Surface mesoscale pico-nanoplankton patterns at the main Fronts of the Alboran Sea


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Abstract
The mesoscale (10-100 km, days-weeks) plays a key role in the Ocean's ecosystem structure and dynamics. This work compares the pico-nanoplankton patterns observed in the Alboran Sea (Western Mediterranean) during three oceanographic cruises. We analyze its response to different expressions of mesoscale circulation associated with the three major hydrodynamic features in the basin; namely the Northwestern Alboran Front (NWAF, surveyed in OMEGA-1 cruise), the Almeria-Oran Front (AOF, surveyed in OMEGA-2 cruise) and the Western Alboran Gyre (WAG, surveyed in BIOMEGA cruise). The first two surveys were carried out under the most typical quasi-stationary twin gyre conditions of the Alboran Sea, whereas the third cruise was performed after an eastward migration of the WAG. The analysis of pico and nanoplankton populations was carried out using flow cytometry. The patchiness observed in the three cruises indicates an association of phytoplankton peaks with the main frontal structures: abundances were higher in the NWAF/upwelling area in OMEGA-1, at the Mediterranean side of the AOF in OMEGA-2, and at a tongue of recent Atlantic Water west of the WAG in BIOMEGA. However, a more detailed analysis reveals that different factors explain the origin of the phytoplankton biomass in each front/cruise. Mixing processes at the Strait of Gibraltar and the subsequent advection of water properties into the Western Alboran Sea were the mechanisms responsible for the abundances observed in the NWAF. The highest concentrations observed in the AOF were related to the intrusion of Mediterranean Surface Waters to the north of the front. During the migrating WAG the phytoplankton distribution was influenced by the formation of a new gyre. The relation between phytoplankton and mesoscale dynamics is further explored in terms of vertical velocity diagnosis. In all cases, intense vertical motion is negatively correlated with the abundance of phytoplankton populations. This resulted from the intense geostrophic background flow associated with large vertical velocities, which drove low residence times of water mass properties and hence a weak biological response. Fast-repeated surveys made during the OMEGA-1 and OMEGA-2 cruises reveal that the surveyed hydrographic features are subjected to significant temporal variability. In this case, the impact on the biology is most evident at taxa level.

Keywords: Phytoplankton; Mesoscale; Patchiness; Physical-biological coupling; Alboran Sea.
1. Introduction

The vertical segregation of the ocean, in terms of biological production, is broken by seasonal vertical mixing or by vertical motions that permit the coincidence of environmental conditions favourable to oceanic primary production by phytoplankton (i.e. light and nutrients). Vertical motion linked to wind driven upwelling is possibly the most understood of these processes. Upwelling fertilizes the surface layer thus favouring biological productivity at all levels of the food chain. Another type of vertical motion relevant for the structure and productivity of biological communities is that associated with mesoscale features, mainly eddies and instabilities of ocean currents (e.g. Klein and Lapeyre, 2009).

The mesoscale (10-100 km, days-weeks) is acknowledged as the most energetic scale of ocean dynamics (Robinson, 1983) and can be described as the “weather” of the ocean. The role played by this ubiquitous dynamic scale in the generation of spatial heterogeneity or “patchiness” in phytoplankton distributions is not well known yet (Martin, 2003). It is at the mesoscale that fronts between water masses become unstable and strong three-dimensional instabilities are set up. The high spatial and temporal variability associated with mesoscale dynamics gives rise to areas of convergence and divergence. Consequently it favours the existence of intense upwelling and downwelling areas with vertical velocities of the order of several tens of metres per day, that is, an order of magnitude higher that the largest vertical velocities usually observed in permanent upwelling areas (Vélez-Belchí and Tintoré, 2001). This is why mesoscale circulation is of great significance to explain the patchiness of nutrient distributions (Lévy, 2008; Martin and Richards, 2001; Woodward and Rees, 2001), chlorophyll (Fielding et al., 2001; Ruiz et al., 2001; Strass, 1992), primary production (Martin et al., 2002; Strass et al., 2002), phytoplankton size structure (Rodríguez et al., 2001), patterns of zooplankton distribution (Huntley et al., 1995) and the life histories of key marine populations (Cowen et al., 2000; Planque, 2005; Werner et al., 1993). At the top end of the food chain, the response of fish abundance to the environment is also more obvious at the mesoscale. This is due to the strong influence of eddies and fronts on physical and biogeochemical properties, and hence on prey distribution (Tew-Kai et al., 2009) and favourable fish reproductive habitats (“ocean triads”; Agostini and Bakun, 2002). Consequently, understanding mesoscale features and their variability is crucial in determining the links between plankton dynamics, primary production, recruitment and...
transport of juvenile fish and larvae of benthic organisms, and biogeochemical fluxes that are undetectable at larger scales.

The Mediterranean Sea is a region where mesoscale processes play a key role in determining the characteristics of the basin-wide marine circulation, the distribution of water masses, and ecosystem functioning (CIESM, 2005). Located at the westernmost Mediterranean basin, the Alboran Sea is the region where water exchanges with the Atlantic Ocean (driven by the inflow of Atlantic Water (AW) through the Gibraltar Strait) have their most conspicuous hydrodynamical effects, generating gyres, fronts and eddies of different spatial scales (Cano, 1978; Tintoré et al., 1991). The quasi-stationary physical framework of the Alboran Sea and its physical-biological coupling has been the subject of numerous studies (Arnone et al., 1990; Rodríguez et al., 1998; Tintoré et al., 1991; among others). The incoming Atlantic Jet (AJ) of AW drives the upper circulation in the region, influencing the coastal upwelling in the NW sector of the basin and feeding two anticyclonic gyres: the quasi-permanent Western Alboran Gyre (WAG) and the less persistent Eastern Alboran Gyre (EAG). The density gradient between the newly injected waters of the AJ (recent AW) and the NW coastal upwelling creates the Northwestern Alboran Front (NWAF). At the eastern limit of the Alboran Sea, the gradient between recent AW from the AJ and older AW that has been circulating in the Mediterranean Sea (whose surface expression is hereafter called Mediterranean Surface Water, MSW) creates the Almeria-Oran front (AOF) (Allen et al., 2001; Gascard and Richez, 1985; Sarhan et al., 2000).

At the mesoscale, the vertical velocities associated with frontal structures in the Alboran Sea are of the order of several tens of meters per day (Allen et al., 2001; Vélez-Belchí and Tintoré, 2001; Viúdez et al., 1996). Upwards is enough to compensate sinking losses of phytoplankton (Rodríguez et al., 2001), and downwards to speed the advection of phytoplankton and heat along isopycnals down to depths of several hundreds of meters (García-Gorriz and Carr, 2001; Peinert and Miquel, 1994). Such motions also have a significant effect on the vertical distribution of zooplankton across the front (Fielding et al., 2001).

