Benthic organism biomass size-spectra in the Baltic Sea in relation to the sediment environment

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Abstract

Biomass size-spectra of benthic organisms (BBSS) were constructed for 44 stations in three basins of the Baltic Sea: Bothnian Bay, Bothnian Sea, and the Baltic Proper, which represents a salinity gradient from about 3‰ to 18‰, respectively. In addition, BBSS were regrouped and analyzed according to an encompassing sediment environmental variable: Loss of weight on ignition (LOI). LOI correlates with many other sediment environmental variables and can characterize the sedimentary environment in a location.

BBSS from the Bothnian Bay were different than those of the Bothnian Sea and Baltic Proper, though BBSS from the latter two basins did not differ from each other. This difference of Bothnian Bay BBSS was indirectly attributed to salinity as it is a region impoverished in both marine and freshwater species; hence individual species size-distributions contribute considerably to the whole resulting in a different BBSS. BBSS grouped according to sediment LOI did not differ from each other. As there were no differences between LOI-grouped size-spectra yet geographical and hence species diversity groupings did differ, it is apparent that the sediment environment is less important than species diversity in determining BBSS patterns in the Baltic Sea. This is in contrast to common environmental explanations for BBSS patterns in other regions.

Published benthic biomass size-spectra (BBSS) of infaunal eukaryotes in coastal marine systems are often bimodal (Schwinghamer 1981; Gerlach et al. 1985; Warwick and Joint 1987). Bimodality of BBSS has been considered a reflection of sediment grain size, with modes corresponding to the optimal body sizes for exploitation of either interstitial living habitats or super-sediment habitats (burrowing and sediment-grain manipulating), respectively (Fenchel 1969; Schwinghamer 1981). These two modes correspond to the commonly recognized benthic size groups meiofauna (8–500 μm) and macrofauna (>500 μm).

This sediment living space argument provides an intuitively satisfying explanation for BBSS bimodality because of its purely physical and external (to the organisms) forcing mechanisms; however, living organisms are not passive particles and have evolved means to overcome some of their bondage to physics and thus may defy simple physical explanations for their patterns. Several workers, therefore, have developed alternative biological explanations for the apparently constant bimodal size-spectra patterns found in different environments—two types of life history strategies of benthic metazoans (Warwick 1984); changes in benthic organism food acquisition strategies with size (Strayer 1991); and complementary coupling between benthic and pelagic

size-spectra (Schwinghamer 1985; Warwick et al. 1986; Warwick and Joint 1987). However, it has been suggested that empirical size-spectra patterns depend on the size intervals and scales used to construct the spectra (Han and Straskraba 1999). Furthermore, a trophic model of pelagic organism size-spectra can generate periodic biomass bump structures over body size (Thiebaux and Dickie 1993) but the validity of trophic bumps remains to be examined in a benthic situation.

Because of the predominant physical explanation for bimodality of marine eukaryotic BBSS, it was hypothesized to exist in freshwater benthos as well, since the sediment constraints there should be similar to marine systems. However, there have been several empirical studies in both marine and freshwater systems showing exceptions to bimodality (*sensu* Schwinghamer 1981)—lentic freshwater (Strayer 1986), lotic freshwater (Bourassa and Morin 1995; Ramsay et al. 1997), brackish (Drgas et al. 1994; Ramsay et al. 1997; Drgas et al. 1998; Duplisea and Drgas 1999), and marine (Edgar 1994). These exceptions to bimodality indicate that a small set of physical constraints, such as sediment grain size, cannot be used to predict the size-spectra pattern in all benthic systems. However, it has been possible to predict pelagic size-spectra patterns from only a few trophic constraints (Platt and Denman 1977; Gaedke and Straile 1994; Sprules and Goyke 1994). However, observed BBSS patterns tend to be similar within certain ranges of conditions identified in single studies, hence BBSS may reflect common processes within a smaller set of conditions than found in pelagic systems. Benthic biomass size-spectra may prove useful for characterization of systems for which little is known about the taxonomic structure, which has been considered as a promising aspect of size-spectra approaches (Platt 1985, Gaedke 1995), since most sediments are poorly characterized taxonomically (Hall 1996; Palmer et al. 1997; Snelgrove et al. 1997). Before BBSS can be accepted as a useful descriptor of a benthic system, patterns of such spec-

tra must be determined in a variety of systems under differing conditions.

Freshwater and marine benthos consist of species which have evolved different strategies of food acquisition, reproduction, and other life histories (Lopez 1988; Strayer 1991). Therefore, it is interesting to examine community BBSS along a stable salinity gradient for any indication of systematic patterns appearing or disappearing as one goes from a marine to a freshwater benthic community.

This study has two major purposes: The first is to examine the patterns of BBSS under different environmental conditions and in different regions of the Baltic Sea. The Baltic Sea is a large semi-enclosed brackish sea with a unique ecology and with only a few localized BBSS descriptions to date (Gerlach et al. 1985; Drgas et al. 1994; Duplisea and Drgas 1999). BBSS studies in the Baltic Sea extends observations to a new type of ecosystem, which represents a transition between marine and freshwater systems. Secondly, this study examines the BBSS pattern along this stable salinity gradient provided by the Baltic Sea for systematic trends in shape in relation to salinity.

Baltic Sea BBSS were grouped according to two independent criteria, sediment environmental variables and geographic location (various Baltic Sea basins), which represents a salinity gradient. Differences in spectra were then examined for trends that could be attributed to grouping criteria.

Methods

Fifty-eight locations were sampled in the Baltic Sea between 55°13′N and 65°27′N and in the depth range 20–130 m between May and June in 1994 and 1995 (Fig. 1). Samples from 44 of these locations were processed for both fauna and environmental data while only environmental data were collected for the remainder. Sampling locations consisted of fine sands, mud and clays which could be adequately sampled with an open-barreled gravity corer. At each sampling station, a 50 cm^2 modified Kajak core sample (Blomqvist and Abrahamsson 1985) and a 0.1 m^2 van Veen grab sample were collected. The top 5 cm of sediment and about 5 cm of overlying water were taken from the core sample and fixed in 4% (final concentration) buffered formaldehyde or glutaraldehyde solution. Grab samples were live-sieved through a 1 mm steel screen and organisms remaining on the sieve were fixed in 4% formaldehyde solution and stained with rose Bengal. An additional sediment sample was taken at each station with a Kajak corer or Askö corer (Ankar and Elmgren 1976) for sediment chemical and physical characterization. Epibenthic water samples were taken at some stations with a Knudsen sampler.

