

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

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4 P. León<sup>a\*</sup>, J.M. Blanco<sup>a</sup>, M.M. Flexas<sup>b\*\*</sup>, D. Gomis<sup>b</sup>, A. Reul<sup>a</sup>, V. Rodríguez<sup>a</sup>, F.  
5 Jiménez-Gómez<sup>c</sup>, J.T. Allen<sup>d</sup>, and J. Rodríguez<sup>a</sup>.

6  
7 <sup>a</sup> Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga,  
8 29071, Málaga, Spain

9 <sup>b</sup> Institut Mediterrani d'Estudis Avançats, IMEDEA (UIB-CSIC), 07190, Mallorca,  
10 Spain

11 <sup>c</sup> Departamento de Biología Animal, Biología Vegetal y Ecología. Universidad de Jaén,  
12 23071, Jaén, Spain

13 <sup>d</sup> School of Earth & Environmental Sciences, University of Portsmouth, Portsmouth  
14 PO1 3QL, UK

15  
16 \*Corresponding author. Present address: Marine Scotland Science, Marine Laboratory  
17 Aberdeen, PO Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK. Tel.: (+44)  
18 (0)1224 295369; fax: (+44) (0)1224 295511

19 \*\*Now at: Jet Propulsion Laboratory, California Institute of Technology, Pasadena,  
20 CA91001, USA.

21 E-mail addresses: pleon@uma.es (P. León), jmblanco@uma.es (J.M. Blanco),  
22 msbert@jpl.nasa.gov (M.M. Flexas), damia.gomis@uib.cat (D. Gomis),  
23 valeriano@uma.es (V. Rodríguez), areul@uma.es (A. Reul), fgomez@ujaen.es (F.  
24 Jiménez-Gómez), john.allen@port.ac.uk (J.T. Allen), jaime@uma.es (J. Rodríguez)

34 **Abstract**

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

64

65 **Keywords:** Phytoplankton; Mesoscale; Patchiness; Physical-biological coupling;  
66 Alboran Sea.

67 **1. Introduction**

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

77 The mesoscale (10-100 km, days-weeks) is acknowledged as the most energetic scale of  
78 ocean dynamics (Robinson, 1983) and can be described as the “weather” of the ocean.  
79 The role played by this ubiquitous dynamic scale in the generation of spatial  
80 heterogeneity or “patchiness” in phytoplankton distributions is not well known yet  
81 (Martin, 2003). It is at the mesoscale that fronts between water masses become unstable  
82 and strong three-dimensional instabilities are set up. The high spatial and temporal  
83 variability associated with mesoscale dynamics gives rise to areas of convergence and  
84 divergence. Consequently it favours the existence of intense upwelling and  
85 downwelling areas with vertical velocities of the order of several tens of metres per day,  
86 that is, an order of magnitude higher than the largest vertical velocities usually observed  
87 in permanent upwelling areas (Vélez-Belchí and Tintoré, 2001). This is why mesoscale  
88 circulation is of great significance to explain the patchiness of nutrient distributions  
89 (Lévy, 2008; Martin and Richards, 2001; Woodward and Rees, 2001), chlorophyll  
90 (Fielding et al., 2001; Ruiz et al., 2001; Strass, 1992), primary production (Martin et al.,  
91 2002; Strass et al., 2002), phytoplankton size structure (Rodríguez et al., 2001), patterns  
92 of zooplankton distribution (Huntley et al., 1995) and the life histories of key marine  
93 populations (Cowen et al., 2000; Planque, 2005; Werner et al., 1993). At the top end of  
94 the food chain, the response of fish abundance to the environment is also more obvious  
95 at the mesoscale. This is due to the strong influence of eddies and fronts on physical and  
96 biogeochemical properties, and hence on prey distribution (Tew-Kai et al., 2009) and  
97 favourable fish reproductive habitats (“ocean triads”; Agostini and Bakun, 2002).  
98 Consequently, understanding mesoscale features and their variability is crucial in  
99 determining the links between plankton dynamics, primary production, recruitment and

100 transport of juvenile fish and larvae of benthic organisms, and biogeochemical fluxes  
101 that are undetectable at larger scales.

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

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

129 On the other hand, the physical processes involved in the migration of the WAG and the  
130 migration/absence of the EAG, have only been studied in a few papers (Flexas et al.,  
131 2006; Renault et al., 2012; Viúdez et al., 1998; among others). Accordingly, less is  
132 known about the impact that the temporal variability of these larger local dynamics have

133 on the biological communities (Macías et al., 2007a, 2008; Vargas-Yáñez and Sabatés,  
134 2007). In particular, there is no up-to-date work addressing the consequences of the  
135 eastward migration of the WAG on the biology of the region.

136 Because of the need for a high-resolution (both in temporal and spatial terms) sampling  
137 design, our knowledge of mesoscale field plankton ecology is almost exclusively based  
138 on proxy estimates for the total community biomass of phytoplankton and zooplankton  
139 (Martin, 2003). In particular, the mesoscale study of phytoplankton is almost entirely  
140 restricted to variables (like chlorophyll) that can be inferred continuously or  
141 synoptically by means of optical sensors. Mesoscale patterns of some phytoplankton  
142 taxa can however be facilitated through the fast, *in situ* flow-cytometry analysis in the  
143 size range of approximately 1-20  $\mu\text{m}$ , covering picoplankton and nanoplankton  
144 (Rodríguez and Li, 1994; Sieburth, 1979). This size-range is relevant, since small cells  
145 are responsible for a fundamental part of oceanic primary production, particularly in  
146 oligotrophic waters (Chisholm, 1992; Platt and Li, 1986; Rodríguez et al., 1998). In this  
147 framework, the mosaic of hydrodynamic structures of the Alboran Sea, which combines  
148 oligotrophic gyres, upwelling areas and energetic frontal systems with a wide range of  
149 mesoscale vertical velocities, represents a unique natural laboratory to examine the  
150 physical-biological coupling of pico-nanoplankton at the mesoscale (Rodríguez et al.,  
151 2001).

