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Benthic Foraminifera biomass production in the Western Baltic *)

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Summary: The biomass (weight of protoplasm) and production of the major species of benthic Foraminifera was calculated for the "Hausgarten" area of Sonderforschungsbereich 95. Data from 440 samples collected between 1971 and 1975 were used for these calculations.

Biomass production of Foraminifera is 10—90 mg wet weight/m²/y in the turbulent zone and up to 5411 mg/m²/y in the basins. Epiphytic species produce 13—26 mg wet weight/m²/y. These values are higher than those recorded in the literature with the exception of the subarctic. The foraminiferal proportion of total meiobenthos biomass ranges between 6% in the turbulent zone and 63% in the basin.

Biomasse-Produktion benthischer Foraminiferen in der Westlichen Ostsee (Zusammenfassung): Für den Bereich des ,,Hausgartens" des Sonderforschungsbereiches 95 in der Kieler Bucht wurden die Biomasse (Protoplasmagewicht) und die jährliche Produktion der wichtigsten Foraminiferenarten berechnet. Daten von 440 Proben zwischen 1971 und 1975 wurden hierfür herangezogen.

Die Biomasse-Produktion durch Foraminiferen beträgt in der Turbulenzzone 10—90 mg Naßgewicht/m²/y und bis zu 5411 mg/m²/y im Beckenbereich. Für epiphytisch lebende Arten wurden 13—26 mg Naßgewicht/m²/y ermittelt. Diese Werte sind höher als alle bisher bekannten, mit Ausnahme einiger aus der Subarktis. Der Biomasseanteil der Foraminiferen am gesamten Meiobenthos beträgt 6% in der Turbulenzzone und bis zu 63% im Beckenbereich.

Introduction

As pointed out by MURRAY (1973, p. 202, 205), most information on living benthic Foraminifera is merely based on standing crop data (number of individuals per unit area, mostly 10 cm²). Only limited information is available on Foraminifera biomass and even less on production. Practically no data are present which permit a comparison of foraminiferal production with that of other marine organisms. It is practically impossible, therefore, to estimate the role of benthic Foraminifera within the mareni food web. Since the "Hausgarten"-area of the Sonderforschungsbereich 95 offers an excellent opportunity to compare the productivity of different groups of organisms, previously published foraminiferal data regarding this area (LUTZE 1974, WEFER 1976a) were recalculated and transformed to reflect mean values of foraminiferal biomass production.

Methods

Direct measurements of foraminiferal live weight are highly time consuming because of the small size and difficulties in separating living Foraminifera from the sediment. It is easier to calculate live weight from the volume of the entire test (MURRAY 1968; 1973, p. 7). MURRAY published size-volume graphs for simple geometrical forms (sphaeroids for *Elphidium*, cones for *Eggerella* or similar genera). Since our main contributor

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of biomass (*Ammotium cassis*) would not fit in such schemes, plastic models were used in the present study to find out size-volume relationships of all species contributing major proportions of biomass in the investigated area. For each species, series of 5—10 models of different sizes were formed. The measured volumes are given in Fig. 1. It is obvious that volume increases logarithmically and that the degree of increase is dependent on the test shape. In other words, one large specimen of a more compact species would exceed in biomass 10—20 smaller individuals. To calculate biomass to a sufficient degree of accuracy, size variation curves are required which cover time and space.

Such curves were given by WEFER (1976a and b), who sampled several stations in the investigation area during the years 1973—1975. Several characteristical "adult" curves were combined for each species to establish a standard variation curve of test size.

Volumes were determined for all size groups (by use of Fig. 1) and multiplied by the number in the group. The sum of group volumes divided by the total number of individuals was considered the mean test volume of the species.

Table 1:

Biomass calculation of average individuals of major species. — Mean test dimensions (largest diameter) and mean test volumes refer to size variation curves given by WEFER 1976a and b. Mean volumes of test walls were calculated from mean test weights (calcareous species divided by 2.71, arenaceous by 2.65). These volumes were substracted from the total volume in order to eliminate differences in wall thickness. The resultant was multiplied by 1.027, the protoplasm specific weight.

