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Cross-slope variations of organic carbon and bacteria in the Gulf of Lions in relation to water dynamics (northwestern Mediterranean)

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ABSTRACT: During November 1994, seawater samples were collected in the Gulf of Lions in the northwestern Mediterranean Sea. Four stations were chosen to cover a range of environments, from coastal seawater near Marseille, France, to open ocean waters 30 miles off the coast. Samples were studied for dissolved and particulate organic carbon (DOC and POC) as well as bacterial abundance and chlorophyll *a* (chl *a*). In the water column, DOC comprized 93 to 99% of total organic carbon, ranged from 65 to 118 µM and was lower in deep waters on the slope. Considering an average 82 µM DOC concentration measured in the surface layer (0 to 70 m) of the slope as typical of the core of the northwestern Mediterranean current, we estimated the DOC load carried by the current to range from 82 to 164 × 10^3 mol C s^{-1}, which was ca 100 times higher than the Rhône River input for the same period. Chl *a* concentrations were up to 224 ng l^{-1} whereas bacterial concentrations ranged from 0.9 to 7.7 × 10^5 cells ml^{-1} making up 17 to 24% of the POC in the surface layer (0 to 70 m). Bacterial-C/phytoplankton-C ratios around the slope were higher than offshore and were in good agreement with bacterial production/primary production ratios. These results indicate a time lag between autotrophic phytoplanktonic and heterotrophic bacterial activities and/or differences in the food web structure from the slope to the seaward end of the section. Although the bacterial-C/phytoplankton-C ratios were lower at the coastal station, the lowest primary production as well as higher bacterial production/primary production ratios were calculated in this area. This suggests that a part of bacterial production was sustained by terrestrial organic matter on the shelf. Variations among stations sampled during comparable climatological conditions revealed the existence of a spatial gradient across the slope.

KEY WORDS: Dissolved organic carbon · Particulate organic carbon · Bacteria · Chlorophyll *a* · Northwestern Mediterranean Sea

INTRODUCTION

Dissolved organic carbon (DOC) represents the largest pool of organic matter in seawater and thus it is important to understand how rapidly and efficiently it is turned over by bacteria (Coffin et al. 1993). In coastal environments, in addition to autochthonous biogenic sources (Wangersky 1978, Romankevich 1984, Jumars et al. 1989), large quantities of DOC are exported from the land to the continental margins through the rivers and the nepheloid layers (Richey et al. 1980, Mantoura & Woodward 1983, Cauwet et al. 1990, Sempéré et al. 1994, Repeta et al. 1995) with varying nutritional value for bacteria (Moran & Hodson 1994). Moreover, vertical (Copin-Montégut & Avril 1993, Carlson et al. 1994)

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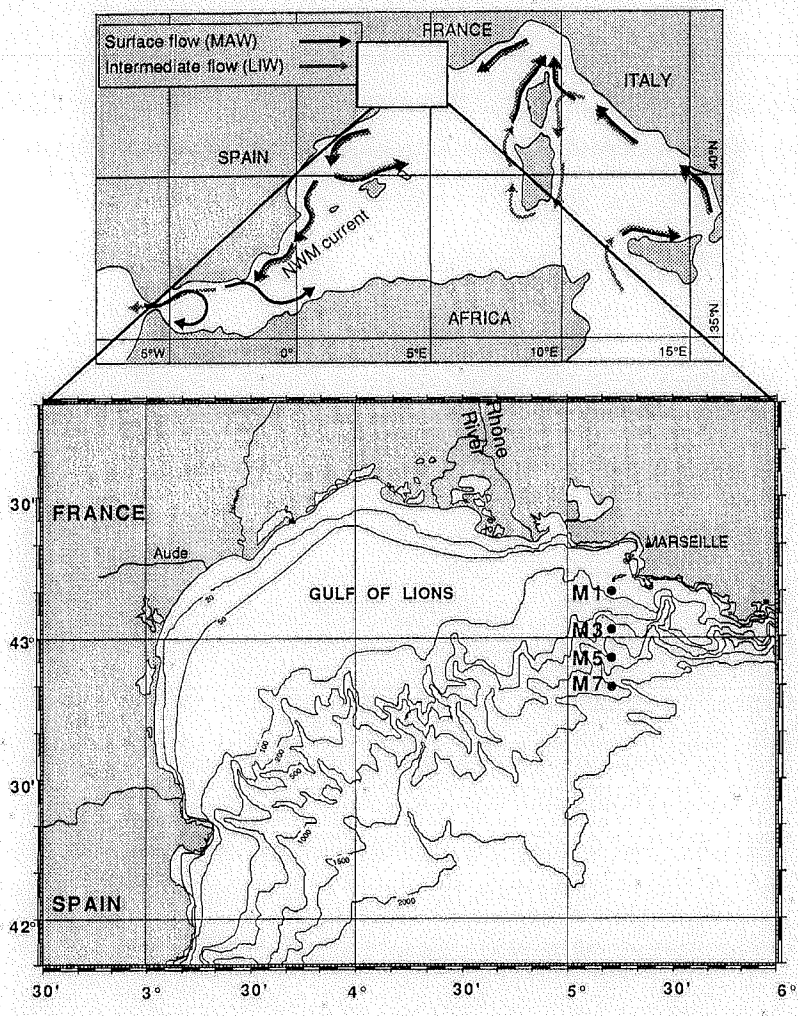

