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Gradients of phytoplankton abundance, composition and photosynthetic pigments across the Almeria–Oran front (SW Mediterranean Sea)

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Abstract

As a part of the interdisciplinary study of the geostrophic front of the eastern Alboran Sea ("Almofront-1", April–May 1991), several characteristics of phytoplankton biomass have been measured at the regional scale to evaluate the gradients between the frontal jet and the surrounding water masses. Microplanktonic diatoms, chlorophyll *a* and fucoxanthin were the most abundant in the front by 1–2 orders of magnitude whereas pico- and nanoplankton, which consist mostly of prymnesiophytes, and 19'hexanoyloxufucoxanthin tended to be the most abundant in the adjacent waters. Correlations between the various phytoplankton components and tracers are examined. The Almeria–Oran front behaves typically as a fertilisation site in an otherwise oligotrophic environment. Frontal fertilisation favored the growth of one or a few opportunistic, autochthonous diatom species, the remainder of the Alboran Sea being occupied by a diversified population of the smallest size-classes of phytoplankton.

1. Introduction

Once the existence of the Almeria–Oran front as a proper oceanic system and its importance on the circulation in the Alboran Sea was discovered (Arnone et al., 1987, 1990; Lohrenz et al., 1988a; Tintoré et al., 1988), high chlorophyll content has been noted in the front area. Evidence for such positive anomalies were provided by remote sensing (CZCS) of the sea surface colour (Arnone and La Violette, 1984, 1986; Wiesenburg and Arnone, 1986; Arnone, 1987; Arnone and Wiesenburg, 1988; Lohrenz et al., 1988a; Arnone et al., 1990) and from direct ship measurements

(Lohrenz et al., 1988b; La Violette, 1989; Arnone et al., 1990; Gould and Wiesenburg, 1990). As pointed out in the last three papers, the chlorophyll anomaly results from a vertical input of nutrients; it is paralleled by increased primary productivity values, and is significant at the regional scale.

Phytoplankton studies in the Almeria–Oran front remain very scarce, however. They mainly consist in the study of a localized diatom bloom observed at a depth of 54 m by Gould and Wiesenburg (1990). This bloom amounted to ca 10^7 cells l^{-1} and a chlorophyll concentration of $23 \mu g l^{-1}$, two amazing values as far as open-sea

Mediterranean waters are concerned. Pending questions regarding phytoplankton include: gradients of phytoplankton abundance and composition, origin (either allochthonous or autochthonous) of the blooming species when present, size and phylogenetic composition of the flora in terms of growth strategies, and the significance of pigment markers in such perspectives. The interdisciplinary cruise “Almofront-1” (Priour et al., 1993; Priour and Sournia, 1994) offered an opportunity to address these questions by deploying several complementary techniques for phytoplankton and pigment analysis.

The present paper is based upon the study of water samples taken in the chlorophyll maximum during the synoptic survey (Leg A). Videau and Birrien (1992) and Videau et al. (1994) report on the primary production measurements and eco-physiological tests performed during Leg B.

2. Methods

2.1. Field sampling

The “Almofront-1” cruise on board R/V *L'Atalante* (April–May 1991) in the eastern Alboran Sea comprised, as its two main steps: (1) a synoptic, multiparametric survey and selected transects (Leg A, April 24–May 12) and (2) a detailed study at selected sites, including experimental work (Leg B, May 13–26). More information on the cruise, together with a preliminary survey, can be found in Priour et al. (1993) and Priour and Sournia (1994). The hydrological aspects are detailed by Priour et al. (1994).

The 83 stations of Leg A (Fig. 1) were spaced by an average distance of 11 km chosen as being slightly less than the first internal radius of deformation (Priour et al., 1993), hence allowing any mesoscale feature to be revealed. Sampling was performed by means of a Seabird® SBE9, CTD-O₂-fluorescence probe and a 12-bottle rosette. Water was sampled during the upward cast at the depth of the fluorescence maximum (or the upper maximum, which was also the strongest, when two or more maxima were encountered).

