

# The meiofauna of a tidal flat in the western part of the Wadden Sea and its role in the benthic ecosystem

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**ABSTRACT:** Composition, abundance and distribution of the meiofauna of a well-studied tidal flat in the western part of the Wadden Sea, The Netherlands, was determined by sampling with 2-monthly intervals at 12 stations during a year. The meiofauna was strongly dominated by nematodes (85 %) and largely restricted to the top 10 cm of the sediment. Clear seasonal variation was observed in harpacticoids and annelids, but not in nematodes. Harpacticoids and annelids were most numerous in the lower parts of the tidal flat, near the main gullies, in areas with coarser sediment, whereas nematodes showed a maximum at intermediate tidal level with average mean particle-size conditions. Low meiofaunal abundances were observed on the high tidal flats with fine sediment and a high organic carbon content. Arguments are given that the role of the meiofauna as consumers of primary organic matter is very restricted in the area and probably much lower than that of the macrofauna. This situation differs from that in most other areas and is largely determined by the relatively small biomass of the meiofauna ( $\pm 0.45 \text{ g C m}^{-2}$ ) as compared to that of the macrofauna ( $\pm 10 \text{ g C m}^{-2}$ ). It seems therefore unlikely that the meiofauna of the tidal flat consumes a large part of the primary organic matter, postulated to be left over by the macrofauna (Kuipers et al., 1981). In fact, evidence is given that the primary food supply to the benthic system of the tidal flat might be much lower than formerly assumed.

## INTRODUCTION

Most studies on the benthic fauna of Balgzand, a well-studied tidal flat area in the western part of the Wadden Sea have been concentrated on the microphytobenthos (Cadée and Hegeman, 1977), the macrofauna (e.g. Beukema, 1974, 1979; Beukema and de Vlas, 1979) or on predators of that fauna (e.g. Kuipers, 1977; de Vlas, 1979; Zijlstra et al., 1982). So far no published information is available on the meiofauna, although the possible importance of that fauna in terms of food-chain dynamics has been highlighted in a recent review by Kuipers et al. (1981). For several other areas, as for instance sublittoral benthic communities in the south-eastern North Sea (Gerlach, 1978) and the Baltic (Elmgren, 1978) or the intertidal mudflats of Lynher estuary (Warwick et al., 1979) and the Ythan estuary (Baird and Milne, 1981) the importance of the meiofauna in terms of metabolic activity has been stressed. Notwithstanding a small biomass as compared to the macrofauna the meiofauna was attributed

a metabolic capacity as high as or even higher than the macrofauna, due to an inverse relationship between metabolic rate per unit of biomass and the size of the organism (e.g. Zeuthen, 1970).

Information on the meiofauna of the Wadden Sea is rather scarce. Smidt (1951) provided some data on the taxonomy and abundance of some meiofaunal groups for the Danish part of the Wadden Sea. Reise (1979) discussed predation of macrobenthos on meiofauna, providing also some information on composition and abundance of the meiofauna near Sylt, Federal Republic of Germany; and in a later paper (Reise, 1981) presented a review of our knowledge on the Wadden Sea meiofauna. New information was also presented on the meiofauna of the Ems Dollard area (Van Es et al., 1980; Bouwman, 1981; Van Es, 1982). The present paper describes the meiofaunal assemblage present on Balgzand, its spatial and seasonal distribution and discusses the metabolic activity of that fauna in relation to other size groups, present in the benthic system.

AREA, METHODS AND MATERIAL

Area

The area studied (Balgzand) is a tidal-flat system of some 50 km<sup>2</sup> in the westernmost part of the Wadden Sea (Fig. 1). The region has been described in earlier papers (i.e. Beukema, 1974; Kuipers, 1977; de Vlas, 1979).

The tidal amplitude in the area is on average about 130 cm, with most of the region situated below MTL. The sediment has a variable grain size, silt and organic carbon content (e.g. Ente, 1969; Cadée and Hegeman, 1977). On the higher parts, along the dikes in the south

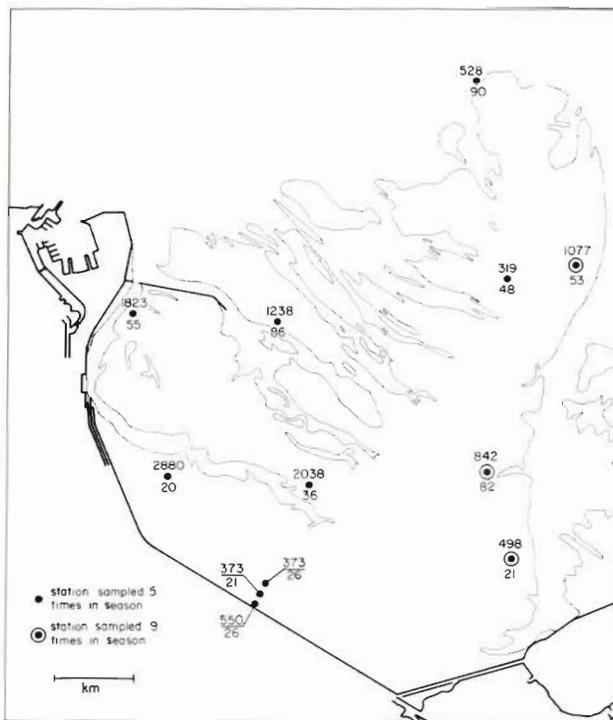


Fig. 1. Map of tidal flats on Balgzand with sampling sites, mean number of nematodes in Feb, Apr, Jul and Sept per 5.3 cm<sup>2</sup> (upper value) and mean number of copepods in Jul and Sept per 5.3 cm<sup>2</sup> (lower value). Stations sampled 5 times (●) and stations sampled 9 times (⊙) between February 1976 and February 1977