Fig. 1. Locations of the 4 stations studied (Stn M1: 43° 10.5' N, 05° 12.5' E; Stn M3: 43° 02.0' N, 05° 12.5' E; Stn M5: 42° 56.0' N, 05° 12.5' E; Stn M7: 42° 49.0' N, 05° 12.5' E) during the EMPS-Pauline cruise in the coastal northwestern Mediterranean Sea, 7 to 15 November 1994. Surface and intermediate circulations in the western Mediterranean Sea are indicated. Cyclonic current in the northern basin is called the northwestern Mediterranean (NWM) or Liguro-Provençal current (after Millot 1987)

and horizontal (Kepkay & Wells 1992) advections may produce large variations in DOC concentrations and should be taken into account when DOC is included in models related to the biological pump.

Pigments and primary production measurements (Lefèvre et al. 1997 and references therein) as well as coastal zone color scanner images (Feldman 1989, Morel & André 1991) have shown that the waters in the Gulf of Lions (northwestern Mediterranean, NWM) are oligo-mesotrophic; however, a higher mass flux and a lower percentage of photosynthetic carbon cycle through bacteria in these waters when compared to oligotrophic waters of the Aegean or southwestern Mediterranean Sea near the Baleares Islands (Bianchi et al. 1996, Turley et al. unpubl.). Interestingly, recent works showed that in the Gulf of Lions waters bacterial growth as well as the microbial food web structure seem to be strongly related to the influence of the wind forcing, the Rhône River inputs (Soto et al. 1993), and the regional circulation (Christaki et al. 1996) i.e. the NWM or Liguro-Provençal current (Fig. 1). However, to our knowledge, there is no report simultaneously dealing with cross-slope variations of organic carbon, autotrophic production and bacterial activity in this area. In this paper, we discuss the vertical and horizontal distributions of DOC, particulate organic carbon (POC), bacterial abundance and chlorophyll a (chl *a*) concentrations related to primary and bacterial production reported by Turley et al. (unpubl.) at 4 stations in the northwestern Mediterranean Sea at 3 to 30 miles from the coast and the city of Marseille (France). We discuss the variations of these parameters in relation to hydrodynamic conditions.

MATERIALS AND METHODS

Study area. Four stations located along a cross-slope transect off Marseille were sampled during the 'EMPS-Pauline' cruise (7 to 15 November 1994) on board the RV 'Tethys II' (Fig. 1). Seawater samples were collected with 12 l Niskin bottles, from the surface to 1000 m depth. Conductivity, temperature and depth (CTD) data were obtained in parallel to the water sampling with a Sea-Bird 19 probe. Three principal water masses are found in this area (Lacombe & Tchernia 1972): the surface Modified Atlantic Waters (MAW), the Levantine Intermediate Water (LIW) and the Deep Western Mediterranean Water (DWMW). The MAW found in the upper 300 m of the water column is characterized by low salinity values between 37.90 and 38.45. Waters with salinity values lower than 37.90 are sometimes observed at the surface and result from the dispersion of freshwater supplied by rivers (Conan 1996). The Rhône River with an annual water discharge of ca 53×10^9 m^3 yr^{-1} (Cauwet et al. 1990) is the main source of freshwater in the northwestern Mediterranean.

The local dynamical features are dominated by the NWM current—which flows westward on the shelf

and along the continental slope—and the wind-induced currents (Millot 1990). The NWM current, whose core essentially encompasses the MAW, is part of the general circulation in the western Mediterranean (Millot 1987). It flows cyclonically along the continental slope following a more or less steady path (Fig. 1), with a flux on the same order of magnitude as the incoming and outgoing fluxes in the Strait of Gibraltar, which are ca 1 to 2 × 10^6 m^3 s^{-1} (Béthoux 1980, Lacombe 1988). The circulation of the LIW and DWMW is likely cyclonic and follows the isobaths. Evidence for mesoscale cross-slope displacements of the NWM current core, due to meanders, was given by Conan & Millot (1995). X. Durrieu de Madron, O. Radakovitch, A. Monaco & S. Heussner (unpubl.) further showed that these fluctuations, which have a typical period of 2 to 10 d, are particularly intense in winter and enhance the shelf-slope exchanges of matter. The winds, which intensify in winter, also lead to highly variable and intense surface currents on the shelf. Four zones of different productivity were defined near the experimental site (Conan 1996 and references therein): (1) the Rhône River plume and its dilution zone with high nutrient concentrations; (2) a coastal eutrophic area in the Gulf of Marseille (eastern end of the Gulf of Lions; Fig. 1, near Stn M1) occasionally enriched by nutrients from the Rhône River or coastal upwelling; (3) a zone of lower productivity within the core of the NWM current on the slope (Fig. 1, between Stns M3 and M7); and (4) a productive frontal zone on the outer edge of the NWM current.