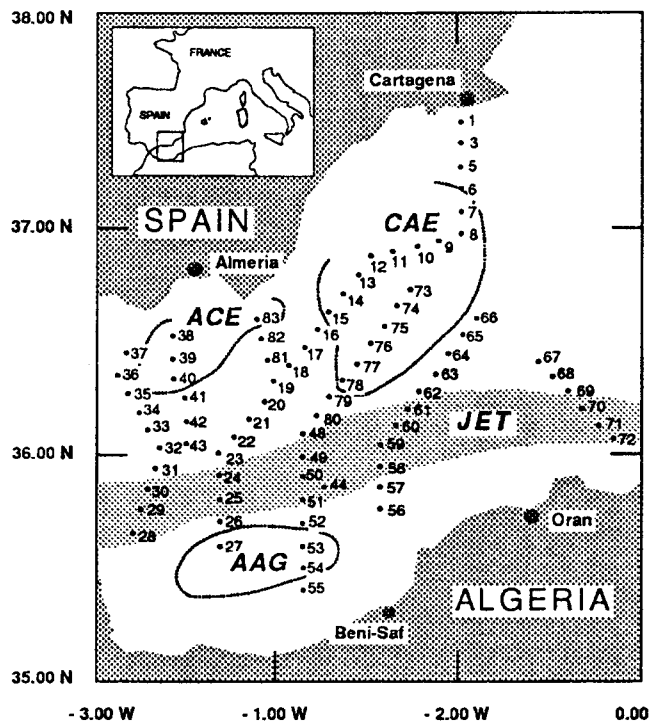


Fig. 1. “Almofront-1” cruise, Leg A (April 24–May 12, 1991): the 83 stations of the synoptic survey and the main hydrological structures. AAG: Atlantic Anticyclonic Gyre; ACE: Almeria Cyclonic Eddy; CAE: Cartagena Anticyclonic Eddy; JET: frontal jet.

2.2. Microscopical cell counting

A 150 ml subsample was fixed with high-quality grade formaldehyde at the final concentration of 1% and kept at dark for further processing within a 4–6 month delay by the Utermöhl method. Microplanktonic algae were identified and enumerated whereas ultraplanktonic organisms were identified at a higher taxonomic level and enumerated globally. According to Fogg (1991), we define here “microplankton” as organisms $> 20 \mu\text{m}$ and “ultraplankton” as organisms $< 20 \mu\text{m}$ including both pico- and nanoplankton.

2.3. Flow cytometry measurements

Samples were fixed with a glutaraldehyde solution (Merck®) at a final concentration of 1% and stored in liquid nitrogen as described by Vaultot et al. (1989). A Bruker® ACR-1000 flow cytometer was used for the analyses. We measured forward light scatter (FLS, an indicator of size),

orange fluorescence from phycoerythrin (580 ± 40 nm) and red fluorescence from chlorophyll (680 ± 20 nm) after excitation by 390–490 nm light of mercury arc-lamp (Steen, 1986). Instrument calibration was frequently monitored by analyzing $0.94 \mu\text{m}$ and $1.96 \mu\text{m}$ fluorescent standard beads (Polysciences®).

2.4. Pigment measurements

Two to four liters (depending on the fluorescence signal) were filtered onto 47 mm Whatman® GF/F glass-fiber filter. Pigments were extracted in 5 ml of cold methanol using a sonication probe. After clarification of the extract by filtration, chlorophylls and carotenoids were analyzed by reverse-phase HPLC, using the procedure described in Williams and Claustre (1991) except that flow rate was set at 1 ml min^{-1} . Two Milton Roy® spectromonitors were used in series, one set up at 440 nm and the other at 667 nm (for phaeopigment detection). Calibration

procedure was performed using pigment standards kindly provided by R. Bidigare.

3. Results

3.1. Dynamic topography of the study area

Dynamic topography, as revealed by the density measurements in the whole study area, showed an eastward flowing jet (Prieur et al., 1993), the envelope of which is represented here in Figs. 1–3 and 5. A high of the dynamic topography was found South (at right) of this jet (Fig. 1) and identified to the classical eastern gyre of Atlantic waters in the Alboran Sea (AAG, Atlantic Anticyclonic Gyre). Surface salinity in this gyre was the lowest of the study area ($< 36.7\text{‰}$), indicating the retention there of Atlantic water which had recently entered the Mediterranean Sea. North of the jet (left to it), two other mesoscale features were found: (1) An anticy-

