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Phytodetritus at the sediment-water interface, NW Mediterranean Basin: spatial repartition, living cells signatures, meiofaunal relationships*

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SUMMARY: The deep-sea phytodetritus at the sediment-water interface was investigated in the continental margin, canyons and interfluves from 260 to 2070 m depth in the northwestern Mediterranean in June 1995. Overlying phytoplankton biomass, hydrodynamics and relationships with meiofauna densities were also evaluated. The phytoplankton biomass was low (< 0.2 μg Chl a l^{-1}), with the lowest standing stocks on the eastern part of the Balearic Basin. Two sedimentary entities were identified: 1) the west coast where pigment concentrations were higher, with an average of 0.38 μg Chl a g^{-1} dry weight and 4.60 Phaeo a g^{-1} dw on the first half cm of sediments; and 2) the eastern part of the North Balearic basin where pigment concentrations were significantly lower (0.15 μg Chl a g^{-1} dw). A north to south gradient was observed, with higher pigment amounts on the Rhodanian slope. Differences were found in the different parts of the studied canyons, with a slight increase in the Axis sites. The vertical pigment repartition was a gradual decrease in the Interfluve sites, whereas concentrations decreased sharply below the first cm in the Axis sites, attesting differences in sedimentation, grazing or bioturbation within the different canyon parts. The north to south gradient in the phytoplankton Chl a/Chl b ratio and sedimented phytodetritus attest geographical differences within phytoplankton assemblages (i.e. diatoms are absent in the south). The epifluorescence tests from the interface revealed the presence of living microphytes at the northern sites, associated with aggregates and faeces. No consistent fluff was evidenced anywhere. The revival tests also agree with a north to south trend. The Meiofaunal density was positively related to the quality of the sedimented layer. A PCA, within the major parameters and factors, illustrates these relationships. All results allow two distinct geographical sectors to be discriminated around the frontal zone: the NW and E sides of the NW Mediterranean Basin, following in particular their contrasted hydrodynamics. The results indicated the relationships within phytoplankton input, underlying phytodetritic layer and meiofauna. They confirm the well-documented statement that demonstrates the deep-sea floor chloropigment concentration to be a good proxy for the overlying primary productivity, but also that some pigment ratios representative of plankton assemblages are preserved on surficial deep sediments, even after sedimentation and grazing.

Key-words: deep-sea phytodetritus, meiofauna, phytoplankton, NW Mediterranean Basin.

RESUMEN: Fitodetritos en la interfase sedimento-agua, Cuenca Mediterránea Nordoccidental: distribución espacial, señales de células vivas, relaciones con la meiofauna. – Se investigó el detrito de agua profunda en la interfase sedimento-agua en el margen continental, caniones y interfluves entre 260 y 2070 m de profundidad en el mar Mediterráneo Noroccidental en junio de 1995. La biomasa de fitoplancton flotante, la hidrodinámica, y las relaciones con las densidades de meiofauna fueron también evaluadas. La biomassa de fitoplancton fue baja (< 0.2 μg Chl a l^{-1}), con los standing stocks mas bajos en la parte oriental de la cuenca Balear. Dos entidades sedimentarias fueron identificadas: 1) la costa occidental donde las concentraciones de pigmento fueron mas altas: 0.38 μg Chl a g^{-1} peso seco (ps) en promedio y 4.60 Phaeo a g^{-1} ps en el 0,5 cm de sedimento, y 2) la parte oriental de la cuenca Balear Norte donde las concentraciones de pigmentos fueron significativamente mas bajas (0.15 μg Chl a g^{-1} ps). Se reconoció un gradiente norte-sur, con valores mas altos de pigmentos en la pendiente Rodaniana. Fueron observadas diferencias en las distintas partes de los cañones estudiados, con un incremento menor en "Eje". La distribución vertical de pigmentos mostró una disminución gradual en los esta-

ciones de "Interfluve", mientras que las concentraciones decrecieron fuertemente debajo del primer centímetro en las posiciones del "Eje", corroborando diferencias en sedimentación, grazing o bioturbación dentro de las diferentes partes del cañón. El gradiente norte-sur en la relación de Chl *a*/Chl *b* de fitoplancton y los fitodetritos sedimentados muestran diferencias geográficas dentro de las asociaciones fitoplanctónicas (i.e. diatomeas están ausentes en el sur). Los tests de epifluorescencia en la interfase revelaron la presencia de microfitas vivientes en los estaciones del norte, asociados con agregados y faeces. Evidencia de un "fluff" consistente no fue encontrada. Los tests de "revival" también coinciden con una tendencia norte-sud. La densidad de meiofauna se relaciona positivamente con la cualidad de la capa sedimentada. Un análisis de componentes principales, con los mayores parámetros y factores, ilustra estas relaciones. Todos los resultados permiten discriminar dos sectores geográficos bien distintos cerca de la zona frontal: los lados NW y E de la cuenca Mediterránea NW siguiendo, en particular, sus contrastantes hidrodinámicas. Los resultados muestran las relaciones dentro del input de fitoplancton, yaciendo debajo de la capa fitodetrítica y la meiofauna. Esto confirma la afirmación que la concentración de cloropigmentos en el fondo del océano profundo es un buen indicador de la productividad primaria en aguas superiores, y también que algunos ratios de pigmentos, representativos de asociaciones planctónicas, son preservados en sedimentos superficiales profundos, aun después de la sedimentación

Palabras clave: fitodetritos de océano profundo, meiofauna, fitoplancton, Cuenca Mediterránea noroccidental.

INTRODUCTION

In the last decade several studies have pointed out the complexity of Mediterranean hydrology, the specificity of each basin and the level of productivity. This productivity is not so dramatically low and uniform as previously reported (Barlow *et al*., 1997). In the northwestern Mediterranean basin (Gulf of Lions and Catalan Sea) the hydrodynamics and associated phytoplankton features have been widely investigated (Estrada, 1985; Margalef, 1985; Estrada and Margalef, 1988; Masó and Duarte, 1989). Whereas the phytoplankton biomass is often described as low in surface Mediterranean waters, it can reach up to 2 µg l^{-1} in the deep chlorophyll maximum (DCM), more or less linked to the dome (Estrada, 1985), and also up to 2 µg l^{-1} in off-shore surface waters near the Catalan front (Estrada and Margalef, 1988). The more or less stable DCM can generate not only POC sedimentation, but also short-term events in surficial water masses. This may have been neglected in the past. These pulse blooms near the fronts may generate enriched near-bottom deep layers. As a probable result of such events, brownish fluffs on the deep-sea sediment surface were sampled in the Gulf of Lions in March-April 1991 (1584 m, 42°21N- 3°55E, 10^5 l^{-1} encysted microphytes, mainly *Chaetoceros* sp; Riaux-Gobin and Descolas-Gros, 1992; Riaux-Gobin *et al*., 1995). Mass sedimentation events may be spatially restricted and escape conventional investigations, whereas the sedimented material may reflect these events: still living cells or encysted cells on the surface of deep sediments may be their fingerprints.

The biochemical characterization of phytodetritus at the water-sediment interface, and its level of preservation or transformation, may provide information on its origin and sedimentation features (Santos *et al*., 1994; Riaux-Gobin *et al*., 1997; Beaulieu and Smith, 1998). Spring blooms, upwelling areas or frontal zones favour such fast or "in pulse" plankton sedimentation, which may generate enriched deep layers (cf. refs. in Cushing, 1992). In temperate areas bio-deposition to the deep-sea floor has been demonstrated to be pulsing with pronounced inter-annual variability (Lampitt, 1985; Rice *et al*., 1986; Thiel *et al*., 1988-89), and to be linked to productive frontal zones. Furthermore, degraded or intact phytoplankton reaching the deep-sea floor may be an important nutritional source for benthic heterotrophs (Billet *et al*., 1983; Thiel *et al*., 1988-89; Lochte and Turley, 1988; Pfannkuche *et al*., 1999; Pfannkuche *et al*., 2000).

