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Density of the major size groups of benthic fauna and trophic input in deep basins of the Atlantic Ocean

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ABSTRACT

Seven deep-sea areas were studied in the Atlantic Ocean. An intensive and comparable benthic sampling program was conducted during several deep-sea biology cruises with IFREMER research ships and mainly with the RV *Jean Charcot*, in the Norwegian Sea, the Bay of Biscay, the Porcupine Seabight, the Vema Fracture Zone, the Demerara abyssal plain, the Cape Verde Basin, the Angola and Cape basins near the Walvis Ridge. A synthesis of community structure data has been realized and the benthic fauna, quantitatively sampled, was separated into three main size categories (meiofauna, macrofauna *sensu stricto* and megafauna). Comparison of population densities in the different stations, dominated by pelagic sedimentation, shows that the range of abundance differs for the three major size groups and that meiofaunal and macrofaunal density are positively linearly related; the biomass of the macrofauna is roughly twice that of the meiofauna. The megafaunal pattern of abundance differs from meiofaunal and macrofaunal abundance and shows an exponential relationship with the two other groups.

The abundance of meiofauna and macrofauna has a positive linear relationship with the "burial" organic carbon flux, which has been evaluated from mean organic carbon concentration in the surface sediment and the rate of sediment accumulation during the Holocene. The relationship observed would be expected if the biomass is dependent of the flux of particulate organic carbon to the deep-sea floor and therefore demonstrates that this flux is the first order parameter which controls biomass distribution in the deep Atlantic Ocean.

1. Introduction

A quantitative knowledge of the abundance of the various size groups of the benthic fauna is essential for a better understanding of the structures and functions of deep-sea communities at the sediment-water interface. An exponential decrease in the abundances of benthic fauna with water depth is generally observed, although some variability in abundance is introduced when distinct bottom topographic (trenches) and geographical locations (such as latitude) are taken into account (Rowe, 1983). These relationships usually are explained in terms of the control of faunal abundances by trophic input (Rowe, 1971; Menzies *et al.*, 1973; Steele, 1974; Thiel, 1975; Thiel, 1979; Rowe and Staresinic, 1979; Khripounoff, 1979; Hinga *et al.*, 1979; Wangersky

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and Wangersky, 1981; Stockton and Delaca, 1982; Vinogradova and Tseitlin, 1983). However, quantitative data are still inadequate to support this assumption. Indeed the control parameter most frequently tested was depth, assumed to be correlated to decrease in food availability.

In this study we compare benthic population density in several soft bottoms dominated by hemipelagic and pelagic sediments. The aim of the present work is to demonstrate quantitatively (1) the range of variability in the abundances of 3 major size groups (meio-, macro-, megafauna) for several deep ocean locations in the Atlantic and the ecological relationships between the distribution of these 3 major size groups, for which data are seldom obtained at the same time and at the same location; (2) the relationship between these faunal abundances and the mean local organic carbon supply.

Most of the faunal abundance data discussed in this paper were reported elsewhere and reprocessed for a general analysis of deep-sea community structure by Sibuet (1987). The present work is a synthesis of the quantitative data obtained during several deep-sea biology cruises in the Atlantic Ocean undertaken in the framework of deep-sea ecology programs at IFREMER. Each site, as described by Dahl *et al.* (1977), Laubier and Sibuet (1979), Dinet (1980), Khripounoff *et al.* (1980), Sibuet *et al.* (1982), Sibuet *et al.* (1984), Sibuet (1985), Dinet *et al.* (1985), Sibuet and Segonzac (1985), Sibuet (1987) has its own faunal characteristics and variability, but here we examine general trends which imply various degrees of simplification of the system studied.

2. Methodology

a. Sampling. Seven deep-sea geographical areas were explored in the Atlantic Ocean since 1972 (Fig. 1): the Norwegian Sea (N), the Bay of Biscay (B), the Porcupine Seabight (P), the Vema Fracture Zone (V), the Demerara Basin (D), the Cape Verde (C), Angola and Cape Basins (W). During these cruises, an intensive sampling program was conducted using two box corers: a Reineck corer (600 cm²) and a modified USNEL spade corer (2500 cm²), a 5 m wide beam trawl and photographic surveys using a variety of equipment such as Troika and R.A.I.E. (Remorquage abyssal d'instruments pour l'exploration). Since 1984, a 6000 m deep inhabited submersible (*Epaulard*), developed by IFREMER, was employed to obtain an extensive coverage by bottom photography (Sibuet *et al.*, 1985).

