Full-depth zooplankton profiles over the deep bathyal of the NE Atlantic*

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ABSTRACT: Vertical profiles of zooplankton (size range less than 5 mm) were taken with a 1 m^2 MOCNESS (333 µm mesh aperture) from the > 4000 m water column at 2 sites in the NE Atlantic. In the upper 1000 m, the profiles tended to exhibit high variability and were influenced by diurnal migrations, but below, the distributions were nearly similar. The standing crop in the upper 400 m was remarkably low, possibly due to a bloom of salps and their grazing pressure on the phytoplankton crop. The non-linear decrease of the normalized zooplankton abundance and biomass below 1000 m in the area investigated could be approximated by a power function. The improved regression 'model' revealed no differences between the slopes when compared to biomass data from other marine locations given by various authors. This indicates that the processes of vertical material flux seem to be similar in many bathypelagic systems of the open sea. The y-intercepts, however, showed differences due to either a higher surface productivity in some ocean areas or differences in sampling methods and evaluation of the material. Possible causes which may have led to less of a decrease in zooplankton abundance at greater depths (below 2500 m) such as food supply, resuspension, upward flux, faunal changes and trophic interactions are discussed.

INTRODUCTION

In the course of the BIOTRANS programme (Pfann-kuche et al. 1990) 2 deep sites in the temperate NE Atlantic were investigated. Special attention was given to small-scale zooplankton distribution below the epipelagic zone. Only a few papers from the NE Atlantic (Angel & Baker 1982, Roe 1988, Roe et al. 1990), the Mediterranean Sea (Weikert 1990, Weikert & Trinkaus 1990) and the Red Sea (Weikert 1982) present quantitative studies below 1500 m at depth sampling intervals ≤ 500 m. Quantitative data from below 6000 m are still rare and generally based on relatively coarse 1000 to 2000 m sample steps (see Vinogradov 1968, Vinogradov & Tseitlin 1983 and literature quoted therein).

The aim of this paper is to present data on the bathymetric distribution of zooplankton and zooplankton standing crops over a depth of 4500 m and to compare these 'fine'-scaled data with those from previous studies at greater depths. The distribution of the zooplankton in the bathypelagic zone is discussed with a view to its description by 2 regression 'models'. Data on the distribution of specific taxa which are involved will be published elsewhere.

MATERIALS AND METHODS

Zooplankton was sampled throughout the water column during Cruise 06, Leg 7A/B, of the RV 'Meteor' at 2 deep oceanic sites in the NE Atlantic: the BIOTRANS area (between 47°N, 19°W and 47°30′N, 20°W; Pfannkuche et al. 1990) and the European Community (EC) station northeast of the BIOTRANS area at 48°50′N, 16°30′W (Fig. 1). The hydrography of the BIOTRANS area was well explored during the NOAMP project (Northeast Atlantic Monitoring Program; Mittelstaedt et al. 1986). Typical for the deep open sea, it exhibits a stable hydrographic environment. Different types of water masses were identified by CTD measurements: surface water from 0 to 150 m, North Atlantic Central water between 150 and 650 m, Mediterranean water between 650 and 1250 m, Labrador water from 1700 to 2000 m, Middle North Atlantic Deep water between 2300 and 2800 m, and bottom water below 4000 m.

Stratified oblique tows were carried out with a 1 m^2 MOCNESS (multiple opening/closing net and environmental sensing system; Wiebe et al. 1985) at standard depth intervals (Table 1). The MOCNESS was equipped with 9 black nets, which could be opened and closed sequentially at discrete depths. The 333 µm mesh nets are not expected to collect animals smaller
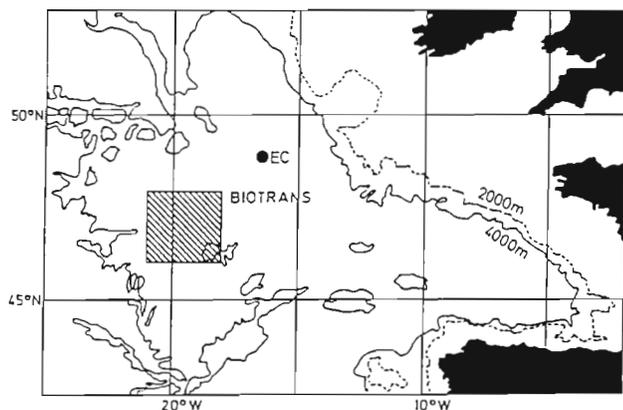
Fig. 1. Sampling sites in the NE Atlantic

than 1 mm quantitatively (e.g. Barnes & Tranter 1965, Böttger 1987). The water volume filtered was estimated by a calibrated flowmeter and corrected for the net frame angle and the angle of the oblique haul through the water. The flowmeter failed in 3 tows (marked with an asterisk in Table 2). For these tows the volume of water filtered was estimated by a geometric formula (Beckmann 1988). The mean filtered volumes and their

standard deviation of each fishing stratum are shown in Table 1.