In the NW Mediterranean margin and deep-sea floor, sedimentation processes, by way of trap deposition and/or sediment accumulation, were studied at different time-scales: the Holocene scale (10,000 years) by Got and Aloisi (1990) and the annual/seasonal scale by Monaco *et al*. (1990) and Puig and Palanques (1998). Radionuclides, mainly ^{210}Pb fluxes, have been successfully used by Heussner *et al*. (1990), and recently by Zuo *et al*. (1997), who give revised rates and a spatial distribution of these annual sedimentation rates corresponding to the present study area (Zuo *et al*., 1997).

The river contribution dominates the deposition system. The Rhone influence in the Gulf of Lions sedimentation (Thomas, 1997) is important, but more or less restricted to the pro-delta and showing a low incidence on the abyssal plain: off-shore sedimentation originates in atmospheric input and oceanic productivity. More or less the same conclusions are given by Bouloubassi *et al*. (1990), using organic markers, about the Ebro impact.

Biological implications of these sedimented layers, such as the relationships with benthic meiofau-
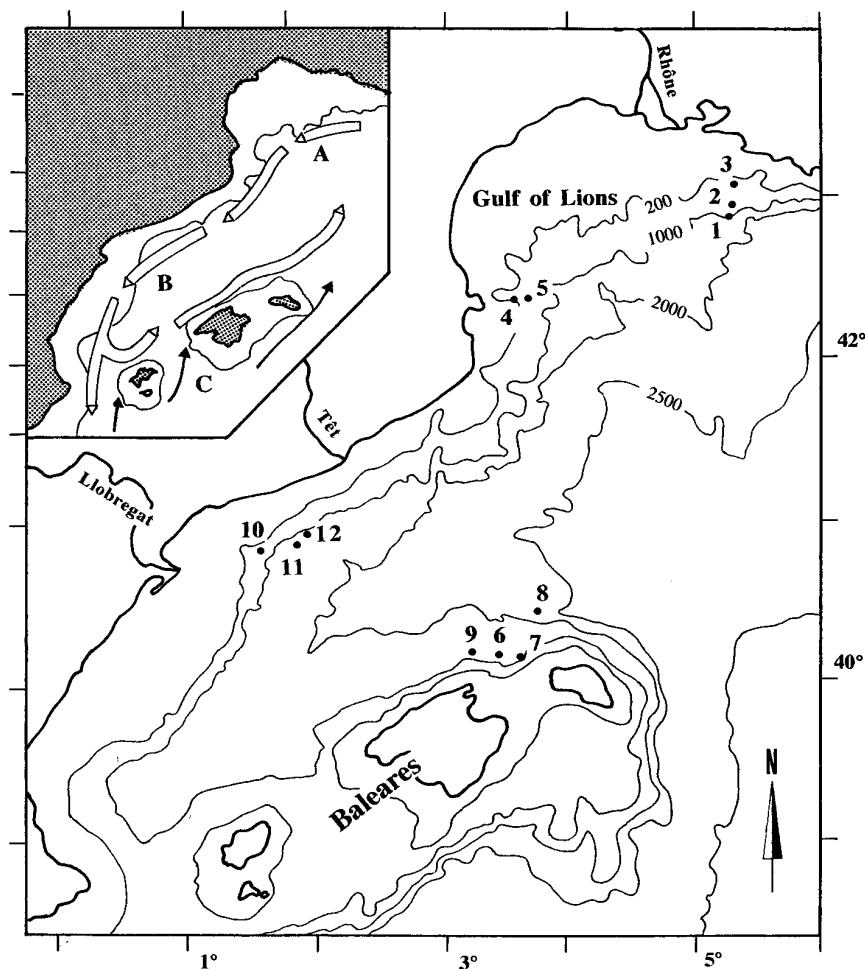
FIG. 1. – Location of the sampling sites in the Gulf of Lions, the Foix canyon and the Balearic Islands sites (cf. Table 1); also indicated are circulation features of interest, including the Liguro-Provençal drift (A), the Liguro-Catalan current (B) and the Northern drift with Atlantic influence (C).

na, have been studied less (Dinet and Khripounoff, 1973; De Bovée *et al.*, 1990).

In the present paper we document the level of preservation of the deep-sea floor phytodetritic material in relation to the oceanographic regime and the overlying phytoplankton biomass in late spring in 3 distinct areas: the Rhodanian slope, the Catalan slope and the North Balearic zone. We discuss the variations linked to the canyon's geomorphology, arguing and illustrating the importance of this phytodetritic material as a food source for meiofauna.

SITES, MATERIALS AND METHODS

During the EUROMARGE'95 cruise aboard the R/V "Suroit" in the north western Mediterranean basin, one major task was a coordinated study of biogeochemical cycles with a prevalent focus on the water-sediment interface.

Samplings took place in three clearly distinct hydrodynamic areas: the Rhodanian slope, the Catalan slope and the North Balearic zone. A permanent nutrient enriched dome or ridge, extending from north of the Gulf of Lions to south-west of the Catalan Sea, is delineated by two "fronts" and their associated opposite currents (see refs in Introduction; Fig. 1). The Catalan front is characterized by a strong salinity gradient and the North Balearic front by a temperature gradient (Font, 1988). Schematically, three water masses coexist: a dense median dome and lighter waters of continental origin on the west side and of Atlantic origin on the east side. The position of the "fronts", central "divergence" and the presence of mesoscale cyclonic cells depend upon seasons and years (Font, 1988). From the hydrological descriptions of this Basin, two major phytoplankton provinces with well-marked differences can be identified: 1) on the western coast, an enriched water mass linked to the Catalan front; and,

2) on the east side (North Balearic zone) phytoplankton with a lower biomass. Different assemblages characterise these two provinces (Estrada *et al.*, 1989; Barlow *et al.*, 1997).

Sampling of sediments and water masses was carried out in late spring (1995 June 5-16). Different canyon parts were sampled at each of the four prospected sites (Fig. 1): Head, Axis and Interfluve (Fig. 2). The sampling locations and dates are summarised in Table 1. Each station can be defined as follows: 1) the Planier station (PL) was at a 260 to 1180 m depth site located on the Rhodanian slope in the south-west Liguro-Provençal derive regime; 2) the Lacaze Duthiers (LD) and 3) Foix stations (FX) were located on the Catalan slope also in the south-west drift; and 4) the Balearic Islands station (BL) was located in the North Balearic basin in a northward drift regime.

Sediments were collected with the 12-core Wuttke multiple corer [described by Barnett *et al.* (1984) and produced by Fa. Wuttke, Hamburg]. This corer enables the sampling of well-preserved sediment-water interface even at deep stations (Thiel *et al.*, 1988-1989). At each site two cores (from two different casts) were analysed (Table 1), with the exception of the LD Interfluve, BL 1650 Axis, FX Axis and PL Head. Differences in pigment concentrations between duplicates (sub-samples from one core) were less than 5%.

Immediately after sampling, cores were transferred to the laboratory. The water interface layer (about 5 mm) was gently siphoned off the cores and sub-sampled for further analyses and tests (5 ml sub-sample filtered onto GF/F Whatman filters and stored frozen at -20°C for subsequent pigment analysis; 10 ml for epifluorescence microscopy study on board and 2 ml isolated for revival test on board, see below). Then, the bottom water (the first 10 to 20 cm above the sediment) was siphoned off and sub-sampled (100 to 500 ml filtered and stored in the same way as for the interface layer) for subsequent pigment analysis. The upper part of the cores was carefully sliced into 6 segments (0-0.5, 0.5-1, 1-2, 2-3, 3-4, and 4-5 cm) and stored frozen at -20°C for subsequent pigment analysis and dry weight evaluation. Storage for several months does not apparently affect the pigment concentrations (Gieskes and Kraay, 1983; Klein and Riaux-Gobin, 1991). A sub-sample (0-0.5 cm) fraction was preserved in formaldehyde for subsequent SEM examination.

