Particle flux in the northeast Atlantic Ocean during the POMME experiment (2001): Results from mass, carbon, nitrogen, and lipid biomarkers from the drifting sediment traps.

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[1] During 48 hour stations during the three Programme Océan Multidisciplinaire Méso Echelle (POMME) cruises in 2001 (late winter, spring, and late summer) at different locations within the region studied (38°–45°N, 15°–21°W), drifting sediment traps were deployed at 200 m and 400 m. Fluxes increased from late winter (POMME 1) to spring (POMME 2), with highest values in the North Atlantic gyre (109.1, 20.1, and 3.5 mg m^{-2} d^{-1} for mass, C, and N, respectively) and decreased during POMME 3 to reach threshold values (19.1 ± 6.0, 4.4 ± 1.1, and 0.7 ± 0.2 mg m^{-2} d^{-1}, respectively). Lipid class tracers and their fatty acid composition analyzed by gaseous chromatography were used to assess the quality and quantity of organic matter fluxes. Wide seasonal variability was observed in biogenic lipid fluxes (0.42 ± 0.19 and 0.39 ± 0.13 mg m^{-2} d^{-1}, 1.78 ± 1.08 and 0.69 ± 0.56 mg m^{-2} d^{-1}, and 0.71 ± 0.14 and 0.45 mg m^{-2} d^{-1} on average at 200 m and 400 m during late winter, spring, and late summer, respectively) in relation with the development of the spring phytoplankton bloom. In a northern persistent anticyclonic eddy a major export of algal matter occurred through zooplankton activity. In contrast with this pattern, the southernmost anticyclonic eddy exhibited the lowest particle fluxes in relation to the low productivity and the high bacterial carbon demand prevailing in the surface waters. In the main cyclonic structure (C4) and the saddle zone (during POMME 2) the pattern of lipid biotracers reflected the permanence of a zooplankton community and likely advective transfer of matter between 43.5°N and 42°N through subsurface water circulation.

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1. Introduction

[2] The flux of particles is a major process of the "biological pump" which transfers photosynthesis products, living cells and detritus down to the sea floor. Only a small fraction (10%) of the organic matter produced in the euphotic productive layer is exported to intermediate waters [*Wakeham and Lee*, 1993] while the remainder is recycled in the epipelagic layer through dynamic trophic webs. Amorphous aggregates, marine snow, fecal pellets and carcasses of crustacean feed the vertical flux of organic material. During intense bloom periods, microalgae can contribute a significant part of the flux through direct sedimentation, without transfer through zooplankton. Processes of particle dissolution and remineralization are very active during transport in the water column. Overall, open ocean flux of organic carbon rarely exceeds 0.1–2% of the net primary production below 2000 m [*Lampitt and Antia*, 1997].

[3] The northeast Atlantic Ocean is known as a sink for carbon CO_2 [*Takahashi et al.*, 1995] suggesting intense mechanisms of primary production removal down to the deep ocean. Part of these mechanisms must be sought in the processes of biogenic particle export to depth. Intense and rapid bloomings of phytoplankton characterize the area [*Honjo and Manganini*, 1993]. In addition, the distribution of water masses varies widely at mesoscale, and subduction of mode waters occurs along a latitudinal gradient [*Reverdin et al.*, 2005]. To what extent such features affect physical/biological coupling and the associated process of biogenic particle export to depth, is not known.

[4] As part of the Programme Océan Multidisciplinaire Méso Echelle (POMME) experiment, the aim of the drifting traps deployment was to quantify and characterize the export of organic matter out of the productive layer. Lipids are good markers of sources and transformation of organic

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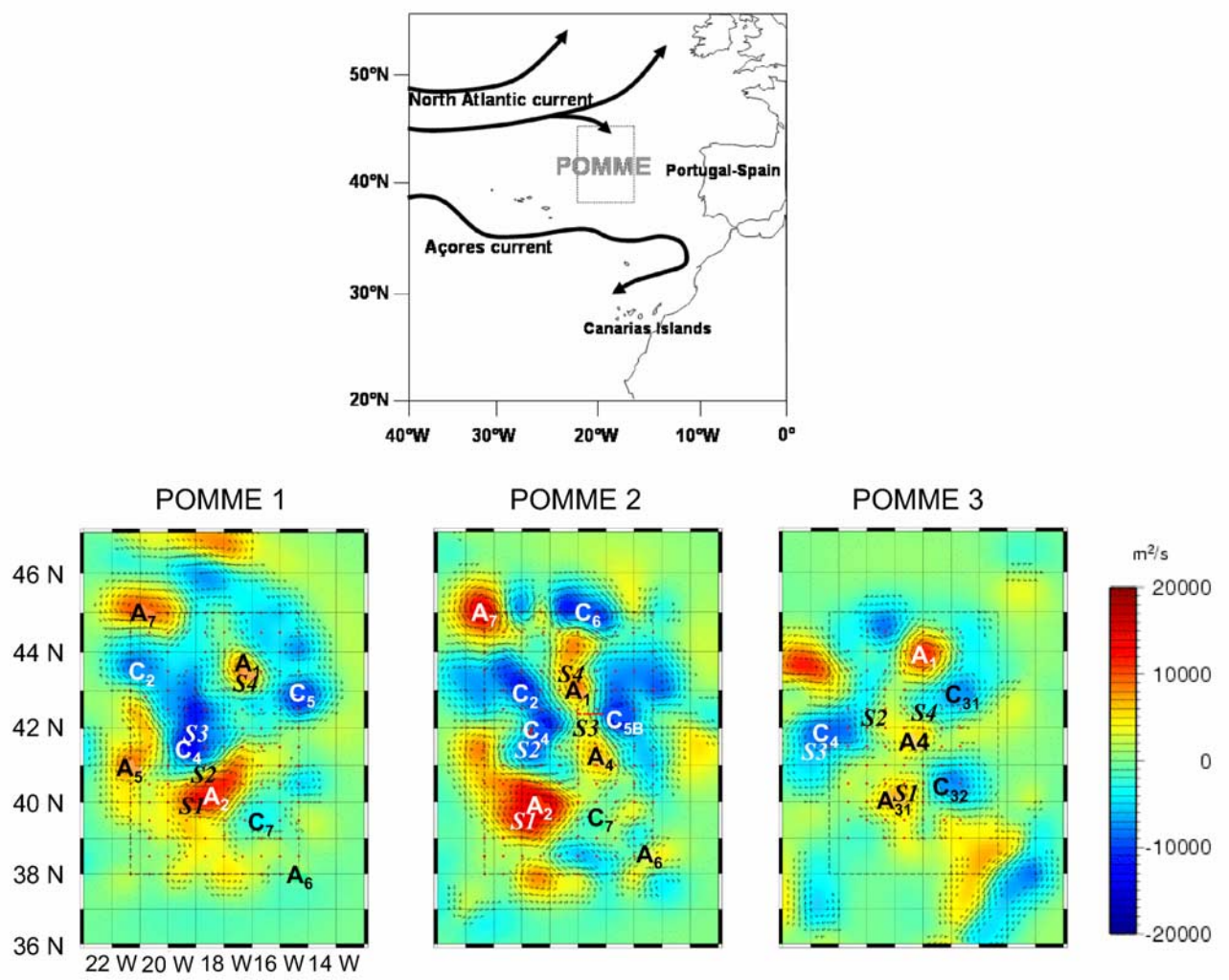

Figure 1. (top) Location of the Programme Océan Multidisciplinaire Méso Echelle (POMME) study area. (bottom) Synoptic maps of current velocity at 100 m depth, depicted as arrows around eddies, estimated during leg 1 (output of the Système Océanique de Prévision Régionale en Atlantique Nord-Est (SOPRANE) model (green frame), M. Assenbaum, Laboratoire d'Etudes en Géophysique et Océanographie Spatiales) showing cyclonic (C) and anticyclonic (A) structures. Time series stations (S1, S2, S3, and S4) are located within these hydrological structures.

matter in marine systems [*Saliot et al.*, 1991; *Wakeham*, 1995]. The dynamic of lipid classes and/or lipid molecular markers in sediment traps has been successfully used to assess the export process in marine systems [*Wakeham et al.*, 1984b; *Goutx et al.*, 2000; *Wakeham et al.*, 2002]. In the present paper, we report on the elemental composition and the lipid content of the particle flux. The pattern of variation of these biogeochemical descriptors is used to assess the role of seasonal biological features and/or hydrodynamic particularities in biogenic matter export to depth.

