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Vertical flux of fatty acids in the North Atlantic Ocean

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ABSTRACT

The quantitative and qualitative composition of fatty acids in particulate material collected in traps deployed during 98 days at 389, 988, 3755 and 5068 m depths in the equatorial North Atlantic was determined. The fatty acid composition indicates a predominantly marine source (14:0, 16:0, 16:1, 18:0, 18:1, 20:5, 20:4, 22:6, 22:5) with possibly a minor terrigenous component in the bathypelagic traps. The vertical fluxes of fatty acids and lipids decrease rapidly with depth. The rate of net loss of carboxylic acids increases with number of double bonds and decreases with number of carbon atoms. Iso- and anteiso- as well as some monoenoic fatty acids are more persistent, probably due to enhanced microbial synthesis during settling which counteracts degradation.

1. Introduction

The settling of particulate matter produced in ocean surface waters has long been inferred as a major supply of organic matter as food and energy for benthic communities in the deep ocean (Maury, 1861; Vinogradov, 1968). Mineralization of particles settling out of the euphotic zone may also account for part of the ocean-wide subsurface nutrient maxima and oxygen minimum (Menzel, 1974). The notion that relatively large particles dominate the vertical flux (McCave, 1975), supported by some earlier evidence, has led to the development of new samplers which collect large particles more efficiently than conventional water bottles. Sampling at different locations with various apparatus such as bottle samplers, large volume filtration systems (Bishop *et al.*, 1977) and sediment traps of various designs (e.g. Honjo, 1978; Hinga *et al.*, 1979) provides samples of different and variable subdivisions of the size spectrum of particulate matter. Most large macroscopic debris from plants or animal carcasses would still escape collection (Isaacs and Schwartzclose, 1975).

The transport of organic matter, such as large rapidly settling fecal pellets, through oceanic ecosystems and its role as food supply for benthic ecosystems, has been mainly studied by measurement of total organic carbon fluxes (Rowe and Gardner, 1979; Hinga *et al.*, 1979). However, microbial activity, biodegradation and zooplankton coprophagy (Paffenhofer and Knowles, 1979) during settling may

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lead to compositional changes in the diet supplied to benthic organisms and would eventually also affect the organic composition of pelagic sediments. Some insight into these compositional changes may be gained by flux measurements of individual compound classes such as lipids or proteins and individual compounds (Crisp *et al.*, 1979; Wakeham *et al.*, 1980; Prahl and Carpenter, 1979; Tanoue and Handa, 1980; Lee and Cronin, 1982). We report here the fatty acid composition and lipid content of material collected in sediment traps at a station in the equatorial North Atlantic. In the course of interpretation we will also use a simple vertical model to further elucidate flux gradients of major fatty acids. A detailed comparison of our results with other lipids such as wax esters, steryl esters, triglycerides, sterols, fatty alcohols, hydrocarbons as well as free amino acids in the same samples will be reported elsewhere (Wakeham, 1982; Lee and Cronin, 1982; Gagosian *et al.*, 1982). Our intent in applying the vertical flux model to a restricted data set for fatty acids is to illustrate an approach to interpretation of organic geochemical data which will be of utility for the larger data sets of multiple compound classes and several sampling locations resulting from studies now in progress.

Changes of biogenic material during settling are due to regeneration and would obviously affect concentrations of carbonate, nutrients and dissolved oxygen in the water column as well as specific organic compounds. As an example we will use the same model for an approximation of the oxygen consumption derived from vertical gradients of earlier reported organic C, H, N fluxes (Honjo, 1980).

2. Methods

a. Sampling. Four traps, each with a 1.5 m^2 opening, were deployed for 98 days (November, 1977-February, 1978) at respectively 389 m, 988 m, 3,755 m and 5,068 m depths in the tropical North Atlantic (Site E) at 13°30.2'N, 54°00.1'W (Honjo, 1980). The bottom depth at the Demerara abyssal plain site is 5,288 m. Sodium azide (NaN_3) poison was applied to each trap during the deployment period. After recovery, the receiving cup with shutter was detached from the cone. The cup was opened on a laminar flow clean air bench for about 20 seconds under subdud light, then ten drops of saturated sodium azide (NaN_3) were added, and the cup sealed with silicon rubber gaskets. The samples and *in situ* seawater were kept at 3°C in the original cup assemblage until returned to the onshore laboratory. The temperature of the samples was raised to a maximum of 15°C and lit by a fluorescent light (500 candle power) for approximately 20 minutes twice for size fractionation and splitting. For each sample, the size fraction greater than 1 mm was separated. In the two lowermost traps, these > 1 mm fractions represent less than 3% of the organic carbon flux (Honjo, 1980), and their fatty acid composition has not been analyzed. The 389 m and 988 m > 1 mm fractions were blended with

a stainless steel high-speed blender for three seconds. All four < 1 mm fractions and the two blended > 1 mm fractions were finally split twice in a four-bin splitter.

b. Extraction. All solvents were reagent grade and distilled one time in an all glass still. All glassware was rinsed with 1M HCl in methanol, toluene and pentane before use. The 1/16 fraction of the particulates (3-400 mg) was centrifuged for 15-30 minutes at 1500 r.p.m. in 50 ml centrifuge tubes with Teflon lined screw caps. The supernatant seawater was poured off and extracted with toluene. Methanol was added, the tubes shaken and stored for 96 hours at 3°C. After centrifugation the methanol extract was decanted into a 250 ml round bottom flask. A 50/50 (v/v) methanol/toluene mixture was added, the tubes were flushed with N_2, sealed and heated in a boiling water bath for 15 minutes. After cooling and centrifuging the extract was decanted. Finally the samples were extracted with methanol, all contents of the tube were filtered through Teflon membrane filters (0.5 μm) in Millipore Pyrex glass vacuum filtration units. The extracts (methanol and methanol/toluene and methanol) were combined and the solvent evaporated under reduced pressure. The resulting lipid fraction was redissolved in 3 × 5 ml hexane and transferred into a 50 ml centrifuge tube. Sodium chloride saturated water (15 ml) was added, the tubes sealed, shaken, centrifuged for 10 minutes at 400 r.p.m., and the hexane fraction transferred into a 100 ml round bottom flask. This was repeated twice, the combined hexane fractions evaporated under reduced pressure and redissolved in 1 or 3 ml toluene. The sodium chloride saturated water fraction was analyzed for free amino acids (Lee and Cronin, 1982). The total hexane soluble lipids concentration of the toluene solution was determined by weighing an aliquot on a Cahn microbalance (Table 1).