Surface water samples were collected with NIO bottles. A 2 l sub-sample was filtered on Wathman GF/F filters and stored frozen at -20°C for subsequent pigment analysis (Table 1). Chlorophyll *a* (including isomers), *b* and *c* (Chl *a*, *b* and *c*) and associated phaeopigments (Phaeo *a*, *b* & *c*) were measured on acetone extracts using the spectrofluo-
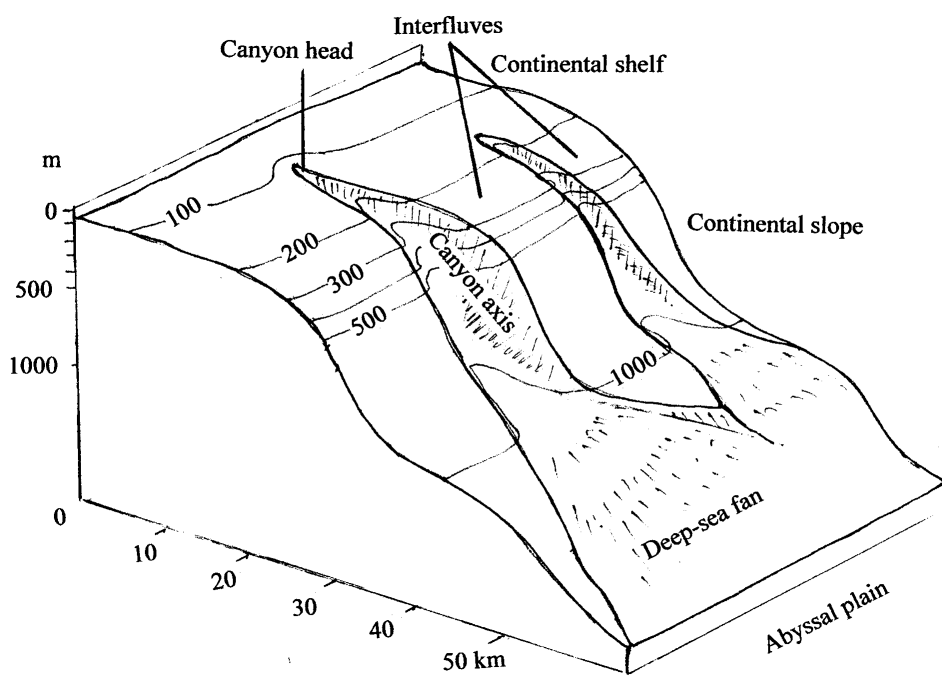

Fig. 2. – Schematic presentation of a canyon, with head, axis and interfluve parts, as mentioned in this study.

TABLE 1. – List of sampling stations, geographical positions and sediment depths. St. N° = number (see Fig. 1) and letter (see PCA Fig. 8); KTB = multiple corer; n.d. = no data; dupl = duplicates). PL = Planier canyon; LD = Lacaze Duthiers canyon; BL = Balearic Islands sites; FX = Foix canyon; Int = interfluve.

St. N°		Cast type	Station	Date	Latitude N	Longitude E	Depth (m)	Phyto. surface
1	A	KTB_{03}	PL Axis	5/6/95	43° 00.72'	5° 11.63'	1180	+
1	B	KTB_{05}	PL Axis	5/6/95	43° 00.62'	5° 11.61'	1180	n d
2		KTB_{06}	PL Int	6/6/95	42° 58.97'	5° 14.67'	915	n d
2	C	KTB_{10}	PL Int	6/6/95	43° 00.47'	5° 16.83'	630	+
3	D	KTB_{11}	PL Head	6/6/95	43° 05.95'	5° 14.79'	260	+
4	E	KTB_{16}	LD Axis	8/6/95	42° 24.25'	3° 37.56'	1175	+
4	F	KTB_{19}	LD Axis	8/6/95	42° 24.29'	3° 37.44'	1180	n d
5	G	KTB_{21}	LD Int.	10/6/95	42° 25.71'	3° 41.93'	775	+
6	H	KTB_{27}	BL Axis	11/6/95	40° 13.02'	3° 25.47'	1220	+
6	I	KTB_{28}	BL Axis	11/6/95	40° 13.01'	3° 25.54'	1220	n d
7	J	KTB_{29}	BL Int	12/6/95	40° 13.95'	3° 37.04'	585	+
7		KTB_{32}	BL Int	12/6/95	40° 14.01'	3° 37.00'	585	n d
8	K	KTB_{33}	BL 2000	13/6/95	40° 27.31	3° 43.38'	2070	n d
8	L	KTB_{34}	BL 2000	13/6/95	40° 27.17'	3° 43.17'	2070	+
9		KTB_{37}	BL 1650 Axis	13/6/95	40° 18.07'	3° 12.26'	1650	n d
10		KTB_{40}	FX Int S	15/6/95	40° 54.02'	1° 47.05'	1040	+(dupl)
10		KTB_{42}	FX Int S	15/6/95	40° 54.04'	1° 47.07'	1045	n d
11	M	KTB_{44}	FX Axis	16/6/95	40° 56.65'	1° 54.68'	1310	+
12	N	KTB_{45}	FX Int N	16/6/95	40° 58.02'	1° 59.43'	1030	+(dupl)
12	O	KTB_{47}	FX Int N	16/6/95	40° 58.02'	1° 59.43'	1040	n d

rometric method of Neveux and Lantoine (1993). GF/F filters were homogenized in 100% acetone (p.a. Merck) and kept cool and dark for 12 h. Wet sediments (1 g ± 0.001 g) were extracted (for 24 h, 4°C, in dark) in 10 ml 90% acetone (p.a. Merck), without grinding or adding $MgCO_3$, only shaking twice during the extraction time (the final concentration of acetone was never below 85%; pigment degradation only appears below 80%). Sub-samples of sediments were oven dried (60°C) for dry weight evaluation. For scanning electron microscopy (SEM), small sub samples of subsurface sediments were filtered on Nuclepore filters (1 μm pore diameter), carefully washed with distilled water to remove salts, oven dried (60°C), gold coated and observed with an Hitachi S 520 scanning electron microscope.

At each sampling station, cultures in 500 ml F/2 medium (Guillard and Ryther, 1962) were initiated immediately after sampling, with a 5 ml inoculum of the water-sediment interface. In the first step these cultures were incubated under natural conditions on the ship deck at the temperature of the surface water masses. At the end of the cruise, the cultures were transferred to the laboratory under similar simulated conditions in a controlled culture chamber. Every 5-8 days these cultures were sampled for later Chl *a* analysis (5 ml GF/F filtered and stored frozen at -20°C) and for microscope examination.

In order to evidence still living microphytes, qualitative epifluorescence tests were applied onboard (Zeiss microscope, obj. 40) on subsurface sediment sub-samples at each site.

Meiofauna was collected with cut-off plastic syringes (5.31 cm² in section) used as small cores. Four sub-samples were taken in two different tubes of each multi-corer performed. The upper 5 cm of each mini-cores were preserved in 4% buffered formalin. The animals were sieved on a 40 μm mesh and sorted by an adapted Silicagel-flotation technique (De Jonge and Bouwman, 1977) using Ludox HS-40. They were counted under a dissecting microscope and identified to higher taxa. Data are expressed in individuals per m^{-2} and mg per m^{-2} (see refs *in EUROMARGE-NB Final Report*: Dinet *et al.*, 1996).