2. Materials and Methods

2.1. Sampling Area and Sediment Traps

[5] The northeast Atlantic area explored during the POMME program extended over 375 10^3 Km^2 between Açores and Spain, from 38° to 45°N and 16° to 22°W (Figure 1 (top)). The water mass circulation created mesoscale structures (front, cyclonic and anticyclonic gyres) and subduction of mode waters [*Mémery et al.*, 2005]. Each survey was carried out during two legs. During the first leg, the sampling of physical and chemical parameters enabled the description of the main hydrodynamic features in the area, whereas during the second leg, typical mesoscale structures identified during the first leg of the surveys were studied for biology and biogeochemistry through long time series stations (2 days), generally four stations for each leg 2. The drifting traps (Technicap PPS5, conical, 1 m^2 section) were deployed at 200 m and 400 m at the beginning of each time series station and during 47 hours. In 2001, the particle flux was collected at three periods of the year, late winter (POMME 1 (P1)), spring (POMME 2 (P2)), and late summer (POMME 3 (P3)). The stations were chosen along a north-south gradient with the aim of characterizing anticyclonic, cyclonic and frontal structures (Figure 1 (bottom)). A southwestward displacement of eddies was noticeable during the three surveys. Notwithstanding, some

Table 1. Geographical Position of Drifting Sediment Traps at Mooring and Recovery During POMME 1 (P1), POMME 2 (P2), and POMME 3 (P3)

Site	Hydrographic Structure	Mooring	Position	Recovering	Position
			POMME 1		
Site 1	southern anticyclonic (A2)	1 Mar 2001	N40°5.916, W18°46.242	3 Mar 2001	N40° 8.326, W18°46.089
Site 2	frontal zone (ZF)	5 Mar 2001	N40°47.72, W18°57.780	7 Mar 2001	N41°9.965, W18°32.999
Site 3	cyclonic (C4)	10 Mar 2001	N41°49.882, W18°20.465	12 Mar 2001	N41°43.412, W19°9.827
Site 4	northeastern anticyclonic (A1)	14 Mar 2001	N43°19.382, W17°30.678	16 Mar 2001	N43°6.611, W17°16.500
			POMME 2		
Site 1	southern anticyclonic (A2)	18 Apr 2001	N39°45.283, W19°44.743	20 Apr 2001	N39°44.350, W19°46.246
Site 2	cyclonic (C4)	22 Apr 2001	N41°59.940, W19°39.384	24 Apr 2001	N41°43.291, W19°44.023
Site 3	saddle (PS)	26 Apr 2001	N42°5.022, W17°39.770	28 Apr 2001	N41°58.047, W17°28.078
Site 4	northeastern anticyclonic (A1)	1 May 2001	N43°19.424, W17°57.000	3 May 2001	N43°21.347, W18°58.830
			POMME 3		
Site 1	southern anticyclonic (A31)	19 Sep 2001	N39°59.889, W19°19.718	21 Sep 2001	N40°7.448, W19°21.367
Site 2	anticyclonic (A4)	23 Sep 2001	N42°10.492, W19°50.201	25 Sep 2001	N42°19.825, W19°51.839
Site 3	cyclonic (C4)	27 Sep 2001	N41°24.417, W22°3.804	29 Sep 2001	N41°33.173, W21°54.653
Site 4	cyclonic (C31)	2 Oct 2001	N42°30.920, W17°57.780	4 Oct 2001	N42°30.920, W17°57.780

structures were sampled several times (the southern anticyclonic eddy A2, the cyclonic eddy C4 and the northern anticyclonic eddy A1) whereas other structures (i.e., the frontal zone and the saddle) were only sampled during one cruise. Table 1 associates each station with a hydrodynamic structure for comparison between the three surveys.

[6] The characteristics of drifting trap deployment and their position in the POMME area are reported in Table 2. The cups of the traps (seven per trap) were poisoned with a 2% buffered formalin solution. Among the seven cups, six sampled during 7 hours and one sampled during 5 hours. After sieving (>1 mm), the largest particles were separated from the sediment fraction and the living organisms removed. The remaining material was subsampled (3–20 mg). Aliquots were prepared by using a Jeacons peristaltic splitter which delivers prefixed volumes of subsamples. During the splitting procedure, the cup content was homogenized by gentle agitation using a magnetic stirrer. The subsamples were concentrated on preweighted glass GF/F fiber filters for mass, calcium carbonate, CHN and lipid biomarkers analyses.

2.2. Chemical Analysis

[7] Filters devoted to mass flux measurement were washed with MilliQ water in order to remove salts, then dried. Dry matter (hygrometric degree below 40%) was weighed (standard deviation below 10%). Elemental analyses (C, H, N) of sediments were performed on a technicon CHN analyzer LECO 900. The carbonate fraction was determined from particulate Ca concentrations [*Guieu et al.*, 2005].

[8] Lipids were extracted from the filters (precleaned 6 hours at 450°C) following the *Bligh and Dyer* [1959] protocol. Lipid classes were separated on chromarods and quantified on a thin layer chromatography/flame ionization detection (TLC/FID) Iatroscan TH10 apparatus model MK-IV (hydrogen flow, 160 mL min^{-1}; air flow, 2000 mL min^{-1}) coupled to a compatible PC equipped with a Boreal integration system (Flotec Company, 1989). Samples (4–6 μL of a 30 μL solution of the lipid extract in dichloromethane) were spotted using a 2 μL Hamilton syringe onto SIII chomarods previously calibrated with standard compounds (Sigma Chemical Ltd., GC grade). Analyses were run in triplicate.

[9] The separation scheme involved five elution steps in solvent systems of increasing polarity: hexane + diethylether + formic acid, acetone, chloroform + methanol and chloroform + methanol + ammonium hydroxide according to a modified procedure of *Goutx et al.* [1990] [*Striby et al.*, 1999]. The use of these elution systems was successful in separating neutral lipid classes (hydrocarbons, sterol esters coeluting with wax esters, ketone as internal standard, triacylglycerols, free fatty acids, alcohols, sterols and diglycerides), chloroplast lipids (pigments, glycolipids), monoglycerides and nonnitrogen containing phospholipids (diphosphatidylglycerides coeluting with phosphatidylglycerides) from nitrogen containing phospholipids (phosphatidylethanolamine and phosphatidylcholine). Under these conditions, the relative standard deviation of replicate analysis (n = 3) of the same sample spotted on adjacent rods for Iatroscan TLC-FID analysis was 3–11%. After lipid class analysis, the remaining lipid extract was subjected to fatty acids marker analysis. Methylations of fatty acids were performed in 10 mL tubes, by addition of 250 μL BF3/methanol (14/86, v/v) and 250 μL toluene, placed at

Table 2. Relationship Between Sites and Hydrological Structures Explored During P1, P2, and P3

	POMME 1 (27 Feb–19 Mar 2001)	POMME 2 (16 Apr–8 May 2001)	POMME 3 (15 Sep–12 Oct 2001)
Site 1	southern anticyclonic (A2)	southern anticyclonic (A2)	southern anticyclonic (A31)
Site 2	frontal zone (ZF)	cyclonic (C4)	anticyclonic (A4)
Site 3	cyclonic (C4)	sill (PS)	cyclonic (C4)
Site 4	northeastern anticyclonic (A1)	northeastern anticyclonic (A1)	cyclonic (C31)

Table 3. Mass, Total Carbon, Carbon Carbonate (and % Contribution to Total Carbon Flux in Brackets), Nitrogen Flux, and C/N Composition From Drifting Sediment Trap Material Deployed at 200 m and 400 m Depth[a]

	200 m Trap					400 m Trap				
	Mass	Total Carbon	C Carbonate[b]	N	C/N, atoms	Mass	Total Carbon	C Carbonate[b]	N	C/N, atoms
					POMME 1					
A2 (S1)	13.6	4.1	0.8 (20)	0.7	5.0	23.9	3.3	1.6 (48)	0.3	9.4
ZF (S2)	14.4	2.4	1.0 (42)	0.3	6.9	nd[c]	nd	nd	nd	nd
C4 (S3)	15.7	2.4	1.1 (46)	0.4	5.1	18.1	2.9	1.3 (45)	0.3	8.3
A1 (S4)	40.8[d]	6.9[d]	2.3[d] (33)	1.0[d]	5.9	55.0	5.6	4.1 (73)	0.6	8.0
					POMME 2					
A2 (S1)	23.6[d]	5.6[d]	1.2[d] (21)	0.9[d]	5.3	26.7	2.6	1.9 (73)	0.3	7.4
C4 (S2)	37.8[e]	11.5[e]	1.1[e] (10)	2.1[e]	4.7	34.2	4.0	2.5 (73)	0.6	5.7
PS (S3)	77.1	9.7	5.0 (52)	1.4	5.9	66.2	13.3	2.7 (20)	2.3	5.0
A1 (S4)	109.1	20.1	3.8 (19)	3.5	4.9	47.1	6.2	2.9 (47)	1.00	5.3
					POMME 3					
A31 (S1)	23.8	3.1	1.7 (55)	0.5	5.3	9.2	1.7	0.7 (41)	0.3	4.9
A4 (S2)	14.4	3.9	0.3 (8)	0.7	4.8	10.5[f]	2.0[f]	0.6[f] (30)	0.3[f]	5.7
C4 (S3)	24.8	5.2	1.3 (25)	0.7	6.4	10.4	2.4	0.6 (25)	0.3	6.9
C31 (S4)	13.4	5.3	0.8 (15)	1.00	4.5	13.7	4.0	1.1 (28)	0.6	5.7

[a]All fluxes are in mg m^{-2} d^{-1}. Two to three cups are mixed for analysis depending on the amount of material collected. Flux are cumulative fluxes per time series sediment trap.
[b]Percent contribution to total carbon flux is in parentheses.
[c]No deployment.
[d]Calculated on five cups.
[e]Calculated on four cups.
[f]Calculated on three cups.