A suite of sediment physical and chemical properties were measured at the stations. In the bottom water collected by the Knudsen sampler, temperature was measured using a mercury thermometer; salinity by conductivity and oxygen concentration by Winkler titration on duplicate samples. Organic C and N were measured with Leco CHN 900 on dried and ground sediment core samples mixed over the top 5 cm of sediment and treated with 0.1 M HCl to remove carbon-

ates. Loss of weight on ignition (LOI) was determined by burning dried ground sediments in a crucible at 550°C for 6 hours.

In the laboratory, organisms from grab samples were picked from remaining sediment and sorted into taxa. Size of individuals was measured using Optimas image analysis software (versions 4–5.2) linked to a black and white camera. Organism size was measured as any or all of longitudinal section area, longitudinal section perimeter, length, and width. These measures were converted to wet weight using published regressions (Ankar and Elmgren 1976; Rumohr et al. 1987), new regressions (Duplisea unpubl. data) or geometric models (Feller and Warwick 1988).

Core samples were sieved through a 500 µm steel sieve into a bucket. The >500 µm fraction was stained with rose Bengal and organisms were picked out and measured as above. The sediment-water mixture that had passed the 500 µm sieve was then subsampled with 60 cm^3 syringe (subsampling factor 60/1,000). This subsample was sieved through a 40 µm steel sieve onto a 5 µm Nitex mesh sieve. Remnants on the 40 µm sieve were washed back into the bucket. The >40 µm fraction was then sieved in small portions onto a 40 µm steel sieve and washed into a 1.5 L Erlenmeyer flask with 1.15 g cm^{-3} (final density in flask) Ludox (colloidal silica). The sediment-Ludox mixture was then shaken and allowed to sit for 1.5 h. Then, the top ca. 100 ml of the mixture was decanted onto a 40 µm sieve then washed and preserved in 2% buffered formaldehyde solution. This process was repeated, allowing the sediment-Ludox mixture to sit >1 h. This method of Ludox extraction for meiofauna-sized benthic organisms (40–500 µm) has >90% efficiency (Ólafsson and Elmgren 1997).

The subsampled core fraction remaining on the 5 µm sieve (about 5 ml of material) was washed into a 50 ml round bottom centrifuge tube with filtered 1.20 g cm^{-3} (final density in tube) Ludox. This was spun in the centrifuge at 1,000 × g for 5 min and the supernatant decanted. The sediment plug was resuspended and spun again at 3,500 × g for 15 min. The decantate from these processes was washed onto a 5 µm sieve with tap water (checked previously for particles by running ca. 20 L through a 5 µm sieve and staining: Negligible material remained on the sieve) to wash it free of Ludox. The remains were then preserved in 2% formaldehyde solution and stained with Acridine Orange (AO; Becton Dickinson No. 4349400) and kept in the dark at 4°C until analysis.

The 6–40 µm AO stained extract was washed into a 50 ml plankton settling chamber, covered and left undisturbed for >4 h. The resulting slide was counted on an inverted plankton microscope with a mercury light source passing through an ultraviolet (UV) light filter to differentially light organisms and ambient detritus. A transect was then run across the slide, counting about 10 fields at ×100, and a subsampling factor was calculated accordingly. A highly sensitive fluorescence detection camera attached to various intermediary devices brought an image to the image analyzer, where organisms were measured automatically based on their brightness threshold with relative ambient detritus. Automatically identified objects in each field were briefly examined and excluded from measurement if they were obvi-
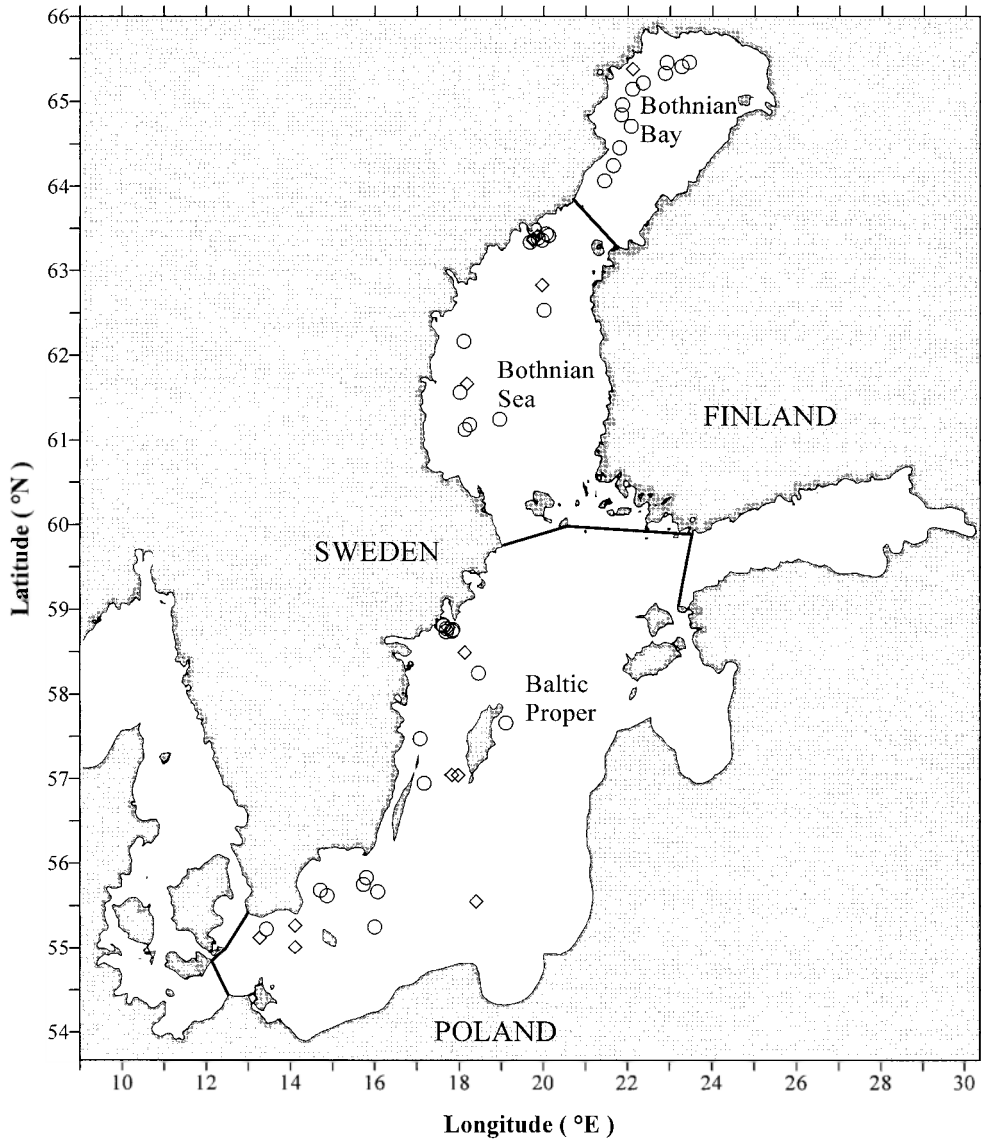
Duplisea