c. Saponification, methylation, liquid chromatography. A 7 to 22% portion (1-10 mg) of the total lipid extract in toluene (~ 200 μl) was placed in a 13 ml centrifuge tube with 1 μg (19:0) fatty acid methyl ester (FAME) internal standard and 2 ml 0.5 M KOH in methanol. The tubes were flushed with N_2, sealed with Teflon lined screw caps and heated for 20 minutes in a boiling water bath. The tubes were then cooled, 2 ml of 14% w/w BF_3 in methanol were added; the tubes were flushed with N_2, sealed, and heated in a boiling water bath for five minutes. Fatty acid methyl esters were extracted into pentane from the reaction mixture in the tube using the procedures of Farrington and Quinn (1971). Fatty acid methyl esters were isolated from lipid or nonsaponifiable lipid extracts by column chromatography on 20 cm length, 0.9 cm i.d. Silica gel columns. The Silicagel 60 (0.063-0.2 mm or about 70-230 mesh ASTM, Merck) was Soxhlet-extracted (50/50 v/v methanol/toluene) for 24 hours, dried at 110°C for 24 hours and 5% deactivated with double distilled water before use. A suite of toluene/ethylacetate/hexane solvent mixtures with increasing polarity was used to elute the column. Three subfractions were collected

Table 1. Weights (in micrograms) of total fatty acid methyl esters collected.

#	FAME		PARFLUX E site (13°30'N, 54W), 98 days							S-1 site (31°32'N, 55W), 75 days		
		Depth (meter)	389		988		3755	5068		5367		
		size fraction (< 1 mm or > 1 mm)	< 1	> 1	< 1	> 1	< 1	< 1	Blank**	All Cup 1	All* Cup 2	Blank
			(all below in micrograms)									
a	14:0		29	7	7	2.5	4.4	5.4	0.3	15	0.58	
b	14:1		< 10	4.3			1.1	1.8				
c	14:1		< 10	4.6		1.8	1.3	1.9	0.3	8.4		
d	14:1				3	2.1			0.3	13.3		
e	14:0	Major	2030	861	460	42	81	54		84	1.7	
f	16:0		24		15		~1					
g	16:1			21								
h	15:1					3.7						
j	15:1					9.3						
k	15:0	Iso	115	46	26	4.5	8.9	6.2		22		
l	15:0	Ante iso	34	16	19	10	6.6	5.6		9.6		
m	15:0	Major	460	185	185	23	20	12	0.7	35.5	0.6	
n	16:1		20	3	23		13.5	9.0				
o	16:1					1.5				14.3	0.07	
p	16:0	(Iso)	120	27	29		2.9	3.8		10.1		
q	16:1	Major	} 2770	470	} 480	} 115	96	} 62		90	0.56	
r	16:1			36			2.1					
s	16:0		83	21	7		2.9	3.5				
t	16:0	Major	9710	3740	5050	285	410	240	16.6	205	19	0.23

#	FAME		389 <1	389 >1	988 <1	988 >1	3755 <1	5068 <1	Blank**	5367 Cup 1	5367 Cup 2	Blank
u	17:1		59	10	20	5.7	8.5	13.5				
v	17:0	Iso	135	34	30	8.9	2	2				
w	17:0	Ante iso	150	48	41	< 1	6.2	4.4				
x	17:1	Major	290	74	110	22.5	13.2	12.2		< 10		
y	17:1		88	29	22	2.9	2.8	2.4				
z	17:0	Major	640	255	450	18.5	14.5	7.5	0.2	< 10	0.25	
A	18:1		120	22	52	5.3	26	27.4		2.3	0.1	
B	18:4		150	29	23	5.4				1.6	0.2	
C	18:2		595	160	115	8.1	9.7	8.6		4.1		
D	18:1	Major	7150	1880	1770	195	280	213		} 45	} 4.3	
E	18:1		670	240	190	33	27.5	25				
F	18:1		33	12	6		1.6	1			1.1	
G	18:0	Major	2240	850	1780	110	120	100	24	26	7.7	0.04
H	20:4	Major	750	170	155	3.1	4.7	3.2				
J	20:5		1720	380	305	12.5	9.6	10.4				
K	20:3		25	11	6							
L	20:4		71	21	5							
M	20:2		210	86	110		3.2	2.2				
N	20:1	Major	590	230	1520		13	12	1.0			
O	20:1		180	58	38		4.3	4.6	2.5			
P	20:0		130	40	82	< 0.1	8.2	6.2	1.0			
Q	22:5		} 5260	} 1170	} 910	} 42	} 23.3	} 23				
R	22:6											
S	22:5		210	36	13		1.5	2.5				
T	22:2		89	22	20							
U	22:1		660	210	56	4.2	} 4.1	} 1.6				
V	22:1		145	46	110	14.5						
W	22:1		60	19	31	0.4	2.3	2.0				
	22:0	Minor amount masked by co-eluting (M = 391) blank contaminant.										

#	FAME	389		988		3755	5068		5367		
		< 1	> 1	< 1	> 1	< 1	< 1	Blank**	Cup 1	Cup 2	Blank
X	24:1	540	135	170	20	5	3.6				
Y	24:1	300									
Z	24:0	440	12	58	11	19	18				
α	26:0					18	19				
	28:0 and 30:0 Not detected in GC/MS (CI) mass search.										
β	Trisnor-hopan-21-one	***	***	190	N.D.	294	280				
Detection limit approx.		12	3	2	0.1	1.0	1.0	0.1	1.0	0.03	0.01
Total FAMEs (mg)		39	11.7	14.4	1.0	1.28	0.93				
Total PUFAs (μg)		7770	1720	1370	58	18.5	15				
Total Lipids (mg)		225	69	170	19	25	12.5				

