International Council for the Exploration of the Sea

C.M. 1983/L: 14
Biological Oceanography Committee

The present state of knowledge on North Sea subtidal Meiofauna.

Carlo Heip, Rudy Herman and Magda Vincx

Marine Biology Section, Zoology Institute, State University of Ghent, Belgium

INTRODUCTION

This report reviews work that has been done on North Sea subtidal meiofauna, from an ecological point of view. In this respect, mainly the hard-bodied meiofauna taxa Nematoda and Copepoda have been studied to any extent. We therefore present also a short review on relevant taxonomic studies of these groups.

TAXONOMIC STUDIES

Harpacticoida

The publication of Lang's "Monographie der Harpacticiden" (1948) has stimulated the study of Harpacticoid Copepods throughout the world, which is reflected in the description of more than 1300 new species since and an increasing interest in the biology and ecology of these copepods in the last decades. Lang's comprehensive work contains the systematic description of all species known till 1944, an extensive morphological study and chapters on the evolution and the biogeography of the harpacticoid copepods. Ecological notes per species were included when they existed.

In 1965 a second important work from Lang appears "Copepoda Harpacticoida from the Californian coast", in which 81 new species are described and some important families and genera are reviewed.

In the last decade Bodin (1967, 1971, 1976a, b & 1979) compiled the taxonomic papers and all descriptions of new species and taxonomical changes are listed in his "Catalogue des nouveau Copépodes Harpacticoides marins" till 1979 which should be consulted for further references. Very useful are the tabular keys published by Wells (1976, 1978, 1981), which are designed for non-specialists in harpacticoid taxonomy.

Although numerous taxonomical papers appeared in the last decades, very few are restricted to the North Sea area proper.

German Harpacticodologists, e.g. Becker, Klie, Kunz, Mielke, Noodt & Scheibel, studied the harpacticoid fauna round Helgoland, the Island of Sylt and the Kieler Bucht in the Baltic.

Other studies on the eastern parts of the North Sea are restricted to the Norwegian coast, with workers as Drzycismki, Geddes and Por.

In the Western zone of the North Sea most of the recent papers are restricted to the intertidal zone or near-shore coastal inlets and estuaries (e.g. Hamond, Wells). Except for some ecological studies of McIntyre on the Fladen Grounds few work has been done in the central and northern North Sea area. In the Irish Sea important harpacticoid work was done around the Isle of Man by Moore.

Finally, the Belgian group works in the Southern Bight of the North Sea (e.g. Claeys, Heip, Herman, Willems). They study the estuaries of the Delta region in The Netherlands and the subtidal zones, where besides ecological work, some taxonomic work is being done.

References

BODIN, Ph. 1967. Catalogue des nouveaux Copépodes Harpacticoïdes marins. Mém.Mus.Nat.Hist.nat., série A, 50(1) : 1-76.
BODIN, Ph. 1971. Catalogue des nouveaux Copépodes Harpacticoïdes marins. Additif n° 1. Téthys, 2(4) : 881-907.
BODIN, Ph. 1976a. Catalogue des nouveaux Copépodes Harpacticoïdes marins. Additif n° 2. Téthys, 7(2-3) : 265-278.
BODIN, Ph. 1976b. Catalogue des nouveaux Copépodes Harpacticoïdes marins. Additif n° 3. U.B.O., Fasc.Sc. Brest (France) : 1-45.
BODIN, Ph. 1979. Catalogue des nouveaux Copépodes Harpacticoïdes marins. (Nouvelle édition). U.B.O., Fac.Sc. Brest (France) : 1-228.
LANG, K. 1948. Monographie der Harpacticiden. Håkan Ohlsson, Lund, 2 vol.: 1-1682.
LANG, K. 1965. Copepoda Harpacticoidea from the Californian coast. K. svenska vetensk.Akad.Handl., 10(2) : 1-566.
WELLS, J.B.J. 1976. Keys to aid in the identification of marine harpacticoid copepods. Depart.Zool.Univ. Aberdeen, U.K., publ. : 1-215.
WELLS, J.B.J. 1978. Keys to aid in the identification of marine harpacticoid copepods. Amendement Bull. N° 1, Zool.Publ., Victoria Univ. Wellington, 70 : 1-11.
WELLS, J.B.J. 1981. Amend. Bull.N° 3, Zool. Publ. Victoria Univ. Wellington, 75: 1-13.

Nematoda

Prior to 1972, 456 nematode species were known from the North Sea (Gerlach, 1980), the number now approximates 735. (See addendum).

Gerlach & Riemann (1973, 1974) published a checklist containing all the systematic references about free-lving marine nematodes till 1973. The more recent references are given in this report.

Systematic research on marine nematodes started in the intertidal zone as this environment is sampled (much) easier than the subtidal region. We will deal with systematic papers on intertidal nematodes, because many species live in the subtidal as well as in the intertidal zone.

Neighbouring seas to the North Sea such as Kiel Bay, the Irish Sea and the Channel are also dealt with because the nematode species composition is similar.

Systematic work in and around the North Sea started at the end of the nineteenth century. The pioneer in North Sea nematode research, Bastian (1865), described several new species from the Falmouth region (Cornwall, U.K.). Most of those species are found back in the sub- and intertidal regions of the North Sea. It was nearly one hundred years later that Wieser (1951-1952) studied the free-living nematodes from the Plymouth area. Today, the British coasts are intensively studied by Jayasree, Lambshead, Moore, Platt, Warwick and Zhan.

The Norwegian coasts especially the fjords, have been studied by Allgen (1925-1960). A lot of species found in those regions have not been found back in other North Sea regions.

The German coasts (German Bight and Kiel Bay) have been studied by Schulz (1931-1938), Schneider (1939), Gerlach (1949-), Riemann (1966-), Lorenzen (1966-), Juario (1973-), Blome (1974-) and Benwell (1981-).

The southern part of the Dutch coast was examined by De Man (1876-1928), Schuurmans Stekhoven (1929-1954), Bresslau (1940), Jensen (1976-), Decraemer (1974-) and by Vincx (1981-).

The French Channel coast was examined by Kreis (1929), De Man (1889-1893), Boucher (1975-), Decraemer (1979-), Luc & De Coninck (1959), Gourbault (1981-) and Vitiello (1967-).

For a review on the current state of the systematics of free-living marine nematodes, we refer to the article of Heip _et al._ (1982).

References

BENWELL, M.P. 1981. A new species of Gonionchus (Nematoda, Xyalidae) from the Firth of Clyde, with a redescription of Enoploides spiculohamatus Schulz (Nematoda, Enoplidae). Cah.biol.mar. XXII : 177-184.