In the first part of this study, we consider the quantitative data on deep-sea meio- and macrofaunal abundances from USNEL box cores. In this case, the number of samples (Table 1) was sufficient for the determination of the mean and standard deviation for each area. Data from the Vema Fracture Zone are excluded from this discussion because the methodology used for meiofaunal abundance analyses was different (Dinet *et al.*, 1985), and the location in a fracture zone with strong easterly

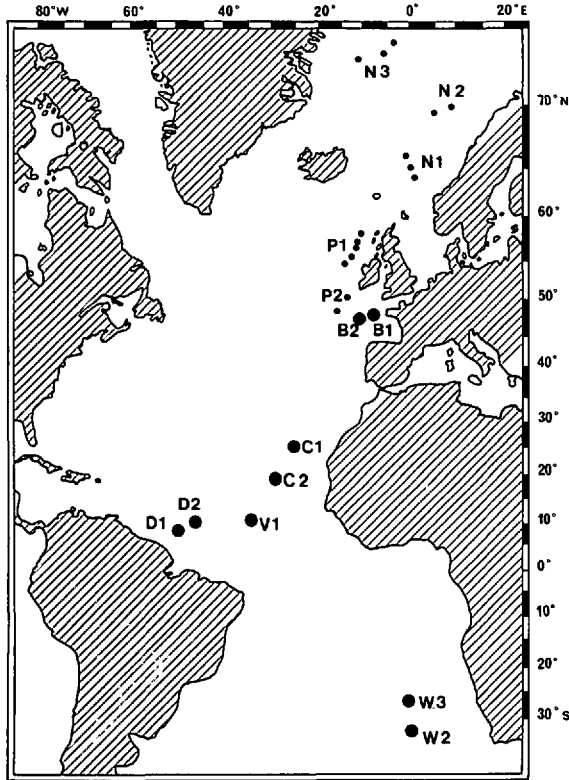


Figure 1. Location of the different abyssal stations studied by the Deep-Sea Ecology Group at IFREMER quoted in this study.

currents is not representative of abyssal plain environments (Khripunoff *et al.*, 1980). In the second part, we use data from samples taken by REINECK as well as USNEL corers. As these two instruments do not have the same sampling efficiency (Dinet *et al.*, 1985), no standard deviations from the mean were calculated.

The trawl transects were used to study the megafauna which corresponds to the large-size organisms generally observed on bottom photographs. This larger size group, not well defined and characterized by relatively low densities, cannot be sampled quantitatively with corers. Abundances were estimated from the width of the trawl and the length of the tract on the bottom determined by acoustic positioning. This gives only a relative value and is not considered as an "absolute" measurement. Indeed, the data obtained from photographs taken with instruments such as the RAIE, Troïka or Epaulard reveal that the trawl usually underestimates the density of large animals (Rice *et al.*, 1979; Sibuet and Lawrence, 1981; Sibuet *et al.*, 1984). However, the trawl and photographic megafaunal data at our most intensively worked stations (Bay of Biscay, Cape Verde, Demerara abyssal plain) were found to be of the same order of

Table 1

Geographic area Name of the cruise	Station	Depth m	Number of cores (1)	Number of trawls
Bay of Biscay				
BIOGAS 1972-74 and	B1	1900	16*	9
BIOGAS 1978-81	B2	3000	17*	3
Demerara Plain				
DEMERABY 1981	D2	4420	8*	6
Cape Verde Basin				
SEABED 1981	C1	5190	6*	6
	C2	4950	7*	2
Vema Fracture Zone				
VEMA 1977	V1	5100	8*	3
Norwegian Sea				
NORBI 1975	N1	2600-3600	3	6
	N2	2900-3200	2	4
	N3	2500-3700	4	4
Porcupine plain				
INCAL 1976	P1	2650	2	2
	P2	4820	1	2
Cape and Angola Basins				
WALVIS 1979-80	W2	4650	4	4
	W3	5250	9	4

(1) REINECK corer was used, unless indicated by *, where a USNEL was used. See Methodology. Locations are indicated on Figure 1.

magnitude (Sibuet, 1985; 1987). We therefore consider that the data obtained from the trawls for some zoological groups can be used for comparative purposes (Sibuet, 1987).