Shorthand Notation: 18:2 means 18 carbon atoms : 2 double bonds.
Ranking according to increasing GC retention time.
h,j,u,f,g Except for molecular ion mass number no GC/MS data.
Short GC retention times might suggest saturated cyclopropyl (h,j,u,f) or isoprenoid (g) rather than assigned monoenoic chains (Boon, pers. comm.).
* Cup 2 (S-1) no NaN_3 bactericide during deployment.
** Blank E to be multiplied with 1.5 and 1.33 for comparison with > 1 mm at 389 resp. 988 m.
*** Minor peak with same GC retention time is an unresolved mixture.
Molecular ion (M = 384 + 1) signal/noise ratio unfavourable (GC/MS-CI).
Total unresolved compound mixture peak area less than 100 μg.
N.D. = non detectable.
PUFAs in S-1 samples not reported.
Fluxes are obtained when dividing above masses by area (1.5 m^2) and deployment period (98 or 75 days).

in correspondence with test runs for FAME standard mixtures and combined for further analysis. Blanks were processed along with the extraction, saponification, methylation and liquid chromatography steps.

d. PARFLUX S-1. Procedures were similar except for those described below. A pair of traps was deployed for 75 days during the low productivity season (October 20, 1976-January 5, 1977) at 5,367 m depth in the Sargasso Sea at 31°32.0′N, 55°00.8′W (Honjo, 1978). The bottom depth of the Sohm abyssal plain site is 5581 m. Bactericide was applied to only one (cup 1) of the traps. Without size fractionation, the samples were split only once in a 4-bin splitter. Seawater was decanted from the resulting 1/4 aliquot. The sample was refilled with 200 ml double-distilled, 0.45 μm Nuclepore-filtered water, and stored for 24 hours at 2°C. This procedure was repeated three times, the supernatants were discarded. Subsequently the samples were extracted twice with ethanol (2 × 200 ml) and three times with acetone (3 × 200 ml). The combined extracts were filtered over 12 cm Whatman filters, evaporated under reduced pressure and redissolved in 5 ml pentane. Nine and twenty-three percent of the lipid fractions of cup 1 and cup 2, respectively, were combined with 50 μg 19:0 FAME standard each, saponified and methylated. The liquid chromatography fraction containing about half of the polyunsaturated fatty acids (PUFA) was not recovered and values for PUFAs are not reported for this station. A blank was processed along with the saponification, methylation and liquid chromatography. About 25% of the lipid fractions was processed similarly, however, without addition of 19:0 internal standard. No significant amounts of original 19:0 could be detected. The amounts of other species (calculated by comparison with coinjected 17:0 FAME standard) were similar to those observed for the 19:0 spiked samples, confirming the overall reproducibility of our procedures.

e. Gas chromatography and mass spectrometry. A 20 m, 0.32 mm i.d. SE-52-coated glass capillary column installed in a Hewlett-Packard 5710 A gas chromatograph equipped with a flame ionization detector was used for developing procedures with FAME standard mixtures. The column was temperature programmed from 100 to 260°C at 2°C min^{-1} with helium carrier gas flow of 6-7 ml min^{-1}. Injector temperature was 250°C and detector temperature was 300°C. A Supergrator-3 (Columbia Scientific Industries) programmable computing integrator was linked to the gas chromatograph. Initially all samples were analyzed with this system, FAMEs were tentatively identified by comparison of retention times to various standards run periodically under the same conditions. Concentrations of FAMEs were determined by ratios of peak areas to the area of the 19:0 internal standard.

Subsequently the samples, blanks and standards were run on a 20 m, 0.32 mm i.d. SE-52 coated, deactivated by persilylation, high temperature glass capillary

column installed in a Carlo Erba 4160 gas chromatograph equipped with an on-column injection port and a flame ionization detector. The column was temperature programmed from 120 to 260°C at 2°C min^{-1} with hydrogen carrier gas pressure of 0.75 kg cm^{-2}. The injection temperature was made with auxiliary cooling and a column oven temperature at 100°C and detector temperature was 300°C. The gas chromatograph was linked with a Supergrator-3 integrator.

All samples, blanks and standards were analyzed by chemical ionization (CI, isobutane, 750 μm source pressure, 130 eV) on a Finnigan 3200 quadrupole mass spectrometer interfaced with a Finnigan 9500 gas chromatograph and a Finnigan 6000 data system. The 17 m, 0.32 mm i.d., SE-52-coated, $BaCO_3$ deactivated glass capillary column was programmed from 100 to 250°C at 4°C min^{-1}. The < 1 mm, 5068 m, sample and standards were also analyzed by electron ionization (EI, 70 eV) with the same GC-MS-C system. Peaks in the reconstructed chromatograms from the CI mode runs were assigned by interpretation of CI and EI mass spectra. Subsequently the corresponding peaks from the Carlo Erba 4160 gas chromatograms were quantified by ratios of peak area to the area of the 19:0 internal standard. Final structure determination and quantification agreed well with the tentative assignments based on the H.P. 5710A gas chromatograms.

3. Results

Both total lipids and fatty acids (Table 1) exhibit a rapid decrease with depth. The fatty acid composition of the fractions < 1 mm and > 1 mm in the uppermost 389 m trap are almost identical. The abundance of polyunsaturated fatty acids (20:5, 20:4, 20:2, 22:5, 22:6, 18:2) provides evidence for a marine input as these are produced almost exclusively by marine organisms (Schultz and Quinn, 1977; among others). The predominance of lower molecular weight compounds 14:0, 16:0, 16:1, 18:0, 18:1 is consistent with a marine input (Sargent *et al.*, 1976). Less than half of the > 1 mm fraction consisted of intact zooplankters which were probably trapped alive (Honjo, 1980). Indeed the FAME distribution of this fraction (as well as the < 1 mm fraction) was similar in composition to that of a zooplankton tow at this station (unpublished results) except for greater relative abundance of polyunsaturated fatty acids in the trap sample. Presumably the fatty acids in the upper trap represent the relatively unaltered planktonic source (zooplankton and phytoplankton). Most likely little transformation or decomposition of fatty acids has taken place before trapping or after collection during the 98-day deployment period.

The labile PUFA segment of the fatty acid pool disappears rapidly with increasing depth (Table 1) in concordance with the virtual absence of PUFA in pelagic surface sediment (Van Vleet and Quinn, 1979; Saliot and Boussuge, 1978).

