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COMMUNITY STRUCTURE AND FUNCTIONAL ROLES OF MEIOFAUNA IN THE NORTH SEA*

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KEYWORDS: meiofauna; North Sea; community structure; energetics; biogeochemical cycles.

ABSTRACT

Knowledge on community structure of North Sea meiofauna has greatly increased recently. A quasi-synoptic picture of meiofauna densities and copepod community structure from 171 stations of the southern North Sea, sampled in April-May 1986, has been obtained during the North Sea Benthos Survey. Latitudinal patterns in meiofauna abundance and copepod weight, abundance and diversity exist in an area between 51°30′N and 58°30′N. Using TWINSPAN-classification five major groups of copepod species can be recognized which are related to sediment type, latitude and depth. The part of the meiofauna in total benthic energy flow, their role in the benthic food web and in biogeochemical cycles is discussed based on existing literature. There are still considerable gaps in knowledge and the field is not progressing rapidly.

INTRODUCTION

Meiofauna are small metazoans and, depending on definition, protozoans, that live in or on a substratum during at least some stage of their life-cycle. The term meiobenthos is most often used for animals living in sediments (infauna), but many meiofauna species are more loosely associated with the substratum, as on rocky bottoms and in algae, and many meiofauna species are regularly found in the water.

Even in the last review of meiofauna (HIGGINS and THIEL, 1988) a rigorous definition of what meiofauna consists of is not given. The Greek stem 'meio' means smaller and was used first by MARE (1942) to describe the animals that passed through a 1 mm mesh sieve, as originally used by PETERSEN (1914) in his quantitative studies of what is now called the macrobenthos. Similarly, a sieve with a mesh size of around 42 μm is used to delimit the lower size of meiofauna. Such arbitrary conventions are very unsatisfactory but reflect the fact that there is a spectrum of animal body size in the benthos spanning many orders of magnitude. It is probably only for reasons of comparison of abundance or biomass that such an artificial set of limits is necessary, although also diversity is sensitive to such definitions (SOETAERT and HEIP, 1990).

Size categories also bear little relationship to taxonomic composition, although there are several phyla of which all or nearly all representatives are in the 1 mm or smaller size fraction, which in itself is a remarkable fact, the reasons for which have been rather unexplored. These include Gastrotricha, Kinorhyncha, Tardigrada, Gnathostomulida and the recently described Loricifera. On the other hand many macrofaunal groups contain species of meiofaunal dimensions and in the deep-sea many species of 'traditional' macrofaunal taxa are of meiofaunal size.

Since SMIDT's (1951) early work on the Danish Wadden Sea and MCINTYRE's (1964) study of the Fladen Ground meiofauna, much information has been gained on the species composition, density and biomass of meiofaunal assemblages from restricted areas in the North Sea (Fig. 1.) HEIP *et al.* (1990) summarized the knowledge, resulting from 40 years of meiobenthos research in the North Sea, and concluded that only the coastal areas of Belgium, The Netherlands and Germany are relati-