70°C during 60 min. The reaction was stopped by adding 2 mL MilliQ water and placing the tubes in the freezer at −20°C. FAME fractions (containing also hydrocarbons and sterols) were extracted from the reaction tubes by 3 times 2 mL hexane/diethylether (9/1, v/v). FAMEs were purified on silicagel Varian microcolumns (sorbant mass: 50 mg). Gas chromatography analysis was performed on a Perkin Elmer autosystem XL equipped with a glass capillary column (polar phase BPX70; thickness 0.25 μm; 30 mL X 0,25 mm i.d.), injector splitless (240°C), detector (280°C), gas vector hydrogen, oven temperature programmed from 50° to 144°C at 3° min^{-1}. Compounds were identified by reference to a standard mixture of marine fatty acids and further confirmed by GC/MS analysis according to *Caradec et al.* [2004]. The coefficient of repeatability of GC analysis is 5.8%.

3. Results

3.1. Mass, Carbon, and Nitrogen Flux

[10] Mass, total carbon (C) and nitrogen (N) fluxes were low during the observation period (Table 3) and their quantification often required the mixing of several cups of the sediment trap in order to get enough material to fulfill the sensitivity requirement of the analytical methods. In the upper 200 m, fluxes increased from P1 to P2 (Table 3) and reached their highest values in spring (P2) (109.1, 20.1 and 3.5 mg m^{-2} d^{-1}, for mass, C and N respectively) in the northern domain. Mass, C and N fluxes decreased during P3 to reach threshold values of 19.1 ± 6.0, 4.4 ± 1.1 and 0.7 ± 0.2 mg m^{-2} d^{-1}, respectively with almost no change in the C/N ratios. Between 200 m and 400 m, changes in the C and N fluxes exhibited two main features. During P1, the variations were not significant except for the southernmost station where the Mass flux and C/N value doubled (6–11). During P2, the C and N fluxes decreased by a factor of 2–4, except at the point saddle (PS, S3) where the reincrease of the C and N flux at 400 m was likely due to fresh biogenic material inputs as shown by the lower C/N ratio at 400 m than at the upper 200 m trap. During P3, similarly to P2 but to a lesser extent, C and N fluxes decreased (1.5 to 3) between 200 m and 400 m depth. The carbonate C contribution to the total C flux was quite high and varied within a wide range (8–55%) in the 200 m traps (Table 3). At 400 m, in most cases, this contribution (20–73%) was similar to or larger than that of the trap above except at the point saddle where it decreased by a factor of 2.

3.2. Total Lipids and Lipid Class Composition

[11] Total lipids (total carbon lipid, C-TL) are the sum of all the lipid classes separated and quantified by Iatroscan TLC/FID, with the exception of hydrocarbons which can constitute contaminations of anthropic origin. They are fatty acid esters of alcohols such as glycerols (acyl-glycerols), fatty alcohols (wax esters) and sterols (sterol esters).

[12] C-TL concentrations were analyzed in each cup. Daily fluxes (mg m^{-2} d^{-1}) were calculated from absolute concentrations cumulated over the 2 day periods. The variability of the flux during each sediment trap time series can be assessed by the percentage variation of the flux within the eleven cups per trap time series (Table 4).

[13] Lipid fluxes represented 4–22 % of the total carbon flux. During P1, the fluxes were quite stable over each sampling period (±11%) but a wider variability was observed in spring (P2) (up to 72%) and late summer (P3) (up to 124%). From south to north in the POMME area, the lipid fluxes showed a similar seasonal pattern, with the highest fluxes in spring in relation with the phytoplankton blooming, particularly noticeable at the sites explored several times (A2, C4, A1). There were two distinct maxima in spring: one

Table 4. Flux of Total Lipids (TL), Phospholipids (PL), Chloroplast Lipids (AMPL), Wax Esters (WE), Triglycerides (TG), and Degradation Metabolites (i.e., the Sum of Free Fatty Acids (FFA), Alcohols (ALC), Diglycerides (DG), and Monoglycerides (MG)), Lipolysis Index (LI), and Percentage Variation of the Flux Within the 11 Cups per Trap Time Series[a]

				TL	%	PL	%	AMPL	%	ST	%	WE	%	TG	%	FFA + ALC + DG + MG	%	LI
P1	200m	A2	S1	446	*8*	62	*22*	124	*10*	5	*26*	0	*0*	46	*13*	206	*11*	0.9
		ZF	S2	151	*9*	9	*26*	94	*7*	8	*12*	0	*0*	0	*0*	40	*13*	0.4
		C4	S3	484	*8*	13	*22*	132	*6*	40	*15*	18	*38*	42	*20*	238	*10*	1.2
		A1	S4	617	*11*	107	*20*	165	*7*	72	*22*	0	*0*	52	*32*	211	*15*	0.7
	400m	A2	S1	425	*7*	29	*13*	90	*9*	44	*14*	15	*38*	125	*12*	120	*11*	0.5
		ZF	S2	nd	*nd*	nd	*nd*	nd	*nd*	nd	*nd*	nd	*nd*	nd	*nd*	nd	*nd*	nd
		C4	S3	499	*9*	4	*38*	134	*14*	29	*20*	17	*38*	101	*16*	214	*8*	0.8
		A1	S4	245	*9*	38	*14*	133	*8*	15	*11*	0	*0*	8	*19*	52	*9*	0.3
P2	200m	A2	S1	462	*13*	28	*122*	188	*29*	33	*45*	30	*164*	56	*56*	128	*39*	0.4
		C4	S2	2446	*72*	340	*96*	579	*82*	148	*78*	107	*106*	715	*125*	557	*57*	0.3
		PS	S3	1361	*64*	116	*90*	539	*111*	99	*77*	82	*59*	64	*74*	461	*63*	0.6
		A1	S4	2869	*46*	336	*35*	999	*62*	248	*37*	280	*50*	218	*116*	787	*52*	0.4
	400m	A2	S1	383	*30*	2	*245*	171	*44*	22	*45*	40	*245*	40	*59*	107	*37*	0.4
		C4	S2	297	*43*	4	*199*	98	*37*	24	*54*	18	*171*	37	*97*	116	*35*	0.7
		PS	S3	1519	*60*	122	*91*	343	*56*	119	*45*	204	*164*	267	*149*	464	*50*	0.5
		A1	S4	571	*27*	74	*50*	210	*36*	79	*58*	57	*78*	37	*57*	113	*32*	0.3
P3	200m	A31	S1	657	*80*	40	*82*	333	*83*	42	*41*	0	*0*	44	*112*	197	*132*	0.5
		A4	S2	700	*68*	71	*89*	336	*87*	54	*67*	10	*185*	39	*126*	190	*66*	0.4
		C4	S3	922	*26*	164	*32*	365	*32*	120	*72*	12	*143*	135	*69*	127	*37*	0.2
		C31	S4	571	*46*	79	*103*	274	*55*	62	*98*	0	*0*	25	*87*	131	*67*	0.3
	400m	A31	S1	375	*85*	35	*39*	184	*84*	25	*53*	5	*186*	16	*36*	110	*146*	0.5
		A4	S2	487	*18*	14	*125*	311	*17*	16	*62*	0	*0*	17	*64*	81	*89*	0.2
		C4	S3	469	*124*	41	*48*	306	*158*	16	*38*	3	*265*	14	*91*	89	*123*	0.2
		C31	S4	482	*70*	91	*79*	223	*58*	27	*51*	17	*109*	13	*111*	111	*97*	0.3

[a]Abbreviations are as follows: TL, biogenic component of total carbon fluxes (4–22%); PL, cell membrane; AMPL, chloroplast (phytodetritus); WE, reserve lipids in zooplankton; TG, reserve lipids in phyto- and zooplankton; nd, no deployment. Flux is in $\mu g\ m^{-2}\ d^{-1}$.

in the upper 200 m, associated with eddies C4 and A1 in the northern part of the area, and the other at 400 m, at the saddle where the flux reincreased at depth. When the fluxes were high as for the C4 and A1 eddy sites (Table 4), a pronounced decrease of the flux with depth occurred.

[14] Global qualitative change in the composition of the lipid fluxes (Figure 2) was studied through the variability of five selected lipid classes, the phospholipids and sterols typical of cell membranes from living organisms, the chloroplast membrane lipids (pigments and glycolipids) characteristic of phytodetritus, the reserve lipids from zooplankton (wax esters and triglycerides) and phytoplankton (triglycerides) and the degradation metabolites of these source lipids indicating the degradation status of the organic material [*Goutx et al.*, 2000, 2003].