Table 2 summarizes the sampling time and procedures at the 2 sites. In the BIOTRANS area (water depth ca 4500 m), a day profile was taken from the surface to 3300 m; at night, 1 profile was taken from 10 m to 4460 m and a second one from 400 m to 1650 m. From the EC station (water depth ca 4800 m), a day profile was available from 150 m to 4000 m. Due to large sampling times, the profiles were composed of shorter profiles from different days. Day and night differences can be disregarded below 700 m (Angel 1979) and 1000 m, respectively (Angel et al. 1982, Longhurst et al. 1989). In our data, there was also no difference evident between the day profiles below 1000 m in the BIOTRANS area and the EC station. Therefore, these data from both sites were combined into a single profile (see Fig. 2b, c).

The plankton samples were preserved in a 4 % seawater-formaldehyde solution buffered with hexamethylenetetramine. The material was sorted in a fluid composed of 0.5 % propylene phenoxetol, 5 % propylene glycol and 94.5 % tap water (Steedman 1976).

The metazoa of the mesozooplankton (upper threshold length 5 mm; see Weikert & Trinkaus 1990) were wet weighed after Tranter (1962). This method allows the subsequent specific analysis of the bathypelagic samples, which were too small in order to make aliquots for a more precise dry weight or carbon determination. Large samples from the upper 1000 m were split by a whirling vessel (Wiborg 1951) into fractions of tenths or hundredths before being sorted. Exoskeletons and carcasses, excluded from the counts, were discriminated according to Wheeler (1967) and Weikert (1977) together with large-sized flocculent material. The composition of this material (phytoplankton, faeces, radiolaria) was similar to that described for the same area from the sea-bottom (see Thiel et al. 1988/

Table 1. Standard sampling intervals in the water column and the mean filtered volumes. SD: standard deviation; n: no. of samples

Strata (m)	Sample intervals (m)	Mean filtered volume (m³)	SD	n
0–450	50	350	185	24
450–1050	150	1100	360	16
1050–2250	200	1370	526	21
2250–3000	250	1930	425	11
3000–5000	250 or 500	2270	981	11

Table 2. Station data. B: BIOTRANS-area; EC: European Community station; (D): Dayhaul; (N): Nighthaul

Haul	Date	Local time	Area	Depth range (m)
MOC-13	11 Apr 88	00:40–01:22 (N)	B	1650–3600
MOC-14	11 Apr 88	13:41–17:45 (D)	B	1450–3300
MOC-15	13 Apr 88	21:32–23:49 (N)	B	400–1650
MOC-16	14 Apr 88	02:57–03:50 (N)	B	10– 400
MOC-17	17 Apr 88	00:48–02:50 (N)	B	400–1650
MOC-18	17 Apr 88	11:18–14:09 (D)	B	400–1650
MOC-20*	22 Apr 88	13:48–14:31 (D)	B	0– 450
MOC-21*	4 May 88	10:18–14:30 (D)	EC	1850–4000
MOC-22*	5 May 88	12:55–15:35 (D)	EC	400–1650
MOC-23	6 May 88	14:00–14:32 (D)	EC	150– 450
MOC-24	10 May 88	00:08–04:23 (N)	B	2750–4460

* Filtered volumes estimated by a geometric formula (Beckmann 1988)

1989). The formation of our material during a bloom of phytoplankton and salps justifies use of the term phytodetritus (Billett et al. 1983, Rice et al. 1986, Thiel et al. 1988/1989). The wet weight of this material was estimated as described above and subtracted from the zooplankton biomass.

The phytodetritus and zooplankton biomass and the animal counts were standardized to a per 1000 m^3 basis and plotted on a logarithmic scale with depth. The mean values and their ranges, if available, are presented at the midpoints of the sampled depth intervals.

RESULTS

Total zooplankton and biomass

In the BIOTRANS area, zooplankton was concentrated during the day in the upper 50 m (ca 80 000 ind. 1000 m^{-3}; Fig. 2a). Numbers decreased to ca 22 500 ind. 1000 m^{-3} at a depth of 200 m, and then increased again to a maximum of more than 90 000 ind. 1000 m^{-3} at 350–400 m. Below 400 m there was a fairly steady decrease in numbers down to 1000 m (2000 ind. 1000 m^{-3}).

The day profile from the EC station commenced at 150 m. The depth-related decrease of zooplankton was more gradual than in the BIOTRANS area. The maximum value in the mesopelagic zone was moderate (ca 55 000 ind. 1000 m^{-3}) and was recorded at 200–300 m.