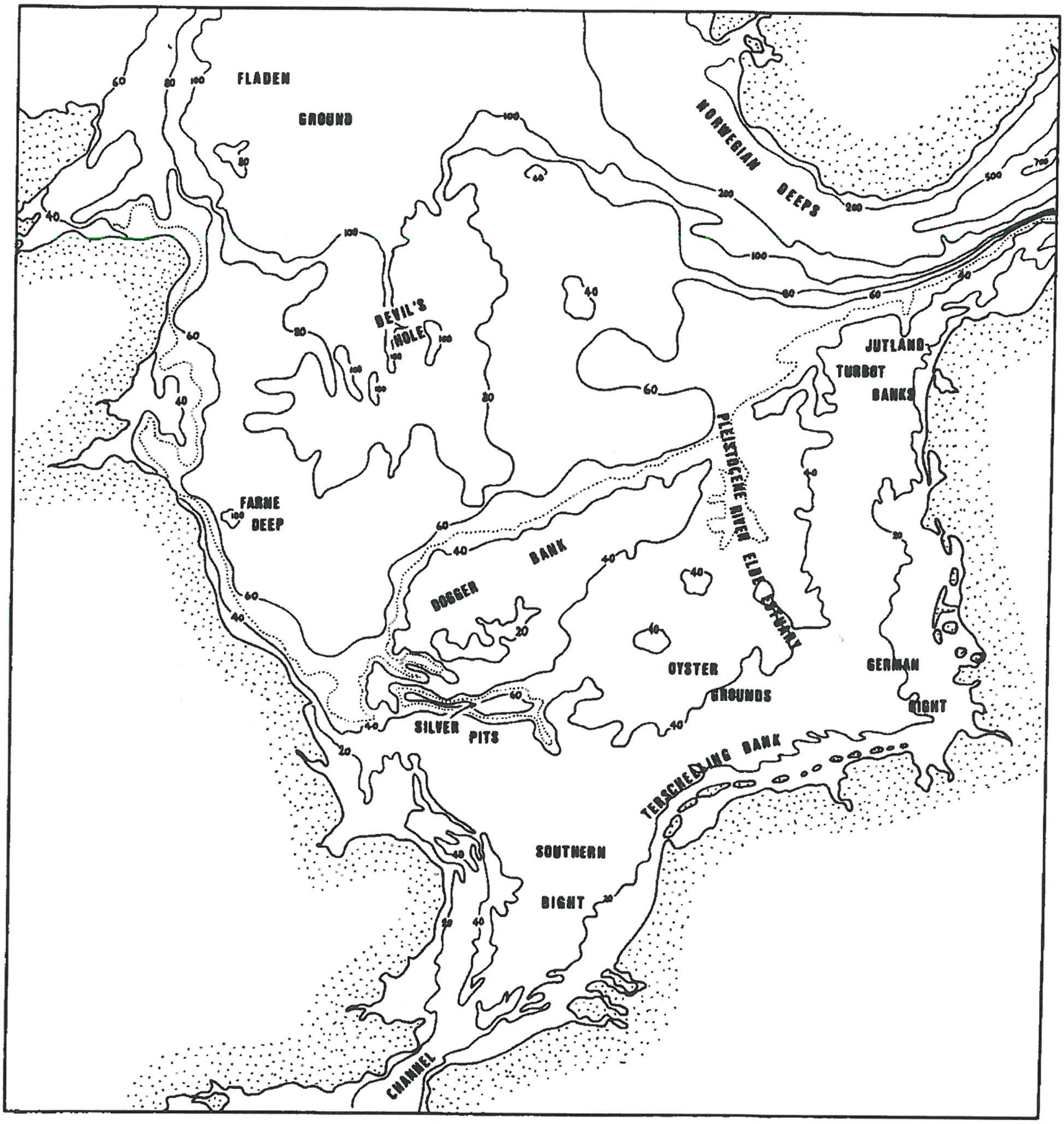

Fig. 1. Map of the North Sea.

vely well-known. Since then the results from the 1986 North Sea Benthos Survey (NSBS) have become available (HUYS *et al.*, 1990; 1992) and these results will form the basis of this paper.

MEIOFAUNAL DENSITIES IN THE NORTH SEA

The abundance (density) of total meiofauna, nematodes and copepods is shown in Fig. 2. Nematodes were the dominant group in virtually all stations, their densities ranging from 60 to 4200 ind. 10 cm^{-2}. They are less abundant in the southern North Sea than elsewhere and become more important with latitude (and thus depth) up to 53°30' N. From this latitude on there is a tendency for nematode density to decrease again towards the north, but the trend is not linear. The relation between total meiofauna density and latitude fits, as expected, the picture obtained for the nematodes. Only in the Southern Bight, where nematode numbers were low, harpacticoids sometimes represented the dominant meiofaunal taxon.

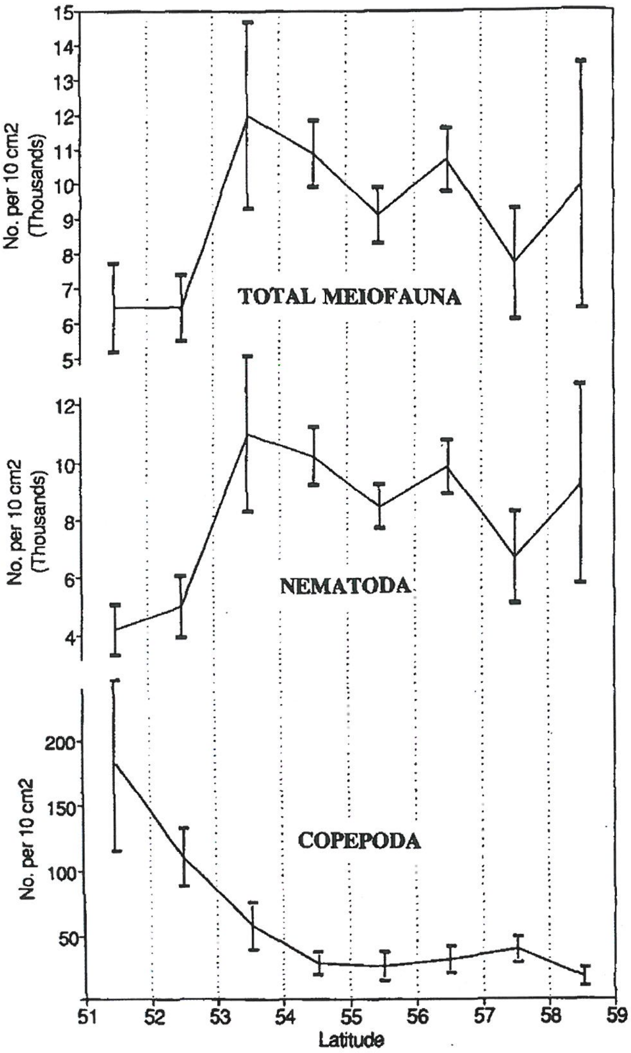

Fig. 2. Density of total meiofauna, nematodes and copepods averaged over latitude. Bars indicate standard errors.