DOC and POC measurements. To avoid contamination, seawater was drained with a Teflon pipe directly from the Niskin bottle into large glass bottles (10 l) that had been cleaned with 2% HCl and rinsed several times with distilled water. Seawater samples were filtered within 6 h in the laboratory under reduced vacuum through an all glass pre-combusted (450°C) fibre filter (Whatman GF/F, 25 mm diameter). Filters were then frozen at –20°C for POC analysis. The first 100 ml of filtrate were discarded, and then 10 ml of filtered seawater samples were transferred into pre-heated (450°C) glass vials, with Teflon-lined screw caps, for DOC measurements. All samples were poisoned with 50 µl of $HgCl_2$ (final concentration: 10 mg l^{-1}) and stored in the dark at room temperature.

For DOC analysis, we used a commercially available Shimadzu TOC 5000 system (high temperature catalytic oxidation; Sugimura & Suzuki 1988) with a catalyst made of platinized-quartz wool. Samples were acidified (pH = 2) with 2 M HCl and bubbled for 10 min with CO_2-free pure air to purge inorganic carbon. Two or three 50 µl replicates for each sample were injected into a column heated at 680°C. The effluent passed through a drying unit (magnesium perchlorate cartridge), a halogen scrubber for eliminating halogen gas and sulphates, a dust-eliminating membrane filter to remove sea-salts and phosphoric acid aerosols, and finally the non-dispersive infra-red (NDIR) cell in which CO_2 was detected. The catalyst bed was preconditioned by injecting 50 µl of acidified and sparged Milli-Q water until the lowest stable integrated area was obtained (between 400 and 600 area units). The analytical precision of the procedure was within 4% (n = 3). Of the replicate samples, 85% showed a dispersion between ±2 and ±8 µM C, and the remaining 15% showed a dispersion between ±10 and ±14 µM C.

Calibration curves were built with a set of standard solutions of known concentrations: 62, 83, 125, and 167 µM C. These solutions were prepared every day prior to analyses of seawater samples by dilution in Milli-Q water from a 'stock solution' of potassium hydrogen phthalate prepared each week. The error introduced by the standard curves was estimated to be less than 4% for the sample determination. The system blank was measured by injecting pyrolyzed and carbon free water in the combustion tube (TC blank check function of the instrument). A series of 5 replicates was made 10 times, producing at the end of the blank checking program 50 DOC measurements of the pyrolized water. The instrument blank determined by this method was 9 µM C. The DOC blank of Milli-Q water was found to be 6 µM C and was subtracted from the DOC standard concentrations for sample DOC calculation.

In preparation for POC analysis, the GF/F filters were oven dried at 50°C and loaded into pre-combusted porcelain combustion boats. They were covered with a few ml of 2 N phosphoric acid and evaporated to dryness at 50°C for 12 h to remove inorganic carbon (Tan & Strain 1979). The filters were then assayed on a CHN analyzer (CHN-800 LECO) with a combustion tube at 850°C. The CO_2 generated by oxidation was measured by a NDIR cell with a standard deviation of 2%.

Enumeration of bacteria. Samples were drawn from the Niskin bottles and immediately preserved in 20 ml vials with 0.2 µm-filtered 2% glutaraldehyde (final concentration). Slides were prepared within 24 h of sampling to avoid underestimation of cell numbers due to possible losses during storage (Turley & Hughes 1992). Samples were sonicated on ice for 30 to 120 s in a 50% on-off cycle using a Vibracell V 600 20 kHz ultrasonicator to ensure good distribution on the filter. An appropriate volume of sample was stained with 0.2 µm-filtered DAPI solution (Porter & Feig 1980) at 1 µg ml^{-1} final concentration for 10 min before filtering onto a black 0.2 µm pore-size 25 mm diameter Nuclepore filter (Hobbie et al. 1977). Slides were kept at –20°C until counting. Standard error between replicate samples was 3 to 20% (30 fields randomly counted per sample).

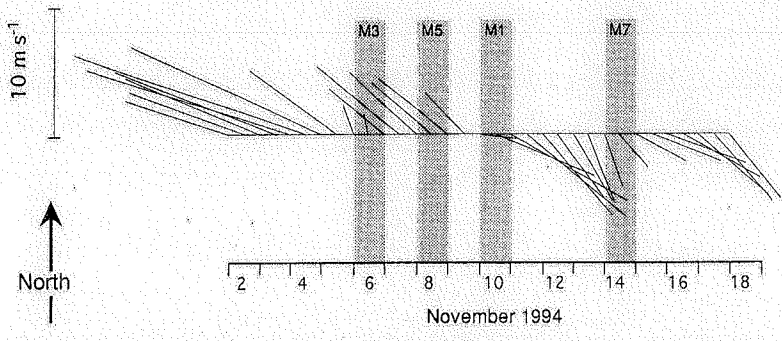

Fig. 2. Stick plot of the wind speed and direction measured near Marseilles between 2 and 18 November 1994. Sticks are rotated by 180° to indicate the leeward direction of the wind. Values are averaged over 12 h periods and are smoothed using 2 repeated passes of a simple hanning window. The days on which the 4 stations were sampled are shown by vertically shaded bars