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

159

## 160 **2. Materials and methods**

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

163 *(1) OMEGA-1 field experiment*

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

#### 172 (2) *OMEGA-2 field experiment*

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

#### 181 (3) *BIOMEGA field experiment*

182 Carried out onboard *BIO García del Cid* (9-17 October 2003), this cruise covered a  
183 migrated WAG. At the time of the cruise the WAG was displaced about 100 km  
184 eastwards from its usual location (Fig. 1, bottom panel). The sampling consisted of 16  
185 meridional transects of 9 CTD stations each, with a distance between stations of about  
186 10 km in both longitudinal and latitudinal direction. The physics were analysed in  
187 Flexas et al. (2006).

### 188 **2.1. Hydrographic data**

189 Hydrographic characterization of surface water masses was performed using potential  
190 temperature, salinity and potential density (calculated at each hydrographic station;  
191 Millero et al., 1980) obtained from hydrographic observations detailed above. The  
192 mesoscale dynamics of each area was evaluated by estimating the geostrophic flow and  
193 the vertical velocity field as follows. Hydrographic data were first interpolated onto a  
194 regular grid using an Optimum Interpolation technique (Bretherton et al., 1976).  
195 Dynamic variables (i.e., dynamic height) were computed with respect to an assumed no-

196 motion depth of 300 m. In order to eliminate non-resolved small scale structures,  
197 horizontal fields were spatially smoothed with a cut-off wavelength of 40 km. This cut-  
198 off wavelength corresponds to structures with a radius of about 10-20 km, similar to the  
199 local internal Rossby radius of deformation (of about 10-15 km). Vertical velocities  
200 were calculated using the quasi-geostrophic form of the OMEGA equation (Hoskins et  
201 al., 1978).

## 202 **2.2. Biological sampling and in situ analysis**

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

212 Chlorophyll concentration was measured with a Turner Fluorometer previously  
213 calibrated with pure chlorophyll a, following the method suggested by Yentsch and  
214 Menzel (1963). Additionally, all samples were analyzed on board using a FacScan  
215 (Beckton-Dickinson) flow cytometer. Flow Cytometry (FC) was used to estimate  
216 abundance, size and functional composition of phytoplankton <20  $\mu\text{m}$  (equivalent  
217 spherical diameter, ESD). In this work each sample run for 5 min under mode "high"  
218 ( $60 \pm 5 \mu\text{L}\cdot\text{min}^{-1}$ ) and the following setting conditions: Forward Scatter (FSC)=E00;  
219 Side Scatter (SSC)=271 and the fluorescence signal at wavelengths of 564-606nm  
220 (FL2) and >650nm (FL3) (FL2=450; FL3=300). The FL2 and FL3 signals (ascribed to  
221 phycoerythrine and chlorophyll-a respectively) together with SSC (related to particle  
222 size) were used to identify the following operative groups (Fig. 2a, c): nanoplankton  
223 larger than 10  $\mu\text{m}$  (henceforth "Nano>10"), ultraplankton (henceforth "Ultra"),  
224 equivalent to nanoplankton 2-10  $\mu\text{m}$ , cryptomonad flagellates (henceforth "Crypto"),  
225 eukaryotic picoplankton (henceforth "Eupico"), and prokaryotic *Synechococcus*  
226 cyanobacteria (henceforth "Cyano"). During the OMEGA-2 cruise, an additional  
227 analysis was carried out with the following setting conditions: Frontal Scatter  
228 (FSC)=E00; Side Scatter (SSC)=402 and Fluorescence (FL2=555; FL3=651). This

229 allowed a quantitative analysis of the prokaryotic *Prochlorococcus* population (Fig. 2b).  
230 Such analysis was not available for OMEGA-1 and BIOMEGA.

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

239

### 240 **3. Results**

#### 241 ***3.1 Macroscale and mesoscale dynamics during the cruises***

##### 242 *3.1.1. Quasi-stationary conditions*

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

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

257 The vertical velocity is mainly related to the edges of the WAG and evolves in time  
258 from the first to the third survey (Fig. 4d) according to changes of the front and WAG  
259 position. Maximum vertical velocities, of  $\pm 45 \text{ m} \cdot \text{d}^{-1}$  at a depth of 50 m, are located in



260 the eastern and western boundaries of the domain (about 36°N) in surveys 1 and 2,  
261 while up to  $-40 \text{ m}\cdot\text{d}^{-1}$  are observed within the AJ (about 36.25°N) in survey 3. They are  
262 located in areas where curvature and advection reach their maximum. The core of the  
263 WAG is characterized by less intense vertical dynamics, in coherence with the low-  
264 energy character typical of a large anticyclonic eddy such as the WAG (Vélez-Belchí  
265 and Tintoré, 2001; Vélez-Belchí et al., 2005). Geostrophic velocities near the surface (at  
266 5 m depth) were up to  $1 \text{ m}\cdot\text{s}^{-1}$  (Vélez-Belchí et al., 2005).

