 200 m (Table 3). For comparison, Siegel et al. (2002) estimated a median critical depth of 181 m as characteristic of the initiation of the spring bloom at latitudes of 40°-45° N in the North Atlantic. If all the CTD casts (including other stations in addition to the biological ones) performed between 21 and 22 March 2009 are considered, the MLD fluctuated from 115 m (a cast at 19:30 on 21 March) to the whole water column depth of approximately 2190 m (a cast at 20:26 GMT on 21 March 2009). In parallel with the increase in MLD, these last stations of F1 presented a decrease of the stratification index and an increment of P\(_{\text{pp}}\). The coincidence on 21 March 2009, of a water column mixed down to the bottom (2190 m) with high P\(_{\text{pp}}\) (1400 mg C m\(^{-2}\) d\(^{-1}\)) and a concentration of 2.33 mg m\(^{-3}\) of Chl a at the surface, typical of a well-developed bloom situation, is intriguing. The MLD values reported here must be taken with caution, not only because of the subjectivity involved in their determination from CTD recordings (de Boyer Montégut et al., 2004), but also because homogeneous variable profiles do not represent evidence of active mixing at the time of sampling (Mourino-Carballedo, personal communication). However, the high variability of MLD determined during the last days of F1 and the agreement between the patterns of variability in hydrographical variables and in vivo fluorescence (Fig. 2) suggests that the changes in the vertical structure of the water column of these stations are due to mesoscale hydrographical forcing occurring after a phytoplankton bloom had already developed. As noted by Lévy et al. (1999, 2000) the winter-spring bloom in the NW Mediterranean is not a steady phenomenon but presents a high spatio-temporal variability from onset to decay. The close relationship between variation in salinity, P\(_{\text{pp}}\) and phytoplankton composition at these last stations of F1 must be taken as a reflection of ecological history (including the interactions with the other components of the food web), not as a direct effect of hydrographical variables such as salinity. As mentioned in Section 3.5, high salinities indicate a stronger mixture with deep, nutrient-rich waters, and therefore, the capability to sustain the development of a high phytoplankton biomass based on fast-growing groups such as diatoms.

In summary, our findings underline the importance of the winter-spring phytoplankton bloom in the deep convection region of the NW Mediterranean as a contributor to phytoplankton biomass and primary production in the region. However, during the bloom period, both phytoplankton biomass and primary production showed considerable variability at the scale of days, in connection with the intense hydrographic mesoscale heterogeneity in the region and with the physiological and ecological history of the planktonic communities associated with each water body. The observation that the relationships between surface phytoplankton biomass and primary production could show substantial variability has implications for estimates of primary production based on remote sensing.

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