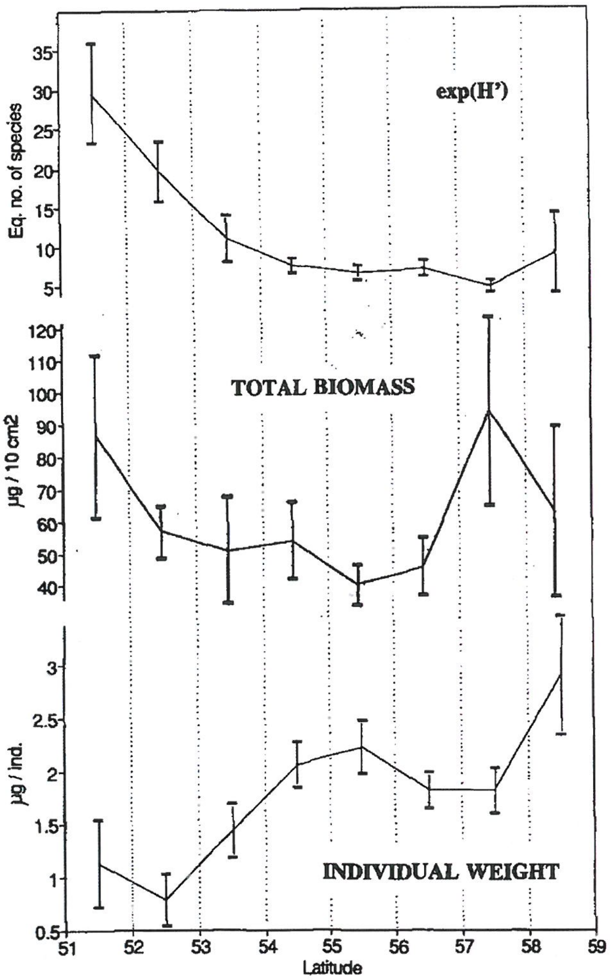

Fig. 3. Diversity (exp H' with H' the Shannon-Wiener index based on ln), biomass (ash-free dry weight) and individual weight of copepods averaged over latitude.

In the central part of the Southern Bight high numbers of interstitial copepods and relatively low numbers of nematodes are found. This community type extends to the coastal zone of Belgium and the Netherlands but is virtually absent from the shallow offshore areas of the Britain although the sediment type is virtually the same, with median grain sized sands (250-300 µm). The Southern Bight community is unique for the North Sea and values of the nematode/copepod ratio are low.

MEIOFAUNA COMMUNITIES

The description of meiofauna distribution in terms of communities dates back to the thirties when REMANE (1933) used meiobenthic species to define benthic communities in the Kiel Bay. Many of the subsequent studies (*e.g.* POR, 1964b; COULL and HERMAN, 1970; SOYER, 1970) attempted to apply the isocommunity concept introduced by THORSON (1957) for macrobenthic communities. This concept was based on the assumption that communities inhabiting the same type of sediment at similar depths are characterised by different species of the same genera, but replacing each other in accordance with the geographical regions. This hypothesis has not stood the test of time and the NSBS survey clearly showed that depth and sediment type are not the only factors that structure copepod communities (HUYS *et al.*, 1990), which are the only communities of the North Sea Benthos Survey that have been studied until now (HUYS *et al.*, 1990). Species distributions of nematodes are presently being studied.

A total of 278 copepod species belonging to 105 genera and 22 families were identified. Over 40% of the species were new to science; new taxa were particularly found among the interstitial families which were most important in terms of