For core samples, the precision of the data, which is a function of the sample size was tested (Jumars, 1976). Detailed reports were given in Dinét and Vivier, 1977; Dinét, 1980; Sibuet *et al.*, 1984; Dinét *et al.*, 1985. For the most heterogeneous stations in the Bay of Biscay, 17 cores (retrieved with undisturbed sediment) were obtained. The number of cores necessary to calculate a significant value of the density for the macrofauna was estimated to be between 5 and 9 cores, depending on the spatial distribution of the species. For the meiofauna, nearly 20 subsamples are necessary, due to the subsample size (5.31 cm²) and their heterogeneity (Dinét *et al.*, 1985). The detailed sampling methodology was extensively described elsewhere (Rowe and Sibuet, 1983; Sibuet *et al.*, 1984; Laubier and Monniot, 1985).

b. Definition of the benthos size groups considered. The benthic fauna is divided according to the conventional size categories in conjunction with the method used for sampling and processing. Schwinghammer (1981, 1983), for instance, demonstrated

that the size groups of benthic fauna should correspond to a characteristic biomass spectrum and to distinct types of habitat.

For the meiofauna, subsampled with a tube of 5.31 cm² surface, the lower size limit corresponds to the definition of Thiel (1975), Vitiello and Dinét (1979) and Dinét (1980) that is > 40 µm mesh size sieve.

For the macrofauna sampled with the box corer, the lower limit was 250 µm mesh size. For all samples, the density of macrofauna was corrected for the number of individuals usually considered as belonging to taxa of the meiofauna (nematodes, ostracods and copepods). The final number obtained in this way (macrofauna *sensu stricto*) shows a closer relationship between abundance and biomass. Indeed, the number of nematodes larger than 250 µm is variable and can constitute up to 50% of the total number of individuals on a sieve. In terms of biomass, however, this large meiofauna was shown to be less than 10% of the total macrofaunal biomass (Khrifounoff, 1979).

For the trawled megafauna, we consider only the large size taxa. The general feeding types of the various taxa allow us to define three major categories: deposit feeders, suspension-feeders (sessile fauna) and swimming carnivores. In this study we consider only the deposit-feeders and swimming carnivores; we have not taken into account the relatively sparse attached filter feeders (hydroids, bryozoans, sponges, actinarians, brachiopods, cirripeds, crinoids, tunicates) because of the scarcity of hard substrates in the study areas, the very low efficiency of trawling for these groups and the dependence on the occurrence of filter feeders in the bottom currents.

3. Results

a. Relationships between the various size groups. The data on faunal abundance reveal the following range of variability in each identified size category.

- 6.6 to 7.2 ind.cm⁻² for the minimum and maximum meiofaunal mean density,
- 106 to 1200 ind.m⁻² for the minimum and maximum macrofaunal mean density,
- 4 to 11940 ind.10⁴m⁻² for the minimum and maximum megafaunal mean abundance.

The densities obtained for the meiofauna and for the macrofauna varied by a factor of 10 and the macrofaunal mean density was three orders of magnitude lower than that of the meiofaunal mean density. The relative estimates of the abundance of the trawled megafauna considered here for the various Atlantic stations showed greater variability. The deposit feeders showed the largest range of variability (10³), whereas the swimming carnivores exhibited a range of variability of 50.

The relationship between the density of the meiofauna and the macrofauna is shown in Figure 2 for the stations which were studied with the most comparable intensive

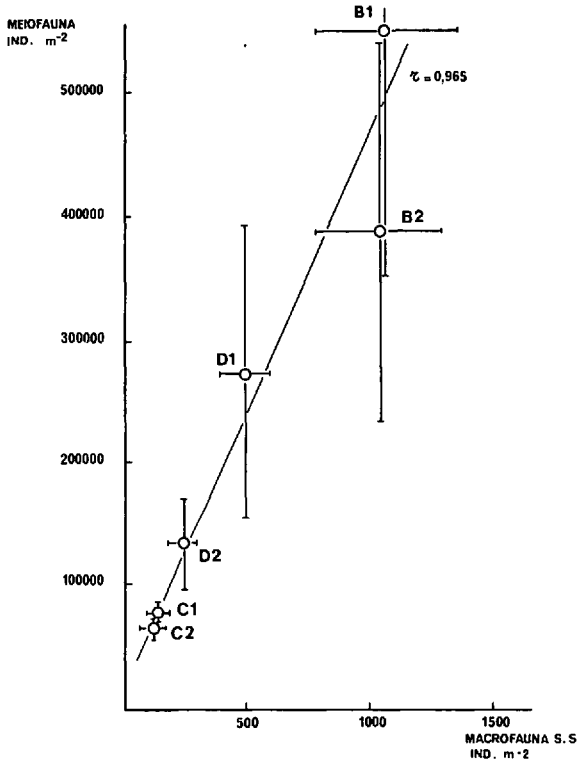


Figure 2. Meiofauna vs macrofauna (*sensu stricto*) abundances at 6 Atlantic abyssal sites (Fig. 1 and Table 1) where the USNEL corer was used.

sampling and sorting strategy. For stations in the Bay of Biscay (2000 and 3000 m), Cape Verde and Demerara Basins (more than 4000 m), there is an excellent linear correlation ($r = 0.96$).