On the other hand, the physical processes involved in the migration of the WAG and the migration/absence of the EAG, have only been studied in a few papers (Flexas et al., 2006; Renault et al., 2012; Viúdez et al., 1998; among others). Accordingly, less is known about the impact that the temporal variability of these larger local dynamics have
on the biological communities (Macías et al., 2007a, 2008; Vargas-Yáñez and Sabatés, 2007). In particular, there is no up-to-date work addressing the consequences of the eastward migration of the WAG on the biology of the region.

Because of the need for a high-resolution (both in temporal and spatial terms) sampling design, our knowledge of mesoscale field plankton ecology is almost exclusively based on proxy estimates for the total community biomass of phytoplankton and zooplankton (Martin, 2003). In particular, the mesoscale study of phytoplankton is almost entirely restricted to variables (like chlorophyll) that can be inferred continuously or synoptically by means of optical sensors. Mesoscale patterns of some phytoplankton taxa can however be facilitated through the fast, *in situ* flow-cytometry analysis in the size range of approximately 1-20 μm, covering picoplankton and nanoplanckton (Rodríguez and Li, 1994; Sieburth, 1979). This size-range is relevant, since small cells are responsible for a fundamental part of oceanic primary production, particularly in oligotrophic waters (Chisholm, 1992; Platt and Li, 1986; Rodríguez et al., 1998). In this framework, the mosaic of hydrodynamic structures of the Alboran Sea, which combines oligotrophic gyres, upwelling areas and energetic frontal systems with a wide range of mesoscale vertical velocities, represents a unique natural laboratory to examine the physical-biological coupling of pico-nanoplankton at the mesoscale (Rodríguez et al., 2001).

This paper analyzes the mesoscale distribution of pico-nanoplankton at three major hydrodynamic features in the Alboran Sea: the NWAF, the AOF and the structures resulting from a migration event of the WAG. Such analysis tries to address questions like: Is the phytoplankton distribution driven by the same physical process in the whole basin? Is there any relationship between mesoscale dynamics and phytoplankton populations? How does temporal variability affect phytoplankton patterns in the short-term?

2. Materials and methods

Three regions of the Alboran Sea were studied at the mesoscale during the following cruises (Fig. 1):

(1) *OMEGA-1 field experiment*
Carried out onboard *BIO Hespérides* (1-15 October 1996), this cruise covered the Northwestern Alboran Front (NWAF). Three fine-scale surveys were carried out with a SeaSoar undulating vehicle equipped with Conductivity-Temperature-Depth (CTD), fluorometer and PAR light sensors. Each survey was completed in about 70 hours and consisted of 10-11 meridional sections (70-80 km long) separated by 10 km in the west-east direction, covering a total area of about 80 km by 100 km (Fig. 1, left panels). Details about the physical sampling and instruments can be found in Vélez-Belchí and Tintoré (2001) and Vélez-Belchí et al. (2005).

(2) *OMEGA*-2 field experiment

Carried out onboard *RRS Discovery* (22 November -29 December 1996), this cruise covered the Almeria-Oran Front (AOF). Three fine-scale surveys were carried out during this cruise, consisting of 10-11 parallel tracks separated about 10 km (Fig. 1, right panels). A SeaSoar undulating vehicle was used to continuously monitor the water column to a depth of ~ 450 m. However, SeaSoar data at 5m depth were not available and near-surface measurements (at 5-m) were obtained from the vessel continuous thermosalinograph. See Allen and Guymer (1997), Allen et al. (1997, 2001) and Fielding et al. (2001) for additional information.

(3) *BIOMEGA* field experiment

Carried out onboard *BIO García del Cid* (9-17 October 2003), this cruise covered a migrated WAG. At the time of the cruise the WAG was displaced about 100 km eastwards from its usual location (Fig. 1, bottom panel). The sampling consisted of 16 meridional transects of 9 CTD stations each, with a distance between stations of about 10 km in both longitudinal and latitudinal direction. The physics were analysed in Flexas et al. (2006).

2.1. Hydrographic data

Hydrographic characterization of surface water masses was performed using potential temperature, salinity and potential density (calculated at each hydrographic station; Millero et al., 1980) obtained from hydrographic observations detailed above. The mesoscale dynamics of each area was evaluated by estimating the geostrophic flow and the vertical velocity field as follows. Hydrographic data were first interpolated onto a regular grid using an Optimum Interpolation technique (Bretherton et al., 1976). Dynamic variables (i.e., dynamic height) were computed with respect to an assumed no-
motion depth of 300 m. In order to eliminate non-resolved small scale structures, horizontal fields were spatially smoothed with a cut-off wavelength of 40 km. This cut-off wavelength corresponds to structures with a radius of about 10-20 km, similar to the local internal Rossby radius of deformation (of about 10-15 km). Vertical velocities were calculated using the quasi-geostrophic form of the OMEGA equation (Hoskins et al., 1978).

2.2. Biological sampling and in situ analysis

Samples for the study of pico-nanoplankton were taken in two different ways. During the OMEGA-1 and OMEGA-2 cruises, samples were collected from the vessel’s continuous non-toxic sea-water pumping system, at a depth of ~5 m. The biological sampling was carried at a rate of 1 sample per hour (i.e., 1 sample every 13-14 Km), increased to 1 sample/30 minutes in the zones of major interest (i.e. frontal areas showing the largest gradients in biological properties). BIOMEGA samples were obtained at depths of 10, 20, 40, 60, 80 and 100 meters from the Rosette-Niskin bottles used to sample the water column at the stations shown in Fig. 1. For obvious comparative reasons only the upper samples (10 m) have been used in this work.

Chlorophyll concentration was measured with a Turner Fluorometer previously calibrated with pure chlorophyll a, following the method suggested by Yentsch and Menzel (1963). Additionally, all samples were analyzed on board using a FacScan (Beckton-Dickinson) flow cytometer. Flow Cytometry (FC) was used to estimate abundance, size and functional composition of phytoplankton <20 µm (equivalent spherical diameter, ESD). In this work each sample run for 5 min under mode “high” (60 ± 5 µL·min⁻¹) and the following setting conditions: Forward Scatter (FSC)=E00; Side Scatter (SSC)=271 and the fluorescence signal at wavelengths of 564-606nm (FL2) and >650nm (FL3) (FL2=450; FL3=300). The FL2 and FL3 signals (ascribed to phycoerythrine and chlorophyll-a respectively) together with SSC (related to particle size) were used to identify the following operative groups (Fig. 2a, c): nanoplankton larger than 10 µm (henceforth “Nano>10”), ultraplankton (henceforth “Ultra”), equivalent to nanoplankton 2-10 µm, cryptomonad flagellates (henceforth “Crypto”), eukaryotic picoplankton (henceforth “Eupico”), and prokaryotic Synechococcus cyanobacteria (henceforth “Cyano”). During the OMEGA-2 cruise, an additional analysis was carried out with the following setting conditions: Frontal Scatter (FSC)=E00; Side Scatter (SSC)=402 and Fluorescence (FL2=555; FL3=651). This
allowed a quantitative analysis of the prokaryotic *Prochlorococcus* population (Fig. 2b). Such analysis was not available for OMEGA-1 and BIOMEGA.

