

Biomass Size Spectra of Near-Shore Shallow-Water Benthic Communities in the Gulf of Gdańsk (Southern Baltic Sea)

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With 4 figures and 5 tables

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Abstract. Biomass size spectra were prepared for benthic (macro- and meiobenthos) communities at 5 stations located in the shallow, coastal area of the Gulf of Gdańsk (Southern Baltic Sea). Stations differed in their sediment characteristics (coarse sand vs. organic matter-enriched fine sand). Spectra were based on measurements of meio- and macrobenthic animals collected with 3 types of gear: 24.4 and 75.0 mm diameter hand-held corers and 0.1 m² VAN VEEN grab. Benthic biomass at the stations consisted mainly of nematodes and oligochaetes among the meiobenthos and of hydrobiid snails and *Mytilus edulis* among the macrobenthos. Regardless of habitat, size spectra peaked initially at the meiofaunal range weight class (251.19–501.19 ng C). The separation between meio- and macrobenthic peaks was, however, not as distinct as that found in other studies. Normalized size spectra demonstrated that most of the variability was introduced by macrobenthos: a rather clear separation between the macrofauna of coarse- and fine-grained sediments was evident as well. However, benthic biomass spectra of all the stations conformed to a common pattern and could be represented by a single, averaged spectrum.

Problem

The implications of individual body size of members of different communities in regard to community structure and function are receiving growing attention among researchers engaged in studies on both terrestrial (GRIFFITHS, 1986) and aquatic (BANSE, 1982) environments. Relationships between body size and parameters of individual performance (intrinsic growth rate, metabolism, fecundity, production *etc.*) extend to the population level and to that of community and ecosystem as well (PETERS, 1983). According to PETERS (1983) the aggregation of populations into mixed-species assemblages of similar body size is a form of community analysis

and should prove useful in treating processes, such as bioaccumulation, site productivity, energy flow, and nutrient processing, which involve all or most members of the ecosystem.

Based on the concept of size spectra developed by SHELDON & PARSONS (1967) and SHELDON *et al.* (1972), a number of attempts have been made to use the SHELDON & PARSONS model to describe portions of freshwater and marine ecosystems to make inferences on interactions between various trophic levels (CYR *et al.*, 1997; BORGMANN, 1982; KERR, 1974), including predator-prey interactions (THIEBAUX & DICKIE, 1993) and energy flow up the trophic structure (BORGMANN, 1987; HAVENS, 1998). Moreover, DICKIE *et al.* (1987b) stated that energy flow within the community can be determined from the distribution of body size, without the necessity of specifying trophic levels of the organisms involved.

The SHELDON & PARSONS model describes community structure by evoking biomass distribution over a sequence of equal intervals of the logarithm of body size (THIEBAUX & DICKIE, 1993). Many workers believe that the model works well for pelagic ecosystems (for which it was originally constructed), as it offers explanation and prediction for various processes (FRY & QUINONES, 1994; POPE *et al.*, 1994; ZHOU & HUNTLEY, 1997), including fisheries yield (BOUDREAU & DICKIE, 1992; DICKIE *et al.*, 1987a; DUPLISEA *et al.*, 1997; MACPHERSON & GORDOA, 1996; SPRULES *et al.*, 1991), although the latter aspect has been recently questioned (CYR & PETERS, 1996). In addition, some authors (RODHOUSE *et al.*, 1994) stress the need of supplementing the analysis of biomass spectra with taxonomic data.

Application of the size spectrum concept to the benthic system, pioneered by SCHWINGHAMER (1981), while supporting the traditional categories of micro-, meio- and macrofauna (WARWICK, 1984; SCHWINGHAMER, 1981), has spawned some controversy as to the utility of the SHELDON & PARSONS model for making inferences on that system. While some data support the model (*e.g.*, CATTANEO, 1993), other workers (STRAYER, 1991; WARWICK & JOINT, 1987) have found the model to be too simplistic (for a summary of those views see DUPLISEA & HARGRAVE, 1996).

Compared to the volume of data sets collected for the pelagic realm, the evidence for benthic systems is still too limited to allow comprehensive conclusions on invoking the role of biomass spectra as a unifying principle for all aquatic ecosystems (POFF *et al.*, 1993; SCHWINGHAMER, 1983; STRAYER, 1991). This explains the need to obtain further data from widely different areas and to improve the methodology of spectra construction (RAMSAY *et al.*, 1997).

Size spectra of Baltic Sea communities were presented by GERLACH *et al.* (1985) working with benthos off the Kiel Bay (and off Helgoland in the North Sea), by WITEK (1986) for plankton, and by WITEK *et al.* (1993) for the entire biocoenoses of two sites in the Southern Baltic. Both GERLACH *et al.* (1985) and WITEK *et al.* (1993) mentioned methodological problems with obtaining representative spectra for benthic communities. The problem, in the case of WITEK *et al.* (1993), even resulted in discontinuities in the spectra.

In this paper, we describe biomass size spectra of shallow-water benthic communities at five stations in a nearshore area of the Gulf of Gdańsk (Southern Baltic Sea); the aim is to supplement the existing body of data on biomass distribution in the Baltic benthic assemblages and to prepare ground for future research on community metabolism in the area. Specifically, we address the following questions: (1) do community size spectra allow distinct separation of ecological categories of

the benthos? and (2) do habitat differences between stations significantly affect benthic size spectra?