The night profile in the BIOTRANS area exhibited the highest concentration in the upper 50 m (ca 280 000 ind. 1000 m^{-3}), which was followed by a rapid decrease to 35 000 ind. 1000 m^{-3} between 100 m and 150 m. Below 150 m the gradient was similar to that of the day profiles. Around 450 m, a small secondary maximum of nearly 33 000 ind. 1000 m^{-3} was detected.

In the bathypelagic zone, i.e. below 1000 m, the individual concentration by day and night decreased drastically from 4000 ind. 1000 m^{-3} at 1000 m to 200 ind. 1000 m^{-3} at 4500 m (Fig. 2b). Irrespective of the time of day there was a distinct increase in abundance at 2750–3000 m in all profiles. The mean of 500 ind. 1000 m^{-3} at this depth exceeded the value for the overlying 2500–2750 m sample interval by 230 %.

Zooplankton biomass could not be estimated for all sampling intervals due to methodology. However, a single mean profile, composed of BIOTRANS day data and, below 1000 m, additional data from the EC day station and the BIOTRANS night profile (Fig. 2c), is available to show the sequence of biomass decrease with depth.

In the upper 100 m, the biomass was ca 8900 mg 1000 m^{-3} wet weight and decreased to 2400 mg 1000 m^{-3} at 200 m depth. The principal biomass maximum of

16 800 mg 1000 m^{-3} occurred between 300 and 500 m. Within the subsequent 200 m, the biomass decreased sharply to 1200 mg 1000 m^{-3} at 700 m. Below 700 m, the decline became less with depth reaching a minimum of 100 mg 1000 m^{-3}.

DISCUSSION

Zooplankton standing crop

Biomass data from the NE Atlantic over the 4000 m water column are sparse, and published fine-scaled individual data do not exist. Our total biomass crop compares fairly well with Roe's (1988) dry weight data (320 μm mesh size), which was converted (conversion factor 1:5) into wet weight after Cushing et al. (1958), from an oligotrophic region (Madeira Abyssal Plain: 7500 mg m^{-2}; this study 6700 mg m^{-2}). Most of the zooplankton biomass (74 %) was distributed in the upper 1000 m. Angel & Baker (1982) yielded a similar ratio of some 75 % from the upper 900 m in the NE Atlantic (330 μm mesh size).

Ninety percent of the individual crop was collected in the upper 1000 m. However, as exemplified by the BIOTRANS day station, the standing crop of counts was remarkably low in the upper 400 m (17 300 ind. m^{-2} of total zooplankton; 13 960 ind. m^{-2} of copepods) as compared with data from other Atlantic regions (Table 3). This may in part be explained by the fact that in our study, only metazoans smaller than 5 mm were considered. However, this methodological difference should only affect calculations of the total zooplankton crop, not the copepod crop because the copepod fraction > 5 mm was negligibly small in numbers. In an adjacent area at 48 °N, 21 °W, Beckmann et al. (1987), using a 300 μm mesh size (multiple closing net; Weikert & John 1981), reported 41 400 to 50 700 ind. m^{-2} (total zooplankton) from the upper 400 m of a cold-core eddy. This concentration is higher by a factor of 3 than that in our study. Higher values were also found by Colman (1962) in the Bay of Biscay of the NE Atlantic (55 260 ind. m^{-2} of total zooplankton and 42 280 ind. m^{-2} of copepods in the upper 500 m) from catches with a 230 μm net. Even in the oligotrophic waters of the Sargasso Sea higher crops were found. Deevey & Brooks (1977) reported some 80 000 copepods m^{-2} in the upper 500 m of the oligotrophic Sargasso Sea using a 202 μm mesh, while the crop of the larger 363 μm net zooplankton equalled our estimate.

The low mesozooplankton abundances in our study were associated with a mass occurrence of salps (predominantly *Salpa fusiformis*) in the fraction larger than 5 mm (2130 ind. m^{-2} during daytime and 730 ind. m^{-2}

during the night in the upper 400 m). Salps are capable of ingesting particles as small as 1 µm (Harbison & Gilmer 1976). They can reduce the phytoplankton stock markedly (Deibel 1982), thus affecting the stock of other, mainly crustacean, zooplankton by competition (Berner 1957, 1967 as quoted by Silver & Bruland 1981). At the BIOTRANS site, high production rates of phytoplankton were found at the same time. Because of the grazing pressure exerted by the salps, the high production rate did not result in a high phytoplankton stock (Stienen et al. 1988). Pfannkuche et al. (1988) found fecal pellets of salps together with phytodetritus at the sea floor of the BIOTRANS area. This indicates that grazing of phytoplankton by salps had commenced some time before our study.