Data on the biomass are extremely difficult to obtain. The limited data obtained on dry weight biomass by subsampling at a few stations are shown in Figure 3. In this figure the macrofauna is taken *sensu stricto*, excluding the meiofaunal taxa greater than the 250 μm mesh size. The meiofaunal biomass is evaluated as the sum of biomasses of individuals greater than 40 μm mesh size plus that of the meiofauna taxa sampled in the macrofaunal samples. The plots of biomass in two size groups in the Demerara and Cape Verde basins indicate that there is a strong correlation between the meiofaunal and the macrofaunal biomass with a slope near 2 (1.96). It is well known that meiofaunal densities remain important with depth (Dinet, 1980; Thiel, 1983) compared to a major decrease in macrofaunal abundances (Rowe, 1971). However, in terms of biomass the macrofauna is still more important than meiofauna in abyssal plains—roughly two times. The biomass of the large meiofauna (> 250 μm)

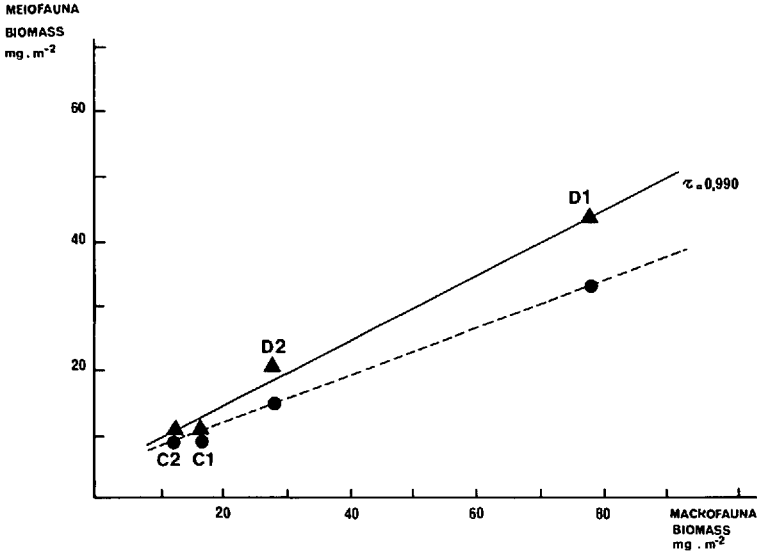


Figure 3. Biomass of macrofauna *sensu stricto* vs meiofauna; triangle: small + large meiofauna; circle: small meiofauna only (40 to 250 μm). The taxa of the meiofauna larger than 250 μm : nematods, copepods, ostracods constitute 20–25% of the meiofauna.

consists of a constant fraction of the total meiofauna (20% to 25%) as indicated by the differences between the symbols shown in Figure 3. Moreover, there is no trend indicating an increase of one group versus the other in poorly populated environments. This is rather surprising as decrease of macro versus meiofaunal with depth has been shown by Thiel (1983) and Snider *et al.* (1984). However, our abundance relationship (Fig. 3) concerns mainly stations situated at more than 4000 m with the exception of the two Bay of Biscay stations. We do not have a relevant set of data to reassess the usual relationship with depth and indeed this was not our strategy. The standard deviation of B_1 and B_2 (Fig. 2) precludes any significant differentiation with the other stations. We intend to show (Section 3b) that the observed relationship is related to food availability.

Megafaunal abundance is seldom obtained together with the abundance of the other size groups. Our data permit an examination of their relationship with the two other size groups. Thus, Figure 4 shows that although megafaunal densities are highly variable at the different sites, the deposit-feeder density is related exponentially to meiofaunal densities. Because of the relationship shown in Figure 2, similar relationships could also be shown with macrofaunal abundances. The correlation between carnivore megafauna and meiofauna (Fig. 4) is less significant. It has been shown (Sibuet, 1987; Mahaut *et al.*, 1989) that this category has to be studied in more detailed subsets related to their mobility and feeding strategy.