Species	Mean Test Size (mm)	Mean Test Volume (mm^3)	Mean Test Weight (mg)	Mean Volume of Test Walls (mm^3)	Mean Volume of Protoplasm (mm^3)	Mean Biomass (Life Weight) (μg)	
Elphidium excavatum clavatum	0.31	0.0086	0.0063	0.0023	0.0063	6.47	Calcareous
E. excavatum excavatum	0.24	0.0035	0.0028	0.0010	0.0025	2.57	
E. incertum	0.41	0.0152	0.0103	0.0038	0.0114	11.7	
E. gerthi	0.325	0.0054	0.00286	0.0011	0.0043	4.42	
Ophthalmina kilianensis	0.44	0.016	0.0063	0.0023	0.0137	14.0	
Ammotium cassis	1.85	0.177	0.266	0.100	0.077	79.1	Arenaceous
Miliammina fusca	0.33	0.0038	0.0033	0.0012	0.0026	2.67	
Crithionina heinckei	0.21	0.0028	0.0015	0.00057	0.0022	2.29	

The volumes of test walls were calculated from mean test weights by dividing calcareous species by 2.71 and arenaceous by 2.65. These volumes were subtracted from the total volume in order to eliminate differences in wall thickness. For example *A. cassis* has larger sand grains which might diminish the protoplasm volume to a greater degree than other foraminiferal tests would. Volume to weight conversion for comparison with data from other organisms was carried out by multiplying plasma volumes with 1.027 as introduced by SAIDOVA (1967). These biomass values were multiplied with average standing crop data for different depth intervals using data from LUTZE (1974) and WEFER (1976a). The result is mean standing biomass (Table 2). For these calculations the assumption was made that all tests are equally filled with protoplasm. This was supported by microscopical observation of whole and manipulated tests.

The biomass data were multiplied by the amount of probable reproductions per year to calculate the mean biomass production for each depth interval (Table 2). The turnover rate of the mean standing crop, depending on the proportion of individuals which reproduce, the frequency of reproduction and the number of new individuals resulting from each reproductive phase is necessary for biomass production calculations (MURRAY 1973). Turnover rates for the different species were taken from size variation curves (WEFER 1976a and b). For *Elphidium incertum*, *E. excavatum excavatum*, *E. gerthi*, *Miliammina fusca*, *Crithionina heinckei* it is once a year, for *E. excavatum clavatum* and *Ammotium cassis* twice a year and for *Ophthalmina kilianensis* 1.3 times a year.

Results

Production in the "Hausgarten"-area

The area under discussion is located in the western part of Kiel Bight (Western Baltic; 54°32′ N, 10°03′ E). The so called "Hausgarten" is a rectangle of 0,6 km², extending from 5 m depth (turbulence zone) down to the rim of a shallow basin with about 26 to 28 m depth. It was investigated by nearly all marine disciplines over a period of 4 years and was shown to be fairly typical for this part of the Baltic Sea. The general environmental conditions can be summarized as follows: hyposaline with a pycnocline in summer and fall generally between 10—15 m, surface water salinities ranging between 12 and $19^0/_{00}$, deep water salinities between 17 and $22^0/_{00}$. Water depth does not exceed 30 m. There is practically no river discharge of sediments. Up to 13 m water depth a glacial till platform covered with a thin and coarse grained layer of residual sediment including boulders is present. The deeper part of the investigation area is a plain, low-silled basin with mud sedimentation (high sedimentation rates) (see Fig. 2).

The mean production of foraminiferal biomass by sediment dwellers is low on the erosional platform and varies between 10 and 90 mg wet weight/m²/y. A slow increase with depth (and decreasing turbulence) is to be observed (Fig. 2, Table 2). The production of epiphytic Foraminifera varies between 13 and 26 mg/m²/y and is limited to the erosional platform since the occurrence of algae is dependent on boulders.