Gross vertical distribution of total zooplankton

Overall, the distribution of zooplankton numbers and biomass at the studied sites was similar to the biomass profiles published by Angel & Baker (1982) from 3 sites in the NE Atlantic. Especially notable is the increase of individuals in the bathypelagic zone at 2750–3000 m by an order of magnitude compared to the contiguous depth intervals (2500–2750 m and 3000–3500 m, respectively). Angel & Baker (1982) found an increase in biomass at similar depths at their 42° N station, but this increase was not detected at their station at 49° N. This may be due to the large sampling intervals of 500 m at the latter location which may have blurred the difference. The increase of individuals in our samples,
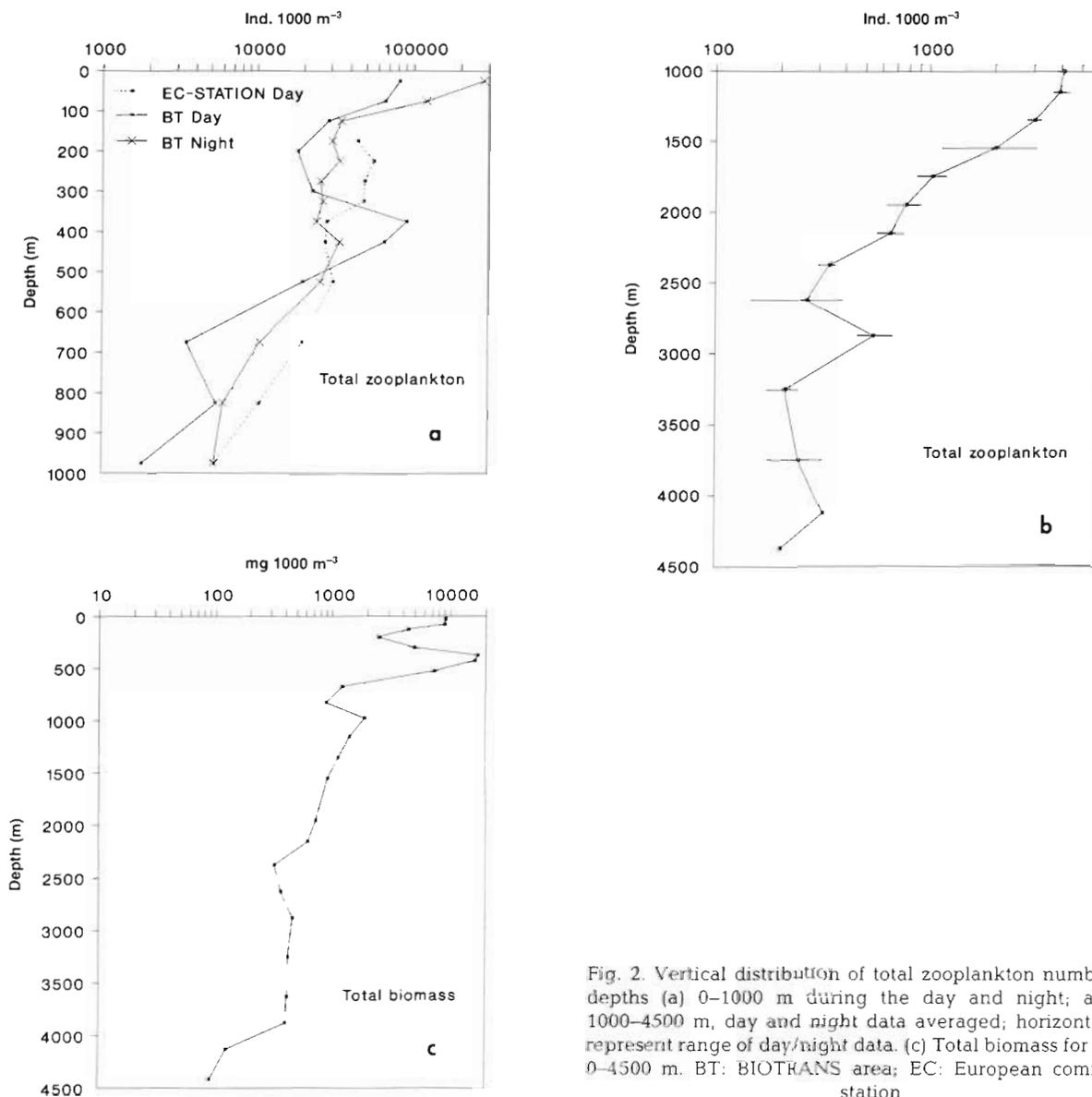

