Rapp. P.-v. Réun. Cons. int. Explor. Mer, 183: 51–56. 1984.

Variability and productivity of meiobenthos in the Southern Bight of the North Sea

C. Heip, R. Herman, and M. Vincx

Marine Biology Section, Zoology Institute
Ledeganckstraat 35, B-9000 Gent, Belgium

The composition and density of meiofauna in the Belgian coastal waters of the North Sea are essentially similar to those over large spatial scales. However, the impact of pollution from the Western Scheldt river is clearly reflected in a decrease in diversity on all taxonomic levels. Nematodes are the only animal group that survives in normal or even greater abundance, albeit it with lower diversity. Total meiofauna production is estimated at 1·5–2·0 g C m^{-2} yr^{-1} and equals or even greatly exceeds macrofauna production in the area.

Introduction

The numerical importance of meiobenthos in marine sediments is well established. Nematodes are the dominant animal taxon in these environments and number between 1 and 3 million ind./m^2 in most shallow waters. Harpacticoid copepods are often second in numerical importance. However, energy flow through the meiobenthos is poorly known, and its part in marine food webs involving commercially important species is still a matter of debate.

Estimations of meiobenthic productivity are based on density and biomass data and use the well-known relationships between the last parameter and production as expressed in a P/B ratio. In benthic ecology the figure proposed by Gerlach (1971), $P/B = 9$, is still widely used. It was based on an average of three annual generations of meiobenthos each having a life-cycle turnover of three (Waters, 1969).

In recent years the relationship between respiration and production proposed by McNeil and Lawton (1970) has also been used to estimate production of meiofauna (Warwick *et al.*, 1979). When individual respiration is known, production can be estimated from density in the field.

Both indirect approaches for the estimation of meiobenthic production in the sea depend ultimately on density. For this reason the spatial and temporal variability of density and biomass has to be studied.

Material and methods

The Belgian coastal zone of the Southern Bight of the North Sea has been studied since 1970. During 1972–1980 ten stations were chosen in order to estimate the influence of pollution in this area (Fig. 1).

Samples were taken with a van Veen grab, subsampled with a core on deck in earlier years, and from 1977 onwards, with a Reineck box corer and also subsampled with a core. Meiofauna from muds was extracted using a centrifugation-flotation technique based on Ludox. Meiofauna from sands was extracted by decantation. In principle all copepods and 100 nematodes were determined to species level in each subsample.

Results and discussion

Spatial variability in the Southern Bight

The meiobenthic communities of the Southern Bight have been described by Govaere *et al.* (1980) who based them on harpacticoid copepods. They distinguished a coastal zone characterized by large epibenthic species (*Microarthridion littorale – Halectinosoma herdmani* association) and an open sea zone characterized by small interstitial species (*Leptastacus*

Table 1. Mean number of higher taxa, total density, and percentage of nematodes and harpacticoids in six subtidal stations, June 1977 – September 1979.

Station	$\bar{n}$ taxa	N_{tot}	% nem	% harp
M 10061	4·11	750	94·98	3·37
M 10481	3·70	1903	98·47	0·82
M 10791	3·22	2571	99·07	0·59
M 11312	2·50	2297	99·52	0·42
M 11672	2·56	1347	97·52	1·01
M 11860	2·10	1372	99·18	0·15