Chl *a* analysis. Seawater samples were collected from the Niskin bottles in 1 l opaque bottles (cleaned with 2% HCl and rinsed several times with distilled water) and refrigerated until their processing on land, which was always within 12 h after sampling. Samples were filtered onto 0.45 µm pore-size Millipore HA filters (45 mm diameter). The filtration volumes ranged from 1.7 to 2.0 l. Pigments were extracted by adding 90% acetone to the homogenate which was then left overnight in the dark. Following the fluorometric determination described by Holm-Hansen et al. (1965), the measurements were performed before and after acidification with 2 drops of 1 N HCl on a Perkin-Elmer LS-5B luminescence spectrometer. Calibration was made with pure Sigma chl *a* standards and a linear instrumental response over the considered range.

RESULTS

Climatological and hydrological conditions

The heavy rainfalls that occurred on the adjacent land area before and during the sampling period led to an unusually high freshwater discharge from the Rhône River (av. 5358 m^3 s^{-1} for November; B. Charrière, R. Sempéré & G. Cauwet unpubl.). Wind measured near the Rhône River mouth indicated that 2 periods of opposite wind regimes dominated during the experiment (Fig. 2). Stns M3 and M5 were sampled while the wind was northwestward, Stn M1 was sampled during the wind reversal period, and Stn M7 while the wind was southeastward. As shown by Estournel et al. (1997), a northwestward wind prevents the surface offshore dispersion of the Rhône River plume by transporting it westward along the shore, whereas a southeastward wind induces a seaward spreading of this plume. Therefore, it appears that the low surface salinity values measured in the water column at Stn M1 (salinity between 37.90 and 37.97; Table 1) and particularly between 5 and 30 m depth at Stn M7 (salinity between 37.52 and 37.56) may be due to the influence of the Rhône River freshwater at these stations during the period sampled. The effect of the wind-induced mixing is also clearly evident at Stn M1 where all parameters (salinity, temperature, DOC, POC, bacteria and chl *a*) varied only slightly down to 70 m deep (Table 1, Figs. 3 & 4), indicating a relative homogenization of the shelf water column. The surface mixed layer over the slope was thickest at Stn M3 (ca 40 m).

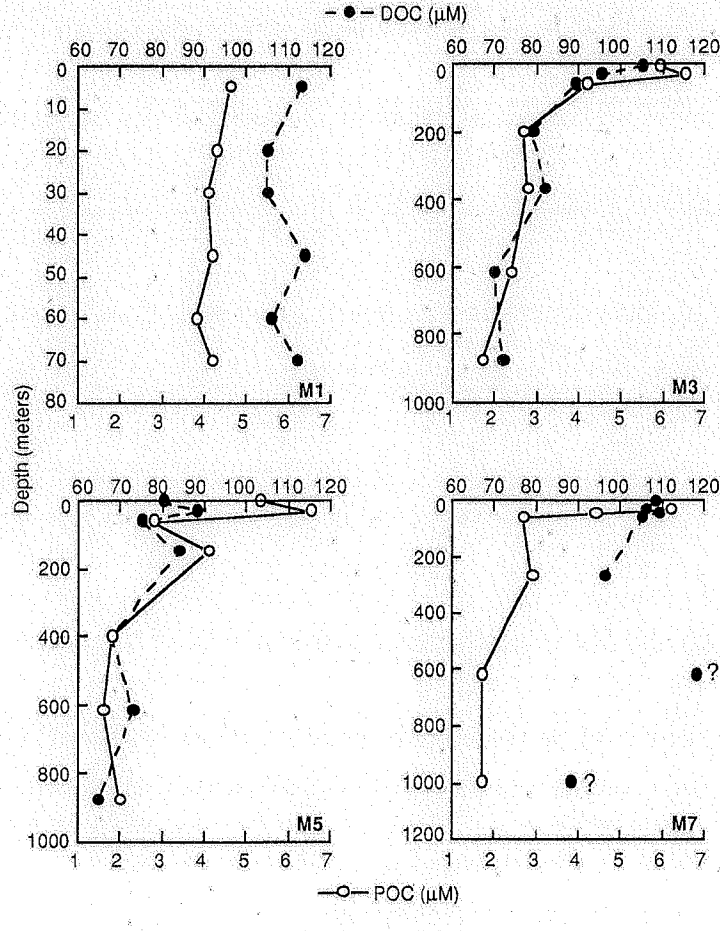

Fig. 3. Vertical distribution of DOC and POC in seawater samples collected at Stns M1, M3, M5 and M7 in the coastal northwestern Mediterranean Sea

Table 1. Sampling dates, sample depth, DOC, POC, bacterial numbers, chl *a* concentrations, bacterial-C/POC (BC/POC) ratio (%), bacterial-C/phytoplankton C (BC/Phyt-C) ratio, salinity, and temperature from seawater samples collected from 4 stations in the northwestern Mediterranean Sea, November 1994. Ratios 1 and 2 were calculated assuming a constant C/chl *a* of 30 (Strickland 1960) and 100 (Fuhrman et al. 1989) in the top 70 m, respectively. nd: not determined. POC values are not corrected for a 50% retention of bacteria on the glass fibre filters used in the filtration