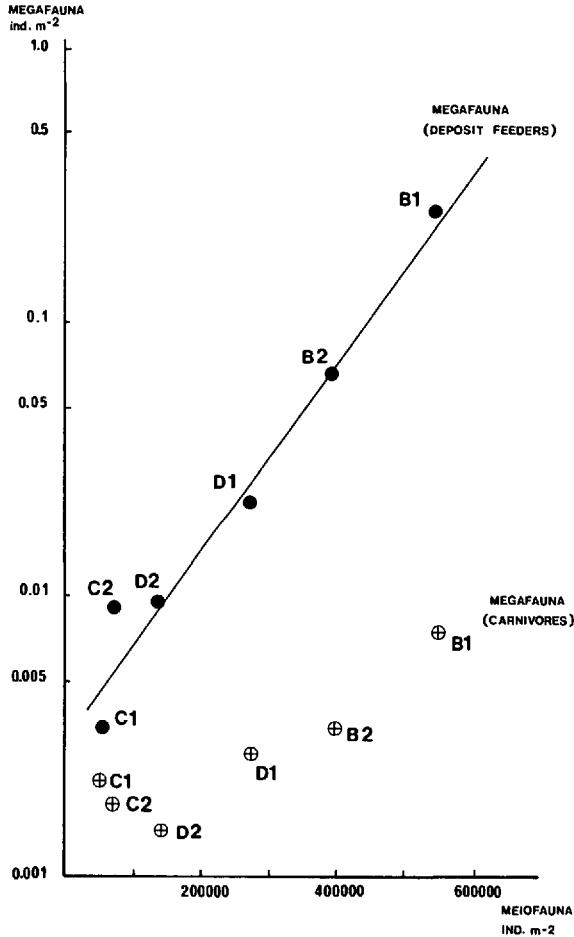


Figure 4. Meiofauna vs. megafauna abundances. Megafauna data on a log scale: Deposit feeders ($r = 0.998$); carnivores.

b. Faunal abundances and carbon supply. As indicated in the introduction, one can expect a relationship between faunal abundances as quantified in this study and the organic carbon supply to the sea floor. To test this hypothesis, we should estimate the various trophic inputs in each geographic area.

How can we evaluate the flux of organic matter available to benthic populations? The first intuitive approach would be to use the primary productivity above each region to get an approximate idea of differences between the origin of food supply. Such data are not available with a suitable precision. It has been estimated that 6% of the primary productivity is transferred from the photic zone to subsurface waters (Wollast, 1981). During their fast settling through the water column, particles undergo remobilization

and degradation (Hargrave, 1985). Only a small fraction of the initial productivity reaches the sediment. It has been shown, however, that the variations of the organic flux at all depths correlate with the variations of primary productivity (e.g. Deuser *et al.*, 1981). The loss of carbon in the water column is related to the importance of degradation and consumption; e.g., by opportunistic consumers (Roe, 1984; Heyraud *et al.*, 1988) and related to the local depth and the sinking velocity. There is therefore a relationship between the primary productivity and the organic matter reaching the seafloor which is by far more important than the quantities of organic matter accumulated in surface sediment. This explains why abundance and organic matter in surface sediments are poorly correlated (Sanders *et al.*, 1965; Khripounoff, 1979).

Recent understanding of how carbon reaches the sediment as well as deep-sea studies using submersibles (Sibuet, 1987) have drawn attention to the possibility that most of the organic matter reaching the interface is consumed before burial within a few months (Honjo *et al.*, 1984; Sibuet *et al.*, 1984).

A quantitative approach was done by Bender and Heggie (1984) showing that more than 90% of the organic carbon reaching the seafloor is readily reduced by oxygen. Contrarily to what happens in coastal zones, the secondary oxidants (NO_3^- , Mn O_2 , Fe_2O_3 , SO_4^{2-}) occurring within the deep sediments oxidize only a small fraction of the raining organic carbon in pelagic environments (Bender and Heggie, 1984).