[15] In all samples, the flux of chloroplast lipids and degradation metabolites was high (90–999 $\mu g\ m^{-2}\ d^{-1}$), these compounds being the major contributors to the lipid pool (21–65% and 13–49%, respectively). In the upper 200 m traps, the seasonal signatures of these two classes were contrasted. The largest contribution of degradation metabolites to the flux was during P1 whereas the highest percentages of phytodetritus lipids were during P2 and P3. Superimposed on this seasonal trend, during P1 a north/south contrast (i.e., more degradation metabolites in the southern site than in the northernmost site) was noticeable likely due to the timing of the bloom which was developing by the end of P1 as the northeast Atlantic Gyre site (A1) was sampled. As an exception to this pattern there was a large contribution of chloroplast lipids in the frontal zone in winter. In spring, because the flux largely increased, by a factor of 4–5 compared to late winter in the northern domain in particular (C4 and A1), the bulk organic matter exported through the particle flux included a major contribution from these phytodetritus. Reserve lipids (wax esters from zooplankton, and triacylglycerols from phyto- and zooplankton) increased from P1 (1.2–13.5%) to P2 (2.7–29.5%) then decreased during P3. During the P2 survey, the zooplankton WE reserves clearly characterized the biogenic material exported out of the euphotic layer and to depth. Both WE and TG reserve lipids were also present in the A2 and C4 400 m traps during the P1 survey whereas in P3, all classes of compounds decreased leaving chloroplast lipids a major contributor to the exported material.

[16] From a quantitative aspect, wax esters fluxes exhibited a remarkable pattern (Table 4). During the P1 survey, at 200 m, the wax esters flux was considerably more intensive in the cyclonic gyre (C4) than in any of the other sites where it was under the detection limit; it remained constant with depth, indicating the rapid transfer of biogenic particles to the mesopelagic layers at this site. During P2, the wax esters flux varied from one site to another but was still high in C4. In the northern anticyclonic Gyre (A1), it

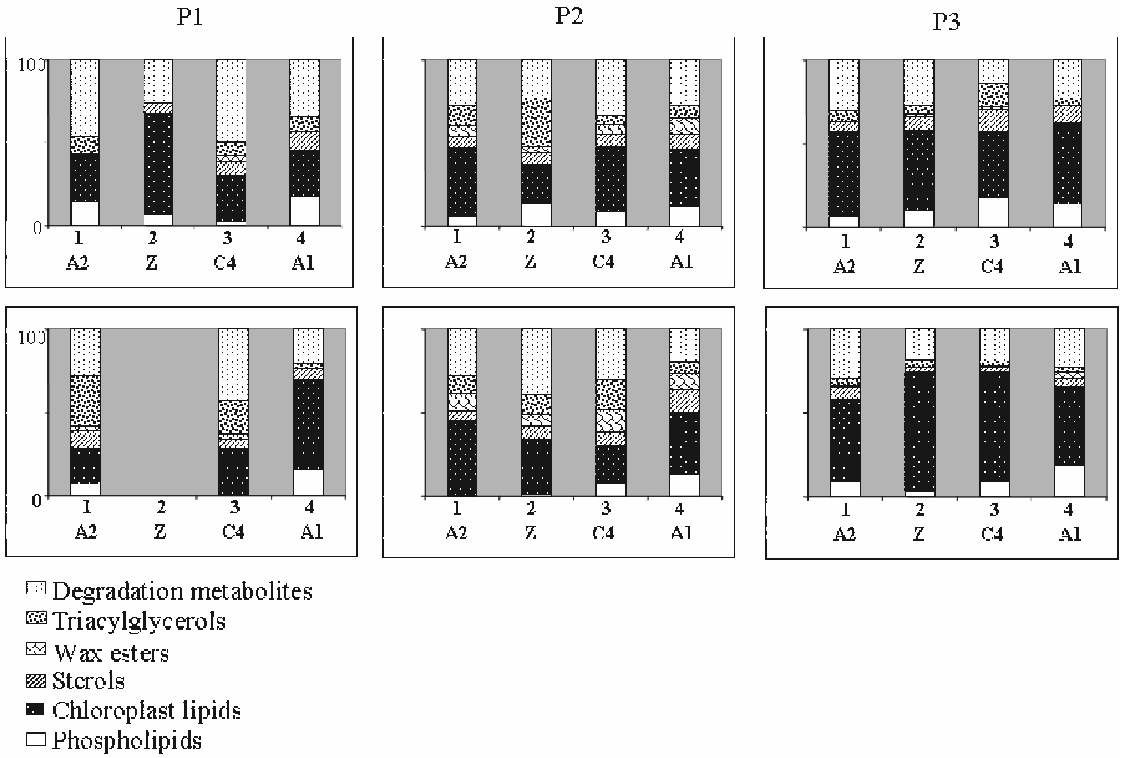

Figure 2. Synoptic view of particle flux quality as given by the percentage distribution of the major lipid classes in the total lipid pool: phospholipids and sterols from cell membranes, chloroplast lipids from phytoplankton, reserve lipids (wax esters and triacyglycerols) from phyto- and zooplankton, and degradation metabolites from these source lipids.

reached a maximum suggesting that a large zooplankton community was feeding on the phytoplankton bloom in the ecosystem above the trap; At this site, between 200 and 400 m, the wax esters flux strongly decreased indicating active removal by mineralization and/or advective transport of the biogenic particles produced in the upper layers. The saddle site (PS) was the only site presenting a reincrease of the WE flux with depth (at 400 m), suggesting advective inputs from adjacent areas and/or the presence of a deep mesopelagic zooplankton community.

3.3. Fatty Acid Biomarkers

[17] Fatty acid (FA) moieties are basic constituents of lipid molecules. Their distribution in marine organisms can be highly characteristic and specific. Fifty fatty acids were identified and quantified by gas chromatography analysis. The qualitative aspect of the fatty acids study was based on selected criteria reported in Table 5 and presented along with the results (Table 6).

3.3.1. Terrestrial Inputs

[18] Fatty acids with an even carbon number higher than 22 carbons like the C24:0 are representative of superior plants and often used as specific markers of contributions from terrestrial sources [*Marty et al.*, 1988]. In the POMME domain, the C24:0 contribution varied from 0.17–1.9% of total fatty acids. Its overall distribution (abundance in the 200 m and 400 m A2 traps during P1, decrease during P2 followed by reincrease during P3) reflected the dilution by the biological inputs (Figure 3).

3.3.2. Phytoplankton Sources

[19] Polyunsaturated fatty acids (PUFA) have two to six double bounds. They are labile molecules and can easily be used as an indicator of freshness of organic matter. They are abundant in microalgae but not synthesized by bacteria. Zooplankton does not synthesize PUFA but accumulates them from food. To better characterize the freshness of organic matter it is convenient to study the variation of the polyunsaturated fatty acids to saturated fatty acids ratio ($PUFA/FA_{SAT}$) and/or the variations of a single polyunsaturated FA such as the C20:5w3 which is an abundant constituent of marine microalgae and zooplankton [*Claustre et al.*, 1989; *Volkman et al.*, 1989].

Table 5. Diagnostic Fatty Acid Biomarkers and Major Sources

Fatty Acid Biomarkers	Sources
C24:0	terrigenous inputs
$PUFA/FA_{sat}$	fresh planktonic organic matter
C20:5w3, % total FA	abundant in marine microalgae and zooplankton
C22:6w3/C20:5w3	dinoflagellates, prymnesiophyceae versus diatoms
C18:1w9 + ΣPUFA (5 + 6)	zooplankton
iC15 + iC17 + aC17, % total FA	bacterial walls
S C16:1/C16:0	bacterial process indicator
$FA_{sat} + FA_{monounsat}$, % total FA	oxidized lipids

Table 6. Distribution (% of Total Fatty Acids) of the Main Classes of Fatty Acid Markers (Saturated, Monoenes, Dienes, Trienes, and Polyenes) and Fatty Acid Diagnostic in the 200 m and 400 m Drifting Sediment Traps During P1, P2, and P3

