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Size spectra of benthic biomass and metabolism

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ABSTRACT: Logarithmic size spectra of animals from subtidal silty sand sediments of Helgoland Bight and Kiel Bay corresponded with the benthic size spectrum elaborated by Schwinghamer (1981). There was a meiofauna biomass peak in size classes from 0.05 to 0.5 µg organic carbon, a trough at about 5 µg, and a biomass increase per size class towards larger macrofauna size classes. Problems are identified regarding analysis of Foraminifera biomass and sampling of juvenile macrofauna (0.1 µg to 0.1 mg organic carbon), small macrofauna (0.1 to 10 mg) and large macrofauna. Mass-specific rates of oxygen consumption, as computed by Banse (1982), were used to construct, for the Helgoland Bight Station, a benthic size spectrum by metabolism. Logarithmic size classes in the range 0.05 to 0.5 µg organic carbon (meiofauna excluding Foraminifera) and in the range 5 µg to 1 g (macrofauna) each consumed about the same amount of oxygen: an equivalent of 0.6 to 1 ml O_2 h^{-1}, calculated per m^2. For a general estimate, the size spectrum by metabolism may be a useful tool.

INTRODUCTION

Since Sheldon & Parsons (1967) established the continuous size spectrum for particulate matter in the sea, biomass spectra of pelagic organisms became the focus of a number of investigations. Biomasses of logarithmic size classes, from the smallest bacteria to the largest vertebrates, decrease from size class to size class. Kerr (1974) calculated that biomasses of 2 connected trophic levels should have a simple proportion to each other: the standing stock of prey organisms should typically be in the order of 1.2 times that of its predators, and typical prey organisms should average 5 % of the body length of their predator. Sheldon et al. (1977) established a correlation between growth rates of prey and predator, and identified the fraction eaten by predators. Silvert & Platt (1978) developed a time-dependent equation for energy flux, with the metabolic rate of organisms as a function of body size and predation as a continuous energy transfer from smaller to larger organisms, so that the energy concentrated in organisms of a certain size will later appear in larger organisms which have preyed upon them.

It is still open for discussion to what extent such generalizations and models provide a good picture of the energy flow in pelagic ecosystems. Conover (1978) points to examples of more specific size preferences and to adaptations; there are examples where a wide range of size classes are accepted as food. Furthermore, there are some problems with the models, when large organisms produce small offspring, and when small bacteria live on the carcasses of larger organisms or are attached to detritus. Unfortunately, since only a very few biomass spectra have been worked out from different ocean areas, it is difficult to verify hypotheses.

Fenchel (1969) noted the absence of 0.01 to 0.1 mg wet-weight animals in the benthos. Schwinghamer (1981b, 1983) confirmed the existence of this trough between meiofauna and macrofauna and found highest biomass per size class in bacteria size classes and in large macrofauna size classes. For zoobenthos, Warwick (1984) found highest species numbers per size class for 0.64 µg dry-mass meiofauna and 3.2 mg dry-mass macrofauna. While Fenchel (1969) argued that the trough between meiofauna and macrofauna might indicate a size range of animals too large to move within the pores of the sediment but not large enough to burrow or to move sediment particles, Warwick (1984) found a similar trough in the size spectrum of animals living in fluid mud without interstitial pores. Warwick points to different life-history characteristics which change more or less abruptly at the body size of about 45 µg dry mass.

In this paper we confirm the general shape of the benthic size spectrum, from meiofauna to macrofauna, as established by Schwinghamer (1981b). We point out some sampling problems regarding the size class

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between meiofauna and macrofauna, and we suggest differentiation between juvenile macrofauna, small macrofauna, and large macrofauna. We advocate presenting the benthic size spectrum by mass, not by volume, and not in log scale. We construct a size spectrum by metabolism and come to the conclusion that all logarithmic size classes, at least within the macrofauna, contribute the same amount to total metabolism.

MATERIAL AND METHODS

Stations. On March 25, 1980, RV 'Victor Hensen' of the Institut für Meeresforschung in Bremerhaven (Federal Republic of Germany) sampled Station '102' SSW of Helgoland in the German Bight (54°01' N; 7°49' E, 34 m water depth, silty sand). Macrofauna of this region has previously been classified as belonging to the *Echinocardium cordatum-Amphiura filiformis* association (Stripp 1969). Seasonal and year-to-year fluctuations of macrofauna at this station have been investigated since 1969 and will be documented later by E. Rachor. Meiofauna was analyzed by Juario (1975, 'silty sand station'); this station is referred to as 'Helgoland Bight Station'. On March 18, 1982, RV 'Littorina' of Kiel University (Federal Republic of Germany) sampled Station A in Kiel Bay east of Boknis Channel (45°35.5' N, 10°16.5' E, 16 m water depth, fine sand with 1.6 % clay and silt below 63 µm); this station is referred to as 'Kiel Bay Station'.

Sampling. Helgoland Bight Station was sampled with the small type (167 cm^2) Reineck box corer to a sediment depth of about 20 cm. Immediately after the core came on deck, the following subsamples were taken:

(a) 0.75 cm^2 meiofauna core, taken by plastic syringe from which the distal part had been cut off. This core was further subdivided in 1 cm horizontal layers from sediment surface to 6 cm depth. Samples were fixed with formalin to which a few drops of Rose Bengal (1 : 100 in 5 % formalin) were added. In the laboratory, the sediment of each sample (0.75 cm^3) was suspended in water and freed from finest particles by washing on a screen with 50 µm mesh. The residue was resuspended in water and, after heavy particles had settled to the bottom, the liquid containing small or light particles including organisms, was sieved through 50 µm mesh. By this conventional meiofauna procedure 2 fractions were separated from each sediment layer: light particles left on the sieve were suspended in water in a Petri dish and sorted under the dissection microscope; one quarter of the heavy grains settled from the suspension was analysed for larger Foraminifera under the dissection microscope.

(b) 25 cm^2 meiofauna core, taken with a 25 cm^2 Thiel-meiofauna-corer (Gerlach 1972): seven 1 cm sediment layers were taken from surface to 7 cm depth, and sieved through 200 µm mesh.

(c) 167 cm^2 macrofauna sample: sediment from the Reineck corer was sieved on ship board through 500 µm mesh, and the macrofauna on the sieve was collected.

(d) Large macrofauna sample: sediment sampled on the same day with two 0.1 m^2 Van Veen grabs and with six 167 cm^2 Reineck box corers (together 0.3 m^2) was sieved through 500 µm mesh. Only the large animals (more than about 0.1 g wet weight, without shells) are considered.

