

SECTION D. THE USE OF MEIOBENTHOS IN POLLUTION MONITORING STUDIES: A REVIEW

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1 INTRODUCTION

The potential of the meiobenthos for pollution monitoring has previously been discussed by Marcotte and Coull (1974), Pequegnat (1975), Gray *et al.* (1980), and Heip (1980).

From a practical point of view, the sampling of meiobenthos in intertidal as well as in subtidal areas is relatively simple and is possible on a small scale: only small amounts of sediment are necessary to elucidate the structure of the meiobenthic communities (using cores). However, because of their small size, meiobenthos species are laborious to sort and to identify; only hard-bodied taxa (especially copepods and nematodes) are recommended in a monitoring context because highly specialized techniques are needed to identify soft-bodied forms such as Turbellaria.

Nematodes and copepods are abundant in almost every marine habitat (normally ranging between 500 and 10 000 individuals/10cm²), making them suitable for ecological and statistical analysis. Nematodes are particularly notable for their persistence as a taxon, and are found in all environmental conditions that can support metazoans. The high diversity of meiobenthic organisms has been used in the past as an argument against the use of these organisms for bio-monitoring purposes, because of the difficulties encountered in identifying the numerous species. The wider use of meiofauna in pollution monitoring studies was therefore facilitated by the publication of comprehensive taxonomic works which made identification much easier for the ecologist (for copepods: Wells, 1971, 1978, 1979, 1981; Bodin, 1979; for nematodes: Gerlach and Riemann, 1973, 1974; Tarjan, 1980; Lorenzen, 1981; Platt and Warwick 1983, 1988).

Another particular advantage of nematodes and interstitial copepods is their conservative life cycle (i.e., the absence of highly mobile pelagic life stages), so that local contamination effects are not hidden by immigration. They have a rapid turnover compared to the macrofauna; they also have a short life-span and are in intimate contact with pore water. Thus, they should demonstrate a fast response to pollution.

Usually, eutrophication and organic pollution will lead to increased food supply and a rise in the total number of benthic organisms. Other types of pollution do not increase the food supply. The difference is important because changes in community structure induced by organic pollution and toxic pollution cannot be identical.

2 DETECTION OF POLLUTION-INDUCED DISTURBANCES

Several methods for the detection of pollution-induced disturbances have been proposed. They all take into account the changes observed in the structural aspects of the community caused by pollution:

- 1) taxon diversity of the meiofaunal components;
- 2) relative abundance of higher taxa of the meiobenthos (e.g., the ratio of nematode to copepod abundance);

- 3) species diversity of dominant taxa (indices, graphical methods); and
- 4) species distribution patterns.

The impact of pollution on the functional aspects of meiobenthic communities (e.g., respiration, productivity) has not been well studied.

2.1 Taxon Diversity

Taxon diversity of the meiofaunal phyla has been proposed as a possible tool for the assessment of pollution effects by Van Damme and Heip (1977) and by Herman *et al.* (1985). Taxon diversity is lower in polluted conditions; this is caused mainly by the disappearance of the rare taxa (e.g., Ostracoda, Gastrotricha, Halacarida, Hydrozoa, Tardigrada). However, because of small sample size, sampling techniques are often not adequate to provide an accurate density estimate of these rare taxa, which sometimes occur in numbers as low as 1 to 10 individuals/10 cm²; the diversity of the meiobenthic community is then much influenced by the presence or absence of these rare taxa. It is well known that sediment composition is also very important in the determination of taxon diversity. Herman *et al.* (1985) examined taxon diversity of the meiobenthic communities at 18 stations along the Belgian coast; in the sandy stations up to seven different higher taxa were found, while in more than 50% of the other stations only one or two taxa (i.e., nematodes and copepods) occurred.

Amjad and Gray (1983) also found a decrease in the number of meiofaunal taxa along an organic enrichment gradient, which was similar to the gradient in the nematode-copepod ratio (see below).