Material and Methods

1. Study area

Benthic organisms were sampled in August and October 1992 at 5 stations (A, B, C, W and Y) located in the shallow, coastal area of the Gulf of Gdańsk (Fig. 1). Apart from season-dependent differences

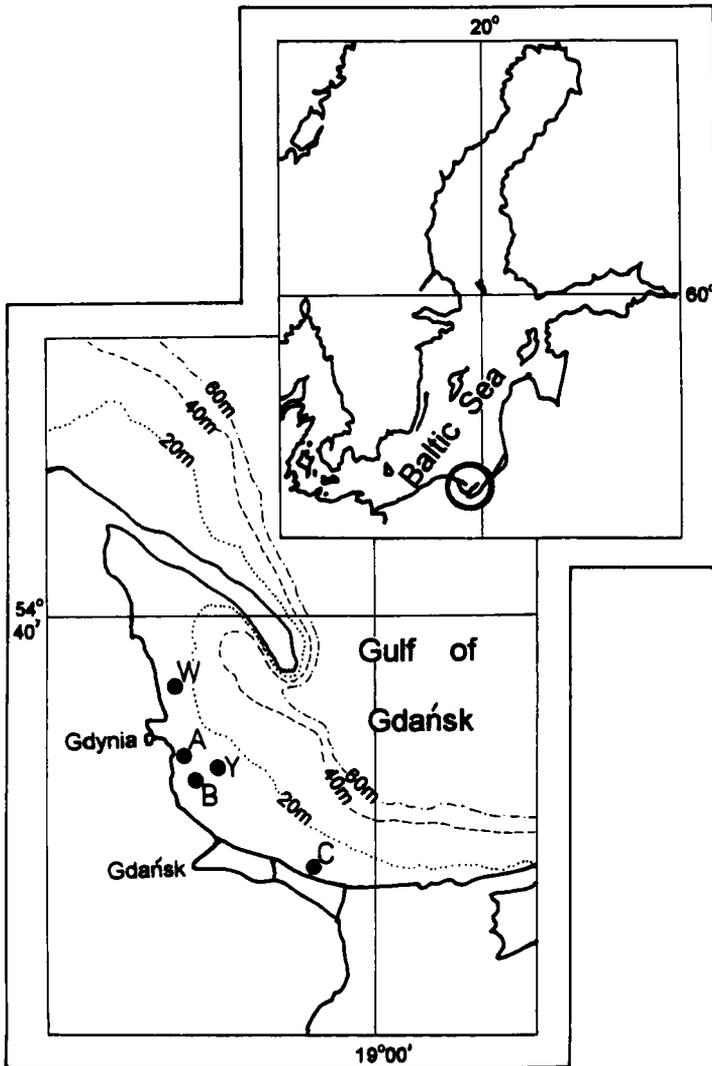


Fig. 1. Location of sampling sites.

in the near-bottom water temperature between stations sampled in August (A, B, C) and October (W, Y), the stations differed mainly in their sediment characteristics. Sediments at stations B and Y were much coarser and contained less organic matter than those at A, C and W (Table 1).

2. Meiofauna

Meiobenthos samples were collected by SCUBA diving. Hand-held corers of two sizes were used: a small diameter corer (24.4 mm i.d., hereafter referred to as the small corer) and a large-diameter one (75.0 mm i.d., henceforth referred to as the large corer) were inserted into the sediment to a depth of 10 cm. At most stations, 3 pairs of cores were retrieved, except at station W where 2 small cores and 3 large ones were taken. The samples were fixed with borax-buffered (PFANNKUCHE & THIEL, 1988) 10% formalin and Rose Bengal-stained. To extract the fauna, the samples were divided into 10 ml portions which were subsequently subjected to the shake-and-decant procedure (ELMGREN & RADZIEJSKA, 1989), repeated 10 times. Small corer sample supernatants were passed through a set of 0.5, 0.2, 0.1 and 0.04 mm mesh size sieves, whereas 1.0 and 0.22 mm mesh size sieves were the coarsest and the finest, respectively, used for the large corer sample supernatants. Animals retained on the 1.0 mm sieve were regarded as macrobenthos. Animals retained on each sieve were identified to the lowest possible taxon, enumerated and sorted for measurement.

Length and width measurements were taken using the OPTIMAS (BioSonic, USA) computer image analysis system. Except for nematodes (see below), all animals were measured.

Prior to biomass calculation, individual weights were determined from the animal volume obtained with the formula given by FELLER & WARWICK (1988):

$$V = L \cdot W^2 \cdot c$$

where: V is the body volume [nl]; L the maximum body length [mm]; and c a taxon-specific coefficient whose value was selected as recommended by FELLER & WARWICK (1988).

To determine nematode biomass, approximately one-third of all nematodes per sample were picked randomly and measured. Nematode biomass obtained from calculations performed on a subset of individuals was extrapolated to include all individuals present in the sample.

Biomass was determined by assuming, after FELLER & WARWICK (1988), 1.13 as the specific weight of the meiobenthos, dry weight being 25% of the wet weight, and organic carbon content making up 40% of the dry weight. For determination of shell-free biomass of hydrobiid snails and bivalves, the length-weight equations of RUMOHR *et al.* (1987) and WARZOCHA & GOSTKOWSKA (1991) were used.

3. Macrobenthos

The macrobenthos was sampled with a 0.1 m² VAN VEEN grab (n = 3 per station). Samples were fixed with borax-buffered 10% formalin. Macrofauna were extracted by passing the sediment through a 1.0 mm sieve. After extraction, organisms were identified, enumerated, and sorted for measuring and biomass determination. Animals were measured under a stereomicroscope equipped with a measuring eyepiece. Individual weights were calculated from published length-weight equations (RUMOHR *et al.*, 1987; WARZOCHA & GOSTKOWSKA, 1991) and converted to carbon biomass using conversion factors available in the literature (ANKAR & ELMGREN, 1978; RUMOHR *et al.*, 1987; BREY *et al.*, 1988).