Simple regressions and a principal component analysis (PCA) were applied to a set of data (n =15) concerning pigments, water content, sampling depth and meiofauna densities from the same cast at each site.

RESULTS

Sediment description

We had the opportunity to work on cores with a well-preserved interface in most cases. No real fluff was observed (only whitish vellum in some cases),

TABLE 2. – Pigment concentrations in water masses (surface, bottom and overlying the sediment), surficial sediment (0-0.5 cm). and batch culture after 20 days (see text for culture conditions). Surface = surficial phytoplankton; bottom = 0-20cm above sediment; interface = 1-5mm above sediment. * duplicates (mean value); ** duplicates (the 2 values). n d = no data. ( ) = dubious data. The duplicates were sampled with two different casts (see Table 1).

Station	Depth m	water masses surface Chl a	bottom Chl a	interface Chl a [µg l⁻¹]	sediment (0-0.5 cm) Chl a	Phaeo a [µg g⁻¹ dw]	Chl a / Phaeo a water surface	water bottom	sediment (0-0.5 cm) Chl a [µg l⁻¹]	Chl a / Chl b water surface	sediment (0-0.5 cm)	culture tests after 20 d
Rhodanian slope												
Planier (PL)												
-Head	260	0.074	0.026	0.662	0.551	4.716	5.239	0.339	0.117	6.09	4.01	400
-Axis*	1180	(0.972)	0.013	1.06	0.642	7.593	5.102	0.206	0.085	(17.06)	2.99	** 300, 500
-Interfluve*	630-915	0.095	0.011	0.070	0.242	3.043	5.185	0.072	0.079	7.17	2.74	** 0.1, 50
x̄		(0.380)	0.017	0.597	0.478	5.117	5.175	0.206	0.094	(10.11)	3.25	
SDV		(0.512)	0.008	0.498	0.209	2.301	0.069	0.133	0.020	(6.04)	0.67	
Catalan slope												
1) Lacaze Duthiers (LD)												
-Axis*	1175	0.288	0.105	0.280	0.422	5.178	3.633	0.599	0.081	12.12	3.03	* 1, 13
-Interfluve	775	0.443	0.010	0.045	0.248	3.532	2.976	0.069	0.070	10.32	2.41	7
2) Foix (FX)												
-Axis	1310	0.172	0.030	0.036	0.826	10.772	5.122	0.104	0.077	5.14	2.62	0.08
-Interfluve N*	1030	0.095	0.011	0.028	0.294	4.500	2.960	0.129	0.061	6.00	2.43	** 0.02, 0.08
-Interfluve S*	1040	0.134	0.008	0.064	0.357	5.050	4.263	0.073	0.071	5.37	2.44	** 0.07, 0.09
x̄		0,226	0.033	0.091	0.429	5.806	3.790	0.194	0.072	7.79	2.59	
SDV		0.141	0.041	0.106	0.231	2.850	0.918	0.227	0.008	3.21	0.26	
North Balearic zone												
Baleares (BL)												
-Axis*	1220	0.069	0.006	0.068	0.161	2.022	6.133	0.006	0.080	5.02	1.74	** 0.3, 5
-Interfluve	585	0.072	0.008	0.023	0.295	3.166	5.007	0.008	0.078	4.21	2.03	** 0.3, 38
-Bal. Ax. 1650	1650	n d	0.005	0.042	0.159	1.870	n d	0.074	0.085	-	1.39	nd
-Bal. 2000*	2070	0.059	0.003	0.009	0.195	2.525	4.718	0.074	0.078	4.5	1.83	** 0.1, 1.7
x̄		0.067	0.006	0.036	0.203	2.395	5.286	0.040	0.080	4.58	1.75	
SDV		0.007	0.002	0.026	0.064	0.585	0.747	0.034	0.003	0.41	0.27	

indicating no recent microphytic sedimentation. Some differences were noticed in the macroscopic appearance of the sediment within each site, but also within the different parts of the canyons. At PL a red surficial layer (2-4 cm deep) due to Pechiney Industrial waste was observed. At BL the sediments appeared grey and more compact than on the Catalan slope and the microscopy test revealed the presence of coccoliths and absence of diatoms (pers. and Dugué obs.; SEM pictures not shown). On the western sites, diatoms were present at the same depth. As a general trend, the interfluve surficial sediments were fluid (high water content) within a more important depth than in the canyon axis. Macrofauna burrows were observed particularly at PL Int, LD axis and LD Int. These burrows suggested an active bioturbation on these sites, with no differentiation between axis and interfluve.

Phytoplankton

During this late spring, surface Chl a concentrations (Table 2; Fig. 3) were relatively low (0.09 to 0.34 µg l⁻¹), with slightly higher values at LD (maximum 0.4 µg l⁻¹). These results are in agreement with those reported by Conan *et al*. (1996) from a cruise a few weeks later at the same sites, with the exception of the high value at PL axis (0.972 µg l⁻¹; Table 2), which may be dubious [such a high pigment concentration on the Rhodanian site was previously only reported on a coastal zone and during summer (M_1; Conan *et al*., 1996)], but the Chl a concentration of the interface water at the same site was also high (Table 2). The North Balearic stations (BL) presented the lowest phytoplankton pigment amounts. The Chl a / Chl c ratio was spatially constant (average: 3.5; no data shown), whereas the Chl a / Chl b ratio decreased significantly from north to south (7-10 to 4; Table 2).

Bottom water and interface

Very low pigment amounts characterised the deep overlying water (bottom water, 20 cm column above the sediment) at all sites (Table 2; highest values at LD axis, up to 0.105 µg Chl a l⁻¹). The Chl a
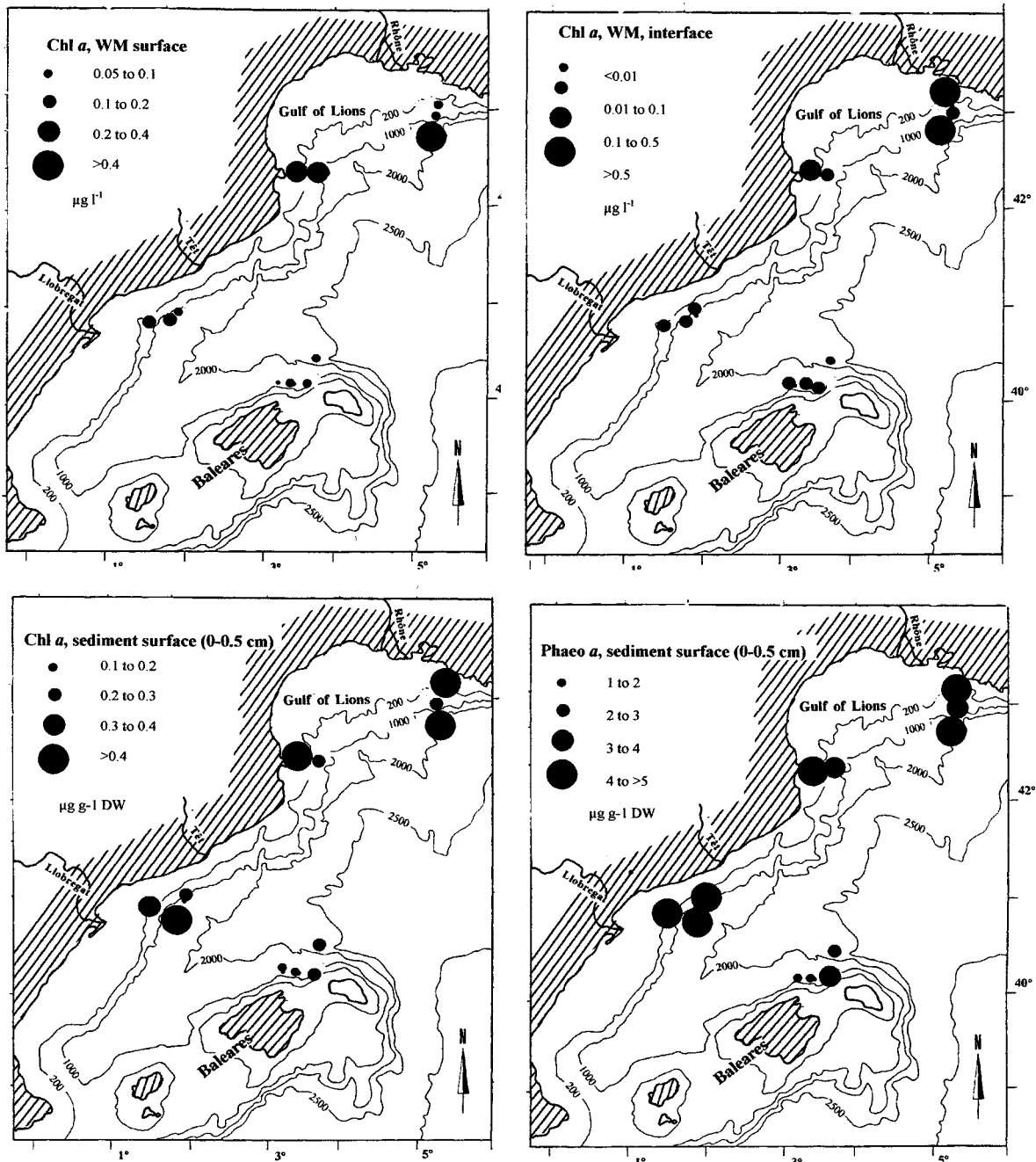
FIG. 3. – Spatial repartition of Chl *a* in surface Water Masses (WM), water sediment interface, sediment surface (0-0.5 cm layer) and Phaeo *a* in sediment surface (0-0.5 cm layer).