and west, the median grain size varies between 80 and 130 μm, with over 5 % silt and up to 1 % organic carbon. In the lowest, northern parts, near to the main gully, and most exposed to wave action and tidal currents, a coarser sediment is found with median particle sizes between 160 and 200 μm, less than 2 % silt and below 0.1 % organic carbon. Salinity in the overlying water varies from about 8 to 31 ‰ (average 20 to 26 ‰; Manuels and Rommets, 1973); maximum temperature variation of that water (during high tide)

ranges from ca. -1.0 °C in winter to over 21 °C in summer.

Sampling

Samples were obtained from 12 sampling sites (Fig. 1), which coincided in general with those of Beukema (1974) for macrofauna. These sampling sites give a reasonable coverage of the depth-range and the substrate-types, encountered on Balgzand. In contrast to Beukema, who sampled mainly along transects, our samples were collected randomly in an area of some 100 m<sup>2</sup> at each marked sampling site.

All 12 stations were sampled on 27 February to 3 March, 14 to 28 April, 7 to 12 July, 20 to 22 September 1976, and on 20 to 31 January 1977. In addition, 3 of these stations were sampled on 1 April, 9 to 12 June, 23 August, and 4 November 1976 (Fig. 1). On these stations the vertical distribution of the meiofauna was studied.

Sampling was carried out a low tide, using a transparent perspex tube with sharpened edges and an internal diameter of 26 mm. A study of the depth-distribution of the main meiofaunal groups indicated, that in accordance with the situation in most other tidal flat areas, about 85 % of the nematodes and over 95 % of the other taxa encountered were present in the top 10 cm. Therefore, sampling was restricted to that depth, which means that nematodes may have been underestimated by ca. 15 %.

Samples collected were preserved in heated formaldehyde 4 % (ca. 70 °C). With this procedure the nematodes were preserved in a stretched position; this facilitated later measurements for computing biomass. The material was stained with rose-bengal for 60 min after sieving the sample over a 1 mm sieve and collecting it on a 50 μm sieve, to eliminate the finer silt particles.

Table 1. 95 % confidence limits of single sample and mean of 3 samples per sampling location, determined on 3 separate locations in September, 1975 for Nematoda and Harpacticoida

| Group         | Location | Number of samples | Limits of single count | Limits of mean of 3 counts | Mean of all counts |
|---------------|----------|-------------------|------------------------|----------------------------|--------------------|
| Nematodes     | a        | 18                | 0.58x - 1.73x          | 0.68x̄ - 1.47x̄            | 1247               |
|               | b        | 18                | 0.33x - 3.02x          | 0.55x̄ - 1.80x̄            | 1499               |
|               | c        | 15                | 0.79x - 1.26x          | 0.83x̄ - 1.20x̄            | 394                |
| Harpacticoids | a        | 18                | 0.01x - 71.89x         | 0.03x̄ - 39.44x̄           | 7.8                |
|               | b        | 18                | 0.04x - 26.58x         | 0.37x̄ - 2.67x̄            | 2.7                |
|               | c        | 15                | 0.08x - 12.82x         | 0.20x̄ - 5.08x̄            | 9.7                |

Separation of meiofauna from the sediment was obtained by elutriation (Uhlig et al., 1973). Microscopic examination of the residue after elutriation indicated a very high recovery of the meiofauna (ca. 95 %). For sorting and measuring of the material a binocular microscope was used at a magnification of 40x. From the sample 10 % was sorted in a counting chamber. Sorting was restricted to larger taxonomic groups such as nematodes, harpacticoids, turbellarians and annelids.

At each sampling site the abundance of the meiofauna was obtained from the mean of 3 samples (cores). The precision in determining abundance of the most numerous nematodes with this method was estimated by taking 18 replicate cores at 3 stations. The nematode counts obtained were log transformed, as the standard deviations were proportional to the means. Table 1 gives the 95 % confidence limits of a single sample and of the mean of 3 samples at each station, showing the limits for single samples to range between 0.57x and 2.00x, and for the mean of 3 samples between 0.69x and 1.49x, on average. The accuracy in determining abundance in other, less numerous groups was much poorer, as is demonstrated for harpacticoids in Table 1.

For the most numerous group of meiofauna, the nematodes, an attempt was made to estimate dry weight biomass, from length and width measurements, following the method of Andr assy (1956) cited by McIntyre (1969):

$$\text{dry weight} = 0.25 (\text{length} \times \text{width}^2) \cdot \frac{1.13}{1.7},$$

in which dry weight is determined in g, length and width in cm. Direct estimates of the weight of nematodes, or other less important groups, could not be made.

Of the substrate parameters median grain size and silt content were determined as described by Beukema (1974).