Fig. 1. Map showing sampling locations examined in this study. Circle (○) symbols represent sites where both benthic organism samples and sediment environment samples were processed. Diamond (◇) symbols represent locations where only sediment environment samples were processed.

ously incomplete organisms. Organisms were classified as nematodes, ellipses, or spheres based on their circularity (perimeter^2/area). Organisms smaller than 30 μm^2 were excluded as they were probably not properly represented by sieving through a 6 μm sieve.

The 6–40 μm fraction, though important to assess for biomass, was largely devoid of ciliates which would be expected in this size range (Fenchel 1967). Small protozoans and protists were present in this fraction but the preservation of samples in formaldehyde is detrimental to obtaining quantitative estimates of protozoan densities. The 6–40 μm sieve fraction from these samples consists largely of the more robust benthic organisms including sedimented phytoplankton and some detritus, pollen was excluded. Certain combination artifacts occur in the spectra due to the inclusion of this

fraction such as sharp changes in biomass in the weight class range of −5 to 2. Therefore, one must take care not to overinterpret structure appearing in the spectrum at these transition points.

The 40–500 μm fraction was usually divided into 40–200 μm and 200–500 μm for measuring, except for a single sample, for which finer sieve gradations were used. Organisms were divided into major taxa (e.g., nematodes, harpacticoids) or into species for most macrofauna. If numerous enough, usually 50 individuals of each taxon in each sieve fraction were measured. Subsampling was carried out by volume if numbers of individuals were large, or by counting if there were fewer individuals of a taxon.

Not all of these procedures were used on all samples, but several replicates of each procedure are usually represented
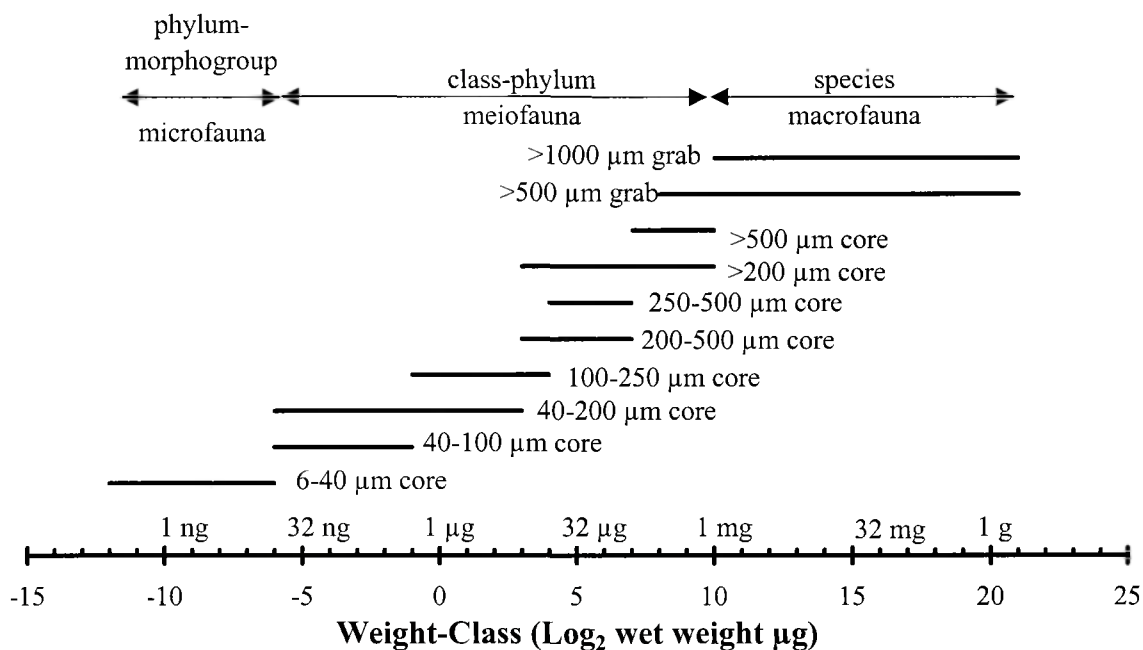
Fig. 2. Organism size ranges effectively sampled by different sieves and gears used in this study. The general level of taxonomic resolution applied to organisms found in different size ranges is demarcated on the upper border.

in the spatially averaged spectra presented here. One should be aware though, that not all points in the average spectra presented have the same number of replicates, even within a spectrum. However, the standard errors presented in figures were calculated according to the actual weight-class specific sample size. Additionally, since different gears and sieve sizes sample different size ranges of organisms, these ranges were used to determine cut-off points for combining spectra from different gears (Fig. 2). Kajak core and van Veen grab BBSS showed the least discrepancy at weight-class 10 and therefore this was chosen as the transition between Kajak and van Veen spectra, with Kajak core data used for weight-classes <10 and van Veen grab data used for weight-classes ≥10.