The Kiel Bay Station was sampled with the large type (600 cm^2) Reineck box corer to a sediment depth of 16 cm. The following subsamples were taken:

(e) Meiofauna core, taken by a plastic syringe to a depth of 8 cm and subdivided into 2 cm^3 subsamples from 1 cm layers. Sediment-layer samples were narcotized with 6 % $MgCl_2$, fixed in 1 % glutardialdehyd, and treated according to Schwinghamer (1981a): the sediment was suspended in 20 cm^3 of a mixture of sea water, $MgCl_2$, sorbitol, tris-HCl and Percoll (Pharmacia Fine Chemicals, Uppsala, Sweden; density 1.15 g cm^{-3}); the suspension was centrifuged at 2700 rpm for 20 min. The fauna was separated from the Percoll-solution by filtration on Sartorius membrane filters with 8 µm pores. Centrifugation was repeated 3 times. Animals retained on membrane filters were fixed with glutardialdehyd, stained with Rose Bengal, and investigated under the inverted microscope.

(f) 560 cm^2 macrofauna sample (sediment left after subsampling), sieved through 500 µm mesh, narcotized with 6 % $MgCl_2$, fixed in 1 % glutardialdehyd, sorted and identified.

Volume analysis.

(a) Foraminifera (Helgoland Bight Station only): for a cursory survey, Foraminifera diameter was roughly identified under the dissection microscope by comparison with a mm scale. Volumes were calculated either as spheres (small animals) or as rotation ellipsoids, assuming the diameter to be 3 times the height of the test. For closer analysis, 141 randomly sorted Foraminifera were mounted on permanent slides; their volumes were calculated by analogy with geometrical models.

(b) Nematoda: the volume of worms with unusual proportions were individually calculated according to geometrical models. Nematodes with normal body proportions were calculated according to Andrassy (1956):

$$\text{volume} = \frac{(\text{maximum diameter})^2 \times \text{length}}{1.7}$$

(c) Other meio- and macrofauna: volumes were cal-

culated from the nearest geometrical model and include the mantle cavity and the shells of bivalves.

Biomass estimates. No weight determinations were made (except for large macrofauna); all biomass data are results of rule-of-thumb calculations: soft-body volume was converted to soft-body wet mass assuming a density of 1.13 g cm^{-3}. Soft-body wet mass was converted to soft-body organic carbon equivalents (C) assuming 10 % carbon. It is evident that data calculated by this procedure are rather crude, as they do not account for varying ash and water contents of living tissues. We assumed that fraction of the volume inside the Foraminifera test which stained red with Rose Bengal to represent the soft body. For 141 individual Foraminifera an estimate was made regarding the percentage of the stained volume in relation to the total test volume; the volume of the soft body amounted to 10 to 90 % of the test volume (mean 32 %). In Bivalvia and thick-shelled Ostracoda only 50 % of the total volume was assumed to be soft body, the remainder is shell and mantle-cavity space filled with water. For Echinodermata 50 % of the total volume was calculated to account for body cavities and skeleton. Large specimens of *Arctica* were calculated according to length-weight correlations.

Scales. Sheldon et al. (1972), working with Coulter Counter particle-size distributions, introduced a logarithmic plot of biomass by volume (unit: total volume of all particles within one size class) against particle diameter. For organisms of non-spherical shape the Equivalent Spherical Diameter (ESD) was introduced. The size classes are organized according to $\log_2$ diameter (with 1, 2, 4 µm . . .). This scale is similar to the Wentworth Scale used by sedimentologists of English speaking countries: here the basis is a particle with 2 mm diameter and diameters decrease (2, 1, 0.5, 0.25 mm . . .). With only small inaccuracies, the Sheldon Scale (term introduced by Schwinghamer 1981b) and the Wentworth Scale can be integrated. This has been done by Schwinghamer (1981b) in such a way, that for smaller sizes the basis for the $\log_2$ series is a particle with a diameter of 1 µm; this scale runs to a diameter of 64 µm. The next step is 0.125 mm and continues with 0.25, 0.5 mm etc. corresponding to steps in the Wentworth Scale. While we classified organisms by volume according to this scale (Fig. 4), we preferred to classify organic carbon mass data according to a $\log_{10}$ scale with steps $10^{0.25}$, $10^{0.5}$, $10^{0.75}$ . . ..

RESULTS

Foraminifera

At Kiel Bay Station, Foraminifera were neglected because they are very scarce. Foraminifera from Helgoland Bight Station are presented in Table 1. Average Foraminifera volume in this sample was 2.1 nl; aver-

Table 1. Size classes, biomasses and estimates of metabolism of foraminiferans and permanent meiofauna at Helgoland Bight Station. Oxygen consumption q (in µl O_2 h^{-1} at 20 °C) calculated for mean individual mass w (in mg AFDW) of size classes according to log q = 0.34+0.74 log w for forams and log q = 0.73+0.76 log w for permanent meiofauna (Banse 1982: Table 1, eucaryote unicellulars, nematodes)

Size class by organic carbon	Mean mass of individual C	Mean mass of individual AFDW	Foraminifera Biomass mg C m^{-2}	Foraminifera O_2 consumption µl O_2 h^{-1} mg^{-1} AFDW	Foraminifera O_2 consumption µl O_2 h^{-1} m^{-2}	Permanent meiofauna Biomass mg C m^{-2}	Permanent meiofauna O_2 consumption µl O_2 h^{-1} mg^{-1} AFDW	Permanent meiofauna O_2 consumption µl O_2 h^{-1} m^{-2}
1.0 – 1.8 ng	1.4 ng	2.4 ng	1	10.50	10	0.1	22.84	2
1.8 – 3.2	2.4	4.3	8	9.02	72	0.4	19.86	8
3.2 – 5.6	4.3	7.6	20	7.78	156	0.0	17.32	0
5.6 – 10	7.7	13	36	6.71	241	0.7	15.12	10
10 – 18	14	24	93	5.78	536	15	13.16	197
18 – 32	24	43	198	4.97	984	23	11.46	246
32 – 56	43	76	300	4.28	1284	58	9.98	578
56 – 100	77	134	288	3.70	1066	131	8.70	1140
100 – 178	137	239	599	3.17	1899	54	7.57	409
178 – 316	243	425	716	2.73	1955	153	6.60	1010
316 – 562	432	756	695	2.35	1633	80	5.74	460
562 – 1000	768	1.3 µg	0	2.03	0	28	5.01	140
1 – 1.8 µg	1.4 µg	2.4	0	1.74	0	25	4.36	109
1.8 – 3.2	2.4	4.3	1086	1.50	1629	31	3.80	118
3.2 – 5.6	4.3	7.6	0	1.29	0	4	3.31	13
5.6 – 10	7.7	13	0	1.11	0	0	2.88	0
Total			*4040*		*11500*	*603*		*4500*

age mass, 0.07 µg C (range 1 ng to 3 µg). Of the total biomass represented by 141 randomly picked Foraminifera, 27 % was provided by 1 individual (39 nl volume, 3 µg C); 27 Foraminifera with 100 to 562 ng C individual mass and with volumes of above 2 nl represented 50 % of the total biomass, and the 113 smaller Foraminifera contributed only 23 % to the biomass.