BLOME, D. 1974. Zur Systematik von Nematoden aus dem Sandstrand der Nordseeinsel Sylt. Mikrofauna Meeresboden, 33 : 1-25.

BLOME, D. 1982. Systematik der Nematoda eines Sandstrandes der Nordseeinsel Sylt. Mikrofauna Meeresboden, 86 : 1-194.

BOUCHER, G. 1975. Nématodes des sables fins infralittoraux de la Pierre Noite (Manche Occidentale). I. Desmodorida. Bull.Mus.natn.Hist.nat. Paris, 3è sér., 285, Zool. 195 : 101-128.

BOUCHER, G. 1976. Nématodes des sables fins infralittoraux de la Pierre Noite (Manche Occidentale). II. Chromadorida. Bull.Mus.natn.Hist. nat. Paris, 3è sér., 352, Zool. 245 : 25-61.

BOUCHER, G. 1977. Nématodes des sables fins infralittoraux de la Pierre Noite (Manche Occidentale). IV. Enoplida. Bull.Mus.natn.Hist.nat., Paris, 3è sér., 468, Zool. 325 : 733-752.

BOUCHER, G. & M.N. HELLEOUET. 1977. Nématodes des sables fins infralittoraux de la Pierre Noire (Manche Occidentale). III. Araeolaimida et Monhysterida. Bull.Mus.natn.Hist.nat. Paris, 3è sér., 427, Zool. 297 : 85-122.

BOUCHER, G. & F. de BOVEE. 1972. Halaphanolaimus harpaga n.sp., espèce nouvelle de Leptolaiminae (Nematoda). Vie et Milieu, 23, 1-A : 127-132.

BOUWMAN, L.A. 1981. A survey of nematodes from the Ems estuary. Part I : Systematics. Zool.Jb.(Syst.), 108 : 335-385.

DECRAEMER, W. 1979. Desmoscolecids from sublittoral fine-sand of Pierre Noire (West Channel) (Nematoda, Desmoscolecida). Bull.Mus.natn.Hist. nat., Paris, 4è sér., 1, sect. A, n° 2 : 299-321.

DECRAEMER, W. & P. JENSEN. 1981. Meyliidae (Nematoda-Desmoscolecoidea) with four new species and two new genera. Bull.K.Belg.Inst.Nat.Wet., Brussel, 53, Biologie, 18 : 1-13.

GERLACH, S.A. & F. RIEMANN. 1973-1974. The Bremerhaven Checklist of aquatic Nematodes. A catalogue of Nematoda Adenophorea excluding the Dorylaimida. Veröff.Inst.Meeresforsch.Bremerh. Suppl. 4 : 1-404 (1973) & 405-734 (1974). *

JAYASREE, K.V. 1976. Two new species of the genus Chitwoodia Gerlacht, 1956 (Nematoda, Asconolaimidae) from a polluted study beach in the Firth of Clyde, Scotland and a revision of the genus. Cah.Biol.mar. 17(4) : 439-446.

JAYASREE, K.V. 1980. A new species of Paracanthonchus Micoletzky, 1924 and a known species of Paracyatholaimus Micoletzky, 1922 (Nematoda, Cyatholaimidae, Paracanthonchinae) from polluted intertidal sand in Scotland. Cah.Biol.mar., 21 : 375-381.

JAYASREE, K.V. 1981. A new and two known species belonging to subfamily Leptolaiminae (Leptomaimidae, Nematoda) from polluted intertidal sand in Scotland. Cah.Biol.mar., 22 : 313-321.

JAYASREE, K.V. & R.M. WARWICK. 1977. Free-living marine nematodes of a polluted sandy beach in the Firth of Clyde, Scotland. Description of seven new species. J.nat.Hist., 11 : 289-302.

JENSEN, P. 1976. Free-living marine nematodes from a sublittoral station in the North Sea of the Belgian coast. Biol.Jb. Dodonaea, 44 : 231-255.

JENSEN, P. 1976. Redescription of the marine nematode Pandolaimus latilaimus (Allgén, 1929). Its synonyms and relationships to the Oncholaimidae. Zoologica Scripta, 5 : 257-263.

JENSEN, P. 1978. Four Nematoda Araeolaimida from the Öresund, Denmark, with remarks on the oesophageal structures in Aegialoalaimus. Cah.Biol. mar., 29 : 221-231.

* HEIP, C., M. VINCX, N. SMOL & G. VRANKEN. 1982. The systematics and ecology of marine free-living nematodes. Helminthological Abstracts Series B 51: 1-31.

JENSEN, P. 1980. Description of the marine free-living nematode Chromadora lorenzini n.sp. with notes on its microhabitats. Zool.Anz. Jena, 205: 213-218.

JENSEN, P. 1981. Species, distribution and a microhabitat theory for marine mud dwelling Comesomatidae (Nematoda) in European waters. Cah.Biol. mar., 22 : 231-241.

JENSEN, P. 1981. Description of the freeliving marine Nematode Dracognomus tinae n.sp. (Draconematoidea : Prochaetosomatidae). Cah.Biol.mar., 22 : 285-289.

JUARIO, J. 1973. Cyartonema germanicum sp.n. (Nematoda : Siphonolaimidae) aus dem Sublittoral der Deutschen Bucht und Bemerkungen zur Gattung Cyartonema Cobb, 1920. Veröff.Inst.Meeresforsch.Bremerh., 14 : 81-86.

JUARIO, J. 1974. Neue freilebende Nematoden aus dem Sublittoral der Deutschen Bucht. Veröff.Inst.Meeresforsch.Bremerh., 14 : 275-303.

LAMBSHEAD, P.J.D. 1981. A revision of the marine nematode genus Tawaia Allgen, 1934 (Nematoda : Tawaiidae). Zoological Journal of the Linnean Society, 73 : 259-272.

LAMBSHEAD, P.J.D. 1982. A new species of free-living nematode from the Firth of Clyde, Scotland. Bull.Br.Mus.nat.Hist.(Zool.), 42(3) : 149-155.

LAMBSHEAD, P.J.D. & H.M. PLATT. 1979. Bathyeurystomina, a new genus of freeliving marine nematodes (Enchelidiidae) from the Rockall Trough. Cah.Biol.mar., 20 : 371-380.

LORENZEN, S. 1973. Freilebende Meeresnematoden aus dem Sublitoral der Nordsee und der Kieler Bucht. Veröff.Inst.Meeresforsch.Bremerh., 14 : 103-130.

LORENZEN, S. 1973. Die Familie Epsilonematidae (Nematodes). Microfauna Meeresboden, 25 : 1-86.