Fig. 2. Vertical distribution of total zooplankton numbers for depths (a) 0–1000 m during the day and night; and (b) 1000–4500 m, day and night data averaged; horizontal bars represent range of day/night data. (c) Total biomass for depths 0–4500 m. BT: BIOTRANS area; EC: European community station

Table 3. Standing crops (ind. m^{-2}) in the upper 400 to 500 m of different oceanic areas. TZ: total zooplankton; C: copepoda.
1: ind. < 5 mm, without Protozoa; 2: day profiles; 3: cold-core eddy; 4: mean value during a longer period

	Atlantic BIOTRANS site (this study)		Atlantic 48° N, 21° W (Beckmann et al. 1987)	Atlantic 46° 30' N, 8° W (Colman 1962)		Atlantic 32° N, 64° W (Deevey & Brooks 1977)	
	TZ	C	TZ	TZ	C	C	C
Depth (m)							
0–400	17 300	13 960	41 400 – 50 700	–	–	–	–
0–500	–	–	–	55 260	42 280	79 700	12 900
Mesh size							
(μm)	333	333	300	230	230	202	363
Remarks	1, 2	1, 2	2, 3	2	2	4	4

which is weakly indicated in the artificially composed biomass profile (Fig. 2), fell within the range of the Middle North Atlantic Deep water. This is mixed with water from the Polar Sea which has a higher oxygen and salinity content (see Harvey 1982, Mittelstaedt et al. 1986) and, as a mere speculation, may contain a larger concentration of potential food particles.

A proposed vertical distribution 'model' of zooplankton

To describe the vertical distribution of zooplankton, many authors used exponential regressions ($\log y = \log a + bx$, where y = concentration and x = depth; Wishner 1980, Angel & Baker 1982, Scotto di Carlo et al. 1984, Roe 1988, Weikert & Trinkaus 1990) probably due to the log-linear graphics introduced by Vinogradov (1968). The underlying hypothesis of this analysis is that the regression constant a is an estimate of the

productivity at the sea surface over a certain period of time and the regression coefficient b is a measure of the flux of organic material to the depth (Wishner 1980, Angel & Baker 1982).

As noted by Angel et al. (1982) and also indicated by our profiles, the variability of the zooplankton in the upper 1000 m is very high and strongly affected by its diurnal migrations, mainly by metridiniids (*Pleuromamma* spp. and *Metridia* spp.). Therefore, these data should be disregarded to avoid migration influences. However, in our study the logarithmic decline of zooplankton numbers with depth is not linear below 1000 m (test on linearity: $p < 0.001$; Sachs 1978). Also the zooplankton biomass distributions from depths > 1000 m, published by Vinogradov (1968) for the Pacific and Indian Oceans, and by Angel & Baker (1982) and Roe (1988) for the NE Atlantic, are not exponential at a closer view. However, these data could not be tested on linearity, because the sample size of the singular profiles is not sufficient for a linearity test. This means that
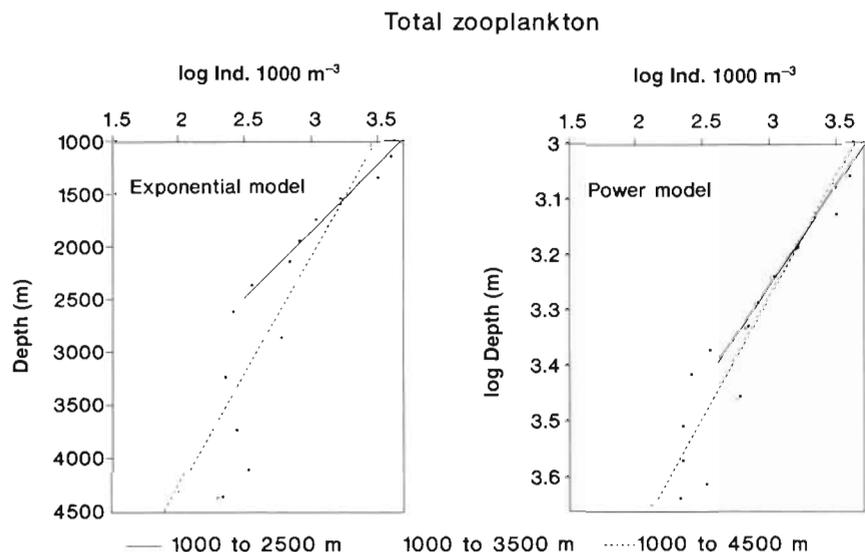
Total zooplankton

Fig. 3. Regression lines for the profiles of zooplankton numbers obtained from the exponential model (left) and the power model (right) assuming different sampling depths

Table 4. Regression analysis for the abundance profiles in Fig. 3 (for further details see text). –: depth-related quotient of slopes obtained by dividing the highest by the lowest value