The quantitative sorting of the 0.75 cm^2 meiofauna core resulted in 3590 'living' Foraminifera (Fig. 1); 460 individuals were found in the 5 to 6 cm sediment layer. It seems very probable that some Foraminifera were living even deeper than 6 cm in the sediment. For a total figure we calculate 52.5 million ind m^{-2}, with a test volume of 860 ml m^{-2} and a biomass of about 4.0 g C m^{-2}. Only 38 out of the total 3590 individuals had tests with more than 550 µm diameter (more than about 29 nl volume or about 1 µg C mass). Small forams below 50 µm diameter seemed to be more abundant in the surface layer of the sediment, while specimens larger than 300 µm were abundant in the 3 to 5 cm layer. Of the Foraminifera, 53 % came from the upper 2 cm layer of the sediment, but their biomass was only 31 %. Of Foraminifera biomass, 55 % was from the 3 to 5 cm sediment layer, 4 % from deeper layers.

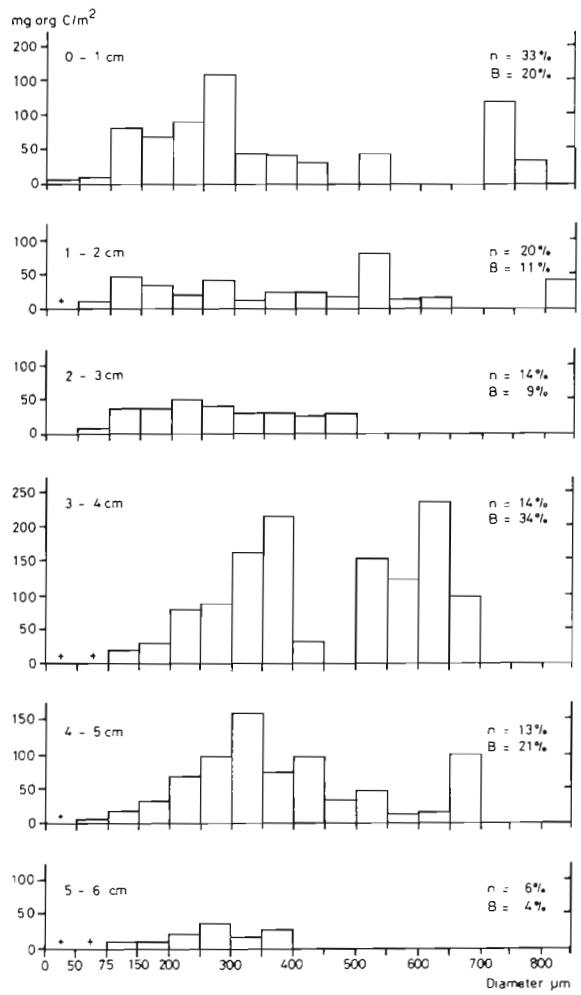

Fig. 1. Non-logarithmic size class distribution of biomass of 3590 foraminiferans found in the 6 layers of the 0.75 cm^2 core collected at Helgoland Bight Station. Volumes converted to organic carbon (C) assuming that: plasma makes up 32 % of the test volume; plasma density is 1.1; organic carbon makes up 10 % of the wet plasma mass. Values at right show percentages of abundance (n) and biomass (B) in different layers

'Brown pellets', other unidentified items, and dinoflagellate cysts

In the 0.75 cm^2 core from Helgoland Bight Station we found items which could not be identified; they stained slightly red with Rose Bengal. They are 150 to 400 µm in size and 0.1 to 50 nl in volume (mostly 1 to 20 nl). Under the dissection microscope they look dark brown or black (Fig. 2A). Of these, 2.5 million m^{-2} were found in the 0 to 6 cm sediment layer. The total volume of 'brown pellets' is about 14 ml m^{-2} corresponding to

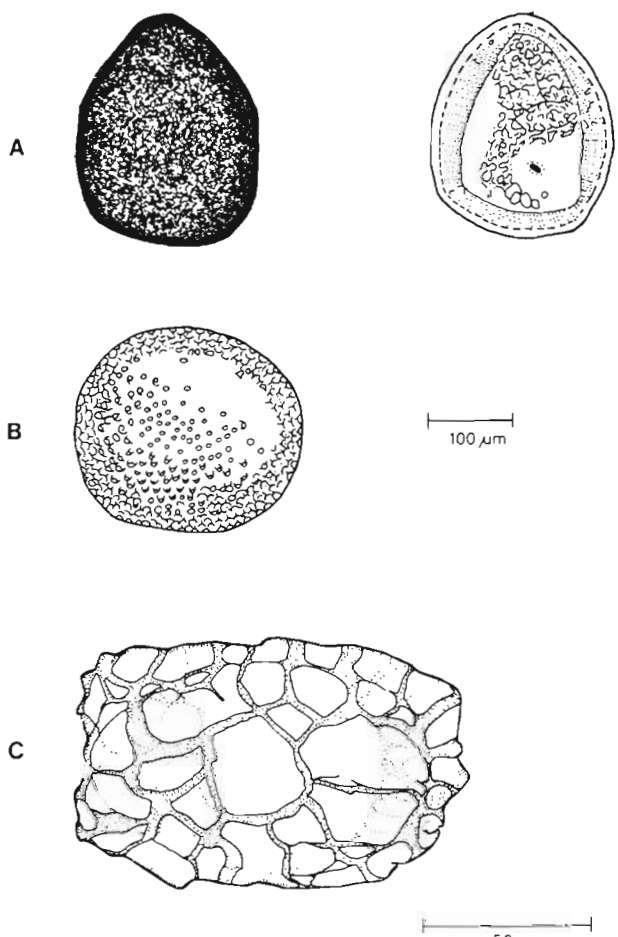

Fig. 2. 'Pellets' from Helgoland Bight Station; (A) 'brown pellets'; (B) 'oblong pellets'; (C) cyst of the dinoflagellate *Polykrikos schwartzii*

about 1.2 g C m^{-2}, i.e. more than the nematode biomass. Similar pellets were found at Kiel Bay Station. It is possible that 'brown pellets' are resting cysts of dinoflagellates, because they resemble figures by Dale (1979). At Helgoland Bight Station some of them (Fig. 2 C) could be identified as *Polykrikos schwartzii* Bütschli, by comparison with photographs published by Reid (1978). We are grateful to Dr. R. Warwick, Plymouth, for this information. Other unidentified items from Helgoland Bight Station are 'oblong pellets', 75 to 230 µm in size (Fig. 2 B) and 'spheres' with a soft surface which disintegrate quickly. All these particles are excluded from our size spectra.