Station and sampling date	Depth (m)	DOC (µM)	POC (µM)	Bacteria ($\times 10^5$ ml^{-1})	Chl *a* (ng l^{-1})	BC/POC (%)	BC/Phyt-C ratio 1	BC/Phyt-C ratio 2	Salinity	Temperature (°C)
M1, 10 Nov 1994	5	113	4.6	5.4	200	19	1.8	0.5	37.90	17.76
	20	105	4.3	5.7	153	22	2.5	0.7	37.95	17.55
	30	105	4.1	5.4	197	22	1.8	0.5	37.94	17.52
	45	114	4.2	6.5	195	26	2.2	0.7	37.94	17.46
	60	106	3.8	7.1	224	31	2.1	0.6	37.95	17.38
	70	112	4.2	6.6	191	26	2.3	0.7	37.97	16.64
M3, 6 Nov 1994	5	105	5.9	5.9	151	17	2.6	0.8	38.00	18.10
	30	95	6.5	5.1	140	13	2.5	0.7	38.00	18.10
	60	89	4.2	5.5	82	22	4.5	1.3	37.90	15.90
	200	79	2.7	1.5	4.0	9	–	–	38.30	13.30
	370	82	2.8	1.4	0.4	9	–	–	38.50	13.50
	620	70	2.4	1.0	0.2	7	–	–	38.50	13.40
	880	72	1.7	0.9	0.0	9	–	–	38.50	13.20
M5, 8 Nov 1994	5	80	5.3	4.9	73	15	4.5	1.3	38.00	17.83
	30	88	6.5	5.9	62	15	6.4	1.9	38.07	17.73
	60	75	2.8	3.5	110	21	2.1	0.6	37.97	13.91
	150	84	4.1	1.5	6.7	6	–	–	38.30	13.27
	400	68	1.8	1.5	0.0	14	–	–	38.55	13.48
	620	73	1.6	1.3	0.0	13	–	–	38.55	13.38
	880	65	2.0	0.9	1.3	7	–	–	38.51	13.22
M7, 14 Nov 1994	5	108	nd	7.7	193	nd	2.6	0.8	37.52	17.49
	30	106	6.2	6.1	145	16	2.8	0.8	37.56	17.55
	45	109	4.4	5.3	131	20	2.7	0.8	38.10	15.24
	60	105	2.7	4.9	132	30	2.5	0.7	38.07	14.28
	270	96	2.9	1.9	1.0	11	–	–	38.53	13.39
	620	118	1.7	1.1	0.9	11	–	–	38.52	13.27
	1000	88	1.7	nd	0.6	nd	–	–	nd	nd

DOC, POC and TOC

DOC concentrations in the water column ranged from 65 to 118 µM (Table 1, Fig. 3) comprising 93 to 99% of the total organic carbon (TOC), with highest values rather found in the photic zone than in the underlying waters. Our DOC data for 620 and 1000 m depths at Stn M7 are doubtful, as they are significantly higher than recent measurements at the same location (50 to 60 µM; R. Sempéré & L. Guilhem unpubl.). This might be due to unsteady conditions of the catalyst during measurement and/or contamination during GF/F filtration. Integrated DOC concentrations in the surface layer (0 to 70 m) showed that the highest stocks of DOC (Fig. 5a) were observed at stations located at the end points of the transect, i.e. coastal Stn M1 (91.2 g C m^{-2}) and offshore Stn M7 (89.6 g C m^{-2}). In the surface layer, DOC was positively correlated with bacteria and chl *a* abundances ($p < 0.01$; Fig. 6a, b) indicating that phytoplankton produced dissolved organic compounds (Lancelot 1979, Søndergaard et al. 1985, Baines & Paice 1991) utilized by bacteria (Cole et al. 1982, Hollibaugh & Azam 1983, Decho 1990, Amon & Benner 1996). POC concentrations ranged from 2.7 to 6.5 µM C in surface waters and decreased down to 1.6 µM C in deeper layers (Fig. 3, Table 1). The cross-slope pattern observed for POC (Fig. 5b) in the surface layer (0 to 70 m) was different from that of the DOC (Fig. 5a). POC content along the section ranged from 3.5 to 4.5 g C m^{-2}, being maximum at Stn M3.

Chl *a* and bacteria

In the water column, bacterial cell numbers ranged from 0.9 to 7.7 $\times 10^5$ cells ml^{-1} (Fig. 4, Table 1). Bacteria in surface samples (0 to 70 m) were slightly more abundant (3.5 to 7.7 $\times 10^5$ cells ml^{-1}) on the shelf (Stn M1: 6.1 ± 0.6 $\times 10^5$ cells ml^{-1}) and on the southmost station (Stn M7: 6.0 ± 1.1 $\times 10^5$ cells ml^{-1}) than at M3 and M5 (5.1 ± 1.1 cells ml^{-1}). However, using a tritiated-leucine incorporation technique, Turley et al. (unpubl.) indicated that bacterial production was lower near the coast (Stn M1: 65 mg C m^{-2} d^{-1}) than at other stations