Depth range (m)	F	Slope	F	95 % confidence limits	y-intercept
Exponential model					
1000–2500		-7.892×10^{-4}	1.36	$\pm\ 1.393 \times 10^{-4}$	4.440
1000–3500	1.77	-5.783×10^{-4}		$\pm\ 0.914 \times 10^{-4}$	4.131
1000–4500		-4.465×10^{-4}	1.30	$\pm\ 0.786 \times 10^{-4}$	3.905
Power model					
1000–2500		-2.805	1.09	$\pm\ 0.542$	12.115
1000–3500	1.21	-2.571		$\pm\ 0.372$	11.382
1000–4500		-2.315	1.11	$\pm\ 0.319$	10.567

the commonly used exponential regression is not appropriate to describe the decrease of zooplankton with depth. Differences or similarities between regression lines may thus be blurred by using this calculation.

We propose a power regression ($\log y = \log a + b \log x$) which is in better accordance with the measured points (test on linearity: $p = 0.014$). This is especially important when results from different sampling depths are compared. Calculating separate regressions for our individual counts assuming arbitrary maximum sampling depths of 2500, 3500 and 4500 m (Fig. 3), the slopes of the exponential regressions for the respective

depths ranges were -7.892×10^{-4}, -5.783×10^{-4}, and -4.465×10^{-4}, but for the power regressions were -2.805, -2.571, and -2.315. Calculating the depth-related quotients of the slopes for each regression by dividing the highest by the lowest values, the largest quotients were obtained from the exponential regressions (Table 4). This result also holds true for our biomass data (Table 5) and those from previous studies (Vinogradov 1968, Angel & Baker 1982, Roe 1988). The conclusion is that the regressions of the power 'model' are more similar than those of the exponential 'model' (Fig. 3), and therefore, data from different sampling

Table 5. Regression analysis of bathypelagic biomass profiles assuming different sampling depths (for further details see text). F-values calculated as in Table 4

Data (Source)	Depth range (m)	Exponential model Slope	Exponential model F-value		Power model Slope	Power model F-value	
NE Atlantic	1000–2500	-4.089×10^{-4}	1.16		-1.421	1.07	
333 µm mesh size	1000–3500	-3.532×10^{-4}		1.28	-1.521		1.13
(This study)	1000–4500	-3.194×10^{-4}	1.11		-1.605	1.06	
NE Atlantic	1000–2500	-5.843×10^{-4}	1.19		-2.020	1.16	
320 µm mesh size	1000–4000	-4.912×10^{-4}		1.60	-2.341		1.15
(Roe 1988)	1000–5400	-3.662×10^{-4}	1.34		-2.316	1.01	
NE Atlantic	1000–2500	-8.822×10^{-4}	1.73		-3.283	1.34	
330 µm mesh size	1000–3500	-5.109×10^{-4}		2.49	-2.450		1.60
(Angel & Baker 1982)	1000–4500	-3.539×10^{-4}	1.44		-2.050	1.20	
NW Pacific	1000–4000	-5.270×10^{-4}	1.44		-2.568	1.04	
380 µm mesh size	1000–6000	-3.662×10^{-4}		1.66	-2.472		1.02
(Vinogradov 1968; Table 16)	1000–8000	-3.174×10^{-4}	1.15		-2.511	1.02	
Tropical Pacific	1000–4000	-3.815×10^{-4}	1.34		-1.992	1.08	
380 µm mesh size	1000–6000	-2.848×10^{-4}		1.44	-1.843		1.04
(Vinogradov 1968; Table 18)	1000–8000	-2.643×10^{-4}	1.08		-1.921	1.04	
Indian Ocean	1000–2000	-7.618×10^{-4}	1.32		-2.766	1.08	
380 µm mesh size	1000–2500	-5.783×10^{-4}		1.50	-2.565		1.12
(Vinogradov 1968; Table 20)	1000–4000	-5.095×10^{-4}	1.14		-2.462	1.04	

depths can be compared by statistical methods. Like nearly all approximations, this calculation is not optimal. Nevertheless, it is closer to the real distribution than the previous calculations.

In the following, we apply the power regression to compare our data with those of other authors. Since data for individual numbers from below 1000 m are scarce, we used biomass data.