267 The OMEGA-2 survey captured the Almeria-Oran front as a sharp transition defined by  
268 the 17.0-15.5°C isotherms and the 36.7-37.0 isohalines (Figs. 5a,b). During the first two  
269 surveys, the AOF separated warmer and fresher AW of the EAG, to the south-west,  
270 from Mediterranean waters with temperature  $<15.5 \text{ }^\circ\text{C}$  and salinity 36.7-37.5 to the  
271 north-east. In the third survey, a tongue of MSW (potential temperature  $> 15.5 \text{ }^\circ\text{C}$ ,  
272 salinity  $> 37.5$ ; Arnone et al., 1990) intruded in the northern area (MSW, Fig. 4b) of the  
273 sampling domain. Published hydrographic analysis showed that during surveys 2 and 3  
274 the tongue of MSW had been subducted and transported across the front (along the 27.9  
275  $\sigma_0$  density isosurface; Allen et al., 2001; Fielding et al., 2001). Another noticeable  
276 change between surveys was the formation of a surface eddy-like feature of lighter old  
277 AW and its intrusion into the Mediterranean side of the AOF (old AW eddy; Figs. 5a,b,  
278 c, central and right panels).

279 The vertical motion within the AOF was of the order of  $14 \text{ m}\cdot\text{d}^{-1}$  (Fig. 5d), with  
280 maximum values at a depth of 77 m. The horizontal distribution of vertical velocity  
281 shows the mesoscale patches of upward and downward velocity by the frontal current  
282 (Allen et al., 2001; Fielding et al., 2001). Geostrophic velocities near the surface (at 13  
283 m depth) were up to  $50 \text{ cm}\cdot\text{s}^{-1}$  (Allen et al., 2001).

### 284 *3.1.2. Migrating WAG conditions*

285 The BIOMEGA cruise sampled a migrated WAG, centred at about 3°W (Fig. 6). The  
286 region was characterized by: (i) a smaller WAG (of about 80 km in diameter), with  
287 salinity significantly lower than published data and the lowest values recorded in  
288 OMEGA-1; (ii) a cold cyclonic structure to the south-east of the WAG (old AW eddy;  
289 Fig. 6a); and (iii) a tongue of old AW to the west (Fig. 6a), that was fresher than the  
290 WAG at the surface but more saline than the WAG below the 40 m depth (Flexas et al.,  
291 2006). Mesoscale vertical velocities (Fig. 6d) showed maximum values of the order of

292  $\pm 18 \text{ m}\cdot\text{day}^{-1}$  at a depth of 80 m. These velocities are significantly lower than the values  
293 observed during OMEGA-1 (Fig. 7) and others reported previously for the WAG. In  
294 contrast, those values were significantly higher than in OMEGA-2 (Fig. 7). Geostrophic  
295 velocities near the surface (at 10-m depth) reached a maximum of  $70 \text{ cm}\cdot\text{s}^{-1}$  (Flexas et  
296 al., 2006).

297

## 298 **3.2. Macroscale and mesoscale biological patchiness**

### 299 *3.2.1. OMEGA-1: The Northwestern Alboran Front*

300 At gyre-scale, there was a clear coherence between total chlorophyll concentration (as  
301 an indicator of total phytoplankton abundance) and the hydrological characteristics of  
302 the surveyed area as described by temperature and salinity surface distributions (Figs. 4  
303 and 8, panel a). Particularly during the first survey, the chlorophyll surface pattern  
304 shows the expected gradient from the oligotrophic waters of the WAG ( $< 0.2 \mu\text{g}\cdot\text{L}^{-1}$ ) to  
305 the more productive north-western waters under the influence of the coastal upwelling  
306 ( $> 2 \mu\text{g}\cdot\text{L}^{-1}$ ). Intermediate concentrations were found at the NWAFF ( $\sim 1\text{-}2 \mu\text{g}\cdot\text{L}^{-1}$ ). At  
307 gyre-scale, the chlorophyll pattern also follows the southward displacement of the AJ  
308 and the start of the WAG migration observed during the second and third survey, a  
309 process that translates in a clear decrease of surface concentration values. At the  
310 mesoscale, phytoplankton biomass takes the form of patches linked to the AJ and  
311 NWAFF. This pattern was particularly clear during the first survey, when chlorophyll  
312 concentration values were the highest. From the first to the third survey phytoplankton  
313 biomass decreased, and were accompanied by a lower manifestation of mesoscale  
314 structures in the chlorophyll signature.