A much higher production is found in deeper parts of the area, where numbers between 3000 and 5000 mg/m²/y were recorded. This striking difference is possibly due to two factors: in shallow water, mechanical stress due to strong turbulence prevents growth of larger species with higher standing crop. The second factor might be a shortage of food in the shallow area as sediments of the erosional platform have a very low content of organic matter. The material produced in the water column, and forming a potential source of food for the main producers of foraminiferal biomass, is mainly deposited in the basins, thereby increasing the food supply in the deeper areas.

Fig. 3 demonstrates that only three species are major contributors of biomass: *Ammotium cassis*, *Elphidium excavatum clavatum* and *Elphidium incertum*. Whereas the main increase of standing crop (number of individuals per 10 cm²) occurs between 22 and 25 m, the biomass increases rapidly between 17 and 18 m depth and is fairly uniform down to 28 m. This increase in foraminiferal biomass and production is mainly due to *Ammotium cassis*, a species producing much larger protoplasm than the rest of the Foraminifera. Macrobenthos biomass increases with depth, is highest between 14 and 20 m and then decreases drastically (ARNTZ et al. 1976). This is also true for meiofauna apart

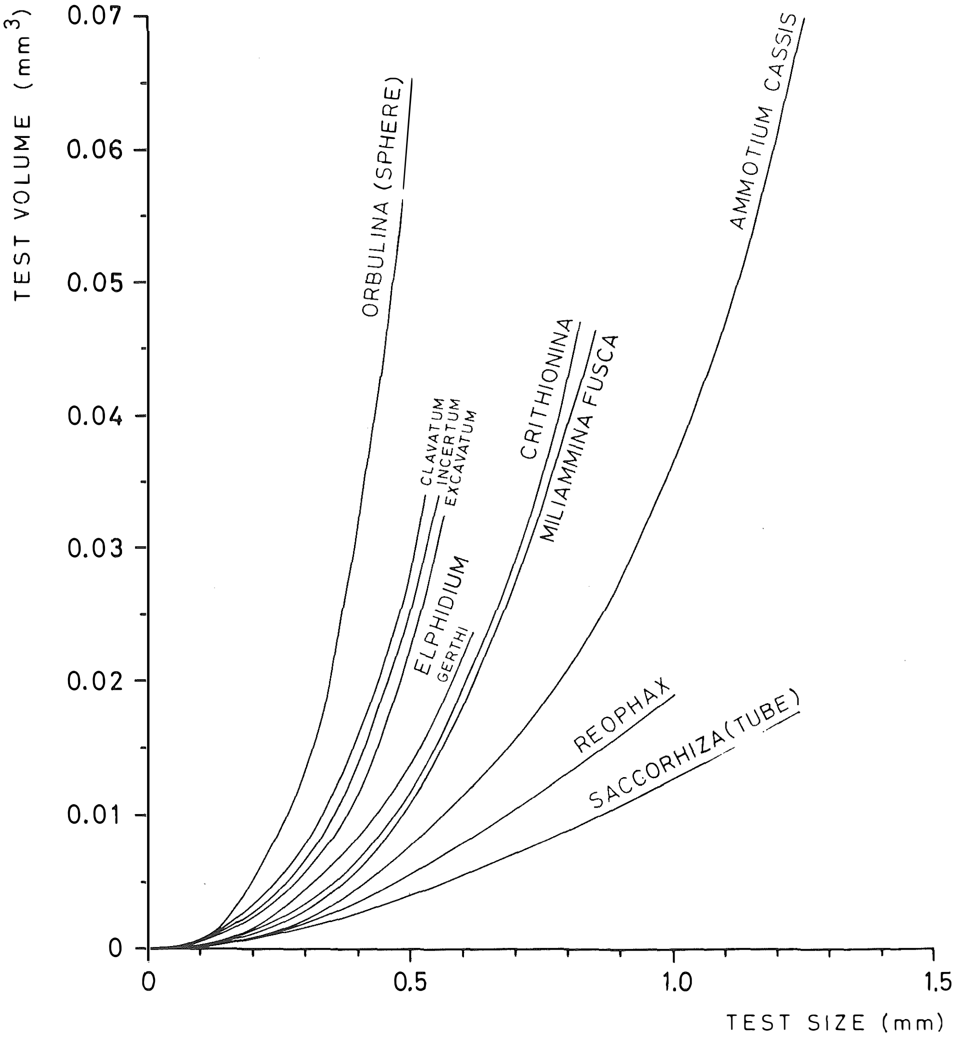

Fig. 1: Size-volume relationship of Foraminifera discussed in this paper. — All volumes were obtained from plastic models. Curves of *Orbulina* (sphere) and *Saccorhiza* (tube) were added to mark the two possible extremes.