## RESULTS

### Meiofaunal composition and abundance

Since our sorting of the samples was directed mainly at the quantitatively more important taxonomical groups, a single specimen of a rare group may have passed unnoticed. This may be partly the reason why the meiofaunal assemblage encountered in our study area was poor in taxa, consisting mainly of nematodes, harpacticoids, turbellarians and annelids. Occasionally immatures of the macrofauna, mainly of molluscs, were encountered, but always in low numbers. Immatures of macrofaunal polychaetes will have been

included in the annelid group, together with parts of macrofaunal polychaetes passing the 1 mm sieve. The abundance of the meiofauna in our area, obtained by averaging the samples of 10 stations during the 5 sampling periods, is shown in Table 2. The numerically most important group appears to be the

Table 2. Abundance (number m<sup>-2</sup>) of the more important meiofauna in the Balgzand-area, averaged for 10 stations during 5 sampling periods

| Group             | n × 10 <sup>3</sup> m <sup>-2</sup> | %    |
|-------------------|-------------------------------------|------|
| Nematoda          | 2,117                               | 86.3 |
| Harpacticoida     | 56                                  | 2.3  |
| Turbellaria       | 36                                  | 1.5  |
| Annelida          | 230                                 | 9.4  |
| Juvenile molluscs | 15                                  | 0.6  |

nematodes, varying between 0.5 and 10 million m<sup>-2</sup>, with over 85 % of the numbers observed. Apart from the metazoan meiofauna, also larger protozoans such as foraminiferans and ciliates were encountered in large numbers. As these groups were, however, incompletely sampled, the smaller individuals passing the 50 µm sieve, the groups are not further considered.

### Variation in time and space

In all groups large numerical variations were observed in the course of the season and/or between stations.

Variations in the course of the sampling season (February 1976–February 1977) (Fig. 2) give straight means of numbers observed on all, usually 12 stations during each of the 5 sampling periods, together with means of the numbers on 3 stations, sampled on 9 occasions. The numerical variation in the nematodes (Fig. 2A) was moderate in both sets of data, considering the sampling error. As, moreover, the 2 sets of data varied independently, it seems doubtful whether much of the variance observed can be attributed to seasonal variation. A similar conclusion can be drawn for the material on turbellarians (Fig. 2D). However, both sets of data suggest a strong seasonal variation in the abundance of annelids (Fig. 2C) and harpacticoids (Fig. 2B), with clearly increased abundance during summer and early autumn. Although less convincing, the data on juvenile molluscs also suggest and increased abundance during summer.

Examples of spatial variations are illustrated in Fig. 1 for nematodes and harpacticoids as these groups were more numerous and showed a somewhat more regular pattern in their seasonal occurrence and spa-

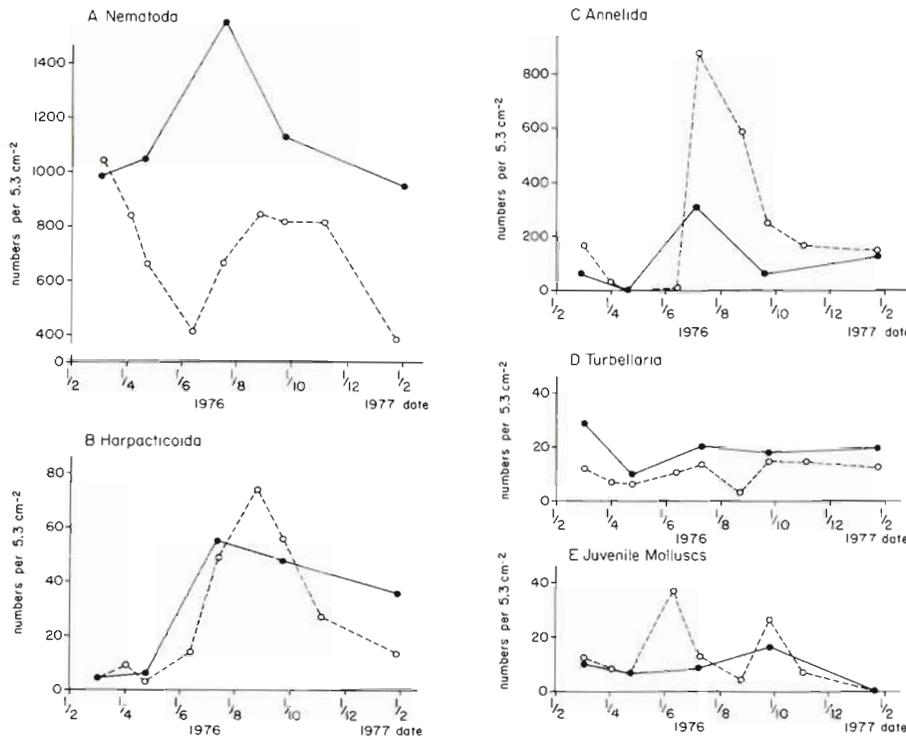


Fig. 2. Meiofaunal numbers per 5.3 cm<sup>2</sup> during 5 sampling periods, averaged over 12 stations (—) and during 9 sampling periods, averaged over 3 stations (----). (a) Nematoda, (b) Harpacticoida, (c) Annelida, (d) Turbellaria, (e) juvenile molluscs (1/2 = February 1st, etc.)

tial distribution. It appears that nematodes were in particular abundant in the western part of the sampling area, whereas harpacticoids were more numerous in the northern and eastern parts.

Seasonal and spatial variation in the abundance of nematodes and harpacticoids were tested with an analysis of variance (Table 3). The analysis showed for harpacticoids that consistent differences between stations and sampling season were responsible for a large part of the variance observed, whereas in nematodes only differences between stations contributed significantly to the variance. Between sampling periods no significant differences could be shown, consistent with Fig. 2a.