	200 m				400 m			
	A2 (S1)	ZF (S2)	C4 (S3)	A1 (S4)	A2 (S1)	C4 (S3)	A1 (S4)	
POMME 1								
S saturated	52.2	68.3	49.4	53.2	48.7	55.4	54.0	
S monoenes	35.0	21.5	34.0	19.8	40.4	37.6	26.6	
S dienes	3.9	4.6	3.5	3.2	7.4	2.9	4.2	
S trienes	0.1	0.3	0.6	2.2	0.0	0.2	1.6	
S polyenes 4	3.0	0.3	0.5	0.8	0.1	0.1	1.0	
S polyenes 5	2.5	2.2	5.0	8.0	0.4	1.6	6.9	
S polyenes 6	3.3	2.7	7.0	12.5	2.9	2.3	5.7	
C24:0, %	2.2	1.9	1.2	0.8	1.8	1.3	1.2	
PUFA/sat	0.25	0.15	0.34	0.50	0.22	0.13	0.36	
C20:5w3, %	2.4	2.1	3.7	6.9	0.4	1.4	6.2	
S C16:1/C16:0	0.46	0.17	0.46	0.18	0.66	0.56	0.28	
C22:6w3/C20:5w3	1.34	1.26	1.88	1.81	7.01	1.61	0.90	
S FA polyenes (5 + 6) + C18:1w9, %	18.6	19.3	25.9	30.5	17.3	18.2	24.6	
iC15 + iC17 + aC17, %	0.2	0.0	0.7	1.5	0.0	0.8	2.6	
FA_{sat} + $FA_{monounsat}$, %	87.2	89.8	83.4	73.0	89.1	92.9	80.6	
	200 m				400 m			
	A2 (S1)	C4 (S2)	PS (S3)	A1 (S4)	A2 (S1)	C4 (S2)	PS (S3)	A1 (S4)
POMME 2								
S saturated	53.4	44.0	64.0	41.0	52.1	60.9	42.8	46.7
S monoenes	25.8	29.3	21.0	35.3	28.6	25.5	30.7	30.8
S dienes	2.9	2.3	1.7	2.1	2.9	2.7	1.9	2.6
S trienes	1.1	1.1	1.4	1.0	1.5	1.0	1.1	0.9
S polyenes 4	1.5	0.9	0.5	0.7	3.8	1.0	1.1	1.2
S polyenes 5	5.9	9.1	4.3	7.9	5.0	4.3	9.3	7.7
S polyenes 6	8.8	12.7	5.9	10.6	5.5	4.5	12.9	8.8
C24:0, %	0.8	0.2	0.8	1.3	0.8	0.9	1.0	1.2
PUFA/sat	0.38	0.60	0.21	0.54	0.36	0.22	0.62	0.45
C20:5w3, %	4.5	7.1	3.8	6.7	4.0	4.2	7.8	6.5
S C16:1/C16:0	0.15	0.08	0.10	0.22	0.16	0.14	0.13	0.22
C22:6w3/C20:5w3	1.97	1.79	1.53	1.59	1.37	1.07	1.66	1.35
S FA polyenes (5 + 6) + C18:1w9, %	28.1	41.1	24.2	43.3	27.0	19.2	43.4	36.2
iC15 + iC17 + aC17, %	0.4	0.7	1.5	1.4	1.4	0.3	0.7	1.4
FA_{sat} + $FA_{monounsat}$, %	79.2	73.2	85.0	76.3	80.7	86.4	73.5	77.5
	200 m				400 m			
	A31 (S1)	A4 (S2)	C4 (S3)	C31 (S4)	A31 (S1)	A4 (S2)	C4 (S3)	C31 (S4)
POMME 3								
S saturated	72.9	70.9	50.1	63.6	72.2	74.5	54.3	61.1
S monoenes	15.7	19.5	22.7	18.0	16.9	18.0	25.2	24.6
S dienes	2.3	2.3	3.6	4.2	3.5	2.2	3.4	6.1
S trienes	0.7	0.2	1.9	1.1	0.4	0.0	0.8	0.8
S polyenes 4	1.2	1.8	2.3	2.2	3.6	3.2	2.1	2.1
S polyenes 5	2.2	1.7	6.7	2.9	1.3	0.5	1.9	1.4
S polyenes 6	3.1	2.5	10.7	4.7	0.7	1.5	3.0	3.1
C24:0, %	1.3	0.9	0.6	1.8	1.5	1.5	1.1	1.8
PUFA/sat	0.13	0.12	0.50	0.24	0.13	0.10	0.21	0.22
C20:5w3, %	2.1	1.4	4.7	2.5	1.3	0.5	1.9	0.9
S C16:1/C16:0	0.10	0.10	0.10	0.12	0.20	0.14	0.20	0.17
C22:6w3/C20:5w3	1.49	1.75	2.28	1.87	0.53	2.70	1.57	3.43
S FA polyenes (5 + 6) + C18:1w9, %	14.9	16.0	33.2	18.8	9.4	12.6	21.8	15.3
iC15 + iC17 + aC17, %	0.2	0.6	1.0	0.6	0.4	1.2	1.4	0.5
FA_{sat} + $FA_{monounsat}$, %	88.7	90.4	72.7	81.6	89.2	92.5	79.5	85.7

[20] PUFA/FA_{SAT} and C20:5w3 (Figure 4) were more abundant at 200 m than 400 m and during P2 than P1. During P3, this signal persisted in the cyclonic gyre (C4) whereas it decreased in all the other sites. As an exception to this pattern, the saddle site (PS) explored during P2 exhibited a consistent reincrease of PUFAs at 400 m, with maximum emphasis (×2) on the C20:5w3 and C22:6W3 fatty acids.

3.3.3. Diatoms Versus Dinoflagellates

[21] Diatoms generally produce more C20:5w3 than C22:6w3 whereas the opposite is true for dinoflagellates [*Viso and Marty*, 1993]. Thus the molecular ratio of these two compounds (C22:6w3/C20:5w3) can be used to assess the relative contribution of these microalgae to the biogenic particle flux. In the upper 200 m traps, the latitudinal variations of this ratio were weak (1.34–1.88, 1.53–1.97, 1.49–2.28 in P1, P2 and P3, respectively). The maximum value observed in the cyclonic gyre (C4) during P3 suggests a higher dinoflagellate/lower diatom lipids contribution to the flux during late summer. In the 400 m traps, a stronger latitudinal contrast was observed during P1 and P3. Maxima were observed in the southern anticyclonic gyre (A2; 7.01)

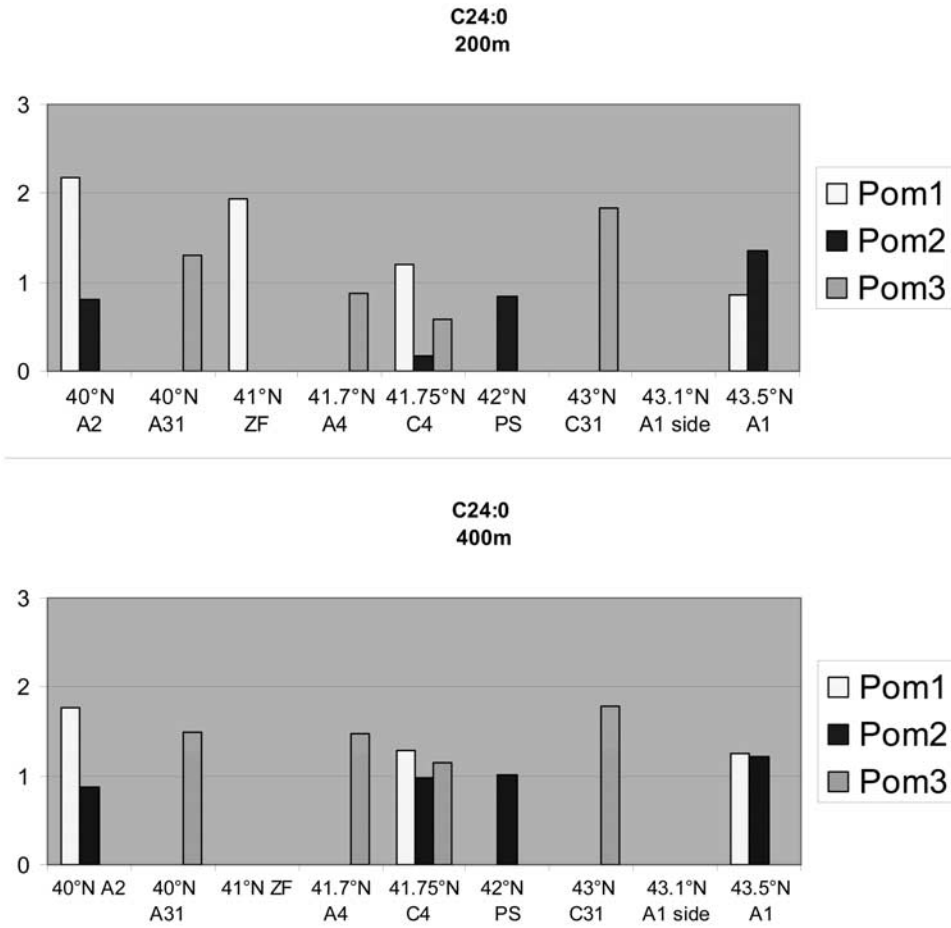

Figure 3. Distribution of the C24:0 fatty acid (% of total fatty acids), marker of terrigeneous inputs.

and the northern cyclone (C31; 3.43) indicating a lower input of diatom material to the drifting traps during the nonbloom periods, a feature which was more pronounced in the southern eddy. In this eddy (A2), the change of the ratio between 200 and 400 m depth, was accompanied by a drop in polyunsaturated fatty acids (polyenes 4 and 5) (Table 6), phospholipids and chloroplast lipids (Table 4), suggesting a specific hydrolysis and utilization of diatom membrane compounds by mesopelagic heterotrophs. In contrast, in the northern cyclone C31 (P3), polyenes 4 and membrane lipid compounds such as phospholipids remained stable reflecting the persistence of fresh organic matter and/or input of heterotrophic biomass in the 400 m trap.

3.3.4. Bacteria

[22] Branched fatty acids (isomeric iso and anteiso C15 and C17) and hydroxy-fatty acids are exclusively synthesized by bacteria in order to produce their own membrane phospholipids [*Wakeham*, 1995]. In detrital organic matter, they can be used as a reliable printing of bacterial cell walls [*Marty et al.*, 1994; *Ramos et al.*, 2003]. In the upper 200 m traps, the contribution of branched fatty acids increased as the season advanced from P1 to P2, then decreased in P3. Reincreases of these markers in the deeper traps may be related to the growth of bacteria attached to the particles during sedimentation. The decrease (by a factor of 2) observed at the PS (site 3, P2) again suggested a decoupling between the 200 m and the 400 m traps material probably due to the hydrodynamics in the area.