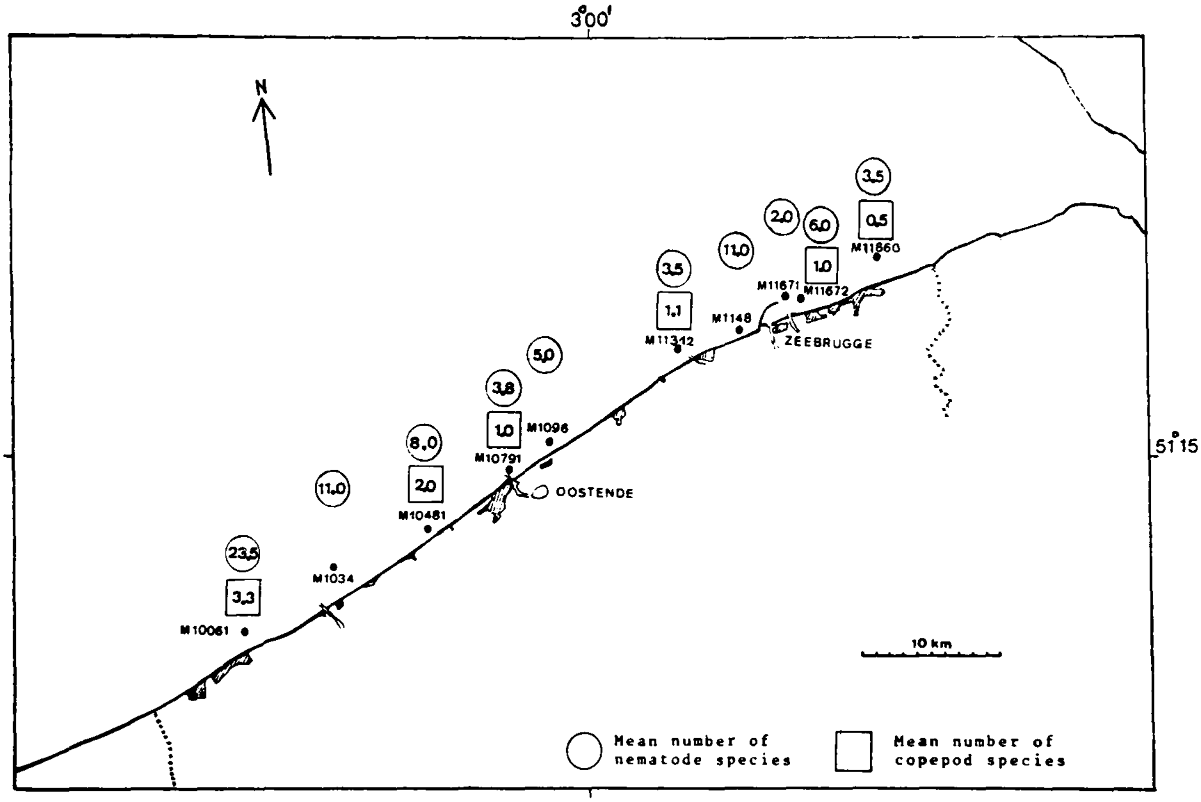

Figure 1. Localization of the ten subtidal stations. Nematode data are from 1972–1978; harpacticoid data are from 1977–1979.

laticaudatus – Paramesochra helgolandica association). Both zones are separated by a transition zone where interstitial and epibenthic species co-occur.

These associations are stable in the sense that species composition and relative abundance are similar over large areas. In the coastal zone nematodes are dominant and represent more than 90 % of the meiofauna on all stations (Table 1). The total number of meiobenthic taxa decreases from west to east (Fig. 2), a phenomenon that can be linked to pollution from the Western Scheldt estuary. This pollution is reflected in the heavy metal content of the sediments (Bouqiaux and Herman, 1977), which is linked with the amount of particles smaller than 37 μm and which decreases from east to west (Table 2).

Nematodes from the coastal zone were compared on the basis of summer samples. The number of nematode species (*S*) and diversity (*H*, Brillouin's index in bits/ind.) are given in Table 3. This table also shows the partitioning of species over the four main feeding types recognized in nematodes (1A: selective deposit-feeders; 1B: non-selective deposit-feeders; 2A: herbi-

Table 2. Silt-clay fraction (< 37 μm), organic matter, and concentration of pollutants on ten coastal stations (data from Bouqiaux and Herman, 1977).

Station	< 37 μm (%)	Org. mat. (%)	S_{tot} (%)	Cr (ppm)	Cu (ppm)	Hg (ppm)	Mn (ppm)	Ni (ppm)	Pb (ppm)	Zn (ppm)
M 10061	5	0·36	0·06	10	2	0·09	102	4	15	41
M 1034.........	23	2·2	0·26	20	4	0·20	205	5	31	52
M 10481	37	2·2	0·35	27	8	0·28	275	8	59	70
M 10791	72	5·9	0·65	56	18	0·75	755	17	124	154
M 1096.........	20	1·8	0·34	20	5	0·15	360	6	54	58
M 11312	67	5·8	0·66	53	20	0·61	625	16	78	138
M 1148.........	21	1·4	0·19	24	8	0·14	290	6	41	70
M 11671	48	4·0	0·39	29	10	0·29	400	8	54	83
M 11672	52	3·9	0·47	36	11	0·58	540	11	71	103
M 11860	41	3·4	0·45	30	11	0·36	400	9	63	98