**Abundance and environmental parameters**

It seems likely that the variation in space observed in nematodes and harpacticoids is related to environmental parameters as silt content, median grain size and level in the tidal zone. Multiple linear regression analysis indicated that about 62 % of the spatial variation in harpacticoids could be explained by the 3 environmental parameters ( $r = 0.79$ ,  $p < 0.05$ ). Harpacticoid abundance increased with increasing depth and median grain size, but with decreasing silt content. Of the 3 parameters, depth was slightly more important than silt and grain size. Fig. 3B shows plots

Table 3. Analysis of variance on abundance estimates of Nematoda and Harpacticoida, considering 8 regularly sampled stations during 4 periods (February, April, July, September)

|                          |          |          |                 |
|--------------------------|----------|----------|-----------------|
| Nematoda                 |          |          |                 |
| Between stations         | F = 6.59 | d.f. = 7 | $p < 0.01$      |
| Between sampling periods | F = 0.74 | d.f. = 4 | $p > 0.05$ n.s. |
| Harpacticoida            |          |          |                 |
| Between stations         | F = 3.28 | d.f. = 7 | $p < 0.05$      |
| Between sampling periods | F = 9.41 | d.f. = 4 | $p < 0.01$      |

of harpacticoid abundance in relation to silt and depth (upper figure,  $r = 0.77$ ,  $p < 0.02$ ) and to median grain size and depth ( $r = 0.72$ ,  $p < 0.05$ ).

Nematode abundance was explained for about 50 % by the 3 parameter model ( $r = 0.70$ ). The relation was, however, not significant ( $p = 0.1$ ), which may be due to the use of a linear regression technique. As can be observed in Fig. 3A, showing nematode abundance in relation to silt and depth ( $r = 0.61$ , n. s.) and to median grain size and depth ( $r = 0.70$ ,  $p < 0.05$ ) there is an indication of non-linearity. Nematode abundance seems to be highest at intermediate grain sizes (around 160  $\mu\text{m}$ ) and silt content (about 5 %) and around mean tidal level (MTL). In the analyses used grain size differences explain most of the variation, but depth very little.

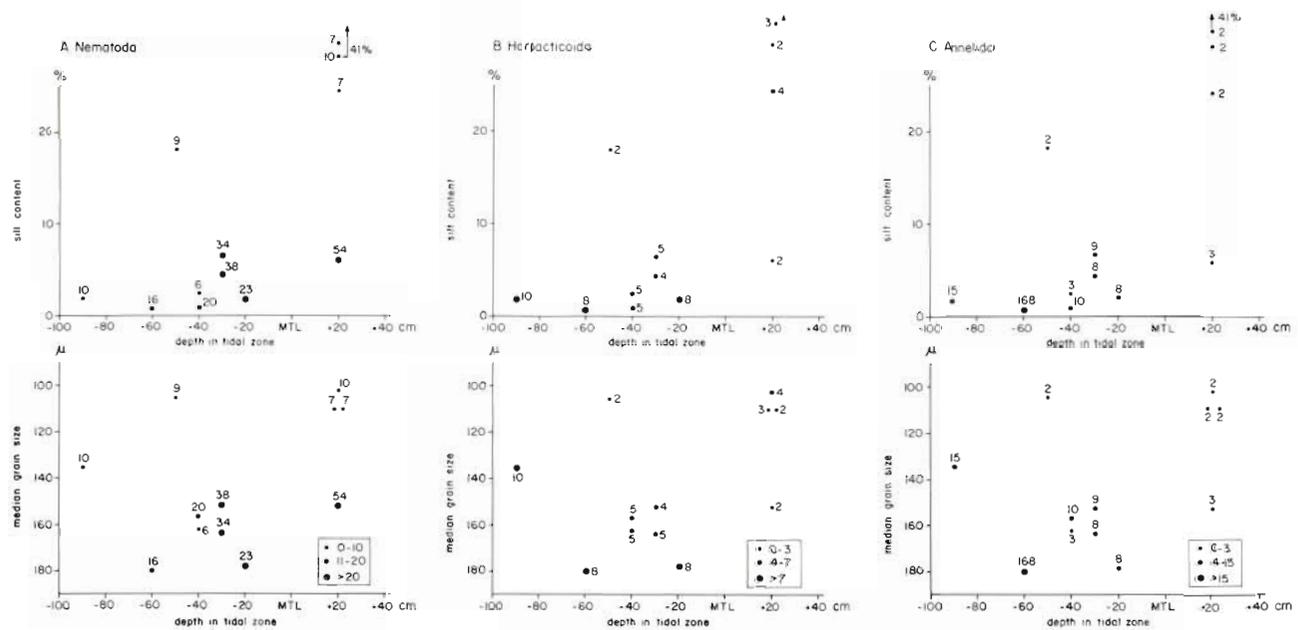


Fig. 3. Distribution of meiofauna in relation to height in tidal zone and silt content (%) of sediment (upper) and in relation to depth in tidal zone and median particle size (lower). (A) Nematoda, numbers  $\times 10^5 \text{ m}^{-2}$ ; (B) Harpacticoida, numbers  $\times 10^4 \text{ m}^{-2}$ ; (C) Annelida, numbers  $\times 10^4 \text{ m}^{-2}$

The abundance variation observed in annelids (Fig. 3C) was poorly explained by the 3 parameter model ( $r = 0.62$ , n. s.), with a suggestion of a similar distribution as observed in harpacticoids.