315 The features observed for the chlorophyll pattern can be extended to those of the  
316 quantified phytoplankton populations (Fig. 8, panels b-f). Nano $>10 \mu\text{m}$  showed  
317 maximum cell density (around  $10^3 \text{ cells}\cdot\text{mL}^{-1}$ ) at the upwelling influenced zone (U, Fig.  
318 4a) where chlorophyll showed maximum concentration; elsewhere the cell density was  
319 at least two orders of magnitude lower, even in the mesoscale eddies along the NWAFF  
320 (Fig. 8, panel b). Ultra (cells  $2\text{-}10 \mu\text{m}$ ) patches linked to mesoscale eddies were more  
321 conspicuous than those of large nanoplankton, reaching  $4\times 10^3 \text{ cells}\cdot\text{mL}^{-1}$  at different  
322 locations and more than  $5\times 10^3 \text{ cells}\cdot\text{mL}^{-1}$  in the region under upwelling influence.  
323 Densities higher than  $2\times 10^3 \text{ cells}\cdot\text{mL}^{-1}$  were also observed in the core of the

324 oligotrophic WAG during the first survey. Eupico mesoscale patterns were very similar  
325 to those previously described, reaching densities higher than  $20 \times 10^3$  cells·mL<sup>-1</sup> in the  
326 upwelling influenced region and slightly lower densities in mesoscale eddies along the  
327 front. Crypto abundance values during the first survey ranged between  $1 \times 10^2$  and  $5 \times 10^2$   
328 cells·mL<sup>-1</sup> with a maximum  $> 1 \times 10^3$  cells·mL<sup>-1</sup> at the core of the oligotrophic WAG.  
329 Cyan also showed a clear mesoscale pattern during the first survey, with a main patch of  
330 density values  $> 2.5 \times 10^4$  cells·mL<sup>-1</sup> in the northwestern sector of the sampling area (U,  
331 Fig. 4a). Short-term variability was particularly evident: Cyano abundance decreased  
332 one order of magnitude from the first to the second survey and another half between the  
333 second and the third one. In survey 3 abundances were very low (of about  $10^2$  cells·mL<sup>-1</sup>  
334 <sup>1</sup>) at the NWAF and undetectable at the core of the WAG.

### 335 3.2.2. OMEGA-2: The Almeria-Oran Front

336 Total chlorophyll concentration showed patches of high and low concentration along the  
337 AOF boundary (Fig. 9, panel a). Concentrations were highest (around  $2.5 \mu\text{g}\cdot\text{L}^{-1}$ ) at the  
338 northeast of the sampling domain (Fig. 9a;  $36.5^\circ\text{N}$ ,  $1^\circ\text{W}$ ). The three fast surveys were  
339 characterised by the presence of mesoscale structures, but with a clear decrease of  
340 concentration values among surveys. Chlorophyll concentration in the intruding MSW  
341 was much reduced ( $< 0.4 \mu\text{g}\cdot\text{L}^{-1}$ ) during the third survey (Figs. 5 and 9, panel a).

342 Nano $>10 \mu\text{m}$  and Ultra showed similar mesoscale patchiness to that of total chlorophyll  
343 (Fig. 9, panels b and c), with maximum population density values of  $4 \times 10^2$  cells·mL<sup>-1</sup>  
344 and  $2.5 \times 10^4$  cells·mL<sup>-1</sup>, respectively. These two groups exhibited a different temporal  
345 evolution: as total chlorophyll, cell density of nanoplanktonic large cells decreased  
346 within successive surveys; ultraplanktonic populations showed a marked increase in the  
347 second survey (up to 1.8-fold), apparently linked to the first signals of MSW. However,  
348 by the time MSW had intruded throughout the survey domain (i.e. during the third  
349 survey), the density values of Ultra linked to the MSW intrusion decreased down to  $<$   
350  $6 \times 10^3$  cells·mL<sup>-1</sup>, while its maximum abundance at that time were coincident with the  
351 patch of maximum chlorophyll concentration. Eupico showed a similar pattern of  
352 change to Ultra (Fig. 9, panel d): maximum abundances were located to the north of the  
353 domain during the second survey and decreased significantly in the MSW during the  
354 third survey.

355 Crypto flagellate patchiness became sharper and denser during successive surveys (Fig.  
356 9, panel e). While the first survey shows poorly defined patches with density values  
357 around  $10^2$  cells·mL<sup>-1</sup>, the third survey shows two well-defined mesoscale patches with  
358 abundances  $> 1.5 \times 10^4$  cells·mL<sup>-1</sup> coincident with chlorophyll patches.

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

### 366 3.2.3. BIOMEGA: *The migrated WAG*

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

372 Nano  $>10 \mu\text{m}$ , Ultra and Eupico had gyre-scale and mesoscale distributions similar to  
373 that of chlorophyll, with mesoscale patches containing maximum cell densities of  $\sim$   
374  $2 \times 10^2$ ,  $10^4$  and  $6 \times 10^4$  cells·mL<sup>-1</sup>, respectively (Fig. 10, panels b, c and d). Crypto and  
375 Cyano showed a more heterogeneous distribution with mesoscale patches distributed  
376 over the entire domain. Maximum cell density values ( $4 \times 10^3$  and  $7 \times 10^4$  cells·mL<sup>-1</sup>) were  
377 found in the tongue of cold surface water located to the west of the WAG (old AW in  
378 Fig. 6a; Fig. 10, panels e and f). All the studied groups showed a significant negative  
379 correlation with temperature ( $P<0.01$ ; Table 1).

380

### 381 3.3. Physical-biological coupling

382 The comparison of vertical velocities with the biological variables from each survey  
383 (Fig. 11) shows the association of maximum concentrations of phytoplankton within a  
384 narrow range of vertical velocities (approx. within  $[-15,+15] \text{ m}\cdot\text{d}^{-1}$ ). However, a  
385 correlation test did not show statistically significant relations between vertical velocities  
386 and biological abundances. In contrast, a significant negative linear relationship was

387 observed between maximum taxa abundance and maximum geostrophic velocities (Fig.  
388 12; Table 2).