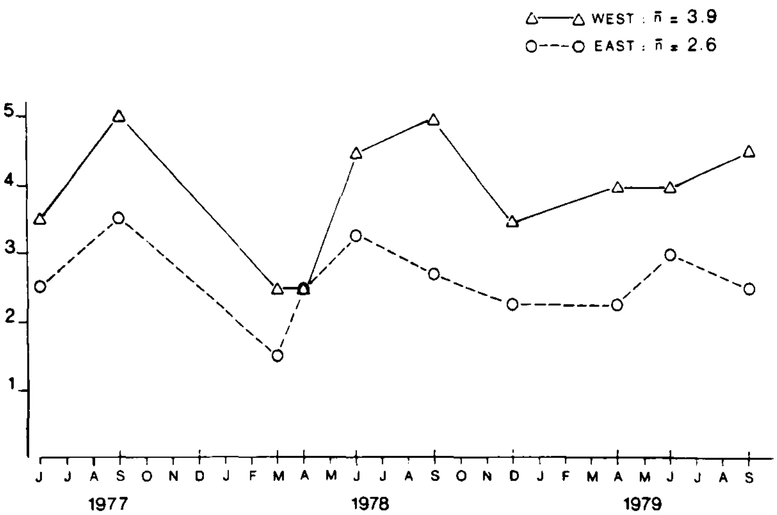

Figure 2. Fluctuation of the mean number of taxa in the western and eastern zones of the Belgian coast.

vores; and 2B: predators and/or omnivores). This partitioning has been summarized in a trophic index $\Sigma\Theta^2$ (Θ = the percentage of each feeding type), varying between 0·25 and 1. $\Sigma\Theta^2 = 1$ indicates that only one trophic type is present; this has only been found when that trophic type was 1B.

A significant correlation has been found between the number of nematode species, the heavy metal content of the sediments, and the sediment type. The trophic index follows the same trend. The relation between the number of species and the trophic index is shown in Figure 3. When non-selective deposit-feeders dominate, the number of species is always low. On moderately polluted stations (M 10481 and M 11672), 1B is already the dominant group, but species number still drops when the heavy metal content of the sediment increases. The less polluted sandy stations are always more diverse, with trophic indices approaching 0·25. The causality of the decrease in diversity of nematodes is not obvious as it is also correlated with the amount of particles smaller than 37 μm. However, a correlation with diversity or species number does not exist for the amount of silt-clay particles (< 63 μm) or the median grain size of the sand fraction of the same stations. Nevertheless, it is remarkable that nematode richness is very significantly correlated with the heavy metal content.

In the coastal zone there are only four families of nematodes with a frequency higher than 50 %: the Comesomatidae, Xyalidae, Linhomoeidae, and Axonolaimidae, with the following species: *Sabatieria* spp., *Daptonema tenuispiculum, Metalinhomoeus* sp.n.A, and *Ascolaimus elongatus. Sabatieria* occurs on all stations. The genus is represented by five species with different abundance. *S. breviseta* occurs on all stations except one (M 10061). *S. vulgaris* is the second most important, whereas *S. celtica* is restricted to sandy sites (dominant in M 10061). *S. hilarula* and *S. granulosa* occur irregularly in low numbers.

Daptonema tenuispiculum is especially dominant on

Table 3. Number of nematode species (*S*), distribution of the four feeding types (% 1A, % 1B, % 2A, % 2B), trophic index ($\Sigma\Theta^2$), diversity (*H*), and evenness (*e*) of the nematodes.

Station	*S*	1A	1B	2A	2B	$\Sigma\Theta^2$	*H*	*e*
M 10061	23·5	3·5	39·5	25·5	30·5	0·32	2·94	0·74
M 1034	11·0	1·0	97·0	2·0	0·0	0·94	1·10	0·35
M 10481	8·0	0·0	100·0	0·0	0·0	1·00	1·14	0·41
M 10791	3·8	0·0	100·0	0·0	0·0	1·00	0·75	0·43
M 1096	5·0	0·0	93·0	6·0	1·0	0·87	1·04	0·47
M 11312	3·5	0·0	100·0	0·0	0·0	1·00	0·78	0·47
M 1148	11·0	0·5	86·5	4·5	8·5	0·76	1·85	0·59
M 11671	2·0	0·0	100·0	0·0	0·0	1·00	0·88	0·91
M 11672	6·0	0·0	98·5	1·0	0·5	0·97	0·81	0·34
M 11860	3·5	0·3	96·3	0·5	2·9	0·93	0·35	0·18