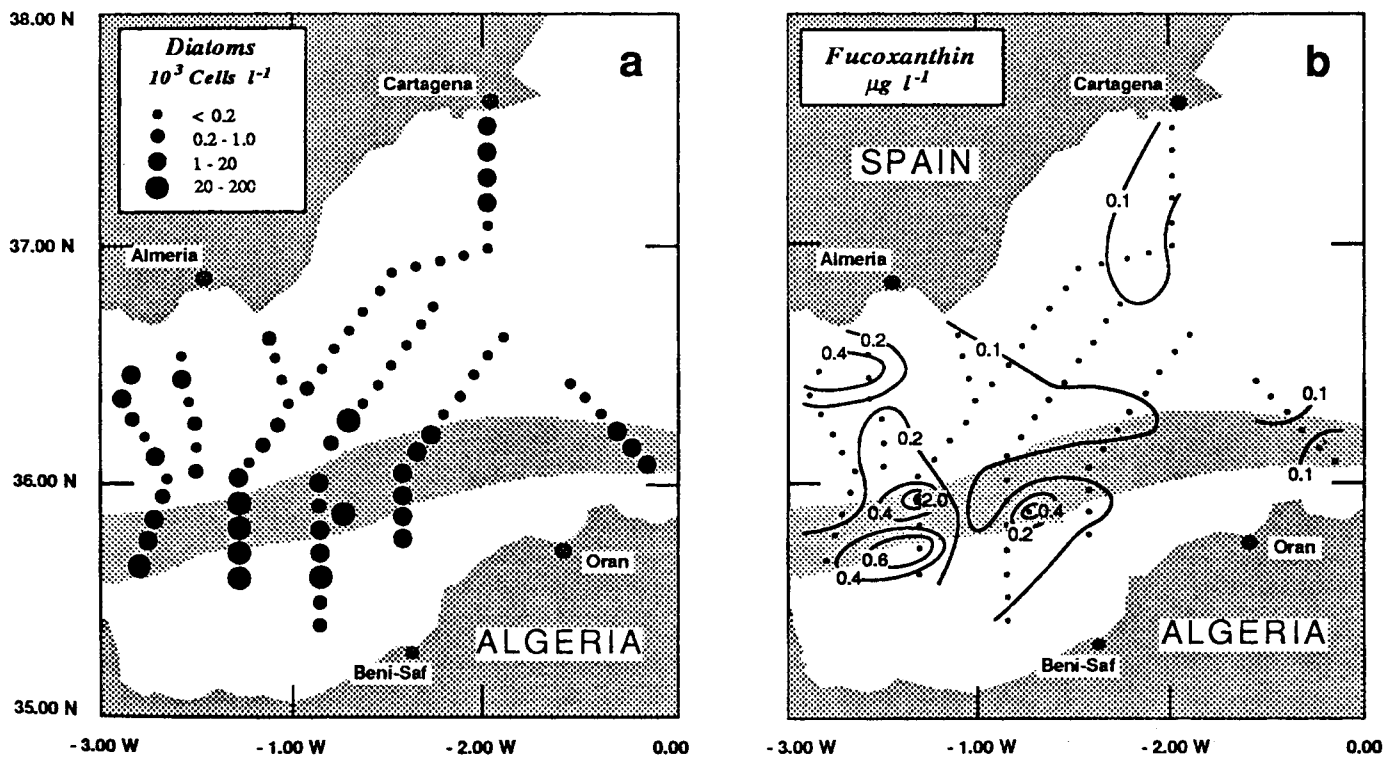


Fig. 2. (a) Distribution of cell numbers of microplanktonic diatoms as measured under the inverted microscope at the depth of the chlorophyll maximum; (b) distribution of fucoxanthin concentration from HPLC measurements at the depth of the chlorophyll maximum.

clonic eddy, south of Cartagena, 60 km in diameter and 200 m deep (there under: CAE, Cartagena Anticyclonic Eddy); this isolates some old Atlantic water from the Mediterranean surroundings (Prieur et al., 1994). (2) A small cyclonic eddy (low dynamic height), south of Almeria (there under: ACE, Almeria Cyclonic Eddy); in this eddy, surface salinity was $> 37\text{‰}$ and the top of the pycnocline was at -30 m against an average depth of 60 m for the whole study area. Direct current measurements by Acoustic Doppler Current Profilers (Prieur and Gratton, 1994) confirmed all the above features. The maximum horizontal velocity was near 1 m s^{-1} in the jet core and about 0.4 m s^{-1} in the gyre and eddies.

3.2. Phytoplankton abundance and composition

Diatoms were quantitatively the dominant fraction of the microplankton ($\geq 20 \mu\text{m}$) at the depth of chlorophyll maximum. Their numbers were highly variable, however (Fig. 2a). There were virtually no diatoms ($\leq 1000 \text{ cells l}^{-1}$) in the

whole region investigated north of the frontal jet if one omits (1) the four northernmost stations off Cartagena that belong to a hydrologically complex coastal area, (2) four western stations in ACE and (3) station 79, in the middle of the study area, where CAE is nearly contiguous to the jet. In counterpart, cell numbers in the jet and south of it range between 1 and $200 \cdot 10^3 \text{ cells l}^{-1}$ with the highest numbers being found in the western part of the jet. Taxonomically, diatoms are typical of the temperate or warm temperate flora, with *Chaetoceros*, *Guinardia*, *Lauderia*, *Nitzschia*, *Rhizosolenia*, *Schroederella*, *Skeletonema*, *Thalassionema* and *Thalassiosira* as the dominant genera. It is noteworthy that the (relatively) high cell numbers ($50\text{--}200 \cdot 10^3 \text{ cells l}^{-1}$) are caused by the dominance of a single diatom species, either *Thalassiosira* cf. *partheneia* Schrader at Station 79 or *Rhizosolenia alata* Brightwell [= *Proboscia alata* (Brightwell) Sundström] in the whole frontal region.