The small amount of 24:0 FAME, decreasing with depth, suggests a minor input

of higher vascular plant waxes of terrestrial origin in the surface waters (Simoneit, 1977). These compounds (22:0, 24:0, 26:0, 28:0) from the same origin are often reported in atmospheric samples and sea surface microlayer samples (Marty *et al.*, 1979; Gagosian *et al.*, 1981). In the 389 m and 988 m trap samples 22:0 and 26:0 could not be detected despite extensive searching of the GC/MS (CI) mass spectra. Biodegradation of nC > 20 aliphatic carboxylic acids or hydrocarbons is apparently more difficult relative to lower molecular weight compounds (Matsuda, 1978; Van Vleet and Quinn, 1979). This could lead to selective enrichment of 24:0, 26:0 FAME in the two lowermost traps.

One triterpenoid co-eluted with the FAME fractions during liquid chromatography (Table 1, β). The GC/MS (EI) mass spectrum of the 5068 m sample is identical to that of a trisnorhopan-21-one standard and is presumably of microbial origin (Simoneit, 1975). Gagosian *et al.* (1982) report matching values of 190, 270 and 255 μg from their analyses of another portion of the lipid extract of 988 m (< 1 mm), 3755 m and 5068 m traps, in agreement with our analyses.

The daily influx of fatty acids is about the same for the lowest traps at Site E (5068 m) and Site S-1 (cup 1, 5367 m) (e.g. 1.7 $\mu g\ m^{-2}\ d^{-1}$ and 1.8 $\mu g\ m^{-2}\ d^{-1}$ respectively for 16:0 major fatty acid). The amounts detected in the nonpoisoned cup 2 are tenfold smaller and the abundance of 16:1 and 18:1 compared to 16:0 and 18:0 is smaller in cup 2. Both of these results are consistent with greater metabolism in cup 2 compared with cup 1. These observations and previously mentioned compositional similarity of fatty acids in fresh plankton and in the 389 m E-site trap, all indicate the biocide was effective. However, more experiments are needed to verify complete preservation of organic matter composition by the biocide.

4. Modeling flux gradients

At the station in the equatorial North Atlantic Ocean (E-site) the fluxes of total organic matter (Honjo, 1980), total lipids and individual fatty acids (Table 1), as well as some of the other lipid subfractions (Wakeham *et al.*, 1980) and various free amino acids (Lee and Cronin, 1982) all show a marked decrease with depth (Fig. 1). For many of the above compound classes one can mathematically describe the net loss during settling with a simple one-dimensional model.

A fit (a) to the data shows quantitatively that the biogeochemical stability of a fatty acid is a function of the numbers of carbon atoms and double bonds in the molecule. Extrapolation of the best fit model to the seafloor (b) gives an estimate of the vertical flux at the sediment/water interface to be compared with rates of sedimentation, oxygen consumption and diagenesis as derived from the literature. More complex mechanisms such as (microbial) degradation or zooplankton metabolism may explain the net loss term of the model and will be dealt with in the discussion.

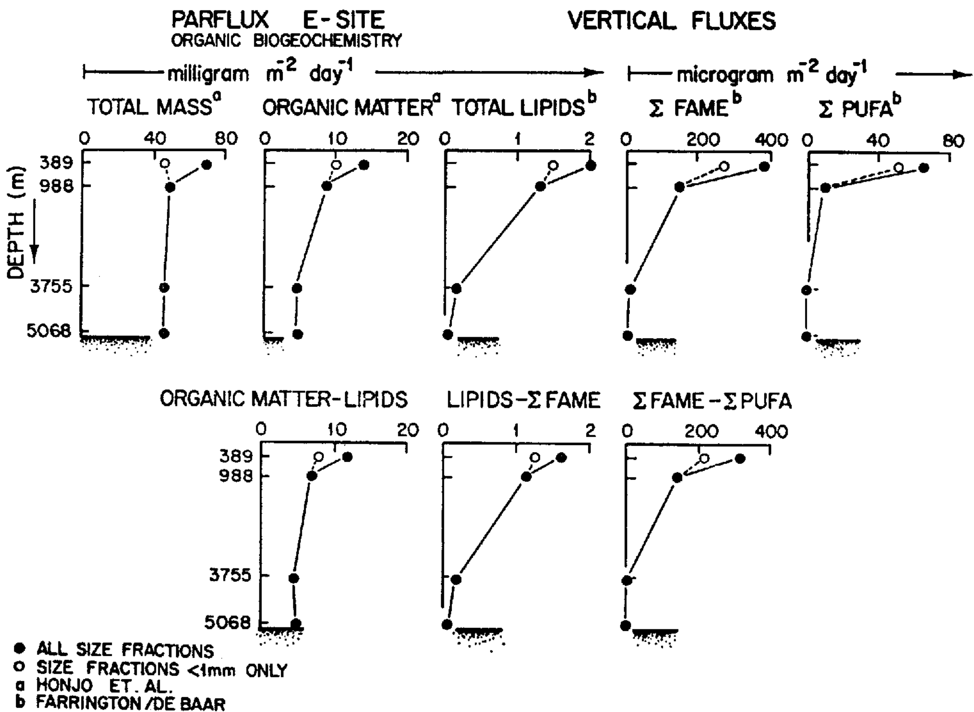

Figure 1. Flux gradients for organic compound classes.

a. Curve fitting. A linear depth function for a steady state

$$\frac{\partial F}{\partial z} = -k_o \tag{1}$$

was compared with an exponential function

$$\frac{\partial F}{\partial z} = -k_1 F \tag{2}$$

where depth is defined positively downward. Given a constant mean settling velocity at all depths, these functions are analogs of respectively zero and first order kinetics. As usual in marine chemistry, the constants k_o ($\mu g \cdot m^{-3} \cdot d^{-1}$) and k_1 (m^{-1}) are defined over ranges of temperature (2-12°C) and pressure (40-500 atm). Increased pressure can cause decreased microbial degradation rates (Jannasch *et al.*, 1971). Temperature might have an important effect on the biochemical reactions associated with marine organisms which could influence flux gradients (Packard *et al.*, 1975). Effects of temperature and pressure would already be included in the first order model (e.g. see Wyrtki, 1962). Integration of (1) and (2) with boundary condition (F_{389}, 389 m) of the uppermost trap respectively produces

Table 2. Comparison of zero order and first order loss models for all size fractions at Station E.