389

## 390 **4. Discussion**

### 391 *4.1. Methodological considerations on the computation of vertical velocities*

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

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

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

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

416

### 417 *4.2. Physical framework*

418 OMEGA-1 and OMEGA-2 were carried out under the quasi-persistent physical regimes  
419 characterizing the Alboran Sea circulation in the summer-autumn period (Renault et al.,  
420 2012) (Fig. 3a and 4): wherein Atlantic water flows jet-like into the Alboran Sea  
421 through the upper layer and forms the WAG and EAG. Two main frontal systems are  
422 linked to these structures. To the northwest, the NWAFF is found at the northern  
423 boundary of the WAG. The NWAFF separates the fresher waters of recent Atlantic origin  
424 (AW) of the WAG from the almost permanent upwelling region filled with upwelled  
425 Mediterranean waters observed along the Spanish coast (Figs. 3a and 4). The AOF is  
426 observed on the eastern side of the EAG, separating the AW of the EAG from MSW  
427 (Fig. 3a, 4).

428 The quasi-steady state of the Alboran Sea circulation described above is subjected to  
429 changes. One of the most interesting is the eastward migration of the WAG (Vargas-  
430 Yáñez et al., 2002; Vélez-Belchí et al., 2005). This was the case studied during the  
431 BIOMEGA cruise (Figs. 3b and 6; Flexas et al., 2006). Situations like WAG  
432 displacements are now considered as transient modes in contrast to annually stable  
433 surface circulation regimes of the Alboran Sea (Peliz et al., 2013; Renault et al., 2012;  
434 Sánchez-Garrido et al., 2013). The migration of the WAG is triggered by changes in the  
435 intensity and direction of the inflow of AW, which would determine the decoupling of  
436 the AJ-WAG system or making the AJ impact directly onto the WAG (Vélez-Belchí et  
437 al., 2005; Viúdez et al., 1998). In this situation the gyre would then migrate eastwards.  
438 The AJ would deflect south (through the implication of the Coriolis force) and start the  
439 formation of a new anticyclonic gyre (a new WAG). However, the factors involved in  
440 this complex migratory process are not totally understood. Studies point to several  
441 sources of variability, including differences in atmospheric pressure over the  
442 Mediterranean (Macias et al., 2008; Ramirez-Romero et al., 2012; Vargas-Yáñez et al.,  
443 2002), blocking of the AJ (Viúdez et al., 1998; Flexas et al., 2006), seasonal variability  
444 (Renault et al., 2012; Ruiz et al., 2013), wind forcing (Peliz et al., 2013) and tides  
445 (Sanchez-Garrido et al., 2013).

446

#### 447 **4.3. Physical versus biological forcing**

448 The phytoplankton distribution patterns clearly reflect an association of abundance with  
449 the main physical features characterizing each cruise: namely, the NWAFF and the  
450 upwelling area in OMEGA-1; the Mediterranean side of the AOF in OMEGA-2; and the

451 western tongue of AW in BIOMEGA cruise. However, differences in hydrology and  
452 time evolution of water masses found among surveys indicate that phytoplankton  
453 abundance owes itself to different factors. In this section we discuss the mechanisms  
454 responsible for the phytoplankton patches in each case study

#### 455 *4.3.1. The Northwestern Alboran Front*

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

476 Otherwise, mixing processes at the Strait of Gibraltar (Gómez et al., 2001, 2004) may  
477 act as a fertilizing mechanism favouring the development of phytoplankton biomass  
478 downstream (Echevarría et al., 2002; Macías et al., 2006; Reul et al., 2008; among  
479 others). According to model simulations (García-Lafuente et al., 2013; Macías et al.,  
480 2007b) and in-situ lagrangian measurements (Vélez-Belchí, 2006), the time scales of the  
481 AJ through the Strait and the Alboran Sea would be consistent with the time-lag needed  
482 to observe a biological response to the fertilizing processes in the Western sector of the  
483 Alboran Sea. However, this hypothesis is partially disregarded by other studies which

484 point to tidally-induced mixing processes in the Strait of Gibraltar (Macías et al., 2006;  
485 Ramirez-Romero et al., 2014) and the advection of coastal chlorophyll-rich waters  
486 through the Strait (Macias et al., 2007b). The generation of internal waves in the  
487 Camarinal Sill causes the suction of coastal waters rich in chlorophyll towards the  
488 center of the channel (Garcia Lafuente et al., 2013; Navarro et al., 2011; Vazquez et al.,  
489 2009;) and enhances the upwelling of deep nutrient-rich waters in the same region  
490 (Echevarria et al., 2002). The coupling of both processes favours the phytoplankton  
491 growth during its advection to the Alboran Sea (Bruno et al., 2013) and would support  
492 the spread by the AJ as the origin of population cell density observed in mesoscale  
493 patches in the NAAF.