/ Phaeo *a* ratio, representative of the degree of degradation of the material, ranged from very low values (< 0.1) at BL to far higher values at PL head and LD axis (0.34 and 0.59 respectively). With the exception of these last two sites, no recent sedimentation has apparently taken place in other areas. Concerning the interface layer (the few mm above sediment; Table 2; Fig. 3), no real fluff was observed, and here again only PL axis and head and LD axis showed high values (0.66 to 1.06 µg Chl *a* l⁻¹), whereas at

the other sites the concentrations were at the detection limit of the method.

Sediment

Duplicates within two different casts at the same site indicated a good reproducibility of results (around 10% variation; cf. Table 2 *in EURO-MARGE-NB Final Report*: Riaux-Gobin *et al.*, 1996). Table 2 and Figure 3 give the pigment distri-
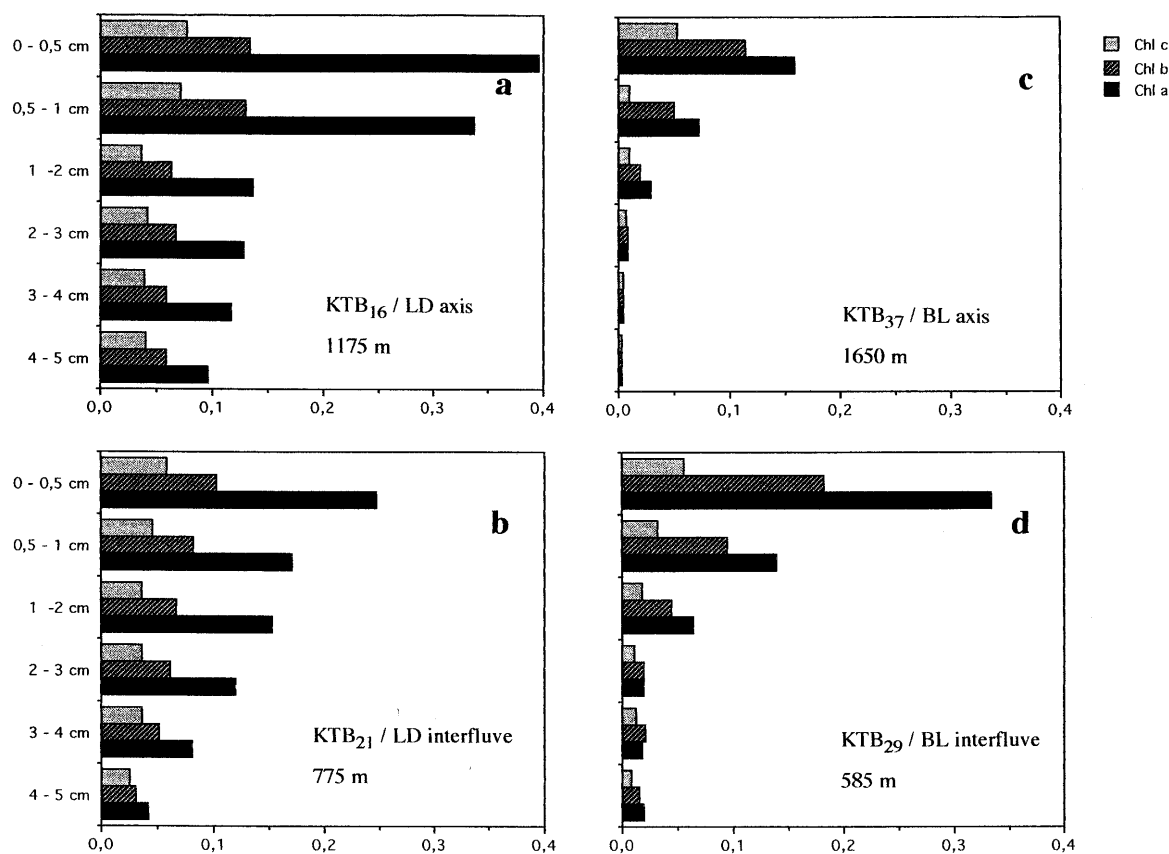
FIG. 4. – Vertical pigment gradients in sediments, in two contrasted zones: the Lacaze Duthiers canyon (enriched zone. 2a: LD axis; 2b: LD interfluve), and the Balearic Islands site (impoverished zone. 2c: BL axis; 2d: BL interfluve).

bution in the first 5 mm of sediments. Pigment concentrations were low (average of 0.37 µg g^{-1} dw Chl a and 4.49 µg g^{-1} dw Phaeo a), with minimum values at BL (0.17 µg g^{-1} dw Chl a). The Chl a / Phaeo a ratio was relatively constant in all layers of all sediments, ranging from 0.06 to 0.12 with no clear trend. Chl a / Chl c ratios were higher than in the overlying water (from 4 to 5; data not shown), whereas the Chl a / Chl b ratio was lower at the sediment surface (from 1.3 to 4), probably due to a better preservation of Chl b (Chl b is more stable than Chl a; Brown et al. 1977). On the other hand, a clear gradient of the Chl a / Chl b ratio was observed from 3.25 in the north to 1.75 in the N Balearic sites. From surface to deeper layers of sediments, a regular gradient of pigments was obvious at the interfluve stations (for example at LD and BL; Fig. 4 b and d), whereas at the axis sites the gradient was more irregular (Fig. 4 a and c).

Epifluorescence qualitative tests

At PL some fluorescent cells (containing chloropigments) were detected on each part of the canyon (only in surface sediment); this fluorescent signal was often associated with faeces and aggregates. At LD some rare but apparently undamaged cells with red well-marked fluorescence (upon which $Chaetoceros$ spore-like cells) were present mostly at LD axis. In contrast, at FX and BL no well-preserved cells were observed, only faeces with a very low, greenish signal.

