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Structure and variability of the microbial community associated to the Alboran Sea frontal system (Western Mediterranean) in winter

JACQUET Stephan [1, 2 *], PRIEUR Louis [3], NIVAL Paul [3], VAULOT Daniel [1]

1)- Université Pierre-et-Marie-Curie (Paris 06) and CNRS, UMR 7144, Station Biologique, BP 74, 29682 Roscoff Cedex, France

2)- INRA, Station d'Hydrobiologie Lacustre, UMR CARRTEL, 74203 Thonon-les-Bains Cedex, France

3)- Laboratoire d'Océanologique de Villefranche-sur-Mer, CNRS and Université Pierre-et-Marie-Curie (Paris 6), 06234 Villefranche-sur-Mer Cedex, France

*) - Corresponding author (S. Jacquet)
E-mail address: stephan.jacquet@thonon.inra.fr

ABSTRACT: The Almofront-2 cruise (22 November 1997 – 18 January 1998) was aimed at documenting physical, chemical and biological characteristics of the Alboran Sea. Both horizontal and vertical distributions of picophytoplankton (*Prochlorococcus* spp., *Synechococcus* spp. and small photosynthetic eukaryotes), heterotrophic prokaryotes and viruses were investigated using flow cytometry (FCM). Three types of ecosystems were discriminated on the basis of physical parameters and picoplankton distribution: the Mediterranean ecosystem (MED) in the Northern part, the anticyclonic gyre of modified Atlantic (ATL) water in the southern part, and the frontal ecosystem in between. MED waters were dominated by *Prochlorococcus* while *Synechococcus* concentration was higher in ATL waters.

High concentrations of both groups were also recorded in dense waters of the front, a likely response to nutrient injection from deeper and/or adjacent waters. Photosynthetic picoeukaryotes concentration was the highest in regions influenced by the front and at the periphery of the gyre. The low biomass of picoeukaryotes in dense waters of the front suggests that this group responded very differently to environmental factors compared to *Prochlorococcus* and *Synechococcus*. Picoplankton contributed up to 50% of total chlorophyll *a* (Chl *a*) in the gyre (mean ca 25%), essentially due to the picoeukaryotes.

The biomass of the picophytoplankton clearly decreased between the two legs. Heterotrophic bacteria concentrations were well correlated to those of picoeukaryotes and reached their maximum in the central part of the Alboran eastern gyre. Two patches of high concentration of heterotrophic bacteria were recorded in frontal-influenced MED waters and were tightly coupled to maximal Chl *a* concentrations following the 28.1-28.2 density excess isolines. At this period of the year, picoplankton could represent up to 50% of the <200 μm living organic carbon in MED waters and up to 35% in modified ATL waters (mean 35 and 23%, respectively). At last, two groups of virus-like particles (VLPs) were discriminated by FCM according to DNA content fluorescence. No major differences in their distribution patterns were recorded between sites. A significant correlation was found between heterotrophic bacteria numbers and VLPs suggesting a tight coupling between the two communities. In

conclusion, picoplankton appears to constitute an important fraction of living matter in the Alboran Sea at the end of fall and early winter and may thus participate significantly to carbon and energy fluxes in the W. Mediterranean Sea.

KEY WORDS:
Alboran sea, frontal structures, picoplankton, virus, microbial communities, carbon biomass.

ACRONYMS
CTD: conductivity, temperature, depth sensors
FCM: flow cytrometer
DML: Depth of mixed layer, DCM: Deep chlorophyll maximum
ATL: Atlantic waters, MAW: Modified Atlantic Water; MED: Mediterranean waters,
LIV: Levantine intermediate water
VLP: virus like particles

Introduction

Hydrological fronts are mesoscale structures, characterized by an important horizontal gradient of salinity and temperature, where physical and biological processes interact with each other. An important characteristic of frontal-jet systems is that the main water mass circulation is not exactly in geostrophic balance. Such small unbalance generates secondary circulations, both horizontally and vertically (Bower & Rossby, 1989) and localized vertical velocities that may be responsible for nutrient enrichment in the mixed layer from adjacent or upwelled waters (Fasham *et al*., 1985). Hence, frontal structures in the ocean constitute a dominant source of phytoplankton heterogeneity and biomass enhancement (Franks, 1992). Rodriguez *et al.* (2001) proposed that the response of phytoplankton can vary with its size structure that may depend more on hydrodynamics than nutrients in frontal ecosystems, while some authors reported that, in a frontal structure, the combination of nutrients and light levels are likely to be the main responsible for both the biomass enhancement and community structure of the phytoplankton (Claustre *et al*., 1994).

In the Alboran Sea, surface Atlantic waters enter the Mediterranean Sea through the strait of Gibraltar. Strong interactions occur between this flow (referred to as the Atlantic jet) and local Mediterranean waters resulting in the geostrophic Almeria (Spain) - Oran (Algeria) frontal jet surrounding an anticyclonic eddy (Cheney & Doblar, 1982; Farmer & Armi, 1988; Tintoré *et al*., 1988). The nutrient-enriched Atlantic inflow has been reported to enhance primary production of Mediterranean waters (Gould & Wiesenburg, 1990; Minas *et al*., 1991). During the Almofront-1 cruise (held in spring 1991), primary production was reported to be 2.5 higher in the frontal zone compared to surrounding waters, essentially due to diatoms (Prieur & Sournia, 1994). Nutrient availability in adjacent waters and an important secondary circulation at the basis of the euphotic zone were shown to be responsible of the frontal fertilization in an environment where surrounding waters remained relatively oligotrophic (Prieur *et al*., 1993).

Marine microbial communities are an important part of the pelagic ecosystem and food web (Azam *et al*., 1983; Thingstad *et al*., 1997). For nearly two decades, numerous laboratory and field studies focused on the ecology of picoplankton (organisms < 3µm in size) revealing the great importance of the picophytoplankton in the global carbon fixation in marine systems (Marañón *et al*., 2001). The cyanobacterium *Prochlorococcus*, the most abundant photosynthetic organism on Earth, is widely distributed both horizontally (between 40°N and 40°S) and vertically (over the whole euphotic zone), with maximum concentrations exceeding 10^5 cell.ml^{-1} (reviewed in Partensky *et al*., 1999; West & Scanlan, 1999). It is mostly associated to oligotrophic and well-stratified provinces of the ocean where it contributes significantly to the primary production (Campbell *et al*., 1994; Li, 1994). The cyanobacterium *Synechococcus* is more widespread since it is less sensitive to temperature than

Prochlorococcus and accommodates to a larger range of trophic status and water column mixing conditions (e.g. Partensky *et al*., 1999) although it is generally restricted to the upper well-lit layer. Compared to *Prochlorococcus*, its concentration is usually lower in the range 10^4-10^5 cell.ml^{-1} and decreases even further in oligotrophic waters. Distribution of photosynthetic picoeukaryotes is less documented than those of photosynthetic prokaryotes because, in contrast to the latter, flow cytometry does not allow identifying their taxonomy on the basis of their sole fluorescence and scatter signatures except for orange-fluorescing cryptophytes. In recent years, however, the use of molecular approaches has permitted to establish the major picoeukaryote taxonomic groups present in marine waters (reviewed in Vaulot et *al*., 2008; Worden & Not, 2008), including the Mediterranean sea (Díez *et al*., 2001; Marie *et al*., 2006; Viprey *et al*., 2008) which include Prasinophyceae, Haptophyta, and Chrysophyceae. Picoeukaryote concentrations reach typically 10^3 cell.ml^{-1}. Heterotrophic bacteria constitute a very diversified community (Torsvik *et al*., 2002). Although these cells colonize the whole water column, their highest concentrations are recorded in the euphotic layer with typically 10^5 to 10^6 cell.ml^{-1} (reviewed in Ducklow, 1999). Viruses have been recently recognized as the most abundant biological particles in the sea with concentration reaching up to 10^8 viruses.ml^{-1} (Bergh *et al*., 1989; Wommack & Colwell, 2000; Suttle, 2007). Although they participate only weakly to the carbon stock, they may have important roles in the genetic control of host diversity and the transfer of organic matter directly from auto- and heterotrophic communities to dissolved organic matter (reviewed in Fuhrman, 1999; Wilhelm & Suttle, 1999; Middelboe, 2008; Jacquet *et al.*, 2010).

We participated to the Almofront-2 cruise which took place in late 1997-early 1998. We documented these biological compartments from a large set of samples analyzed by flow cytometry. Our main goal was to document the coupling of picoplankton and virus-like particles with biological, chemical or physical processes in a region characterized by strong hydrological and trophic situations.

Materials and methods

Sample collection

The Almofront-2 cruise held in the Alboran Sea (Western Mediterranean Sea). Sampling took place in the eastern part of the Alboran Sea, between 0° and 3°W longitude and between 35° and 37°N latitude (Fig. 1). During leg-1 of the cruise (1st – 21th December 1997), one north-south transect was sampled at 24 stations during 3 days (referred to as CTD 252 to 275) separated from each other by about 3 nautical miles (see Cuttelod & Claustre, 2010) when crossing the frontal jet – gyre system, 5 miles otherwise. In the rest of the text, we will refer to stations or CTD as synonymous terms. This transect was designed to obtain a general description of the whole area and to localize precisely the jet-front-gyre system. Twelve depths between 0 and 200 m were sampled for each station. During leg-2 (23 December 1997 – 15 January 1998), 8 representative sites of the range of hydrodynamical and biogeochemical situations encountered during leg-1, were occupied for a period of 36 h and sampled between 8 and 10 times (Fig. 1). For each site, we selected 3 different profiles between 0 and 200 m depth every 12 h (at general around 8:00 and 20:00 the first day and 8:00 the second day, local time) to document the picophytoplanktonic fraction plus 1 profile describing the entire water column, from surface to bottom (20:00), to obtain counts of both heterotrophic bacteria and virus-like particles. From 12 to 18 samples were taken for each CTD profile using 10L-Niskin bottles from an oceanic CTD Rosette (SEABIRD SBE32, Seattle, USA). The CTD was equipped with a SEABIRD O2 probe (SBE911+and rosette, Seattle), a CHELSEA fluorometer (Aquatracka III, U. K.), a SEA-TECH transmissiometer (Corvallis, USA) and two sensors for PAR (Photosynthetic Active Radiation, ref. QSPL2/4S) and SPAR (Surface Photosynthetic Active Radiation, ref. QSR 240) measurements (Biospherical Inst., San Diego, USA).