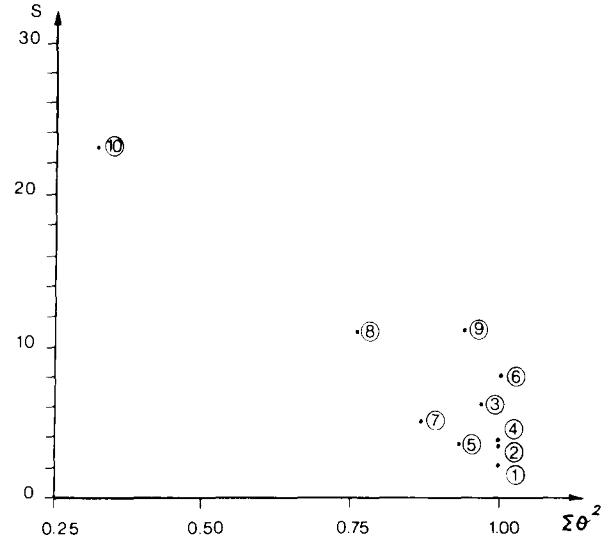

Figure 3. Degree of heavy metal pollution from highest (1) to lowest (10). Number of nematode species (S); trophic index ($\Sigma\Theta^2$); see text.

the highly polluted stations (M 10791, M 11312, and M 11671). It occurs regularly in low numbers on the other stations. A vertical profile of nematode species on M 11860 shows that *Daptonema* is restricted to the upper centimeters of the sediment. This is always the case. We assume that *Daptonema,* which is a monhysterid and therefore a good swimmer, is able to survive in the flocculent upper layer of the sediment decribed by Billen *et al.* (1977). This flocculent layer still contains some oxygen, whereas the deeper layers in these very polluted stations quickly become anoxic.

The influence of organic carbon content, heavy metal pollution, and sediment characteristics on the nematodes of sublittoral muds and sandy muds has been examined by Warwick and Buchanan (1970); Boucher (1972); Vitiello (1974); and Tietjen (1977, 1980). In none of these studies has a 100 % dominance of non-selective deposit-feeders (1B) been found, although high dominance of 1B is characteristic of most shallow marine muds. A combination of the trophic index and species richness provides a good indication of the influence of pollution on sediments near the Belgian coast, which must be among the most polluted subtidal marine areas of the world.

The impoverishment of the nematode community along the Belgian coast following a west to east increase in pollution can be explained by the gradual elimination of species as stress increases. The same can be found in harpacticoid copepods. All stations in the Belgian coastal zone yield species belonging to the *Microarthridion littorale – Halectinosoma herdmani* association described by Govaere *et al.* (1980). Six out of a total of eleven species are common to eastern and western stations, with *M. littorale* being extremely dominant on all stations and making up on average 87 % of all harpacticoids in the west and 94 % in the east. One species is restricted to the east: *Halectonisoma propinquum,* whereas another ectinosomid, *Pseudobradya beduina,* and two other species are present only in the west. The impoverishment of the harpacticoid fauna from west to east is also reflected in the average diversity which decreases from $H' = 0{\cdot}87$ bits/ind. in the west to $0{\cdot}43$ bits/ind. in the east, and in the fact that 14 out of 15 stations in the west yielded harpacticoids against 21 out of 30 in the east.

We may summarize by stating that meiofauna associations do occur with rather great consistency over large areas and that the composition of these associations is mainly determined by sediment characteristics. In the Belgian coastal zone, pollution from the Western Scheldt estuary may be responsible for a significant decrease in diversity from west to east. This decrease is reflected over all taxonomic levels.

Productivity of meiobenthos in the Southern Bight

As it was impossible to measure production of meiobenthic populations in the sea with the means that were at our disposal, only indirect measures based on density and biomass were used. When estimating production from biomass, life-cycle turnover is the more stable parameter: it was found by Waters (1969) to vary between 2 and 5 with a modal value of 3·5. The annual number of generations is less stable. While it is true, as Gerlach (1971) assumed, that there are many meiofauna species which produce only one or a few generations each year, this need not always be the case. Species of the nematode genus *Monhystera* have been studied in our laboratory by Vranken and Van Brussel (unpublished) and could produce between ten to fifteen generations annually in the field. Nematode com-

Table 4. Number of harpacticoid copepod species and average relative frequency (%) in six subtidal stations along the Belgian coast, June 1977 – September 1979.