Size-spectra in this paper are presented with a $\log_2$ wet weight μg binning on the x-axis and $\log_{10}$ wet biomass in g

m^{-2} on the y-axis. The x-axis scaling represents the smallest size of organisms in the integer weight-class, e.g., a $\log_2$ weight-class of -2 encompasses organisms with individual weights $\geq 2^{-2}$ and $<2^{-1}$ μg or ≥ 0.25 and <0.50 μg wet weight. True zero biomass values are considered to be those zero values in the body size range which is adequately sampled by the gear and laboratory methods used (Fig. 2). The organism size sampling range for all gear types combined is considered to be $2^{-12} - 2^{22}$ μg (0.25 ng to 4.2 g) wet weight. Zero biomass values are considered as such for all averaging and statistical analyses. For graphical representation and analyses, true zero biomass values in the averaged spectrum are represented as points on the x-axis (0.0001 g wet wgt m^{-2}).

Grouping of data—To overcome obstacles created by missing data in a dimensional reduction of the multivariate environmental dataset, Spearman rank order nonparametric correlation between environmental variables was conducted using pair-wise deletion. These correlations indicated that there is considerable redundancy in the environmental data set of stations, and a grouping of Baltic Sea stations based on the near complete data set of LOI values captures most of the differences in the environmental data set (Table 1). Though N had a stronger correlation than LOI with most other measured variables, LOI was measured at almost all stations and therefore was chosen as the grouping variable. Three LOI groupings were selected which divided the LOI range into roughly three equally spaced intervals and which gave sample sizes >10 for each of the three groups of Baltic Sea stations (Table 2); geographic regions included in each group are shown in Table 3. These three groups were created in order to examine the behavior of BBSS under a range of environmental conditions yet which did not require a fine

Table 1. Spearman rank order correlations between sediment environmental variables in the Baltic Sea. Correlation coefficients (r) values are reported in upper triangle, sample size is reported in the lower triangle. Significant values (P < 0.05) are made bold. C = organic carbon. N = organic nitrogen. LOI = loss on ignition. O₂ = bottom water oxygen concentration. H₂O = water content. SAL = bottom water salinity. DPT = water depth. Missing data were pairwise deleted.

	C	N	LOI	H₂O	O₂	SAL	DPT
C		**0.98**	**0.90**	**0.84**	**−0.81**	0.34	**0.59**
N	30		**0.85**	**0.83**	**−0.74**	**0.42**	**0.54**
LOI	30	30		**0.87**	−0.45	0.24	**0.30**
H₂O	14	14	34		**−0.50**	**0.46**	0.17
O₂	17	17	33	30		**−0.50**	**−0.65**
SAL	30	30	55	34	35		−0.15
DPT	30	30	55	34	35	58	

Table 2. Environmental variables for station groupings. LOI = loss on ignition group (*see text*). C = organic carbon. N = organic nitrogen. H_2O = water content. Values are means ± SE. and values in italics are sample sizes. All sampled stations are represented here, therefore sample sizes vary from the organism data.

	Depth m	C % dry wt.	N % dry wt.	LOI % dry wt.	Salinity ‰	Oxygen mg L⁻¹	H_2O % wet wt.
LOI L	57.8 ± 3.7 (21)	1.22 ± 0.23 (13)	0.13 ± 0.03 (13)	2.77 ± 0.24 (23)	5.89 ± 0.48 (23)	8.90 ± 0.56 (11)	50 ± 3 (14)
LOI M	57.4 ± 5.6 (18)	2.38 ± 0.19 (8)	0.22 ± 0.02 (8)	6.06 ± 0.21 (19)	5.51 ± 0.32 (21)	9.86 ± 0.64 (12)	62 ± 3 (9)
LOI H	75.7 ± 7.4 (15)	4.44 ± 0.14 (10)	0.49 ± 0.04 (10)	12.3 ± 0.40 (14)	9.56 ± 1.28 (15)	5.86 ± 1.18 (12)	84 ± 1 (11)
Baltic Proper	59.8 ± 4.5 (26)	3.00 ± 0.48 (14)	0.35 ± 0.06 (14)	8.15 ± 0.96 (23)	9.39 ± 0.67 (26)	7.88 ± 0.75 (10)	69 ± 15 (23)
Bothnian Sea	55.3 ± 5.8 (14)	2.30 ± 0.08 (3)	0.25 ± 0.01 (3)	4.28 ± 0.49 (19)	5.43 ± 0.06 (19)	8.95 ± 0.60 (10)	53 ± 16 (11)
Bothnian Bay	75.4 ± 6.7 (14)	2.17 ± 0.36 (14)	0.19 ± 0.03 (14)	5.85 ± 0.93 (14)	3.39 ± 0.18 (14)	*11.5 ± 0.29 (4)	*61 ± 9 (4)

* Taken from a subset of the same stations but sampled in 1987 (Leonardsson 1988).

Table 3. Redundancy of LOI and geographic basin grouping regimes for Baltic Sea basins only. Measured as number of station of each group in one regime appearing in each group of the other regime.

	Baltic Proper	Bothnian Sea	Bothnian Bay
LOI L	5	7	6
LOI M	5	7	3
LOI H	8	0	3

and hence questionable partitioning of a continuous environmental variable.