Phytoplankton populations were additionally discriminated along a size axis related with the light scatter properties as described in Fig. 2c. Previously, the SSC signal was calibrated for cell size using cultures of microalgal species and latex spheres (Coulter Calibration Standard). In all cases at least 200 cells/spheres of each species and sphere size class were measured on a VIDS IV analysis semi-automatic system and FC. All the cytograms previously acquired have been reanalysed under the same criteria to minimize the uncertainty in the discrimination of phytoplankton groups between cruises.

### 3. Results

#### 3.1 Macroscale and mesoscale dynamics during the cruises

**3.1.1. Quasi-stationary conditions**

The macroscale hydrological pattern observed during OMEGA-1 included (Figs. 3 and 4): (i) part of a well developed WAG with a diameter of approximately 100 km occupying most of the southwestern sector of the basin (centred at about 4ºW), where recent AW (S<36.6) accumulates; (ii) part of the upwelling area (U, in Fig. 4a) located along the Spanish coast, to the NW of the gyre; and (iii) the NWAF separating both structures and associated with the AJ.

The surface distributions of temperature and salinity (Figs. 4a,b) show the existence of mesoscale disturbances mainly linked to the NWAF and the AJ. The latter appears as a surface band bounded by the 18-19.5ºC isotherms with minimum surface salinity (Vélez-Belchí et al., 2005). The second and third surveys (Fig. 4) show a southward displacement of the NWAF that indicates the start of a WAG migration process, with the AJ impinging directly on the WAG (Vélez-Belchí et al., 2005). While the WAG is pushed eastward, the area of new AW to the northwest of the sampling area increased in size.

The vertical velocity is mainly related to the edges of the WAG and evolves in time from the first to the third survey (Fig. 4d) according to changes of the front and WAG position. Maximum vertical velocities, of ± 45 m·d⁻¹ at a depth of 50 m, are located in
the eastern and western boundaries of the domain (about 36°N) in surveys 1 and 2, while up to -40 m·d⁻¹ are observed within the AJ (about 36.25°N) in survey 3. They are located in areas where curvature and advection reach their maximum. The core of the WAG is characterized by less intense vertical dynamics, in coherence with the low-energy character typical of a large anticyclonic eddy such as the WAG (Vélez-Belchí and Tintoré, 2001; Vélez-Belchí et al., 2005). Geostrophic velocities near the surface (at 5 m depth) were up to 1 m·s⁻¹ (Vélez-Belchí et al., 2005).

The OMEGA-2 survey captured the Almería-Oran front as a sharp transition defined by the 17.0-15.5°C isotherms and the 36.7-37.0 isohalines (Figs. 5a,b). During the first two surveys, the AOF separated warmer and fresher AW of the EAG, to the south-west, from Mediterranean waters with temperature <15.5 °C and salinity 36.7-37.5 to the north-east. In the third survey, a tongue of MSW (potential temperature > 15.5 °C, salinity > 37.5; Arnone et al., 1990) intruded in the northern area (MSW, Fig. 4b) of the sampling domain. Published hydrographic analysis showed that during surveys 2 and 3 the tongue of MSW had been subducted and transported across the front (along the 27.9 σ₀ density isosurface; Allen et al., 2001; Fielding et al., 2001). Another noticeable change between surveys was the formation of a surface eddy-like feature of lighter old AW and its intrusion into the Mediterranean side of the AOF (old AW eddy; Figs. 5a,b, c, central and right panels).

The vertical motion within the AOF was of the order of 14 m·d⁻¹ (Fig. 5d), with maximum values at a depth of 77 m. The horizontal distribution of vertical velocity shows the mesoscale patches of upward and downward velocity by the frontal current (Allen et al., 2001; Fielding et al., 2001). Geostrophic velocities near the surface (at 13 m depth) were up to 50 cm·s⁻¹ (Allen et al., 2001).

3.1.2. Migrating WAG conditions

The BIOMEGA cruise sampled a migrated WAG, centred at about 3°W (Fig. 6). The region was characterized by: (i) a smaller WAG (of about 80 km in diameter), with salinity significantly lower than published data and the lowest values recorded in OMEGA-1; (ii) a cold cyclonic structure to the south-east of the WAG (old AW eddy; Fig. 6a); and (iii) a tongue of old AW to the west (Fig. 6a), that was fresher than the WAG at the surface but more saline than the WAG below the 40 m depth (Flexas et al., 2006). Mesoscale vertical velocities (Fig. 6d) showed maximum values of the order of
±18 m·day⁻¹ at a depth of 80 m. These velocities are significantly lower than the values observed during OMEGA-1 (Fig. 7) and others reported previously for the WAG. In contrast, those values were significantly higher than in OMEGA-2 (Fig. 7). Geostrophic velocities near the surface (at 10-m depth) reached a maximum of 70 cm·s⁻¹ (Flexas et al., 2006).

3.2. Macroscale and mesoscale biological patchiness

3.2.1. OMEGA-1: The Northwestern Alboran Front

At gyre-scale, there was a clear coherence between total chlorophyll concentration (as an indicator of total phytoplankton abundance) and the hydrological characteristics of the surveyed area as described by temperature and salinity surface distributions (Figs. 4 and 8, panel a). Particularly during the first survey, the chlorophyll surface pattern shows the expected gradient from the oligotrophic waters of the WAG (< 0.2 µg·L⁻¹) to the more productive north-western waters under the influence of the coastal upwelling (> 2 µg·L⁻¹). Intermediate concentrations were found at the NWAF (~ 1-2 µg·L⁻¹). At gyre-scale, the chlorophyll pattern also follows the southward displacement of the AJ and the start of the WAG migration observed during the second and third survey, a process that translates in a clear decrease of surface concentration values. At the mesoscale, phytoplankton biomass takes the form of patches linked to the AJ and NWAF. This pattern was particularly clear during the first survey, when chlorophyll concentration values were the highest. From the first to the third survey phytoplankton biomass decreased, and were accompanied by a lower manifestation of mesoscale structures in the chlorophyll signature.