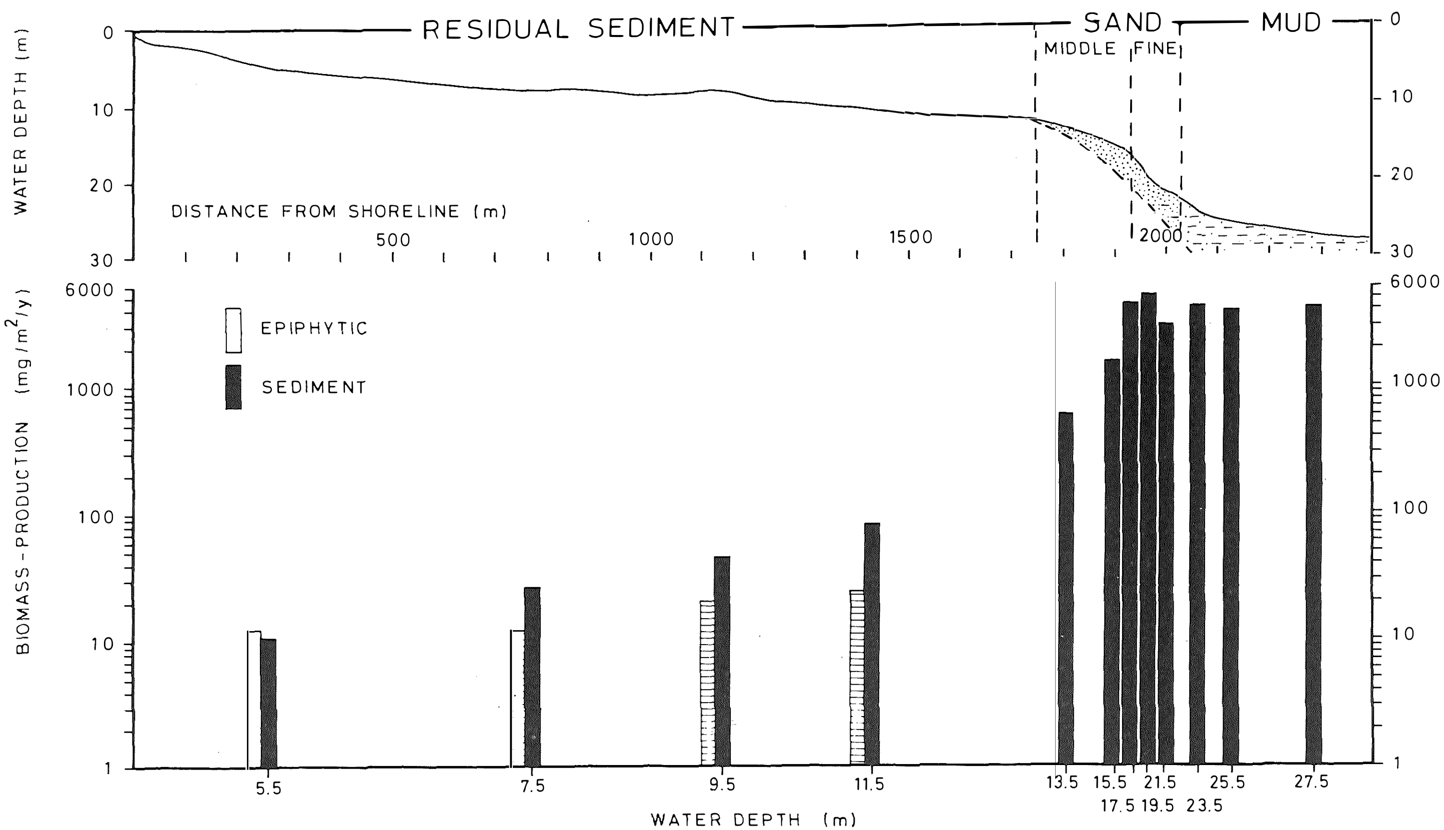

Fig. 2: Foraminiferal biomass production at the "Hausgarten" area in the Eckernförder Bucht. — At the top profile showing the erosional platform with low production and the edge of a small basin with extremely high production has been given.

Table 2:

Calculation of foraminiferal biomass production according to water depth and species. — Mean standing crop data (SC) from LUTZE 1974 (1; 1971—1973) and WEFER 1976a (2; 1973—1975) were averaged for two meter intervals and then multiplied by a) mean biomass values as taken from table 1, and b) the amount of probable reproductions per year, as discussed by WEFER 1976a and in the present paper. The data are based on 440 samples.

Standing crop data refer to either the number of individuals per 10 cm² (for the sediment community) or to 10 g wet algae (for the epiphytic community). The latter were converted for 10 cm² sea floor through multiplication by 0.0263 (this conversion factor was obtained from average algal weight per m²). Thus all biomass production data are expressed as mg wet weight per m² and year.

		E. exc. clavatum sc × 6.47 × 2				E. incertum sc × 11.7 × 1				E. exc. excavatum sc × 2.57 × 1				E. gerthi sc × 4.42 × 1				A. cassis sc × 79.1 × 2				M. fusca sc × 2.67 × 1				Total
	Depth (m)	standing crop 1	2	Ø	Prod.	standing crop 1	2	Ø	Prod.	standing crop 1	2	Ø	Prod.	standing crop 1	2	Ø	Prod.	standing crop 1	2	Ø	Prod.	standing crop 1	2	Ø	Prod.	Production mg/m²/y