Revival tests

The revival tests (Culture tests; Table 2) were positive for the northern sampling stations (PL, LD), whereas at FX and BL they were not significant (see illustration in $EUROMARGE-NB$ $Final$ $Report$: Riaux-Gobin et al., 1996). The duplicates (cultures initiated with samples of 2 different casts at the same site; Table 2), even if not exactly similar, roughly indicated the same tendency. There was no revival at FX, very low response at BL, positive but low response at LD and rapid response at PL head and PL axis, whereas the response at PL interfluve was less positive. The level of response was apparently not linked to the depth. Moreover, the highest

pigment concentrations in the sediment were not always linked to a positive response of the culture (i.e. FX axis; Table 2). These cultures attest that at the PL and LD stations some microphytes were still living when sampled. Some light microscope investigations on these cultures were performed at the end of the experiments: these assemblages were dominated by well growing planktonic microalgae, particularly *Chaetoceros* spp (the culture makes the determination at species rank difficult).

DISCUSSION

Geographical areas in the NW Mediterranean basin

Following the present phytoplankton data, and in agreement with the previous works (i.e. refs. cit.), the east part of the North Balearic Basin (BL) is an impoverished (oligotrophic) area, whereas the Rhodanian slope (PL) and the Catalan slope (LD and FX) exhibited higher pigment concentrations, partly related to river discharge (Masó and Duarte, 1989). Moreover, the Chl *a* / Chl *b* ratio decreased from north to south. Chl *b* is a marker of *Chlorophyta* and *Prochlorophyta* (Rowan, 1989; Buma *et al.*, 1991). The low Chl *a* / Chl *b* ratio characterises the dominance of population by these organisms. Thus, the results suggest that different assemblages are linked to each water mass, its origin and its hydrodynamics, in agreement with previous studies (Estrada *et al.*, 1989; Barlow *et al.*, 1997). The Chl *a* / Phaeo *a* ratio also exhibited differences within areas: on the Rhodanian slope (PL site) this ratio was homogenous from the coast to off-shore, though this was not the case at the other sites, indicating different origins of the water masses (i.e. refs. cit.) or the presence of meso-scale hydrodynamic cells.

An interesting new fact is that the deep-sea benthos reflects not only the differences between the pigments richness (a), but also the pigment diversity (b) of the overlying water masses of the three areas, even after particle sedimentation and grazing.

a) Figure 5 illustrates the relationships between the phytoplankton biomass in surface waters and in deep-sea sediment surface. A significant correlation appears within BL, PL and FX (r = 0.74, significant at P = 0.01). When LD is also taken into account, the correlation is not significant (r = 0.39). During the sampling period, the sediments of the Lacaze Duthiers canyon (LD) do not reflect the richness of the overlying phytoplankton. On the other hand, the

meiofauna is particularly abundant at this site, probably with intense grazing. A similar trend is also noticed if we compare the bottom water (20 cm water column overlying the sediments) and the overlaying surface water pigment concentrations: a positive (direct) correlation exists (not illustrated), but with a weak significance (r = 0.3924, n = 10); here again, if LD is not included in the calculations, the relationship is stronger (r = 0.57).

Observations in epifluorescence and revival tests roughly agree with these assumptions: a better preservation at the sediment-water interface seems to occur in the areas where the overlying waters are phytoplankton-enriched (northern stations), with no well marked relation to depth. In the north Balearic zone (BL) all parameters (even the meiofaunal density, Fig. 6 A) indicated a reduced richness of the interface, related to the low phytoplankton concentrations in the upper water masses.

b) The geographical gradient in the Chl *a* / Chl *b* ratio in sediment surface roughly follows those of the overlying phytoplankton (Table 2). Moreover, the absence of diatom frustules in deep-sea sediments in the south part of the NW Mediterranean basin (BL), and coccoliths present everywhere, reflect the geographical diversity of the phytoplankton assemblages.

Moreover, the degree of compaction and appearance of BL sediments (light/whitish grey colour), which are different from those of the west part of the Basin, are also noticeable. The Balearic platform is carbonate-enriched (Canals and Ballesteros, 1997), partly due to a lack of fluvial inputs, favouring the settlement of carbonate benthic communities and carbonate particles, whereas the north-west Mediterranean margin is dominated by terrigenous inputs. The phytoplankton assemblages of the south part of the NW Mediterranean, mainly lacking large diatoms (refs. cit.) may also explain the carbonate-dominated sedimentation at BL.

Variations linked to canyon geomorphology

In Table 3 we compare the results for different parts of a canyon during spring-summer (unpublished data from MEDIMAR cruises and present study): The Axis and Interfluve of the Lacaze-Duthiers canyon (LD). We had the opportunity to sample this canyon over several years, from 1991 to 1995 (present data), in similar conditions, using a multiple corer and the same pigment analysis methodology.

	AXIS						INTERFLUVE					
Date	lat N	long E	Depth m	Chl a [µg g^{-1}dw]	Phaeo a	Chl a/ Phaeo a	lat N	long E	Depth m	Chl a [µg g^{-1}dw]	Phaeo a	Chl a/ Phaeo a
April 199	142°21.91' "	3°55.50' "	1540	0.141 0.176	3.722 3.654	0.038 0.048	42°26.43' "	3°40.88'	760 "	0.076 0.145	1.839 3.852	0.041 0.038
July 1991	"		"	0.138 n. dupl	3.118	0.044	" "		" "	0.128 0.084	3.342 2.033	0.038 0.041
May 1992	" "		" "	0.125 0.303	2.534 5.844	0.093 0.052	" "		" "	0.198 0.136	4.301 4.058	0.046 0.034
Mar. 1993	"		"	0.098 n. dupl.	2.763	0.035	" n. dupl.		"	0.076	1.839	0.041
June 1995 (present study)	42°24.25' 42°24.29'	3°37.57' 3°37.44'	1175 1180	0.396 0.447	5.059 5.296	0.078 0.084	42°25.71' n. dupl..	3°41.94'	775	0.248	3.531	0.070
x̄ SDV				0.228 0.135	3.998 1.245	0.059 0.023				0.138 0.062	3.099 1.034	0.044 0.011

Pigment concentrations are higher in the axis of the canyon, but very slightly and with exceptions (Table 3). The Chl a / Phaeo a ratio does not show any significant differences within the two parts of the canyon. As previously suggested (Monaco e*t al.*, 1990; Buscail *et al.*, 1990; Courp and Monaco, 1990), advection and channelisation may not be the only sedimentation and accumulation processes involved. In frontal zones, "pulse" sedimentation may also induce temporary higher particulate material concentrations in axis canyons, as well as in deep interfluves. In agreement with this hypothesis,

FIG. 5. – Relationships between pigment content of the sediments (0-0.5cm layer; µg g^{-1} Chl a dw) and the surface water masses (µg l^{-1} Chl a).

numerous macrofauna burrows (pers. obs. during MEDIMAR campaign, and present cruise) suggested an active bioturbation at these sites, with no differentiation between axis and interfluve. These observations (burrows not restricted to canyon axis) fit closely to those extensively reported *in EUROMARGE-NB Final Report* by Grehan and Keegan (1996).

At BL, where phytoplankton biomass is low, the underlying sediments were also impoverished (cf. Fig. 5), and no difference appeared within axis or interfluve pigment concentrations. Bioturbation (as suggested from Macrofauna burrows presence) was scarcer at BL than in the Catalan or Rhodanian zones.