The cell numbers of dinoflagellates (not shown) never exceed $4 \cdot 10^3 \text{ cells l}^{-1}$ and the species

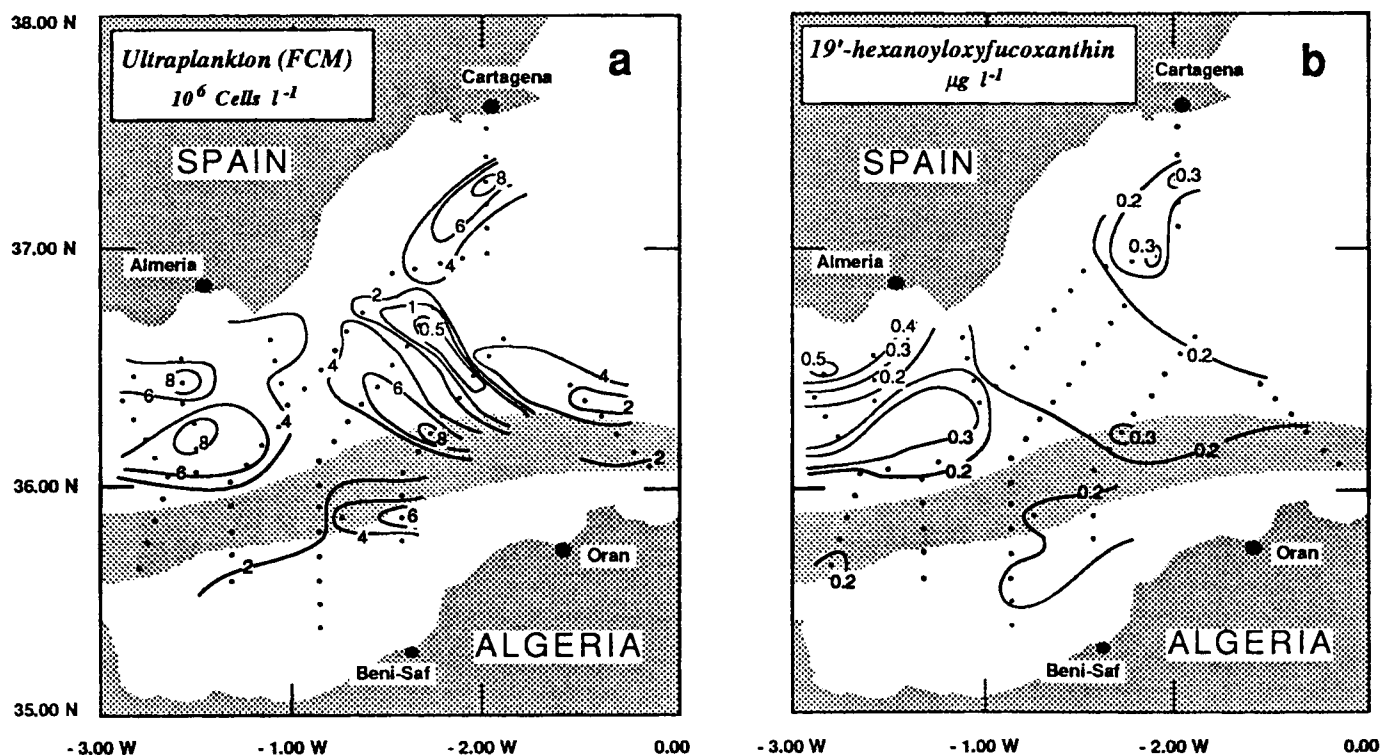


Fig. 3. (a) Distribution of ultraplanktonic cell numbers as measured by flow cytometry (FCM) at the depth of the chlorophyll maximum; (b) distribution of 19'-HF concentration from HPLC measurements at the depth of the chlorophyll maximum.

composition is that of temperate or warm stratified waters. Besides cosmopolitan species such as *Prorocentrum micans* Ehr. or *Ceratium furca* (Ehr.) Clap. and Lachmann, the presence of the following taxa is significant in this respect: *Achradina pulchra* Lohmann, *Ceratium belone* Cleve, *C. limulus* (Pouchet) Gourret, *C. teres* Kofoid, *Ceratocorys armata* (Schütt) Kof., *Kofoidinium velloides* Pav., *Noctiluca scintillans* (Macartney) Kof., *Pyrocystis* spp., *Prorocentrum rostratum* Stein and *Schuetziella mitra* (Schütt) Balech [= *Gonyaulax mitra* (Schütt) Kof. = *Oxytoxum gigas* Kof.]. We were not able to identify any clear-cut distribution of cell numbers or taxonomical composition along the geographical or hydrological dimensions.

Microplankton also included a few isolated colonies of the prymnesiophyte *Phaeocystis globosa* Scherrfel that were found in the frontal jet.