		Zero order		First order uncorrected		First order efficiency corrected	
		k_0	r	k_1	r	k_1	r
e	14:0	0.46	.75	0.78 10^{-3}	.95	0.77 10^{-3}	.94
f	16:0	2.27	.86	0.86 —	.99	0.85	.98
G	18:0	0.57	.94	0.79 —	.98	0.79	.98
m	15:0	0.27	.73	0.84 —	.99	0.83	.98
z	17:0	0.16	.91	1.07 —	.99	1.1	.99
q,r	16:1 Group	0.49	.74	0.77 —	.95	0.76	.94
D	18:1 Major	1.37	.76	0.75 —	.95	0.74	.94
E	18:1 Minor	0.14	.77	0.74 —	.95	0.73	.94
H	20:4	0.14	.75	1.2 —	.97	1.19	.96
J	20:5	0.31	.73	1.1 —	.95	1.12	.94
Q,R	22:5 + 22:6	0.97	.73	1.6 —	.99	1.59	.99

$$F_{389} - F = k_o\,(z - 389) \tag{3}$$

and

$$\ln(F_{389}/F) = k_1\,(z - 389) \tag{4}$$

By comparison of measured ^{230}Th flux vs. ^{230}Th-production from dissolved ^{234}U Brewer *et al.* (1980) estimated 0.70-0.78-0.78-0.67 trapping efficiencies for the 389-988-3755-5068 m depth traps. Using both efficiency corrected and uncorrected fluxes F for the major fatty acids (as methyl esters) in all size fractions the coefficients of correlation (r) favor the first order equation (4) over the zero order model (3) (Table 2). The efficiency correction is close to 0.7 for all traps and does not significantly alter the closeness of the first order fit. Consequently, the constants k_1 are not affected by the trapping efficiency.

Most of the organic matter flux is associated with settling large particles. However, intact crustaceans, euphausiids and pteropods in the greater than 1 mm fraction of the mesopelagic traps (Honjo, 1980) might suggest the collecting of living zooplankton. In the 389 m trap no more than half of the particles greater than 1 mm were of intact zooplankton. A first order model fitted exclusively to the size fractions smaller than 1 mm leads to only a slight decrease of the rate constants k_1 (Table 3). In other words, the first order rate constants are barely affected by trapping of intact zooplankters. In the following we will consistently use the first order rate constants derived from the efficiency corrected (unless otherwise indicated) total mass fluxes in all size fractions.

The stability of a fatty acid molecule is expected to increase with chain length and decrease with the number of double bonds in the chain (e.g. Farrington *et al.*,

Table 3. First order rate constants, half-depths and percentages of top trap reaching the sea floor for individual fatty acids.

	PARFLUX E traps		First order decay model					
			All size fractions			Size fractions < 1 mm only		
	Fatty acid methyl ester		k_1 (meter^{-1})	Half depth (meters)	$100\,F_{5288}/F_{389}$ (%)	k_1 (meter^{-1})	Half depth (meters)	$100\,F_{5288}/F_{389}$ (%)
e	14:0		0.77 10^{-3}	960	1.1	0.71 10^{-3}	1040	1.7
f	16:0		0.85 —	820	1.3	0.8 —	870	1.8
G	18:0		0.78 —	890	2.1	0.73 —	950	2.9
Z	24:0		0.6 —	1160	2.5	0.57 —	1220	2.6
m	15:0		0.83 —	840	1.3	0.77 —	900	1.8
z	17:0		1.06 —	650	0.5	1.01 —	690	0.8
q,r	16:1	Group	0.76 —	910	1.3	0.72 —	960	1.6
D	18:1	Major	0.74 —	940	1.5	0.7 —	990	2.3
E	18:1		0.79 —	880	1.6	0.67 —	1030	2.4
F	18:1		0.31 —	2240	1.5	0.64 —	1080	2.2
U,V	22:1	Group	1.36 —	510	0.09	1.3 —	530	0.1
X,Y	24:1	Group	1.26 —	550	0.18	1.16 —	600	0.2
C	18:2		0.91 —	760	0.6	0.87 —	800	0.8
M	20:2		1.08 —	640	0.4	1.03 —	670	0.6
B	18:4*		1.18 —	590		1.05 —	660	—
L	20:4		1.19 —	580	0.2	1.16 —	600	0.2
J	20:5		1.12 —	620	0.2	1.09 —	640	0.3
Q,R	22:5	22:6	1.59 —	440	0.03	1.55 —	450	0.04
k	15:0	Iso	0.6 —	1160	2.8	0.53 —	1310	4.1
l	15:0	Ante iso	0.84 —	830	0.5	0.37 —	1870	13.3
p	16:0	(Iso)	0.76 —	910	1.3	0.73 —	950	1.6
w	17:0	Ante iso	0.75 —	920	1.5	0.71 —	980	2

* Concentrations in two lower traps assumed at detection limit 0.1.
All data corrected for trapping efficiency.

1977). The rate constants k_1 of the major saturated fatty acids indeed decrease with chain length (Table 3, e, f, G, Z). In contrast the long chained monounsaturated FAMEs (22:1, 24:1) have larger rate constants than the shorter chained (16:1, 18:1) monounsaturated species (Table 3, U, V, X, Y, resp. q, r, D, E, F). The polyunsaturated fatty acids (PUFAs) decrease much more rapidly than the saturated or monounsaturated FAMEs. The half depths ($z_{1/2} = \ln(2/k_1)$ = depth range over

Table 4. First order rate constants, half depths and percentages of top trap reaching the sea floor for various compound classes.

PARFLUX E traps	First order decay model All size fractions		
	k_1 (meter^{-1})	Half depth (meters)	$\frac{100\,F_{5288}}{F_{389}}$ (%)
Mean values fatty acids			
Alkanoic (6)	0.82 10^{-3}	900	1.5
Monoenoic (6)	0.87 —	1000	1.0
Dienoic (2)	1.00 —	700	0.5
Polyenoic (4)*	1.27 —	560	0.14
Branched chains (4)	0.74 —	960	1.5
Compound class			
Σ FAME	0.84 10^{-3}	870	1.0
Σ PUFA	1.38 —	500	0.07
Total lipids	0.68 —	1080	3.3
Organic C	0.28 —	2480	20.8
Organic matter	0.21 —	3300	30.7
Differences			
Σ FAME −Σ PUFA	0.80 10^{-3}	920	1.3
Lipids −Σ FAME	0.66 —	1110	3.8
Organic matter—lipids	0.16 —	4250	43

* Polyenoic fatty acids are commonly referred to as polyunsaturated fatty acids (PUFA).

which 50% has been lost) range from 400 m to 700 m for individual PUFAs (Table 3). As a group (Σ PUFA) their half depth is 500 m, a dramatic difference from the 3300 m half depth for the organic matter as a whole (Table 4).