Wishner (1980) determined depth-related wet weight biomass from catches at 10 and 100 m above the sea bottom with a 183 µm mesh in different areas of the Atlantic and Pacific Oceans, respectively. Dry weight

Fig. 4. Regression lines for the profiles of biomass (power function) below 1000 m from different parts of the world ocean. 1: NE Atlantic (this study); 2: Atlantic/Pacific (Wishner 1980); 3: NE Atlantic (Roe 1988); 4: NE Atlantic (Angel & Baker 1982); 5: NW Pacific (Vinogradov 1968, Table 16); 6: Tropical Pacific (Vinogradov 1968, Table 18); 7: Indian Ocean (Vinogradov 1968, Table 20)

data (mesh size 320 µm) from the NE Atlantic (31° 17' N, 25° 24' W) by Roe (1988) were converted (conversion factor, 1 : 5) into wet weights after Cushing et al. (1958). Angel & Baker (1982) used displacement volumes for their data from the NE Atlantic (42° N, 17° W) taken with a 330 µm mesh. These values were converted (conversion factor, 1 : 0.73) into wet weights after Wiebe et al. (1975). Wet weight data (380 µm mesh) from the NW Pacific, the tropical Pacific and the Indian Ocean were taken from Vinogradov (1968).

Fig. 4 shows the regression lines, and Table 6 the corresponding values. The regression coefficients of the slopes are between 1.6 and 2.5. Although they seem to show a high similarity, especially between Lines 1 (our data), 2 (Wishner 1980), 3 (Roe 1988), 6 (Vinogradov 1968; Tropical Pacific) and 7 (Vinogradov 1968; Indian Ocean), significant differences exist between the regressions ($p = 0.045$, df = 6, 194, analysis of covariance: Sokal & Rohlf 1969, Weber 1986). An *a posteriori* test (Table 7) (Sokal & Rohlf 1969) shows no significant difference between the slopes of the lines. This means that the processes of material flux seem to be similar in most bathypelagic systems of the open ocean, as discussed by Wishner (1980) and Roe (1988) who applied the exponential regression. The concurrence of the slopes exists despite the use of different mesh sizes, i.e. different size groups of zooplankton were compared. However, there are significant differences between the y-intercepts of Group A [Lines 4 (Angel & Baker 1982; NE Atlantic) and 5 (Vinogradov 1968; NW Pacific)] and Group B (Lines 1, 2, 3, 6 & 7), but no differences exist within the 2 groups. These differences may result from either a higher surface productivity in some ocean areas or differences in methods of sampling and evaluation of material.

Although the power regression was found empirically, we will propose biological interpretations which may have led to less of a decrease in deep-living zooplankton at depths below 2500 m as compared to the strong exponential decrease seen at depths above 2500 m. Similar profiles were presented from the NE
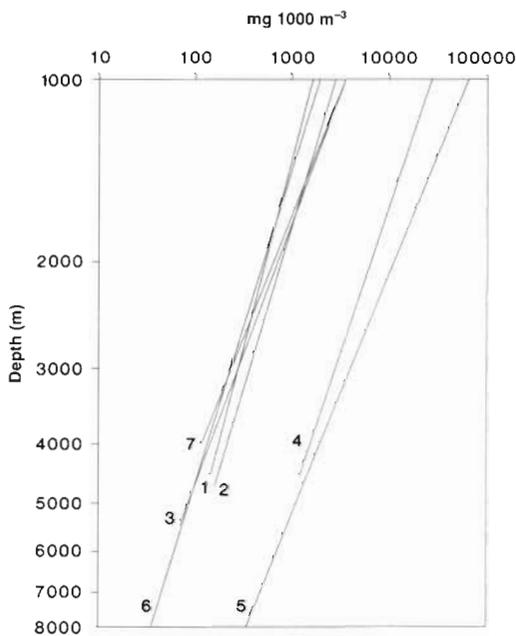
Table 6. Linear regression coefficients for biomass as a function of depth below 1000 m in the open oceans, calculated by the power function ($\log y = \log a + b \log x$). CL: confidence limits of the regression coefficients. 'No.' corresponds to profile no. in Fig. 4

No.	Area	y-intercept	Slope	95 % CL	r^2
1	NE Atlantic	8.03	−1.605	±0.429	0.640
2	Atlantic Pacific	8.99	−1.847	±0.568	0.807
3	NE Atlantic	10.50	−2.316	±0.576	0.853
4	NE Atlantic	10.58	−2.050	±0.712	0.731
5	NW Pacific	12.34	−2.511	±0.244	0.871
6	Tropical Pacific	9.05	−1.921	±0.603	0.509
7	Indian Ocean	10.94	−2.462	±0.625	0.692

Table 7. *A posteriori* test of the regressions for regional biomasses after Sokal & Rohlf (1969). The sums of squares (SQ) of the slopes are presented in the upper right triangle, and the SQ of the y-intercepts in the lower left triangle. $SQ_{crit.\ 0.05} = 0.997$. Group no. corresponds to no. and source in Fig. 4. Bold values denote significant differences