[23] In aerobic bacteria, the ratio of C16:1/C16:0 is high [*Méjanelle*, 1995]. Whatever the site and the depth of the trap deployment, the values for this ratio were much higher in winter than in spring, in A2 and C4 than in the northernmost site (A1), and at 400 m than at 200 m. The presence of this bacterial marker reflects the printing of export matter by bacterial biomass and/or activity. The highest values of this parameter were directly related to the presence of lipid degradation metabolites and to the ratio of these metabolites to entire lipids (see Table 4, LI) which constitutes a good index of lipid hydrolysis by bacterial ectoenzymes [*Goutx et al.*, 2003]. In addition to the latter indicator, saturated and monounsaturated fatty acids (FA_{sat} + $FA_{monounsat}$) reflected the organic matter degradation status, the double bonds of freshly biosynthesized fatty acids being easily oxidized. As for the C16:1/C16:0 ratio, values were higher in winter and in the south and generally higher at 400 m than at 200 m, with the exception of the saddle site.

3.3.5. Zooplankton

[24] The C18:1W9 fatty acid is characteristic of zooplankton according to *Sargent and Falk-Peterson* [1981] and often used as a specific biogeochemical marker for zooplankton [*Wakeham et al.*, 1984b]. In addition, five and

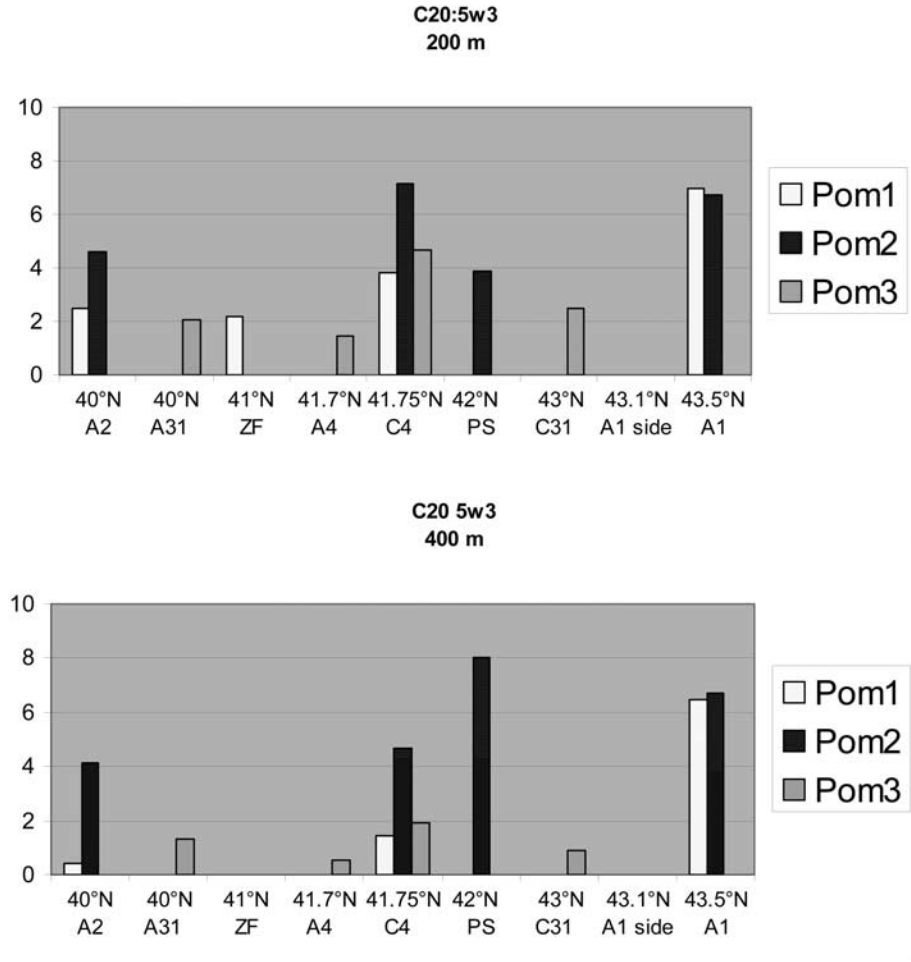

Figure 4. Distribution of the C20:5W3 fatty acid (% of total fatty acids), markers of fresh biological production.

six unsaturated fatty acids are molecular compounds of dietary interest for higher trophic levels, which are also abundant in zooplankton due to their feeding activity. We used the variations of the sum of these fatty acids as an indicator of zooplankton contribution to the material of the traps. The pattern of variation of this parameter was quite simple (Table 6). It increased from winter to spring, and from south to north, clearly in relation with the development of biological production. The contribution of these biomarkers to the flux decreased with depth at all seasons and at all sites, indicating their rapid consumption and mineralization. As an exception, a marked reincrease of these biomarkers ($\times 2$) at depth, characterized the saddle site (PS) in spring. In general, ecosystems in the northern domain, which was characterized by high fluxes and a strong contribution of polyunsaturated fatty acids to these fluxes, were an important source of matter and energy for the deep heterotroph communities. Zooplankton markers in the range C20:1 and C22:1 are characteristic of copepods and zooplankton feeding on them [*Virtue et al.*, 2000]. They were minor contributors to the fatty acid flux (<3%) in the POMME domain. An increase to the highest values was observed in spring in both the 200 m and 400 m traps in the southern A2 anticyclonic eddy and in the upper trap in the cyclonic C4 gyre.

4. Discussion

4.1. Hydrology

[25] During the POMME experiment the hydrographic surveys, carried out by deployment of drifters, floats and altimetry [*Assembaum and Reverdin*, 2005] coupled to intensive measurements of nutrients [*Fernández et al.*, 2005a, 2005b], provide a reliable hydrological background to the biogeochemical studies. Geostrophic current velocities derived from this data set and analyzed through the Système Océanique de Prévision Régionale en Atlantique Nord-Est (SOPRANE) model provided a basis for monitoring the temporal development of mesoscale features during (and between) the surveys [*Assembaum and Reverdin*, 2005]. Typically, a permanent frontal zone was observed at 41°–42°N, characterized by intense isopycnal displacement. This frontal zone separates the POMME domain into two regions: the northern domain characterized by high energy and deeper mixed layer depths progressing from on average 100 m in winter to 75 m in spring and high nutrient

Table 7a. Seasonal and Mesoscale Variability of Particle Flux During the POMME Experiment: Total Carbon (TC) and Total Carbon Lipid (C-LT) Fluxes per Survey[a]

	POMME 1		POMME 2		POMME 3	
Drifting Traps Depth	CT	C-LT	CT	C-LT	CT	C-LT
200 m	3.9 (2.1)	0.42 (0.19)	11.7 (6.1)	1.78 (1.08)	4.4 (1.0)	0.71 (0.14)
400 m	3.9 (1.4)	0.39 (0.13)	6.5 (4.7)	0.69 (0.56)	2.5 (1.0)	0.45 (0.05)

[a]Fluxes are in mg m^{-2} d^{-1}. Values in parentheses are the standard deviations to the mean data, giving an indication of the extent of variability.

surface concentrations due to vertical mixing [*Fernández et al.*, 2005a]. South of the front, waters were warmer and the nutrients were depleted at the surface due to biological activity. Besides the front (FZ), surface geostrophic currents depict the mesoscale structures encountered during the study (see Figure 1). The largest structures (50–100 km) were studied: a cold core cyclonic eddy (C4) close to the northern border of the front and two warm core anticyclonic eddies (A2 and A31) in the southern part of the domain were explored during P1, P2 and P3. At the northeast of C4, a northern anticyclonic eddy (A1) was explored during P1 and P2 only. During P3, shipboard constraints occurred in the highest latitude of the POMME domain and time series stations were positioned south from A1 (sites A4 and C31). Traps were also deployed in the frontal structure (FZ, S2) during P1, and at the so-called point saddle (PS) (S3, P2) observed at the boundary of four eddies.

4.2. General Characteristics of the Flux

[26] During the POMME experiment, the intensities of mass, carbon and nitrogen fluxes (9.2–109.1, 2.0–20.1, 0.3–3.5 mg m^{-2} d^{-1}, respectively) were not corrected from trapping efficiency. For the moorings deployed at the boundary of the POMME domain, ^{230}Th was used to estimate sediment trap efficiency, revealing values ranging from 18 to 58% [*Guieu et al.*, 2005]. As the location of the drifting and moored traps were quite different, comparison between the two data sets was only possible for a very restricted number of samples collected at 400 m. On these limited sets of data, the comparison between noncorrected fluxes obtained from moored traps and drifting traps was promising and similar patterns of variations of mass and carbon fluxes were observed. It is thus likely that drifting trap fluxes are underestimated, but the overall pattern of change in flux intensity and proportions between the different components are correct. Flux estimations fall within the range of values reported by *Moran et al.* [2003] for the Atlantic province. They were below values reported for the Peru upwelling (February–March 1978 [*Wakeham et al.*, 1984a]), and lower than the spring fluxes reported by *Peinert and Miquel* [1994] for the Almeria-Oran front. C-lipid fluxes (0.4–2.9 mg m^{-2} d^{-1}) are comparable to C-lipid fluxes reported for various areas of the Mediterranean Sea in winter, the Alboran Sea [*Striby*, 2000], the Aegean Sea [*Chronis et al.*, 1996] and the Ligurian Sea [*Marty et al.*, 1994], these basins being globally oligotrophic at that time of the year.