Aissa and Vitiello (1984) examined the meiofauna of the lagoon of Tunis which is influenced by the discharge of sewage arising from the urbanized area. Densities decreased according to an increasing gradient of organic pollution (and a rise of the redox potential discontinuity layer). Nematodes and polychaetes were the most resistant meiobenthic organisms; indeed, nematodes were the only surviving metazoans at the most severely affected sites.

Keller (1984, 1985) described the effect of domestic sewage on the structure of the meiobenthic communities along a transect off Marseille, France. She differentiated three areas: (1) a heavily polluted coastal zone, where sediments were devoid of macrobenthic animals, and supported a relatively poor meiofauna (nematodes, copepods and acari). The copepods were uncommonly large in size and constituted most of the total benthic biomass; the nematodes were mainly freshwater species; (2) an intermediate zone, which was much richer in meiofauna and also more diversified. Polychaetes increased in number, while acari became scarce and copepods decreased in size. 0.4-1 km away from the outfall, where the sediment was strongly polluted, the nematode community consisted of large individuals which contributed greatly to the biomass; (3) an offshore, slightly polluted, zone, where meiofauna densities were reduced and individuals decreased in size with increasing depth. Generally, an enrichment in the meiofauna was evident from the coastal to the intermediate zone. Enrichment induced by urban pollution had been recorded previously, but not at a distance of more than 1 km away from the outfall.

Huys *et al.* (1984) and Smol *et al.* (1986) found that nematodes and copepods were more abundant in a dumping area for waste from titanium dioxide (TiO₂) manufacture; also, that there was a significantly lower taxon diversity of the meiofaunal groups.

Frithsen *et al.* (1985) examined in detail the response of benthic meiofauna to long-term, low-level inputs of fuel oil, such as may be present at the heads of urbanized estuaries and bays. They used mesocosms (outdoor tanks) containing sediment and sea water from Narrangansett

Bay, Rhode Island, USA. The abundances of metazoan meiofauna decreased during periods of oil addition; ostracods and harpacticoid copepods were the most sensitive metazoan groups. Abundances of most meiofaunal groups returned to levels similar to those of the controls within 2 to 7 months after the termination of oil additions. However, the abundance of kinorhynchs and halacarids remained depressed for more than 1 year after the last oil addition, presumably due to residual oil in the sediments.

Moore *et al.* (1987) found a sharply reduced density and species richness of all intertidal meiofaunal taxa within 320 m of the discharges of hydrocarbons in the Firth of Forth. However, at 600-900 m, meiofaunal densities were enhanced or depressed, relative to clean sediments, depending upon the seasonal pattern of the redox potential discontinuity layer. Oil platform discharges resulted in strongly reduced nematode densities in the near vicinity. By contrast, copepod densities were greatly enhanced, which was considered to be due to the epibenthic habit of the species involved, enabling them to flourish in conditions of an enhanced food supply and/or low predation and competition.

In a review of field experimentation in meiofaunal ecology, Coull and Palmer (1984) referred to fourteen papers which described pollution experiments in the field or in meso- or microcosms. It was evident from this work that changes in structural parameters of the most important taxa of the meiofauna differed according to sediment type, the nature of the pollutant (oil, sewage, nutrients), sampling techniques and time.

The ability to discriminate between stations along a putative pollution gradient in two Norwegian fjords was just as efficient when the meiofauna data were pooled into taxonomic groups higher than the level of the species (Heip *et al.*, 1988a).

2.2 The Nematode-Copepod Ratio

The use of ratios to observe trends in marine data sets was suggested by Margalef (1975, 1978). He found that a number of ratios describing planktonic ecosystems decreased in response to disturbance (stress, upwelling, and pollution). Amongst the ratios were the numbers of dinoflagellates to diatoms, zooplankton biomass to phytoplankton biomass, and carnivore biomass to herbivore biomass.

Parker (1975) and, in more detail, Raffaelli and Mason (1981) proposed the nematode-copepod ratio as a tool for pollution monitoring using meiobenthic organisms. However, these two studies interpret this ratio in an opposite way.