SEDIMENT	5-6									0.3	3.2	1.8	5	0.5	0.2	0.3	1	0.0	0.02	0.01	2	0.04	2.2	1.1	3	11
	7-8									0.8	6.4	3.6	9	0.9	0.2	0.6	2	0.0	0.10	0.05	8	0.1	5.0	2.6	7	26
	9-10					0.4		0.4	5	6.6		6.6	17	4.5		4.5	20	0.04		0.04	6	0.8		0.4	1	49
	11-12					0.3	0.2	0.2	3	4.6	8.1	6.3	16	1.5	0.2	0.8	4	0.05	0.77	0.41	65	0.1	0.8	0.5	1	89
	13-14					1.4	0.9	1.1	13	4.9	7.9	6.4	16	0.6	0.2	0.4	2	2.6	4.2	3.4	544	0.2	3.5	1.9	5	581
	15-16	0.3		0.3	3	2.2		2.2	26	6.2		6.2	16	0.3		0.3	1	9.9		9.9	1563	0.02		0.0	0	1610
	17-18	0.8		0.8	10	10.3		10.3	120	5.9		5.9	15	0.3		0.3	1	28.7		28.7	4540	0.3		0.3	1	4687
	19-20	1.1		1.1	15	29.8		29.8	349	1.4		1.4	4					31.9		31.9	5043	0.3		0.3	1	5411
	21-22	5.8		5.8	74	31.9		31.9	374	2.5		2.5	6					17.1		17.1	2705	0.9		0.9	2	3162
	23-24	15.2	8.5	11.9	154	72.4	74.1	73.2	857	0.1		0.1	<1					23.6	33.9	21.9	3465	1.0	0.6	0.8	2	4478
	25-26	92.0		92.0	1190	88.0		88.0	1030									12.0		12.0	1898	1.6		1.6	4	4123
	27-28	158.0	233.4	195.7	2533	43.5	82.3	62.9	736									6.2	7.6	6.9	1092	0.6	0.0	0.3	1	4361
EPIPHYTIC		Cr. heinckei sc × 0.0263 × 2.1 × 1				O. kilianensis sc × 0.0263 × 14.0 × 1.3				sc × 0.0263 × 2.57 × 1				sc × 0.0263 × 4.42 × 1				sc × 0.0263 × 79.1 × 2				sc × 0.0263 × 2.67 × 1				
	6			91	5.0			15.7	7.5			2.3	0.2			2.8	0.3						1.0		0.07	13
	8			107	5.9			13.8	6.6			2.0	0.1			4.5	0.3						0.5		0.03	13
	11			278	15.3			11.4	5.5			5.9	0.4			1.5	0.1						0.2		0.01	21
	13			374	20.6			9.1	4.3			1.2	0.1			2.9	0.2		0.1	0.1	0.4		0.4		0.03	26