LORENZEN, S. 1973. Theristus-Arten (freilebende Nematoden) mit unsymmetrischen Spicularapparat als Charakterarten mariner Sandbiotope in Nordsee und Kieler Bucht. Veröff.Inst.Meeresforsch.Bremerh., 14 : 87-101.

LORENZEN, S. 1974. Die Nematodenfauna der sublittoralen Region der Deutschen Bucht, insbesondere im Titan-Abwasser-Gebiet bei Helgoland. Veröff.Inst.Meeresforsch.Bremerh., 14 : 305-327.

LORENZEN, S. 1975. Rhynchonema-Arten (Nematoden-Monhysteridae) aus Südamerika und Europa. Mikrofauna Meeresboden, 55 : 1-29.

LORENZEN, S. 1977. Haftborsten bei dem Nematoden Haptotriconema arenaria gen.n., sp.n. (Desmoscolecidae) aus sublittoralem Sand bei Helgoland. Veröff.Inst.Meeresforsch.Bremerh., 16 : 117-124.

LORENZEN, S. 1977. Revision der Xyalidae (freilebende Nematoden) auf der Grundlage einer kritischen Analyse von 56 Arten aus Nord- und Ostsee. Veröff.Inst.Meeresforsch.Bremerh., 16 : 197-261.

LORENZEN, S. 1978. Postembryonalentwicklung von Steineria- und Sphaerolaimidaen-Arten (Nematoden) und ihre Konsequenzen für die Systematik. Zool.Anz., Jena, 200(1/2) : 53-78.

LORENZEN, S. 1979. Marine Monhysteridae (sensu stricto, Nematodes) von der südchilenischen Küste und aus dem küstenfernen Sublitoral der Nordsee. Studies on Neotropical Fauna and Environment, 14 : 203-214.

LORENZEN, S. 1981. Entwurf eines phylogenetischen Systems der freilebenden Nematoden. Veröff.Inst.Meeresforsch.Bremerh., Suppl. 7 : 1-449.

MOORE, P.G. 1977. Additions to the littoral fauna of Rockall, with a description of Araeolaimus penelope sp.nov. (Nematoda : Axonolaimidae). J.mar.biol.Ass.U.K., 57 : 191-200.

PLATT, H.M. 1973. Freeliving marine Nematodes from Strangford Lough, Northern Ireland. Cah.Biol.mar., 14 : 295-321.

PLATT, H.M. 1982. Revision of the Ethmolaimidae (Nematoda : Chromadorida). Bull.Br.Mus.nat.Hist. (Zool.), 43(4) : 185-252.

PLATT, H.M. & Z.N. ZHANG. 1982. New species of marine nematodes from Loch Ewe, Scotland. Bull.Br.Mus.nat.Hist. (Zool.), 42(4) : 227-246.
VINCX, M. 1981. New and little known Nematodes from the North Sea. Cah. Biol.mar., 22 : 431-451.
VINCX, M., J. SHARMA & N. SMOL. 1982. On the identity of "Paracanthonchus caecus (Bastian, 1865)" with a redefinition of the genus Paracanthonchus Micoletzky, 1924. Zoologica Scripta, 11(4) : 243-263.
WARD, A.R. 1973. A new species of Pterygonema (Nematoda : Ceramonematoidea) from sublittoral sand in Liverpool Bay. Mar.Biol., 19 : 204-205.
WARD, A.R. 1974. Three New Species of free-living Nematodes from sublittoral sediments in Liverpool Bay. Mar.Biol., 24 : 93-96.
WARWICK, R.M. 1969. Two new species of Pseudonchus (Nematoda, Choanolaimidae) from the British Coast. Cah.Biol.mar., 20 : 375-382.
WARWICK, R.M. 1969. The marine Nematode Eurystomina terricola (De Man, 1907) and its distribution on British Shores. Hydrobiol., 34(3/4) : 392-400.
WARWICK, R.M. 1970. Two new species of free-living marine nematodes from the Northumberland Coast. J.nat.Hist., 4 : 593-598.
WARWICK, R.M. 1970. Fourteen new species of free-living marine Nematodes from the Exe estuary. Bull.Brit.Mus.Zool., 19 : 139-177.
WARWICK, R.M. 1971. The Cyatholaimidae (Nematoda, Chromadoridae) off the coast of Northumberland. Cah.Biol.mar., 12 : 95-110.
WARWICK, R.M. 1977. Some free-living marine nematodes from the Isles of Scilly. J.nat.Hist., 11 : 381-392.
WARWICK, R.M. & J.W. COLES. 1975. Notes on the free-living marine genus Euchromadora de Man, 1886 and its alies, with descriptions of two new species (Chromadoridae : Nematoda). J.nat.Hist., 9 : 403-412.
WARWICK, R.M. & H.M. PLATT. 1973. New and little known marine nematodes from a scottish sandy beach. Cah.Biol.mar., 14 : 135-158.

ECOLOGY

In the Proceedings of the First International Meiofauna Conference in Tunis, McIntyre (1971) reviewed the existing literature on subtidal meiofauna. In all, twenty relevant papers published within the last 50 years were mentioned, and only two of them are from the North Sea : Smidt's (1951) work from the Danish Wadden Sea and McIntyre's (1964) own work from the Fladen Ground. Since 1971 the situation has improved a little, with work being done on the East coast of England (Warwick & Buchanan, 1971), the German Bight (several authors) and the Southern Bight (several authors). However, the largest part of the North Sea remains unexplored, and some of the existing data on density and biomass are to be treated with extreme caution.

The first quantitative estimates of Smidt (1951) are from the Danish Wadden Sea, not a typical North Sea environment. As with all earlier work, his estimates are certainly much too low and will consequently not be referred to. McIntyre (1961) as well gives far too low densities for the Fladen Ground but corrects in a later publication (McIntyre, 1964).

The Danish Waddensea

Smidt (1951) took core samples from the channels and the intertidal flats of the Danish Waddensea. Sorting in the laboratory was done by stirring up the material in a glass dish : the organisms were supposed to form the upper layer of the settled material. In our experience such a procedure will greatly underestimate densities and Smidt's figures are therefore nearly worthless.

Wet weights were determined for Harpacticoida (9.9 µg/ind.), Ostracoda (12 µg/ind.) and small (0.6 µg/ind.) and large (7.8 µg/ind.) nematodes. Nematodes were not determined. Harpacticoïds were more abundant on the waddens than in the channels. Species that were found exclusively or chiefly on sandy bottoms were *Asellopsis intermedia*, *Harpacticus flexus*, *Laophonte spp.* (?) and *Tachidius discipes*. On muddy bottoms the following species occurred: *Amphiascus spp.*, *Ectinosoma curticorne*, *Platychelipus littoralis* and *Microarthridion littorale*.