#### 494 4.3.2. The Almeria-Oran Front

495 An analogous mechanism may explain the peaks of cell concentrations associated with  
496 several phytoplankton groups in the northern part of the AOF in OMEGA-2. During the  
497 third survey a significant increase of Cyano and especially of *Prochlorococcus* was  
498 detected linked to an intrusion of MSW. Although slight signals of Mediterranean  
499 waters were already observed in the preceding survey (i.e. three days before; Allen et  
500 al., 2001), MSW flowed firstly westward along the Spanish coast, reaching the AOF  
501 region between the second and third survey. Similar peaks of abundance for  
502 *Prochlorococcus* associated with Mediterranean waters have been described by Jacquet  
503 et al. (2002) in the Almeria-Oran Front. These authors suggest the injection (or favoured  
504 horizontal spreading) of nutrients into the surface layer as the mechanism responsible  
505 for the peak. Examining our analyses it seems unlikely that the peak observed in  
506 OMEGA-2 was due to *in situ* growth or to local vertical motion. The growth rates  
507 described for those taxa in the AOF suggest less than one division per day (Jacquet et  
508 al., 2002). Such rate would be consistent with the observed enhancement of Cyano,  
509 from  $\sim 3 \times 10^4$  to  $4 \times 10^4$  cels·mL<sup>-1</sup>, but is too low to explain the more than 10-fold increase  
510 in *Prochlorococcus* abundance between the second and third survey. On the other hand,  
511 the MSW intrusion was characterized by very low vertical motions, which would  
512 dismiss a local ageostrophic origin. Instead, the correlation between Cyano and  
513 *Prochlorococcus* (see section 3.2.2.) with proper MSW (only detected during the third  
514 survey) suggest that other factors were involved. According to Allen et al. (2001), the  
515 net south-westward advection of MSW during OMEGA-2 occurred for at least 6 days  
516 before the second survey. Considering the growth rates described by Jacquet et al.,



517 (2002), this time would be enough to obtain the phytoplankton abundances observed  
518 during the third sampling. Thus, the lower intensity of the frontal jet (Allen et al., 2001),  
519 compared to OMEGA-1 (Vélez-Belchí et al., 2005), and the previous history of the  
520 MSW could determine the spatio-temporal coupling to force the biological response  
521 observed during the third survey.

#### 522 *4.3.3. The migrated WAG*

523 The biological pattern observed in BIOMEGA was different to that described in the  
524 NWAFF under stationary conditions. Biological mesoscale patches were concentrated on  
525 the western side of the domain, associated with the tongue of old AW (Figs. 6 and 10).  
526 This relation is also supported by the strong correlation between the main  
527 phytoplankton groups and colder waters (Table 1) corresponding to the old AW tongue  
528 (CIESM 2001; Flexas et al., 2006). The differences with respect to OMEGA-1 seem to  
529 be a direct consequence of the absence of the AJ-WAG system observed during  
530 BIOMEGA. The formation of a new WAG (Fig. 3b) in the westernmost side of the  
531 basin during the cruise could have drawn the old AW tongue around the migrated  
532 WAG. Previously located further north, this water was advected to the southeast of the  
533 gyre following the anticyclonic circulation of the new WAG (Flexas et al., 2006).  
534 Therefore, contrary to the situation observed during OMEGA-1 (see discussion above;  
535 Ruiz et al., 2001), the high phytoplankton biomass observed in BIOMEGA could have  
536 its origin in the advection of coastal upwelled waters.

#### 537 *4.3.4. Implications of the mesoscale temporal scale*

538 Although space and time are intrinsically linked at any scale (Haury et al., 1978),  
539 progress in understanding the biological mesoscale has mostly concentrated on  
540 increasing the spatial resolution of the sampling. Conversely, information about the  
541 associated temporal variability is very scarce. To our knowledge the study of mesoscale  
542 temporal scales in the Alboran Sea is restricted to a few works. The later include the  
543 analysis of particle light attenuation, chlorophyll-a and gelbstoff fluorescence, optical  
544 plankton size distribution and acoustic measurements taken during the two OMEGA  
545 cruises also studied in this paper (Ruiz et al., 2001; Fielding et al., 2001). Later, Jacquet  
546 et al. (2002) examined the short-term time variability of picoplankton cellular  
547 parameters in the AOF. More recently, Macías et al. (2008) studied the influence of  
548 zonal wind forcing and atmospheric pressure on the mesoscale variability of

549 hydrodynamic and chlorophyll patterns in the NW sector of the Alboran Sea. Our  
550 results represent the first description of the short-term variability associated with the  
551 mesoscale patchiness of phytoplankton cell populations and functional groupings.

552

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

573

#### 574 ***4.4 Common versus site-specific patterns and processes***

575 Mesoscale frontal structures not only influenced the phytoplankton patchiness (section  
576 4.3) but were also responsible for the differences in abundance observed between  
577 cruises, with both chlorophyll and identified groups showing higher concentrations in  
578 OMEGA-2 and BIOMEGA than in OMEGA-1. In this section we discuss the biological  
579 response, in terms of phytoplankton abundance, to the mesoscale dynamics in the basin.