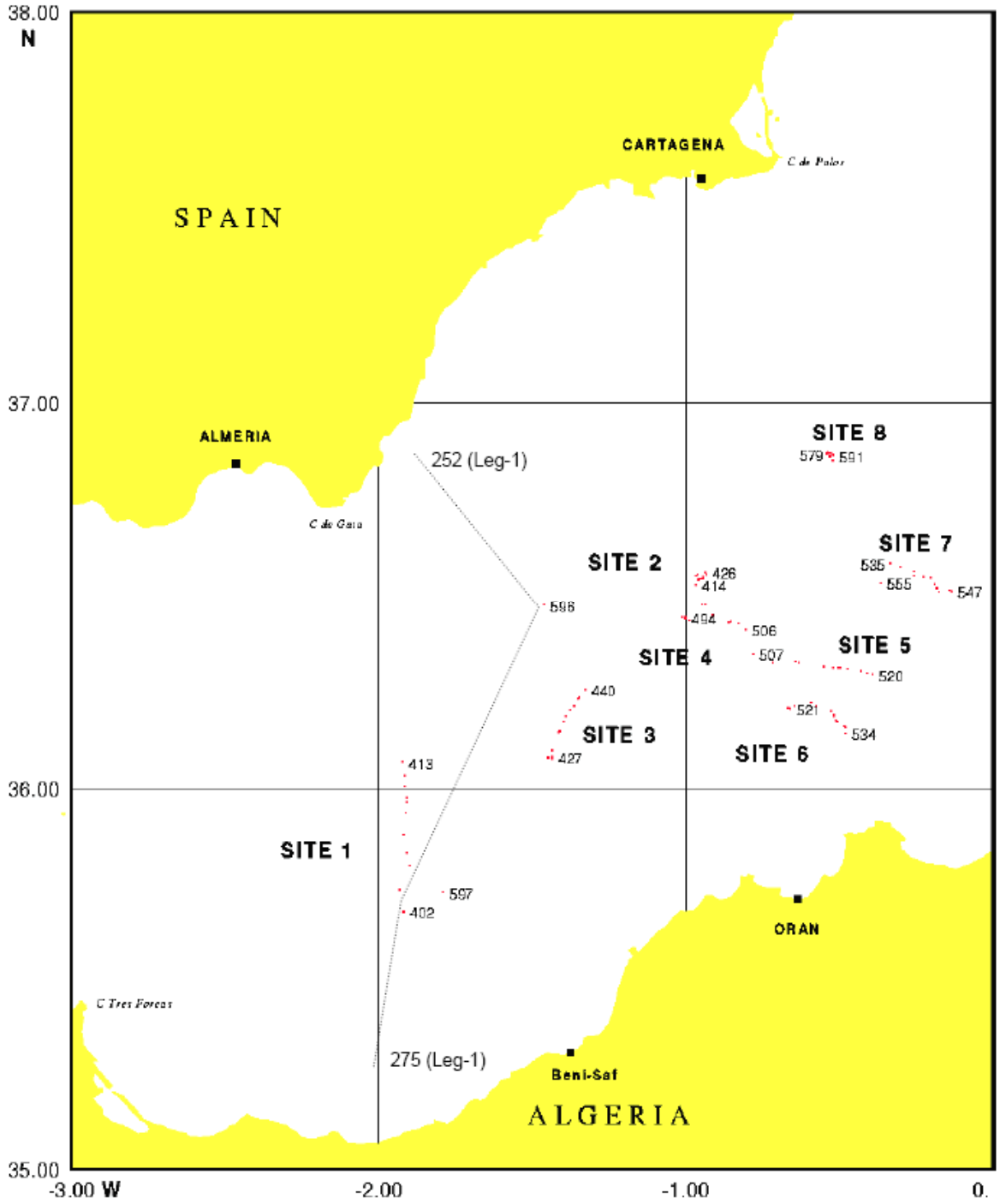

Figure 1 : Sampling locations of the Almofront-2 cruise in the Alboran Sea (SW Mediterranean Sea).

During the first leg of the cruise, a north-south transect was intensively sampled as symbolized by dashed lines. The 24 stations referred to as CTD 252 to 275 (see Cuttelod & Claustre, 2010) were separated from each other by about 5 nautical miles but CTD 260 to 269 by 3 n. miles and sampling was performed over the 0-200 m water column at 12 different depths.

During the second leg, 8 sites characterized by several stations were occupied for 36 h near the drift of the sediment trap line (0-400 m) deployed at starting time of each site. Both the photic and the aphotic layers were sampled in 'Mediterranean waters' (sites 2, 8), the front (site 7), the Atlantic baroclinic jet (sites 1, 4, 5) and the eastern Alboran gyre (sites 3, 6).

Sample processing

Samples were fixed during the cruise using a mixture of glutaraldehyde and paraformaldehyde (0.05 and 1% final concentration respectively) for 20 min and immediately frozen in liquid nitrogen (see Jacquet *et al*., 1998). Back to the laboratory, samples were stored at -80°C. Prior to analysis, samples were rapidly thawed at 37°C and divided into two aliquots: one for natural fluorescence analysis to get counts of autotrophic population, the other to enumerate heterotrophic bacteria after 10 min incubation of the samples with the fluorescent nucleic acid dye SYBR™Green I (Molecular Probes, 1/10,000 final concentration, Marie *et al*., 1997). Samples collected during the surface to bottom profile were divided into 3 aliquots, the last one being used to estimate titers of virus-like particles according to Marie *et al*. (1999). Briefly, samples were diluted from 1:5 to 1:10 in TE buffer (Tris 10 mM, EDTA 1 mM, pH 7.5), then incubated with SYBR™Green I at a final concentration of 1/20,000 for 15 min in subdued light.

Flow cytometric analysis and data processing

Samples were analyzed with a FACSort™ flow cytometer (FCM, Becton Dickinson, San Jose, CA). Setup for natural fluorescence was as previously described (Partensky *et al*., 1996). *Prochlorococcus* had low red chlorophyll fluorescence and could be easily discriminated from both the photosynthetic picoeukaryotes community and the background noise (Fig. 2A, B). *Prochlorococcus* and photosynthetic picoeukaryotes were discriminated from *Synechococcus* cyanobacteria on the basis of the orange phycoerythrin fluorescence of the latter (Fig. 2B). On stained samples, both photosynthetic picoeukaryotes and *Synechococcus* could be discriminated from other bacteria because of their higher red chlorophyll fluorescence (Fig. 2C). It was not the case for *Prochlorococcus* because of dim red fluorescence of the cells (Fig. 2C). Because, when stained, the two communities of *Prochlorococcus* and heterotrophic bacteria could not be discriminated by flow cytometry, the actual abundance of heterotrophic bacteria was determined by substracting the *Prochlorococcus* concentration determined on non-stained samples from the sum of the two populations obtained on stained samples. Two groups of virus-like particles referred to as V-I and V-II, following Marie *et al.* (1999), were discriminated according to the green dye-DNA fluorescence *vs*. right angle scatter (Fig. 2D). 0.95 µm fluorescent beads (Polyscience) were added to all samples and FCM parameters were normalized to them. Data were collected on "listmode files" and then analyzed using CYTOWIN (Vaulot, 1989, available freely at http://www.sb-roscoff.fr/Phyto/).

Confocal microscopy analysis

Confocal Laser Scanning Microscopy (CLSM, Fluoview, Olympus Optical Co., Tokyo, Japan) and image analysis were used to estimate the size of heterotrophic bacteria (Jacquet *et al*., 2002). Several samples from different depths and different hydrological situations were filtered onto 0.2 µm pore size inorganic membrane filters (Anodisc, Whatman™, Maidstone, UK). The filter disk was placed onto a slide. A 20 µl mixture (50%-50%) of normal PBS (Phosphate Buffer Saline, Sigma, Saint-Quentin Fallavier, France) and bi-distilled glycerol (d=1.26, Fisher scientific, Elancourt, France) was added with a drop of SYBR™Green I (1/1,000 final concentration). A 22 x 40 mm coverslip was overlaid on preparation. Images were acquired with the Fluoview software and processed using Image Tools. The average size (i.e. spherical equivalent) of bacteria was found to be 0.48 µm (SD=0.14, n=194).

Carbon biomass estimation

For heterotrophic bacteria, we used a conversion factor of 20 fgC.cell^{-1} (Lee & Fuhrman, 1987) that appears appropriate for cells ranging between 0.4 and 0.5 µm in diameter. Typical JGOFS values were used for the other groups, i.e. 53 fgC.cell^{-1} for *Prochlorococcus*, 250 fgC.cell^{-1} for *Synechococcus* and 2,108 fgC.cell^{-1} for photosynthetic picoeukaryotes (see Campbell *et al*., 1994 and references therein). To integrate carbon biomass through the water column, a uniform depth of 100 m was chosen rather than the mixed layer (that could vary between stations) or the euphotic zone (since low cell concentrations were often recorded below 60-70 m, i.e. the depth of 1% light). For viruses, we used 0.08 fgC.particle^{-1}, according to Bratbak *et al*. (1992).

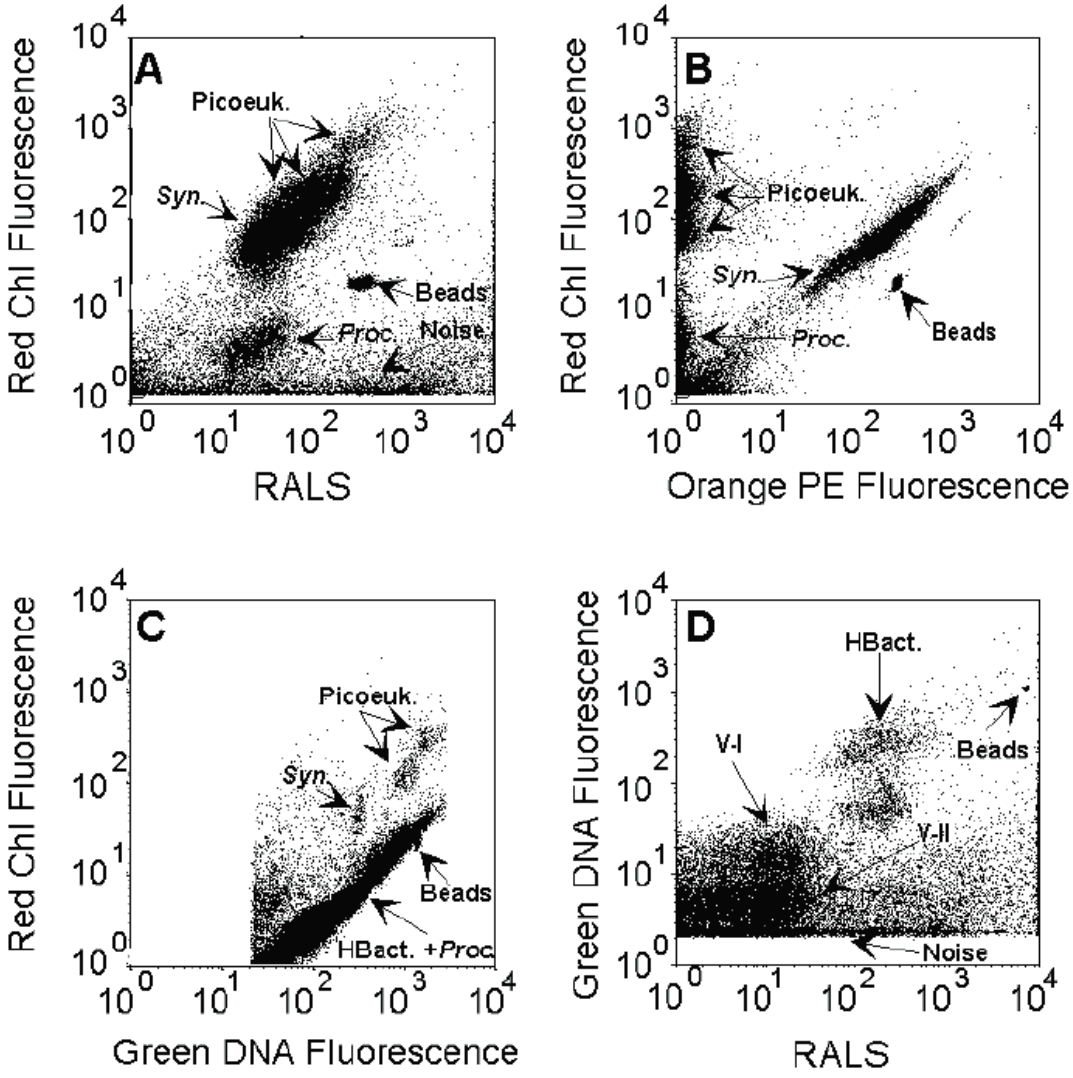

Figure 2 : Flow cytometric analysis of natural populations sampled in the Alboran Sea. Prochlorococcus, Synechococcus and picoeukaryotes were discriminated on the basis of their right angle light scatter (RALS) vs. their red chlorophyll fluorescence (A) or phycoerythrin orange fluorescence (B) from unstained samples. Heterotrophic bacterial populations were discriminated on the green DNA fluorescence vs. red fluorescence (C) and RALS (D) from SYBR Green stained samples. Viruses referred to as V-I and V-II (D) were discriminated on the basis of the green DNA-dye complex fluorescence vs. their RALS.

Other data sets

Density and chlorophyll fluorescence profiles were obtained from CTD instrumentation that measured these parameters continuously (see figures 3, 4). Density excess ($kg.m^{-3}$) was obtained from UNESCO standard equations. Chlorophyll *a* fluorescence was measured with the Chelsea fluorometer and converted to biomass ($mg.m^{-3}$) using appropriate conversion factor (i.e. 1.85 x F according to Cuttelod & Claustre, 2010). Horizontal current profiles was acquired with 2 ADCP 75 and 300 kHz vessel-mounted RDI® Acoustic Doppler Current Profiler (ADCP results shown in Sempéré *et al.*, 2003). Measurements of inorganic nutrient concentrations (nitrate, nitrite, phosphate) were carried out using a Technicon AutoAnalyser II according to standard colorimetric methods and following the procedures given in Tréguer & Le Corre (1975).