Canuella furcigera was found in both sandy or muddy sediments, as were several indetermined representatives of the Cletodidae and Ectinosomatidae.

Ostracoda were found in very low numbers in the channels, they were especially common on the sand waddens.

Fladen Ground

Nematodes and harpacticoids predominated in all samples studied by Mc Intyre (1964). These samples were obtained with a corer at a station situated at 58°20'N, 0°30'E, at a depth of 101 m. Fourteen cores were collected from three surveys. Samples were sieved alive over a 76 µm sieve but the filtrate was examined as well, using resuspension and subsampling. 60% in number and 22% in weight of the nematodes passed alive through the sieve and other, fixed samples in which the filtrate was discarded were corrected consequently. It should be noted that McIntyre (1964) cites different correction measures in the abstract of his article.

The results are shown in table 1. Average meiofauna density was 1959 ind./10 cm^2, nematodes numbered 1845 ind./10 cm^2. The average biomass was 0.43 g dwt/m^2 for nematodes and 0.76 g dwt/m^2 for meiofauna as a whole.

TABLE 2. FLADEN. NUMBERS OF ANIMALS PER 10 CM² IN 14 CORES

	29 April 1962				15 January 1963						8 August 1963				
	F 1	F 2	F 3	F 4	F 5	F 6	F 7	F 8	F 9	F 10	F 11	F 12	F 13	F 14	Mean
Nematoda	2215	1867	2027	1852	1258	1115	1715	2392	3020	2695	1491	1535	1895	755	1845
Kinorhyncha	5	8	5	3	15	15	18	3	23	8	10	—	3	5	9
Ostracoda	8	5	5	5	10	5	8	3	—	3	5	3	—	3	5
Copepoda	38	35	33	50	43	70	105	65	53	55	90	18	33	40	52
Nauplii	3	—	5	13	15	10	15	—	13	8	18	3	10	35	11
Others	3	—	10	3	3	25	5	3	8	8	3	8	10	40	9
Total	2272	1915	2085	1926	1344	1240	1866	2466	3117	2777	1619	1567	1951	878	1931
Polychaeta	5	3	3	10	10	35	10	18	13	15	10	8	3	3	10
Lamellibranchiata	3	3	—	3	15	30	63	20	33	13	18	10	13	23	18
Total	8	6	3	13	25	65	73	38	46	28	28	18	16	26	28
Grand total	2280	1921	2088	1939	1369	1305	1939	2504	3163	2805	1647	1585	1967	904	1959

Species composition of the nematodes is unknown. The harpacticoids are better described. 41 species were found, the dominant ones being *Amphiascus tenuiremis*, *Cletodes pusillus*, *Zozime valida*, *Stenhelia* sp. A and *Pseudotachidius coronatus*. Among the Kinorhyncha Homalorhagae were poorly represented and species of *Echinoderes* were dominant, followed by *Centroderes multispinosus*, *Semnoderes armiger* and juvenile Cyclorhagae. Mollusks and most polychaetes were young stages of only a few species.

The density data obtained by McIntyre may be compared with estimates obtained from a cruise of RV. Knorr with a box-corer in the same area (Herman, Sharma, Vincx and Heip, unpublished). The average density and biomass for five stations sampled in May 1976 are given in table 2. In general these figures are higher than McIntyre's : on average the meiofauna numbers 2552 ind./10 cm^2, with nematodes 2447 ind./10 cm^2, the biomass figures are 1.14 g dwt/m^2 for the entire meiofauna and 0.56 g dwt/m^2 for the nematodes. However two stations had meiofauna densities over 3000 ind./10 cm^2.

Density of the principal meiobenthic taxa on Fladen Ground (N per 10 cm^2). Means of two samples.

	St 19	St 22	St 32	St 44	St 59	Mean
Nematoda	3875	2964	2429	1334	1733	2467
Copepoda	26	49	37	43	66	44
Polychaeta	13	4	3	10	20	9
Kinorhyncha	3	2	2	3	4	3
Ostracoda	3	3	2	1	7	3
Others	9	50	9	19	42	26
Total	3929	3072	2481	1409	1868	2552

McIntyre (1964) mentions that the Fladen Ground is one of the poorest known in terms of standing stock of the macrofauna, with only 1.6 g dwt/m^2. Meiobenthos production, assuming a P/B-ratio of ten, will be greater than macrobenthos production, and McIntyre hypothesises that competition exists between nematodes and the larger (and economically valuable) macrofauna.

The Northumberland coast

The qualitative distribution of nematodes of various sediment types in the Northumberland coastal waters has been investigated by Warwick & Buchanan (1970, 1971). Average densities were 185 ind./10 cm^2 on a fine sand station (- 35 m), 815 ind./10 cm^2 on another fine sand station (-54 m) and 713 ind./10 cm^2 on a silt station (-80 m). On the fine sand station A the dominant species were Sabatieria ornata, Dorylaimopsis punctatus, Actinonema pachydermatum, Mesacanthion sp., Terschellingia longicaudata, Sphaerolaimus sp. and Theristus sp. 1, which together accounted for 54% of all individuals. On the fine sand station B the dominant species were Sabatieria ornata, Odontophora longisetosa, Terschellingia longicaudata, Mesacanthion sp., Sabatieria hilarula and Theristus setosus, together accounting for 51% of all individuals. On the silty station C the dominant species were Dorylaimopsis punctatus, Leptolaimus elegans, Sabatieria cupida, Sabatieria ornata, which accounted for 52% of all individuals. The first three of these species were considered to be typical of muddy sediments. For the sandy stations Odontophora longisetosa was characteristic.

In their second paper Warwick & Buchanan (1971) investigated the temporal stability of the nematode community on the muddy station C. There appeared to be no seasonal fluctuations in the relative dominance of the different species and the three dominant species mentioned above remained dominant in most months. Juveniles dominated the populations at all times and gravid females were present in all seasons. Asynchronous, continuous reproduction thus seemed to prevail, at least in these dominant species. Although significant fluctuations in density were found, they were thought to result from patchiness rather than represent true fluctuations.

The average weight of a nematode was 0.45 µg/ind., the biomass of the entire taxocene varied between 0.3 and 0.7 g dwt/m^2.