### Biomass

As already mentioned, an attempt was made to estimate the dry weight of nematodes on the basis of length and maximum girth width. The average individual weight of nematodes, obtained by this method, is shown in Table 4 for each major sampling period, including data of all stations. Between periods the mean dry weight per individual ranged from 0.23 to 0.42  $\mu\text{g}$ , with a mean of 0.28  $\mu\text{g}$ . This figure should be compared with an estimate of 0.25  $\mu\text{g}$ , given by Gray

(1976) or 0.17  $\mu\text{g}$ , mentioned by Warwick et al. (1979). From the average individual dry weight a biomass estimate was obtained for the whole area per sampling period and for the year, by averaging estimates of 10 stations, which together should give a fair representation of the whole sampling area (Table 4). Nematode biomass estimates were found to range between 0.40 and 0.77  $\text{g m}^{-2}$  with an annual average of 0.60  $\text{g m}^{-2}$ .

Table 4 also includes biomass estimates for the sampling area ( $\text{g m}^{-2}$  dry weight) for harpacticoids and turbellarians. These were obtained by attributing for all sampling dates an individual dry weight value for these groups of 2  $\mu\text{g}$ , as suggested by Gray (1976). The biomass of harpacticoids would then range from 0.02 to 0.22  $\text{g m}^{-2}$  with an annual mean of 0.10  $\text{g m}^{-2}$ , whereas turbellarian biomass was rather steady around 0.08  $\text{g m}^{-2}$  (range 0.05 to 0.10  $\text{g m}^{-2}$ ).

Table 4. Biomass estimates of major taxa of the meiofauna on Balgzand, with individual dry weight of nematodes. Estimates are shown for the 5 main sampling periods, taking means of 10 stations, together representative for the whole area

| Major taxa  | Sampling period |      |      |      |      | Annual mean |
|---|-----------------|------|------|------|------|-------------|
|   | Feb-Mar         | Apr  | Jul  | Sep  | Jan  |             |
| Nematoda, individual dry weight ( $\mu\text{g}$ )   | 0.42            | 0.29 | 0.24 | 0.23 | 0.23 | 0.28        |
| Nematoda, total dry weight ( $\text{g m}^{-2}$ )  | 0.77            | 0.58 | 0.71 | 0.56 | 0.40 | 0.60        |
| Harpacticoida, total dry weight ( $\text{g m}^{-2}$ )   | 0.02            | 0.01 | 0.19 | 0.21 | 0.05 | 0.10        |
| Turbellaria, total dry weight ( $\text{g m}^{-2}$ )   | 0.10            | 0.05 | 0.09 | 0.08 | 0.08 | 0.08        |
| Annelida, total dry weight ( $\text{g m}^{-2}$ )  | 0.17            | 0.03 | 0.89 | 0.31 | 0.37 | 0.35        |
| Total biomass meiofauna on Balgzand (dry weight, $\text{g m}^{-2}$ ) (juvenile molluscs excluded) | 1.06            | 0.67 | 1.88 | 1.16 | 0.90 | 1.13        |

No reliable estimate was available for the individual dry weight of annelids (polychaetes + oligochaetes). The figure provided by Gray (1976) of 150  $\mu\text{g}$  was obviously far too high, considering the size of the animals encountered in our samples. This can be attributed to differences in handling the samples after collection; different from Gray's technique, in our case the material was sieved over a 1 mm screen prior to elutriation, so that larger animals were removed. To obtain an estimate of dry weight, part of the annelid material was measured computing dry weights according to the method applied for nematodes. The material originated from samples, in which annelids were numerous and covered all seasons. Some 130 measurements indicated an individual mean dry weight of 1.55  $\mu\text{g}$ . Justification for the use of the method was found in determining the carbon content of 4 larger annelids with a C-analyser (wet oxidation method, Menzel and Vaccaro, 1964) converting the estimate to dry weight by assuming a ratio carbon/dry weight of 0.4 and comparing it with a dry weight estimate obtained from the dimensions. The 2 estimates agreed reasonably well taking into account the largely different methods, the average weight of the 'carbon method' being 60  $\mu\text{g}$  and of the 'measurement method' 88  $\mu\text{g}$ . It could be, therefore, that our annelid dry weights are somewhat overestimated.

Our material showed 2 modes in the weight distribution of annelids with about 80 % of the animals weighing around 0.12  $\mu\text{g}$ , while the remaining 20 % consisted of larger worms with an average weight around 7.12  $\mu\text{g}$ . Because of the restricted number of animals measured, a single estimate for the individual dry weight of annelids was used in all seasons and samples (1.55  $\mu\text{g}$ ). Table 4 gives biomass estimates for the whole area during the 5 sampling periods, showing a range in dry weights between seasons of 0.03 to 0.89  $\text{g m}^{-2}$ , with an annual average of 0.35  $\text{g m}^{-2}$ .

Having thus obtained biomass estimates of all major meiofaunal taxa, with the exception of the small group of juvenile molluscs, the total meiofaunal biomass can be assessed, showing a range of 0.67 to 1.88  $\text{g m}^{-2}$  for the seasons with an annual average of 1.13  $\text{g m}^{-2}$ . Nematodes are indicated as contributing most (about 53 %) to this biomass, followed by annelids (ca. 31 %) and harpacticoids (8 %). Nematodes dominate in all seasons, except in July, when annelids are more abundant.