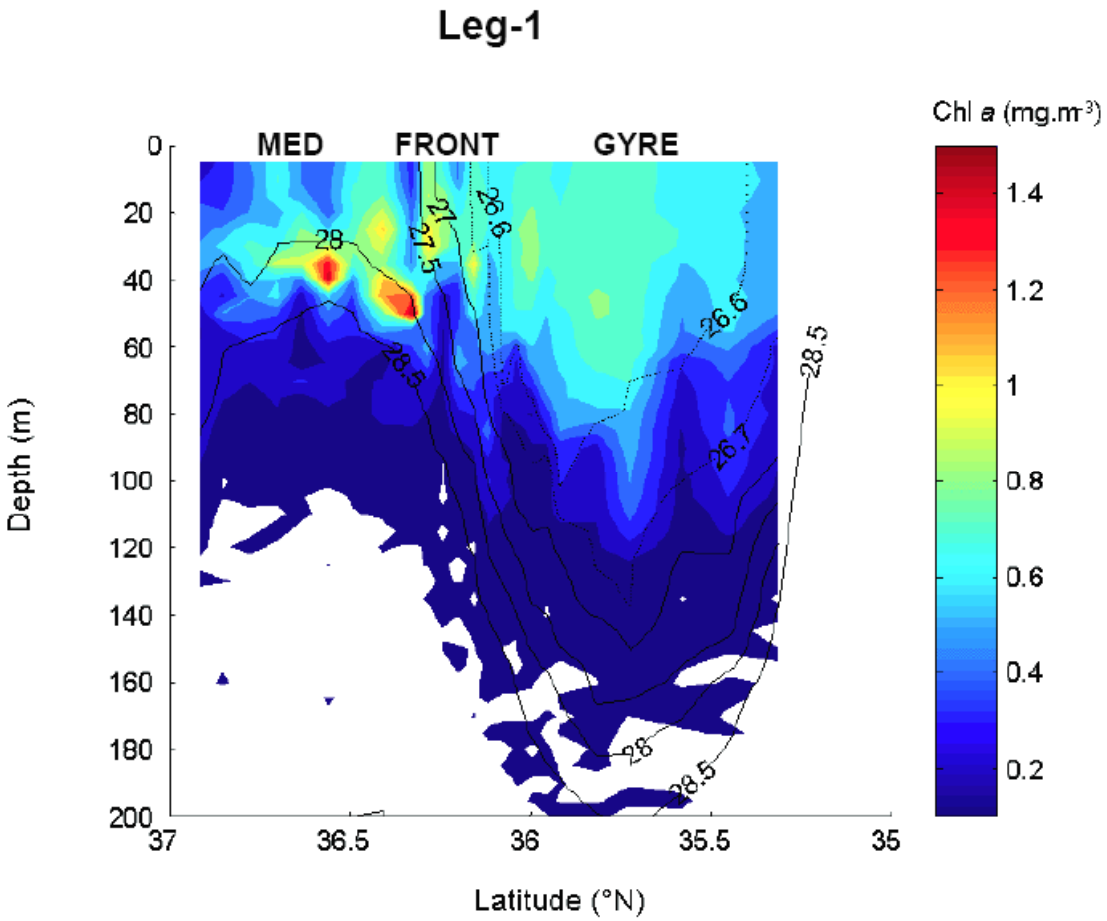

Figure 3 : Density profiles (kg.m^{-3}) and chlorophyll *a* distribution (mg.m^{-3}) along the CTD 252- 270 transect of leg-1 of the Almofront-2 cruise (between 13 and 16 December 1997).

Results

Hydrological conditions and chlorophyll distribution

Surface Atlantic water flowing into the Mediterranean Sea does not mix immediately with Mediterranean waters but their characteristics change progressively to the modified Atlantic waters (MAW) which are found in the western Mediterranean basin.

The North South transect crossed three types of hydrological structure (*leg 1*) :

(1) the Mediterranean waters (MED), cold and very saline, could be divided into two types referred to as MED-1 waters (CTD 252 to 255) from the Spanish coastal current that originated from the North Mediterranean and, more to the south, MED-2 waters (CTD 255 to 259, Conductivity, Temperature, Depth profiles are here the name of sampling stations);

(2) the Atlantic jet, the maximum current speed being found at CTD 260 to 268. The frontal structure was located between CTD 260 and 263, the gradient of temperature and salinity being particularly clear in surface waters at CTD 260 and 261. The core of the jet, as revealed by maximum current speed (up to 80 cm.s^{-1}), correspond to CTD 264 and 265 (see Fig. 3 in Sempere *et al.*, 2003).

(3) the Eastern Alboran anticyclonic gyre was revealed by surface warm water and density profiles with a deep mixed layer (CTD 269 to 275). The central part of the gyre for which current speed is weak, is sampled by CTD 271-272.

The bottom depth of surface mixed layer shifted from 30-40 m to about 110-130 m between the dense MED waters and the central part of the gyre. The maximum of Chl *a* concentration was tightly coupled to the 28.1–28.2 density excess isolines with two important patches (>1.2 mg.m-3) recorded in MED-2 waters and in the dense waters near the front between 30 and 50 m (Fig.. 3). In surface waters, significant concentrations of Chl *a* were mostly recorded in Atlantic and frontal influenced waters.

During the second leg, a well-stratified water column with excess density close to 28.0 (S>37.5 and T<16°C) and a 25 m deep surface mixed water characterized MED waters at sites 2 and 8 (Fig. 4 A, B).

In contrast, the water column profile in the frontal structure (site 7 corresponding to both the left side of the jet in surface and to MED waters at depth, see Fig 5) was more heterogeneous (Fig. 4C). A clear stratification was observed at the depth of 10-15 m, followed by a constant increase of density with depth until 100 m. However, two discontinuities in both temperature and salinity occurred between 15 and 60 m and between 60 and 100 m, respectively. An important Chl *a* maximum was recorded between 20 and 30 m (Fig. 4). However the amplitude and depth position of the maximum is changing between the 3 casts shown although small distance between these casts. The two first casts exhibit the strongest maxima, the third few hours after, with a deeper maxima around 40-50 m depths. It could be noted that the Chl *a* remains noticeable near 70-80 m depths (S>28.2) although inside the Med waters below the surface jet flow of MAW.

Closer to the jet core, but always on its left side looking downstream, the water column was homogenous over the first 30 m and a broad pycnocline developed between 30 and 150 m (site 4, Fig. 4D). Only weak variation in the profile structure between the 2 first relevant stations of site 4 and a Chl *a* fluorescence was recorded constant in mixed layer and weak at below depths. The third station exhibits a 50 m mixed layer and abrupt change in Chl *a* below, so during this site exploration the mixed layer increase the depth of mixed layer at constant Chl *a* concentration in.

In the core of the jet where surface current velocity was the highest (site 5), water column was homogeneous over the first 50-70 m and the pycnocline began at 80 m (Fig. 4E). The concentration of chlorophyll is constant from surface to 80 m although some variation occurs at the bottom of mixed layer.

The right side of the jet sampled at site 1 was characterized by a constant vertical gradient in density, temperature and salinity, between 30-45 m and 150 m and by a contrasted profile in Chl *a* with a minimum at 60 m and a strong maximum at 80 m for two among three profiles (Fig. 4F).

A well-mixed water column over the first 100 m characterized the outer side of the Alboran eastern gyre (site 6) with weak deep maximum for one among the 3 profiles of this site. Finally, near the centre of the gyre (site 3), the water column was well mixed over 80-100 m (Fig. 4G, H). The chlorophyll concentration was constant in the mixed water column and there was no deep maximum Chl *a* fluorescence at these two sites.

Other relevant characteristics recorded during leg-2, i.e. depths of the mixed layer (DML) and of chlorophyll maximum (DCM), as well as concentrations in inorganic nutrients in surface and at DCM are reported in Table 1.

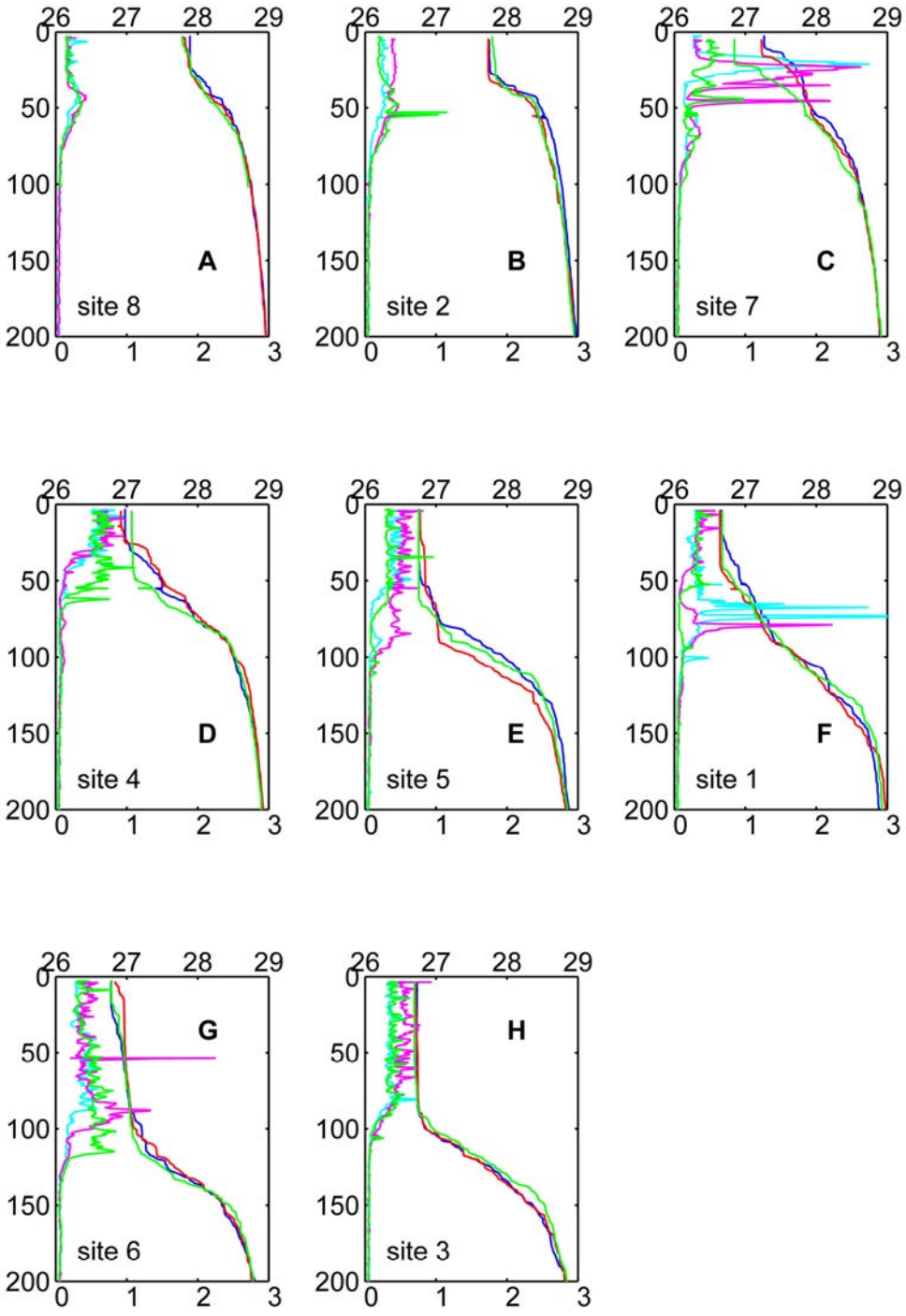

Figure 4. Density excess (26 to 29 kg.m^{-3}) and chlorophyll a calibrated fluorescence (1 to 3 mg.m^{-3}) vertical profiles recorded at 3 selected stations for each of the 8 sites investigated during leg-2 of Almofront-2 cruise. Blue, red and green color line respectively stands for the 1st,2nd and 3rd density profiles listed in table 1, and corresponding Chl *a* color are cyan, mauve and green.

Table 1: Hydrographical characteristics of the 3 selected stations per site during leg 2:
Site number;
Stations: (CTD numbers) ;
Latitude;
Longitude;
DML : depth of the mixed layer (m);
DCM : depth of the chlorophyll *a* fluorescence maximum (m);
Concentration of nitrates (N-NO3), nitrites (N-NO3), phosphates (P-P04) at surface and DCM (µM).