Three geographic groupings of Baltic Sea BBSS were chosen which represent the three major basins of the Baltic Sea sampled in this study (Fig. 1). These regions are separated by sills and have both geological and biological justification for their separation (Elmgren 1984; Wallentinus 1991). LOI values were highest in the Baltic Proper and lowest for the Bothnian Sea; however, organic carbon and nitrogen were lowest in the Bothnian Bay while still highest in the Baltic Proper (Table 2). Salinity was highest in the Baltic Proper and decreased toward the Bothnian Bay, in keeping with the Baltic Sea salinity gradient. Oxygen content was lowest in the Baltic Proper and highest in the Bothnian Bay; however, average depth was greater in the Bothnian Bay than in either the Baltic Proper or Bothnian Sea, indicating that differences between basin environmental variables were not simply due to sampling above or below a halo- or thermo-cline.

Grouping of Baltic Sea stations by both geographic basin and by LOI group cannot be considered a redundant analysis as stations belonging to most LOI groups are present in all basins (Table 3). That is, the groupings do not overlap excessively, despite similarities of the sample size of the grouping regimes. The one exception is that no stations in LOI H, with the highest organic content, came from the Bothnian Sea. This indicates that the two grouping schemes have the potential to reveal different information.

Statistical analyses—Statistical analyses were performed using Statistica 5.2 and Splus 4.5 software. Statistical significance is reported for $\alpha = 0.05$. BBSS between various groups were compared using discriminant analysis (DA). DA is the same as MANOVA but post hoc analyses tend to differ (Duarte-Silva and Stam 1995). To obtain the complete matrix of values for DA, stations where not all sieve fractions were examined were removed from the analysis. DA was computed on the log transformed summed biomass in 5 adjacent weight-classes starting at weight-class −6: (−6 to −2), (−1 to 3), (4 to 8), (9 to 13), (14 to 18), (19 to 24). This reduced the matrix to contain six variables which is equivalent to testing BBSS containing 6 weight-classes and reduces the potential for an ill-conditioned matrix. Assumptions of homogeneity of variances were tested with Levene's test: variable (14 to 18) was marginally heteroscedastic while variable (19 to 24) was quite heteroscedastic. Probability plots were examined for assumptions of normality with which all variables complied. The body size location of maximum difference between two cumulative distributions (D_{max}), was
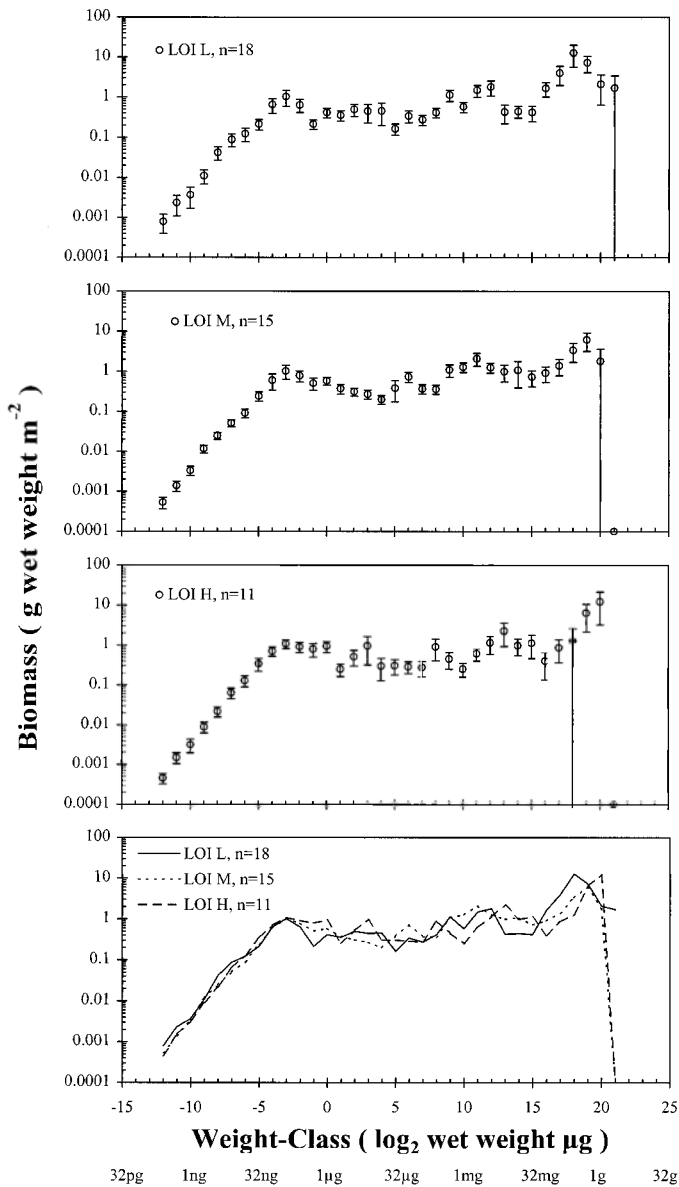
Fig. 3. Benthic biomass size-spectra of eukaryotes when stations were grouped according to three ranges of sediment loss on ignition (LOI) values. Values are means ± 1 SE. True 0 values are represented as points on the x-axis (0.0001). Linear individual wet weight at major ticks is presented below the primary x-axis scaling in $\log_2$ wet weight. Note logarithmic scaling of biomass on the y-axis.

used as an indicator of the body size class where two spectra differed most from each other. D_{max} reported here provides a type of cross validation with DA results.

Results

Station grouping characteristics—The group with the lowest LOI values (LOI L) had an average LOI value of 2.8%; the middle LOI group (LOI M), 6.1%; and the highest LOI values (LOI H), 12.3% (Table 2). Organic carbon (C) and nitrogen (N) follow LOI very closely. C/N ratios were

Table 4. Result of DA and body weight-class of D_{max} values between biomass size-spectra, grouped according to loss on ignition value (LOI Low, Medium, and High) and location. BP = Baltic Proper, BS = Bothnian Sea, BB = Bothnian Bay. ns = not significant ($P > 0.05$).