The features observed for the chlorophyll pattern can be extended to those of the quantified phytoplankton populations (Fig. 8, panels b-f). Nano>10 µm showed maximum cell density (around 10³ cells·mL⁻¹) at the upwelling influenced zone (U, Fig. 4a) where chlorophyll showed maximum concentration; elsewhere the cell density was at least two orders of magnitude lower, even in the mesoscale eddies along the NWAF (Fig. 8, panel b). Ultra (cells 2-10 µm) patches linked to mesoscale eddies were more conspicuous than those of large nanoplankton, reaching 4x10³ cells·mL⁻¹ at different locations and more than 5x10³ cells·mL⁻¹ in the region under upwelling influence. Densities higher than 2x10³ cells·mL⁻¹ were also observed in the core of the
oligotrophic WAG during the first survey. Eupico mesoscale patterns were very similar
to those previously described, reaching densities higher than 20x10^3 cells·mL^{-1} in the
upwelling influenced region and slightly lower densities in mesoscale eddies along the
front. Crypto abundance values during the first survey ranged between 1x10^2 and 5x10^2
cells·mL^{-1} with a maximum > 1x10^3 cells·mL^{-1} at the core of the oligotrophic WAG.
Cyan also showed a clear mesoscale pattern during the first survey, with a main patch of
density values > 2.5x10^4 cells·mL^{-1} in the northwestern sector of the sampling area (U,
Fig. 4a). Short-term variability was particularly evident: Cyano abundance decreased
one order of magnitude from the first to the second survey and another half between the
second and the third one. In survey 3 abundances were very low (of about 10^2 cells·mL^{-1})
at the NWAF and undetectable at the core of the WAG.

3.2.2. OMEGA-2: The Almeria-Oran Front

Total chlorophyll concentration showed patches of high and low concentration along the
AOF boundary (Fig. 9, panel a). Concentrations were highest (around 2.5 µg·L^{-1}) at the
northeast of the sampling domain (Fig. 9a; 36.5ºN, 1ºW). The three fast surveys were
characterised by the presence of mesoscale structures, but with a clear decrease of
concentration values among surveys. Chlorophyll concentration in the intruding MSW
was much reduced (< 0.4 µg·L^{-1}) during the third survey (Figs. 5 and 9, panel a).

Nano>10 µm and Ultra showed similar mesoscale patchiness to that of total chlorophyll
(Fig. 9, panels b and c), with maximum population density values of 4 x 10^2 cells·mL^{-1}
and 2.5x10^4 cells·mL^{-1}, respectively. These two groups exhibited a different temporal
evolution: as total chlorophyll, cell density of nanoplanktonic large cells decreased
within successive surveys; ultraplanktonic populations showed a marked increase in the
second survey (up to 1.8-fold), apparently linked to the first signals of MSW. However,
by the time MSW had intruded throughout the survey domain (i.e. during the third
survey), the density values of Ultra linked to the MSW intrusion decreased down to <
6x10^3 cells·mL^{-1}, while its maximum abundance at that time were coincident with the
patch of maximum chlorophyll concentration. Eupico showed a similar pattern of
change to Ultra (Fig. 9, panel d): maximum abundances were located to the north of the
domain during the second survey and decreased significantly in the MSW during the
third survey.
Crypto flagellate patchiness became sharper and denser during successive surveys (Fig. 9, panel e). While the first survey shows poorly defined patches with density values around $10^2$ cells·mL$^{-1}$, the third survey shows two well-defined mesoscale patches with abundances $> 1.5 \times 10^4$ cells·mL$^{-1}$ coincident with chlorophyll patches.

Phototrophic prokaryote showed the most interesting mesoscale spatial and temporal changes. Both Cyanobacteria and Prochlorophytes mesoscale patchiness (Fig. 9, panels f and g) became sharper and denser from the first to the third survey. Both Cyano and Prochlorococcus reached their maximum density ($\sim 8 \times 10^4$ cells·mL$^{-1}$) during the third survey with the intrusion of MSW (Fig. 5a). Their abundances showed a positive significantly correlation with saltier waters (Cyano, $r=0.34$, $P<0.05$, $n=75$; Prochlorococcus, $r=0.41$, $P<0.05$, $n=75$) corresponding to proper MSW.

3.2.3. BIOMEGA: The migrated WAG

Surface chlorophyll concentrations higher than 0.4 $\mu$g·L$^{-1}$ were limited to the western side of the domain (old AW, Fig. 6a), exhibiting mesoscale patches with concentrations of $\sim 2$ $\mu$g·L$^{-1}$ (Fig. 10, panel a). The rest of the sampled domain, including the migrated WAG and the old AW eddy (Fig. 6a) appeared as an oligotrophic environment with very low concentrations of chlorophyll.

Nano $> 10$ $\mu$m, Ultra and Eupico had gyre-scale and mesoscale distributions similar to that of chlorophyll, with mesoscale patches containing maximum cell densities of $\sim 2 \times 10^3$, $10^4$ and $6 \times 10^4$ cells·mL$^{-1}$, respectively (Fig. 10, panels b, c and d). Crypto and Cyano showed a more heterogeneous distribution with mesoscale patches distributed over the entire domain. Maximum cell density values ($4 \times 10^3$ and $7 \times 10^4$ cells·mL$^{-1}$) were found in the tongue of cold surface water located to the west of the WAG (old AW in Fig. 6a; Fig. 10, panels e and f). All the studied groups showed a significant negative correlation with temperature ($P<0.01$; Table 1).

3.3. Physical-biological coupling

The comparison of vertical velocities with the biological variables from each survey (Fig. 11) shows the association of maximum concentrations of phytoplankton within a narrow range of vertical velocities (approx. within $[-15,+15]$ m·d$^{-1}$). However, a correlation test did not show statistically significant relations between vertical velocities and biological abundances. In contrast, a significant negative linear relationship was
observed between maximum taxa abundance and maximum geostrophic velocities (Fig. 12; Table 2).

4. Discussion

4.1. Methodological considerations on the computation of vertical velocities

The computation of vertical velocities from hydrographic measurements contains large uncertainties. Spatial interpolation of observations always implies some sort of spatial filtering that affects the diagnosed variable, in this case, vertical velocities: smaller cut-off wavelengths usually result in sharper, smaller structures with larger vertical velocities (e.g., Gomis et al., 2001). The vertical velocities presented in this work were calculated using the same spatial interpolation parameters to ensure optimal comparison among cruises.

Observational errors also have an impact on the diagnosed vertical velocities, but they are small compared with that of spatial filtering (Gomis and Pedder, 2005). Moreover, they can be assumed to be similar for the three cruises, since the instrumentation used to measure hydrographic variables had similar accuracies.

Another source of errors is the lack of synopticity. The fast (3-day) cruises carried out in OMEGA-1 and OMEGA-2 can be assumed quasi-synoptic (Allen et al., 2001; Gomis et al., 2005). The BIOMEGA sampling took longer (9 days), but a sequence of Sea Surface Temperature and Sea Level Anomaly satellite images showed that the WAG remained roughly in the same position during the cruise: although it showed some distortion to the west of the domain, that sector of the gyre was surveyed before the deformation and therefore errors derived from the lack of synopticity are also considered acceptable for that cruise (Flexas et al, 2006).