Site	CTD #	Lat. (°N)	Long. (°W)	DML (m)	DCM (m)	$NO_{3\ surf}$ (µM)	$NO_{3\ DCM}$ (µM)	$NO_{2\ surf}$ (µM)	$NO_{2\ DCM}$ (µM)	$PO_{4\ surf}$ (µM)	$PO_{4\ DCM}$ (µM)
	581	36.861	0.529	50	25	0.06	2.73	0.01	0.14	0.01	0.07
8	584	36.849	0.520	47	30	0.03	3.04	0.01	0.11	0.00	0.05
	588-7	36.871	0.535	50	30	0.03	1.78	0.00	0.17	0.00	0.02
	416	36.542	0.958	42	35	0.06	3.20	0.02	0.12	0.00	0.04
2	419	36.554	0.959	45	35	0.06	2.48	0.01	0.15	0.00	0.04
	423-2	36.543	0.943	45	32.5	0.06	2.35	0.00	0.17	0.00	0.04
	537	36.584	0.333	40	15	0.24	1.37	0.02	0.09	0.00	0.03
7	540	36.562	0.256	37	17	0.12	0.76	0.02	0.06	0.00	0.01
	544-3	36.519	0.181	35	22	0.09	0.09	0.02	0.02	0.00	0.00
	496	36.438	1.001	47	28	0.37	0.37	0.08	0.08	0.00	0.00
4	499	36.475	0.937	37	26	0.43	0.43	0.11	0.11	0.01	0.01
	503-2	36.430	0.857	67	50	1.01	1.22	0.09	0.10	0.02	0.02
	509	36.346	0.78	72	55	0.56	0.56	0.21	0.31	0.01	0.01
5	512	36.325	0.632	62	42	0.51	0.51	0.23	0.23	0.01	0.01
	516-5	36.311	0.502	82	65	0.64	0.64	0.25	0.25	0.01	0.01
	403	35.667	1.917	40	35	0.77	1.05	0.35	0.09	0.03	0.02
1	406	35.831	1.906	60	42	0.80	0.71	0.36	0.09	0.04	0.02
	410-9	35.962	1.909	57	40	0.78	0.78	0.28	0.27	0.02	0.01
	523	36.206	0.66	55	30/80	0.53	0.31	0.32	0.25	0.02	0.04
6	526	36.212	0.573	42	25/80	0.43	0.65	0.25	0.29	0.02	0.03
	530-1	36.175	0.507	50	30/90	0.55	1.4	0.33	0.30	0.02	0.05
	429	36.078	1.417	110	100	0.78	0.78	0.27	0.27	0.01	0.01
3	432	36.140	1.411	92	100	0.74	0.74	0.27	0.27	0.04	0.05
	436-5	36.200	1.375	100	97	0.71	0.8	0.34	0.32	0.01	0.02

3.2. Comparison between legs

Characteristics and positions of stations (leg-1) and sites (leg-2) were compared based on density profiles, ADCP measurements and GPS data (Global Positioning System). The meander-gyre system clearly moved eastwards during the second leg (about 56 miles between 22 December and 16 January, see VanWambeke, 2004), so that geographical positions did not correspond to the same water masses at any period of time throughout the period of study. Nevertheless, vertical profiles sampled during leg-2 could be compared to those obtained on the north-south transect of leg 1 (Table 2). It has to be noted that the initial location of each site was chosen after a 12 hours survey at 12 knots as for Almofront 1 cruise (Prieur & Sournia, 1994; Claustre *et al.*, 2000) in order to follow this slow North Eastwards drift of the whole frontal jet –eddy structure using real time information from ADCP profiles and Thermosalinograph. Therefore the long-time stations can be referred to one of the typical situation observed along the North-South transect of leg 1. They illustrate as a virtual frontal system (Fig 5), the real one which is in Alboran basin continuously stretching or compressing under the effect of the large scale forcing factors.

Table 2: Correspondence between sites from Leg 2 and stations from Leg 1 transect. Sites are ranked as to follow the North-South structure observed in the transect. Stations are named by the CTD number.

Sites (Leg 2)	Stations (Leg 1)	Characteristics
2	259-263	Mediterranean (MED2) waters
8	258-259	Mediterranean (MED 2) waters
7	260-262	Left side of the jet near surface front meander crest
4	262-263	Left side of jet core (south-eastward current)
1	262-263	Right side of jet (northward current, meander through)
5	264-265	Right side of jet core (south-eastward current)
3	266-267	Eddy (weak northward current)
6	266-267	Eddy (weak north-easterly current)

Mediterranean sites 2 and 8 show the same density profiles than MED-2 waters in leg 1's transect. Sites 7, 4, 5 are representative of the frontal gradient structure. Site 4 and 7 represent the left side of the jet. More precisely, the first day spent at site 7 could be related to the left side of the jet whereas the second day was more towards the core part of the jet. The current direction (south-east ward) suggests the site 7 is on the eastern part of the meander crest of the frontal jet-eddy system. Site 5 was a southeast current is also observed is similar to the right side of the jet core. Site 1 is typical of a frontal structure but the northward current indicate that it is in the western part of the front-eddy system and near the through of the jet meander.

The anticyclonic gyre with a weak Atlantic water mixed layer stratification is sampled by site 6 with a southeast current in surface, and site 3 where a weak north-eastwards current was observed. The position of the successive CTD profiles, made at each site on the drifting ship by following the sediment trap drifting line, illustrate the current pattern in this part of Alboran Sea (Fig 1).

So, by relocating the leg2 sites in a moving frame (Fig. 5) of the frontal jet-gyre system and using physical properties (density, mixed layer depth, horizontal currents) and Chl *a*, it is straightforward to compare how the bacterial communities change or not between the leg 1 and leg 2 cruise (Table 2). By comparing Chl *a* section of figure 3 and profiles obtained at each sites (Fig. 4) it easy to confirm that the repartition horizontal and vertical of Chl *a* were similar. In addition the intra-site variability between profiles were already proved much below the inter-site variability on physical properties (Van Wambeke *et al*., 2004), suggesting that physical and hydrodynamical forcing drive the biomass distribution through the system, despite of its North eastwards drift.

Table 3: Characteristics of the mixed upper layer at the different sites in Leg 2. Depth of the homogeneous layer (Z) for water density and picoplankton cells abundance.

Sites	Types	Z-Excess density (m)	Z-Prochlorococcus (m)	Z-Synechococcus (m)	Z-picoeucaryotes (m)
8	Med	25	40	30	20
2	Med	30	30	25	20
7	Front outside jet	15	20	10	10
4	Front inside jet	25	20	25	20
5	Jet	55	70	70	70
1	Jet	45	50	35	40
6	Gyre border	gradient	110	gradient	110
3	Gyre center	90	90	90	100

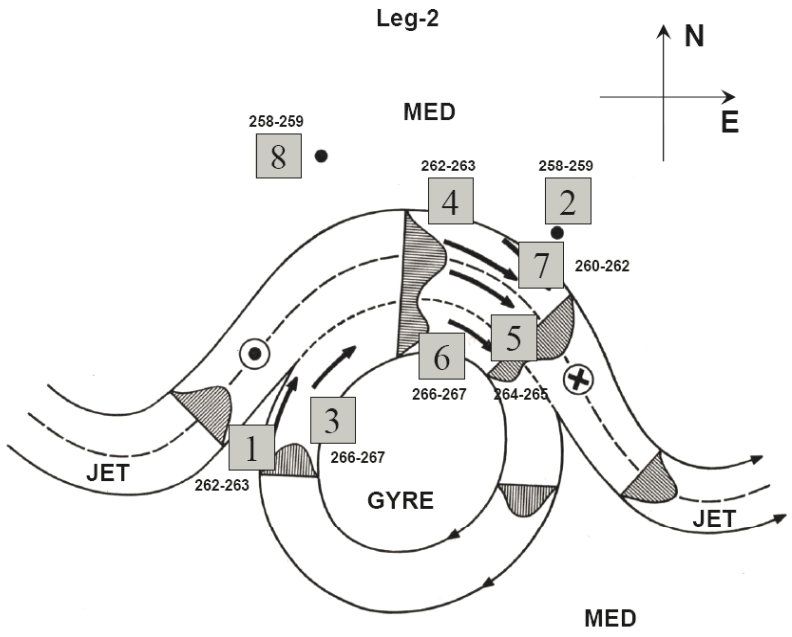

Figure 5: Schematic positions of sites in a moving frame of the jet-front-gyre system explored during leg-2.

Arrows symbolize horizontal current strength of the horizontal flow in different parts of the meandering frontal jet – gyre structure, as measured by ADCP.

In addition, a circle point and a cross are set near the curved axis of the meandering jet to symbolize some upward (circle point) and downward flow (cross) currently observed in such system (Bower & Rossby, 1989). However other kind of secondary circulations, involving vertical velocities and transverse to frontal system, are possible at submesoscale as suggested in text and by Prieur et al.(1993) or Klein and Lapeyre (2009).

Structure of the microbial communities

North South transect (Leg 1)

Along the transect *Prochlorococcus* cells were more abundant in Mediterranean waters (MED1, 6.3 10^3.ml^{-1}) than in the gyre waters (Fig. 6A). They are relatively abundant in the north side of the front. More south, abundances are low and similar in the jet and in the centre of the gyre (31 10^3 cells ml^{-1}).

Synechococcus displayed the same spatial trend as *Prochlorococcus* in the north part of the transect (max in MED1, 40 10^3.ml^{-1}) (Fig. 6B), except a more rapid decrease of abundance with depth. In contrast to *Prochlorococcus*, *Synechococcus* concentrations are relatively abundant (45 10^3.ml^{-1}) in the jet and inside the gyre.

Photosynthetic picoeukayotes concentration is relatively low in MED waters (1 10^3 .ml^{-1}). These cells were abundant in the frontal waters where *Prochlorococcus* and *Synechococcus* were relatively less abundant than in other places. The highest concentration was recorded in the centre of the gyre (23 10^3 cells ml^{-1}) and the high concentrations layer extend deeper. The spatial distribution of these cells appears to follow the isopycnal distribution

Heterotrophic bacteria show an increasing concentration from north to south (Fig. 6 D) High concentrations are found in the gyre core where their pattern appears to be shaped by the density pattern, as for picoeukaryotes. In the Northern part of the transect the low abundance of heterotrophic bacteria in the MED 1 waters but quite high concentration in MED 2 waters contrasts with the *Prochlorococcus* and *Synechococcus* abundances. Spots of high concentrations are found at the depth of 30 m in MED 2 water and deeper in the front (50 m).