The shorter monounsaturated fatty acids (16:1, 18:1) exhibit net loss rates which are near, or even smaller than the rates calculated for fully saturated species (Table 3). The moderate flux gradients of short monounsaturated fatty acids (16:1, 18:1) may be explained by a larger (microbial) biosynthesis term;

$$\text{net flux change} = \text{degradation} - \text{biosynthesis } (\text{mass} \cdot \text{m}^{-3} \cdot \text{d}^{-1}) \qquad (5)$$

which would counteract the degradation during settling. As for the 18:1 FAME, Brooks *et al.* (1976) appreciated that this may often include an unresolved mixture of oleic acid (18:1 ω9), a common component of animals, and cis-vaccenic acid (18:1 ω7), an abundant bacterial constituent (Perry *et al.*, 1979). Microbial biosynthesis before and during settling is most plausible for the branched chain fatty acids which are rather persistent with depth (Table 3, k,l,p,w) and are known to be synthesized mostly by bacteria (Perry *et al.*, 1979).

b. Extrapolation to the sea floor. Fluxes at the sediment/water interface can be predicted by extrapolation of the first order model to the sea floor (5288 m). From the vertical flux passing the 389 m horizon we extrapolate from the model that 31% of the total organic matter, 3% of the lipid fraction and about 1% of the fatty acids would reach the sea floor (Table 4). The lipid fraction as a whole (half depth 1000 m) represents 15% of the total organic matter (half depth ≈ 3300 m) in the mesopelagic traps (Table 1). This implies that the remaining fraction (organic matter-lipids) is highly refractory with a 4250 m half depth, i.e. the nonlipid organic flux at the sea floor compares to 43% of the nonlipid organic flux at 389 m depth.

Above and elsewhere (Wakeham *et al.*, 1980) we demonstrated some of the compositional changes of the organic matter during settling in the water column. By extrapolation to the sea floor and comparison with a sediment piston core (Van Vleet and Quinn, 1979) we can also gain insight in the compositional changes occurring between arrival at the sea floor and final burial. The flux of organic carbon to the sea floor, benthic energy requirements, and infaunal oxygen respiration were discussed previously (Hinga *et al.*, 1979; Honjo, 1980; Suess, 1980). The extrapolated influx of organic carbon is 1.4 $mg \cdot m^{-2} \cdot d^{-1}$ and much larger than the accumulation rate at the surface (0.38 $mg \cdot m^{-2} \cdot d^{-1}$) or at depth (0.26 $mg \cdot m^{-2} \cdot d^{-1}$) in the sediment core (Table 5). The difference exceeds the 0.2-0.8 $mg \cdot m^{-2} \cdot d^{-1}$ consumption rate derived from *in situ* oxygen utilization (Smith, 1978; Hinga *et al.*, 1979). However, these oxygen utilization rates are from the Sargasso Sea benthos at depths similar to the PARFLUX E water depth. There are no data available for an equatorial station. Other sinks such as epibenthic fauna probably make up some or all of the calculated difference between the extrapolated influx and utilization and burial of organic matter (Grassle *et al.*, 1975; Rowe and Gardner, 1979).

Only 1% of the fatty acids (Σ FAME) passing the 389 m horizon reach the sea floor, 0.1% escapes benthic consumption and 0.01% is finally buried (Table 5). The major saturated fatty acids (14:0-15:0-16:0-18:0) exhibit a fairly consistent pattern. Whether during settling in the water column, benthic residence or diagenesis, the losses tend to be smaller with increasing chain length of the molecule (Table 6). The branched chain 15:0 group (iso + anteiso) is more persistent than its straight chained counterpart. This persistence is again ascribed to microbial biosynthesis at the benthic boundary layer and within the sediment (Perry *et al.*, 1979).

5. Regeneration and oxygen consumption

Application of above derived model to earlier reported organic C, H, N-fluxes (Honjo, 1980) yields best fit *rate* terms

$$J = k_1 F = J_0 \exp(-k_1 z) \text{ [micromol} \cdot m^{-3} \cdot d^{-1}] \quad (6)$$

whose ratios agree well with ratios reported by Redfield *et al.* (R.K.R.) (1963)

Table 5. Extrapolated influx at sediment/water interface compared with sedimentation rate.

	Organic carbon flux			Σ FAME flux		
	$mg \cdot g^{-1}$ dry wt.	$mg \cdot m^{-2}$ day^{-1}	%	$\mu g \cdot g^{-1}$ dry wt.	$\mu g \cdot m^{-2}$ day^{-1}	%
Primary productivity[1]		200[2]				
Vertical flux 389 m		6.8[2]	100		490	100
Sedimentation 5574 m (extrapolated)	30	1.4	20.6	85	4.0	0.8
Surface sediment 0-2 cm	5.4[3]	0.38[4]	5.6	5.6[3]	0.39[4]	0.08
Burial 50-1000 cm	3.7[3]	0.26[4]	3.8	0.8[3]	0.06[4]	0.01
Sedimentation—burial		1.1	16.8		3.9[4]	0.79
Benthic oxygen consumption[5] at 5100-5200 m: 0.5-1.7 $ml \cdot m^{-2} \cdot d^{-1}$		0.2-0.8	3-12			

[1] The Steeman-Nielsen method has artifacts (Carpenter and Lively, 1980). Using different methods values as high as 1400 $mg \cdot m^{-2} \cdot d^{-1}$ were reported (Gieskes *et al.*, 1979) for the tropical Atlantic Ocean.

[2] PARFLUX-E 13°5′N, 54W (Honjo, 1980). All size fractions, efficiency corrected.

[3] Van Vleet and Quinn (1979). Their station 7 (pers. comm.) at 6°24′S, 25°36′W rather than published average values stations 6 and 7. Depth 5574 m.