	Location of D_{max}	N	DA P
LOI L vs. LOI M	18	11, 7	ns
LOI L vs. LOI H	18	11, 11	ns
LOI M vs. LOI H	18	7, 11	ns
BP vs. BS	20	9, 7	ns
BP vs. BB	20	9, 9	0.03
BS vs. BB	18	7, 9	0.05

9.4, 10.8, and 9.1 for LOI L, M, and H, respectively indicating that all locations are similar in proportions of variables and hence differ only in absolute amounts. Salinity and depth were greatest, and bottom water oxygen concentration lowest in LOI H, which is consistent with sampling below the primary halocline (50–70 m) in the Baltic Sea (Wallentinus 1991). However, bottom water oxygen was on average 5.8 mg L^{-1} which is well within the range tolerated by most benthic organisms (Rosenberg et al. 1991). Sites with low oxygen concentrations that were considered in the BBSS probably experience only periodic hypoxia, which is tolerated by most Baltic benthic organisms (Rosenberg et al. 1991). This conjecture is supported by examination of the station with the lowest bottom water oxygen concentration at the time of sampling (0.74 mg L^{-1}). This station had a biomass (17.3 g wet weight m^{-2}) above several other well oxygenated locations and 13 different taxa including 10 taxa in weight-classes <10, and 4 taxa in weight-classes ≥10. Hence BBSS differences in this study cannot be attributed to sampling sites suffering from known problems caused by low oxygen in the Baltic Sea (Elmgren 1989; de Jonge et al. 1994). Sediment water content increased with LOI as depositional areas tend to have fine sediments with higher organic and water content.

Biomass size-spectra based on LOI groupings—BBSS in all groupings show an increase in biomass from weight-class −12 to a first peak in weight-class −3 (Fig. 3). After the initial peak, spectra oscillate by approximately half an order of magnitude around a biomass of ca. 0.4 g wet weight m^{-2} for all LOI groups until weight-classes >10. At weight-classes >10 biomass increases in all groups to an initial local maximum at weight-classes between 11 and 13, followed by a decrease and a global maximum at weight-classes between 18 and 20. The LOI H spectrum has maximum biomass in the ultimate weight-class, whereas LOI L and M spectra peak before the ultimate weight-class. Generally, variability at single points in the spectra were low relative to the biomass range of data but weight-class specific biomass after the global maximum tended to be more variable than that before the maximum. None of the LOI spectra were significantly different from each other (DA, $P > 0.73$). The body size location of D_{max} occurred at weight-class 18, well within the macrofauna domain of the size spectrum (Table 4).
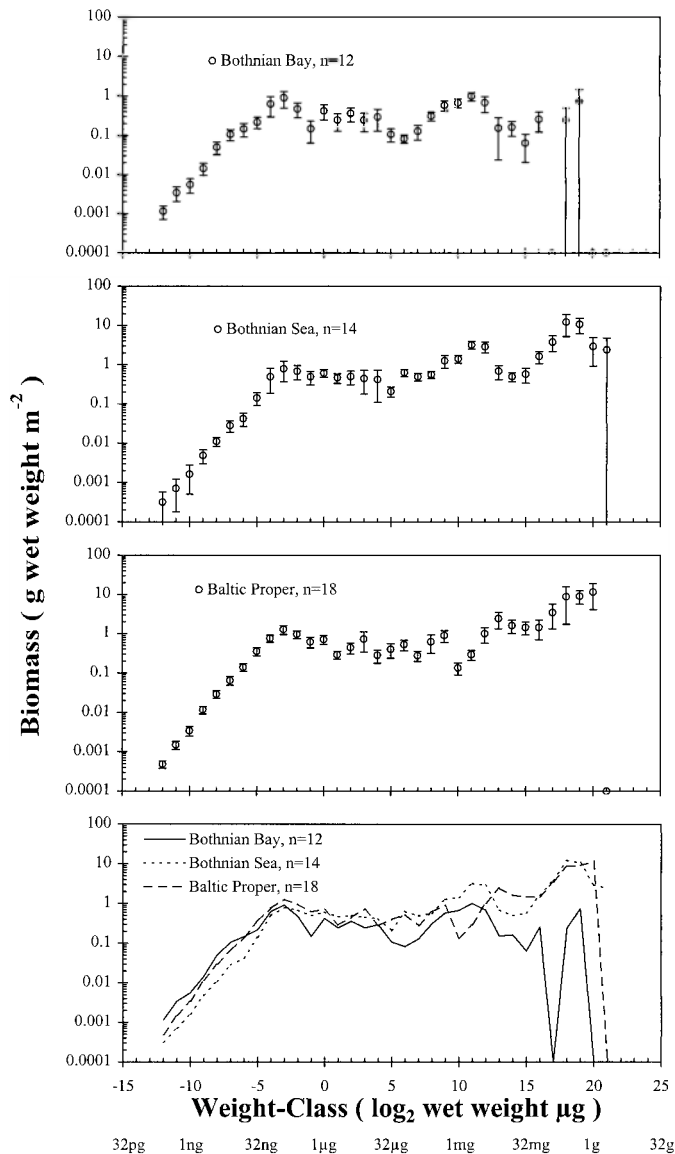
Fig. 4. Benthic biomass size spectra of eukaryotes when stations were grouped according to geographic region. Values are means ± 1 SE. True 0 values are represented as points on the x-axis (0.0001). Linear individual wet weight at major ticks is presented below the primary x-axis scaling in $\log_2$ wet weight. Note the logarithmic scaling of biomass on the y-axis.

Biomass size-spectra based on geographic groupings—BBSS in Baltic Sea basins increased in biomass to peak at weight-class -3 at about 1 g wet weight m^{-2} (Fig. 4). In the Baltic Proper BBSS, biomass decreased after weight-class -3 by about half an order of magnitude to oscillate about that level until weight-class 10, after which biomass increased again to a secondary peak of the same order of magnitude as the first. In the Baltic Proper and Bothnian Sea spectra, a global maximum of >10 g wet weight m^{-2} was found in weight-classes 20 and 18, respectively but in the Bothnian Bay spectrum, a low variability biomass peak of ca. 1 g wet weight m^{-2} was found in weight-class 11 and

Table 5. Standardized discriminant coefficients to distinguish Baltic Sea basins on the basis of their benthic biomass size-spectra patterns. Variables are summed organism biomasses in the weight-class ranges indicated (*see* methods for details). Z = canonical variable; SZ = canonical variable determined by forward stepwise DA. % Contribution is the contribution to group separation by each canonical variable; a P-value > 0.05 indicates that the canonical variable as well as any further canonical variables do not contribute significantly to discrimination between groups.