In summary, total errors associated with vertical motion estimations are, in a best-case scenario, of the order of 20-30% of the field variance and could reach up to 50% (Gomis and Pedder, 2005; Gomis et al., 2005). Previous published literature shows vertical velocities similar in magnitude to those presented here (references for each cruise are given in Section 2.1).

4.2. Physical framework
OMEGA-1 and OMEGA-2 were carried out under the quasi-persistent physical regimes characterizing the Alboran Sea circulation in the summer-autumn period (Renault et al., 2012) (Fig. 3a and 4): wherein Atlantic water flows jet-like into the Alboran Sea through the upper layer and forms the WAG and EAG. Two main frontal systems are linked to these structures. To the northwest, the NWAF is found at the northern boundary of the WAG. The NWAF separates the fresher waters of recent Atlantic origin (AW) of the WAG from the almost permanent upwelling region filled with upwelled Mediterranean waters observed along the Spanish coast (Figs. 3a and 4). The AOF is observed on the eastern side of the EAG, separating the AW of the EAG from MSW (Fig. 3a, 4).

The quasi-steady state of the Alboran Sea circulation described above is subjected to changes. One of the most interesting is the eastward migration of the WAG (Vargas-Yáñez et al., 2002; Vélez-Belchí et al., 2005). This was the case studied during the BIOMEGA cruise (Figs. 3b and 6; Flexas et al., 2006). Situations like WAG displacements are now considered as transient modes in contrast to annually stable surface circulation regimes of the Alboran Sea (Peliz et al., 2013; Renault et al., 2012; Sánchez-Garrido et al., 2013). The migration of the WAG is triggered by changes in the intensity and direction of the inflow of AW, which would determine the decoupling of the AJ-WAG system or making the AJ impact directly onto the WAG (Vélez-Belchí et al., 2005; Viúdez et al., 1998). In this situation the gyre would then migrate eastwards. The AJ would deflect south (through the implication of the Coriolis force) and start the formation of a new anticyclonic gyre (a new WAG). However, the factors involved in this complex migratory process are not totally understood. Studies point to several sources of variability, including differences in atmospheric pressure over the Mediterranean (Macias et al., 2008; Ramirez-Romero et al., 2012; Vargas-Yáñez et al., 2002), blocking of the AJ (Viúdez et al., 1998; Flexas et al., 2006), seasonal variability (Renault et al., 2012; Ruiz et al., 2013), wind forcing (Peliz et al., 2013) and tides (Sanchez-Garrido et al., 2013).

4.3. Physical versus biological forcing

The phytoplankton distribution patterns clearly reflect an association of abundance with the main physical features characterizing each cruise: namely, the NWAF and the upwelling area in OMEGA-1; the Mediterranean side of the AOF in OMEGA-2; and the
western tongue of AW in BIOMEGA cruise. However, differences in hydrology and
time evolution of water masses found among surveys indicate that phytoplankton
abundance owes itself to different factors. In this section we discuss the mechanisms
responsible for the phytoplankton patches in each case study

4.3.1. The Northwestern Alboran Front

Explaining mesoscale patchiness of phytoplankton is basically a matter of physical
versus biological mechanisms or, better, a combination of both kinds of processes
(Martin, 2003). This possibility is examined by Ruiz et al. (2001) in the NWAF through
the study of the mesoscale distribution of fluorescence during the OMEGA-1 survey.
On the basis of observed horizontal jet velocities and assumed temperature-dependent
phytoplankton growth rates, they estimate the distance that a phytoplankton population
in the jet is displaced before doubling in size. Their conclusion is that it is very
improbable that upward velocities associated with ageostrophic motion result in high
local concentrations of phytoplankton in the zone where the upward velocity is
occurring. Due to the time needed for phytoplankton to grow, the intense horizontal
velocities associated with the jet can decouple the sectors where deep nutrient-rich
waters reach the surface from sectors where high values of the recorded concentrations
are observed (Ruiz et al. 2001). Despite its influence during the first survey, the T-S
characteristics and time evolution of water masses during OMEGA-1 dismiss the
advection of coastal upwelling waters as the origin of phytoplankton abundances in the
surveyed area. The increasing salinity with decreasing temperature pattern of the coastal
upwelling does not fit the hydrological characteristics of the biologically richer waters
for the sampled domain. In addition, a lower manifestation of the upwelling situation
was observed during the second and third surveys while the jet was still biologically
rich (Ruiz et al., 2001).

Otherwise, mixing processes at the Strait of Gibraltar (Gómez et al., 2001, 2004) may
act as a fertilizing mechanism favouring the development of phytoplankton biomass
downstream (Echevarría et al., 2002; Macías et al., 2006; Reul et al., 2008; among
others). According to model simulations (García-Lafuente et al., 2013; Macías et al.,
2007b) and in-situ lagrangian measurements (Vélez-Belchí, 2006), the time scales of the
AJ through the Strait and the Alboran Sea would be consistent with the time-lag needed
to observe a biological response to the fertilizing processes in the Western sector of the
Alboran Sea. However, this hypothesis is partially disregarded by other studies which
point to tidally-induced mixing processes in the Strait of Gibraltar (Macías et al., 2006; Ramirez-Romero et al., 2014) and the advection of coastal chlorophyll-rich waters through the Strait (Macías et al., 2007b). The generation of internal waves in the Camarinal Sill causes the suction of coastal waters rich in chlorophyll towards the center of the channel (Garcia Lafuente et al., 2013; Navarro et al., 2011; Vazquez et al., 2009;) and enhances the upwelling of deep nutrient-rich waters in the same region (Echevarría et al., 2002). The coupling of both processes favours the phytoplankton growth during its advection to the Alboran Sea (Bruno et al., 2013) and would support the spread by the AJ as the origin of population cell density observed in mesoscale patches in the NWAF.