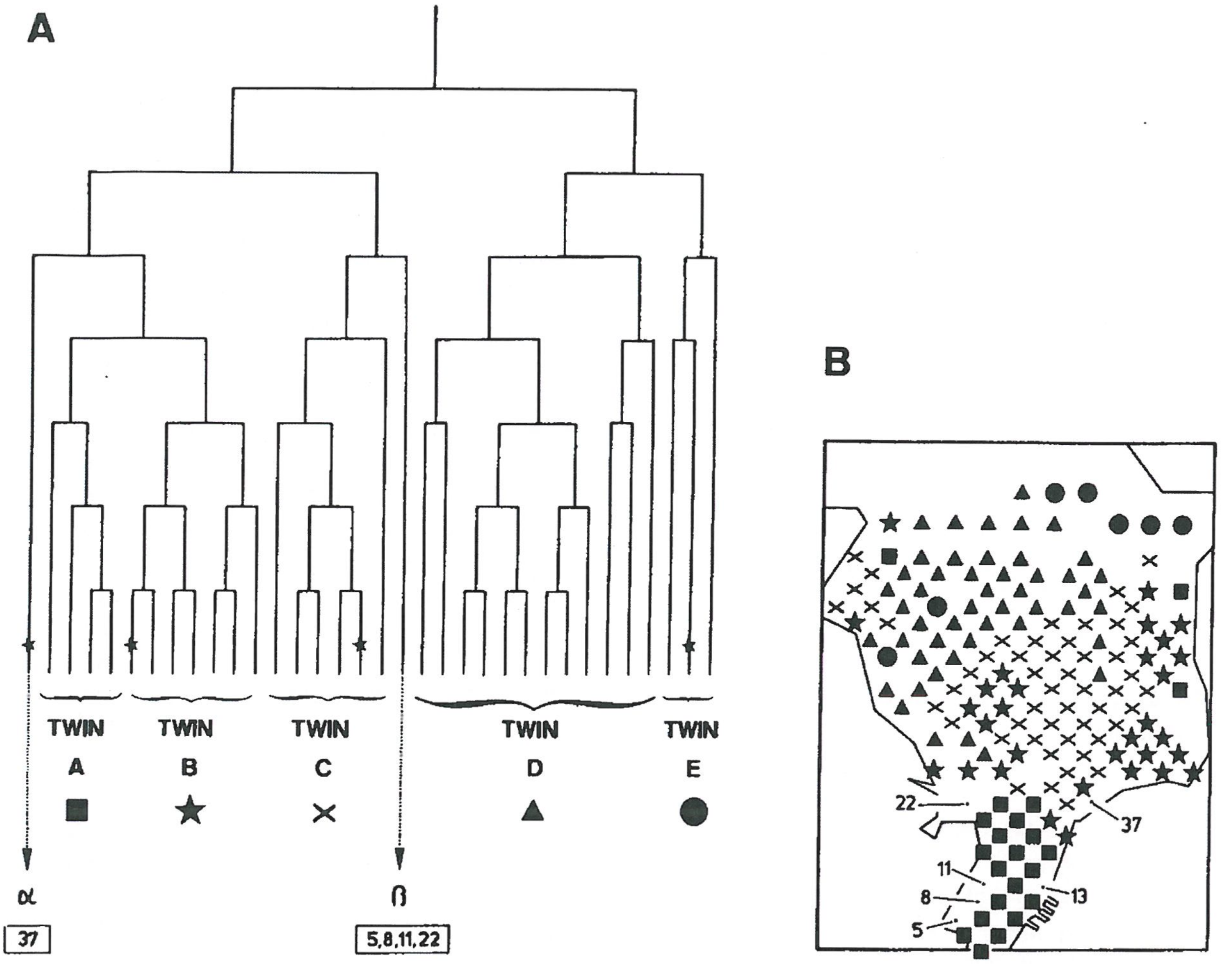

Fig. 4. TWINSPAN classification of stations based on copepod species (A) and spatial arrangement of the TWIN-groeps in the North Sea (B).

species diversity. Copepod density decreased rapidly to the north and this trend was followed by diversity (Fig. 3).

Individual ash-free dry weight was determined for 98 species of copepods. Total biomass reached a peak in the south (low individual AFDW, high density) and in the north (high individual AFDW, low density), but was low in the Central North Sea where the copepod communities were impoverished both qualitatively and quantitatively.

Using Two-Way Indicator Species Analysis TWINSPAN (HILL, 1979), it was impossible to define meaningful clusters on the basis of the 18 major meiofaunal taxa. However, seven distinct communities could be recognised on the basis of the copepod composition (Fig. 4 and 5): (1) TWIN A largely coincided with the Southern Bight and showed high densities of predominantly interstitial species (Cylindropsyllidae, Paramesochridae, Cyclopinidae) and a few characteristic taxa from coarse sediments; (2) TWIN B was found in the coastal zone of the Netherlands, Germany and Denmark, and in the Dogger Bank, and was dominated by large Ectinosomatidae and Ameiridae, and by interstitial Leptastacidae; (3) TWIN C represented an impoverished community north of the Dogger Bank and consisted of large pelophilic species belonging to the Diosaccidae, Laophontidae and Ameiridae; (4) between the Scottish coast and Norwegian Deeps and in the Silver Pits Zosimidae, Cletodidae and Idyanthidae were the most important families (TWIN D); (5) TWIN E grouped the Norwegian Deeps, Devil's Hole and Farne Deep and showed a typical deepwater fauna represented by Ancorabolidae, Cerviniidae, Stenocopiinae and bathyal cletodid genera. Two minor clusters (α; ß) coincided with the Dutch Wadden Sea (one station) and the river outlets (Thames, Wash, Meuse/Scheldt) whose meiofauna is subject to pollutants.