580 In the three datasets studied here (OMEGA-1, OMEGA-2, and BIOMEGA) the vertical

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

592 Large vertical velocities induced by mesoscale structures are generally associated with  
593 large horizontal velocities (Gomis et al., 2001; Tintoré et al., 1991). These energetic  
594 horizontal flows could therefore be responsible for the observed spatial decoupling  
595 between maximum vertical velocities and the most conspicuous expression of  
596 phytoplankton response (i.e., maximum phytoplankton abundance). Such an effect was  
597 already pointed out by Ruiz et al. (2001) in the analysis of the origin of chlorophyll  
598 concentrations observed during OMEGA-1 (see section 4.3.1) and it may also explain  
599 the biological response observed in the phytoplankton group abundances studied here.  
600 Our data shows significant negative linear relationships between maximum taxa  
601 abundance and maximum geostrophic velocities (Fig. 12; Table 2), indicating a  
602 decrease of cell concentrations with increasing flow intensity. Variations in biological  
603 abundance coincident with changes in the mean flow have also been described by  
604 Echevarría et al. (2002) in the Strait of Gibraltar. These authors justify the lower  
605 abundance of phytoplankton in the southern section compared with the northern side  
606 with stronger hydrodynamics as a result of lower residence times of the water masses.  
607 Phytoplankton would have less time to incorporate nutrients, even in favourable trophic  
608 conditions, and hence a weak biological response. However, later studies have  
609 described different mechanisms which include differences in the advection of coastal  
610 waters between the margins of the Strait (García-Lafuente et al., 2013; Macías et al.,  
611 2007b) and the existence of sub-mesoscale structures on the northern section of the  
612 channel (Bruno et al., 2013). These features would increase the residence time of water  
613 masses, explaining the high levels of chlorophyll on the northern side of the Strait of

614 Gibraltar.

#### 615 ***4.5 Mesoscale variability at taxon level***

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

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

636 The distribution pattern found by Jacquet et al. (2002) in the AOF is consistent with this  
637 idea. Based on the analysis of cell abundance of picophytoplankton, Jacquet et al.  
638 (2002) distinguished two major types of systems: mesotrophic conditions dominated by  
639 eukaryotes and *Synechococcus*, and oligotrophic areas dominated by *Prochlorococcus*  
640 and, to a lower extent, by *Synechococcus*. Cell concentrations in OMEGA-1 (first  
641 survey) and OMEGA-2 are consistent with those previously observed in the basin.  
642 According to the scheme by Jacquet et al. (2002), abundances in the AOF would  
643 correspond to a mesotrophic system dominated by eukaryotes and *Synechococcus*. In  
644 Jacquet et al. (2002), as in our study, the highest abundances of *Prochlorococcus* were  
645 observed in Mediterranean waters, which they related to poor-nutrient content. Similar

646 conclusions were obtained by Echevarria et al. (2009), who found lower densities of  
647 both picoplankters in the NW region of the Alboran Sea in comparison with the  
648 adjacent and more oligotrophic basin of the Gulf of Cadiz.

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

661

## 662 **5. Conclusions**

663 The characterization of the major hydrodynamic features in the Alboran Sea and of the  
664 associated biological features shows a strong influence of physical processes on  
665 phytoplankton patchiness. The pico-nanoplankton biomass is mainly associated with the  
666 frontal structures of the NWAF, the AOF and the WAG. Different factors and the  
667 influence of water from surrounding basins seem to explain the origin of the peaks in  
668 each region. The patchiness in the NWAF is mainly related to mixing processes in the  
669 Strait of Gibraltar and subsequent advection by the AJ into the Western sector of the  
670 Alboran Sea. In the eastern limit of the basin the phytoplankton distribution is driven by  
671 the interaction between recent AW from the AJ and Mediterranean Surface Waters  
672 along the AOF. The physical structures associated with the migration and formation of  
673 new WAGs have a strong impact on the patchiness in the westernmost side of the  
674 region. The biological impact of mesoscale dynamics extends to the phytoplankton  
675 abundances in the Alboran Sea. Our observations indicate that phytoplankton  
676 populations tend to accumulate in areas of low vertical motion. The relationship  
677 between pico-nanoplankton concentrations and the geostrophic flow associated with the  
678 mesoscale dynamics explain the spatial decoupling between the largest vertical

679 velocities and local peaks of abundance. Areas with strong vertical motion are related to  
680 strong geostrophic flow that result in rapid advection and lower residence times driving  
681 a weak biological response.

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

694

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934 **Figures.**

935

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

940

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

946

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

955

956 Figure 4. OMEGA-1 cruise. (a) Potential temperature (°C), (b) Salinity and (c) Potential  
957 density ( $\text{kg}\cdot\text{m}^{-3}$ ) at a depth of 5 m. (d) Vertical velocity ( $\text{m}\cdot\text{d}^{-1}$ ) at the depth of 50 m.  
958 Negative/positive signs indicate downward/upward velocities, respectively. Survey1: 1-  
959 4/10/1996; Survey2: 6-9/10/1996; Survey3: 9-11/10/1996. The main hydrography  
960 structures are indicated: North-Western Upwelling (U), Atlantic Jet (AJ), Western  
961 Alboran Gyre (WAG), and Northwestern Alboran Front (NAAF). Note: Vertical  
962 velocities correspond to the level at which their magnitude is maximum (i.e., at a depth  
963 of 50-m, in OMEGA-1).

964

965 Figure 5. OMEGA-2 cruise. (a) Potential temperature (°C), (b) Salinity and (c) Potential  
966 density ( $\text{kg}\cdot\text{m}^{-3}$ ) at a depth of 5 m. (d) Vertical velocity ( $\text{m}\cdot\text{d}^{-1}$ ) at a depth of 77 m.  
967 Negative/positive signs indicate downward/upward velocities, respectively. Survey1:  
968 16-20/12/1996; Survey2: 21-24/12/1996; Survey3: 26-28/12/1996. The main  
969 hydrography structures are indicated: Eastern Alboran Gyre (EAG), Almeria-Oran  
970 Front (AOF), Mediterranean Surface Water intrusion (MSW), and old Atlantic Water  
971 eddy-like feature (old AW eddy). Note that the maps at 5-m (a-c) correspond to  
972 measurements obtained from the vessel continuous thermosalinograph, since SeaSoar  
973 data at 5-m were not available for OMEGA-2. Note: Vertical velocities correspond to  
974 the level at which their magnitude is maximum (i.e., at the depth of 77 m, in OMEGA-  
975 2).