Group	1	2	3	4	5	6	7
			SQ slope				
1	–	0.023	0.259	0.073	0.725	0.072	0.287
2	0.143	–	0.079	0.012	0.224	0.002	0.112
3	0.064	0.074	–	0.024	0.027	0.094	0.008
4	**10.658**	**5.537**	**7.194**	–	0.098	0.007	0.047
5	**27.569**	**12.684**	**16.622**	0.555	–	0.417	0.001
6	0.013	0.380	0.130	**13.717**	**40.957**	–	0.129
7	0.082	0.147	0.030	**10.518**	**29.294**	0.127	–
			SQ y-intercept				

Atlantic by Angel & Baker (1982), who however did not take notice of this pattern. Not unexpected, the bathymetric distribution of zooplankton does not appear as a mere function of depth, but is likely influenced by additional factors such as faunal changes, interactions between organisms and, last but not least, food supply.

The species-specific analysis, which is still in progress, revealed that at about 2000 m a number of new species occurred among the copepod fauna, such as *Benthomisophria* spp., *Hyalopontius* spp., *Foxtonia barbatula* Hülsemann & Grice 1963 and some unidentified calanoids. Whether or not this faunal alteration is symptomatic, its relation to trophic interactions is still to be investigated. Since the concentration of organisms declines with increasing depth, predator-prey relationships are believed to be secondary to an omnivorous/ detritivorous lifestyle (Vinogradov & Tseitlin 1983) because of energetical and/or behavioural reasons (see Childress et al. 1990 for discussion of this issue).

The source of food supply to the deep sea is almost exclusively from the autotrophic surface regime. Data provided by sediment traps assumed an exponential decrease of sinking organic matter with depth (e.g. Honjo 1980, Berger et al. 1988). However, resuspension and upward flux can be seen up to 2000 m above the seabed and are induced by physical and biological agents [see discussion of Angel (1990) and literature cited therein]. The intensity and constancy of the upward flux is little understood. Without a doubt, however, a pathway from great depths towards the ocean surface exists for a variety of organisms and their ontogenetic stages which allows edible material to be recycled by their own bodies and their gut contents (Bouchet & Waren 1986, Roe et al. 1990). Smith et al. (1989) used inverted sediment traps at 2 bathyal stations in the North Pacific and found an upward flux of particles and eggs which was two-thirds of the concurrently measured downward flux, although entrapped

larvae of deep-sea euphausiids were omitted from the calculation. At some times and latitudes, upward fluxes by the seasonal release of planktonic larvae of benthic opportunists can be considered to be important (Tyler 1988); dietary studies of surface-feeding birds in the Southern Ocean revealed that up to 70 % of the food consisted of deep-sea benthopelagic animals (Ridoux & Coic 1988).

As exemplified by one profile of detrital material (phytodetritus) from our May data, there is a significant coherence (rank correlation analysis p = 0.001) between phytodetritus and zooplankton (Fig. 5). We cannot appraise how quantitatively the material was caught by nets; however, it is a first presentation of the distribution of large-sized flocculent material at bathyal depths. It has been suggested that old phytodetritus
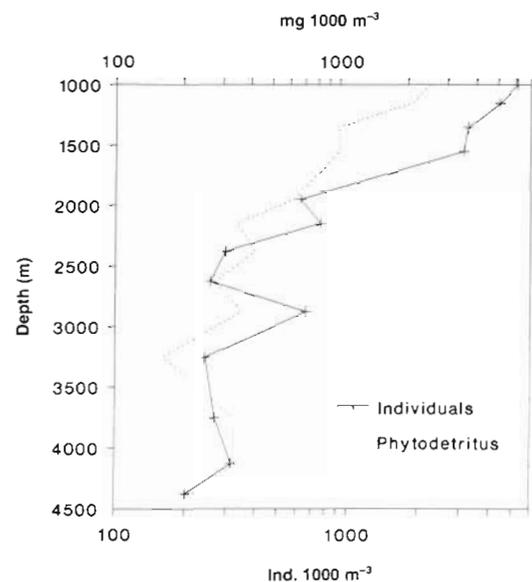

Fig. 5. Vertical distribution of phytodetritus (mg 1000 m^{-3}) and zooplankton (ind. 1000 m^{-3}) below 1000 m during May 1988

is more easily subjected to resuspension than freshly settled material (Angel 1990). The respective microscopic study of our material and cytochemical analyses is in process.

In conclusion, the tendency of 'arrested' zooplankton numbers and biomass with depth commencing at about 2000 m above the sea floor seems to be a reliable and biologically plausible feature. Theoretically, the upward flux of dead and alive particles compensates for the downward gradient of individuals and biomass until losses by predation will predominate with increasing distance to the seabed. Due to the better adaptation, which describes the obviously natural distribution pattern more exactly, the power regression should be superior to an exponential one.

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