In order to estimate the organic matter available to the benthic fauna, the ideal therefore would be to use sediment traps just above the bottom, but there is no extensive data set as yet in the Atlantic. Sibuet *et al.* (1984) and Khripounoff and Rowe (1985) have shown that by comparing sediment traps and surface sediments samples, about 85% of the raining organic carbon was utilized before burial. This implies that the organic carbon within the surface sediments mainly represents what the biomass did not consume and not, as previously thought, what is available for consumption. However the flux of carbon buried is still related to the rain of carbon. According to Bender and Heggie (1984), this relation could still hold with a maximum uncertainty of a factor of 4. Indeed 0–5 to 2% of the organic carbon reaching the seafloor is finally preserved in the sediment. We will make the assumption that the preserved carbon flux in the sediment is proportional to the carbon consumed by the biomass at the sediment water interface. The second assumption is that the sedimented carbon is homogeneously preserved. Reimers and Suess (1983) have shown that a large fraction of the settling organic matter is buried and oxidized within the sediments. Since most of the raining organic carbon is then remineralized, we can neglect in our calculations the variations in organic carbon percentage at the surface of the sediment and consider, as a first approximation, the average of remaining organic carbon over the Holocene period to calculate an average burial flux of carbon. The very low percentage of organic carbon which resides in surficial sediments can grossly represent the fraction preserved since the beginning of the Holocene. The average burial (or sedimented) flux of carbon during the Holocene (Table 2) is therefore grossly

Table 2

Stat.	Depth m	Sed. rate cm. 10^{-3} yr	Dry. sed. density $g \cdot cm^{-3}$	POC $mg \cdot g^{-1}$	POC $mg \cdot cm^{-3}$	C.FLUX $mg \cdot m^{-2} yr^{-1}$
B1	1900	2.0(1)	0.6	5.1(7)	3.1	61
B2	3000	2.0(1)	0.5	4.0(7)	2.0	40
D1	4420	1.8(1,2)	0.5	5.5(1,8)	2.8	50
D2	4850	0.4(1,2)	0.6	4.3(1,8)	2.6	10
C1	5190	0.7(1)	0.7	2.5(1)	1.8	13
C2	4950	0.9(1)	0.7	2.5(1)	1.8	16
V1	5100	1.0(3)	0.3	5.5(9)	1.7	17
N1	2600-3600	1.9(4)	0.7	6.5(7,10)	4.6	86
N2	2900-3200	1.9(4)	0.7	5.4(7,10)	3.8	72
N3	2500-3700	1.9(4)	0.7	6.6(7,10)	4.6	88
P1	2650	2.6(5)	0.5	4.8(11)	2.4	62
P2	4820	2.6(5)	0.5	3.1(11)	1.6	40
W2	4650	0.8(6)	0.5	3.4(11,12)	1.7	14
W3	5250	1.0(6)	0.5	1.6(11,12)	1.0	10

See references hereunder.

(1) Mauviel, 1982; Mauviel *et al.*, 1982.

(2) Bé *et al.*, 1976.

(3) Damuth, 1977.

(4) Streeter *et al.*, 1982; Duplessy *et al.*, 1975; Duplessy *et al.*, 1980; Moyes *et al.*, 1977.

(5) Grousset, 1983; Grousset and Chesselet, 1986.

(6) Auffret, pers. comm.

(7) Laubier and Sibuet, 1979; Khripounoff *et al.*, 1985.

(8) Sibuet *et al.*, 1984.

(9) Khripounoff, 1979; Khripounoff *et al.*, 1980.

(10) Dahl *et al.*, 1977.

(11) Dinet, 1980; Le Coz, pers. comm.

(12) Khripounoff, pers. comm.

estimated from

$$F_{POC} = (POC) \times S$$

Where *POC* is the mean organic carbon concentration in the surface sediments per cubic centimeter, and *S* is the rate of sediment accumulation during the Holocene, estimated by measurements of ^{230}Th , ^{221}Pb (done by gamma spectrometry) or paleofaunal records. We selected the Holocene interval because it has been well identified in the large number of Atlantic locations (Table 2). A comparison between faunal abundances and the organic carbon burial flux can only indicate general trends.

Despite these uncertainties and the potential problems arising from a comparison of data representing different time scales (modern fauna vs organic carbon content averaged on a geological time scale of several thousand years), we observe in Figure 5,