Ultraplankton as estimated under the light microscope by the Utermöhl method (data not shown) range from 75 to $600 \cdot 10^3$ cells l^{-1} . A significant part of this size fraction consisted of coccolithophorids (Prymnesiophyceae) belonging to the genera *Discosphaera*, *Emiliania*, *Helicosphaera*, *Ophiaster*, *Rhabdosphaera*, *Scyphosphaera* and *Syracosphaera*. The remaining organisms belong to naked dinoflagellates (*Gymnodinium* and *Gyrodinium* spp.), Cryptophyceae and unidentified flagellates. No quantitative or qualitative difference in the horizontal distribution was obvious.

Total cell numbers (excepted Cyanobacteria) as estimated by flow cytometry (thereunder FCM) ranged from 350 to 8800 cells ml^{-1} (Fig. 3a). The maximum densities are localized in the northern half of the study area, more precisely: (1) in ACE, (2) in the complex area off Cartagena and (3) in the central area. Inside the jet, cell numbers are lower than 4000 ml^{-1} , excepted at stations 57 and 61 (> 6000 cells ml^{-1}). The values of the forward light scatter (FLS) showed that cell diameters are in the majority $< 10 \mu m$ and mostly $< 5 \mu m$.

Cyanobacteria are characterized under FCM by their low phycoerythrin fluorescence and their small size (0.8–2 μm). They were poorly represented (from 50 to $200 \cdot 10^3$ ml^{-1}) and mainly located in ACE (data not shown).

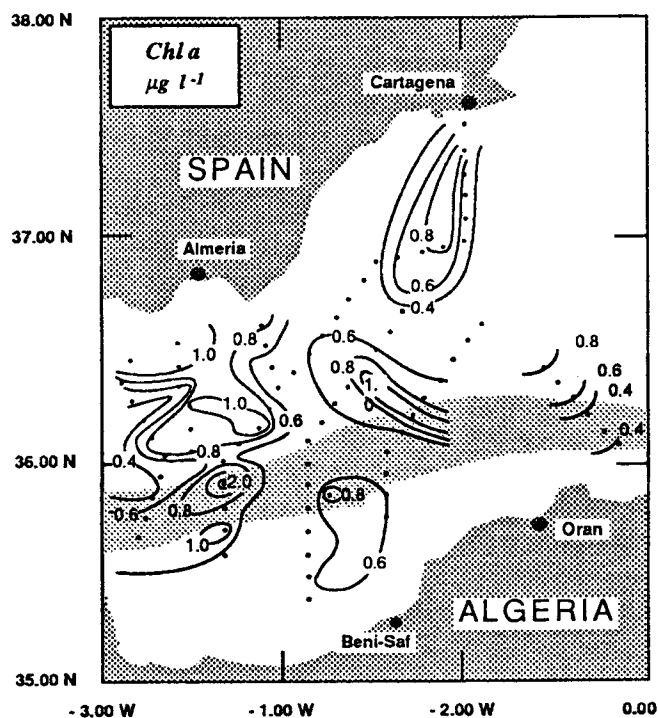


Fig. 4. Distribution of chlorophyll *a* concentration from HPLC measurements at the depth of the chlorophyll maximum.

3.3. Photosynthetic pigments

The distribution of HPLC-measured chlorophyll *a* concentrations at the depth of the chlorophyll maximum is shown in Fig. 4. Values range within a factor of about 25 (0.2 – $2.6 \mu g l^{-1}$). The horizontal distribution is much more patchy than that of the integrated concentrations as deduced from in vivo fluorescence (Prieur et al., 1993, 1994) as an obvious consequence of the irregularities of vertical profiles (Videau et al., 1994). Concentrations higher than $1 \mu g l^{-1}$ were all found in the jet and in ACE (Fig. 4).

Fucoxanthin, a carotenoid pigment characteristic of diatoms (Diatomophyceae) and occasionally found in Chrysophyceae and Prymnesiophyceae, was found in the wide range of < 0.01 (trace concentration) to $2.1 \mu g l^{-1}$ (Fig. 2b). It was virtually absent in the central part of the study area and reached its maximum concentration in the jet region, hence paralleling diatom distribution.

The carotenoid pigment 19'-hexanoyloxyfucoxanthin (here under 19'-HF), is a characteristic

pymnesiophyte antenna pigment (Arpin et al., 1976; Haxo, 1985), also found in a very few dinoflagellate species. Its concentrations range from 0.05 to 0.50 $\mu\text{g l}^{-1}$ (Fig. 3b), with the highest values in the northern half of the study area, namely in the ACE surroundings and in the coastal area off Cartagena. Similarities with the distribution of FCM ultraplankton (Fig. 3a) are obvious.