Nematoda and other permanent metazoan meiofauna

Permanent meiofauna at Helgoland Bight Station (Table 1) are dominated by Nematoda (Fig. 3). Their abundance is 7.4 million ind m^{-2}, with a biomass of about 0.6 g C m^{-2}. The range of volumes of individual nematodes is 0.01 to 20 nl; individual masses range from 0.6 ng to 2.1 µg C. Nematodes below 50 ng C are rarely found deeper than 3 cm in the sediment. The

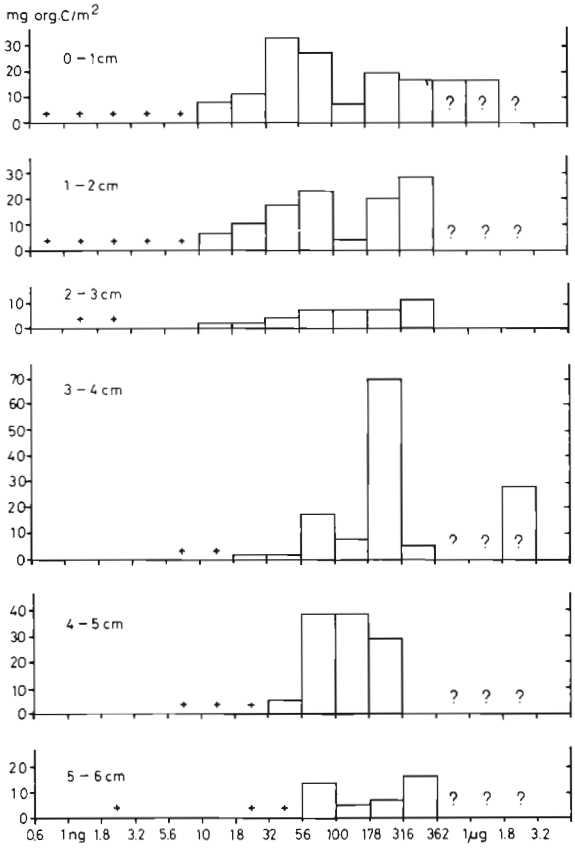

Fig. 3. Logarithmic size spectrum of biomass of 557 nematodes found in the 6 layers of the 0.75 cm^2 core collected at Helgoland Bight Station and sieved through 50 µm mesh

nematode population in the 3 to 6 cm stratum is mostly composed of individuals with 50 to 500 ng C individual mass (about 0.5 to 5 nl volume). Nematode biomass is distributed about equally in the 0 to 2 cm layer and in the 3 to 5 cm layer. It remains an open question how abundant large nematodes are above 500 ng C mass (or about 10 nl volume). Obviously, a 0.75 cm^2 core covers too small an area to give a representative picture of the rare larger members of the meiofauna, and from the 2 nematode specimens found with 1237 and 2133 ng C mass, extrapolation is not permissible. We obtained other nematode data from the 25 cm^2 core of Helgoland Bight Station which was sieved through 200 µm mesh, but contained fewer large nematodes than could be expected from the 0.75 cm^2 core. Even large nematodes have diameters below 50 µm, hence they may pass a 200 µm mesh-size screen.

'Other permanent meiofauna' at Helgoland Bight Station was composed of 'soft meiofauna' (Gastrotricha and Turbellaria), Kinorhyncha, Harpacticoidea and Ostracoda. Data from the 0.75 cm^2 core, owing to very small figures, cannot be extrapolated. Data from the 25 cm^2 core probably are too low owing to the 200 µm mesh size used. Sampling and sorting procedures were not adequate for 'soft meiofauna'. At Kiel Bay Station, 692 members of the permanent meiofauna (from 0 to 8 cm depth) were analyzed. Total abundance was about 3.5 million ind m^{-2}; biomass, 221 mg C m^{-2}. Nematodes represented 82 % of the total meiofauna biomass; their individual sizes ranged from 0.3 ng to 1.2 µg C. Sizes were about equally distributed at different depths, no shift was evident towards larger nematodes in deeper layers. In 6 to 8 cm depth, fewer individuals were found than in the other layers. But even at 15 cm a few very long and very thin nematodes and a few Gnathostomulida were found (P. Jensen, Helsingør, pers. comm.).

Juvenile macrofauna or temporary meiofauna

At Helgoland Bight Station, larvae and juveniles of macrofauna are present in the 0.75 cm^2 core sieved through 50 µm mesh, in the 25 cm^2 core sieved through 200 µm mesh, and in the 167 cm^2 macrofauna sample sieved through 500 µm mesh. It seems that a 25 cm^2 core gives the best result, at least for the size range 0.1 µg to 0.1 mg C (Table 2), disregarding very small bivalves of 0.01 to 0.1 µg C mass which pass through 200 µm mesh. They are better collected together with permanent meiofauna.

In the 25 cm^2 core sieved through 200 µm mesh, 1 Priapulida larva was the only animal of a size below 0.1 µg C. We omitted this larva and a few animals larger than 100 µg C. For the size class 0.1 µg to

Table 2. Macrofauna at Helgoland Bight Station. Biomasses and estimates of metabolism, expressed via respiration of different size classes. Oxygen consumption q (in µl O_2 h^{-1}) at 20 °C calculated for mean individual mass (w) (in mg AFDW) of size class according to log q = 1.29+0.74 log w (Banse 1982: Table 1, poikilotherms)

Size class by organic carbon	Mean mass of individual		Biomass mg C m^{-2}	O_2 consumption µl O_2 h^{-1}	
	C	AFDW		mg^{-1} AFDW	m^{-2}
Juvenile macrofauna					
100 – 178 ng	137 ng	239 ng	0.4	28.29	14
178 – 316	243	425	0.4	24.36	10
316 – 562	432	756	3	20.97	63
562 – 1000	768	1.3 µg	5	18.07	90
1 – 1.8 µg	1.4 µg	2.4	5	15.55	78
1.8 – 3.2	2.4	4.3	18	13.39	241
3.2 – 5.6	4.3	7.6	49	11.52	564
5.6 – 10	7.7	13	127	9.93	1261
10 – 18	14	24	123	8.54	1050
18 – 32	24	43	133	7.36	979
32 – 56	43	76	68	6.33	430
56 – 100	77	134	152	5.46	830
Small macrofauna					
100 – 178 µg	137 µg	239 µg	120	4.70	564
178 – 316	243	425	77	4.04	311
316 – 562	432	756	73	3.48	254
562 – 1000	768	1.3 mg	81	3.00	243
1 – 1.8 mg	1.4 mg	2.4	320	2.58	826
1.8 – 3.2	2.4	4.3	346	2.22	768
3.2 – 5.6	4.3	7.6	458	1.91	875
5.6 – 10	7.7	13	1162	1.65	1917
Large macrofauna					
10 – 18 mg	14 mg	24 mg	220	1.42	312
18 – 32	24	43	180	1.22	220
32 – 56	43	76	280	1.05	294
56 – 100	77	134	590	0.91	537
100 – 178	137	239	880	0.78	686
178 – 316	243	425	1830	0.67	1226
316 – 562	432	756	1100	0.58	638
562 – 1000	768	1300	0	0.50	0
Total			*8401*		*15300*

0.1 mg C we obtained 74 000 ind m^{-2}; biomass, 684 mg C m^{-2}; average individual mass, 9.2 µg C. For the same station, Juario (1975) reported as 'juveniles' only 18 000 ind m^{-2}; average individual mass, 1 µg C. We suppose that Juario picked all larger specimens from his sample and eliminated them. All specimens of juvenile macrofauna were found in the upper 3 cm of the sediment. The dominating species *Scalibregma inflatum* was restricted to the upper 2 cm of the sediment.