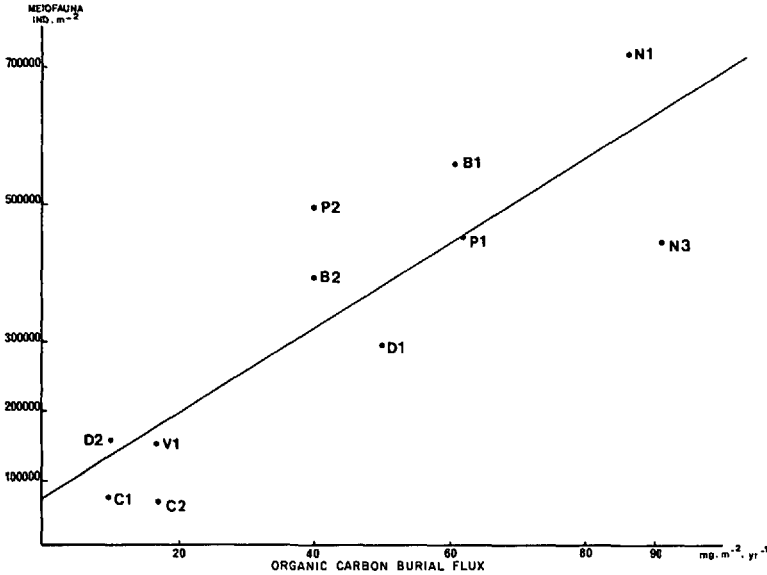


Figure 5. Organic carbon burial flux vs meiofauna ($r = 0.865$). (*): This is 0.5 to 2% of the fresh organic flux at the sediment surface (based on Bender and Heggie, 1984).

6 and 7 a good correlation between the abundances of the present fauna and the computed burial flux of organic carbon (F_{POC}). While the abundances of meio- and macrofauna are linearly related to the organic carbon burial flux (Figs. 5 and 6), the deposit feeders and carnivore abundances are exponentially related to this burial flux of organic carbon (Fig. 7).

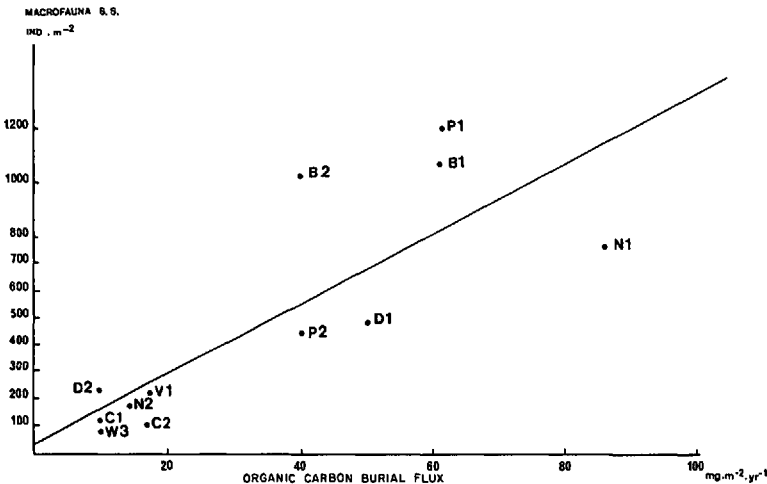


Figure 6. Organic carbon burial flux vs macrofauna ($r = 0.809$). (*) see comment Figure 5.

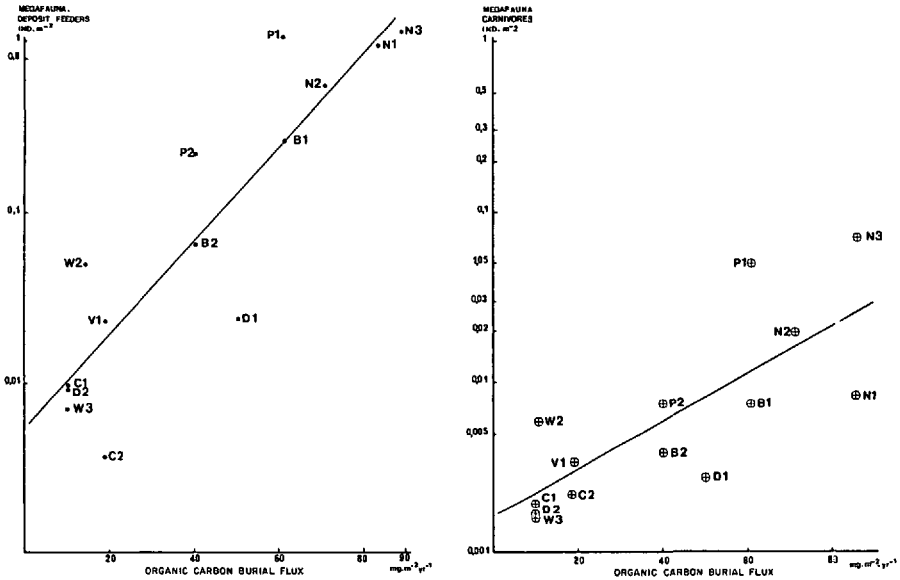


Figure 7. Organic carbon burial flux vs megafauna. (a) deposit feeders ($r = 0.895$); (b) carnivores ($r = 0.802$). (*) see comment Figure 5.