4.3.2. The Almeria-Oran Front

An analogous mechanism may explain the peaks of cell concentrations associated with several phytoplankton groups in the northern part of the AOF in OMEGA-2. During the third survey a significant increase of Cyano and especially of Prochlorococcus was detected linked to an intrusion of MSW. Although slight signals of Mediterranean waters were already observed in the preceding survey (i.e. three days before; Allen et al., 2001), MSW flowed firstly westward along the Spanish coast, reaching the AOF region between the second and third survey. Similar peaks of abundance for Prochlorococcus associated with Mediterranean waters have been described by Jacquet et al. (2002) in the Almeria-Oran Front. These authors suggest the injection (or favoured horizontal spreading) of nutrients into the surface layer as the mechanism responsible for the peak. Examining our analyses it seems unlikely that the peak observed in OMEGA-2 was due to in situ growth or to local vertical motion. The growth rates described for those taxa in the AOF suggest less than one division per day (Jacquet et al., 2002). Such rate would be consistent with the observed enhancement of Cyano, from $3 \times 10^4$ to $4 \times 10^4$ cels·mL$^{-1}$, but is too low to explain the more than 10-fold increase in Prochlorococcus abundance between the second and third survey. On the other hand, the MSW intrusion was characterized by very low vertical motions, which would dismiss a local ageostrophic origin. Instead, the correlation between Cyano and Prochlorococcus (see section 3.2.2.) with proper MSW (only detected during the third survey) suggest that other factors were involved. According to Allen et al. (2001), the net south-westward advection of MSW during OMEGA-2 occurred for at least 6 days before the second survey. Considering the growth rates described by Jacquet et al.,
(2002), this time would be enough to obtain the phytoplankton abundances observed during the third sampling. Thus, the lower intensity of the frontal jet (Allen et al., 2001), compared to OMEGA-1 (Vélez-Belchí et al., 2005), and the previous history of the MSW could determine the spatio-temporal coupling to force the biological response observed during the third survey.

4.3.3. The migrated WAG

The biological pattern observed in BIOMEGA was different to that described in the NWAF under stationary conditions. Biological mesoscale patches were concentrated on the western side of the domain, associated with the tongue of old AW (Figs. 6 and 10). This relation is also supported by the strong correlation between the main phytoplankton groups and colder waters (Table 1) corresponding to the old AW tongue (CIESM 2001; Flexas et al., 2006). The differences with respect to OMEGA-1 seem to be a direct consequence of the absence of the AJ-WAG system observed during BIOMEGA. The formation of a new WAG (Fig. 3b) in the westernmost side of the basin during the cruise could have drawn the old AW tongue around the migrated WAG. Previously located further north, this water was advected to the southeast of the gyre following the anticyclonic circulation of the new WAG (Flexas et al., 2006).

Therefore, contrary to the situation observed during OMEGA-1 (see discussion above; Ruiz et al., 2001), the high phytoplankton biomass observed in BIOMEGA could have its origin in the advection of coastal upwelled waters.

4.3.4. Implications of the mesoscale temporal scale

Although space and time are intrinsically linked at any scale (Haury et al., 1978), progress in understanding the biological mesoscale has mostly concentrated on increasing the spatial resolution of the sampling. Conversely, information about the associated temporal variability is very scarce. To our knowledge the study of mesoscale temporal scales in the Alboran Sea is restricted to a few works. The later include the analysis of particle light attenuation, chlorophyll-a and gelbstoff fluorescence, optical plankton size distribution and acoustic measurements taken during the two OMEGA cruises also studied in this paper (Ruiz et al., 2001; Fielding et al., 2001). Later, Jacquet et al. (2002) examined the short-term time variability of picoplankton cellular parameters in the AOF. More recently, Macías et al. (2008) studied the influence of zonal wind forcing and atmospheric pressure on the mesoscale variability of
hydrodynamic and chlorophyll patterns in the NW sector of the Alboran Sea. Our results represent the first description of the short-term variability associated with the mesoscale patchiness of phytoplankton cell populations and functional groupings.

The comparison between fast-repeated surveys during OMEGA-1 and OMEGA-2 cruises reflects sharp changes in the spatial distribution of phytoplankton groups related to rapidly evolving fluctuations of the main hydrographic structures. Short-term changes were not restricted to spatial patterns, but also extended to the abundance of phytoplankton groups. In the NWAF a progressive decrease in maximum concentrations, up to 92% for Cyano, was observed from the first survey to the third one coinciding with an increase of the inflow of AW in the region. These significant changes were directly related to a southward displacement of the jet in OMEGA-1 which characterized the very initial stages of a migration event of the WAG (Vélez-Belchí et al., 2005). It is worth noting that lower fluorescence signals have also been reported in upwellings driven by a southward AJ than under particular wind stress regimes in the northwestern Alboran Sea (Sarhan et al., 2000). During OMEGA-2 phytoplankton groups also showed a temporal evolution that matched the short-term variability of the AOF. Apart from slight variations in the position and the shape of the front (Fig. 5a; Allen et al., 2001) the main change consisted of the intrusion of MSW into the Mediterranean side of the front before the third survey. This MSW tongue was linked to a decrease of eukaryotic taxa and to a significant enrichment of prokaryotic groups (Cyano and Prochlorococcus). Although less intense than for the NWAF, time differences in phytoplankton abundances were also coincident with changes in the magnitude of the geostrophic dynamics through OMEGA-2 surveys.

4.4 Common versus site-specific patterns and processes

Mesoscale frontal structures not only influenced the phytoplankton patchiness (section 4.3) but were also responsible for the differences in abundance observed between cruises, with both chlorophyll and identified groups showing higher concentrations in OMEGA-2 and BIOMEGA than in OMEGA-1. In this section we discuss the biological response, in terms of phytoplankton abundance, to the mesoscale dynamics in the basin.

In the three datasets studied here (OMEGA-1, OMEGA-2, and BIOMEGA) the vertical
velocities showed a mesoscale pattern of alternating sign, but their magnitude was significantly different from case to case: it was more intense in OMEGA-1 than in OMEGA-2, while BIOMEGA showed intermediate values (Fig. 7). Our data show that phytoplankton populations tend to accumulate in areas of low vertical motion (Fig. 11). According to our observations, differences in the magnitude of vertical motions (Fig. 7) play an important role in explaining the diverse biological responses to mesoscale ageostrophic dynamics: the high intensity in the NWAF did not result in a local peak of phytoplankton, while the highest cell concentrations in the AOF were partially related to lower vertical velocities (section 4.3). However, the lack of statistically significant correlations between vertical velocities and biological abundances suggests that other factors are also involved.

Large vertical velocities induced by mesoscale structures are generally associated with large horizontal velocities (Gomis et al., 2001; Tintoré et al., 1991). These energetic horizontal flows could therefore be responsible for the observed spatial decoupling between maximum vertical velocities and the most conspicuous expression of phytoplankton response (i.e., maximum phytoplankton abundance). Such an effect was already pointed out by Ruiz et al. (2001) in the analysis of the origin of chlorophyll concentrations observed during OMEGA-1 (see section 4.3.1) and it may also explain the biological response observed in the phytoplankton group abundances studied here. Our data shows significant negative linear relationships between maximum taxa abundance and maximum geostrophic velocities (Fig. 12; Table 2), indicating a decrease of cell concentrations with increasing flow intensity. Variations in biological abundance coincident with changes in the mean flow have also been described by Echevarría et al. (2002) in the Strait of Gibraltar. These authors justify the lower abundance of phytoplankton in the southern section compared with the northern side with stronger hydrodynamics as a result of lower residence times of the water masses. Phytoplankton would have less time to incorporate nutrients, even in favourable trophic conditions, and hence a weak biological response. However, later studies have described different mechanisms which include differences in the advection of coastal waters between the margins of the Strait (García-Lafuente et al., 2013; Macías et al., 2007b) and the existence of sub-mesoscale structures on the northern section of the channel (Bruno et al., 2013). These features would increase the residence time of water masses, explaining the high levels of chlorophyll on the northern side of the Strait of
4.5 Mesoscale variability at taxon level

Chlorophyll-\(a\) concentration is used extensively in oceanography as a descriptor of phytoplankton biomass (Smayda, 1978). However, the analysis of patchiness using only this descriptor hides significant information regarding phytoplankters heterogeneity, particularly at the mesoscale.