Zeaxanthin, a carotenoid found in cyanobacteria (Guillard et al., 1985), prochlorophytes (Chisholm et al., 1988) and some prasinophytes (Gieskes et al., 1988) was only found occasionally and at low concentrations at the depth of the chlorophyll maximum (data not shown). This agrees with the fact that few cyanobacteria and no prochlorophytes were detected by flow cytometry at this depth. In counterpart, zeaxanthin was encountered more frequently in the surface waters during this cruise (Claustre et al., 1994).

The longest transect made during Leg A, namely: the Cartagena transect (st. 1–27) was also the most representative as it crossed all the hydrological regions, ACE excepted. The integrated concentrations (mg m^{-2} , 0–150 m) of chlorophyll *a*, fucoxanthin and 19'-HF are represented on Fig. 5. The highest chl. *a* concentrations were again found in the jet (st. 24) together with a strong peak of fucoxanthin but coincidentally with a drop of 19'-HF. On the remaining part of the transect, peaks of chl. *a* and 19'-HF were found to be coincident. Among the three pigments considered, fucoxanthin exhibited again the highest range of variation, with concentrations ranging within a factor of 20 (Fig. 5).

3.4. Correlation between the different biomass components or tracers

Correlations between the various phytoplankton components or phytoplankton-related variables are summarized on Table 1. Some of these correlations are detailed below by reading Table 1 horizontally.

The correlation between chlorophyll content and diatom cell numbers is confusing if all stations are considered indifferently (Table 1). Obviously, two trends are to be distinguished. On one

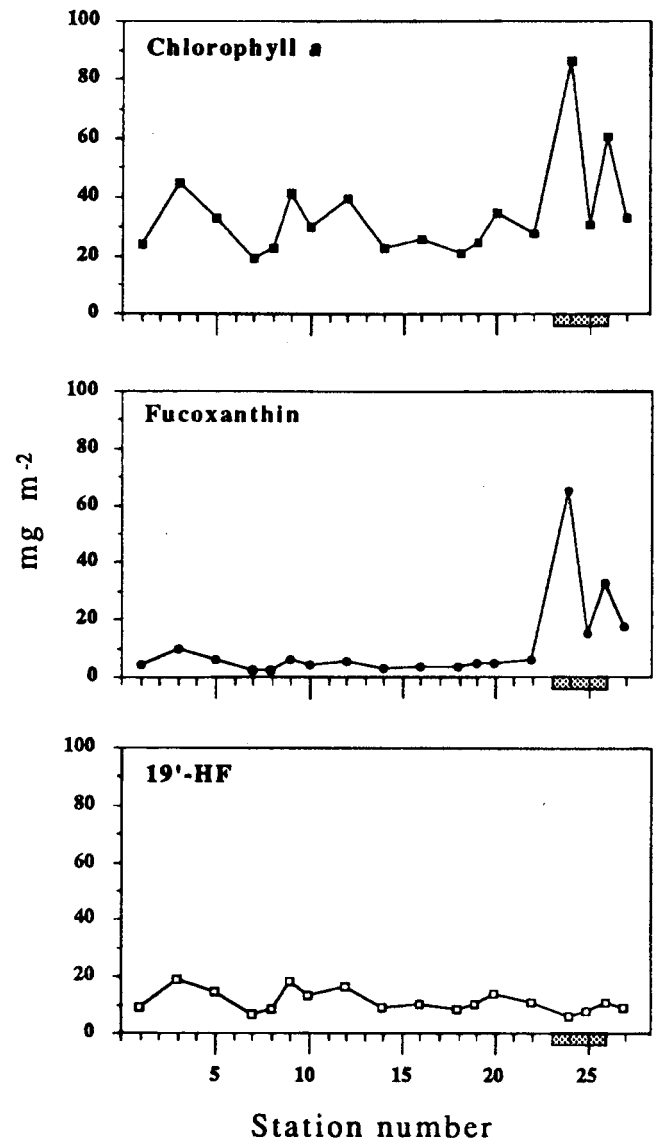


Fig. 5. Integrated chlorophyll *a*, fucoxanthin and 19'-HF in the 0–150 m water column along the transect between stations 1 and 27. The dark bar on abscissa indicates the limit of the frontal jet.

hand, the two variables are uncorrelated when cell numbers are less than $10^3 \text{ cells l}^{-1}$, which is the most frequent case. In other words, diatoms do not contribute significantly to phytoplankton biomass at most stations. On the other hand, a significant correlation is observed (Table 1) for the restricted group of stations located in the frontal jet. No significant correlation was found between chlorophyll content and dinoflagellate numbers (Table 1). Chlorophyll content is positively correlated with both ultraplankton as ob-

served under the light microscope and as estimated by flow cytometry.

Diatom numbers are significantly correlated with fucoxanthin content, as could be expected, particularly in the jet region. They are poorly correlated with dinoflagellate numbers in the jet region, and not correlated with any of the other variables examined.