4. Size spectra

Individual weight-based carbon biomass values provided the basis for community size spectra, whereby the carbon biomass was determined for 27 logarithmic individual carbon weight (mass) classes. The width of each class is equal to $0.3 \log_{10}(W)$ (where W is body carbon weight), which approximately corresponds to classes of a width of $1 \log_2(W)$ (see Table 2 for class intervals) (WITEK *et al.*, 1993). Data from different samplers provide different collecting efficiencies which are reflected as overlaps and

Table 1. Near-bottom water and sediment characteristics at stations sampled in this study.

station	sampling date	depth [m]	salinity [PSU]	temp. [°C]	dissolved oxygen content*	mean grain size [mm]	sediment type	% silt/clay	% organic matter [LON]**
A	4 Aug 1992	9.5	7.068	16.0	6.63	0.165	fine sand	5.3	0.9
B	4 Aug 1992	9.5	7.052	17.6	7.06	0.259	medium sand	2.78	0.59
C	5 Aug 1992	10.8	7.038	18.0	7.36	0.114	very fine sand	3.1	1.16
W	21 Oct 1992	9.8	7.188	9.55	7.38	0.187	fine sand	1.7	0.93
Y	21 Oct 1992	8.0	7.132	9.42	7.95	0.717	coarse sand	0.7	0.8

* expressed in $10^{-3} \text{ dm}^3 \text{ O}_2 \cdot \text{dm}^{-3}$

** LON = loss on ignition

Table 2. Size classes identified in this study and their biomass dominants (% domination).

class no.	weight class		station A	station B	station C	station W	station Y
	weight interval (C units)						
1	2-3.98 ng	-	-	-	-	-	Gastrotricha (100)
2	3.98-7.94 ng	Nematoda (100)	Nematoda (62.1)	Nematoda (100)	Nematoda (100)	Nematoda (100)	Nematoda (100)
3	7.94-15.85 ng	Nematoda (100)	Nematoda (71.4)	Nematoda (100)	Nematoda (100)	Nematoda (100)	Gastrotricha (79.7)
4	15.85-31.62 ng	Nematoda (100)	Nematoda (88.9)	Nematoda (100)	Nematoda (100)	Nematoda (100)	Nematoda (100)
5	31.62-63.10 ng	Nematoda (98.2)	Nematoda (79.2)	Nematoda (100)	Nematoda (100)	Nematoda (100)	Nematoda (78.9)
6	63.10-125.9 ng	Nematoda (97)	Nematoda (94.8)	Nematoda (99.8)	Nematoda (99.8)	Nematoda (100)	Nematoda (75.6)
7	125.9-251.19 ng	Nematoda (96.3)	Nematoda (96.7)	Nematoda (98.2)	Nematoda (98.2)	Nematoda (99.7)	Nematoda (89.2)
8	251.19-501.19 ng	Nematoda (95.7)	Nematoda (86.2)	Nematoda (99.3)	Nematoda (99.3)	Nematoda (99.6)	Nematoda (86.8)
9	501.19 ng-1 µg	Nematoda (79.3)	Nematoda (62.5)	Nematoda (96.4)	Nematoda (96.4)	Nematoda (90.3)	Nematoda (46.2)
10	1-2 µg	Nematoda (47.8)	Ostracoda (30.6)	Polychaeta (40.8)	Polychaeta (40.8)	Nematoda (55.6)	Turbellaria (55.6)
11	2-3.98 µg	Ostracoda (31.6)	Bivalvia (33.8)	Oligochaeta (45.8)	Oligochaeta (45.8)	Bivalvia (24.2)	Turbellaria (73.8)
12	3.98-7.94 µg	Nematoda (60.6)	Oligochaeta (37.4)	Oligochaeta (84.7)	Oligochaeta (84.7)	Hydrobiidae (47.6)	Oligochaeta (68.6)

13	7.94–15.85 µg	Polychaeta (50.6)	Oligochaeta (66.5)	Oligochaeta (74.2)	Hydrobiidae (56.7)	Oligochaeta (79.5)
14	15.85–31.62 µg	Polychaeta (53.7)	Oligochaeta (74.8)	Oligochaeta (89.1)	Hydrobiidae (51.4)	Oligochaeta (98.5)
15	31.62–63.1 µg	Polychaeta (56.7)	Oligochaeta (76.3)	Oligochaeta (64.6)	Polychaeta (43.9)	Oligochaeta (89.4)
16	61.10–125.89 µg	Hydrobiidae (81.0)	Oligochaeta (52.7)	Oligochaeta (70.7)	Hydrobiidae (41.8)	Oligochaeta (88.5)
17	125.89–251.19	Hydrobiidae (95.9)	Hydrobiidae (86.2)	Hydrobiidae (66.4)	Hydrobiidae (94.5)	Hydrobiidae (48.0)
18	251.19–501.19	Hydrobiidae (80.3)	Hydrobiidae (86.8)	Hydrobiidae (91.9)	Hydrobiidae (85.8)	Hydrobiidae (50.5)
19	501.19 µg–1 mg	Bivalvia (56.8)	Bivalvia (79.2)	Polychaeta (53.8)	Polychaeta (61.3)	Bivalvia (76.1)
20	1–2 mg	Bivalvia (67.1)	Bivalvia (91.3)	Polychaeta (51.4)	Bivalvia (81.7)	Bivalvia (77.5)
21	2–3.98 mg	Polychaeta (74.7)	Bivalvia (81.6)	Polychaeta (81.3)	Polychaeta (72.5)	Bivalvia (90.1)
22	3.98–7.94 mg	Polychaeta (90.2)	Bivalvia (94.1)	Bivalvia (90.0)	Oligochaeta (58.9)	Bivalvia (92.5)
23	7.94–15.85 mg	Bivalvia (100)	Bivalvia (100)	Polychaeta (91.9)	Bivalvia (100)	Bivalvia (90.2)
24	15.85–31.62 mg	Bivalvia (100)	Bivalvia (95.1)	Polychaeta (92.6)	Bivalvia (100)	Bivalvia (100)
25	31.62–63.10 mg	Bivalvia (100)	Bivalvia (100)	—	Bivalvia (100)	Bivalvia (100)
26	63.10–125.89 mg	Bivalvia (100)	—	—	Bivalvia (100)	—
27	125.89–251.19 mg	Bivalvia (100)	—	—	—	Bivalvia (100)