In the 167 cm^2 macrofauna sample, sieved through 500 µm mesh, were only a few animals of a size below 10 µg C because they are not held back by 500 µm mesh. However, even animals of 10 to 100 µg C were not well represented: their abundance – as calculated from 500 µm mesh – was 1920 ind m^{-2}, compared with 19 200 ind m^{-2} from the 25 cm^2 core sieved through 200 µm mesh.

At Kiel Bay Station no 'juvenile macrofauna 0.1 µg to 0.1 mg C' was found in the meiofauna core. We found some juvenile macrofauna in the 560 cm^2 core, but this was sieved through 500 µm mesh, and most juvenile macrofauna probably disappeared through the meshes. This size class is underrepresented in Fig. 4.

Small macrofauna

For the size classes 0.1 to 10 mg C, we established the compartment 'small macrofauna'. In the 167 cm^2 macrofauna sample from Helgoland Bight Station, sieved through 500 µm mesh, 73 animals were found

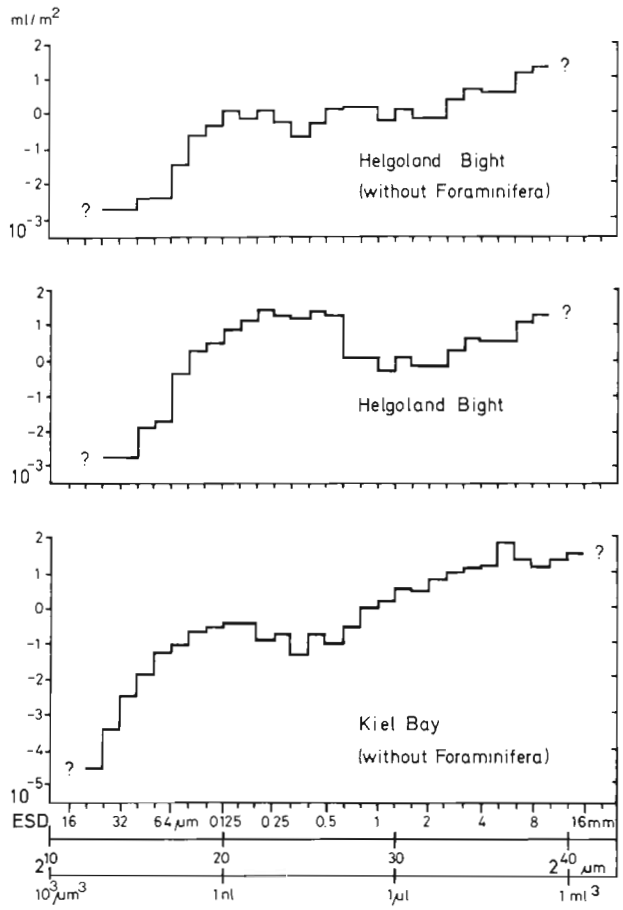

Fig. 4. Logarithmic size spectrum by volume, plotted for Helgoland Bight Station, with and without foraminiferans, and for Kiel Bay Station

which traditionally might be counted as macrofauna. Calculated per unit area, they amount to 4380 ind m^{-2} and have a biomass of 15.5 g C m^{-2}. However, if the 'juvenile macrofauna 0.1 µg to 0.1 mg C' is eliminated (see preceding section) and if 5 large animals above 10 mg C individual mass are eliminated from the sample and transferred to the compartment 'large macrofauna' (see following section), the compartment 'small macrofauna 0.1 to 10 mg C' has an abundance of 2260 ind m^{-2}, and a biomass of 2.6 g C m^{-2} (Table 2). By traditional evaluation, the 560 cm^2 core from Kiel Bay yielded 1144 macrofauna animals, or 20 400 ind m^{-2}, with 35 g C m^{-2} biomass. However, if we subtract animals of 0.1 µg to 0.1 mg C (juvenile macrofauna) and eliminate 11 animals with masses above 10 mg C (large macrofauna), the compartment 'small macrofauna 0.1 to 10 mg C' amounts to 9308 ind m^{-2}, and 9.0 g C m^{-2} biomass.

Large macrofauna

By separating animals of 10 mg to 1 g C mass from the 'small macrofauna', we tried to define the separate compartment 'large macrofauna' for larger members of the macrofauna. In the 167 cm^2 macrofauna sample from Helgoland Bight Station (see preceding section), 5 large macrofauna animals were found: *Goniada maculata, Chaetopterus variopedatus, Ophiura albida, Ophiura texturata,* and a nemertinean. This sample was too small to be representative. But from the same station, 0.3 m^2 of sediment was sampled, and 16 large animals were picked by hand and analyzed for wet weight. We calculated 53 ind m^{-2} and a biomass of 5.1 g C m^{-2} for 'large macrofauna'; 2.9 g was represented by *Echinocardium cordatum* (Table 2).

In the 560 cm^2 core from Kiel Bay Station, 11 animals were found with masses above 10 mg C: *Nephtys caeca, Mya arenaria, Macoma baltica, Macoma calcarea, Arctica islandica.* The compartment 'large macrofauna 10 mg to 1 g C' contained 196 ind m^{-2} with 25.3 g C m^{-2} biomass.

In Kiel Bay *Arctica islandica* larger than 1 g organic carbon mass were to be found; and in Helgoland Bight, larger *Echinocardium cordatum.* These were not sampled.

Spectrum by volume (Sheldon spectrum)

In Fig. 4, $\log_2$ volume spectra are presented which cover meiofauna to macrofauna; biomass is expressed logarithmically by volume. Sea water in mantle cavities etc. and shell material is included, therefore this 'biomass by volume' is a very rough measure. At both stations analyzed, the general trend of biomass by volume is to increase from small size classes to large size classes. However, this increase is not steady, and a meiofauna peak in the range of Equal Spherical Diameter (ESD) 125 to 250 µm can be identified. At both stations the size class ESD 250 to 500 µm is underrepresented, as long as Foraminifera are not included. At Helgoland Bight Station, all Foraminifera which stained red with Rose Bengal are included, with the result that the size class 250 to 500 µm ESD is as well represented as the size class 125 to 250 µm. When Foraminifera are included, biomass by volume in the meiofauna size classes is higher than in the macrofauna size classes, and only the largest macrofauna size classes have nearly as much biomass as the meiofauna size classes.

Spectrum by biomass

In principle, the spectrum by biomass is similar to that by volume. Differences occur due to the neglect of volumes (tests, shells, cavities) filled by fluids. We prefer to present the biomass spectrum with a linear scale for biomass per logarithmic size class, because

this makes it possible to demonstrate the respective contributions of Foraminifera, permanent meiofauna, and macrofauna to total biomass (Fig. 5 & 6). Nematodes (the dominant group of permanent meiofauna) and Foraminifera have about the same size-class distribution. Their mass ranges from 1 ng to 10 µg C, mostly between 10 ng and 3 µg, with a peak between 50 and 500 ng. The biomass spectrum at Kiel Bay Station is dominated by large macrofauna size classes. Some smoothing has been applied to account for irregularities (explained in legend to Fig. 5). Similarly, smoothing was applied to construct the biomass spectrum of Helgoland Bight Station (Fig. 6). The original data are presented in Tables 1 and 2.