4.3. Seasonal Variability

[27] In February, nutrient conditions due to the circulation of water masses become favorable to the growth of biomass [*Mémery et al.*, 2005]. Nutrients exhibited a strong depletion between winter and spring, related to primary production (PP) values ranging from 10 to 60 mg m^{-3} d^{-1} [*Fernández et al.*, 2005b]. The bloom started in the southern latitude during P1 and developed toward the northern latitude during P2. In the phytoplankton community, small size phytoplankton (pico- and nanoautotrophs) was the major contributor to the PP, except during the spring period [*Claustre et al.*, 2005]. The diatom contribution to PP increased northward from 10% in the southern A2 eddy up to 100% in the northern A1 eddy (where a Pseudo-Nitzschia bloom was observed) during spring. It then dropped to 2–4% in winter [*Leblanc et al.*, 2005, Figure 8]. The general effect of the biological carbon production was identified in the change of the survey mean fluxes of carbon and lipids (Table 7a). Their drastic increase (×2.5–4) between P1 and P2 reflected the development of the spring bloom in the surface layers, whereas decreases during P3 were related to the bloom decay. Besides this strong seasonal signal, the south-north productive gradient [*Fernández et al.*, 2005a], and the lack of synopticity resulting from the time lag between northern and southern sampling periods [*Lévy et al.*, 2005], were responsible for significant variability per season (23–73% on average (Table 7a)).

[28] Cross comparison of lipid class tracers and specific fatty acid biomarkers reflected the effect of the season on the functioning of pelagic ecosystems and its impact on the quality of the material exported to depth. During spring, in the northernmost latitudes, the short-term variations of chloroplast lipids observed in the cups of the time series samples (data not shown) revealed bursts of phytoplankton aggregates, in agreement with the characteristics of blooms from the North Atlantic Ocean already reported by *Honjo and Manganini* [1993]. Typically, the particles exported during the development of the bloom were enriched with freshly biosynthesized lipids of phytoplankton origin and depleted in C carbonate compared to P1 indicating the increasing contribution of diatoms [*Leblanc et al.*, 2005] to the particle flux. The only signature of dinoflagellates that we identified in the trap material was observed in the export material at 200 m in the cyclonic gyre (C4) in late summer. In general, the pattern of distribution of the diatoms and dinoflagellates Iatroscan-analyzed biomarker (the chloroplast lipid to sterol ratio) was less contrasted than in previous investigations [*Caillau et al.*, 1999; *Goutx et al.*, 2000] reflecting a lack of size/species relationship (i.e., large/diatoms and small/nanoflagellates), the overall phytoplankton community including diatoms, being dominated by small size species during the POMME investigations [*Leblanc et al.*, 2005].

[29] Trends in heterotrophic signatures were easier to sort out, indicating the general control exercised by the grazing and degradation process on the export of organic matter

in the POMME area. Zooplankton markers, C18:1W9 associated with 20:5W3 and 22:6W3 and wax esters, were strongly represented in the particle flux during the development of the bloom (P2). This is in accordance with V. Andersen (see the POMME program web site, http://www.lodyc.jussieu.fr/POMME) who observed a threefold increase of the macrozooplankton biomass between P1 and P2 in the 0–700 m layer within the whole POMME area. The strongest contribution of these tracers in the northern part of the domain is related with its higher productivity and the increase diatom contribution to primary production and export in relation to the deeper mixed layer depth. Similarly, the moored trap "NE" located in the vicinity of the A1 gyre, was shown to present particular features including a strong summer particulate organic carbon (POC) export pattern [*Guieu et al.*, 2005] and a higher number of swimmers of variable quality compared to other sites at both 400 m (average of 942 individual against 800 for the other sites) and 1000 m (average of 370 individuals against 230 for the other sites) (Figure 5). After the maximum export during the spring, this abundance increased as a function of time (1000 m) or stayed constant (400 m) whereas the mass flux was decreasing (C. Guieu, personal communication, 2004). In the 400 m fixed traps, the transition between winter and spring was accompanied by a shift in the dominant species of swimmers from copepods and gastropods to ostracods. However, no relationship could be evidenced between the contribution of C carbonates to the carbon flux and the potential flux of ostracod shell debris that may occur in the northern drifting traps. Similarly, *Andersen et al.* [2003] observed an abundance of pteropods in spring and summer compared to winter, which was not reflected in the drifting traps carbonate trends.

[30] Two classes of bacterial indicators were studied resulting from either bacterial biomass growth (isoC15, isoC17, aC17) or ecto-enzymatic activity on biopolymers (the lipolysis index that co varied with the C16:1/C16:0 ratio) which composed the particle flux. The contribution of these tracers to the trap material reflected a contrasted situation with regard to the utilization of sinking particles by heterotrophs in the POMME domain. During late winter (P1) in the south (A2), sinking particulate matter was highly hydrolyzed, whereas, in the northern part of the POMME domain, markers of bacterial biomass predominated (A1). These contrasted signatures must be related to the structure and functioning of the planktonic trophic web in the pelagic ecosystem above the traps. In the northern part of the POMME domain, the microphytoplankton bloom (diatoms and others phytoplankton) fueled an active microbial web dominated by tintinnid ciliates [*Karayanni et al.*, 2005] while bacteria carbon demand was satisfied by the release of small labile molecules. It is a very efficient system for channeling carbon to metazooplankton and thus for exporting primary production. Under such conditions, fresh organic matter was transferred to depth and bacterial biomass efficiently colonized particles as reflected in the biomarkers distribution. During spring, similar trends were observed with probably a dilution of the bacterial biomass markers by additional plankonic tracers derived from the bloom. In contrast, in the southern domain in winter, the carbon resources were limited for bacteria and the major part of the primary production was channeled through the bacterial loop [*Karayanni*, 2004]. In the waters below, bacteria achieved their adaptation to the system by an active metabolism of larger particulate biopolymers to supply their food.

4.4. Terrigeneous Inputs

[31] Fatty acids with an even carbon number greater than 22 carbons are rarely present in the marine environment, except for river mouths and sea surface microlayers where material of terrestrial origin is concentrated [*Bouloubassi et al.*, 1997]. Thus C24:0 is often used as a specific marker of terrestrial sources [*Tanoue and Handa*, 1979; *Reetsma et al.*, 1990; *Marty et al.*, 1994]. At the Dyfamed station (northwestern Mediterranean) in May 1995, when there was no advection, the occurrence of this marker in the surface waters was strongly associated with a rain event [*Striby*, 2000]. For the samples collected during P1, we observed a significant contribution of this terrigeneous material to the particle flux (Figure 3). A similar pattern of aluminum distribution in the drifting traps was observed (N. Leblond, personal communication, 2004). This input may be related to the meteorological event of Saharan dust deposit that took place in the area in mid-February, 15 days before the beginning of the leg 2 of P1. The year before (28 February 2000), a comparable event had occurred. This suggests a potential impact of aeolian dust fluxes in periods preceding blooms in the North Atlantic as reported by *Blain et al.* [2004]. There was an efficient transfer of this material through repackaging and/or aggregation of fine suspended particles down to 400 m.

4.5. Role of Mesoscale Features

[32] Although there are major uncertainties concerning the oceanic variability of eddies and the energy that may be attributed to these structures, they have prompted great interest among scientists because they have their own trajectories [*McWilliams and Flierl*, 1979] which drive water particles and associated physical and biogeochemical properties with them [*Paillet*, 1999; *Garçon et al.*, 2001]. In the POMME area, the biogeochemical properties of anticyclonic and cyclonic structures A2, C4 and A1 are depicted by the mean carbon and lipid fluxes and their standard deviation computed at each site during the whole period of investigation (Table 7b). At 200 m, the south-north increase ($\times 2-3$) of the flux and its wide variability per site (28–73%) underline the weakness of the mesoscale properties in controlling the particle flux in the structures investigated. There was a strong discrepancy between the biogeochemical characteristics of the two anticyclonic structures A2 and A1, the biological functioning of which was largely controlled by the S/N gradient of production, in relation with the depth of the mixed layer and seasonality. We observed a net increase (by a factor of 3) of the mean fluxes of biogenic matter between the southern anticyclonic eddy (A2) and the northern A1 anticyclonic eddy, due to a major export of fresh algal material in A1. The latter eddy is associated with a deepening of the permanent thermocline but also with a shoaling of the seasonal thermocline and of the associated nitracline that produces a significant refilling of the photic zone with nitrate during the summer [*Fernández et al.*, 2005a]. This high nitrate level induces high primary production compared to the rest of the zone and allows for a strong summer POC export. In contrast, the southern