discontinuities in the spectra, if data are used indiscriminately (DRGAS *et al.*, 1994). To address this problem we developed a technique which coincidentally retained information supplied by each of the samplers, eliminated overlaps and discontinuities, and avoided an unduly heavy weighing on, *e.g.*, single individuals present in a size class. This would be the case if biomass values produced by 2 or 3 samples were simply averaged. Pitfalls of averaging were avoided by developing a procedure for constructing the so-called derived (as opposed to averaged) size spectra. The rationale and procedure for constructing those spectra from data supplied by 3 different types of gear were described by DRGAS *et al.* (1994). Briefly, if – in a meiobenthos size class range for which taxon biomass data were available from two corers – the biomass produced by the small corer was higher than that obtained from the large one, the former was used (the latter might have been an underestimate due to the coarse sieve used). On the other hand, if the large corer produced biomass higher than that obtained from the small corer in a size class, it was assumed that the coarse sieve had no effect on the biomass from that particular size class, and the two biomass values were averaged. Furthermore, if the biomass data obtained by using the large corer and the VAN VEEN grab overlapped over a size class range, the final derived biomass depended on a taxon. Polychaete and oligochaete biomasses were in most cases higher in the corer samples than in the grab, which might have resulted from a gentler handling of the former. Whenever the large corer produced higher biomass for polychaetes and oligochaetes, these were taken as representative of a size class. If the value from the grab was higher, the derived value was an average of the data obtained with the two samplers. In the case of bivalves and the *Hydrobia* snails, the grab samples were assumed to yield reliable values for larger individuals, while the large corer data were used for the smaller individuals. Whenever there were no corer data on the latter, while a grab sample did yield small individuals, their biomass was entered into the spectrum calculations.

Spectra were normalized by dividing biomass of each weight (mass) interval by the width of the weight class, and plotting these values against the upper limit of their respective weight class.

5. Statistical treatment

Significance of between-station differences in meio- and macrobenthos density, biomass and diversity was tested with the KRUSKAL-WALLIS test, a non-parametric analogue of the 1-way analysis of variance (SOKAL & ROHLF, 1981). Significance of differences between slopes of regression lines for normalised biomass spectra were tested using the T'-method, which is an unplanned test for significance of differences between regression coefficients (SOKAL & ROHLF, 1981). The tests and regression analyses were performed using the NCSS statistical package (HINTZE, 1992).

Results

1. Benthic community description

The benthic communities consisted of a total of 16 identified taxa, together with unidentified polychaetes and bivalves in the meiofauna (Fig. 2). The basic characteristics of the communities are given in Table 3.

Mean densities of the meiobenthos ranged between 3.67×10^4 – 23.4×10^5 indiv. \cdot m⁻² (small corer data, Table 3a). Both corers revealed significant differences between mean station densities. Meiobenthic assemblages at stations A, C and W were more abundant than those at B and Y, which suggests sediment type- and/or organic enrichment-related effects (Table 1). Meiobenthos at all stations was numerically dominated by nematodes (Tables 3a,b). There were statistically significant between-corer differences in the number of taxa per station. This was particularly evident at stations C and W, where sampling with the large corer substantially improved the picture of the meiobenthos taxon richness. The appli-

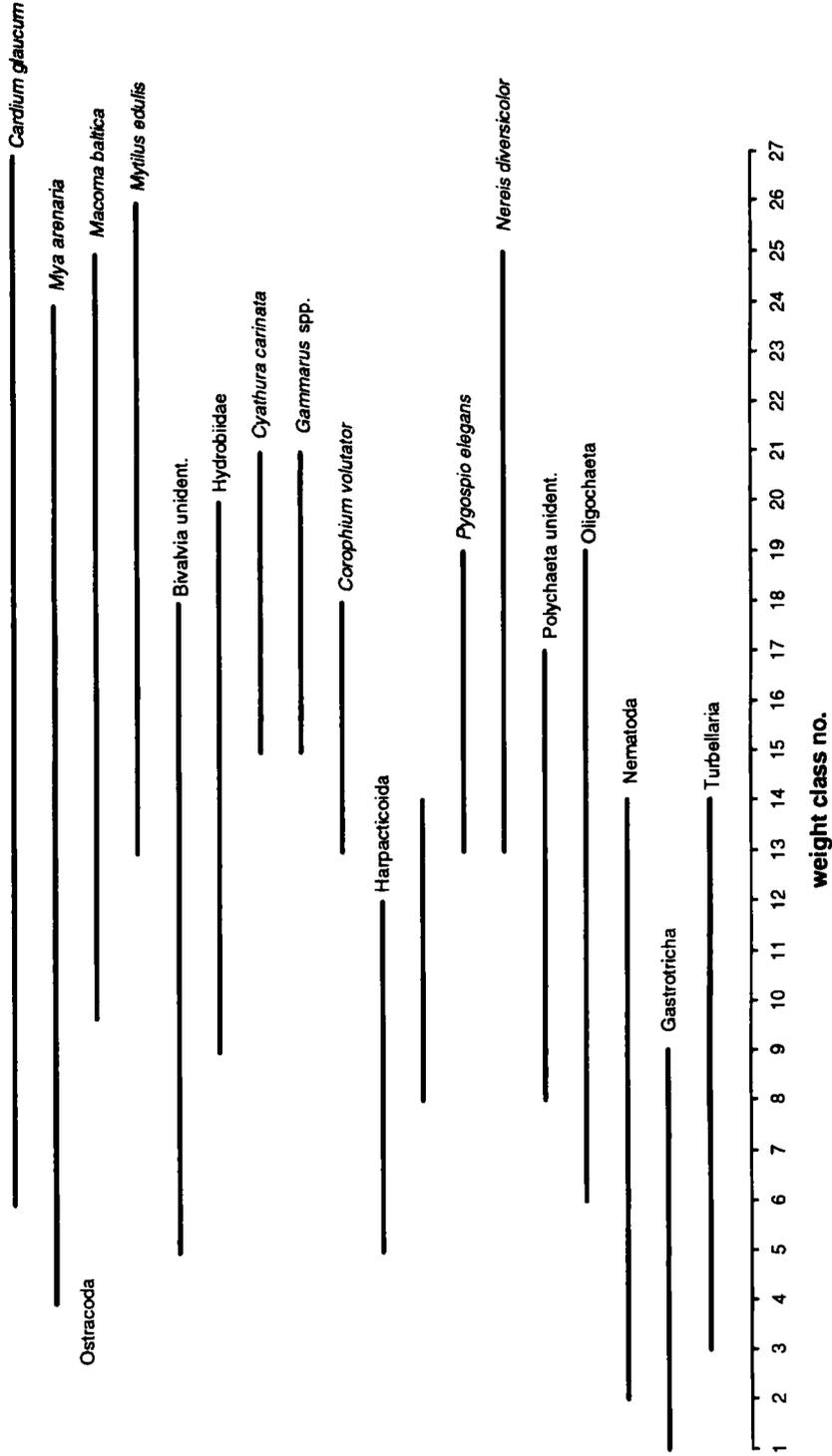


Fig. 2. Size ranges of taxa identified in the study.