Canonical Correspondence Analysis CCA (TER BRAAK, 1986) clearly separated the five major twin groups. TWIN A - C were significantly correlated with sediment and could be arranged along a gradient of decreasing median grain size and increasing silt/clay content. TWIN D was clearly related

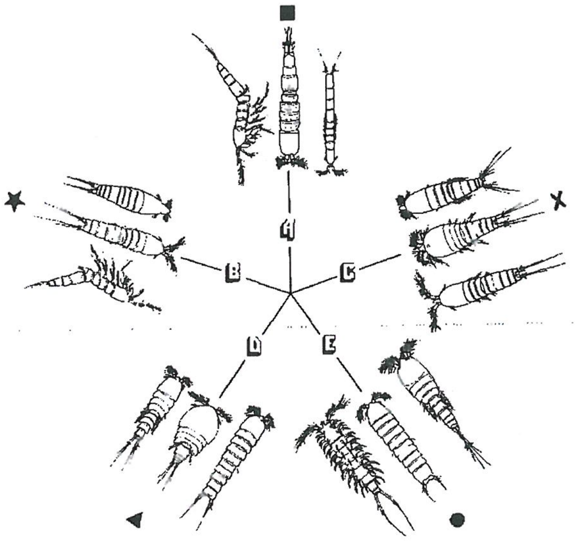

Fig. 5. Dominant copepod ecotypes representative of the five TWIN-groups.

to latitude whilst TWIN E showed a clear preference for depth.

It is striking that the development of a characteristic interstitial fauna of mesopsammic copepods is not found, except on a few locations, in the German Bight and the west coast of Denmark. Particularly in the entrance of the Skagerrak some very coarse sediments are found but here other ecotypes seem to replace the tiny mesopsammic forms.

The distribution of the kinorhynch genera is clearly related to the median grain size. Four genera were recorded, and these can be assigned to two ecological groups. *Echinoderes* and *Semnoderes* are typical representatives of sandy sediments and particularly the latter genus is known to inhabit coarse substrates. These genera were found only in the Southern Bight and in the entrance to the Firth of Forth. Conversely, species of the genera *Pycnophyes* and *Kinorhynchus* were recorded in the central part of the North Sea and never in the Southern Bight. Their distribution was largely confined to the eastern part of the central area. These genera are associated with very fine sediments. The same area was also characterized by the occurrence of Priapulida (larvae of *Priapulus caudatus*), a taxon that was entirely absent in the Southern Bight and occurred only sporadically in the western part of the North Sea (HUYS *et al.*, 1992).

LATITUDINAL PATTERNS

There is a distinct and significant trend for copepod density to decrease towards the north (Fig.2). Diversity (expressed as Hill's number N_1 = exp H and calculated as equivalent number of species, see HEIP *et al.*, 1988) also decreases with latitude in the Southern Bight but increases again towards the north with a minimum around the 100 m isobath (Fig. 3). Mean individual ash-free dry weight shows a completely opposite trend. Towards the north individual biomass is considerably larger due to the gradual replacement of interstitial by large epibenthic species. Total biomass peaks both in the north and the south due to the different combination of large numbers of small species in the south and small numbers of large species in the north.

Canonical correspondence analysis on the major twin groups of the copepods showed that sediment characteristics (median grain size, silt and clay content) are highly intercorrelated but are uncorrelated with depth. Depth is correlated with latitude. The five twin groups are clearly found back in the ordination. The three southern groups show a close correlation with the sediment and can be arranged along a gradient of decreasing grain size and increasing silt and clay content. The position of the northern twin groups is related to latitude and depth.

The topography of the North Sea (Fig. 1) is an important factor in determining the pattern of water movements, and thus the environmental conditions to which the animals and plants in the various areas are subjected. ADAMS (1987) recognised seven subdivisions of the North Sea by using certain depth contours and a combination of physical and biological properties of the water masses. Adams used the 40 m contour which approximately marks the boundary between stratified and well mixed water during the summer, the 50 m contour which along part of its course coincides with the northern flank of the Dogger Bank, the 100 m contour along which the water masses of the Fair Isle-Orkney current tend to flow and the 200 m contour which marks the western boundary of the Norwegian Deeps.