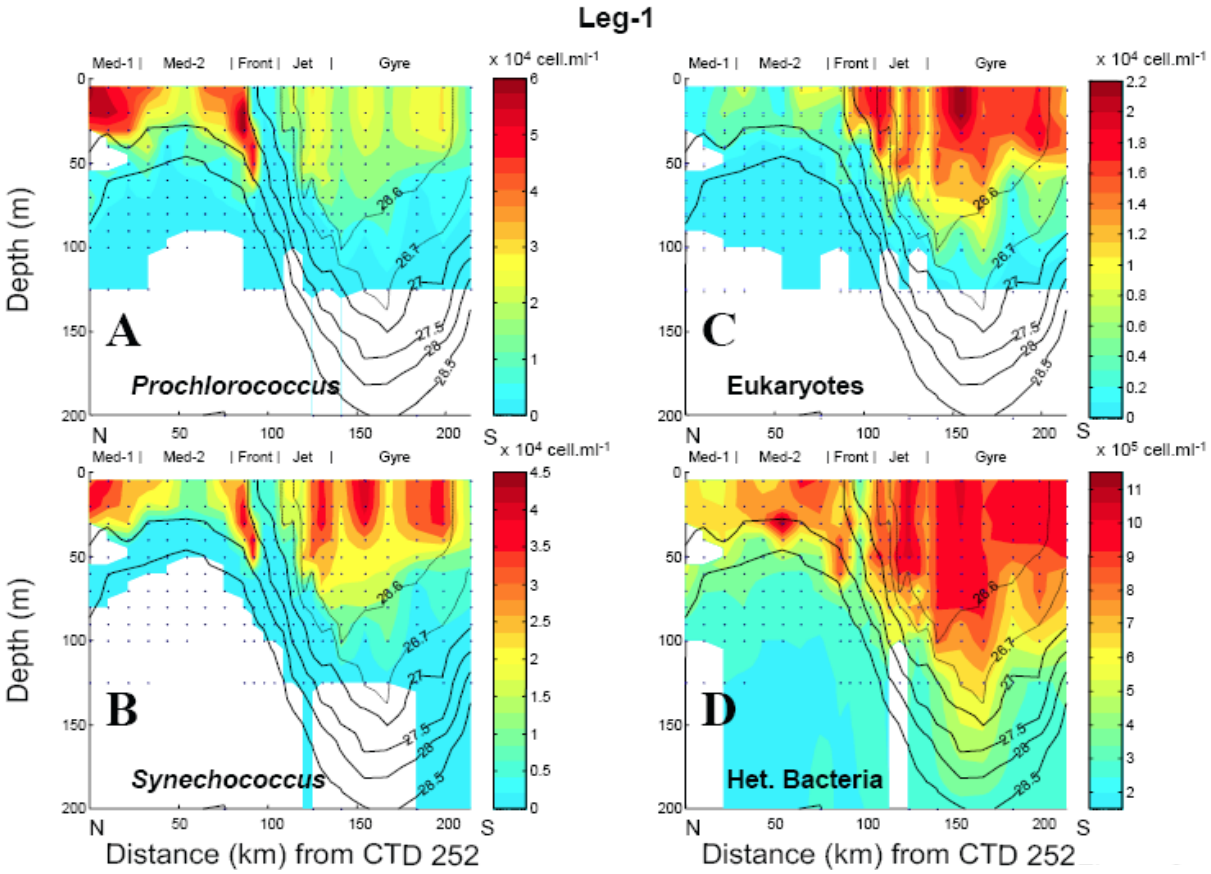

Figure 6 : Distribution of picoplanktonic populations along the transect 2 of leg-1 of the Almofront-2 cruise. (A) *Prochlorococcus*, (B) *Synechococcus* , (C) picoeukaryotes, (D) heterotrophic bacteria. Distances are given in km from CTD 252 (North). Density isolines are expressed in kg.m^{-3}. Note that the color scale varies with groups.

A common pattern to all groups (except *Prochlorococcus*) is a relatively high abundance in the deep water in the gyre, reaching 100 m which suggest there a downwelling effect. Nevertheless the higher abundance in surface water might be the consequence of a growth rate higher enough to compensate the loss rate a downward flux in the gyre core. Another common feature is low concentrations in the front part of the jet which could sign upward advection of water in the 27 -27.5 isopycnal band.

Sites (Leg 2)

The second leg observations confirm the spatial structure observed on the transect. The three profiles obtained at each site provide a visual estimation of the time and space variation in the cells distribution at the same location relative to the front.

Although *Prochlorococcus* stays the most abundant primary producer, its variation in abundance in surface is lower than on the transect. Figure 7 gives, for each site, three profiles which show a similar pattern except in site 4. A 40 m upper layer with constant concentrations, suggesting some amount of mixing, a gradient declining progressively to nearly 100 m and deeper, when sampled, low concentrations constant with depth. The upper mixed layer (Fig.4 and Table 3) is 30 m in Mediterranean waters (sites 8 and 2), 10-20 m in the north side of the jet (site 7), deepens at sites 4 and 5 and is 80 – 110 m in the gyre border and centre (sites 6 and 3). The sites related to the jet show a more complex vertical profile. A 20 to 30 m homogeneous layer is observed above a constant gradient of declining concentrations. The three profiles appear more different between them than do in the other sites. Although it is expected a difference between the morning and evening profiles, a spatial heterogeneity in the abundances in these frontal and jet site are suggested. The downward component

of the jet current which drives, along the isopycnes surface properties to the depth might be the origin of this heterogeneity. The deep maximum found in these profiles (70, 90, 120m) might be clues of such an entrainment on the isopycnic surfaces. The variability shown by these profiles should the result of sampling in the sub-mesocale structures associated with fronts and eddies (e.g. Klein & Lapeyre, 2009)

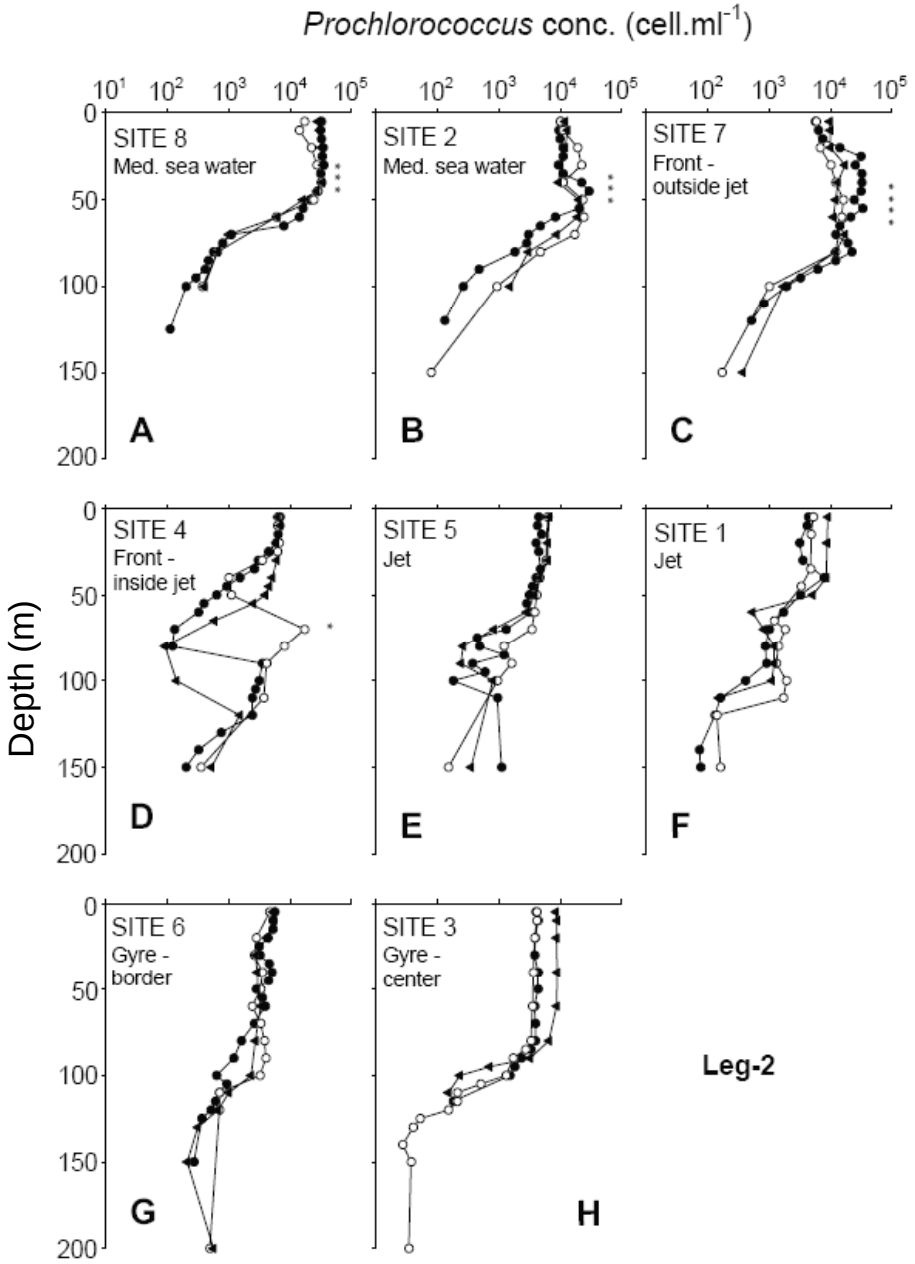

Figure 7: Vertical profiles of *Prochlorococcus* at the different sites investigated during leg-2. The three selected CTD were sampled at 8:00 (○) and 20:00 (●) of day 1 and at 8:00 (◀) of day 2 (local time). Small stars symbolize depths where two populations of *Prochlorococcus* were observed.

Profiles from sites 2 and 7 suggest a maximum of concentrations centred to 30 m and 40 m respectively, but clearly the deep maxima at site 7 is below the mixed layer depth there. The flow cytometer allowed us to observe there two distinct populations of *Prochlorococcus* with different chlorophyll fluorescence (e.g. Moore et al., 1998) at the bottom of homogeneous layer in Mediterranean waters (sites 8 and 3) and at the north side of the front (site 7), as well as in one sample in site 4.

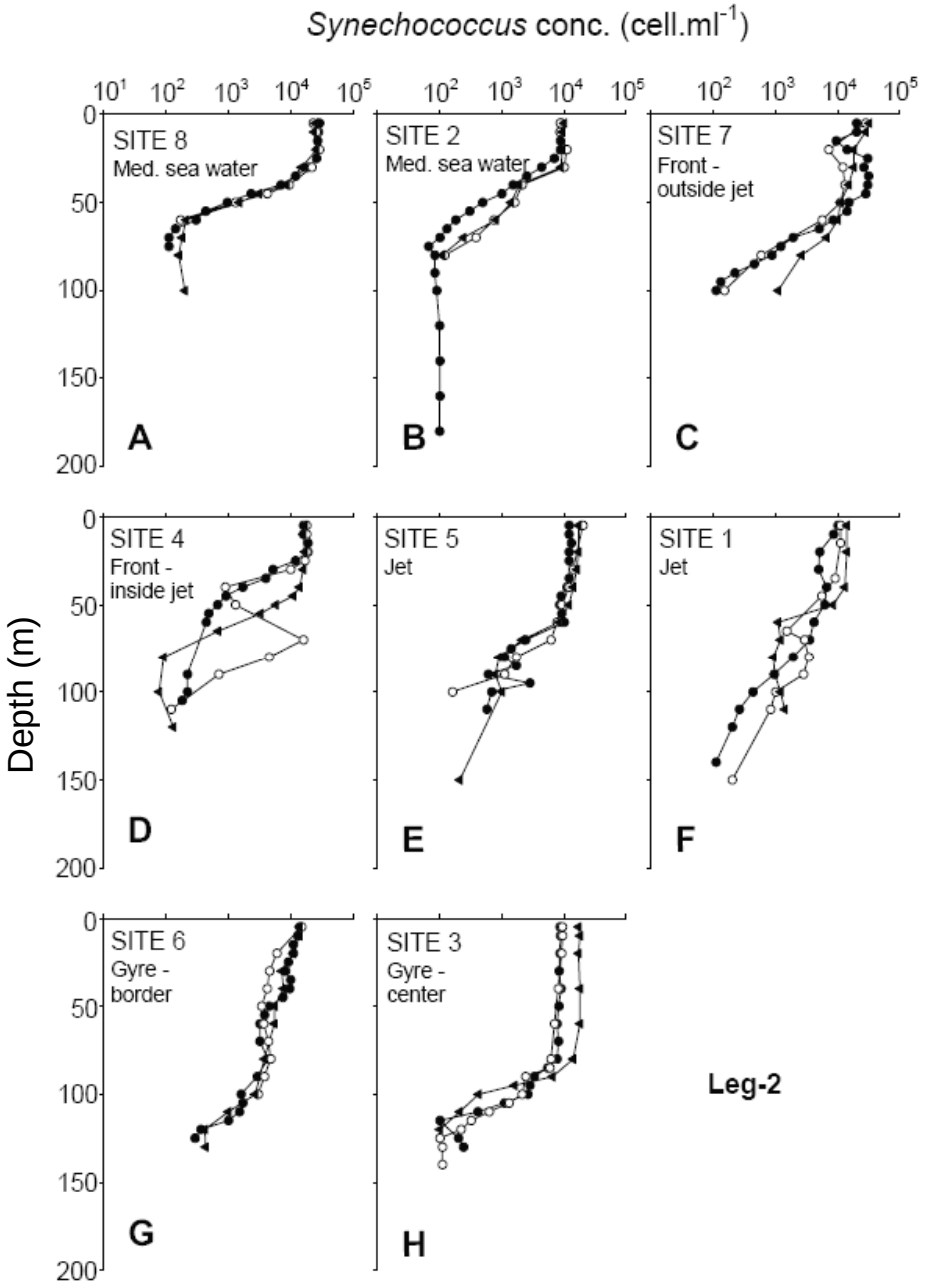

Figure 8 : Vertical profiles of *Synechococcus* at the different sites investigated during leg-2. The three selected CTD were sampled at 8:00 (○) and 20:00 (●) of day 1 and at 8:00 (◀) of day 2 (local time).