The Yorkshire coast

Moore (1971) studied the rather specialized fauna of holdfasts of Laminaria from fifteen sites. 61 species of nematodes were found. The order Enoplida was clearly dominant, with as important species : Enoplus communis (45%), Anticoma acuminata (17%), Thoracostoma coronatum (13%) and Phanoderma albidum (5%).

The German Bight

Stripp (1969b) gives estimates of density and biomass of meiofauna from three stations in the Helgoland Bight. As his samples were subsamples from a Van Veen grab his results are underestimates. They served nevertheless as a basis for Gerlach's (1971) seminal paper on the importance of marine meiofauna in a trophic sense. The large mesh size used by Stripp (1969a) (100 µm) will again severely underestimate the nematode fraction and it is therefore advisable to distrust his results on total density and biomass.

Individual wet weight figures are given for large nematodes (4.2 µg/ind.), intermediate nematodes (1.2 µg/ind.) and small nematodes (0.3 µg/ind.). Weight determinations of other meiofauna were made with scale models and gave : Harpacticoida : 8 µg ; Halacarida : 6 µg and interstitial Polychaeta : 5 µg.

In all stations there was a yearly cycle in density with maximum values in summer and a minimum in March. Summer densities and biomass were on average 1.5-1.6 times higher than winter values. They averaged between 81 and 349 ind./10 cm^2 in sand, between 694 and 750 ind./10 cm^2 in silt and between 833 and 1311 ind./10 cm^2 in silty sand. Corresponding wet weight biomasses were 0.2-0.5 g/m^2 in sand, 1.1-1.3 g/m^2 in silt and 0.9-2.0 g/m^2 in silty sand.

The same area was studied in much more detail as far as the nematodes are concerned by Lorenzen (1974) and Juario (1975). Lorenzen (1974) compared nematode faunas from a TiO_2 dumping ground in the German Bight after dumping started in 1970. The area is 23-27 m deep, the sediment consists of fine sand with a median grain size round 200 µm. The residual current in the area is to the north with a velocity of 5-10 cm/sec. The macrofauna of the area belongs to the Venus gallina-community.

Fifty species of nematodes are common in the area. Lorenzen's procedures did not permit density estimates from most samples, but he found that juveniles represent about 50% of the populations the year round. On the whole 191 species were found, 42 were new to science.

Some samples were taken quantitatively and yielded average densities superior to the values of Stripp (1969b). For fine sand the average density was 530 ind./10 cm^2, for silty sand 2310 ind./10 cm^2 and for mud 920 ind./10 cm^2. There were no clear winter-summer fluctuations.

The coarse sand was dominated by Chromadorita obliqua, Paracyatholaimus occultus, Prochromadorella attenuata, Monhystera spp.. Fine sands were dominated by Daptonema leviculum, Richtersia inaequalis, Sabatieria celtica and Viscosia rustica. Silty sands were dominated by Microlaimus turgofrons, Longicyatholaimus complexus, Sabatieria celtica and Sabatieria pulchra. Muds were dominated by Sabatieria pulchra, Terschellingia longicaudata and Desmolaimus aff. bulbulus.

Several of the dominant species showed a higher reproductive activity in spring. Adults of Mesacanthion diplechma were found only in June-July, indicating that this species has a one year life-cycle.

A silty sand station in the same area was investigated in great detail by Juario (1975). The macrofauna of the area belonged to the Echinocardium cordatum-Amphiura filiformis-community. Subsampling a Van Veen grab will yield biased estimates ; the use of a sieve of 50 µm allows for good estimates of all animals but the smallest nematodes in the subsamples. Total meiofauna fensity varied between 3047 and 5261 ind./10 cm^2, much higher values than found by previous authors. Nematodes made up between 93 and 99% of this. A peak in meiofauna abundance was found in April and in August. Biomass varied between 0.5 and 0.9 g dwt/m^2 with most values close to 0.8 g dwt/m^2.

Nematodes varied between 2867 ind./10 cm^2 in February and 5037 ind./10 cm^2 in August. Harpacticoids were next in dominance, varying between 26 to 179 ind./10 cm^2. From the other groups only the Kinorhynchs and Polychaetes had some importance.

Only nematodes were studied systematically. In general the common species are eurytopic and were similar to those found by Lorenzen (1974). There is no seasonal pattern in species dominance, gravid females and juveniles are present throughout the year and juveniles make up a constant proportion of the total community, indicating year-round continuous reproduction. In most species higher numbers were found in summer, but in Microlaimus turgofrons highest density occurred in winter.

Individual biomass of nematodes was very stable, between 0.13 and 0.19 µg/ind. This indicates clearly the predominance of very small species. A total of 87 species was found, the most abundant being Microlaimus turgofrons, Sabatieria pulchra, Microlaimus torosus, Microlaimus aff. honestus. Diversity was very high. Comparing his data with those of Lorenzen (1974), Juario (1975) proposes the following average values for different sediment types in the German Bight :

- coarse sand : 5.11 bits/ind.
- fine sand : 5.38 bits/ind.
- silty sand : 4.30 bits/ind.
- mud : 2.55 bits/ind.

He distinguishes the following communities in the German Bight :

- a coarse sand community dominated by Prochromadorella attenuata, Chromadorita obliqua and Monhystera sp.
- a fine sand community dominated by Sabatieria celtica, Metadesmolaimus heteroclitus and Paracanthonchus caecus.
- a silty sand community dominated by Microlaimus turgofrons, Sabatieria pulchra and Microlaimus torosus.
- a mud community dominated by Sabatieria pulchra.

The Southern North Sea

There exist no published data on the Southern North Sea proper. Herman (unpublished) gives the following densities from two box-core samples on station AUR 10 situated 54°00'N and 3°40'E, depth 46 m, median grain size of the sand fraction 113 µm, 12.7% silt.

	Nematoda	Harpacticoida
Core A	3723	11
Core B	3024	16

Eight harpacticoid species were found in both samples.

The Southern Bight

Much work has been done since the 70's on meiofauna of the Southern Bight by Belgian workers. A summary of some of the results has been presented by Govaere et al. (1980). They found three zones on bases of the harpacticoid copepods :

- A Microarthridion littorale-Halectinosoma herdmani-community found in very shallow water not exceeding 10 m depth. It inhabits a zone of sedimentation polluted by material derived from the Western Scheldt estuary. The harpacticoids are large epibenthic species with Microarthridion littorale extremely dominant, followed by Pseudobradya beduina, Halectinosoma sarsi, Halectinosoma herdmani, Canuella perplexa and others. Nematodes are dominated by the genus Sabatieria and to a lesser degree Theristus (Daptonema) in very muddy sediments. In more sandy stations a richer fauna occurs with the genera Spilophorella, Rhips and Hypodontolaimus.
  Turbellarions from this zone were studied by Degadt who described numerous species with the Macrostomida dominant.
  Nematodes from the southern part of the area have been studied by Heip & Decraemer (1974). They found 140 species in five stations, with only two species common to all stations : Sabatieria sp. and Richtersia inaequalis.