Spectrum by metabolism

To convert biomass to metabolism we used the data on mass-specific oxygen consumption computed by Banse (1982). Data for 'eucaryote unicellulars' have been used for Foraminifera, data for nematodes for

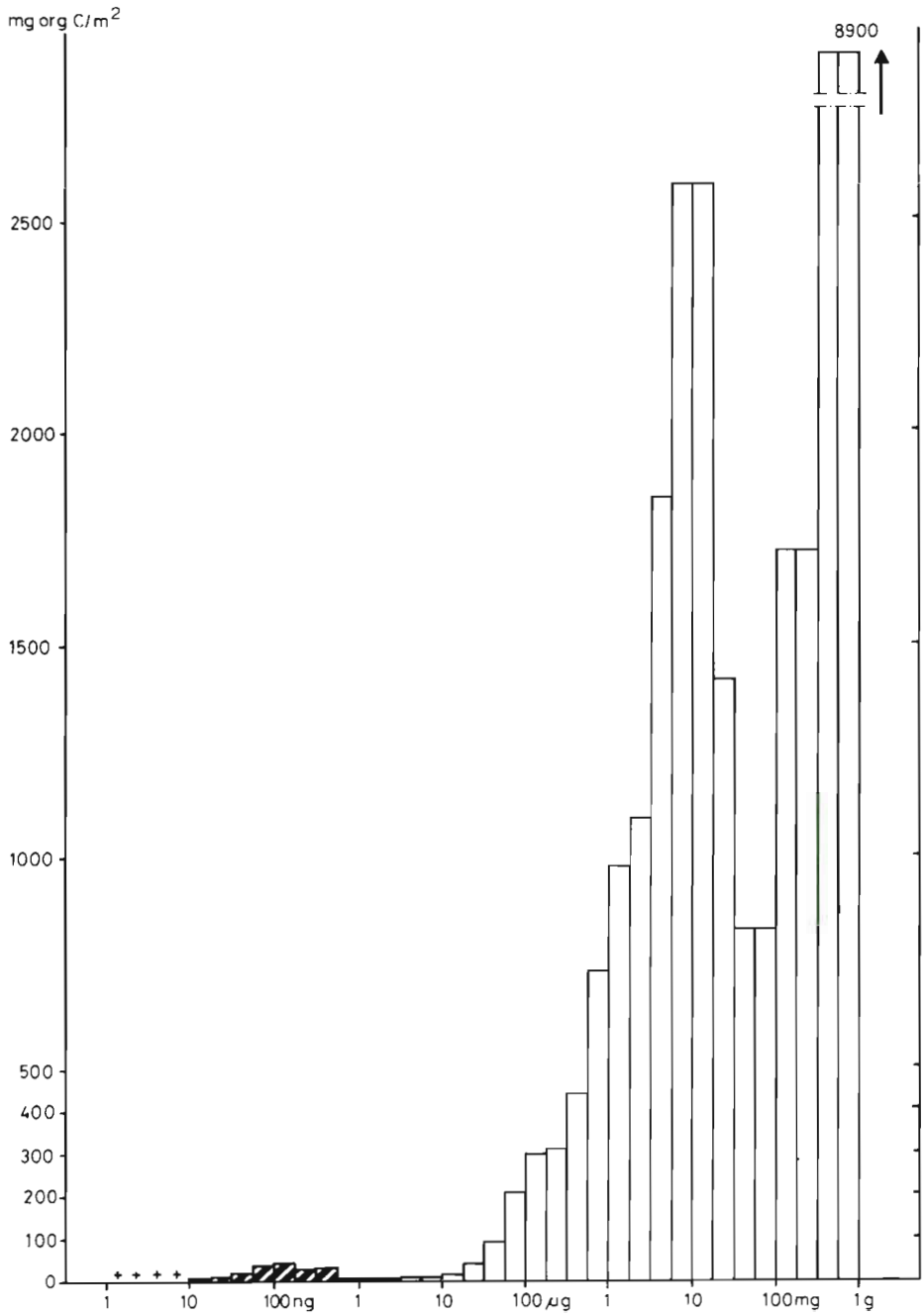

Fig. 5. Logarithmic size spectrum by biomass for Kiel Bay Station. Scale for biomass of size classes is linear. Size range 1 to 100 µg org. C underrepresented due to mesh size. Size ranges 5.6 to 18 mg and 32 to 100 mg organic carbon are calculated together Size range 100 mg to 1 g represented in the original sample by only 2 large *Arctica islandica;* even larger *A. islandica* occur in the region

'permanent meiofauna', data for 'poikilotherms' for macrofauna (including 'juvenile macrofauna'). Values calculated for the metabolism of individual size classes are listed in Tables 1 and 2. For Fig. 7 the smoothed biomass values of Fig. 6 served as basis for calculations. From Fig. 7 it is evident that a peak of meiofauna metabolism occurs at size classes 50 to 500 ng C, corresponding to the meiofauna peak of biomass. Mac-

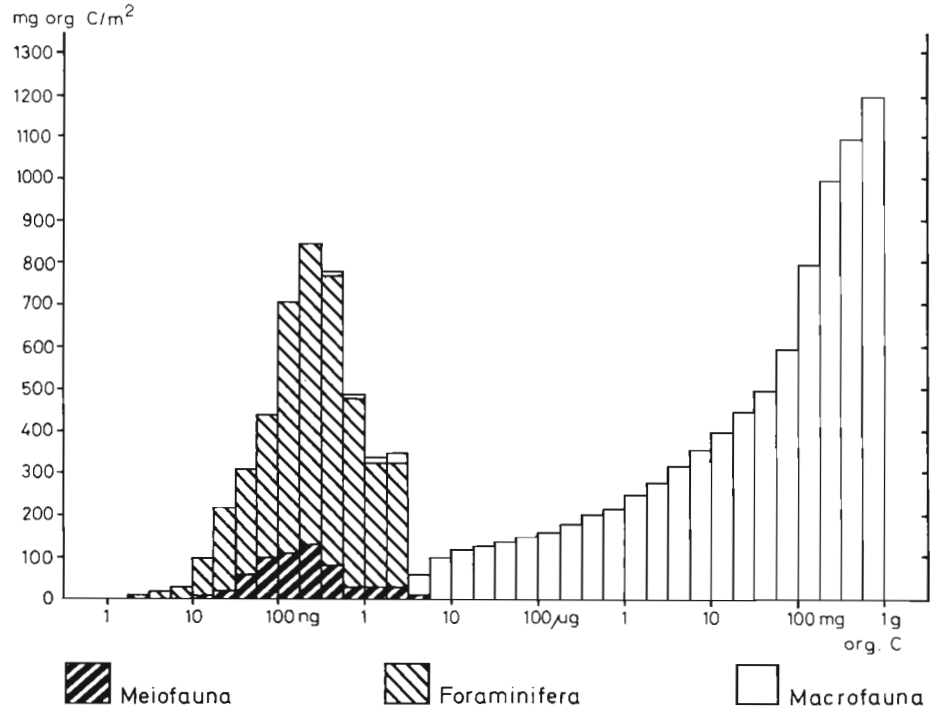

Fig. 6. Logarithmic size spectrum by biomass for Helgoland Bight Station. Smoothed data; for original data consult Tables 1 and 2