Table 3. Parameters of benthic communities at the sampling sites (\pm SD).

parameter	station A	station B	station C	station W	station Y	significance of differences
a. Meiobenthos, small corer						
density [indiv. · m ⁻²]	2340872.33 ± 122319.41	898674.33 ± 92305.07	2218156.0 ± 511769.96	936118.50 ± 77163.03	367315.0 ± 154597.24	P < 0.001
density dominant [%]	Nematoda (96.0 ± 1.85)	Nematoda (82.77 ± 3.57)	Nematoda (98.60 ± 0.96)	Nematoda (100)	Nematoda (66.21 ± 14.57)	
number of taxa	7	8	4	1	5	P < 0.001
H'	0.0948 ± 0.0376	0.3235 ± 0.0386	0.0355 ± 0.0232	0	0.4387 ± 0.1244	P < 0.001
biomass [g C · m ⁻²]	0.6568 ± 0.1316	1.1095 ± 0.6923	0.6260 ± 0.0898	0.1878 ± 0.0202	1.3518 ± 0.7997	P < 0.001
biomass dominant [%]	Nematoda (69.3 ± 21.4)	Oligochaeta (61.55 ± 12.49)	Nematoda (58.42 ± 15.86)	Nematoda (100)	Oligochaeta (90.56 ± 5.27)	P < 0.1
b. Meiobenthos, large corer						
parameter	station A	station B	station C	station W	station Y	significance of differences
density [indiv. · m ⁻²]	738405.67 ± 52891.24	153671.67 ± 125641.49	1274093.67 ± 301464.99	457495.33 ± 86846.92	187943.33 ± 93140.094	P < 0.001
density dominant [%]	Nematoda (90.16 ± 2.12)	Nematoda (46.51 ± 5.0)	Nematoda (95.10 ± 1.74)	Nematoda (88.21 ± 1.43)	Nematoda (74.41 ± 0.45)	
number of taxa	7	7	7	8	6	P > 0.05
H'	0.2009 ± 0.0364	0.6422 ± 0.0707	0.1112 ± 0.0334	0.2520 ± 0.0224	0.3437 ± 0.0514	P < 0.001
biomass [g C · m ⁻²]	0.8837 ± 0.1801	1.1397 ± 0.6708	0.9226 ± 0.1108	0.6313 ± 0.0559	0.6292 ± 0.5442	P < 0.05
biomass dominant [%]	Polychaeta (45.81 ± 5.65)	Oligochaeta (44.99 ± 1059)	Oligochaeta (44.58 ± 11.31)	Oligochaeta (34.65 ± 11.78)	Oligochaeta (81.28 ± 6.83)	

c. Macrobenthos						
parameter	station A	station B	station C	station W	station Y	significance of differences
density [indiv. · m ⁻²]	15053.33 ±2902.16	31590.03 ±2527.85	5056.67 ±2613.13	11853.33 ±2069.84	13593.33 ±9057.33	P < 0.05
density dominant [%]	Hydrobiidae (96.0 ± 1.85)	Hydrobiidae (85.73 ± 2.52)	Hydrobiidae (57.35 ± 2.31)	Hydrobiidae (65.45 ± 9.94)	<i>Mytilus edulis</i> (35.73 ± 30.16)	
number of taxa	7	6	6	6	9	
H'	0.2321 ± 0.0343	0.4401 ± 0.0557	0.4565 ± 0.0737	0.2057 ± 0.0300	0.5946 ± 0.1640	P > 0.05
biomass [g C · m ⁻²]	3.9023 ± 0.8227	80.8867 ± 107.2808	1.5379 ± 0.5980	3.0825 ± 1.5090	23.9517 ± 31.4558	P < 0.01
biomass dominant [%]	Hydrobiidae (41.01 ± 4.61)	<i>Mytilus edulis</i> (74.14 ± 32.75)	Hydrobiidae (39.97 ± 17.62)	Hydrobiidae (39.97 ± 17.62)	<i>Mytilus edulis</i> (66.33 ± 31.34)	P < 0.05

cation of the large corer was also reflected in the meiobenthos taxon diversity (SHANNON-WIENER index, H') for each station. Noteworthy is the fact that H' values were significantly different between stations (Tables 3a,b), higher values yielded by both corers being typical of coarser-grained sediment at stations B and Y.

The mean values of the total meiobenthos carbon biomass ranged from 0.19–1.35 $\text{g C} \cdot \text{m}^{-2}$ (small corer) and 0.63–1.14 $\text{g C} \cdot \text{m}^{-2}$ (large corer). No statistically significant differences were detected between the stations by either of the corers due to a high within-station variability. Nevertheless, particularly in the small corer data set, biomass recorded at stations A, C and W was consistently lower than that at B and Y. Biomass dominants differed between corers at the fine-grained stations. While the small corer showed nematodes as the dominant taxon in the biomass, the large corer, with the elimination of numerous smaller-sized nematodes during processing, emphasised the contribution of larger-bodied polychaetes and oligochaetes.

The macrobenthos (Table 3c) showed significant differences between stations in mean densities and biomasses. The mean density ranged from 556 to 31590 $\text{indiv.} \cdot \text{m}^{-2}$. Coarser-sediment stations accommodated a more abundant macrofauna, which contrasts with the meiofauna. Hydrobiid snails numerically dominated at most stations, except for station Y where the blue mussel *Mytilus edulis* dominated.