Six species occurred in four stations. The authors found a linear relationship between diversity as calculated by the Shannon-Wiener index and the median grain size of the sand fraction given by $H = -0.261 + 15\ Md$ with H in bits/ind. and Md in mm.

- A Halectinosoma herdmani-Leptastacus laticaudatus community.

This community inhabits a transition zone with stations between 15 and 10 m depth. Organic matter in the sediment is lower, but the stations often contain large amounts of detritus. The most frequent harpacticoids are the two species after which the community is named, i.e. a large epibenthic and a small interstitial species. Other harpacticoids are Halectinosoma sarsi, Canuella perplexa, Dactylopodia vulgaris, Ectinosoma dentatum, Euterpina acutifrons (in fact a planktonic species), Thompsonula hyaenae etc. Nematodes from this zone have been studied by Jensen (1974) from seven samples of one station. The dominant species was Sabatieria, followed by Richtersia inaequalis, Microlaimus and Theristus spp.
Turbellarians from this zone were studied by Degadt (1973). Otoplanidae and Acoela were dominant.
Several interstitial polychaetes are important in this zone, with Hesionura augeneri and Streptopsyllis websteri. Nemertineans, Olifochaeta and Archiannelida occur regularly, Hydrozoa, Gastrotricha and Halacarida are rare. Kinorhyncha were never found.

- A Leptastacus laticaudatus-Paramesochra helgolandica-community.

This community is found in stations from depths exceeding 20 m. The sediment consists of clean sand, except in some places were gravel is found. The median grain size varies with decreasing velocity of the tidal currents from larger than 350 µm south of 52°N, between 300-350 µm between 52°N and 52°12'N and between 250-300 µm between 52°12'N and 52°25'N.
In fourteen stations 54 species of harpacticoids were found, the most common being small interstitial species such as Leptastacus laticaudatus, Paramesochra helgolandica, Arenosetella germanica, Kliopsyllus paraholsaticus, Psammotopa phyllosetosa, Intermediopsyllus intermedius and Evansula incerta. The average number of species per station was 13.7, the average diversity 2.7 bits/ind.
Most nematodes in the area are epigrowth feeders with dominant genera such as Chromadorita, Neochromadora, Hypodontolaimus and Dichromadora (Jensen, 1974). Other meiofauna groups are also present : among the Turbellaria the Coelogynoporidae (Proseriata) are dominant, followed by Schizorhynchidae, Acoela and Macrostomida. A number of truely interstitial polychaetes occur : Exogone naidina and Hesionura augeneri are dominant, followed by Exogone hebes, Microphthalmus listensis, Sphaerosyllis hystrix and Streptopsyllis websteri. A number of interstitial gastropods was found : Caecum glabrum, Microhedyle spp., Pseudovermis papillifera and Philinoglossa helgolandica were determined. In most samples the genus Halammohydra was found. Gastrotrichs were common. Archiannelids included Polygordius spp., Saccocirrus, Protodrilus and Protodriloides. Batillipes mira (Tardigrada) was found in this zone as well. On one station the interstitial sea cucumber Leptosynapta minuta was found. Kinorhyncha and Ostracods are rare.

Table 3. Total density and biomass of meiobenthos in three zones of the Southern Bight. N: ind./10 cm^2 · B: g dwt/m^2

Year	Coastal zone		Transition zone		Open sea zone	
	N	B	N	B	N	B
1971 (summer)	934	1.21	1739	2.44	1640	2.24
1972	1182	1.51	2735	1.81	1340	1.75
1973	1261	1.60	774	1.02	852	1.24
1974	1092	1.39	761	1.04	803	1.02
1975 (winter)	1129	1.43	623	0.84	757	0.97

Total density and biomass in the three communities are given in table 3. However, as these are subsamples from a Van Veen grab, bias is present. The biomass calculations are based on a individual weight of 1.24 µg dwt/ind. for a nematode. Later determinations by Bisschop (1977) on nematodes from the coastal area gave a much lower value of 0.59 µg, indicating that in the 1972-1975 survey the smaller nematodes are again underestimated.

Later work has been summarized in Heip et al. (1979, in press) and Herman et al. (in press). Heip et al. (1979) summarized data from 18 stations in the Belgian coastal zone (the Microarthridion littorale-Halectinosoma herdmani-community). An analysis of variance on nematode density data showed that nematode communities are stable in space and time (not in time when the data were not transformed). Highest densities were found in muddy sand (2100 ind./10 cm^2). In sandy stations 20-30 species of nematodes per station were present, in muddy stations 4-12 species. Nematode communities in mud were dominated by species from the Sabatieria pulchra-group, Daptonema tenuispiculum, Theristus and Monhystera spp. In sandy stations other species become important such as Spirinia parasitifera, Richtersia inaequalis, Ascolaimus elongatus, Microlaimus marinus, Tubolaimoides tenuicaudatus and Enoplolaimus propinquus.

A still more detailed analysis of the meiofauna in the Belgian waters is presented by Herman et al. (in press). 280 species of nematodes from 121 genera and 28 families were found in the grid described by Govaere et al. (1980). The nematode fauna was analysed on a family basis. Based on the Sörensen similarity index the region can be divided in six zones, which are a very good representation of the sediment composition. Nematodes thus appear to be more sentitive to slight changes in sediment composition than either macrofauna or harpacticoids, since only three zones could be distinguished in the same grid with the same analysis when the latter were used.

A remarkable difference exists in the distribution of nematode feeding types according to the zones. The coastal area is characterized by a large amount of non-selective deposit-feeders, which are the only group present in very polluted stations north-east of Ostend. The open-sea zone has the four feeding types in about equal proportions, with epigrowth feeders most numerous.

In the coastal zone ten major taxonomic groups were found. In this zone only 2.9 to 3.4 taxa were present per station. Overall density of the meiofauna is 1800 ind./10 cm^2, with on average 96% nematodes. Mean densities of the nematodes were :

- sand : 1190 ind./10 cm^2
- silty sand : 1920 ind./10 cm^2
- mud : 1830 ind./10 cm^2

Individual biomass was slightly higher in sand (0.32 µg/ind.) than in muddy sand (0.30 µg/ind.) or mud (0.25 µg/ind.) and was higher in winter than in summer. Total biomass of the nematodes was :

- sand : 0.38 dwt/m^2
- silty sand : 0.57 dwt/m^2
- mud : 0.45 dwt/m^2

The average biomass over the whole area is 0.50 g dwt/m^2 or approximately 0.2 g C/m^2.