[4] The concentrations (3) ($mg \cdot g^{-1}$ dry wt.) were multiplied with the efficiency corrected flux $47/0.67 = 70$ $mg \cdot m^{-2} \cdot d^{-1}$ at the lowermost trap (5067 m).

[5] 34°N, 66W (Smith, 1978).

(Table 7). Organic nitrogen compounds are relatively labile (Lee and Cronin, 1982) and ΔN decreases with increasing depth. Values slightly less than 16 would be required for the more intense regeneration in shallower (< 500 m) waters, in order to balance the budget with respect to the global 'depth average' R.K.R.-value of $\Delta N = 16$. It was shown previously that flux gradients of individual fatty acids are in agreement with their expected stabilities. Now it is also evident that changes in elemental composition of the bulk organic matter in the very same samples are just as well compatible with the common understanding of regeneration in the oceans.

In situ oxygen consumption in the water column may be described more realistically with a multi-step model (Knauer and Martin, 1981) rather than just one vertical term (e.g. Wyrtki, 1962). For instance in a two box model the oxygen consumption rate in the uppermost box (e.g. 80-400 m) would have a very steep gradient with depth, possibly analogous to models by Riley (1951) and Jenkins (1980) which apply mostly to the upper part of the water column. The lower box (e.g. 400-5000 m) with more gentle gradients would then be represented by the model and data in this paper (Table 7). Flux gradients of organic matter collected in our traps yield predicted rates for deep water oxygen consumption ranging from 0.04 $\mu mol \cdot kg^{-1} \cdot yr^{-1}$ at 2000 m to 0.02 $\mu mol \cdot kg^{-1} \cdot yr^{-1}$ at 4000 m depth. The *total* oxygen consumption rate for deep water (> 2000 m) is generally assessed

Table 6. Extrapolated influx at sediment/water interface compared with sedimentation rate for individual fatty acids.

Fatty acid methyl ester	14:0			15:0 (iso and anteiso)			15:0		
	ng • mg^{-1} dry wt.	ng • m^{-2} • d^{-1}	%	ng • mg^{-1} dry wt.	ng • m^{-2} • d^{-1}	%	ng • mg^{-1} dry wt.	ng • m^{-2} • d^{-1}	%
Vertical flux* 389 m	283	28,100	100	20.7	2,050	100	63	6,280	100
Vertical flux* 5068 m	7.8	548	2.0	1.7	120	6	0.9	64	1
Sedimentation									
(extrapolated) 5574 m	3.7	260	0.9	0.97	68	3.3	0.8	57	0.9
Surface sediment 0-2 cm	0.8**	58	0.2	0.6**	43	2.1	0.3**	21	0.3
Burial 8-11 m	0.12**	8.5	0.03	0.07**	5	0.2	0.05**	4	0.06

Fatty acid methyl ester	16:0			18:0			18:1		
Vertical flux* 389 m	1318	130,700	100	303	30,000	100	974	96,600	100
Vertical flux* 5068 m	35	2,470	2	14	1,015	3.4	34	2,416	2.5
Sedimentation									
(extrapolated) 5574 m	17	1,188	0.9	6.4	450	1.5	15	1,063	1.1
Surface sediment 0-2 cm	1.9**	133	0.1	0.6**	38	0.1	0.4**	31	0.03
Burial 8-11 m	0.3**	23	0.02	0.13**	9	0.03	0.04**	3	0.003

* Total fluxes (all size fractions) corrected for trapping efficiency.
** 6°24′S, 25°36′W (Van Vleet and Quinn, 1979). Their station 7 (pers. comm.) rather than published average values stations 6 and 7. Depth 5574 m.

Table 7. Organic flux data, first order fit parameters, and comparison with R.K.R.-regeneration rates.

Depth	C*	H*	N*	O_2*	O_2-equivalents**
389	563	860	64.3	159	699
988	329	600	37	118	600
3755	144	390	13.6	80	406
5068	141	390	13.6	83	372

	k_1(km^{-1})	J_0(μmol • kg^{-1} • day^{-1})***
O_2 consumption	0.3	-191×10^{-6}
N_{org}—NO_3	0.33	18.3×10^{-6}
C_{org}—CO_2	0.29	54×10^{-6}

Depth	ΔO_2	:	ΔC_{org}	:	ΔN
500	138		107.8		13
1000	138		108.6		13
2000	138		109.6		12.4
3000	138		111		12.1
4000	138		112.6		11.7
Redfield, Ketchum, Richards Ratio					
	138	:	106	:	16

* (Honjo, 1980) (micromole • m^{-2} • d^{-1}). Not corrected for trapping efficiency.
** O_2-equivalents = C + 4H + 1.25N − O_2.
*** Model valid only below 389 m, but J_0 defined at sea surface ($z = 0$) for sake of comparison.

at about 0.1 μmol • kg^{-1} • yr^{-1} in the North Atlantic region (Arons and Stommel, 1967; Kuo and Veronis, 1973; Kroopnick, 1980). Thus, 20 to 40% of the total consumption may be accounted for by flux gradients of material collected in our traps. Quite independently Brewer *et al.* (1980) reported that the same material may also account for about 70% of the total ^{230}Th-production in the water column. Although all above estimates (as well as our own) are based on necessarily simplistic models, they do suggest that the amount of material collected and preserved in traps is significant.

Obviously further experiments are required to resolve the problems of trapping efficiency and sample preservation. However, the above arguments with respect to R.K.R.-rates and oxygen consumption, as well as previously mentioned differences between two cups at site S-1 and agreement between a fresh plankton tow and the 389 m E-site trap, all indicate some integrity of our samples. This evidence supports the validity of our fatty acid data and interpretations, and also supports interpretations for different compound classes in the same samples (Lee and Cronin, 1982; Gagosian *et al.*, 1982).

6. Discussion

By means of quantification with a simple model we have primarily attempted to illustrate an approach for unravelling "mechanisms and rates of processes controlling the distribution of organic compounds in the sea" (Gagosian and Lee, 1981). The actual values of the derived parameters have a large uncertainty when considering the various assumptions and the unknown standard deviation of data for four depths for one time interval. In other marine environments the loss during settling model would yield different rate constants. In addition for areas such as the Sargasso Sea the seasonality would negate the steady state assumption (Deuser *et al.*, 1981). In nearshore areas horizontal transport of labile particulate organic matter may be more significant. In fact, horizontal transport from continental margin areas to our station may explain part of the observed distribution of more stable 24:0, 26:0 fatty acids which have a predominantly land plant source (Simoneit, 1975, 1977).