Parker (1975) compared the subtidal meiofaunal composition of two estuaries in North America: one was polluted by industrial waste from the Dow Chemical Company factory (the Brazos River Estuary) and the other was almost completely undisturbed (the Colorado Estuary). He found that under disturbed conditions 'benthic copepods predominate at their trophic level, while under normal conditions nematodes predominate'. However, only 'surface material from an undisturbed grab sample sufficient to fill a 6-ounce jar' was examined; this may have resulted in overestimation of the copepods, since these animals are mostly restricted to the upper cm of the sediment, while nematodes occur much deeper.

Raffaelli and Mason (1981) compared the response of nematodes and copepods to organic pollution in intertidal areas along the British coast. They sampled to a depth of 35 cm and found that the ratio of nematode to copepod densities was highest where sewage pollution was most obvious. In particular, an increase in the abundance of deposit-feeding nematodes (capable of using the high amount of organic material) was noted, while the copepods decreased in number.

Organic pollution causes an immediate increase in food supply so that, in such areas, extremely high densities of meiobenthos (mainly nematodes) can occur.

Raffaelli and Mason's publication (above) stimulated a large response in the literature concerning the use of meiofauna in pollution monitoring studies, because a very simple, and therefore attractive, tool had been proposed. Most studies were carried out on organically enriched beaches along the British coasts; within these areas, the nematode to copepod ratio increased in response to the presence of large quantities of organic wastes (Warwick, 1981; Raffaelli, 1982; Lamshead, 1984; Shiells and Anderson, 1985). Similar observations were made in the Oslofjord by Amjad and Gray (1983).

The ratio of nematodes to copepods also increased with decreasing particle size, but ratios from polluted sites were always extremely high. Ratios from clean beaches were low and always less than 100, even for muddy sites; all intertidal sites (comprising fine as well as coarse sediments) with ratios exceeding 100 were polluted with organic material (sewage). Some sublittoral ratios from unpolluted sites were high, but never approached the very high values characteristic of polluted intertidal areas. The sublittoral ratios also increased with depth. It is obvious that this ratio must be used with caution as the index is also strongly affected by sediment granulometry.

Coull *et al.* (1981) thoroughly discussed the validity of the nematode/copepod ratio and pointed out that spatial and temporal variations, as well as other ecological processes (such as predation) could alter the ratio independently. The authors rightly pointed out that it is not permissible to reduce the complex meiofaunal community structure to a single ratio.

Warwick (1981) proposed a refinement of the ratio based on trophic dynamic aspects of the meiofauna. He assumed that food is the factor which limits energy flow through the nematode and copepod communities; in that case, the total number of copepods should be proportional to the number of type 2A nematodes (epigrowth-feeders) only, as only 2A nematodes are dependent on the same food source as the copepods. If copepods are indeed more sensitive to the effects of pollution than nematodes, then changes in the proportion of copepods relative to type 2A nematodes might be a useful indicator to separate the effects of pollution from any changes or differences in sediment type. Warwick (1981) suggested that pollution might be indicated by nematode/copepod ratios of around 40 for fine sediments, and 10 for sands. These values are considerably lower than the values of over 100 proposed by Raffaelli and Mason (1981).

Platt *et al.* (1984) and Lamshead (1986) suggested that the ratio should be abandoned as a practical pollution indicator, because (1) it oversimplifies a highly complex set of relationships, and (2) nematode and copepod populations may react independently to a variety of environmental parameters (of which pollution is only one).

Shiells and Anderson (1985) proposed a possible improvement to the ratio whereby only interstitial forms are included, so that only those animals occupying the same micro-habitat are compared.

An increase in copepods due to pollution (as found by Parker, 1975) was recorded by Vidakovic (1983), Moore and Pearson (1986), and Hodda and Nicholas (1986).

Vidakovic (1983) examined Adriatic sublittoral stations, which are constantly influenced by sewage; in this area, the number of copepods increased more than the number of nematodes.