In the coastal area species number of nematodes varied between 1 and 16. The diversity decreases significantly from south to north. In the NE-region the mean number of nematode species is only 5.4, in the SW it is 14.3. Sabatieria spp. (six species) predominate. Species of Daptonema may also be very abundant. Also the harpacticoid fauna is extremely impoverished. In the mud stations only five species were found with Microarthridion littorale extremely dominant. Sandy stations are characterized by the transition community described by Govaere et al. (1980).

The meiofauna of a sandbank in the transition zone has been studiedby Willems et al. (1982a). In nematodes three species groups could be distinguished with high diversity and low density (384 ind./10 cm^2). Harpacticoids are more diverse and more numerous in the coarser sands at the northern end of the sandbank than in the finer sands at the southern end. 65 species were identified with an average diversity of 2.3 bits/ind. and an average density of 162 ind./10 cm^2. Willems et al. (1982b) demonstrated that meiofauna abundance was not correlated with sediment mean grain size. This holds for nematodes and copepods in particular ; ostracods and halacarids were more numerous in coarser sediments.

PRODUCTIVITY OF MARINE MEIOBENTHOS IN THE SOUTHERN BIGHT

A first attempt to calculate energy flow through meiobenthic populations has been attempted for nematodes and harpacticoids in the Southern Bight by Van Damme & Heip (1977), Heip et al. (in press), Herman et al. (in press) and Heip et al. (1983). These estimates are based on density and biomass and on literature data on production and respiration. Using a mean P/B-value of 9, Van Damme & Heip (1977) calculated meiobenthic production in the coastal zone as 5 g $C.m^{-2}$, meiobenthic respiration as 5.7 g $C.m^{-2}$ with an average biomass of 0.6 g $C.m^{-2}$. In the open sea zone, with a standing stock of 0.7 g $C.m^{-2}$, production would be 4.2, respiration 4.3 g $C.m^2.y^{-1}$. These figures were based on very crude approximations. In later years direct production estimations have been obtained for the ostracod Cyprideis torosa and for several harpacticoids (see Heip et al., 1983 for a review). Respiration rates for many harpacticoids have been determined (see Herman & Heip, in press) and also for nematodes much better estimates are available (Warwick & Price, 1979). In the Belgian coastal waters nematodes are extremely dominant and average densities are high. On the Kwintebank meiofauna in general is less abundant and nematodes less dominant. Based on the average temperatures in the Southern Bight, 6°C in winter and 16°C in summer,individual respiration can be calculated based on the knowledge of individual weight. Yearly respiration of nematodes amounts to 5.75 l $O_2.m^{-2}$ in the coastal waters and 2.71 l $O_2.m^{-2}$ on the Kwintebank. These data are based on respiration measures of Warwick & Price (1979). From total respiration production can be calculated using the regression obtained by Humphreys (1979) for non-insect invertebrates $\log P = 1.069 \log R - 0.601$ with P and R in calories. Converting with 1 l O_2 = 0.402 g C, 1 g C = 12 kcal, one then obtains a yearly production of 2.92 g $dwt.m^{-2}$ in the coastal area and 1.31 g $dwt.m^{-2}$ on the Kwintebank. These values are very low, and compare disfavorably with estimates obtained e.g. by using a P/B-ratio of nine as proposed by Gerlach (1971). However, it has become clear that even the proposition P/B = 9 has no real value in determining the production of meiobenthos. Data obtained from culture experiments indicate clearly that the productivity of the smaller nematode species is much larger and a P/B-ratio of 30-40 may not be unrealistic.

These estimations thus remain subject to considerable uncertainty. The figure of 8.6 g $C.m^{-2}.y^{-1}$ in the coastal zone and 5.5 g $C.m^{-2}.y^{-1}$ on the Kwintebank has been arrived at for the total carbon requirements of the meiofauna in these zones (Herman et al., in press).

References

BISSCHOP, G. 1977. Bijdrage tot de studie van de nematodenfauna van de Noordzee en de Westerschelde ter hoogte van haar monding. Thesis, State University Gent, 129 pp.

DEGADT, D. 1973. Bijdrage tot de faunistiek van de Turbellaria in de Noordzee. Thesis, State University Gent, 73 pp.

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

GERLACH, S.A. 1980. Development of Marine Nematode Taxonomy up to 1979. Veröff.Inst.Meeresforsch.Bremerh., 18 : 249-255.

GOVAERE, J.C.R., D. VAN DAMME, C. HEIP & L.A.P. DE CONINCK. 1980. Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. Helgoländer wiss.Meeresunters., 33 : 507-521.

HEIP, C. & W. DECRAEMER. 1974. The diversity of nematode communities in the southern North Sea. J.Mar.biol.Assoc.U.K., 54 : 251-255.

HEIP, C., P.M.J. HERMAN & A. COOMANS; 1983. The productivity of marine meiobenthos. Academiae Analecta, 44(2) : 1-20.

HEIP, C., R. HERMAN, G. BISSCHOP, J. GOVAERE, M. HOLVOET, D. VAN DAMME, C. VANOSMAEL, K. WILLEMS & L. DE CONINCK. 1979. Benthic studies of the Southern Bight of the North Sea and its adjacent continental estuaries. Progress Report I. ICES CM L/9 : 133-163.

HEIP, C., R. HERMAN & M. VINCX. . Variability and Productivity of Meiobenthos in the Southern Bight of the North Sea. Proc.Verb.Réun.Cons. Int.Eplor. Mer (in press).

HEIP, C., M. VINCX, N. SMOL & G. VRANKEN. 1982. The Systematics and Ecology of the Free-Living Marine Nematodes. Helminth.Abstr. Series B, 51 : 1-31.

HERMAN, P.M.J. & C. HEIP. . The respiration of five brackish-water harpacticoid copepod species. J.exp.Mar.Biol.Ecol. (in press).

HERMAN, R., M. VINCX & C. HEIP. (198). Benthic studies of the Southern Bight of the North Sea and its Adjacent Continental Estuaries. IV. Meiofauna of the Belgian Coastal Water : Spatial and Temporal Variability and Productivity. ICES CM (in press).

HUMPHREYS, W.F. 1979. Production and respiration in animal populations. J.Animal.Ecol., 48 : 427-453.

JENSEN, P. 1974. Bijdrage tot de kennis van de nematodenfauna uit een slibrijke en zandrijke zeebodem in de zuidelijke Noordzee. Thesis, State University Gent, 95 pp.