976

977 Figure 6. BIOMEGA cruise. (a) Potential temperature (°C), (b) Salinity and (c) Potential  
978 density ( $\text{kg}\cdot\text{m}^{-3}$ ) at a depth of 10 m. (d) Vertical velocity ( $\text{m}\cdot\text{d}^{-1}$ ) at the depth of 80 m.  
979 Negative/positive signs indicate downward/upward velocities, respectively. Note:  
980 Vertical velocities correspond to the level at which their magnitude is maximum (i.e., at  
981 a depth the 80 m depth, in BIOMEGA). The main hydrography structures are indicated:  
982 Western Alboran Gyre (WAG), western tongue of old Atlantic Water (old AW), and old  
983 Atlantic Water eddy (old AW eddy).

984 Figure 7. Relative distribution of vertical velocities from OMEGA-1 (at 50 m depth,  
985 grey bars), OMEGA-2 (at 77 m depth, white bars), and BIOMEGA (at 80 m depth,  
986 black bars). Gaussians fitted to the distribution of vertical velocities clustered in 10 m·d<sup>-1</sup>  
987 bins are shown as black lines (OMEGA-1, dashed-dotted line; OMEGA-2, dashed  
988 line; OMEGA-1, solid line). The average value of the vertical velocity is virtually zero  
989 for all cruises; when averaging absolute values the mean values and standard deviations  
990 are  $11.04 \pm 11.6 \text{ m}\cdot\text{d}^{-1}$  for OMEGA-1,  $2.18 \pm 2.4 \text{ m}\cdot\text{d}^{-1}$  for OMEGA-2, and  $5.20 \pm 4.4$   
991  $\text{m}\cdot\text{d}^{-1}$  for BIOMEGA.

992

993 Figure 8. (a) Chlorophyll ( $\mu\text{g}\cdot\text{L}^{-1}$ ), (b) Nano >10  $\mu\text{m}$ , (c) Ultra, (d) Eupico, (e) Crypto  
994 flagellates and (f) Cyanobacteria ( $\text{cells}\cdot\text{mL}^{-1}$ ) at 5 m depth during OMEGA-1 surveys.

995

996 Figure 9. (a) Chlorophyll ( $\mu\text{g}\cdot\text{L}^{-1}$ ), (b) Nano >10  $\mu\text{m}$  (c) Ultra, (d) Eupico, (e) Crypto  
997 flagellates, (f) Cyanobacteria and (g) Prochlorophytes ( $\text{cells}\cdot\text{mL}^{-1}$ ) at 5 m depth during  
998 OMEGA-2 surveys.

999

1000 Figure 10. (a) Chlorophyll ( $\mu\text{g}\cdot\text{L}^{-1}$ ), (b) Nano >10  $\mu\text{m}$ , (c) Ultra, (d) Eupico, (e) Crypto  
1001 flagellates and (f) Cyanobacteria ( $\text{cells}\cdot\text{mL}^{-1}$ ) at 10 m depth during BIOMEGA survey.

1002

1003 Figure 11. Relationship between Chlorophyll, Nano >10  $\mu\text{m}$ , Ultra, Eupico, Crypto  
1004 flagellates, Cyanobacteria, Prochlorophytes and Vertical velocity for OMEGA-1,  
1005 OMEGA-2 and BIOMEGA cruises. Vertical velocities correspond to the level at which  
1006 their magnitude is maximum in each cruise (50 m, 77 m and 80 m depth, respectively).

1007

1008 Figure 12. Relationship between maximum abundances ( $\text{cells}\cdot\text{mL}^{-1}$ ) of Nano >10  $\mu\text{m}$ ,  
1009 Ultra, Eupico, Crypto flagellates, Cyanobacteria and maximum geostrophic velocity  
1010 ( $\text{m}\cdot\text{s}^{-1}$ ) from OMEGA-1, OMEGA-2 and BIOMEGA. Maximum geostrophic velocity  
1011 corresponds to the depths of 5 m, 13 m and 10 m, respectively. Considering the wide  
1012 range of phytoplankton abundances data were log-log transformed to allow a better  
1013 comparison.

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## 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.

<b>Phytoplankton Group</b>	<b>n</b>	<b>r</b>	<b>P</b>
Nano>10	77	-0.628	**
Ultra	77	-0.686	**
Eupico	77	-0.601	**
Crypto	77	-0.311	**
Cyano	77	-0.439	**

**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.

<b>Phytoplankton Group</b>	<b>n</b>	<b>y-intercept</b>	<b>Standard deviation</b>	<b>Slope</b>	<b>Standard deviation</b>	<b>R<sup>2</sup></b>	<b>P</b>
Nano>10	7	1.849	0.139	-2.615	0.605	0.789	***
Ultra	7	3.624	0.066	-2.370	0.287	0.932	***
Eupico	7	4.193	0.139	-0.950	0.607	0.329	***
Crypto	7	2.752	0.129	-1.827	0.560	0.648	***
Cyano	7	3.991	0.141	-2.467	0.614	0.763	***