Species	Coastal zone	West	East
Longipedia coronata	0·1	0·2	–
Canuella perplexa	1·2	1·5	0·5
Halectinosoma sarsi	2·1	2·2	1·9
Halectinosoma herdmani	4·5	6·0	0·5
Halectinosoma propinquum	0·5	–	1·9
Pseudobradya beduina	1·0	1·5	–
Microarthridion littorale	88·8	86·8	94·3
Thompsonula hyaenae	0·7	0·9	–
Evansula pygmaea	0·3	0·2	0·5
Paraleptastacus espinulatus	0·5	0·5	0·5
Enhydrosoma propinquum	0·3	0·4	–
Number of species	11	10	7
H' (bits/ind.)	0·78	0·87	0·43

Table 5. Mean density (N̄), biomass (B), individual biomass (Bi) and production (P) of harpacticoids and nematodes in six coastal stations along the Belgian coast, June 1977 – September 1979.

Station	Harpacticoida N̄ 10 cm^{-2}	Harpacticoida B gC m^{-2}	Harpacticoida P gC m^{-2} yr^{-1}	Nematoda N̄ 10 cm^{-2}	Nematoda Bi µg dwt	Nematoda B gC m^{-2}	Nematoda P gC m^{-2} yr^{-1}
M 10061	45·1	0·036	0·252	706	0·31	0·09	0·81
M 10481	17·9	0·014	0·101	1878	0·29	0·22	1·98
M 10971	6·0	0·005	0·044	2472	0·25	0·25	2·23
M 11312	10·8	0·009	0·062	2285	0·24	0·22	1·98
M 11672	10·1	0·008	0·056	1337	0·25	0·13	1·19
M 11860	1·6	0·001	0·008	1368	0·28	0·15	1·37

munities dominated by small bacterial feeders may have P/B ratios well in excess of ten, and a figure of 30–40 may not be unrealistic. However, as it is impossible to estimate the number of annual generations in the field and as production in nature cannot always reliably be induced from laboratory experiments, we used Gerlach's minimum value $P/B = 9$. For an average biomass of 0·18 gC m^{-2} for nematodes, production will be 1·60 gC m^{-2} yr^{-1}. For harpacticoid copepods, a figure of $P/B = 7$ (Herman, unpublished) was used. Total production of harpacticoids is insignificant when compared with that of nematodes and amounts to only 0·09 gC m^{-2} yr^{-1}.

A second method of evaluating production indirectly is to use the relationship between this parameter and respiration. Respiration of nematodes has been studied mainly by Warwick and Price (1979), who demonstrated that it differs according to feeding type. These values have been used to calculate individual respiration of nematodes. A non-selective deposit-feeder has a low respiration of about 1·8 nl O_2 µg dwt^{-1} h^{-1}. As the average biomass of an individual nematode in the Belgian coastal area is only 0·27 µg, its respiration amounts to 0·46 nl O_2 h^{-1} in summer and to 0·24 nl O_2 h^{-1} in winter. This gives an annual respiration of 5·32 l O_2 m^{-2} for the whole nematode community, or 2·16 gC m^{-2} yr^{-1}. Using Humphreys' regression between production and respiration, $\log P = 1 \cdot 069 \log R - 0 \cdot 601$ (Humphreys, 1979) (in cal), production would amount to 1·09 gC m^{-2} yr^{-1}, a very low value. Using $K_2 = 0 \cdot 38$ as found by Marchant and Nicholas (1974), production will be $P = 0 \cdot 613\ R$ or 1·32 gC m^{-2} yr^{-1}. Using the K_2 values found by Warwick (1981) for the opportunistic nematode *Diplolaimelloides brucei* ($P = 2 \cdot 3 - 5 \cdot 7\ R$), production would be accordingly higher. Using the same relationships as established for harpacticoid copepods, their production can be calculated as 86 mgC m^{-2} yr^{-1}, a value which is again negligible when compared with nematode production.

Table 6. Mean density (N̄), biomass (B), production (P) and respiration (R) on six coastal stations, June 1977 – September 1979.