However, at our equatorial station the 'black box' model describes quantitatively the net loss of fatty acids during settling. What would be the underlying mechanism? Continuous physical breakup of settling fecal pellets would be a simple explanation but is rejected as the size distribution (Honjo, 1980) and total mass flux (Fig. 1) are constant with depth. On the other hand, the agreement with expected stabilities of straight chained carboxylic acids, the consistency with early diagenesis, as well as the agreement with the Redfield-ratio all strongly support some biochemical mechanism. The relative persistence of branched chained fatty acids and the presence of trisnorhopan-21-one in the deep traps indicate input of microbial biosynthetic or transformation products. Zooplankton coprophagy with or without vertical migration (Wiebe *et al.*, 1979) may also account for part of the observed compositional changes with depth.

Tanoue and Handa (1980) have studied fatty acids in sediment trap particulate material and suspended matter filtered from seawater at a station in the North Pacific at 47°51.1′N, 176°20.6′E, 5300 m deep. They reported that "no significant vertical trend in the fatty acid concentration was found in trap sediments," and "no vertical variability in the composition of fatty acids was found in the trap sediments collected from these depths." Their sampling depths for sediment traps were 100, 1100, 2200, 4400 and 5250 m and deployment time was 45 days. We do not know the reasons for this difference between their results and ours which show significant vertical quantitative and qualitative gradients. Many hypotheses are possible including the obvious that the stations are in two markedly different oceanic regimes. We are investigating fatty acid and other organic compound distributions in samples from various oceanic regimes, e.g. PARFLUX P of Honjo (1980), the Peru coastal area and the California coastal area off Monterey. The results from these investigations should assist in elucidating the mechanisms for the aforementioned differences.

There are three areas of important agreement between our data and that of Tanoue and Handa (1980). First, both sets of results show that sediment trap material contains higher proportions of unsaturated fatty acids relative to saturated fatty acids in comparison to the relative proportion of unsaturated fatty acids in suspended matter from the water column below the euphotic zone (Tanoue and Handa, 1980; Williams, 1965). Second, a comparison of both sets of data with surface sediment data of Van Vleet and Quinn (1979) and Saliot and Boussuge (1978) for the Equatorial Atlantic show that surface sediments contain much lower concentrations of fatty acids, a lower ratio of fatty acids to organic carbon and a much lower relative abundance of unsaturated fatty acids. Third, both sets of sediment traps recorded a predominance of fatty acids with a marine plankton source, minor to moderate contributions of branched chain fatty acids of bacterial origin, and minor to trace amounts of higher molecular weight fatty acids 22:0, 24:0 and 26:0 of terrigenous origin.

Our data from the Equatorial Atlantic traps strongly support the conceptual model discussed in the Introduction which has euphotic zone organic matter of primary planktonic origin transported rapidly via fast sinking particles such as fecal pellets, through mesopelagic and bathypelagic depths to the sediment water interface. The comparison of quantitative and qualitative compositions of fatty acids in plankton, sediment trap particles, and deep ocean sediments places the sediment trap particulates in a vertical gradient which progresses logically from plankton to surface sediment based on our knowledge of the biogeochemistry of fatty acids as previously discussed. The nonlipid segment of the settling organic matter taken as a whole is rather persistent with a 4250 m half depth in the water column. However, we do not know the detailed composition of this material and by analogy to our investigation of fatty acids and lipids there are probably reactive portions within the nonlipid material which undergo marked compositional change with increasing depth of traps.

The application of the model we have described, or modification thereof, to different classes of organic compounds in samples from a variety of oceanic regions should provide good quantitative measurements of various processes acting on organic matter transported through the oceans. We think that a major contribution of this approach will be an evaluation of the components of the net flux change term in equation (5). The components of this term can be expanded to

$$\text{net flux change} = \text{decomposition} + \text{remineralization} - \text{“de novo” biosynthesis} - \text{transformation production} \quad (7)$$

where decomposition refers to alteration of a chemical structure by biological or chemical means to another organic structure, e.g. hydrocarbon oxidation to an alcohol and further oxidation to an acid or oxidation of a sterol to a steroid ketone. Remineralization refers to metabolism of organic compounds to CO_2, NO_3^-, NH_3,

i.e. inorganic nutrients. Transformation production is the synthesis of one organic compound from another—by analogy the inverse of decomposition. Further subdivisions of these terms giving more details of the biogeochemistry of organic matter can be written into equation (7). Unraveling the contributions of each term requires multiple measurements of a variety of organic compounds judiciously chosen to be key indicators of certain source terms (e.g. see Simoneit, 1977) or processes (e.g. see Gagosian and Lee, 1981).

The results of our study of fatty acids described above and previously discussed studies of other classes of organic compounds in sediment trap material all demonstrate that detailed chemical characterization and quantitative measurement of organic compounds is a prerequisite for understanding such topics as benthic food supply and early diagenesis of organic matter in sediments. The importance of conducting such studies in conjunction with other geochemical and biological research is illustrated by the use of radiochemical constraints (Brewer *et al.*, 1980) and sample description (Honjo, 1980) in our model and interpretation.

7. Conclusions

(1) The fatty acid composition indicates an almost exclusively marine source with possibly a minor terrigenous component in the bathypelagic traps.

(2) The vertical fluxes of fatty acids and total lipids decrease rapidly with depth.

(3) The flux gradients of fatty acids increase with number of double bonds and decrease with number of carbon atoms.

(4) Iso- and anteiso as well as some monoenoic fatty acids behave differently. Their relative persistence with depth is consistent with microbial synthesis during settling which somewhat counteracts degradation.

(5) Similar trends (3, 4) are continued during benthic residence and early diagenesis.

(6) Vertical fluxes ($\mu g \cdot m^{-2} \cdot d^{-1}$) of fatty acids are similar for the deepest traps in the equatorial Atlantic (E) and the Sargasso Sea (S-1).

(7) Regeneration rates of organic C, H, N during settling depart slightly from the Redfield ratio with increasing depth.

(8) Flux gradients of large particles collected in our traps may account for about 20-40% of the oxygen consumption in the deep water and 10% or less in the lower (> 400 m) thermocline region.

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