Mean carbon biomass of the macrobenthos ranged from 1.5 to 80.89 $\text{g C} \cdot \text{m}^{-2}$. Increased biomass also occurred in coarser-grained sediment, where *M. edulis* contributed, on average, 66.3–74.1% of the organic carbon. Carbon biomass at the finer-grained stations A, C and W was dominated by hydrobiids, averaging from about 40 to 63.4% (Table 3c).

We conclude that benthic biomass depended mainly on nematodes and/or oligochaetes among the meiobenthos, and on hydrobiid snails and *M. edulis* among the macrobenthos. The relative predominance of one or the other component in each size range was apparently related to the sediment type.

2. Biomass spectra

As already mentioned, we identified a total of 16+2 taxa in this study. The size (weight) ranges of the taxa varied over 8 orders of magnitude (Table 2; Fig. 2).

Figure 3 shows biomass spectra obtained at each station. At first glance, there is an apparent difference between the shape of the spectra representing the finer-grained sediment (stations A, C and W) and the coarser sediment (stations B and Y). While all spectra showed an increase in biomass with individual weight (the primary size spectrum structure *sensu* BOUDREAU & DICKIE, 1992), secondary structure (showing an internal variability in the form of troughs and peaks) is more clearly visible in spectra representing biomass distributions at stations A, C and W.

In all the spectra, there is a very clear biomass peak at the 251.19–501.19 ng C weight class, although that peak is less pronounced at stations B and Y. This peak is dominated by nematodes (Tables 2 and 4). As shown by Table 4, subsequent peaks – rather than forming a consistent pattern of macrofauna-dominated peaks –

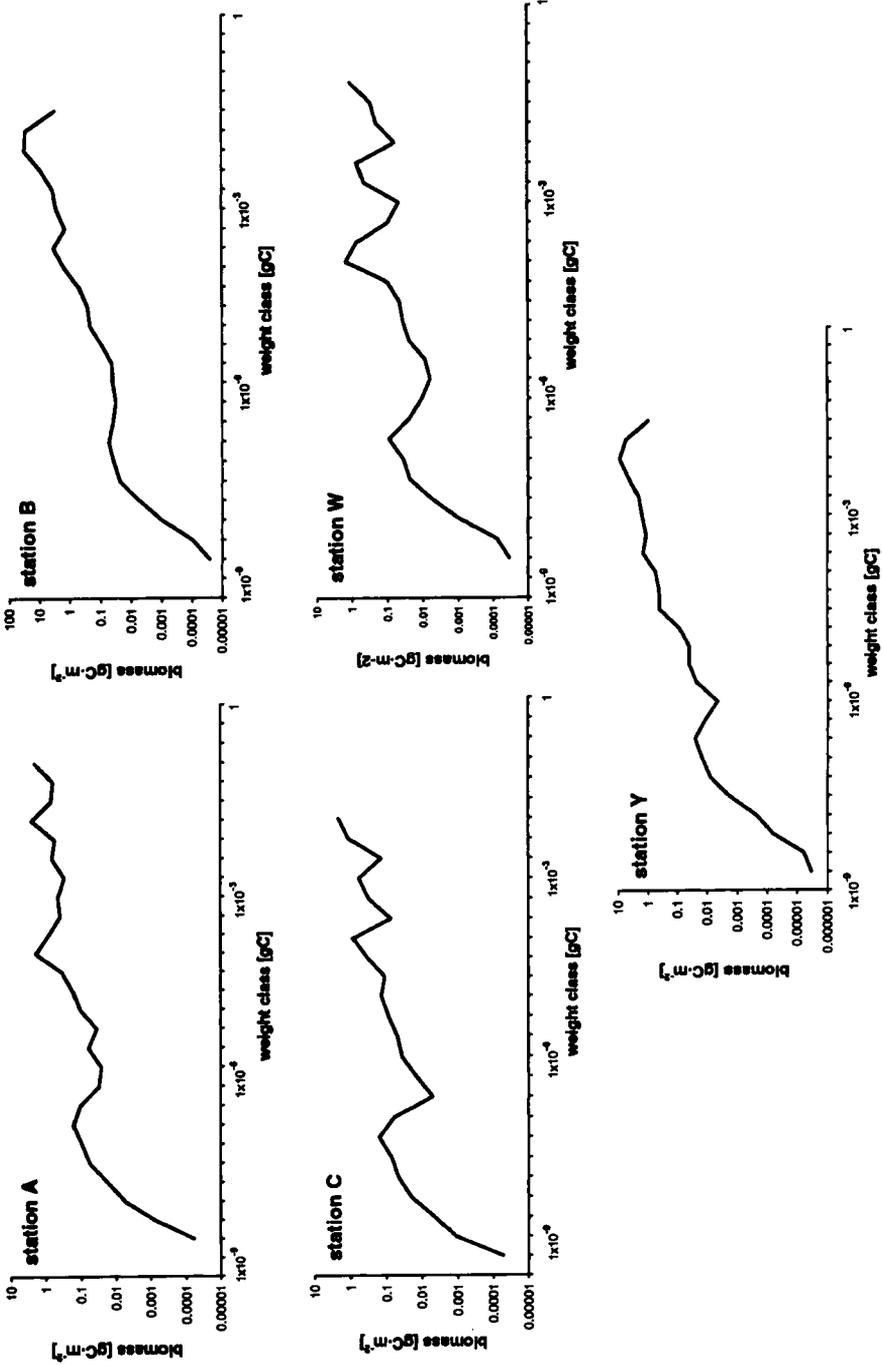


Fig. 3. Biomass size spectra of the benthos at the stations sampled.