Furthermore, a seasonal trend seems to exist in these deep-sea sediments: the higher pigment concentrations at LD were reported in late spring (May-June, whenever axis or interfluve), whereas in March-April concentrations were low (Table 3), and very low concentrations were observed in winter (LD interfluve, 1991: 0.022 to 0.08 µg Chl a g^{-1} dw). Such seasonality in phytodetritus deposition in the Gulf of Lions has been previously documented in relation to meiofauna (De Bovée *et al.*, 1990).

Sedimented phytodetritus as a food source for meiofauna

Another interest of this study was to point out connexions within phyto-biodeposits and Meiofauna, and to discriminate the influence of hydrology, geomorphology (particularly in canyons) and depth
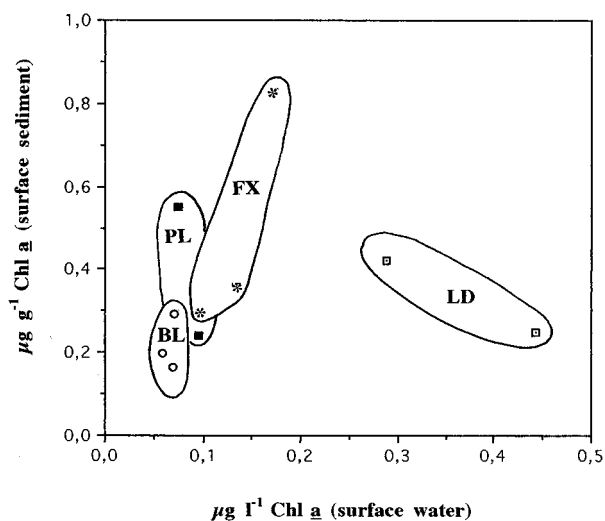
TABLE 4. – Meiofauna (0-5 cm layer). Data from the same cores cast as for pigments data (see Table 2, and ACP). Duplicates from different cores. n. d. = no data

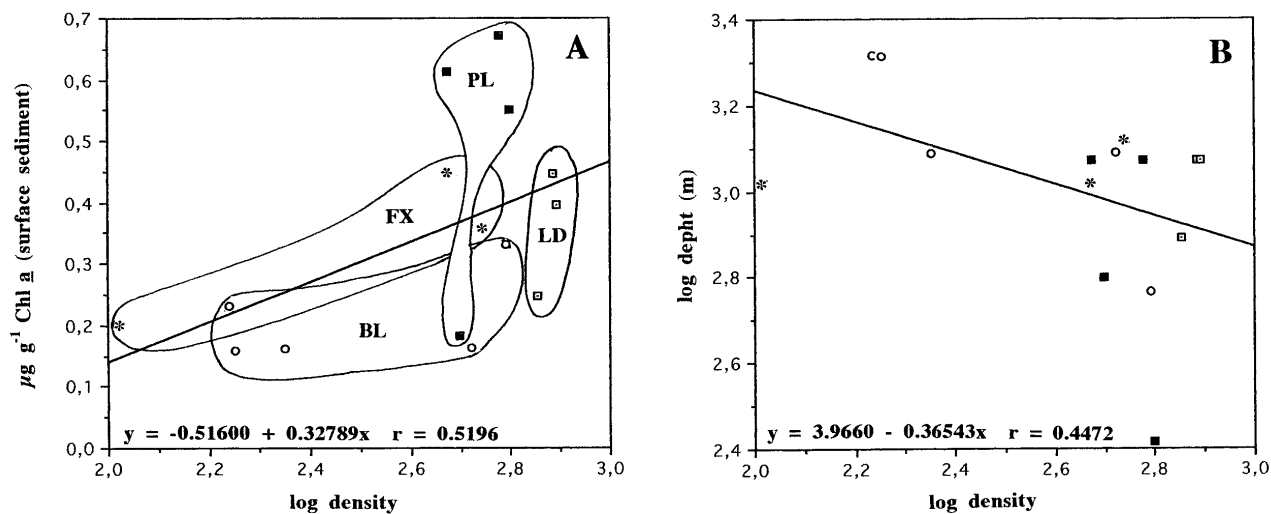| Station	Depth m	map N°	nematodes indiv. 10 cm⁻²	copepods indiv. 10 cm⁻²	total Meiofauna 10 cm⁻²	biomass Meiofauna mg m⁻²
Rhodanian slope						
Planier (PL)						
-Head	260	3	1028	117	1190	304.9
-Axis	1180	1	1047	45	1130	237
-Axis	1180	1	838	30	889	183
-Interfluve	630	2	855	34	936	190
-Interfluve	630	2	1049	58	1154	250
Catalan slope						
1) Lacaze Duthiers (LD)						
-Axis	1175	4	1397	58	1470	314
-Axis	1175	4	1360	36	1440	285
-Interfluve	775	5	1230	58	1350	284
2) Foix (FX)						
-Axis	1310	11	1049	15	1140	207
-Interfluve N	1030	12	804	9	885	157
-Interfluve N	1030	12	190	0	196	35
-Interfluve S	1040	10	987	13	1040	194
North Balearic zone						
Baleares (BL)						
-Axis	1220	6	384	21	42.2	91
-Axis	1220	6	934	38	99.6	209
-Interfluve	585	7	1098	40	116	240
-Bal. Ax. 1650	1650	9	n. d.	n. d.	n. d.	n. d.
-Bal. 2000	2070	8	292	17	32.6	70
-Bal. 2000	2070	8	288	13	33.5	66

FIG. 6. – A) relationships between Meiofauna density (log ind. 5.31 cm⁻²; see Table 4) and the pigment content of the surface sediments (µg g⁻¹ Chl *a* dw; see Table 2). B) relationships between Meiofauna density (log ind. 5.31 cm⁻²; see Table 4) and the depth (log m).

of the sites. Previous works in the NW Mediterranean (Dinet *et al*., 1973; De Bovée *et al*., 1990) pointed out the relatively low Meiofaunal densities. The relationships within biodeposition and Meiofauna have been documented in the Mediterranean (De Bovée *et al*., 1990) and also in other sea margins or deep-sea sediments (Dinet and Khripounoff, 1982), and were recently documented by

Pfannkuche *et al*. (1999) in the north-east Atlantic, and by Pfannkuche *et al*. (2000) in the deep Arabian Sea. The present data (Table 4; Fig. 7), point out relationships within meiofauna and (a) abiotic and (b) biotic factors (Table 5).

a) The good relationships between copepods and sediment pore water content (significant at P = 0.05) may be explained by their preference for fluid sedi-

TABLE 5. – Linear regression coefficients between major parameters in surficial sediments of the studied sites (PL, LD, BL, FX), i.e.: Chl *a*, Chl *b*, Phaeo *a* concentrations, sediment pore water content (% p.w.), total Meiofauna abundance, nematodes and copepods abundance (and pigment ratios as indication, see comments in text, and PCA illustration). n =15; ∗ = significant at p = 0.05