Historically much research has been devoted to abundance and biomass of meiofauna and their relationship to sediment characteristics. Many studies have shown that the median grain size and the silt content of the sediment are often dominant factors that explain a significant part of the variance in species abundance and diversity. A very important qualitative barrier is formed by the 300 µm grain size below which interstitial fauna becomes rare.

MEIOFAUNA AND BIOLOGICAL MONITORING

The suggestion that meiofauna may be used for detection and quantification of perturbation in general and anthropogenic perturbation in particular has been made since the seventies (HEIP, 1980). The relatively recent development of meiofauna research and the plethora of taxonomic difficulties initially caused a certain unfamiliarity with meiofauna among pollution biologists. Yet much of the ecological literature has now been summarized in several extensive reviews (GIERE and PFANNKUCHE, 1982; HICKS and COULL, 1983; HEIP *et al.*, 1985) and the literature on the taxonomy of the major meiofaunal groups has been equally prolific, resulting in the publication of useful identification guides in the Linnean Society 'Synopses of the British Fauna' series (PLATT and WARWICK; 1983; 1988; other volumes on harpacticoid copepods, gastrotrichs and kinorhynchs are forthcoming).

The advantages of using meiofauna in pollution monitoring have been summarized by *e.g.* REES *et al.* (1991). Meiofauna generally has a higher species diversity than macrofauna so that trends may be easier to discern, particularly in areas where macrofauna diversity is low. The time-consuming identification of meiofauna species seems to be unnecessary in many instances and higher taxonomic levels may provide sufficient information (HEIP *et al.*, 1988; WARWICK, 1988). Macrofauna communities may persist due to recruitment from elsewhere, whereas only a few meiofauna species have a planktonic life-history stage and the whole life-cycle is normally passed *in situ.* Generation times are short and meiofauna is theoretically capable of a faster response to perturbation; reductions in fecundity and growth caused by various toxicants manifest themselves faster in community parameters (density, diversity, biomass).

In general, copepods are more strongly influenced by environmental factors, such as organic enrichment, that cause the redox potential discontinuity layer to rise, than any other meiofauna taxon. Benthic copepods as a group appear intolerant to hypoxia; copepod density decreases well before nematode density, when oxygen is depleted in sediments. Interstitial copepods are living deeper into the sediment and disappear first in organically enriched areas (SHIELLS and ANDERSON, 1985) whereas epibenthic species may bloom in similar sediments as long as the overlying water is not hypoxic as well (MOORE and PEARSON, 1986). With regard to inorganic pollution VAN DAMME *et al.*, (1984) suggested that harpacticoid copepods are suitable early warning indicators since no other estuarine group, either meiobenthic, macrobenthic or planktonic, was so clearly affected by heavy metal pollution in the Westerschelde estuary. The different response of copepods and nematodes was illustrated by recent mesocosm experiments using controlled levels of organic enrichment (GEE *et al.*, 1985) and the impact of hydrocarbon and copper pollution (WARWICK *et al.*, 1988) on meiofauna. Both studies revealed a clearer response of the harpacticoids which perhaps offer the best potential for a better estimation of pollution impact in the field.

MEIOFAUNA ENERGETICS IN THE NORTH SEA

The energetic role of meiofauna can be deduced from their production and respiration, provided there is some constancy in assimilation efficiencies. This has been well developed for the North Sea by HEIP *et al.* (1990) and no new data have become available since this review. In practice it is often impossible to use any of the described methods for measuring production (HOLME and MCINTYRE, 1984) directly for meiofaunal populations.

Direct production estimates of field populations only exist for five harpacticoid species (FELLER, 1982; FLEEGER and PALMER, 1982; HERMAN *et al.* 1984a; HERMAN and HEIP, 1985; CECCHERELLI and MISTRI, 1991), and an ostracod species (HERMAN *et al.*, 1983).

Indirect approaches to estimate production from either respiration or biomass have been reviewed by HEIP and HERMAN (1988) and HEIP *et al.* (1990) and will be summarized here again. Respiration measurements, which for meiofauna are technically difficult, may be used to estimate production, assuming proportionality between production and respiration of a population. The log-log relationship between population production and respiration with a slope equal to one proposed by HUMPHREYS (1979) (but with no meiofauna data included) was substantiated by HERMAN *et al.* (1984b) who were able to compare respiration and field production of three meiofaunal populations (one ostracod and two harpacticoid copepods) and found indeed a constant value $P/(P+R) \approx 0.4$.