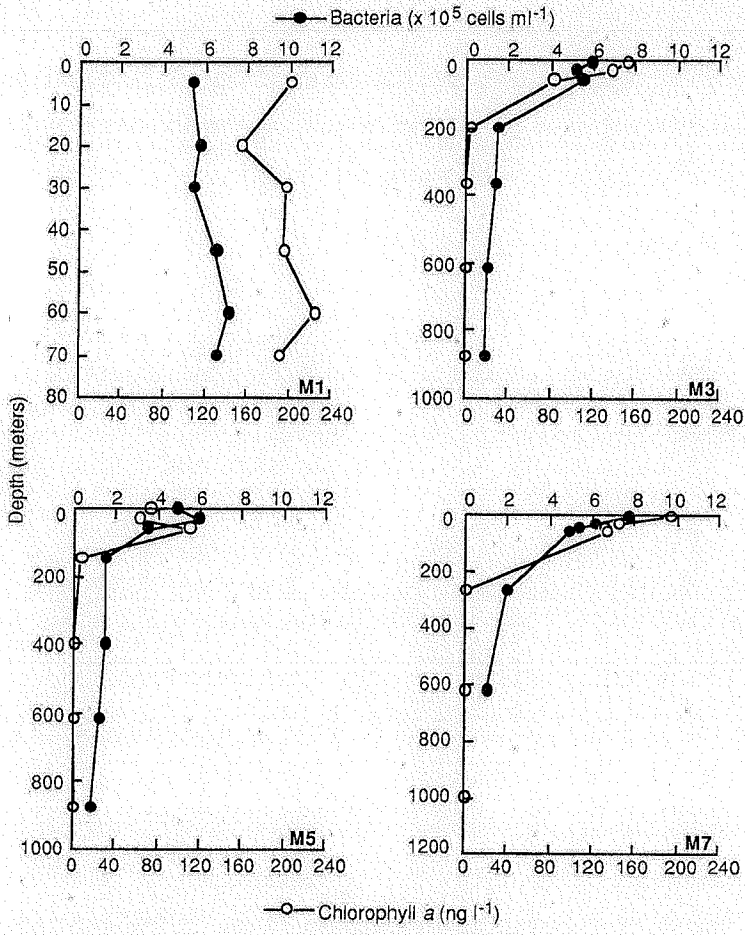

Fig. 4. Vertical distribution of bacterial numbers and chl *a* concentrations in seawater samples collected at Stns M1, M3, M5 and M7

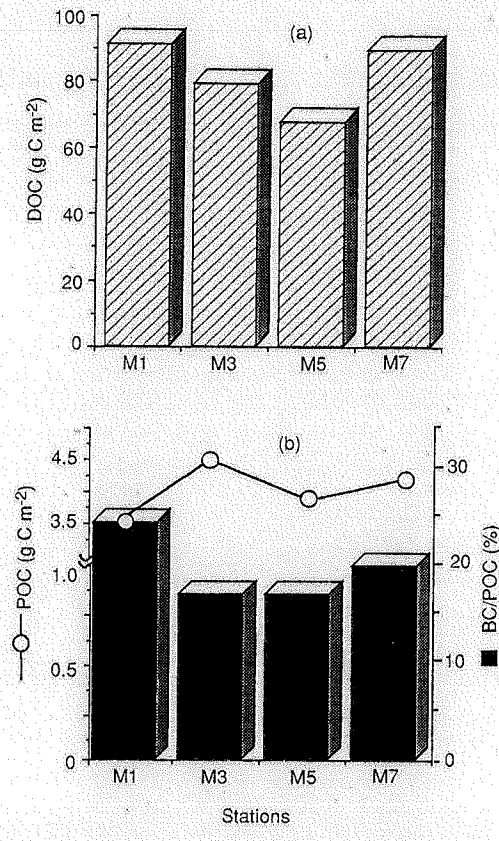

Fig. 5. Integrated concentrations (between 0 and 70 m depth) of (a) DOC and (b) POC and bacterial-C/POC (BC/POC) (%) in seawater samples collected at Stns M1, M3, M5 and M7. BC calculated assuming 20 fg C cell^{-1} (Lee & Fuhrman 1987)

(maximum at Stn M5: 89 mg C m^{-2} d^{-1}). Assuming a conversion factor of 20 fg C per bacterium (Lee & Fuhrman 1987), we found that in the surface layer, the C contribution of free living bacteria to suspended POC ranged from 17 to 24% (Fig. 5b). These ratios are higher at the end points of the transect (Stns M1 and M7) than at Stns M3 and M5 and are on the same order of magnitude as results reported in Atlantic Ocean (20 to 30%, Ducklow et al. 1993; 25 to 33%, Turley & Mackie 1994). Integrated bacterial biomass-C in the surface layer ranged from 0.6 to 0.8 g C m^{-2}.