To our knowledge only few efforts have been made to analyse the mesoscale distribution of phytoplankton taxa in the Alboran basin. Prieur et al. (1993) carried out the chromatographic analysis of pigments associated with particular types of phytoplankton (small flagellates or diatoms); Fiala et al. (1994) combined pigment measurements with FC and microscope cell counting; later, Echevarria et al. (2009) also used FC to describe the picoplankton taxa distribution in the NW sector of the Alboran Sea. Their results demonstrate that patchy chlorophyll \(a\) distributions contain yet more spatial (and temporal) structure at the taxa level. This is confirmed by the chlorophyll a distribution described here (section 3) and it is particularly clear for the picoplanktonic populations of Cyano, but also for Ultra (mainly small flagellates) and Crypto (nanoplanktonic flagellates). These groups show clear mesoscale patchiness even in areas where bulk chlorophyll values are low and homogeneous (see Figs. 8-10). This is coherent with observations of the comparatively higher contribution of picoplankton to total chlorophyll concentration under oligotrophic conditions, where very small sized cells are the main component of the phytoplanktonic community (Chisholm, 1992; Rodríguez et al., 1998; Li et al., 2002; among others).

The distribution pattern found by Jacquet et al. (2002) in the AOF is consistent with this idea. Based on the analysis of cell abundance of picophytoplankton, Jacquet et al. (2002) distinguished two major types of systems: mesotrophic conditions dominated by eukaryotes and *Synechococcus*, and oligotrophic areas dominated by *Prochlorococcus* and, to a lower extent, by *Synechococcus*. Cell concentrations in OMEGA-1 (first survey) and OMEGA-2 are consistent with those previously observed in the basin. According to the scheme by Jacquet et al. (2002), abundances in the AOF would correspond to a mesotrophic system dominated by eukaryotes and *Synechococcus*. In Jacquet et al. (2002), as in our study, the highest abundances of *Prochlorococcus* were observed in Mediterranean waters, which they related to poor-nutrient content. Similar
conclusions were obtained by Echevarria et al. (2009), who found lower densities of both picoplankters in the NW region of the Alboran Sea in comparison with the adjacent and more oligotrophic basin of the Gulf of Cadiz.

The cyanobacteria concentrations in OMEGA-1 would match the spring conditions in the north-western Alboran Sea, in agreement with the seasonal characterization of Reul et al. (2005). However, Eupico and Cyano abundances (up to $6 \times 10^4$ and almost $7 \times 10^4$ cels·mL$^{-1}$ respectively) were significantly higher in BIOMEGA. Such values are comparable to those reported under mesotrophic conditions in other regions (Partensky et al., 1996; Zubkov et al., 2000), suggesting a more favourable situation for phytoplankton associated with the transient modes of the Alboran Sea circulation. The agreement of our concentrations with previous studies in the same region covering different times of the year may suggest little variation over a large temporal scale in phytoplankton abundance. According to Jacquet et al. (2002), this is a clear indicator that short-term variability (i.e. days) would dominate over large temporal scales in mesoscale systems.

5. Conclusions

The characterization of the major hydrodynamic features in the Alboran Sea and of the associated biological features shows a strong influence of physical processes on phytoplankton patchiness. The pico-nanoplankton biomass is mainly associated with the frontal structures of the NWAF, the AOF and the WAG. Different factors and the influence of water from surrounding basins seem to explain the origin of the peaks in each region. The patchiness in the NWAF is mainly related to mixing processes in the Strait of Gibraltar and subsequent advection by the AJ into the Western sector of the Alboran Sea. In the eastern limit of the basin the phytoplankton distribution is driven by the interaction between recent AW from the AJ and Mediterranean Surface Waters along the AOF. The physical structures associated with the migration and formation of new WAGs have a strong impact on the patchiness in the westernmost side of the region. The biological impact of mesoscale dynamics extends to the phytoplankton abundances in the Alboran Sea. Our observations indicate that phytoplankton populations tend to accumulate in areas of low vertical motion. The relationship between pico-nanoplankton concentrations and the geostrophic flow associated with the mesoscale dynamics explain the spatial decoupling between the largest vertical
velocities and local peaks of abundance. Areas with strong vertical motion are related to strong geostrophic flow that result in rapid advection and lower residence times driving a weak biological response.

The physical and biological data collected during OMEGA-1, OMEGA-2 and BIOMEGA cruises represent a significant effort towards resolving the physical-biological coupling at the mesoscale in the Alboran Sea. The high-resolution sampling has been crucial to resolve the short-term changes (i.e. days) associated with the mesoscale in the Alboran Sea. Short-term impacts of physical features on phytoplankton were more evident at phytoplankton group level. Our study demonstrates that resolving the mesoscale greatly improves the understanding of biological-physical interactions. However, it also shows that an isolated survey only provides an isolated picture of a highly dynamic phenomenon, and that, as predicted by theory, mesoscale biological patchiness change rapidly within only a few days. Repeated, fast surveys are therefore essential to unravel the relative importance of physical versus biological mechanisms in the understanding of the upper ocean ecosystem.

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Figures.

Figure 1. Areas covered by the OMEGA-1 (O1), OMEGA-2 (O2) and BIOMEGA (BIO) cruises. Positions of the biological sampling stations (dots) and tracks of the continuous surveys (continue lines) are also indicated (OMEGA-1, left panels; OMEGA-2, right panels; BIOMEGA, bottom panel).

Figure 2. Flow cytometry scatter diagrams (FL3 vs. FL2) used to identify the Prochlorococcus populations under common setting conditions (a), and the Pseudonanochloris (FL3) population during OMEGA-2 survey (b). Fluorescence signal at wavelength of 564-606nm (FL2) and >650nm (FL3). (c) Additional size discrimination of studied cell populations (SSC, Side Scatter).

Figure 3. Sampling areas (marked as black boxes) over Sea Surface Temperature (ºC) (NOAA-AVHRR provided by DLR, Germany, in color) and geostrophic currents (AVISO products, black arrows) in the Alboran Sea during (a) OMEGA-1 and OMEGA-2 surveys carried out during almost stationary dynamical conditions (SST images and geostrophic current weekly composite 30/09-6/10/1996). (b) BIOMEGA survey carried out during a WAG migration event (SST images and geostrophic current weekly composite 6-12/10/2003). A new WAG was forming over the western Alboran basin (new WAG).