Synechococcus vertical profiles show nearly the same pattern as those from *Prochlorococcus* (Fig 8). However a closer examination shows some differences. In Mediterranean waters (site 8, 2), the homogeneous surface layer is shallower and the gradient steeper. The deep layer with constant concentration appears to start at 70 m. In the gyre waters (site 3) the gradient is the same as for *Prochlorococcus*. In the gyre border (site 6) the concentrations are declining slowly from surface to depth, as a remnant of the jet profile (site 1) which shows a constant declining gradient from surface to 150 m. The same type of variability in the profiles in the same site is found in the front inside the jet (site 4), strengthening the hypothesis on a physical entrainment of surface populations to depth.

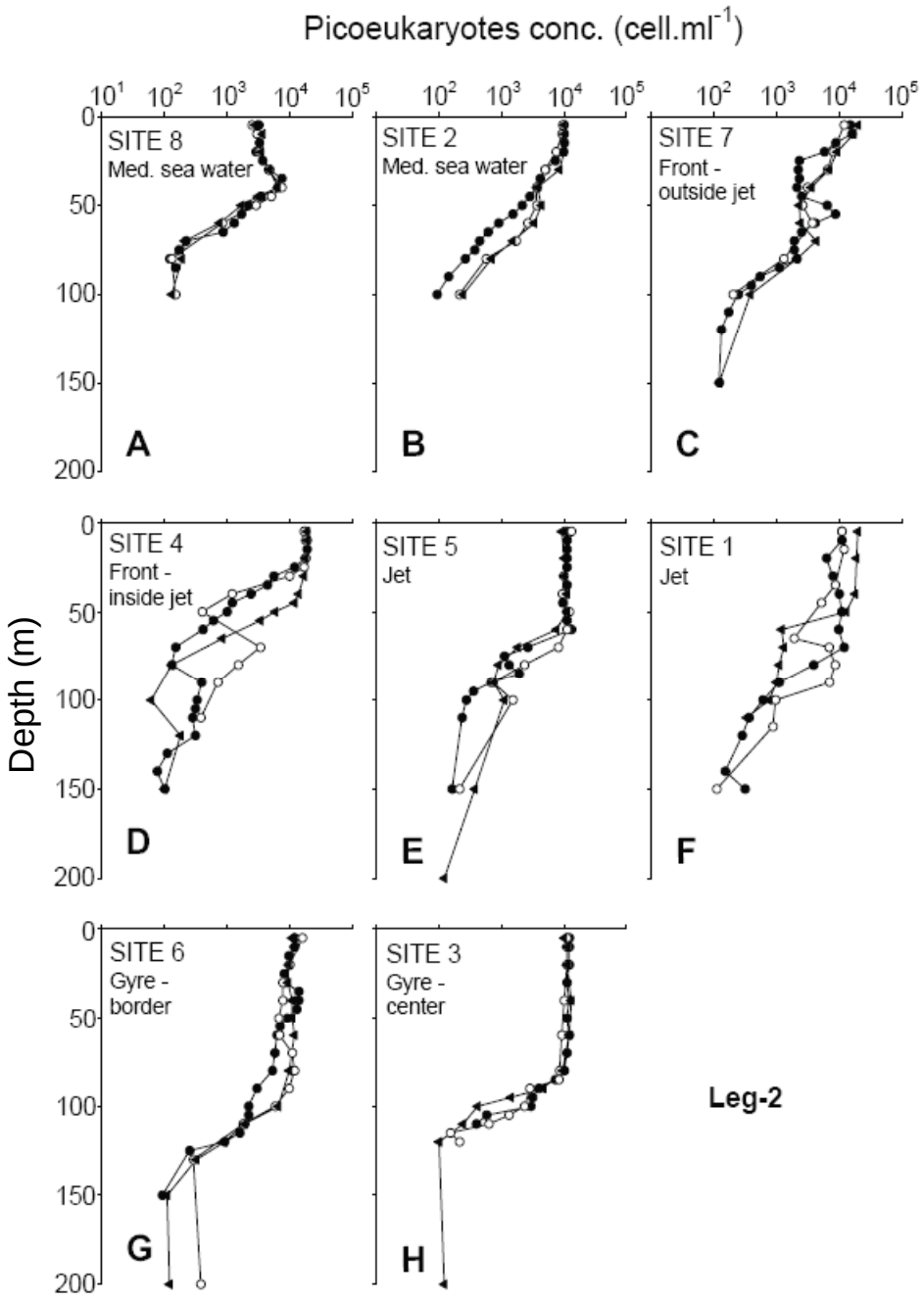

Figure 9: Vertical profiles of picoeukaryotes at the different sites investigated during leg-2. The three selected CTD were sampled at 8:00 (○) and 20:00 (●) of day 1 and at 8:00 (◀) of day 2 (local time).

The same remarks can be done about vertical profiles of picoeukaryotes concentrations (Fig 9). The general patterns are similar to the ones of the cyanobacteria. However in Med. waters there is a sub surface maximum in concentration (40 m), a shallow homogeneous layer in sites 2, 7 and 4, and a clear mixed surface layer down to 60 m in the jet (site 5). It should be noted that at site 3, in the gyre, the constant concentration layer of picoeukaryotes is deeper than observed in Leg 1. As for the other primary producers a large variation between successive profiles under the jet influence is observed at site 4 and also at site 1.

The primary producers profiles follow the density profile at most sites. The homogeneous layer depth is nearly the same as the mixed layer depth. At site 6 (gyre border) the profiles suggest a homogenous layer in *Prochlorococcus* and picoeukaryotes abundances when the density profile shows a gradient (Fig. 4). *Synechococcus* profile at the same site suggest also a gradient of abundance instead of an homogeneous concentration

Heterotrophic bacteria and VLPs which have been counted in surface layer (0-200 m) and in the deep layer (500-2000 m) show the same pattern of decrease with depth (Fig. 10)**.** Heterotrophic bacteria at surface show a nearly constant concentration (1 10^6 cells.ml-1) except in the Mediterranean site 8 (0.8 10^6 cells.ml-1) and in the gyre site 3 (0.09 10^6 cells.ml-1). The concentrations in deep water (2000 m) are approximately two orders of magnitude less than in surface layer. The general pattern of the vertical profile for the two groups is a constant exponential decrease in abundance in surface layer which continues to 1000 m and below a constant concentration. It could be noted that the Levantine Intermediate water (LIW) observed at 400-500 m depths exhibit higher concentrations than the deep water of the western Mediterranean Sea. However no LIW, i.e. no deep salinity and temperature maxima was observed below the eastern gyre (eddy) (data not shown).

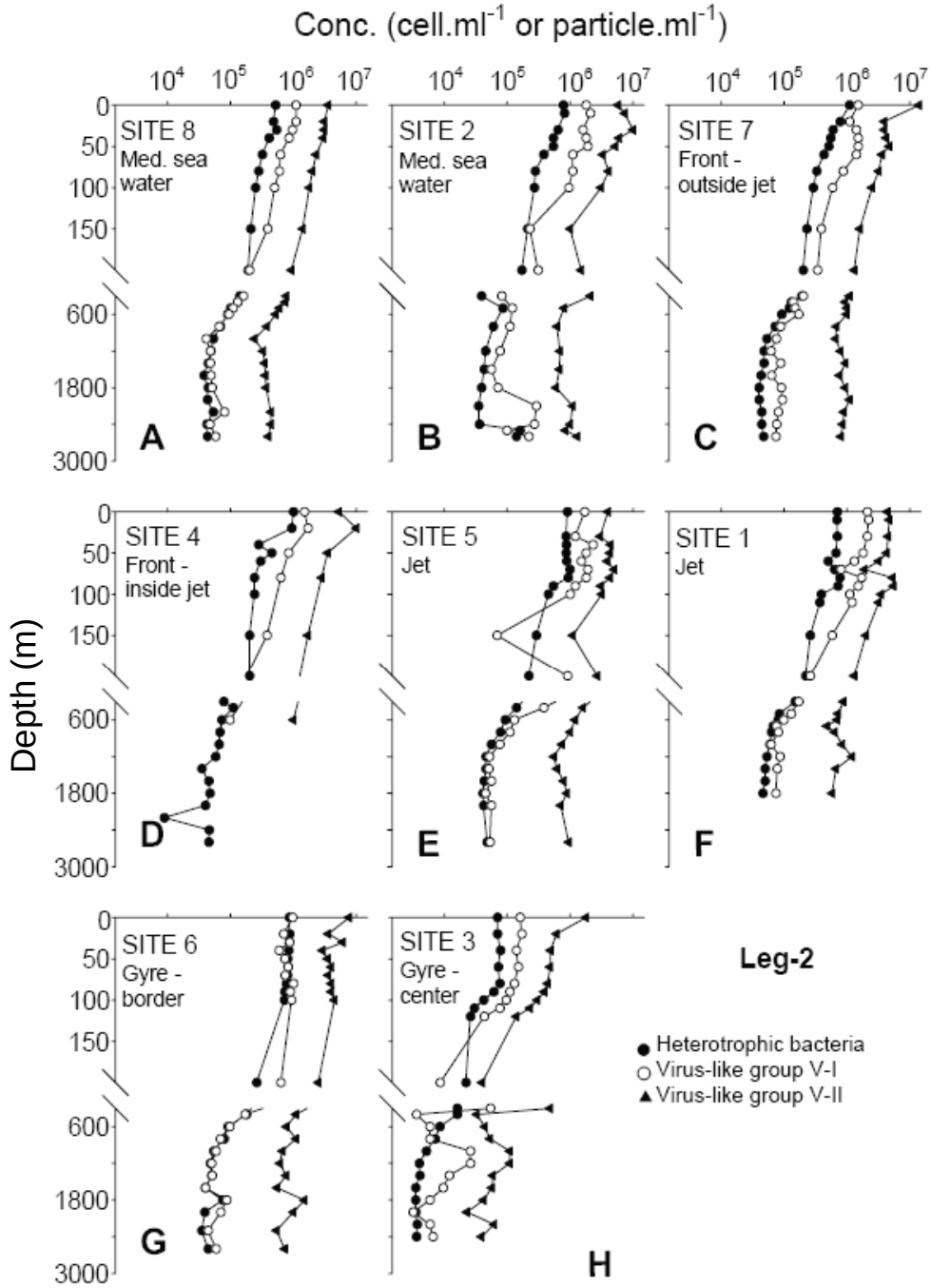

Figure 10:: Vertical profiles of heterotrophic bacteria and viruses over the entire water column at the different sites investigated during leg-2. This station was sampled at early night (between 20:00 and 22:00 local time).

The two groups of virus-like particles appear to decline with depth in the same way although the concentration of group V-I is nearly one order of magnitude smaller than group V-II. In the deep layer the abundance of V-I is much lower than V-II (1.5 orders of magnitude less), except in the gyre center (site 3). Some clear maxima can be observed in the deep layer at sites 2 and 3. This suggests some biological heterogeneity in the body of Mediterranean deep water in Alboran Sea. The ratio of total viruses to bacteria (VBR) was varying between 2 and 55 (12 on average). In surface waters (0-200 m) at site 6, viruses V-I and bacteria show the same abundance, whereas at other sites, viruses V-I were always more abundant than the bacterial community. At nearly all sites this difference was attenuated with depth (see sites 8, 7, 5, 1 and 6).

Carbon biomass distribution

Photosynthetic picoeukaryotes and bacteria contributed mostly to total carbon biomass (Fig. 11). There is a strong contrast between Mediterranean waters where bacteria biomass is larger than picoeukaryotes biomass, and the jet and gyre waters where the picoeukaryote biomass dominates. Carbon biomass of bacteria remained relatively constant in MED waters at ~100 µgC.cm^{-2}, increased regularly to the South crossing the front, and is nearly constant in the jet and gyre waters at ~200 µgC.cm^{-2}. However the increase in bacterial biomass from Med waters to gyre waters (nearly two fold) is clearly lower than that recorded for photosynthetic picoeukaryotes (5 to 6 fold increase, from 70 to 320 µgC.cm^{-2}).