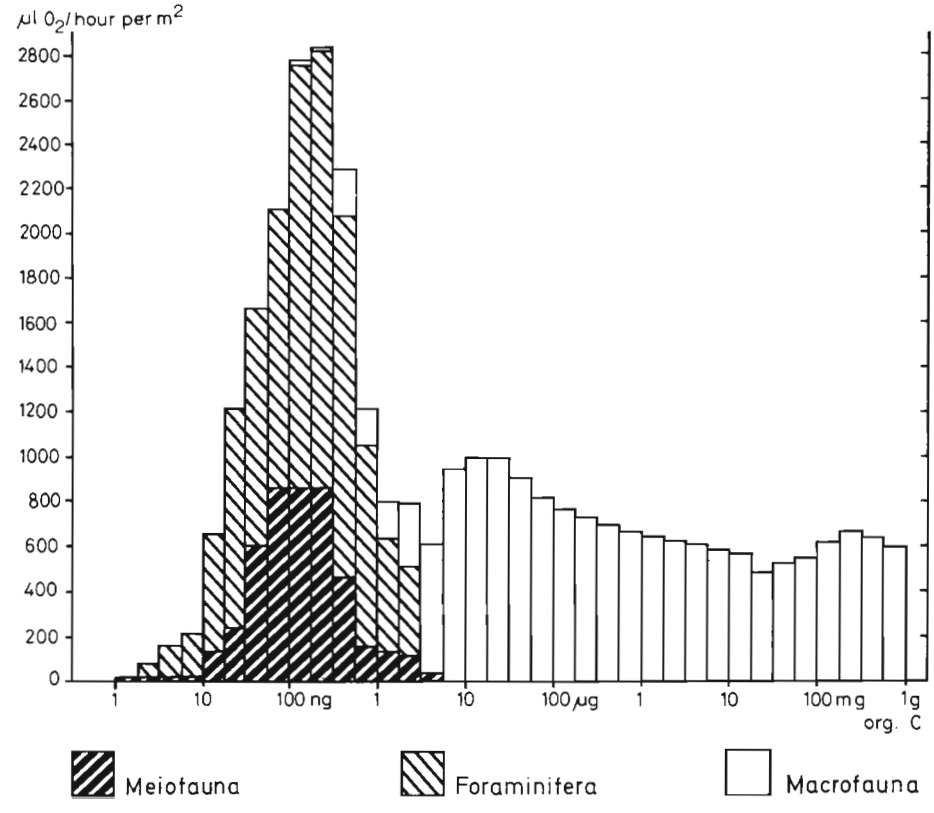

Fig. 7. Logarithmic size spectrum by metabolism for Helgoland Bight Station, based on biomass data from Fig. 6. For original data consult Tables 1 and 2

rofauna contribution to metabolism is about equal within size classes from 0.01 mg to 1 g C individual mass.

DISCUSSION

Sample size

In all size classes there is the problem of how to treat rare and large individuals found in small samples. Let us assume that logarithmic size classes (Fig. 6) represent biomasses of 100 mg C m^{-2} each, or 10 µg cm^{-2}. We then can expect to find 100 individuals of 0.1 µg C mass, or 10 individuals of 1 µg, or only 1 individual of 10 µg in a sample of 1 cm^2. This sample size is obviously not large enough to represent, in a significant way, animals of more than ca 1 µg C mass. Enlarging the sample size to 10 cm^2 would result in unnecessary work to sort and identify 1000 individuals of 0.1 µg mass. A 10 cm^2 sample, therefore, should be sieved through coarser mesh to collect the 100 individuals of 1 µg or the 10 individuals of 10 µg C mass, and another sample of 100 cm^2 should be sieved through even coarser mesh to collect the 100 individuals of 10 µg or the 10 individuals of 100 µg C mass which can be expected to be found in the model sediment. To define optimum sample areas and mesh sizes is a task for the future; Reish (1959) and Bovee et al. (1974) have discussed the problem.

Instead of sieving the sediment it is better to collect rather large sediment samples and to separate the fauna from the sediment by flotation techniques. Subsamples of different sizes may then be processed with size-specific sorting or sieving methods (Schwinghamer 1981b, Warwick 1984).

We use the term 'juvenile macrofauna' for the size classes 0.1 µg to 0.1 mg C which cannot be sampled satisfactorily with 0.5 mm mesh. Marshall (1979) coined the rather unsuitable term 'minifauna' for small members of the deep-sea macrofauna, body size 0.5 to 5 mm, which are collected on 0.42 mm mesh. These deep-sea animals have been classified as meiobenthos by USSR authors ('Russian meiobenthos') but should better be ranked under 'small macrofauna'. Large macrofauna has a low abundance; it must be sampled from large areas of the sea bottom. Adequate methods should be elaborated to sample animals even larger than 1 g C, because large macrofauna seems to have great ecological importance in terms of biomass.

Nematode and Foraminifera data

At Helgoland Bight Station, 7.4 million nematodes m^{-2} were found; biomass is about 0.6 g C m^{-2}. This is more than Juario (1975) recorded in 1971/72 in the same region, but we were probably more careful in sorting small nematodes. However, even our data may be underestimates because we used a grab deployed from a research vessel. Jensen (1983) worked with a similar grab (Haps Corer) and found on muddy sediment in the Sound that the corer provided only 66 % of nematode numbers and 48 % of harpacticoid numbers, compared with SCUBA sampling. Losses are spectacular from the 0 to 1 cm surface layer of the sediment. For conversion from wet weight to organic carbon, Jensen (1984) found 12.4 % instead of the 10 % used by us. Therefore, nematode biomass may actually be higher at our stations than we calculated. Data given by Jensen (1983) for size classes of nematodes refer to nl volume, not µl.

For Foraminifera, the method of protoplasma-volume estimation and the assumption that all volumes staining red with Rose Bengal represent living tissue, may well be criticised. Professor G. Lutze (Geological Institute of Kiel University) kindly informed us that it needs long practice to distinguish living from dead Foraminifera on the basis of Rose Bengal staining; some Foraminifera stained red could be dead, while others with little stain could be alive. We have no long-standing practice, hence our data may be wrong. Our value of about 5000 forams cm^{-2} at Helgoland Bight Station is much higher than hitherto reported from nearby stations. The area distinctly stained inside the test was calculated to represent the 'living soft body'; its proportion of the total test volumes ranged from 10 to 90 % with a mean of 32 %. This percentage is less than the protoplasma volume identified by Wefer & Lutze (1976) via subtracting the test wall from the total test volume: for most genera they achieve values for the plasma volume between 70 and 80 % of total test volume; they calculate wet plasma mass with a density of 1.027 g cm^{-3}.