Table 4. Biomass spectra peaks and their dominant contributors at the stations sampled.

station	carbon biomass peak (weight class)	dominant
A	251.19–501.19 ng C	Nematoda
	125.89–251.19 μ g C	Hydrobiidae
	15.85–31.62 mg C	Bivalvia
B	125.89–251.10 mg C	Bivalvia
	251.19–501.19 ng C	Nematoda
C	7.94–63.10 mg C	Bivalvia
	251.19–501.19 ng C	Nematoda
	251.19–501.19 μ g C	Hydrobiidae
	2–3.98 mg C	Polychaeta
W	15.85–31.62 mg C	Polychaeta
	251.19–501.19 ng C	Nematoda
	125.89–251.19 μ g C	Hydrobiidae
	3.98–7.94 mg C	Oligochaeta
Y	63.10–125.89 mg C	Bivalvia
	51.19–501.19 ng C	Nematoda
	7.94–31.62 mg C	Bivalvia

shift between stations and their dominants vary, particularly among the fine-grained sediment stations A, C and W. Following the meiofaunal peak, the spectra for stations B and Y are much less structured and show only one macrofaunal peak each, the final weight class coinciding with apparent troughs in the spectra.

3. Normalized size spectra

Normalized size spectra (Fig. 4) simplify comparisons of biomass distributions in different habitats. There was a consistent trend in the distribution of normalised biomasses over individual weight classes. All the regressions of log biomass on log individual weight were highly significant, but the residual variations were moderately high, ranging from $r^2 = 0.51$ to 0.85. The slopes varied from -0.36 (station Y) to -0.61 (station A) and indicated an increase in biomass towards the larger weight classes. The highest residual variations (lower r^2) and shallower slopes were clearly typical of stations B and Y. In spite of these differences, slopes were not significantly different one from another according to the T'-method results (Table 5). Thus the second question posed in the introduction has to be answered negatively.

Consequently, we plotted an averaged normalized biomass spectrum (the bottom right panel in Fig. 4), with a slope of -0.45 and a rather low residual variation ($r^2 = 0.74$). The scatter of data points around the regression line showed that macrobenthos was responsible for most of the variability and that there was a clear separation between the macrofauna of coarse-grained (open symbols) and fine-grained sediment (filled symbols).

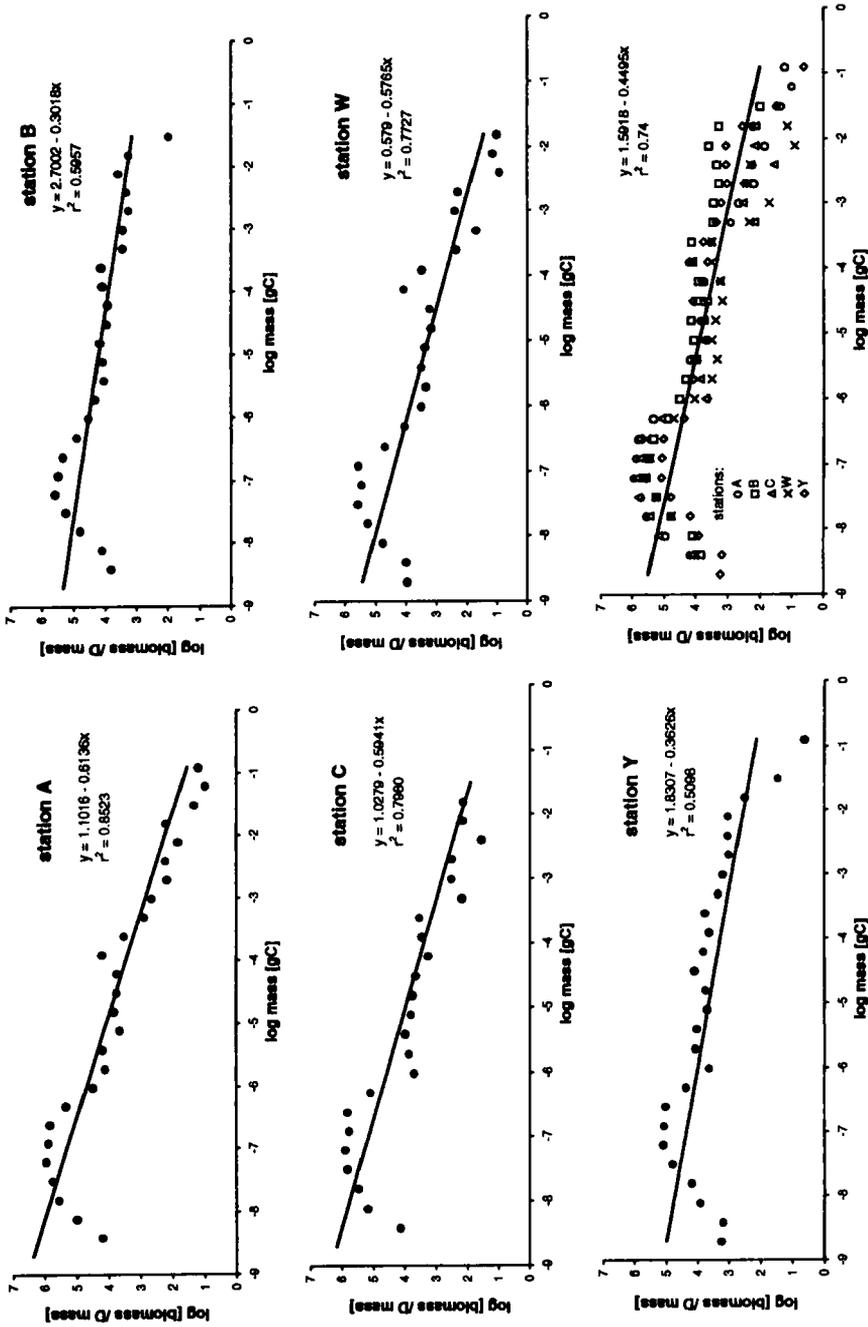


Fig. 4. Normalized biomass size spectra of the benthos at the stations sampled; bottom right panel shows the averaged normalized biomass spectrum of the shallow-water coastal benthos of the Gulf of Gdańsk.