	Harp.	Nem.	Tot.
N̄ 10 cm^{-2}	15	1 675	1 690
B̄ (ind.) µg dwt	2	0·27	–
B̄ gC m^{-2}	0·012	0·18	0·19
P̄ gC m^{-2} yr^{-1}	0·086	1·60	1·69
R̄ nl O_2 ind.$^{-1}$ h^{-1}	12·48	0·65	–
R̄ gC m^{-2}	0·32	1·81	2·13

Total meiofanua production in the order of 1·5 to 2·0 gC m^{-2} yr^{-1} may be compared with macrofauna production in the area as calculated by Govaere *et al.* (1980). The macrobenthic *Abra alba* community in the region has a mean biomass of 1·46 g ash-free dry weight and a mean production of 4·25 g ash-free dry weight, or about 1·70 gC m^{-2} yr^{-1}. This is of the same magnitude. However, in very poor stations near the coast where a *Macoma* community exists, macrobenthic production drops to values as low as 0·1 gC m^{-2} yr^{-1}. As nematodes remain abundant even in these sediments, meiofauna production will greatly exceed macrofauna production there.

Acknowledgements

We are grateful to the Management Team of the Mathematical Model North Sea (Ministry of Public Health, Belgium) who have always assisted us with much competence. We thank the crew of the research vessel "Mechelen" for assistance at sea. Technical assistance from Alex Braeckman, Mark De Keere, Anita Van Bost, and Dirk Van Gansbeke is gratefully acknowledged. This research was supported by the Concerted Actions Oceanography Program of the Ministry of Scientific Policy. Two authors, C. Heip and M. Vincx, acknowledge a grant from the Belgian Foundation for Scientific Research (N.F.W.O.).

References

Billen, G., Vanderborght, J. P., and Wollast, R. 1977. Modèles diagénétiques des substances nutritives dans les sédiments marins côtiers. *In* Projekt Zee, Report to Min. of Science Pol. in Belgium, part 4, pp. 163–186. Ed. by J. Nihoul and F. Gullentops.

Boucher, G. 1972. Distribution quantitative et qualitative des Nématodes d'une station de vase terrigène côtière de Banyuls-sur-Mer. Cah. Biol. mar., 13: 457–474.

Bouqiaux, J., and Herman, P. 1977. Niveaux de pollution du réseau hydrographique et de la zone côtière belge. *In* Projekt Zee, Report to Min. of Science Pol. in Belgium, part 6, pp. 1–98. Ed. by J. Nihoul and I. Elskens.

Gerlach, S. A. 1971. On the importance of marine meiofauna for benthos communities. Oecologia (Berl.), 6: 176–190.

Govaere, J. C. R., Van Damme, D., Heip, C., and De Coninck, L. A. P. 1980. Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. Helgoländer wiss. Meeresunters., 33: 507–521.

Humphreys, W. F. 1979. Production and respiration in animal populations. J. animal Ecol., 48: 427–453.

Marchant, R., and Nicholas, W. L. 1974. An energy budget for the free-living nematode *Pelodera* (Rhabditidae). Oecologia (Berl.), 16: 237–252.

McNeil, S., and Lawton, J. H. 1970. Annual production and respiration in animal populations. Nature, 225: 472–474.

Tietjen, J. H. 1977. Population distribution and the structure of the free-living nematodes of Long Island Sound. Mar. Biol., 43: 123–136.

Tietjen, J. H. 1980. Population structure and species composition of the free-living nematodes inhabiting sands of the New York Bight Apex. Estuar. coast. mar. Sci., 10: 61–73.

Vitiello, P. 1974. Peuplements de Nématodes marins des fonds envasés de Provence. I. Sédiments vaseux de mode calme et vases terrigènes côtières. Ann. Inst. océanogr., Paris, 50 (2): 145–172.

Warwick, R. M. 1981. The influence of temperature and salinity on energy partitioning in the marine nematode *Diplolaimelloides brucei.* Oecologia (Berl.), 51: 318–325.

Warwick, R. M., and Buchanan, J. B. 1970. The meiofauna off the coast of Northumberland. I. The structure of the nematode population. J. mar. biol. Ass. U.K., 50: 129–146.

Warwick, R. M., Joint, I. R., and Radford, P. J. 1979. Secondary production of the benthos in an estuarine environment. *In* Ecological processes in coastal environments, pp. 429–450. Ed. by R. L. Jefferies and A. J. Davey. Blackwell Sci. Publ.

Warwick, R. M., and Price, R. 1979. Ecological and metabolic studies on free-living nematodes from an estuarine mud-flat. Estuar. coast. mar. Sci., 9: 257–271.

Waters, T. F. 1969. The turnover in production ecology of freshwater invertebrates. Am. Nat., 103: 173–185.