The much higher values in the order of production efficiency of 60-90 % found by SCHIE-

MER *et al.* (1980), TIETJEN (1980), WARWICK (1981), SCHIEMER (1982a,b) and HERMAN and VRANKEN (1988) seem to be a consistent feature, but these figures are based on a selection of easily cultured, so-called 'weed species' and are probably not representative for most marine nematodes. On the other hand, WARWICK and PRICE (1979) showed that, after correction for temperature, the community respiration of nematodes nearly equalled 6 l O_2 g^{-1} wwt yr^{-1}. This figure was found in several habitats, where individual nematode weight differed by an order of magnitude.

GERLACH (1971) provided the first estimate of annual P/B = 9 for meiofauna in general. The figure has two components, a life cycle turnover of three and three generations annually. HERMAN *et al.* (1984b) showed that for nematodes under certain conditions (neonate weight is production, juvenile growth is exponential, adult growth is not too important and the generation time is defined as the development time of juveniles) a P/B = 3 per generation (juvenile period) may be expected.

Scaling of annual P/B to body size has been proposed by BANSE and MOSHER (1980), who showed a log-log relationship between the two variables. It was applied to meiofauna by HEIP *et al.* (1982) and to nematodes by VRANKEN and HEIP (1986). Both compilations of meiofauna data show that the weight dependence coefficient in meiofauna is similar to the general value found by Banse and Mosher (1980). However, the intercept values are much lower, in the order of 1/10 of the intercept values of the macrofauna. This feature was anticipated by BANSE and MOSHER (1980), and discussed by HEIP *et al.* (1982) and VRANKEN and HEIP (1986). However, no conclusive arguments have been found to explain it.

Since the P/B per generation (juvenile developmental period) is around three, a fairly accurate indirect estimation of production may be obtained by multiplying the number of generations produced annually by this figure. The reviews of HEIP *et al.* (1985) and HICKS and COULL (1983) give data on the annual number of generations in nematodes and copepods, respectively. For both these groups it is clear that a uniform value for the number of generations produced annually does not exist and that each population has to be studied in its own right.

For nematodes the existing data from laboratory cultures have been reviewed by VRANKEN *et al.* (1986) who proposed the following equation relating the egg to egg development time T_{min} to temperature and adult female weight W:

$$\log T_{min} = 2.202 - 0.0461\,t + 0.627 \log W$$

When multiplied by the constant biomass turnover per generation $(P/B)_g = 3$, development rate $1/T_{min}$ can be used as a predictor of daily P/B.

PRODUCTION AND BIOMASS OF MEIOFAUNA IN THE NORTH SEA.

Energy flow models for the North Sea use meiobenthic biomass to evaluate the trophic role of the meiofauna. Usually, the biomass (around 1-2 g dwt m^{-2} for subtidal sediments) is multiplied by a constant factor (often 8-10) to obtain a production of 8-20 g dwt m^{-2} yr^{-1} and energy consumption, which is perhaps around five times this value, *i.e.* 40-100 g dwt m^{-2} yr^{-1}, or 16-60 g C m^{-2} yr^{-1}. If no other information is available a P/B of 10-20 for nematodes and 14 for copepods could be used. Gross uncertainties are present in such extrapolations and the use of a single P/B. ratio has been strongly discouraged by VRANKEN and HEIP (1986).

The reasonably constant production efficiency, the production to assimilation ratio $P/A \approx 0.4$, found in 'aerobic' meiofauna populations may be used to obtain estimates of production from respiration measurements. In order to evaluate the energy consumption of a population one may try to obtain similar constants for P/C, the production to consumption ratio. Very few data exist on which such extrapolations might be based. HEIP *et al.* (1985) summarized the data for nematodes. Consumption of bacteria and algae by three species of nematodes varied between 14 and 60.10^{-2} µg C d^{-1}. ADMIRAAL *et al.* (1983) estimated that a nematode eats about double its own carbon content each day. A community with a standing stock of 0.3 g C m^{-2} would then consume about 220 g C m^{-2} yr^{-1}. However, it is unreasonable to extrapolate the (spring) rates from a highly productive intertidal community to subtidal communities without *in situ* primary production.

ROLE IN THE FOOD WEB

The role of the meiofauna in ecosystems has been the subject of investigation since the mid seventies. A summary of such studies (COULL, 1988) has shown that in only a few of these attempts have been made to determine the food of meiofauna in the field and that conclusions from such studies are generally vague. Laboratory studies are more numerous. The most important food source for meiofauna are bacteria, diatoms and other microalgae, but the effect of meiofaunal grazing on the microbial community is largely unknown (MONTAGNA, 1984). The grazing pressure seems to be high enough to stimulate microbial activity. MONTAGNA (1984) showed that 3% of bacteria and 1% of diatoms were removed per hour, which would suggest that meiofauna could maintain bacteria and diatoms in the log phase of growth. Meiofauna and microalgal populations share nearly identical spatial patterns (PINCKNEY and SANDULLI, 1990), suggesting that meiofauna may structure microalgal populations.