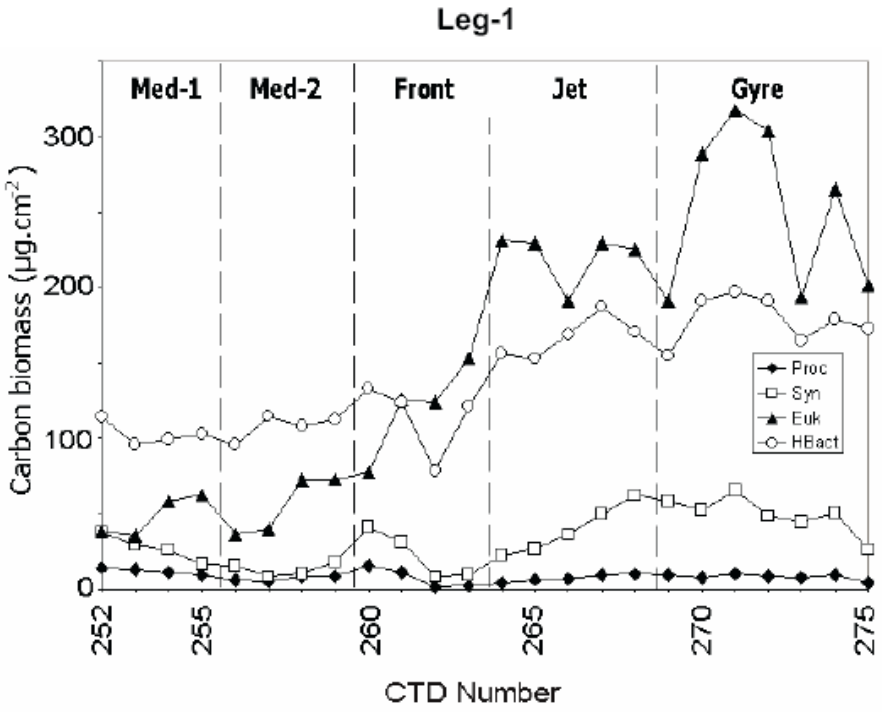

Figure 11: Carbon biomass concentration (µgC.cm^{-2}) of *Prochlorococcus*, *Synechococcus*, picoeukaryotes and heterotrophic bacteria integrated over 0-100 m at each station of the transect 2 of leg-1.

Highest values recorded for carbon biomass were associated to the community of photosynthetic picoeukaryotes that dominated the C pool that increased significantly from Mediterranean waters towards the gyre (from 70 to 320 µgC.cm^{-2}). It is noteworthy that in MED-1 waters near the Spanish coast, the contribution of photosynthetic picoeukaryotes equalled that of *Synechococcus* at about 38 µgC.cm^{-2}. (Fig. 11). Highest C values for *Synechococcus* (65 µgC.cm^{-2}) were recorded inside the gyre. *Prochlorococcus* carbon contribution was 2 to 3 fold higher at MED and frontal sites than in modified ATL waters (gyre waters) but that never exceeded 7% of the total (CTD 252 and 260, max 15 µgC.cm^{-2}).

Summing contributions of all picoplankton groups in the 0-100 m layer the highest total carbon biomass was recorded on Leg 1 in the southern part of the transect. Total carbon biomass of picoplankton was highest, first in the gyre (up to 590 µgC.cm^{-2} at CTD 271) and second in the jet (up to 475 µgC.cm^{-2} at CTD 267). By comparison, total carbon biomass was clearly less in the front (~290 µgC.cm^{-2} at CTD 261) and in MED waters (<220 µgC.cm^{-2}).

A decrease in the total carbon biomass was measured between leg-1 and leg-2, especially in the gyre (up to 30%). However photosynthetic picoeukaryotes and bacteria still contributed mostly to total carbon biomass of picoplankton and the total contribution of other groups (i.e. *Prochlorococcus* + *Synechococcus* + viruses) never exceeded 20% (Fig. 12). There was a weak decrease of the contribution of bacteria to total picoplanktonic carbon biomass (from 50 to 40%) from Mediterranean sites to gyre sites.

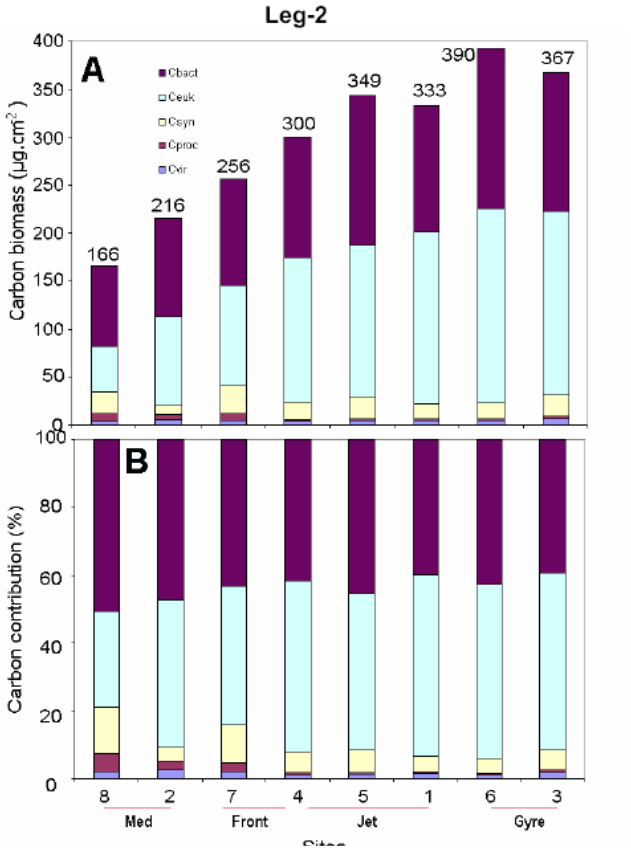

Figure 12 : Absolute (A) and relative (B) averaged carbon biomass integrated over 0-100 m for each site of the leg-2, given in µgC.cm^{-2} and % respectively of the whole microbial compartment composed of *Prochlorococcus*, *Synechococcus*, picoeukaryotes, heterotrophic bacteria and viruses.

As for leg 1, during leg-2, photosynthetic picoeukaryotes biomass increased significantly from north to south, from Mediterranean waters, site 8, to gyre waters, site 3 (from 45 to 200 µgC.cm^{-2}). *Synechococcus* contribution to the C pool never exceeded 12% and the highest contribution was recorded at sites 8 and 7 (with 25-30 µgC.cm^{-2}).

In ATL waters, from jet to gyre sites, *Synechococcus* contribution was very similar for the different sites and remained <10%.

Although very small, *Prochlorococcus* carbon contribution was 2 to 3 fold higher at MED and frontal sites than in jet and gyre site. The contribution of viruses to carbon was very small and varied between 4.5 (site 4) and 10.5 µgC.cm^{-2} (site 3).

The proportion of particulate carbon (Cp) in the picoplankton fraction (<2 µm) compared to the <200 µm size fraction is summarized in table 4. The picoplankton contribution varied between 11% at site 4 and 53% at site 8.

Table 4: Contribution (in %) of picoplankton (fraction < 2 µm) to the total (>0.2 µm):
Chlorophyll *a* (Chl *a*); particulate carbon (Cp); particulate nitrogen (Np) at the depth of maximum of Chl *a* and 50% of surface light.
The corresponding concentrations at the depth of sampling for *Prochlorococcus* (*Proc*), *Synecococcus* (*Syn*), picoeucaryotes (Euk) and heterotrophic bacteria (H bact.) are given (numbers in 10^3 cell.ml^{-1}). Chla<2 µm, Cp<2 µm, and Np<2 µm were not measured at site 1.

Site	CTD	Depth	Chl *a* < 2 µm	Cp < 2 µm	Np < 2 µm	*Proc.* ---	*Syn.* -x 10^3	Euk. cell.ml^{-1}	Hbact. ---
2		50% light	22	35	27	11	10	10	810
2		max chl *a*	18	28	22	32	0.77	2.6	440
8	580	50% light	22	53	55	43	13	9.5	710
8	580	max chl *a*	24	27	32	41	31	3.5	600
7	536	50% light	26	31	26	35	36	4.4	520
7	536	max chl *a*	24	29	23	34	19	9.0	540
4	495	50% light	18	22	23	5.5	15	18	130
4	495	max chl *a*	4	11	20	0.98	0.71	1.4	630
5	508	50% light	16	34	28	4.2	13	13	1000
5	508	max chl *a*	16	19	20	4.2	12	13	1000
6	522	50% light	20	30	30	2.4	7.3	7.5	910
6	522	max chl *a*	12	33	20	5.9	1.5	13	830
3	428	50% light	18	20	23	4.9	11	11	1000
3	428	max chl *a*	49	19	46	4.0	9.2	11	980

Discussion

During the first part (leg-1) of the Almofront-2 cruise (winter 1997), the Almeria-Oran frontal – gyre structure was well marked with the Atlantic jet passing north of the anticyclonic gyre. This situation was different from the one recorded during the Almofront-1 cruise (spring 1991) where a second anticyclonic gyre was observed north of the Atlantic jet close to the Spanish coast. However the position of the jet north to the eastern anticyclonic gyre can fluctuate strongly in latitude (see figure 1 in Prieur & Sournia, 1994).

Clearly, no anticyclonic gyre was observed north to the jet during Almofront-2, but the southern one was fully developed and the frontal zone was observed as also found by Viudez *et al*. (1998) in 1992 and by Allen *et al*. (2001) in 1996. During the second leg, the anticyclonic gyre system moved slowly eastwards. In order to choose the sites for 36 h observations of leg-2, quick surveys were performed using an ADCP and a thermosalinograph. Then the ship was positioned in different part of the moving jet-eddy structure.

Correspondence between leg-2 sites and hydrodynamical structures recorded on the north-south transect (leg-1), is given by Cussat-Legras *et al*. (2001) and Prieur *et al*. (2003) and shown on figure 5.

Three physical zones could be discriminated and three types of systems, based on picoplankton distribution, could be defined: the Mediterranean system in the Northern part, the Atlantic water anticyclonic gyre system in the southern part, and the frontal system in-between. In the following paragraphs, we discuss each situation and document how frontal mesoscale features strongly influence the environment which controls picoplankton distribution (i.e. nutrient, light, and mixing).

Mediterranean ecosystem

Typical MED waters were relatively oligotrophic with concentrations of nitrates and phosphates in surface layer lower than 0.06 and 0.02 µmol.l^{-1}, respectively (Table 1), resulting in the lowest carbon biomass registered in the Alboran Sea during the cruise (Fig. 12). Not surprisingly, *Prochlorococcus* was found to be the most abundant picophytoplankton group (e.g. Partensky *et al*., 1999), especially at depth larger than 30 m (site 2) and in typical MED waters. This result is in agreement with the observations of Moran *et al.* (2001) in typical MED waters surrounding the Algerian current, further East, on October 1996, who showed the dominance of *Prochlorococcus* over the other picophytoplankters in the 0-90 m layer.

It is noteworthy that, at site 2, the differences of concentrations between *Prochlorococcus*, *Synechococcus* and picoeukaryotes in the 0-30 m surface layer were very small and *Prochlorococcus* only dominated over the two other groups from 30 m to nearly 100 m, the bottom of the euphotic layer. This suggests that this site was not highly oligotrophic and that the frontal hydrodynamical structure (as inferred from gradients of temperature, salinity and current speed) and internal waves induced an horizontal spreading or injection of nutrient in the nearby Mediterranean surface waters (Fasham *et al*., 1985). A similar fertilization had already been reported during Almofront-1 (Videau *et al*., 1994). Site 8 was clearly more oligotrophic with picoeukaryotes one order of magnitude less concentrated than *Synechococcus* in surface waters. In a parallel study, Van Wambeke *et al*. (2004) also showed clear differences between sites 2 and 8 with primary production 3 time higher and bacterial production 1.5 times higher at site 2 than at site 8. The two groups of *Prochlorococcus* with different chlorophyll fluorescence signatures regularly observed at depths about 30 to 50 m in MED waters, correspond probably to genetically distinct ecotypes (Moore & Chisholm, 1999; Ahlgren et *al.*, 2006; Zwirglmaier et *al.*, 2008) The absence of variations in water density profiles at MED stations (site 2 and 8) suggests that these populations do not originate from different water masses, in agreement with previous records for the NW Mediterranean Sea (Vaulot & Partensky, 1992).