	$Z1$	$Z2$	$SZ1$	$SZ2$
-6 to -2	-0.83	0.55	-0.72	-0.40
-1 to 3	0.19	-0.44	—	—
4 to 8	-0.83	0.24	-0.77	-0.17
9 to 13	0.03	-1.15	-0.07	1.07
14 to 18	-0.13	0.35	—	—
19 to 24	-0.39	-0.58	-0.53	0.24
Eigenvalue	1.33	0.26	1.29	0.22
% Contribution	83.6	16.4	85.4	14.6
P	0.05	0.47	0.01	0.26

high variability peak of ca. 0.75 g wet weight m^{-2} in weight-class 19.

DA between geographically grouped BBSS indicated that the Bothnian Bay was significantly different from the other two basins, but that the Bothnian Sea and Baltic Proper spectra did not differ from each other (Table 4). D_{max} values were found in weight-class 20 when the Baltic Proper was compared with the other two basins and weight-class 18 when the Bothnian Sea was compared with the Bothnian Bay. The first two discriminant functions in DA explained most of the variance in location, with the first accounting for 83% (Table 5). Summed weight-classes (-6 to -2), (4 to 8), and (19 to 24) were the most important for distinguishing location in the first discriminant function while (9 to 13) was overwhelmingly the most important for the second discriminant function (Table 5). A stepwise DA removed variables (-1 to 3) and (14 to 18) from the resulting function and decreased the model P-value to 0.01; however, no real increase in discriminating power resulted from the stepwise DA as the new canonical variable still could not distinguish the Bothnian Sea from the Baltic Proper with any greater success. For both DA procedures, only the first canonical variables ($Z1$) were significant for distinguishing groups (Table 5).

Repeating the DA while leaving out the two heteroscedastic variables, (14 to 18) and (19 to 24), decreased the model P-value to 0.01, yet still the resulting discriminant function made a 15–20% error in classifying spectra as coming from the Bothnian Sea or the Baltic Proper. Hence, heteroscedasticity was not important in the interpretation of spectra using DA.

Discussion

BBSS examined in this study had characteristic shapes which can be generally described as an increasing function of body size. The relationship was not strictly linear but roughly increased in biomass to a meiofauna peak/plateau, then continued at that biomass to increase again in the ma-

crobenthic size range. This pattern was generally found both for groupings of BBSS based on loss on ignition values of sediments and for major geographic basins of the Baltic Sea.

Baltic Sea BBSS found in this study, although quite similar to each other, differed from the bimodal metazoan size-spectrum pattern sometimes found in aquatic sediments (Schwinghamer 1981; 1988; Gerlach et al. 1985; Warwick and Joint 1987; Poff et al. 1993) (Gerlach, for the Helgoland location only). The Baltic Sea spectra in this study were very similar in form to the BBSS described by (Drgas et al. 1994) for the Gulf of Gdansk in the southern Baltic Sea and from Kiel Bay in the Baltic Sea (Gerlach et al. 1985). The present study and other Baltic Sea BBSS studies (Gerlach et al. 1985, Drgas et al. 1994; 1998) indicate that the Baltic Sea BBSS do not display the characteristic meiofauna-macrofauna trough described by Schwinghamer (1981) but rather show a step-like increase in biomass first to meiofauna then to macrofauna. If ciliates were better accounted for in these studies, the initial increase in biomass to the meiofauna peak would appear more curved (like an inverted parabola) rather than linear; however, it is unlikely that the biomass of ciliates would account for a large amount of biomass in these fine sand and mud sediments.

BBSS similar to those found in this study have been reported in freshwater (Strayer 1986; Ramsay et al. 1997), whereas other freshwater studies have found unimodal abundance size-spectra (Bourassa and Morin 1995), in some cases for epilithic organisms only (Morin and Nadon 1991; Morin et al. 1995). Several freshwater studies that dealt only with macrobenthic size ranges have shown bimodality (Hanson et al. 1989; Rasmussen 1993; Rodriguez and Magnan 1993), which are usually due to the presence of a few key taxa, as well as the unimodality for a single benthic group, expected from Schwinghamer's hypothesis (Rasmussen 1993). A bimodal macrobenthic size-spectrum was found in shallow-water Antarctic benthos due to the presence of large filter-feeding taxa which are not present in deeper waters where pelagic food sources are scarce, hence a unimodal spectrum (Saiz-Salinas and Ramos 1999).

Since the bimodal eukaryote BBSS was described by Schwinghamer (1981), subsequent BBSS studies have often been interpreted as either conforming or not conforming to a bimodal spectrum. Close examination of Schwinghamer's data reveals that the difference in biomass between the meiofauna peak and the meiofauna-macrofauna trough is less than an order of magnitude. This level of difference can be found even in the center portion of the spectra presented in this study, though at varying body sizes. However, data presented in this study do not appear to be bimodal. A composite plot in Schwinghamer (1981) which includes data from many different ecosystems indicates that two studies (Fenchel 1969; Warwick et al. 1979) have a very high biomass within the meiofauna-macrofauna trough region. In many regards these studies resemble the increasing biomass spectrum found in Mirror Lake (Strayer 1986), but it is difficult to say how Strayer's BBSS would appear if grab sample data were also included in his spectrum. Therefore, the generalization of a bimodal eukaryotic size-spectrum (*sensu* Schwinghamer 1981) does not seem entirely supported by

the composite data and is now proving applicable only to a minority of BBSS studies.