In the surface layer, averaged chl *a* concentration followed the same pattern as that for bacteria, being higher at Stns M1 (193 ± 21 ng l^{-1}) and M7 (150 ± 25 ng l^{-1}) than at Stns M3 and M5 (123 ± 30 and 81 ± 21 ng l^{-1}, respectively). By contrast, the integrated primary production measured by the ^{14}C technique was almost 3 times higher offshore (Stn M7: 367.4 mg C m^{-2} d^{-1}) than near the coast (Stn M1: 132.4 mg C m^{-2} d^{-1}). Intermediate values were found at other stations (Stns M3 and M5: 205 ± 8 mg C m^{-2} d^{-1}) (Turley et al. unpubl.; Table 2). Two factors of C/chl *a* conversion were used to estimate phytoplankton-C biomasses (30: Strickland 1960; 100: Fuhrman et al. 1989) in the top 70 m. These results indicated that phytoplankton makes up 2 to 50% of POC. Moreover, these results suggested that bacterial-C/phytoplankton-C ratios ranged from 0.5 to 6.4, being higher at Stns M3 and M5 than at Stns M7 and M1 (Table 1).

DISCUSSION

DOC, bacteria and chl *a* distribution

DOC concentrations measured at Stns M1, M3 and M7 were very close to those already reported in the Rhône River plume (Cauwet et al. 1990, Cauwet & Oriol 1994). By contrast, the lower values observed at Stn M5 were rather similar to those reported for the oligotrophic offshore DYFAMED station (Copin-Montégut & Avril 1993). Bacterial cell numbers as well as

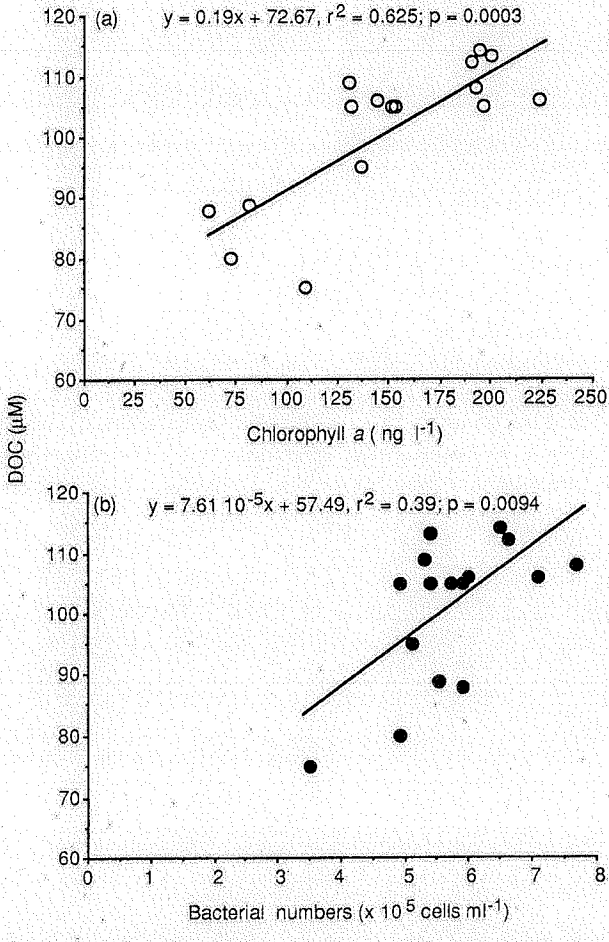

Fig. 6. Regressions between 0 and 70 m depth of (a) DOC vs chl *a* and (b) DOC vs bacterial densities in seawater samples collected at Stns M1, M3, M5 and M7

chl *a* measured here are in the same range as those previously reported in the Mediterranean Sea (Kirchman et al. 1989, Zohary & Robarts 1992, Soto et al. 1993, Bianchi & Giuliano 1996). However, it should be noticed that the spatial distributions of integrated DOC, bacteria and chl *a* biomass-C did not vary conservatively with distance from the coast. Moreover, the low surface salinity data measured at Stns M7 (37.52) and M1 (37.90) may be due to inputs of freshwater from the Rhône River in the whole water column and for the 5 to 30 m layer respectively during the period sampled. Indeed, the southeastward direction of the wind was reported to induce a seaward spreading of the plume (Estournel et al. 1997). Moreover, this spreading was enhanced by the strong rains which occurred during November 1994, yielding an unusually high Rhône water discharge. However, since integrated primary production offshore (Stn M7) was 2 or 3 times higher than near the coast (Stn M1) or the slope (Stns M3 and M5), it is likely that primary production contributed more to the DOC production offshore than at other stations during the period sampled.