The two independent estimates of ultraplankton (“Utermöhl” and “FCM”) are mutually correlated. Each of them is correlated with the concentrations of 19'-HF and cyanobacteria numbers in the jet stations, and not correlated with any of the other variables.

4. Discussion

At first glance, several of the above variables reveal a dramatic contrast between the frontal region and the adjacent waters north and south of it. As the Almeria–Oran front was met in a southern position during the Almofront-1 cruise, the contrast may be characterized in terms of a global comparison between the northern half of the study area on one hand and the frontal-jet system on the other hand. Then, the ranges found at the depth of the chlorophyll maximum can be expressed as follows, the location of the maximum being indicated between brackets:

0–200 · 10³ diatom cells l⁻¹ (Jet)

75–600 · 10³ cells l⁻¹

ultraplankton cells (Utermöhl) (North)

350–8500 · 10³ cells l⁻¹ (FCM) (North)

0.1–2.6 µg chl *a* l⁻¹, (Jet)

0.01–2.1 µg fucoxanthin l⁻¹ (Jet)

0.05–0.50 µg 19'-HF l⁻¹ (North)

No front/adjacent waters contrast was found for the other phytoplankton variables, even though the values were highly variable, but the primary production measurements performed during the second leg of Almofront-1 are relevant here. For the same groupings of stations, orders of magnitude are 0.5–2.0 g C m⁻² day⁻¹ for carbon uptake (Videau and Birrien, 1992; Videau et al., 1994) and 0.07–0.24 mmol N–NO₃ m⁻² h⁻¹ for nitrate-based (“new”) production (L'Helguen et al., 1992, 1994), maxima being found in the jet area. It is also worth remembering here that the top of the nitracline was found at the depths of 18–30 m in the frontal stations and 30–60 m in the adjacent Atlantic or Mediterranean waters (L'Helguen et al., 1992; Videau et al., 1994), which is clearly indicative of frontal fertilisation (Prieur et al., 1993; Prieur and Sournia, 1994).

There is thus no doubt that the front-jet system is a site of increased biological “productivity” in the broad sense. Such a fertilizing effect is a common, though not universal, property of fronts (Franks, 1992). It is particularly obvious in the case of the Alboran Sea where both water masses

Table 1
Correlation matrix between phytoplankton variables

	19'-HF	Fucoxanthin	Cyanobacteria	Dinoflagellates	Ultraplankton (FCM)	Ultraplankton (Uterm.)	Diatoms
Chl <i>a</i>	n.s. (n.s.)	0.69 ** (0.87 **)	n.s. (n.s.)	n.s. (n.s.)	0.54 ** (0.58 *)	0.37 ** (0.63 **)	0.27 * (0.81 **)
Diatoms	n.r. (n.r.)	0.70 ** (0.96 **)	n.s. (n.s.)	n.s. (0.57 *)	n.s. (n.s.)	n.s. (n.s.)	
Ultraplankton (Uterm.)	0.52 ** (0.84 **)	n.r. (n.r.)	n.s. (0.67 **)	n.s. (n.s.)	0.38 ** (0.85 **)		
Ultraplankton (FCM)	0.47 ** (0.88 **)	n.r. (n.r.)	0.27 * (0.87 **)	n.s. (n.s.)			

Upper figures: all stations; lower figures (between brackets): stations in the frontal jet only. * 0.01 < p < 0.05; ** p < 0.01. n.s.: not significant; n.r.: not relevant.

adjacent to the front —impoverished surface Atlantic waters and impoverished surface Mediterranean waters—are typically oligotrophic (Prieur et al., 1993, 1994).

The maximum values reached by the chlorophyll and diatom numbers during “Almofront-1” do not reach, by far, those observed by Gould and Wiesenburg (1990) and mentioned in the Introduction. The latter values were obtained in late autumn (November–December, 1987) whereas ours refer to spring (April–May, 1991). The differences may thus be a matter of seasonality as the bulk of hydrological data and infrared satellite pictures available so far indicate that the strongest physical gradients are encountered in autumn (Arnone and La Violette, 1986; Arnone, 1987; Arnone and Wiesenburg, 1988; La Violette, 1989; Prieur et al., 1990; Le Vourch et al., 1992).

In spite of the moderate cell numbers and chlorophyll content, the diatom maxima observed during “Almofront-1” do have the two characteristics usually attributed to phytoplankton “blooms”, namely: quasi-monospecificity (of either *Rhizosolenia alata* or *Thalassiosira* cf. *partheneia*, as detailed above), and opportunism in the sense that the responsible species are known as fast-growing microalgae with a low chlorophyll content per cell (Guillard and Kilham, 1977). Furthermore, both species have already been recorded as blooming organisms in various parts of the world ocean (*R. alata*: Sournia, 1968; Marshall, 1972; Fanuko, 1983; Clemons and Miller, 1984), in the northeastern African upwelling (*Th.* cf. *partheneia*: Schrader, 1972; Grall et al., 1976) and in the Almeria–Oran front itself (*Th.* cf. *partheneia*: Gould and Wiesenburg, 1990).