Another question that arises is what is the sort of meiofaunal biomass production. MCINTYRE and MURISON (1973) and HEIP and SMOL (1975) suggested that meiobenthic prey were consumed mainly by meiobenthic predators and thus were not available to higher trophic levels. MCINTYRE (1964) and MARSHALL (1970) concluded that there was competition for food between macrofauna and meiofauna and that the main role of meiofauna in the ecosystem is in catalyzing nutrient regeneration. However, since these earlier studies a lot of evidence has been gathered showing that meiofauna is important prey for some macrofaunal- and fish species, although the total proportion of meiofauna entering higher trophic levels may be limited (GEE, 1987).

COULL (1990) has recently reviewed the problem again. The evidence that meiofauna serve as food comes mainly from gut contents. Many authors have shown that especially copepods occur in the guts of fish, even when nematodes are the most abundant meiofaunal group. Selection of copepods over nematodes by juvenile fish is found by COULL (1990) and NELSON and COULL (1989). Many predators prefer to forage in the superficial rediment layers. Copepods are most abundant in the upper 2 mm of the sediment and relatively easy to catch. Nematodes in contrast are more abundant in subsurface layers and move to deeper layers when the upper sediment layer is disturbed (PALMER and MOLLOY, 1986). For the same reason meiofauna seem to serve as food for higher trophic levels more in mud than in sand (SMITH and COULL, 1987). In muddy sediments meiofauna is concentrated in the upper few millimeters. In sandy sediments, however, meiofauna is distributed over a larger depth. In muddy sediments, therefore, meiofauna is more available for predators and predation will be far more efficient than in sandy sediments.

The role of such predation on meiofaunal populations is largely unknown. Some authors found a significant decrease of the harpacticoid population in presence of predators (ELLIS and COULL, 1989; HEDQVIST-JOHNSON and ANDRÉ, 1991), but no effects were found on nematode populations. In contrast, WEBB (1991) did not find any effect of predation on copepod densities.

THE ROLE IN BIOGEOCHEMICAL CYCLES

The role of meiofauna in nutrient regeneration is complex and only some aspects are studied. There is evidence that certain meiofauna species make detritus available to macroconsumers (TENORE *et al.*, 1977). Net incorporation rates of five month-aged eelgrass detritus by the polychaete Nepthys were nearly doubled in cultures containing meiofauna. Meiofauna may influence nutrient cycles either directly by grazing on phytodetritus (RUDNICK, 1989) or indirectly by stimulating the microbial community. RUDNICK (1989) found two competing meiofaunal assemblages segregated by depth in the first few millimeters of the sediment. Meiofauna in the uppermost layer, mostly harpacticoid copepods, feeds on freshly deposited phytodetritus. Meiofauna in the subsurface layer is largely dependent of the older phytodetritus, which is burried and aged in the sediment.

Although the mechanism is unclear, meiofauna can enhance decomposition and mineralization of carbon and nitrogen. Some studies about the effect of bacterivorous nematodes on the mineralization of macrophytal detritus are available. FINDLAY and TENORE (1982) found higher carbon-mineralization rates of *Spartina* and *Gracilaria* detritus in the presence of nematodes. A higher decomposition rate of seaweed detritus in presence of nematodes was found by RIEPER-KIRCHNER (1989). Carbon and nitrogen loss from *Spartina* detritus was enhanced in the presence of bacterivorous nematodes indicating a higher mineralization rate of both carbon and nitrogen (ALKEMADE *et al.*, in press).

The role of nematodes in the sulphur cycle is unknown. Many nematode and other meiofaunal groups are specifically adapted to anoxic sediments. Some nematode species contain endosymbiotic sulphur-oxidising bacteria (DANDO *et al.*, 1991), which makes it possible for nematodes to live under high sulphide concentrations. Nematodes of the family Stilbonematinae are characterized by their association with ectosymbiotic microorganisms. They live on the interface between the oxic and the anoxic sediment layers and may travel between those two layers. (OTT and NOVAK, 1989)

Meiofauna may influence other diagenetic processes. Small burrow-like structures built by nematodes and copepods have been described by

CULLEN (1973) and NEHRING *et al.*, (1989). These structures may alter the microstructure of the sediment. Diffusion between the sediment and the watercolumn will be facilitated through this microscale burrows. A significant increase in diffusion of oxygen in presence of nematodes was recently found (Alkemade *et al.*, unpubl.). The movements of the nematodes through burrows or in the interstitial water may result in bioturbation and increase the oxygen supply in the subsurface layers. The microbial community may be stimulated by the increased oxygen supply, and mineralization of detritus is enhanced. However, these suggested mechanisms still require careful experimental study before their importance in biogeochemical cycles can be evaluated.

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