## DISCUSSION

The meiofaunal assemblage encountered on our tidal flat area is rather poor in taxa with only 4 major taxonomic groups (nematodes, copepods, annelids,

turbellarians). In addition, immature individuals of the macrofauna were encountered (Table 2), together with larger-sized protozoaners such as foraminiferans and ciliates, not considered in this paper. With the exception of a few individuals no ostracodes were recorded, in contrast to the observations of Smidt (1951), Reise (1979), and Bouwman (1981) who mentioned ostracodes, although only in small numbers. The dominant group observed in our area are the nematodes which on average make up over 85 % in numbers and over 50 % in biomass estimates. In Smidt's samples from the Danish Wadden Sea the nematodes were less dominant, but his samples were obtained from the upper 3 cm. As shown by Reise and Ax (1979) the vertical distribution of nematodes extends to below that depth, so that Smidt may have underestimated this group seriously. Near Sylt the nematodes were found to be about as equally dominant (77 %) as in ours are (Reise, 1979).

Abundance of the meiofauna, observed on Balgzand is rather high compared to most other areas, in particular for nematodes (e.g. McIntyre, 1969). Areas with comparable or even higher numerical densities are usually found in other well sheltered intertidal regions with fine sediments (e.g. mudflats, salt-marshes).

Notwithstanding a rather high abundance of the meiofauna, the biomass estimates obtained for Balgzand appear to be below average for tidal areas (Table 6). This can probably be explained by the large contribution of nematodes with a low mean weight (Table 4) to the meiofaunal assemblage of the area.

Variations in abundance, related to season, were only clearly indicated for harpacticoids and annelids, with maximum numbers during summer. Neither nematodes nor turbellarians showed seasonal variation, whereas variations observed in the abundance of juvenile molluscs might be related to season, with higher abundances in the summer. The lack of seasonality in nematode abundance is a common feature (McIntyre, 1969), although exceptions have been recorded (Warwick and Price, 1979). Individual species may show seasonal variation (e.g. Wieser and Kanwisher, 1961).

The distribution of the meiofauna on Balgzand showed some relation to environmental parameters such as silt content, median particle size and depth in the tidal zone. Harpacticoids, and possibly annelids, were most numerous in areas with a low silt content, relatively high median grain size, and well below mean tidal level. As these 3 parameters were interrelated, in particular silt content and depth in the tidal zone, it is hard to decide which factor mainly determines the distribution. Moreover, some parameters not mentioned – such as  $\text{O}_2$ -concentration, depth of the anoxic layer, etc. – related to one or more of the

parameters considered, might also be of importance (McIntyre, 1969).

By contrast, nematodes seem to be most numerous at intermediate values of silt content and median grain size encountered in the area and at a depth around mean tidal level (Fig. 3A). Abundance appears to be depressed in areas low in the tidal range with coarser sediment, but in particular in regions with a relatively fine sediment and a high silt content, found on the higher part of the tidal flat. A similar strong reduction in nematode abundance in an area with fine-grained sediment and a high organic matter content was observed at one location in the Dollard (de Jonge and Bouwman, 1977). However, at a similar site they found nematodes to be much more abundant, but this location was strongly affected by organic waste, discharged by a nearby fresh-water outfall. Nematode distribution on Balgzand bears a certain similarity with the distributional pattern, described by Beukema (1976) for macrofaunal biomass and species number, as confirmed by a plot of nematode numbers on macrofaunal biomass (Fig. 4). This implies that on Balgzand

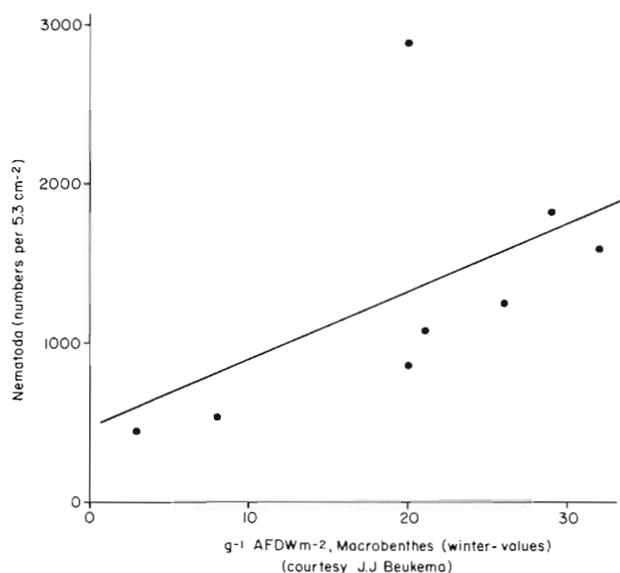


Fig. 4. Relation between ash-free dry weight of macrobenthos and numbers of Nematoda (numbers per 5.3 cm<sup>2</sup>, Spearman's Rank  $r = 0.74$ ,  $p < 0.025$ )

densities of nematodes and macrofauna tend to coincide, whereas copepods and annelids differ in their distribution from the main macrofaunal biomass.

In the introduction we mentioned the possible importance of mei faunal metabolic activity in the benthic ecosystem of Balgzand. In terms of the primary energy available – as Beukema (1974, 1981) and Kuipers et al. (1981) conclude from the existing evidence – the food requirements of the macrofauna most likely underscore considerably the primary food supply, con-

sisting of local phytoplankton and benthic microflora production and organic matter, imported into the area (de Jonge and Postma, 1974; Cadée, 1980). Beukema, de Jonge and Postma and Kuipers et al. estimate food demands of the macrofauna at some 80 to 90 g C m<sup>-2</sup>yr<sup>-1</sup> and the supply at about 400 g C m<sup>-2</sup>yr<sup>-1</sup>.