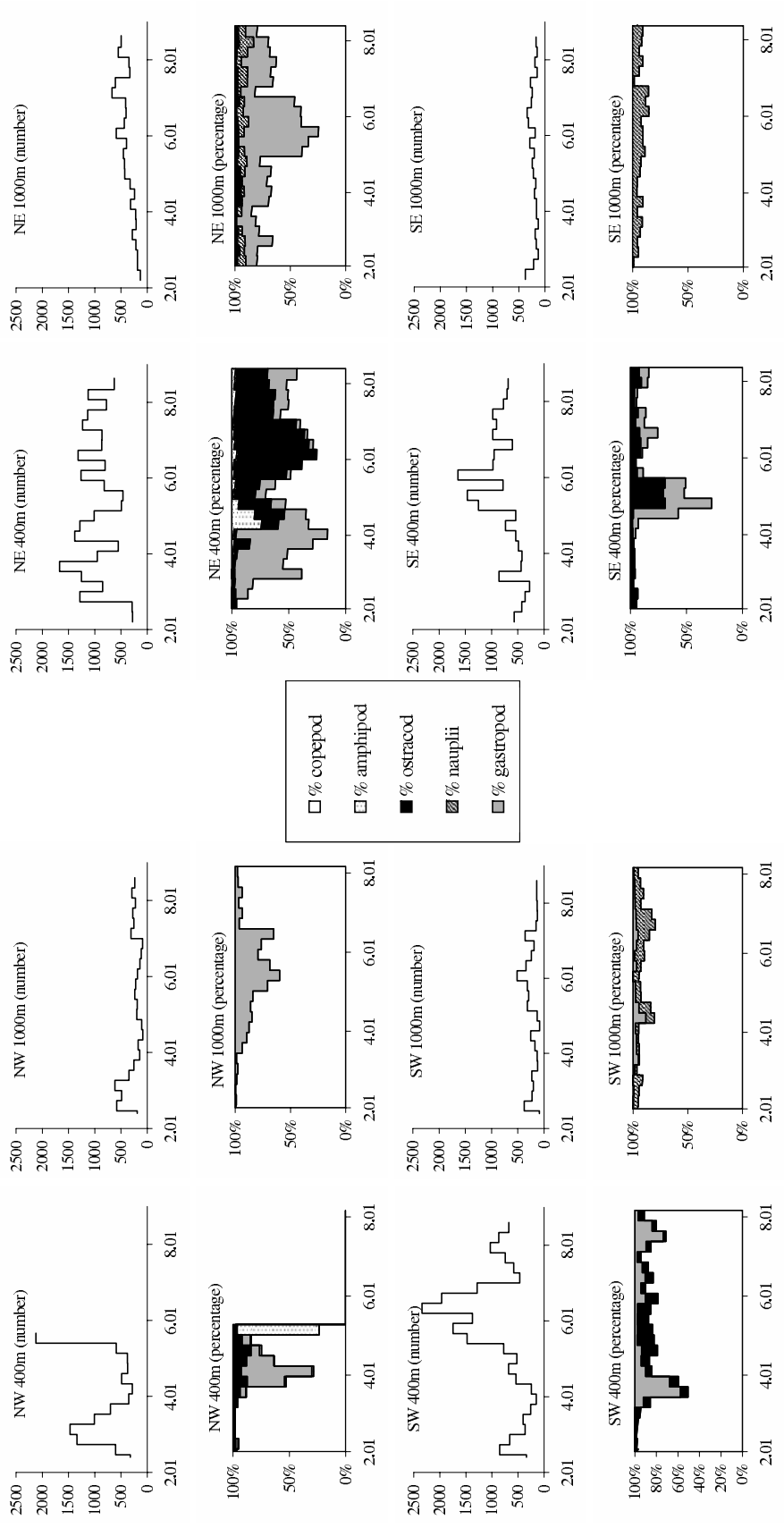

Figure 5. Quantity and quality of swimmers collected in four fixed sediment traps between February and August 2001 at 400 m and 1000 m. For each site, the upper figure indicates the number of swimmers per cup; the lower figure indicates the partitioning into five main categories.

Table 7b. Seasonal and Mesoscale Variability of Particle Flux During the POMME Experiment: Total Carbon (TC) and Total Carbon Lipid (C-LT) Fluxes per Site[a]

	Southern Anticyclone (A2 + A31)		Cyclone (C4)		Northern Anticyclone (A1)	
Drifting Traps Depth	CT	C-LT	CT	C-LT	CT	C-LT
200 m	4.3 (1.2)	0.52 (0.11)	6.3 (4.5)	1.28 (1.03)	13.5 (9.3)	1.74 (1.59)
400 m	2.5 (0.7)	0.39 (0.03)	3.1 (0.8)	0.42 (0.11)	5.9 (0.4)	0.41 (0.23)

[a]Fluxes are in mg m^{-2} d^{-1}. A2 and A31 are considered together. Values in parentheses are the standard deviations to the mean data, giving an indication of the extent of variability.

domain exhibited the lowest fluxes, due to the low productivity of the surface waters and subsequent strong utilization of particulate matter by bacteria. This bacterial carbon demand exceeded the primary production in the Anticyclone area (A2, site 1) and in the frontal zone (ZF, site 2) [*Karayanni*, 2004]. These observations support results from the POMME experiment at P1 and P2 [*Mémery et al.*, 2005] showing that the area was divided into two zones of distinct production regime, located north and south of the frontal zone (41°N and 42°N). At 400 m, the mean carbon and lipid flux was less contrasted (2.9–6.5 and 0.39–0.42, respectively) and exhibited lower-latitudinal variability (7–52%) (Table 7b) due to heterotrophic utilization of biogenic matter during its transport in the water column and/or advection of sinking particles during sedimentation. The transfer to depth was also contrasted between the two anticyclones with a good coupling in A2 compared to A1. In the northern domain, the possibility of advective transfers of matter must be considered. Mass fluxes slightly increased at 400 m in the northern anticyclone A1. At the point saddle (PS), reincrease of fresh biogenic material resulting from/or associated with zooplankton activity (lower C/N ratio, C20:5w3 (×2), wax esters (×2.5), triglycerides (×4) and fatty acids from zooplankton (×2)), characterized the 400 m trap. In this trap, the composition of the flux was comparable to the composition of the shallower 200 m traps, of the northern domain (A1) in particular. The possibility that a layer of sinking matter could have been collected in the 400 m trap, which was already below 200 m when the drifter was launched, must be considered. In this layer, the potential sources for particles might be examined. Although the direct transfer of particles from the A1 200 depth to the PS 400 m depth cannot be assumed, several observations indicate strong biological activity in the mesopelagic layers at 42°/43°5, likely to give rise to a transfer of fresh material from northernmost upper layers to deeper depth in the area of the saddle. First, in the north of the domain (site A1), the distribution of large particles recorded by the video profiler (G. Gorsky, personal communication, 2004) shows an accumulation of the whole range of large particles in the 0–250 m layer. In addition, the large particles' profiles included several reincreases at depth suggesting advection. Further south, at the PS site, a layer of moderate size aggregates was observed in the 300–500 m depth band. Secondly, *Andersen et al.* [2003] reported that a deep zooplankton mesopelagic community including migrants, were living in the northern part of the POMME domain. This deep zooplankton community could likely repackage fresh biological material issued from shallower layers. In this highly dynamic area, this process would not only contribute to enhancing the coupling between surface and depth as suggested by *Conte et al.* [2003], but also between high and lower latitudes along a latitudinal gradient through an intermediate circulation. Thus an advective transfer of matter could probably occur between 43°5 and 42°N through interactions between physical and biological processes. Interestingly, a similar advective transfer of matter is suggested by the distribution of siliceous rich particles in moored sediment traps [*Mosseri et al.*, 2005].

[33] In the intermediate zone, the cyclone C4 exhibited a permanent zooplankton signature in its traps and a decrease of the flux with depth due to organic matter hydrolysis. This suggests that meso-zooplankton grazing was a major process of particle export in this structure. The zooplankton signature, namely the wax esters, are reserve compounds that organisms synthesize during periods of abundant food to store energy for reutilization during starvation periods and/or for reproduction. It is likely that within the oligotrophic POMME domain, the cold cyclonic eddy and associated production represented an interesting habitat for a specific zooplankton community in this latitude.

5. Conclusions

[34] In conclusion, the fluxes of matter and their biogeochemical signatures enabled us to depict the characteristics of the systems and associated export in the various mesoscale structures and along the latitudinal dimension of the POMME area. The coupling between the lipid class tracers and the fatty acid biomarkers method proved to be complementary in this study of the particle flux.

[35] Vertical fluxes of matter exhibited a wide qualitative and quantitative variability related to the biological functioning of the structures studied, which was largely controlled by the south/north gradient of production, in relation with the depth of the mixed layer and the seasonality. During winter, the flux of organic matter was dominated by degraded material, in the southern region in particular. In spring, following the water column stratification, the organic matter in the traps was directly related to plankton production. Spring 2001 was a period of abundant primary production with minor contributions from large diatoms. The particle flux appeared to be the most intensive in the northern domain providing the deeper layers with energy rich material through vertical sedimentation and advection. A deep zooplankton community may likely take benefit from this food supply.

[36] The variability which could have been induced by the mesoscale structures was not fully observed in these spots like observations done within a wide north/south gradient. However, the effect of the functioning mesoscale structures on the quality and the quantity of organic matter

exported to depth (through the trophic behavior of a zooplankton community in the C4 cyclonic eddy and of deep mesopelagic species potentially linked to advective transfer in the area of the A1 anticyclonic eddy) was noticeable in the intermediate POMME area. Further investigations at shorter spatial and temporal scales on these specific mesoscale structures would be required to complete observations recorded during the POMME investigation.

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