Such a high correlation between *Prochlorococcus* and *Synechococcus* concentration was previously reported in Mediterranean waters in winter, suggesting that the two populations may respond very similarly to changes in their environment including nutrient, light and temperature (Vaulot *et al*., 1990; Zwirglmaier et *al.*, 2008). HPLC analysis also revealed that zeaxanthin (mostly characteristic of cyanobacteria, Claustre, 1994) was a major pigment in these waters. Thus, it is not surprising that the contribution of picoplankton to the total <200 µm fraction reached nearly 55% in terms of carbon and 24% in terms of Chl *a* in agreement with Morán *et al*. (2001). The lack of large cells as inferred from results obtained with an automatic counter of particles (Sciandra, person. com.), low abundance of zooplankton (Youssara & Gaudy, 2001) as well as important absorption and regeneration rates for ammonium (Madec *et al*., person. com.) in addition to the previous features suggest that MED waters were characteristics of a relatively oligotrophic ecosystem, possibly influenced by nutrient-richer adjacent or deeper waters. At last, local enrichment could also be inferred from the presence during leg-1 of a clear maximum of Chl *a* at 30-40 m in MED-2 waters.

Frontal ecosystem

The Alboran frontal system is a near permanent structure created by the jet current entering the Mediterranean sea. The eastern part of the front is located between Almeria (Spain) and Oran (Algeria) but its geographical extension to the north varies. During the Almofront 2 cruise it is detected to the south of the Almeria-Oran area. The strong gradients, which are its major characteristic, occurs as a 10 to 30 km wide meandering strip in the 100 to 200 m deep upper layer. It is a typical mesoscale structure. A consequence of the secondary circulation is an upward advection of water rich in nutrients and as expected a primary production in this region essentially based on diatoms (Claustre *et al*., 2000) This biological enhancement was clearly observed in the left side of the frontal system, where water is upwelled and not on the right side, near the gyre, where water is downwelled (see figures 3 and 6). Such high diatom production had already been recorded in May 1991 during Almofront-1 (Claustre *et al*., 1994, Videau *et al*., 1994) suggesting that it is a permanent frontal feature in the Alboran Sea.

High concentrations of both *Prochlorococcus* and *Synechococcus* were also observed in the left side of the front although high concentrations of both populations recorded at this place could thus be due to MED populations exported downward in the secondary circulation, along the isopycnals and benefiting of the mixing with upward transport of nutrient rich water, as suggested by Zakardjian & Prieur (1998) in the Ligurian Sea frontal system's and modelized by Zakardjian (1994) in the Alboran Sea. Consequently, the contribution of picoplankton to Chl *a* was significant at site 7, reaching 25%. Cyanobacterial enhancement could also be explained by other factors such as sufficient light reaching the cells or the impossibility for potential grazers to adapt rapidly (Jacquet *et al*., 2002). Van Wambeke *et al*. (2004) observed indeed clear differences among sites in terms of grazing efficiency by heterotrophic nanoflagellates, with very low values in the front. The potential role of light control could be inferred from the distribution of picoeukaryotes. Indeed, the absence of any peak of eukaryotes, in contrast to cyanobacteria, both recorded during leg-1 and 2 suggested indeed that this group was controlled differently than cyanobacteria. As nutrients were likely not to be limiting (see table 1), inefficient grazing and water stability were more likely factors affecting cyanobacteria such as *Prochlorococcus* (Partensky *et al*., 1999).

It is possible that the MED picoeukaryotic populations could only sustain rapid growth at higher level of light (Jacquet *et al*., 2002). In the central part of the front, the low concentration of *Prochlorococcus* was probably related to the lack of column stability that seems to be a prerequisite for *Prochlorococcus* growth and development (Lindell & Post, 1995; Bustillos-Guzman *et al*., 1995). In contrast, maximum *Synechococcus* abundances were recorded within these semi-mixed water conditions where nitrates were in excess. Such high *Synechococcus*/*Prochlorococcus* ratio in nitrates rich waters has been often reported (Tarran *et al*., 1999; Partensky *et al*., 1999; Furnas & Crosbie, 1999).

Heterotrophic bacteria concentration clearly increased from MED-1 to the jet waters from Leg 1 transect. The high concentration of heterotrophic bacteria recorded at 40-50 m in the north side of the front was clearly associated to the maximal concentration of Chl *a* as observed also in MED-2 waters. As heterotrophic bacterial and primary productions were well correlated (Van Wambeke *et al*., 2004), it is possible that the former was dependent on the later (see above). Alternatively, bacteria could also take advantage of the high level of nutrients advected by the secondary circulation since they were nutrient limited in MED waters. Interestingly, during Almofront-1, phytoplankton production was not used by local bacteria in surface waters of the front in spring (Fernandez *et al*., 1994). During Almofront-2, heterotrophic bacteria concentration, inside the front, remained relatively low, contrasting with high bacterial production (Van Wambeke *et al*., 2004). Such a de-coupling between biomass and production could to be due to an efficient top down control, i.e. grazing pressure by protozoans but this apparently was not the case (Van Wambeke *et al*., 2004). Hence, the likely explanation is that both strong vertical (up to 5 $m.day^{-1}$) water mass motions could transfer the produced bacterial biomass towards the right side of the jet, i.e. toward the gyre water, before grazing pressure could efficiently proceed. Such a hypothesis holds when considering the large amount of heterotrophic bacteria recorded in the south side of the front. Such an increase of bacterial abundance and carbon biomass through the front has also been recorder in leg-2 observations (Fig. 11).

Modified atlantic waters and gyre ecosystems

From the transect as well as from sites profiles it is clear that inside the gyre, the carbon biomass of picoplankton was the highest compared to MED and frontal waters. At this place (site 6), the highest value for phytoplankton depth integrated biomass was also recorded (Tolosa *et al.*, 2004; Leblanc *et al.*, 2004). The contribution of picoplankton to total carbon and Chl *a* was as high as 33% and 49%, respectively (see Table 4). It was essentially due to picoeukaryotes, especially in the centre of the gyre. HPLC measurements revealed that there was an important concentration of the carotenoids 19'HF and 19'BF, revealing the potential predominance of prymnesiophytes and pelagophytes (Claustre, 1994; Vaulot *et al.*, 2008). Correlations between picoeukaryote abundance and 19'HF pigment suggesting a fixed contribution of Prymnesiophytes to picoeukaryotes were previously observed in the Alboran Sea

by Barlow *et al.* (1995, 1997) and during Almofront-1 (Fiala *et al*., 1994). In fact, prymnesiophytes seem to be a major and relatively diverse eukaryotic component in many oceanic provinces (Wilmotte *et al.*, 2002; Fuller e*t al.*, 2006; Mc Donald *et al.*, 2007).

Bacterial biomass was the highest of the 3 ecosystems although bacterial production was only half that recorded in the frontal zone (Van Wambeke *et al*., 2004). Such a situation was already recorded during Almofront-1 (Fernandez *et al*., 1994) and was likely due to different grazing efficiencies and biomass exportation (Van Wambeke *et al.*, 2004). Interestingly, we found that nitrites were clearly higher in these modified ATL waters than in the two previous ecosystems (Table 1). Such a relationship between heterotrophs and nitrites strongly suggest that these waters were characterized by high rates of regeneration processes. Bianchi *et al*. (1994) reported the same observation during Almofront-1 in spring suggesting that the gyre may keep these characteristics in time and space. Van Wambeke *et al*. (2004) showed that bacteria were not limited by any food resource in these modified Atlantic waters. Thus the gyre ecosystem appeared as a mesotrophic system in which bacterial production was likely sustained by lateral incomes from the frontal area. The distribution of *Synechococcus*, also well represented in surface layers of the gyre, corresponds to that usually found in a mesotrophic ecosystem (e.g. Partensky *et al*., 1996, 1999). In view of the elevated concentration of picoplankton in the gyre and of the gradient of concentration recorded between the three ecosystems, it is likely that its production was important in these waters. These observations show that the gyre ecosystem appeared as a mesotrophic system.

Distribution and potential role of viruses

Virus concentrations fell in the range previously reported for Mediterranean waters by Marie et al. (1999) from FCM measurements, but considerably higher than those of Alonso et al. (2001) who used both epifluorescence and electron transmission microscopy. They reported concentrations varying between 3 10^3 and 8 10^4 virus ml^{-1} in summer in the Alboran Sea which are much lower than those reported in the literature and we suspect them to be biased. Our measurements of the total viral concentration ($3x10^5$ to $2x10^7$ virus ml^{-1}) and of viruses to bacteria ratios (VBR, between 2 and 55) are in agreement with typical values now accepted (see reviews by Maranger & Bird, 1995; Fuhrman, 1999; Wommak & Colwell, 2000; Weinbauer et al., 2003; Suttle, 2005, 2007). The higher number of viral particles in surface waters and their exponential decrease with depth, following that of bacteria and other organisms in the 0-200m layer, indicated that viruses were closely related to biological activity (Hara *et al.*, 1996). The existence of the two populations referred to as V-I and V-II is in agreement with a previous profile obtained for the Mediterranean Sea by Marie et al. (1999). According to FCM scatter and fluorescence, V-I particles were larger than V-II, suggesting that the V-I could be infectious to eukaryotic phytoplankton while V-II could be bacteriophages (Jacquet *et al.*, 2002; Marie *et al.*, 1999).

However, clear significant statistical correlations were only found between viruses and heterotrophic bacteria (N total virus versus N bacteria : r=0.72, p=0.05, n=385) as often reported (Boehme et al., 1993; Cochlan et al., 1993; Alonso et al., 2001; Middelboe, 2008). This suggests that heterotrophic bacteria were the main hosts of the viruses. The lack of significant correlations between virus V-I as well as V-II and bacterial abundances, when considering the whole water column, is not surprising because in the Ligurian sea, Winter *et al.* (2009) have shown that viruses are related to prokaryotes in very different ways in epi-, meso- and bathypelagial domains. High VBR could suggest high infection rates, high number of viral particles for each bacterial host and/or low virus decay rates.

Vertical profiles of bacterial abundance in the Alboran Sea are similar in shape to those obtained in the Ligurian Sea by Tanaka *et al.* (2005). The deep maximum in viral abundance observed at some sites (site 3 at 1000 m; site 2 at 2000 m) has also been observed in the Ligurian Sea (Weinbauer *et al.*, 2003)

Conclusion

The Alboran Sea constitutes a perfect area to investigate the coupling between biological and physical processes mainly because the major structures (front and anticyclonic eddies) are more or less stationary in space. The transect across Alboran sea (leg-1) and the sites sampling (leg-2) have shown that spatial structure can be represented by 3 typical elements

(1) Med ecosystem influenced by Mediterranean water from the north of Balearic-Algerian basin:

(2) Gyre ecosystem accumulating Atlantic water progressively modified by mixing with Mediterranean waters,

(3) Frontal ecosystem at the boundary of the two previous systems, characterized by strong horizontal gradients in the physical and biological parameters.

The secondary circulation associated with the jet current gives this system dynamical properties through upwelling and downwellings along isopycnals. Nutrient enrichment as well as dynamic stationarity provided by the upward transport is favourable to autotrophic growth.

Fronts are relatively frequent in the ocean and their influence may be significant at regional and global scales. Our data on picoplankton contribute to the quantification of role of fronts in upper layer of the sea. To date, only a few data on the distribution of microbial communities are available for the open Mediterranean Sea (Magazzu & Decembrini, 1995; Martín-Cuadrado *et al.*, 2007) by comparison to coastal waters (Ghiglione *et al.*, 2005; Sala *et al.*, 2006; Alonso-Sáez *et al.*, 2007).

Almofront-2 cruise allowed us to obtain an unprecedented synoptic view of the distribution and standing stocks of picoplanktonic groups and viruses, analyzed by flow cytometry, which revealed a high variability. During winter season, relatively oligotrophic areas were dominated by *Prochlorococcus* whereas *Synechococcus* and picoeukaryotes were more common in the upper layer well illuminated and nutrient rich of the "modified Atlantic waters" related to the eastern Alboran gyre.

Alboran Sea has been a good model to test the paradigm of phytoplankton. This paradigm states that picoplankton constitute a constant background community limited by diffusive processes, water stability and top down control while opportunistic species (larger cells) respond rapidly to nutrient enrichment with a clear de-coupling of control by higher trophic levels (Fiala *et al.*, 1994). If the data obtained during Almofront-2 cruise do not change this general scheme, it is noteworthy however that picoplankton represents a sizeable part of the total living carbon biomass and seems to display very variable response to the hydrodynamically active frontal structures. This should be considered in the development of predictive models dealing with the coupling between physical and biological variables, especially for quantifying carbon fluxes.

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