However, the biomass of the mei fauna, ranging from 0.7 to 1.9 g m<sup>-2</sup> dry weight in the course of the year, is not particularly high, when compared to that of the benthic macrofauna. As mentioned in the introduction this small biomass might be deceptive, as metabolic activity could be high because of the small size of the mei faunal organisms (Zeuthen, 1970). To investigate this possibility an attempt was made to estimate respiration and production of the macro- and mei fauna of Balgzand (Table 5). Respiration, expres-

Table 5. Respiration and production of macro- and mei fauna on Balgzand. For calculation see text

| Group  | Respiration<br>(g C m <sup>-2</sup> yr <sup>-1</sup> ) | Production<br>(g C m <sup>-2</sup> yr <sup>-1</sup> ) |
|--|--|---|
| Macrofauna<br>(biomass 10 g C m <sup>-2</sup> )  | 59.0   | 11.8  |
| Mei fauna<br>(biomass 0.45 g C m <sup>-2</sup> ) | 13.7   | 3.6   |

sed in g C m<sup>-2</sup>yr<sup>-1</sup> at ambient temperature (ca. 10 °C), was computed according to the general relationship (Banse, 1982) between respiration and biomass for larger invertebrates  $q = 19.5 M^{0.75}$  and for mei fauna  $Q = 5.4 M^{0.75}$ , in which  $q$  = respiration in nl O<sub>2</sub> h<sup>-1</sup> at 20 °C and  $M$  = body mass as dry weight (μg). For the calculation the assumption was made that 1 ml O<sub>2</sub> consumed is equivalent to 0.4 mg C metabolized (Crisp, 1971) and that  $Q_{10} = 2.05$ . Production estimates for the macrofauna were obtained from Beukema (1981). For the mei fauna, P/B-ratios given by Warwick et al. (1979) were adopted, with a ratio of 8.5 for nematodes, of 18 for harpacticoids, and of 5 for annelids and turbellarians. For both macro- and mei fauna a carbon:dry weight ratio of 0.4 has been assumed.

The estimates in Table 5 admittedly have to be considered with some reservation, due to the use of very general equations and ratios. Our respiration estimates per unit of biomass, for instance, appear to be high when compared with those of Warwick et al. (1979), which were partly based on actual measurements for the species present. However, if respiration was overestimated in this exercise, it affected the mei fauna (1.9×) more than the macrofauna (1.4×). Our production estimates, in terms of P/B-ratios, are

Table 6. Comparison of macro- and meiofauna biomass ( $\text{g m}^{-2}$  dry weight) in 4 intertidal (\*) and 3 subtidal areas

| Area            | Biomass (dry weight, $\text{g m}^{-2}$ ) |               | Ratio a/b | Source  |
|-----------------|--|---------------|-----------|---|
|                 | Macrofauna (a)                           | Meiofauna (b) |           |   |
| Balgzand*       | 27                                       | 1.13          | 23.9      | This paper  |
| Lynher estuary* | 16                                       | 4.0           | 4.0       | Warwick et al. (1979)   |
| Dollard*        | 4.7 <sup>1)</sup>                        | $\pm 2.0^2)$  | 2.3       | <sup>1)</sup> van Es et al. (1980)<br><sup>2)</sup> van Es (1982) |
| Ithan* estuary  | 66.8                                     | 5.1           | 13.1      | Baird & Milne (1981)  |
| Northern Baltic | 4  | 1.4           | 2.9       | Elmgren (1978)  |
| Helgoland Bight | 9.2                                      | 0.8           | 11.5      | Gerlach (1978)  |
| Gullmar Fjord   | 3.8                                      | 0.5           | 7.6       | Evans (1983)  |

very similar to those of Warwick et al. (1979). Therefore, the estimates in Table 5 are probably correct in indicating that both respiration and production of the meiofauna and hence consumption are very modest in comparison to that of the macrobenthos.

This conclusion is different from that for many other areas (e.g. Gerlach, 1978; Warwick et al., 1979) where meiofauna metabolism was thought to be about equal or even to surpass that of the macrofauna. The difference is explained by the data collected in Table 6, showing a relatively small contribution of the meiofauna to be biomass of the benthic community of Balgzand. Therefore, there is little evidence suggesting that the meiofauna utilizes a substantial part of the food supply thought to be left over by the larger benthic animals on Balgzand.

This view finds support in the spatial distribution of the potential primary food supply in the tidal flat area compared to that of the macro- and meiobenthos. As mentioned earlier, this primary food supply is supposed to consist of phytoplankton, microphytobenthos and allochthonous organic matter, imported from the bordering open sea area and fresh water outlets (de Jonge and Postma, 1974; Cadée, 1980). Two of these potential food sources for the benthic fauna show a trend in the Balgzand area, as microphytobenthos production and sedimentation of particulate organic matter are at maximum in the most shallow parts of the area, near to the mainland, where the silt content is high and median grain size of the sediment low (Cadée and Hegeman, 1977). Notwithstanding a high supply of primary organic matter, macrobenthic biomass and growth rate are below average in such areas, probably due to the relatively long emersion times (Beukema, 1976; Beukema et al., 1977). Therefore the excess primary food supply not utilized by the macrofauna will be concentrated in particular on these high parts of the tidal area. Consequently, if the meiofauna were to occupy the niche left over by the larger benthic animals, it should be found in the shallow parts of the tidal region. On the contrary, the data presented here indicate nematodes to be most abundant in roughly the

same area as the macrofauna and annelids and harpacticoids on the lower parts of the tidal flat. The large amount of organic matter, produced on and transported onto, the high tidal flats are therefore most likely largely utilized by the microbenthos, as evidenced by increasing bacterial counts at higher organic matter contents in the sediments of the Dollard (van Es et al., 1980; van Es, 1982). The high parts of the tidal zone, rich in organic material, seem to be poorly exploited by metazoans, for which partly the long period of emergence, responsible for extreme physical conditions (de Wilde and Berghuis, 1979) and partly the generally anoxic state of the sediment with a high concentration of sulphides may be responsible.