According to our calculation, based on 141 randomly picked Foraminifera, the mean test volume is 2.1 nl, and the average mass of an individual is 0.07 µg organic carbon. This value is less than the assumption made by Gerlach (1978) that forams have a mass of 1 µg organic dry weight. It is less than the 1 to 2 µg organic carbon analyzed for 400 to 600 µm diameter *Elphidium* by A. Altenberg (Geological Institute of Kiel University, pers. comm.). The value of 0.07 µg C is biased by the large number of small forams in the sample. Most species are represented by both small and large individuals; it is not realistic to calculate average mass values for different species.

At Helgoland Bight Station we found ca 60 % of the foraminiferan biomass living deeper than 3 cm in the sediment, probably in suboxic or even anoxic layers. Living forams have frequently been found in deeper

layers of marine sediments (see bibliography in Severin & Erskian 1981). After burial, *Quinqueloculina* is able to migrate, within 4 to 5 d, from 5 cm depth to the surface, where it lives in well-defined burrows in the top layer of the sediment (Severin et al. 1982); *Nonion* migrates vertically to the sediment surface at a speed of 3 mm h^{-1}; and *Ammonium* (syn. *Streblus*) moves on the sediment surface (Richter 1961).

Size spectrum by volume and biomass

From our analyses of Helgoland Bight Station and Kiel Bay Station a picture emerges which confirms the findings of Schwinghamer (1981b): a meiofauna peak, a trough between meiofauna and macrofauna, and increasing biomass per size class in larger macrofauna. At 16 stations from the subtidal Bay of Fundy, Schwinghamer (1983) invariably found a meiofauna peak at 0.25 to 0.5 mm Equal Spherical Diameter (ESD). At Helgoland Bight Station, we found the same peak. At Kiel Bay Station (Fig. 4), we found this peak at a somewhat smaller body size, corresponding to 0.125 mm ESD. The trough between meiofauna and macrofauna was at 0.5 to 2.0 mm ESD in the Canadian subtidal; we found the same at Helgoland Bight Station, while at Kiel Bay Station the trough was at about 0.5 mm ESD. Warwick (1984) calculated a trough in the spectrum of species size distribution at 0.73 mm ESD (45 µg dry mass) for 7 subtidal and intertidal British stations. At the intertidal Pecks Cove Station in the Bay of Fundy, Schwinghamer (1983) recognized the trough between meiofauna and macrofauna at all seasons of the year, but with varying intensity. Similar variations might be expected for the Helgoland Bight Station and for the Kiel Bay Station owing to seasonal macrofauna patterns, resulting in different numbers of juveniles. The trough between meiofauna and macrofauna is in the size range of ca 5 to 500 µg organic carbon, or 0.01 to 1 mg dry mass, or 0.05 to 5 mg wet mass, the size range of juvenile macrofauna.

It is an open question whether this type of benthic size spectrum is universal. Deep sea and Bothnian Bay may be examples of very low food availability, and with a dominance of very small and very large animals at the expense of medium-sized species (Thiel 1983, Elmgren 1984). But for less 'extreme' ecosystems, such as intertidal and subtidal silty sand sediments, in general there seems to be a gradual increase of biomass of logarithmic size classes with increasing body mass.

In the pelagic zone, in contrast, biomass of logarithmic size classes decreases with increasing body mass. To explain this general difference of size spectra in the pelagial and the benthal, one should consider sinking speed: large particles sink faster than small ones. Animals unable to compensate sinking by buoyancy or by jellyfish type adaptations have to counteract sinking by active locomotion. Adult Antarctic krill *Euphausia superba* of 60 mm length with about 0.5 g dry body mass have to spend 2.5 J d^{-1} in order to counteract, by upward swimming, a sinking rate of 500 m in 3 h (Kils 1982).

Size spectrum by metabolism

We take oxygen consumption at 20 °C as a measure of metabolism and use regressions published by Banse (1982) for eucaryotic unicells, nematodes and poikilotherms. We realize that the regression for eucaryotic unicells was computed from 21 experiments with amoeba, ciliates and flagellates, and that no data on foraminiferans are available. The regression for poikilotherms was computed from a few macrobenthos experiments, but mostly from data of terrestrial animals including insects. The regressions published by Banse (1982) refer to animals from very different environments; it is legitimate to question whether marine benthic animals, on average, have the same level of metabolism as a generalized type of animal.

In Tables 1 and 2 we reproduce regressions in log form, according to Banse (1982). Confidence intervals (at $p = 0.05$) for a (intercept of equation $q = a\ w^b$) are:

for nematodes	5.37	(4.37 to 6.46)
for poikilotherms	19.50	(14.13 to 26.92).

However, the underlying principle is not a scatter of data, but the fact that among animals of the same size there are active species which respire more, and sluggish species which respire less than the average animal represented by the regression. Warwick & Price (1979) analyzed the oxygen consumption of 16 nematode species from Tamar Estuary. The intercept a (calculated for nl O_2, nl body volume) was in active species 1.0 to 1.5, in most species 0.7 to 1.0, but only 0.4 to 0.7 in sluggish nematode genera like *Terschellingia, Sabatieria* and *Metachromadora* which live deeper in the sediment. If one computes the regression for all nematodes, the predicted mean is 0.8. A variation of about 50 to 200 % from the predicted mean seems realistic, characterizing (1) species which live at the surface of the sediment, move quickly and are partially carnivorous and (2) species which live several cm deep in the sediment and most probably live anaerobically for prolonged periods of their life.

Unfortunately, anaerobic metabolism cannot be measured by respirometric methods, thus heat loss must be determined. As long as this has not been done for a variety of animals under realistic conditions as in sediments, generalisations about metabolism in the field are probably not safe. Such caution is valid not

only for meiofauna and foraminiferans living in deeper layers of the sediment, but also for a number of macrofauna animals, e.g. *Arctica islandica*, reported by Taylor (1976) to disappear every week or so for a couple of days from the sediment surface and surviving anaerobically deep in the sediment.

If one disregards criticism of respiration measurements and takes foraminiferan biomass data as fact, the benthic size spectrum by metabolism (Fig. 7) is characterized by higher metabolism per size class in the meiofauna size range, compared with macrofauna. The larger macrofauna size classes have a somewhat lower metabolism than the smaller macrofauna size classes. But in general the differences of metabolism per logarithmic size class from meiofauna to large macrofauna are small. We may conclude that food resources are about equally available and are about equally utilized by all logarithmic size classes of the benthos fauna.

For silty-sand subtidal sediments, Gerlach (1971) generalized that meiofauna makes up ca 3 % of macrofauna biomass, but is responsible for about 15 % of macrofauna metabolism. This general statement has been used, since then, by many authors. It is based on the assumption that meiofauna metabolism per unit of mass is 5 times higher than macrofauna metabolism (Gerlach 1978). The elaboration of a benthic size spectrum allows better precision: at Helgoland Bight Station, metabolism of meiofauna (Foraminifera not included) per unit of mass is 4 times higher than the metabolism of macrofauna (up to size 1 g organic carbon).

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