Besides this regional heterogeneity, are there mesoscale gradients in the distribution of any phytoplankton variable? Because it was conceived as a routine survey, the examination of microplankton by the Utermöhl method during “Almofront-1” cruise does not reveal anything more than a flow of opportunistic diatoms through an oligotrophic sea; a narrower sampling grid and large-volume samples would have been necessary to tell more on microplankton gradients. However, further insight into the meso-scale gradients

is provided by the analysis of the pigment tracers throughout the water column (Claustre et al., 1994). This clearly revealed an asymmetry or anisotropy within the jet, as a consequence of the front-related upwelling on the left border of the jet. Chlorophyll *a*, fucoxanthin and phaeophytin were all observed to increase from left to right, indicating that diatom production as well as grazing activity evolved parallelly from the left (north) to the right (south) border of the frontal jet.

Flow cytometry analysis provided additional information on phytoplankton populations and particularly on their smallest size classes. Although this technique does not permit to measure the absolute size of cells, it appears that the fraction $< 10 \mu\text{m}$ is dominant in the whole area investigated, with the possible exception of stations 24–27 (see below). The significant correlation found with chlorophyll concentration also suggests that these populations contribute greatly to total biomass. From our cell counts, it appears that these ultraplanktonic algae are underestimated under light microscopy by a factor of 5 to 15 times as compared to FCM results. Both estimates are significantly correlated with each other, however (Table 1), which indicates that the underestimated figures are still meaningful.

Pigment analysis using HPLC method provides some indication on the identity of these small populations. The similarity between their distribution and that of the 19'-HF concentration, along with their significant correlation, show that these cells belong mostly to the Prymnesiophyceae. These small flagellates predominate in the northern part of the study area. In the jet, they are masked by the development of large diatoms that are largely responsible for the increase of biomass.

The taxonomic composition of the above-mentioned groups found in the jet does not depart from the western Mediterranean flora as extensively studied by the Spanish oceanographers (e.g., Margalef, 1969; Estrada, 1982; Estrada and Salat, 1989; Delgado, 1990; Delgado and Fortuño, 1991). The two species responsible for the highest cell numbers deserve special attention here. One of them, *Rhizosolenia alata*, is well known in the southwestern Mediterranean Sea (references as above) and was already mentioned in the coastal

waters of the Alboran Sea by Paulsen (1931). Obviously, this is an autochthonous plankter in the study area. Concerning *Thalassiosira* cf. *partheneia*, world records are so few that little can be said except that such very small and mucilaginous diatoms need further investigation. Anecdotally, the presence of *Schuetziella mitra*, a large, thermophilic dinoflagellate, is recorded here for the first time in the Mediterranean Sea. The sporadic presence of *Phaeocystis* under its colonial stage is also noteworthy as this peculiar prymnesiophycean genus has only been mentioned once of the Alboran Sea (Kashkin, 1964) and is poorly known in the Mediterranean Sea (Ignatiades and Mimicos, 1977; Estrada, 1991). It may be responsible for the enigmatic flashes on the CTD-fluorescence probe (Videau et al., 1994; Claustre et al., 1994).

In quantitative terms, the smallest size fractions are the dominant or major contributors of biomass. This may even hold true for the group of stations 24–27 where microplanktonic diatoms attain their maximum numbers, if both cell characteristics and cell numbers are considered. A *Rhizosolenia alata* cell is 250–500 μm long but only 10 μm wide and contains a few, 3 μm -large chloroplasts each, whereas most ultraplanktonic cells are about 5 μm large with little or no vacuole space. Then, one *Rhizosolenia* is roughly equivalent to ten nanoplankters in terms of plant biomass. If the approximate concentrations of 10^5 *Rhizosolenia* and 10^6 nanoplankters per liter are retained, then both components contribute equally to phytoplankton biomass at stations 24–27.

The abundance of ultraplankton as measured under the inverted microscope and under FCM as well is much less variable than that of the microplanktonic diatoms; Utermöhl-ultraplankton showed no regional trend whereas FCM-ultraplankton tended to be the more abundant in the northern half of the study area, that is: where microplankton was the less abundant. On the whole, the size composition of phytoplankton in the Almeria–Oran region may serve to illustrate the current paradigm on planktonic food webs, namely: on one hand, a background of steady-state ultraplankton, the development of which is

limited by molecular diffusion and tightly coupled with grazers within the microbial loop, on the other hand, blooms of opportunistic, nutrient- and turbulence-limited microplankton on which the higher trophic levels exert but a loose control because of a high space–time variability (Goldman, 1988; Stockner, 1988; Fogg, 1991).

Acknowledgements

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