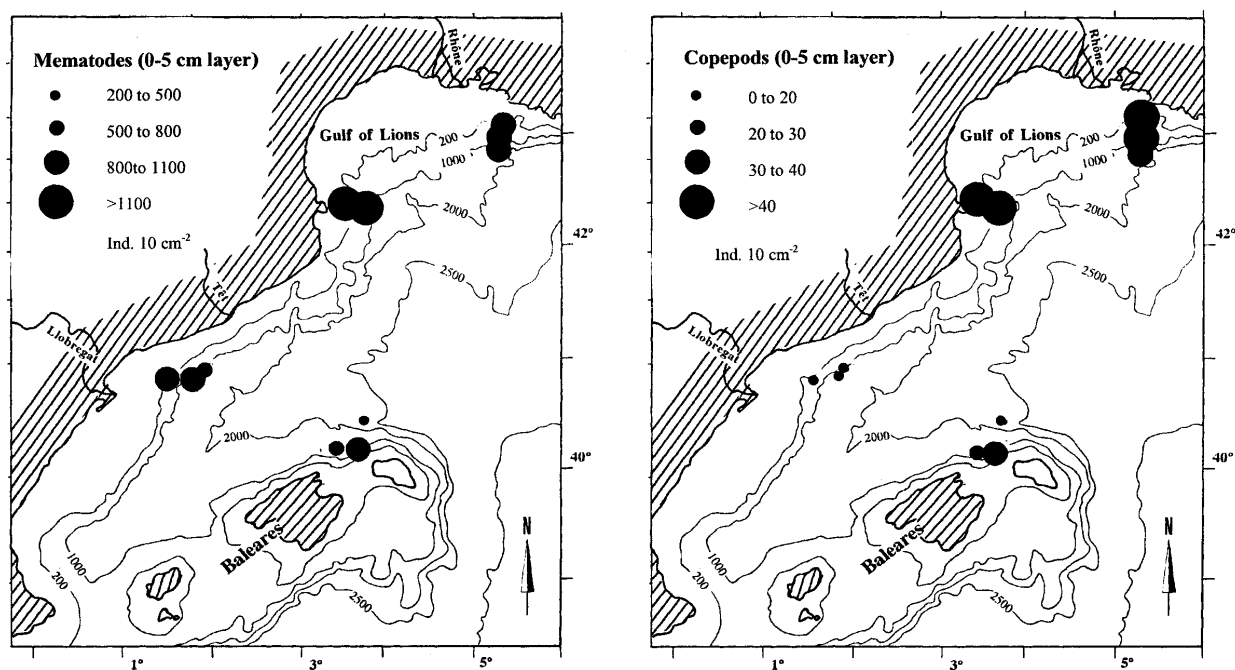|	Chl *a*	Phaeo *a*	Chl *b*	Nem.	Cop.	Meio.	%p.w..	Depth	Chl *a* / Chl *b*	Chl *a* / Phaeo *a*
Chl *a*	1	.95*	.87*	.49*	.41	.50*	.15	.28	.75	.46
Phaeo *a*		1	.88*	.47	.18	.46	.36	.15	.64	.18
Chl *b*			1	.39	.11	.38	.38	.09	.34	.29
Nem.				1	.58*	.99*	.06	.52*	.51	.28
Cop.					1	.62*	.57*	.60*	.68	.77
meio.						1	.08	.54	.54	.32
% p.w.							1	.57*	.29	.54
Depth								1	.53	.50
Chl *a* / Chl *b*									1	.52
Chl *a* / Phaeo *a*										1

FIG. 7. – Spatial distribution of nematodes and copepods in the sediment surface (0-5 cm layer).

ments. In agreement with previous works (see refs. *in* De Bovée *et al.*, 1990), meiofauna density is classically negatively related to depth (but with a low significance p = 0.1; Fig. 6B). Between the axis and interfluve canyon parts, the Meiofauna densities were not significantly different (Table 4).

b) As illustrated by simple correlations (Table 5; Fig. 6A) and PCA (Figs 8 A & B), Meiofauna abundance was positively related to Chl *a* concentration in surficial sediments (significant at P = 0.05), this relation being more strong/significant than those with depth. Chl *a* concentration was more or less independent of depth (Table 5). Moreover, a stronger relationships exists between Meiofauna and Chl *a* than within degraded pigments (Phaeo *a*). Thus, Meiofauna seemed to respond rapidly to freshly sedimented material. These results fit well with the relationships also described by Alongi
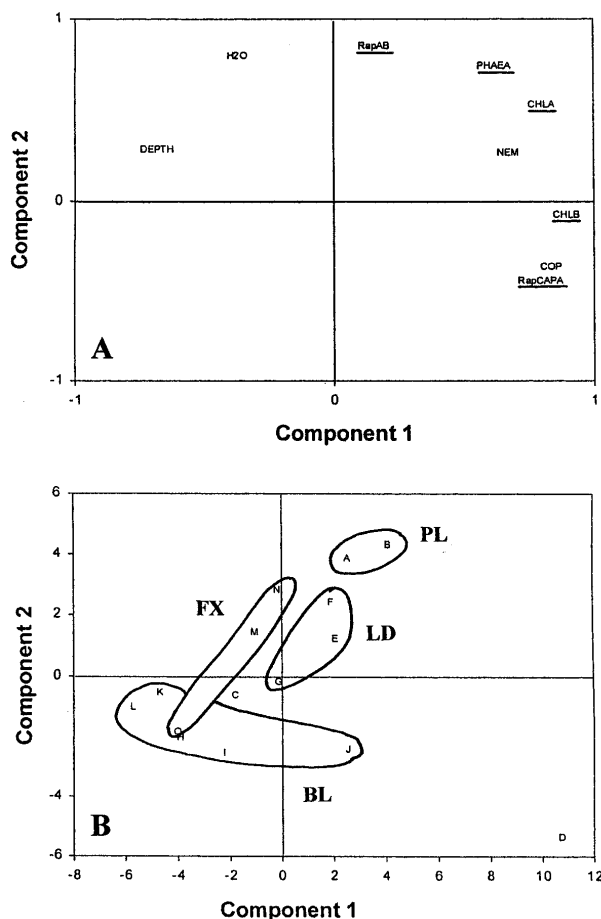
FIG. 8. – Principal Component Analysis (PCA). Illustration of the 2 first axes. A) parameters (RapAB = Chl *a*/chl *b* ratio; RapCAPA = Chl *a*/Phae ratio; CHLA = Chl *a*; PHAEA = Phaeo *a* and CHLB = Chl *b*). B) sampling sites (for abbreviations, see Table 1).

(1992) and Danovaro *et al*. (1995) between deep-sea benthic communities and available organic biodeposits. On the other hand, nematodes (major component of Meiobenthos) and copepods seem to have a dissimilar response to similar factors (PCA, Figs 8 and Table 5): copepods seem to be positively related to the Chl *a* / Phaeo *a* ratio, and to the freshness of the biodeposit. As they are in part detritivorous (McIntire, 1969; Pfannkuche *et al*., 2000), nematodes seem to be less dependent than copepods upon the freshness of the pigmented material. The Chl *a* / Chl *b* ratio also seems to influence the Meiobenthos spatial repartition (see Table 5).

CONCLUSION

Two different sectors in the NW Mediterranean basin are evidenced from the spatial distribution of pigments in surface water and the deep-sea floor:

- The NW and W margins (Rhodanian and Catalan slopes) were phytoplankton-enriched, and exhibited a relatively high pigment content in sediments, with the exception of the southern part (Foix canyon), and high Meiofauna densities.

- The North Balearic zone was phytoplankton-impoverished, and exhibited very low pigment concentrations in sediments, associated with lower Meiofauna densities.

These results, also confirmed by the revival tests, fit well with the presence of the median Catalan front (see refs. cit., Introduction), separating two well-defined zones with contrasted hydrodynamics: 1) The Liguro-Provençal derive on north with major river discharges, and 2) the northward Balearic drift with Atlantic influence on the south (see Fig. 1).

The present data confirm that organic compounds such as microphyte pigments, as well as their ratios, can be used as a reliable proxy for present—or recent—sedimentation events, and can be the fingerprints of the hydro-climatic conditions that prevailed in the overlying water masses in the weeks before. The frontal Catalan zone, as defined by Estrada and Margalef (1988; see Introduction), which is demonstrated to be phytoplankton-enriched despite a relatively low biomass in surficial waters, particularly during the present EUROMARGE 95 cruise, seems to induce local sedimentation and accumulation of Particulate Organic Carbon, and particularly chloropigments, which support the settlement and an active development of deep-sea Meiofauna.

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