from Foraminifera, although the decrease is less marked with depth (SCHEIBEL 1976). For the deepest part of the basin *A. cassis* and *E. incertum* biomass production decrease and *E. excavatum clavatum* standing crop and biomass production increase (Fig. 3). This increase might be caused by less competition, since most other groups of organisms suffer considerably under seasonal oxygen deficiencies caused by the excess supply of decaying organic matter.

Comparison with foraminiferal biomass data given by other authors

MURRAY (1973, p. 202) summarized available data on foraminiferal biomass. For both lagoons and temperate open shelf seas biomass data range between 0 and 900 mg wet weight/m^2. The mean maximum value for 3 lagoons is ca. 500, for 7 shelf sea areas 400 mg/m^2. Production can only be estimated from these values. Assuming one generation per year as the minimum and three generations as an average for temperate shelf seas, the possible maximum production by these Foraminifera would range between 500 and 1500 mg wet weight/m^2/y. The productivity found in the present investigation for shallow basins in the Western Baltic is much higher, since 4000 to 5000 mg wet weight/m^2/y were recorded as mean values. This coincides with the well known high sedimentation rate of phytoplankton in the Western Baltic (ZEITZSCHEL 1965). The high Western Baltic productivity is surpassed in Sub-Antarctic waters, where BASOV (1974) reported a "standing" foraminiferal biomass up to 30.000 mg wet weight/m^2 from the Falkland Islands area.

Comparison with biomass data of other meiofauna organisms

SCHEIBEL (1976) presented detailed biomass data of the meiofauna in the "Hausgarten" area. The groups included are Nematoda, Harpacticoida, Ostracoda, Halacarida, Tardigrada and Gastrotricha. Maximum values of 560 mg dry weight (= 2800 mg wet weight, taking 80% as water content) were found on muddy sand in depths between 20 and 22 m (mainly nematodes). As turnover rates for these organisms are unknown (according to GERLACH 1971 the number of generations per year vary from 1 to 12), only biomass data are comparable. Table 3 shows a comparison with data from the same area given by SCHEIBEL (1976, Tab. 1). It has to be taken into

Table 3:

Meiofauna biomass in the Hausgarten area according to SCHEIBEL 1976, compared with foraminiferal biomass. — The Foraminifera reach percentages up to 63% of the total meiofauna.

Water depth	6—8 m	12—15 m	20—22 m	26 m
Meiofauna without Foraminifera mg dry weight/m^2	50	116	560	308
The same in wet weight (× 5, regarding 80% as the water content)	250	580	2 800	1 540
Foraminifera mg wet weight/m^2	16	398	2 328	2 578
Total meiofauna	266	978	5 128	4 118
% Foraminifera	6%	41%	45%	63%