Table 5. 95% comparison interval limits by T'-method for the regression coefficients of normalised biomass spectra; intervals of all the regression coefficients overlap, hence the coefficients are not significantly different.

station	A	B	C	W	Y
lower interval limit	-0.93	-0.61	-0.90	-0.89	-0.66
upper interval limit	-0.31	+0.01	-0.28	-0.27	-0.01

Discussion

In terms of composition, abundance and biomass, the communities in this study were typical of meio- and macrobenthos of coastal sandy habitats of the Gulf of Gdańsk (DRGAS, 1993; HERRA & WIKTOR, 1985; SZYMELFENIG, 1990; WARZOCHA, 1982; WIKTOR, 1985). WIKTOR's (1985) detailed description of benthic trophic types in the area shows that the communities at the sites we sampled were dominated by detritus feeders – nematodes, oligochaetes and hydrobiids (stations A, C and W) – and by detritus and suspensions feeders – nematodes and the blue mussel, respectively (stations B and Y). Nematodes are treated here as detritus feeders because, although we are aware of the diversity of feeding modes within that taxon (JENSEN, 1987), the nearshore Baltic nematode assemblages seem to be dominated by the detritus-feeding guild (SZULWINSKI *et al.*, pers. comm.). The array of taxa identified herein lacks macrofaunal predators such as the hyperbenthic *Crangon crangon*, *Palaemon adspersus* and fish (WIKTOR, 1985). Methods adopted here precluded sampling of the hyperbenthos, hence no data on predator pressure from those animals could be included. The local benthic assemblages are sustained by a constant supply of detritus and, thus, participate in and contribute to the detrital pathways within the trophic structure of the Gulf of Gdańsk ecosystem; this is fuelled by the high phytoplankton primary production and sedimentation of the resultant phytal biomass (WITEK *et al.*, 1993).

Meiofauna-sized animals have long been recognised as an important trophic link in detritus-based food webs (GIERE, 1993). Meiofauna gains a special prominence in coastal depositional habitats of the Baltic (RADZIEJEWSKA, unpubl. data). This prominence was supported by the results of this study: each biomass spectrum, regardless of habitat differences, showed a peak within the meiofaunal size range (251.19–501.19 ng C). Thus our results corroborate the conclusions of SCHWINGHAMER (1981) and WARWICK (1984) that the meiofauna forms a distinct ecological entity.

In this context it is remarkable to note that the meiofaunal peak identified in this study is almost identical with that reported by WARWICK (1984) from a range of fully marine and estuarine sites worldwide with sediment types ranging from silt to medium sand, by GERLACH *et al.* (1985) from silty and fine sand habitats off Helgoland and in the Kiel Bay (34 and 16 m depth, respectively), and by POFF *et al.* (1993) from a Virginia, USA, stream system. On the other hand, it is also noteworthy that the separation between meio- and macrobenthic peaks in the spectra is not as distinct as that found in other studies, most probably due to the use of the large corer.

Macrobenthos produced different peaks shifting in their position within each spectrum from 125.89 $\mu\text{g C}$ to 251.19 mg C, depending on the major species. But again, the peaks generally coincided with those recognised by the first two studies mentioned above.

At the coarse-sand station Y, macrofaunal biomass was dominated by *M. edulis*, which contributed to the spectrum peak. As stated by some authors (KAUTSKY & EVANS, 1987), this species seems to be excluded from predation pressure under the Baltic conditions. On the other hand, there is evidence that the blue mussel in the southern Baltic is heavily preyed upon by long-tailed ducks (*Clangula hyemalis*) and other sea ducks wintering in the Pomeranian Bay; the predation is, however, quite selective and affects the smaller *M. edulis* size classes only (1–10 mm shell length) (KUBE, 1996). Although those ducks do winter in the Gulf of Gdańsk as well, their impact on the blue mussel population there is far less acute than in the Pomeranian Bay, bivalves other than *M. edulis* providing most of the diet for the ducks (STEMPNIEWICZ, 1986, 1994, 1995). Thus *M. edulis* might be expected to represent a biomass 'sink', processing the sedimenting phytal matter and enriching the sediment with the resultant detritus.

Perhaps the most important result of this study is the fact that benthos biomass spectra conformed to a common pattern and could be represented by a single, averaged spectrum, in spite of habitat and community structure differences between the stations (Fig. 4). This supports the view that biomass spectra can be regarded as a unifying concept in community ecology (CATTANEO, 1993). However, it should be remembered that, under specific Baltic conditions, the benthic communities living in well-oxygenated areas above the halocline are distinctly different from those found below the halocline, which are stressed by hypoxia (ELMGREN, 1984). For this reason, challenges for understanding biomass spectra in the Baltic remain and require more studies encompassing a wider depth range; this will allow future research on production and respiration patterns of benthic communities to draw from ecosystem-wide evidence.

Summary

The concept of size spectra, developed by SHELDON & PARSONS (1967) and SHELDON *et al.* (1972), seeks to describe community structure by evoking the distribution of biomass over a sequence of equal intervals of the logarithm of body size. In this study, biomass size spectra were prepared for benthic (macro- and meiobenthos) communities at 5 stations, differing in their sediment characteristics, located in the shallow, coastal area of the Gulf of Gdańsk (Southern Baltic Sea). The purpose of this study was to determine whether the community spectra would allow distinct separation of ecological categories of the benthos and whether habitat differences between stations would significantly affect benthic size spectra.

Benthic biomass at the stations sampled depended mainly on nematodes and oligochaetes among the meiobenthos and on hydrobiid snails and *M. edulis* among the macrobenthos. Regardless of habitat, size spectra peaked initially at the meiofaunal range weight class (251.19–501.19 ng C), identical to that reported in other studies. The separation between meio- and macrobenthic peaks, however, was not as pronounced as that found in other studies. Normalized size spectra demonstrated

that most of the variations in the spectra between stations was introduced by macrobenthos, which differed between the coarse- and fine-grained sediments. Nonetheless, those differences were not strong enough to significantly affect the spectra. In consequence, the benthic biomass spectra of all the stations were found to conform to a common pattern and could be represented by a single, average spectrum.

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