1 # Surface mesoscale pico-nanoplankton patterns at the main Fronts

2 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

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 (NWAF). 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 μm, 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 NWAF, 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 (NWAF). 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 µm (equivalent
217   spherical diameter, ESD). In this work each sample run for 5 min under mode "high"
218   ($60 \pm 5$ µL·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 µm (henceforth "Nano>10"), ultraplankton (henceforth "Ultra"),
224   equivalent to nanoplankton 2-10 µm, 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 4ºW), 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 NWAF 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 NWAF and the AJ. The latter appears as a
251 surface band bounded by the 18-19.5ºC 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 NWAF 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 m·d$^{-1}$ at a depth of 50 m, are located in

260    the eastern and western boundaries of the domain (about 36ºN) in surveys 1 and 2,

261    while up to - 40 m·d$^{-1}$ are observed within the AJ (about 36.25ºN) 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 m·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 17.0-15.5ºC 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 ºC and salinity 36.7-37.5 to the

271    north-east. In the third survey, a tongue of MSW (potential temperature > 15.5 ºC,

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 m·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 cm·s$^{-1}$ (Allen et al., 2001).

284    *3.1.2. Migrating WAG conditions*

285    The BIOMEGA cruise sampled a migrated WAG, centred at about 3ºW (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    ±18 m·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 cm·s$^{-1}$ (Flexas et

296    al., 2006).

297

**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 µg·L$^{-1}$) to

305    the more productive north-western waters under the influence of the coastal upwelling

306    (> 2 µg·L$^{-1}$). Intermediate concentrations were found at the NWAF (~ 1-2 µg·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    NWAF. 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 µm showed

317    maximum cell density (around 10$^3$ cells·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 NWAF

320    (Fig. 8, panel b). Ultra (cells 2-10 µm) patches linked to mesoscale eddies were more

321    conspicuous than those of large nanoplankton, reaching 4x10$^3$ cells·mL$^{-1}$ at different

322    locations and more than 5x10$^3$ cells·mL$^{-1}$ in the region under upwelling influence.

323    Densities higher than 2x10$^3$ cells·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$^{-1}$ 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$^{-1}$ with a maximum $> 1 \times 10^3$ cells·mL$^{-1}$ 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$^{-1}$ 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$^{-}$

334 $^{1}$) 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 µg·L$^{-1}$) at the

338 northeast of the sampling domain (Fig. 9a; 36.5ºN, 1ºW). 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 ($< 0.4$ µg·L$^{-1}$) during the third survey (Figs. 5 and 9, panel a).

342 Nano>10 µm 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$^{-1}$

344 and $2.5 \times 10^4$ cells·mL$^{-1}$, 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$^{-1}$, 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.

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 x$10^4$ 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 (~ 8x$10^4$ 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 μg·L$^{-1}$ were limited to the western side of the domain (old AW, Fig. 6a), exhibiting mesoscale patches with concentrations of ~ 2 μg·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 μm, Ultra and Eupico had gyre-scale and mesoscale distributions similar to that of chlorophyll, with mesoscale patches containing maximum cell densities of ~ 2x$10^2$, $10^4$ and 6x$10^4$ 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 (4x$10^3$ and 7x$10^4$ 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

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 NWAF is found at the northern
423    boundary of the WAG. The NWAF 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 NWAF 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 NWAF 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 NWAF.

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 ~$3x10^4$ to $4x10^4$ cels·mL$^{-1}$, 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 NWAF 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 fontal 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 NWAF 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

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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 $6x10^4$ and almost $7x10^4$
652 cels·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

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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

705

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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 phytoplankton populations under common setting conditions (a), and the *Prochlorococcus* 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. Samplings 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).

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$^{-1}$
987     $^{1}$ 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 ± 11.6 m·d$^{-1}$ for OMEGA-1, 2.18 ± 2.4 m·d$^{-1}$ for OMEGA-2, and 5.20 ± 4.4
991     m·d$^{-1}$ for BIOMEGA.
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993     Figure 8. (a) Chlorophyll (μg·L$^{-1}$), (b) Nano>10 μm, (c) Ultra, (d) Eupico, (e) Crypto
994     flagellates and (f) Cyanobacteria (cells·mL$^{-1}$) at 5 m depth during OMEGA-1 surveys.
995

996     Figure 9. (a) Chlorophyll (μg·L$^{-1}$), (b) Nano >10 μm (c) Ultra, (d) Eupico, (e) Crypto
997     flagellates, (f) Cyanobacteria and (g) Prochlorophytes (cells·mL$^{-1}$) at 5 m depth during
998     OMEGA-2 surveys.
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1000     Figure 10. (a) Chlorophyll (μg·L$^{-1}$), (b) Nano >10 μm, (c) Ultra, (d) Eupico, (e) Crypto
1001     flagellates and (f) Cyanobacteria (cells·mL$^{-1}$) at 10 m depth during BIOMEGA survey.
1002

1003     Figure 11. Relationship between Chlorophyll, Nano>10 μm, 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 (cels·mL$^{-1}$) of Nano >10 μm,
1009     Ultra, Eupico, Crypto flagellates, Cyanobacteria and maximum geostrophic velocity
1010     (m·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.

| Phytoplankton Group | n | r | P |
|---|---|---|---|
| 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.

| Phytoplankton Group | n | y-intercept | Standard deviation | Slope | Standard deviation | $R^2$ | P |
|---|---|---|---|---|---|---|---|
| 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 | *** |