4. Discussion

The first order relationship between meiofauna and macrofauna abundances (Fig. 2) indicates either a common dependence of these groups on another factor (trophic input) and/or a real interdependence of the macrofauna and meiofauna. A decrease by a factor of 2 in meiofauna density thus corresponds to the same decrease in macrofauna density. Thiel (1975) suggests that generally the decrease in meiofauna abundance with depth is smaller than that of the macrofauna. This was not observed in these deep abyssal environments. The interdependence of the two groups, for example the use of the meiofauna as food by the macrofauna, cannot be excluded, although little is known about the trophic relationships between the meio- and the macrofauna in the deep sea (Rex, 1981). This point has also been theoretically discussed by Hessler (1974). On the other hand, it is generally believed that meiofauna use food resources that are also part of the diet of macrofaunal deposit-feeders (Schwinghammer, 1983). If this is the case, we then observe a balance in the utilization of food resources as the biomass of the two groups increases or decreases. These two size groups also show direct relationships with the trophic input as was shown in the second part of this work by our organic carbon flux calculations. This seems to confirm that the first order relationship between meiofaunal and macrofaunal abundances is more likely due to this common direct relationship with the food input than a result of any close interaction between these two size groups. However, as we know that such interaction probably does exist, (for example part of the meiofauna could use small debris or

dissolved organic matter, the meiofauna/macrofauna ratio could also be interpreted as the net result of these trophic interactions.

The megafauna exhibits exponential relationships with the meiofauna and the macrofauna. Deposit-feeder abundances range over a factor of 100 (Fig. 4), whereas meio- and macrofauna vary by a factor of 5. An exponential relationship is found as well between deposit-feeder abundances and trophic input. Carnivores exhibit the same type of relationship with a shallower slope shown in Figures 4 and 7b in each case. Carnivores feed not only on bottom fauna but also in the water column on different types of prey including large carcasses of pelagic animals. The relationship between megafauna and the trophic input certainly is the most indirect of all the faunal groups studied here. This may be due to a lower foraging efficiency of the megafauna and/or the tendency of megafauna to aggregate when they occur in greater number. The megafauna may also have a different metabolic cost than the macrofauna and meiofauna and are thus less able to efficiently exploit food resources, particularly in nutrient-poor environments. When food is more abundant, megafauna aggregation poses sampling and statistical problems, masking the exact relationship between their abundance and the food input.

Using our biomass data (Fig. 3) and the organic carbon burial flux data (Figs. 5, 6), one can approximate the flux of new organic carbon that would be necessary to sustain these populations. We use the Bender and Heggie (1984) relationship where sedimented carbon flux represents 0.5 to 2.0% of the new carbon flux. For example, a permanent biomass of 50 mg.m^{-2} (meiofauna + macrofauna at D2 on Fig. 3) would be sustained by a flux of $10 \text{ mg.m}^{-2}.\text{yr}^{-1}/0.005$ to $0.02 = 0.5$ to $2 \text{ g.m}^{-2}.\text{yr}^{-1}$ of fresh carbon, which is in good agreement with the fluxes calculated and quoted by Suess (1980) at the sediment-water interface at similar water depths and by Vangriesheim and Khrpounoff (1989) from sediment trap measurements in the Bay of Biscay ($1.6 \text{ g org.C m}^{-2}.\text{yr}^{-1}$).

An important parameter is thus introduced by the organic carbon flux calculation and its relationship with the faunal abundances. The settling carbon seems to be the main factor controlling the biomass distribution at various trophic levels. This may be the explanation for the high correlations we observed in this study.

5. Conclusions

The first comparison of the abundances of the three major size groups of benthic fauna at several deep Atlantic stations and their relationships with carbon input leads to the following conclusions:

1. There is a constant proportional relationship between the faunal abundance of the different size groups for all the locations studied. This possibly indicates the occurrence of a dynamic equilibrium between these groups.
2. The pattern of the abundance of megafauna differs from meiofaunal and

macrofaunal abundances. The first order relationship between meiofauna and macrofauna abundance can be explained by a direct relationship with a common trophic input. The megafauna on the other hand exhibits exponential relationships with the two other groups and with the organic carbon input. The situation for the megafauna is less definable, possibly as a result of different metabolic costs and a lower foraging efficiency.

3. The flux of organic carbon settling in the water column at the sediment interface is the first order parameter which controls the biomass distribution in the deep Atlantic Ocean.

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