Therefore, the suggested moderate metabolic activity of the meiofauna, the low ratio of meiofauna on macrofauna, and the low abundance of meiofauna in areas of suggested excess primary food supply make it difficult to consider the true meiofauna as a major consumer of primary organic matter on Balgzand.

Our data show that the temporary meiofauna, consisting of juveniles of the macrofauna, is hardly impressive in terms of numbers (Table 2), although part of the juvenile, large polychaetes are probably included in the estimates for annelids.

Unless the abundance of this dynamic group was highly underestimated by our sampling programme, it seems therefore unlikely that its metabolic activity will add substantially to that of the meiofauna.

The data presented here thus indicate that the food intake (assimilation) of the macrobenthos and meiofauna together might be on the order of some 80 to 100  $\text{g C m}^{-2} \text{ yr}^{-1}$ , and thus well below the annual supply of primary organic matter of about 400  $\text{g m}^{-2}$ , estimated for the western part of the Wadden Sea (Cadée, 1980). This supply is, however, not restricted to the benthic system of the area, but is also at the disposal of planktonic heterotrophs. Vosjan and Olančuk-Neyman, 1977 found indications that mineralization in the water phase of the western Wadden Sea was low, possibly 1 or 2 orders of magnitude lower than that in the benthic system. However, this suggestion

was based on observations at only 1 location on a tidal flat with a moderately high carbon-content during 1 mo and can therefore hardly be considered as being representative for the whole area during the year. More recent observations in the water phase, covering 3 stations and 4 tidal cycles spread over the year, suggest an actual  $O_2$  consumption of  $20.7 \mu\text{mol } O_2 \text{ l}^{-1} \text{ d}^{-1}$ , averaged over the year (Vosjan, 1981). The spatial and in particular the annual variation observed was large, with a low estimate in November ( $2.4 \mu\text{mol } O_2 \text{ l}^{-1} \text{ d}^{-1}$ ) and a high one in June ( $63.8 \mu\text{mol } O_2 \text{ l}^{-1} \text{ d}^{-1}$ ), so that the estimated annual mean will only be a rough approximation of the true value. However, an earlier observation made on 2 of the 3 stations in April, in which ETS (Electron Transport System) activity was determined, fits the annual pattern of  $O_2$  consumption in the water ( $\pm 12.5 \mu\text{mol } O_2 \text{ l}^{-1} \text{ d}^{-1}$ ) (Vosjan and Tijssen, 1978), if an ETS/ $O_2$  consumption ratio of 2 is accepted (Vosjan, 1981). The new estimate of the annual  $O_2$  consumption in the water column of the western Wadden Sea, based on a better coverage in space and time than in the earlier observations of Vosjan and Olańczuk-Neyman, 1977 suggests – at a mean water depth of 4 m and a conversion factor of 0.86 from mol  $O_2$  to mol C (van Es, 1982) – an annual  $O_2$  consumption in the water column equivalent to about  $300 \text{ g C m}^{-2}$ . A small part of the  $O_2$  consumption has to be attributed to algal respiration, possibly 10 % of the  $150 \text{ g C m}^{-2} \text{ yr}^{-1}$  produced by the phytoplankton (Parsons et al., 1977). Compared to the estimated supply of  $400 \text{ g C m}^{-2} \text{ yr}^{-1}$  to the area (Cadée, 1980) the observations indicate that a large part of the mineralization in the western Wadden Sea could occur in the water column. This tentative conclusion is supported by observations of van Es (1982) for the Dollard estuary, where about 60 % of the organic carbon was found to be mineralized in the pelagic system. As the water depth in the western part of the Wadden Sea is on average 4 times that in the Dollard, it is to be expected that the proportion of organic matter mineralized in the water is significantly higher. However, a large part of the organic carbon, mineralized in the water of the Dollard, consisted of organic waste discharged in the estuary, so that the situation is not quite comparable to that in the western part of the Wadden Sea. Also in estuarine areas outside the Wadden Sea mineralization in the water column was found to be more important than that in the benthic system (e.g. Long Island Sound, Aller and Yingst, 1980).

A proportionally large mineralization of organic carbon in the pelagic system as suggested by Vosjan's observations, would mean that the primary food supply to the benthic fauna in the western part of the Wadden Sea could be much lower than formerly assumed by Beukema (1981) and Kuipers et al. (1981). The organic

material, fuelling the benthic system, will be divided over the subtidal and tidal part of the western Wadden Sea. A recent study has shown the benthic biomass (macrofauna) to be very similar in the 2 benthic regions of the area (R. Dekker, pers. comm.), so that we may assume a more or less equal distribution per unit surface of the primary food supply. However, on Balgzand a major part of the allochthonous organic matter seems to settle on the high tidal flats with a reduced benthic macro- and meiofauna (Cadée and Hegeman, 1977). As the contribution to the intermediate and lower levels of the tidal flats seems to be moderate (Cadée and Hegeman, 1977) one wonders whether the food supply to the benthos of Balgzand could be rather restricted and even be limiting at periods of high benthos density.

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