JUARIO, J.V. 1975. Nematode species composition and seasonal fluctuation of a sublittoral meiofauna community in the German Bight. Veröff.Inst. Meeresforsch.Bremerh., 15 : 283-337.

LORENZEN, S. 1974. Die Nematodenfauna der sublitoralen Region der Deutschen Bucht, insbesondere im Titan-Abwassergebiet bei Helgoland. Veröff. Inst.Meeresforsch.Bremerh., 14 : 305-327.

MOORE, P.G. 1971. The nematode fauna associated with holdfasts on kelp (Laminaria hyperborea) in north-east Britain. J.mar.biol.Ass.U.K., 51 : 589-604.

McINTYRE, A.D. 1961. Quantitative differences in the fauna of boreal mud associations. J.mar.biol.Ass.U.K., 41 : 599-616.

McINTYRE, A.D. 1964. Meiobenthos of sublittoral muds. J.mar.biol.Ass.U.K., 44 : 665-674.

McINTYRE, A.D. 1971. Observations on the status of subtidal meiofauna research. In : N.C. Hulings, ed. Proceedings of the First International Conference on Meiofauna, Smithson.Contr.Zool. N° 76 : 149-154.

SMIDT, E.L.B. 1951. Animal production in the Danish Waddensea. Medd.Danm. Fisk.Havundersøg., Bd II(6) : 151 pp.

STRIPP, K. 1969a. Jahreszeitliche Fluktuationen von Makrofauna und Meiofauna in der Helgoländer Bucht. Veröff.Inst.Meeresforsch.Bremerh., 12 : 65-94.

STRIPP, K. 1969b. Das Verhältnis von Makrofauna und Meiofauna in den Sedimenten der Helgoländer Bucht. Veröff.Inst.Meeresforsch.Bremerh., 12 : 143-148.

VAN DAMME, D. & C. HEIP. 1977. Het meiobenthos in de zuidelijke Noordzee. In : Nihoul, C.F. & L. De Coninck. Nationaal onderzoeks- en ontwikkelingsprogramma - Projekt Zee, Vol. 7 : 1-114.

WARWICK, R.M. & J.B. BUCHANAN. 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. & J.B. BUCHANAN. 1971. The meiofauna off the coast of Northumberland. II. Seasonal stability of the nematode population. J.mar.biol.Ass.U.K., 51 : 355-362.

WARWICK, R.M. & R. PRICE. 1979. Ecological and metabolic studies on free-living nematodes from an estuarine mud-flat. Estuar.coastl.mar.Sci., 9 : 257-271.

WILLEMS, K.A., M. VINCX, D. CLAEYS, C. VANOSMAEL & C. HEIP. 1982a. Meiobenthos of a sublittoral sandbank in the Southern Bight of the North Sea. J.mar.biol.Ass.U.K., 62 : 535-548.

WILLEMS, K.A., C. VANOSMAEL, D. CLAEYS, M. VINCX & C. HEIP. 1982b. Benthos of a sublittoral sandbank in the Southern Bight of the North Sea : general considerations. J.mar.biol.Ass.U.K., 62 : 549-557.

Addendum

Faubel, Hartwig & Thiel (Meteor Forschungsergebnisse, in press) studied the meiofauna over six dates at five stations in the Fladen Ground in the framework of the programs PREFLEX (1975) and FLEX (1976). A complete yearly cycle was obtained from three stations.

Meiofauna abundance was fairly uniform at all stations and varied between 751 and 3490 ind./10 cm^2. Stations 1 and 2, which contained more than 80 % silt and clay, had the highest numbers. Nematodes were the dominant group comprising between 79 and 94 % of the meiofauna. In general meiofauna abundance was highest in December, lowest in April. However, at station 1 (58°20'N, 0°07'W) a minimum was reached in June. Over all samples the density increased from 1457 ind./10 cm^2 in April to 2067 ind./10 cm^2 in July. The average density over all samples was 1945 ind./10 cm^2. The trend for other meiofauna taxa is similar as for the nematodes.

At station 1, which was examined in more detail, the average abundance of the nematodes was 2367 ind./10 cm^2, with an average individual weight of 0.63 µg and an average total biomass of 1.5 g dwt/m^2. From these figures an attempt was made to estimate annual production of the meiofauna. The concept of minimal production, defined as the difference between the highest and lowest biomass found during the year, was used. However, as the authors acknowledge, this concept bears no relationship with real production and the term is ambiguous. A more sound approach was followed by estimating the number of generations annually. On the Fladen Ground, with low annual temperatures and low food input, this was estimated as between one and two for nematodes. With 1.5 generations annually and a life-cycle turnover of three (Waters, 1969), annual P/B would be 4.5 and production of nematodes would amount to 6.75 g dwt/m^2/yr, instead of 3 as claimed by Faubel et al., who multiplied the average standing stock with the annual number of generations only. This will introduce a considerable error and the value of P/B = 2 proposed by the authors will certainly be too low.

During the Spring bloom on the Fladen Ground about 40 g C/m^2 is produced by the phytoplankton. The energy demand of the meiobenthos can be estimated roughly as 4.9 times production (Heip et al., in press) (based on nematodes) and thus amounts to more than 40 g dwt/m^2 or 24 g C/m^2 when accepting that carbon makes up 57 % of the dry weight as found by Faubel et al. It is clear that a large part of the primary production has to pass through the meiofauna.

Another striking result of the paper concerns the amount of organic matter in the sediment, as determined by weight loss after combustion at 550 °C. From April to August 1976 this amount increases roughly by 3 % in the upper two centimeters of the sediment. Accepting that the sediment has a density of 1.5, this indicates that during these months about 1.2 kg of organic matter enters the sediment per m^2 and is reworked over the rest of the year. Assuming that this organic matter contains 40 % of carbon, the yearly turnover of organic carbon would reach the high amount of 300 g C/m^2/yr. There are two possible errors. Wollast (1977) found for sediments in the Belgian coastal zone that the weight loss is about double the amount of organic matter; secondly, combustion at 550 °C may be slightly too high. When halving the figure obtained by Faubel et al., there is still 150 g C/m^2/yr that is metabolized by the benthos. As the primary production in the area is around 90 g C/m^2/yr (Steele, 1974) another source of organic matter seems to be necessary to account for the figure obtained.

Ref. FAUBEL, A., E. HARTWIG & H. THIEL (in press). On the ecology of benthos in sublittoral sediments, Fladen Ground, North Sea. I. Meiofauna standing stock and estimation of production. Meteor Forschungsergebnisse.