The bimodal eukaryote BBSS pattern described by Schwinghamer (1981) was explained as arising from physical constraints placed on organisms living in sediments (*see above*). Schwinghamer's own data, from the coasts of Nova Scotia and New Brunswick, showed remarkable regularity prompting the hypothesis. The physical theory outlined by Schwinghamer (1981) is testable. The theory as first proposed suggested that in sediments where grain size or, more exactly, pore-space size, was large, the meiofauna-macrofauna trough would be shifted to a larger body size; if sediment average pore size was small, the position of the trough would be shifted to smaller body sizes (Strayer 1991). Schwinghamer (1981) sampled silt/clay, sand, and mixture sites and did not find notable differences in the shapes of the size-spectra. Similarly, species size-spectra show no obvious relationship with sediment grain size (Warwick 1984). Both older and more recent research suggests that interstitial organisms are more likely to respond to other sediment chemical and physical factors such as interstitial oxygen concentration (Jansson 1967; Snelgrove and Butman 1994; Strayer et al. 1997) and that response to pore space is species-specific (Williams 1972). Sites with a wide range of sediment properties, including water content, were included in this study (Table 2). These sediment characteristics usually covary, including sediment grain size and organism-available pore space (Williams 1972; Snelgrove and Butman 1994). Therefore, within the confines of sediments that can be sampled with a modified Kajak corer, a wide variety of sediment grain sizes were sampled. BBSS grouped according to LOI values did not differ significantly from each other (Table 6), and thus it does not appear that differences in sediment grain size strongly influence the shape of the BBSS in the Baltic Sea. This has been supported by a separate study in the Baltic Sea (Duplisea and Drgas 1999) and at a site along the English coast (Parry et al. 1999).

In locations where the organism community contains members of both marine and freshwater systems that coexist in a stable community (i.e., assemblages are not ephemeral and change with the tide or float downstream), it is interesting to examine BBSS for patterns that could reflect the relative influence of each organism group. The Baltic Sea has a relatively stable bottom salinity for a fixed location, it is contiguous with both fresh and marine waters, and therefore is an ideal location for this type of examination. The Baltic benthos is known to contain species that evolved in both marine and freshwaters and which coexist at the same locations (Wallentinus 1991).

Despite the ideal natural experiment provided by the Baltic Sea, there is little evidence of a transition in BBSS shape as salinity changes. However, it has been shown that a single pattern characterizing a system is often not the case (*see above*) and that makes spotting a transition difficult. Broad patterns do appear though, such as the absence of large bivalves in the low salinity Bothnian Bay. This is a result of organisms which evolved in marine environments not coping with low salinity; however, the effect lacks the subtlety that one might expect from fundamental differences in food acquisition behaviors between some marine and freshwater

benthos (Lopez 1988; Strayer 1991). This concept rephrased as a question would be: can BBSS patterns of marine and freshwater benthos be attributed to differences in body size feeding strategy niches afforded by the two environments? The effect observed in the Baltic Sea is likely an osmotic stress combined with low calcium stress of the Bothnian Bay for marine bivalves. DA did show that the Bothnian Bay was unique while the spectra from the Baltic Proper and Bothnian Sea were sometimes quite similar. It could be that the Baltic Sea has such a low species diversity (macrobenthic species number in this study: Baltic Proper 5.3 ± 0.9; Bothnian Sea 4.2 ± 0.3; Bothnian Bay 2.2 ± 0.2) that niches are too broad to reveal such differences at the community scale. Such differences would be best examined in high diversity benthos with a stable salinity gradient and by examining the size distribution of feeding types along the gradient. It is questionable if this sort of environment exists in nature.

Past work has shown that meiofauna biomass decreases by less than a factor of 6 from the southern Baltic Proper to the Bothnian Bay, while macrofauna biomass decreases as much as 100-fold over the same range (Elmgren 1978). This work corroborates this, as the discrepancy between the Bothnian Bay BBSS and the two more southern basins' BBSS diverge with increasing body size (Fig. 4). A threefold explanation was offered for this pattern: (1) The absence in the Bothnian Bay of large filter-feeders which actively couple pelagic production to the benthos more efficiently than does purely passive organic material deposition; (2) meiofauna are favored in carbon-poor systems like the Bothnian Bay because they are more efficient at selecting small, high-quality food particles than are macrofauna, as thought to apply to deep sea benthos (Thiel 1979; Soltwedel et al. 1996); and (3) in areas where nonselective deposit feeders are common, meiofauna may be reduced in biomass due to passive predation.

The first explanation is supported by this study, as modal body weight for two dominant filter feeders, *Macoma balthica* and *Mytilus edulis*, fall into the large-body-size classes where basin BBSS diverged most (Fig. 4). Furthermore, these bivalves decrease in abundance going from the Baltic Proper to the Bothnian Bay.

The second explanation is not supported by this study: BBSS based on LOI groupings (where food availability, measured as organic content, decreases from LOI H to LOI L) do not show that small organisms are favored over large organisms at locations with low organic content (Fig. 3). This theory, however, was originally developed for the deep sea and testing it with LOI grouped spectra may not be correct in more hydrodynamic areas like the Baltic Sea because small food particles are more susceptible to removal by water currents.

The third explanation for differences between meiofauna–macrofauna biomass between Baltic Sea basins is not directly examined here since an analysis of functional groups constituting the spectrum was not made.

Despite the observation that macrofauna biomass differs considerably more between basins than meiofauna biomass, it was the biomass variables in the meiofauna size range that contributed most to the basin separation in the discriminant

analysis (Table 5). This is likely owing to the low variability of biomass in the meiofauna size range relative to that of the macrofauna (Figs. 3, 4). Relatively high variability in the macrobenthic size ranges probably results from the influence of single species effects as described above, as well as sampling at a grain smaller than the scale of heterogeneity of large macrobenthic organisms (Wiens 1989; Duplisea 1998).

The present study indicates that a robust BBSS pattern is not present in different locations of the Baltic Sea, and did not vary predictably in relation to sediment characteristics. Explanations for BBSS patterns based on purely external forcing (such as sediment environment characteristics) are inadequate to explain observations. If a more general explanation can be developed to explain BBSS patterns in different systems, it will likely include internal (biotic) interactions between organisms, evolutionary mechanisms, as well as external (physical) factors.

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