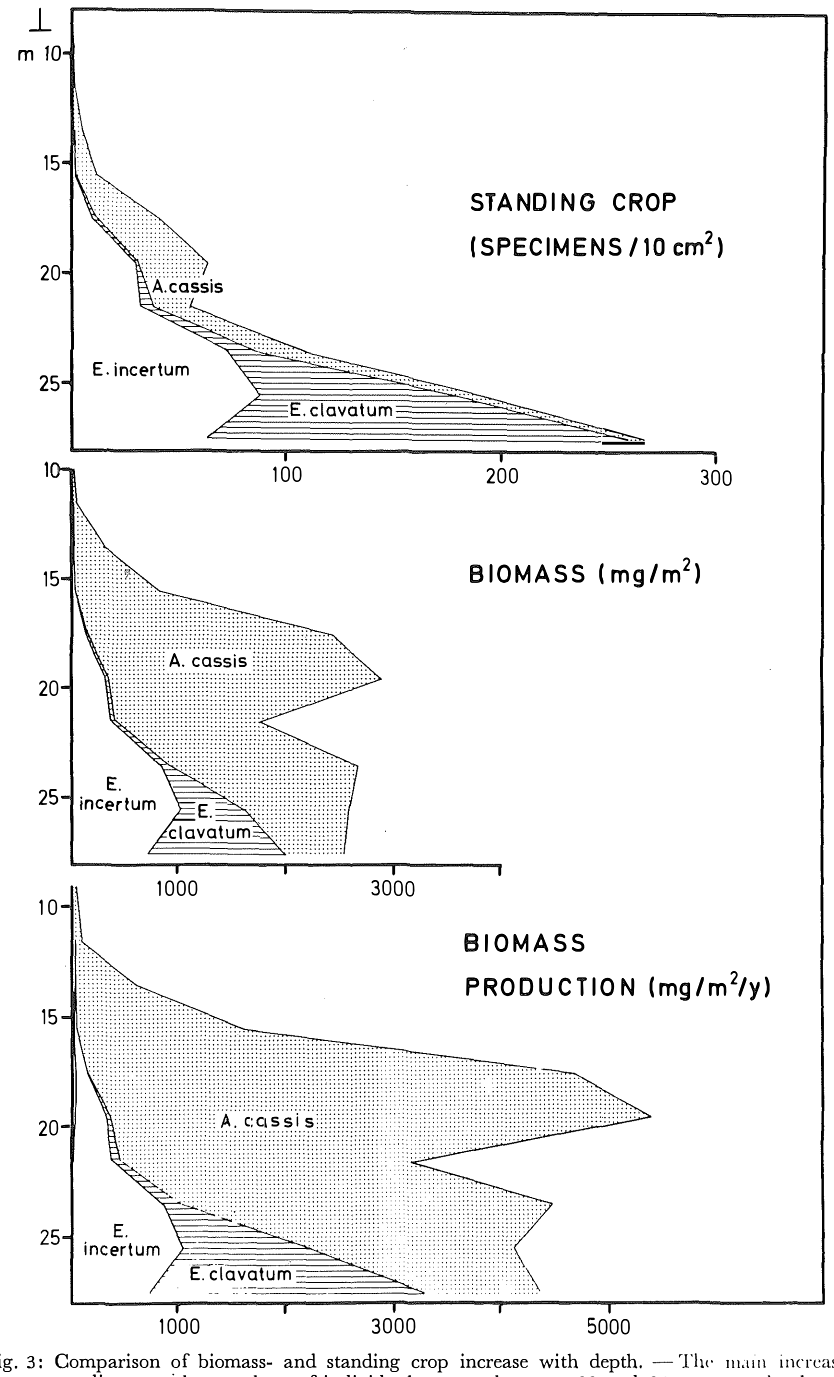

Fig. 3: Comparison of biomass- and standing crop increase with depth. — The main increase of standing crop by numbers of individuals ranges between 22 and 25 m water depth and is mainly caused by growing numbers of *Elphidium exclavatum clavatum*. In contrast the biomass — and even more the production — rises between 15 and 18 m due to the larger species *Ammotium cassis*.

account, that data compared here are acquired by entirely different methods (wet pipetting of the "normal" meiofauna, dry evaluation of stained foraminiferal samples).

Foraminiferal percentages of total biomass in this comparison range from 6% in the turbulence zone to 63% in the mud basin and are much higher than hitherto anticipated. It can be concluded that Foraminifera form a significant part of total meiobenthos biomass and thus must play an important role in the food web.

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