Table 2. Estimates of integrated primary production (PP) and integrated bacterial production (BP) from the sea surface to the base of the deep chlorophyll maximum (DCM: 60 m depth) in the northwestern Mediterranean Sea (data summarized from Turley et al. unpubl.). Bacterial carbon demand (BCD) is calculated assuming a 40% bacterial growth efficiency (Bjørnsen & Kuparinen 1991)

	Stn M1	Stn M3	Stn M5	Stn M7
BP (mg C m^{-2} d^{-1})	64.9	74.2	89.3	75.5
PP (mg C m^{-2} d^{-1})	132.4	212.4	197.3	367.4
BP/PP (%)	49	35	45	20
BCD/PP (%)	123	88	113	50

Interestingly, integrated bacterial production comprized 20% offshore (Stn M7) and 49% near the coast (Stn M1) of the integrated primary production. Assuming a growth efficiency of 40% (Bjørnsen & Kuparinen 1991), then 50 and 123% of primary production may be routed through the DOC reservoir and support the bacterial carbon demand (BCD) at Stns M7 and M1 respectively. This suggests that, during the sampling period, a greater proportion of primary production flowed to the microbial food web near the coast than offshore and/or that additional sources of DOC such as Rhône River organic compounds substantially sustained bacterial production at Stn M1. Such figures are probably underestimates since recent work suggested that the bacterial growth efficiency might range from less than 10 to 25% (del Giorgio et al. 1997). Similar calculations for Stns M3 and M5 indicate integrated bacterial production to comprise 35 and 45% respectively of the integrated primary production. As a consequence, 88 and 113% of primary production should be required to support the BCD, which is much higher than that reported at Stn M7. Since the area including Stns M3 and M5 is very likely under the influence of the NWM current (Conan 1996) with a small influence from the Rhône River, these results suggest a difference in the food web structure between the slope (Stns M3 and M5) and offshore (Stn M7).

Bacterial-C/phytoplankton-C ratio was found to be maximum at Stn M1 which is probably due to the organic carbon input from the Rhône River as suggested above. Interestingly, this ratio is higher at Stns M3 and, particularly, M5 than at Stn M7, being in good agreement with bacterial production/primary production ratios. This suggests that, during the sampling period, heterotrophic bacterial biomass was relatively more important on the slope than offshore when compared to phytoplanktonic biomass. More generally, it seems that the predominance of heterotrophic

biomass over autotrophic biomass is typical of oligotrophic systems (Fuhrman et al. 1989, Cho & Azam 1990, Booth et al. 1993), with an exception reported for the eastern Mediterranean (Robarts et al. 1996). This seems to be consistent with physical measurements (T, S) indicating that during the period sampled, Stn M3 and, more likely, M5 are characteristic of the oligotrophic NWM current, being in agreement with the study of Conan (1996).

Higher bacterial production when compared to primary production as well as the lower DOC value at Stn M5 supports the study of Christaki et al. (1996), which concluded that the oligotrophic NWM current induced a predominance of the heterotrophic biomass over the autotrophic biomass at Stn M3. One explanation for this heterotrophic predominance may be a time lag between peaks of primary production and heterotrophic utilization of the labile DOC (Ducklow et al. 1993, del Giorgio et al. 1997). This explanation might be consistent with the lower DOC values observed at Stns M3 and M5 than at Stn M7. Another possibility may be a higher zooplankton activity at Stns M3 and M5 than at Stn M7. High zooplankton activity may favour the bacterial activity by excretion, sloppy feeding as well as by removal of bacterivores (Peduzzi & Herndl 1992, Christaki et al. 1996, Van Wambeke et al. 1996). In addition to the spatial variability, temporal variability cannot be precluded in this area as was previously shown for the Stn M3 (Christaki et al. 1996).

Considering an 82 µM DOC concentration in the surface layer (0 to 300 m) at M5 as typical of the NWM current in this area, and a NWM water flux of 1 to 2 × 10^6 m^3 s^{-1} (Béthoux 1980, Lacombe 1988), we estimated the DOC flux of the NWM current for November 1994 to range from 82 to 164 × 10^3 mol C s^{-1}. Such a DOC flux is ca 100 times higher than that generated by the Rhône River (Cauwet et al. 1990, Charrière et al. unpubl.) and shows that the NWM current plays a significant role on the organic carbon distribution in the Gulf of Lions.

Conclusion

Investigations at 4 stations located offshore from Marseille in the western Mediterranean showed cross-slope variations in organic carbon, bacterial and chl *a* biomass as well as bacterial and primary production. Wind data measured during the cruise and surface salinity values observed suggest that Stns M3 and M5 located on the slope were likely representative of the oligotrophic NWM current. During the period sampled, the offshore Stn M7 was located on the outer edge of the current. However, the Rhône River influence was also suggested on the shelf (Stn M1) as well as offshore (Stn M7). We observed higher concentrations of DOC at these 2 opposite stations than on the slope (particularly at Stn M5). Although average chl *a* was higher on the shelf than on the slope, integrated primary production was maximum offshore and minimum on the shelf. At this station, the proportion of primary production required to support the bacterial production was higher (123%) than at other stations where the BCD was 50 to 113% of the primary production. This over-utilization could be fuelled by inputs of terrestrial DOC carried by the Rhône River onto the shelf. Differences between the BCD offshore (50%) and within the NWM current (113%, Stn M5) may be due to a time lag between peaks of primary and bacterial production during the period sampled and/or higher zooplanktonic activity on the slope which can enhance bacterial activity by grazing and sloppy feeding as well as by bacterivorous predation. Such difference in the food web structure might be explained by hydrological and chemical conditions (T, S, nutrients) generated by the intensity of the Rhône River influence and the NWM current. Further works should examine temporal variations of organic carbon and bacteria in such a dynamic area.

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