Figure 4. OMEGA-1 cruise. (a) Potential temperature (ºC), (b) Salinity and (c) Potential density (kg·m⁻³) at a depth of 5 m. (d) Vertical velocity (m·d⁻¹) at the depth of 50 m. Negative/positive signs indicate downward/upward velocities, respectively. Survey1: 1-4/10/1996; Survey2: 6-9/10/1996; Survey3: 9-11/10/1996. The main hydrography structures are indicated: North-Western Upwelling (U), Atlantic Jet (AJ), Western Alboran Gyre (WAG), and Northwestern Alboran Front (NWAF). Note: Vertical velocities correspond to the level at which their magnitude is maximum (i.e., at a depth of 50-m, in OMEGA-1).

Figure 5. OMEGA-2 cruise. (a) Potential temperature (ºC), (b) Salinity and (c) Potential density (kg·m⁻³) at a depth of 5 m. (d) Vertical velocity (m·d⁻¹) at a depth of 77 m. Negative/positive signs indicate downward/upward velocities, respectively. Survey1: 16-20/12/1996; Survey2: 21-24/12/1996; Survey3: 26-28/12/1996. The main hydrography structures are indicated: Eastern Alboran Gyre (EAG), Almeria-Oran Front (AOF), Mediterranean Surface Water intrusion (MSW), and old Atlantic Water eddy-like feature (old AW eddy). Note that the maps at 5-m (a-c) correspond to measurements obtained from the vessel continuous thermosalinograph, since SeaSoar data at 5-m were not available for OMEGA-2. Note: Vertical velocities correspond to the level at which their magnitude is maximum (i.e., at the depth of 77 m, in OMEGA-2).

Figure 6. BIOMEGA cruise. (a) Potential temperature (ºC), (b) Salinity and (c) Potential density (kg·m⁻³) at a depth of 10 m. (d) Vertical velocity (m·d⁻¹) at the depth of 80 m. Negative/positive signs indicate downward/upward velocities, respectively. Note: Vertical velocities correspond to the level at which their magnitude is maximum (i.e., at a depth the 80 m depth, in BIOMEGA). The main hydrography structures are indicated: Western Alboran Gyre (WAG), western tongue of old Atlantic Water (old AW), and old Atlantic Water eddy (old AW eddy).
Figure 7. Relative distribution of vertical velocities from OMEGA-1 (at 50 m depth, grey bars), OMEGA-2 (at 77 m depth, white bars), and BIOMEGA (at 80 m depth, black bars). Gaussians fitted to the distribution of vertical velocities clustered in 10 m·d⁻¹ bins are shown as black lines (OMEGA-1, dashed-dotted line; OMEGA-2, dashed line; OMEGA-1, solid line). The average value of the vertical velocity is virtually zero for all cruises; when averaging absolute values the mean values and standard deviations are 11.04 ± 11.6 m·d⁻¹ for OMEGA-1, 2.18 ± 2.4 m·d⁻¹ for OMEGA-2, and 5.20 ± 4.4 m·d⁻¹ for BIOMEGA.

Figure 8. (a) Chlorophyll (µg·L⁻¹), (b) Nano>10 µm, (c) Ultra, (d) Eupico, (e) Crypto flagellates and (f) Cyanobacteria (cells·mL⁻¹) at 5 m depth during OMEGA-1 surveys.

Figure 9. (a) Chlorophyll (µg·L⁻¹), (b) Nano >10 µm (c) Ultra, (d) Eupico, (e) Crypto flagellates, (f) Cyanobacteria and (g) Prochlorophytes (cells·mL⁻¹) at 5 m depth during OMEGA-2 surveys.

Figure 10. (a) Chlorophyll (µg·L⁻¹), (b) Nano >10 µm, (c) Ultra, (d) Eupico, (e) Crypto flagellates and (f) Cyanobacteria (cells·mL⁻¹) at 10 m depth during BIOMEGA survey.

Figure 11. Relationship between Chlorophyll, Nano>10 µm, Ultra, Eupico, Crypto flagellates, Cyanobacteria, Prochlorophytes and Vertical velocity for OMEGA-1, OMEGA-2 and BIOMEGA cruises. Vertical velocities correspond to the level at which their magnitude is maximum in each cruise (50 m, 77 m and 80 m depth, respectively).

Figure 12. Relationship between maximum abundances (cells·mL⁻¹) of Nano >10 µm, Ultra, Eupico, Crypto flagellates, Cyanobacteria and maximum geostrophic velocity (m·s⁻¹) from OMEGA-1, OMEGA-2 and BIOMEGA. Maximum geostrophic velocity corresponds to the depths of 5 m, 13 m and 10 m, respectively. Considering the wide range of phytoplankton abundances data were log-log transformed to allow a better comparison.
Tables

Table 1
Correlation (Pearson Product Moment) between phytoplankton abundances and water temperature in BIOMEGA. Correlation coefficient (r) and significance of correlation are indicated, P<0.01**, n: number of samples analysed.

<table>
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<th>Phytoplankton Group</th>
<th>n</th>
<th>r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nano&gt;10</td>
<td>77</td>
<td>-0.628</td>
<td>**</td>
</tr>
<tr>
<td>Ultra</td>
<td>77</td>
<td>-0.686</td>
<td>**</td>
</tr>
<tr>
<td>Eupico</td>
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<td>-0.601</td>
<td>**</td>
</tr>
<tr>
<td>Crypto</td>
<td>77</td>
<td>-0.311</td>
<td>**</td>
</tr>
<tr>
<td>Cyano</td>
<td>77</td>
<td>-0.439</td>
<td>**</td>
</tr>
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</table>

Table 2
Results of the regression of Log-transformed maximum phytoplankton concentrations and maximum geostrophic velocities. Coefficient of determination (R^2) and significance of regression model are shown, P<0.001***. n: number of samples analysed.

<table>
<thead>
<tr>
<th>Phytoplankton Group</th>
<th>n</th>
<th>y-intercept</th>
<th>Standard deviation</th>
<th>Slope</th>
<th>Standard deviation</th>
<th>R^2</th>
<th>P</th>
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</thead>
<tbody>
<tr>
<td>Nano&gt;10</td>
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<td>1.849</td>
<td>0.139</td>
<td>-2.615</td>
<td>0.605</td>
<td>0.789</td>
<td>***</td>
</tr>
<tr>
<td>Ultra</td>
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<td>0.287</td>
<td>0.932</td>
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</tr>
<tr>
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<td>0.607</td>
<td>0.329</td>
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<tr>
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<td>0.763</td>
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