Moore and Pearson (1986) also found an enhancement of copepod density resulting from sewage pollution. They concluded that the nematode to copepod ratio is mainly determined by the avail-

ability of high dissolved oxygen levels to the copepod fauna. In both studies (Vidakovic, 1983; Moore and Pearson, *op. cit.*), the overlying water contained high levels of dissolved oxygen.

Coull and Wells (1981) found no relationship between the ratio of nematodes to copepods and pollution. However, they sampled sediments only to 1-2 cm depth. A comparison with data from the Southern Bight of the North Sea (unpublished results) suggests that these authors may, as a result, have missed up to 90% of the nematodes.

Hodda and Nicholas (1985) also found that the ratio was not related to pollution; they examined the meiofauna associated with mangroves in southeastern Australia, which was strongly influenced by inorganic pollution; nematode as well as copepod densities decreased as pollution increased.

In mesocosm experiments with organically enriched sublittoral soft sediments, Gee *et al.* (1985) found that the nematode to copepod ratio was unreliable as a biomonitoring tool. The authors suggested that the differential responses in community structure between the nematode and copepod components of the meiofauna might be a better indication of stress at the community level.

Raffaelli (1987) discussed the variable behaviour of the nematode/copepod ratio in organic pollution studies. It was concluded that differences in the habitat requirements of nematodes, mesobenthic and epi-/endobenthic copepods affected the responses of these groups to organic pollution.

Thus, it is clear that the ratio of nematodes to copepods is not *a priori* a valid tool for pollution monitoring, because the ratio is much influenced by the type of sediment, the nature of the pollution (organic/inorganic), and the location of the habitat (intertidal/subtidal).

We conclude with the following quote from Raffaelli (1987): "Whatever the merits of the nematode/copepod ratio for marine pollution monitoring, it is interesting that so many experienced investigators should feel disposed to test the index, and this has itself highlighted some important relationships in meiobenthic ecology".

2.3 Oligochaeta

Although oligochaetes never dominate in marine meiofaunal communities, it may be noted that Hodda and Nicholas (1985) found that the relative abundance of oligochaetes was significantly correlated to levels of pollution in the mangroves of the Hunter River Estuary.

The oligochaete *Limnodrilus* sp. was found to be overwhelmingly dominant in some heavily polluted estuaries, accounting for up to 70% of all meiofauna (Brinkhurst and Jamieson, 1971; Coull and Wells, 1981).

Coates and Ellis (1980) proposed as 'the most practical index for marine pollution' the percentage of total adult enchytraeids represented by *Lumbricillus lineatus*. Unfortunately, in many marine biotopes, this species is completely absent; it occurs mostly in estuarine conditions.

2.4 Gastrotricha

The gastrotrich genus *Turbanella* is an indicator of organic enrichment on beaches (Gray, 1971; Raffaelli, 1982).

2.5 The Relative Abundance of Species

Changes in the relative abundance of species have been advocated as a useful means of demonstrating pollution effects at the community level. This can be done by the simple use of diversity indices, or by plotting the distribution of individuals among different species.

The nematode and copepod assemblages are commonly studied at the species level, and different analytical techniques have been proposed to detect sublethal effects of pollution on the species distribution within these groups.

2.5.1 Diversity indices

The use of a variety of diversity measurements in order to assess the relative complexity of a community in relation to the degree of pollution has increased enormously during the 1970s. Heip *et al.* (1988b) reviewed the use of the different diversity indices that are available; opinions about the different methods of measuring diversity are almost as numerous as the number of articles discussing them.

A coherent system of diversity and evenness indices is the series of diversity numbers proposed by Hill (1973), which includes species richness (number of species), exp H (H = Shannon-Wiener index) and Simpson's index (see Heip *et al.*, 1988b).

The Shannon-Wiener diversity index has been used to indicate long-term changes in community structure (e.g., Heip, 1980) and generally has lower values in polluted situations. The Shannon-Wiener index is often coupled with a measurement of evenness which, independently of the number of species in the sample, will approach a maximum value when the individuals are divided more evenly among species. Platt *et al.* (1984) remarked that the Shannon-Wiener information function is currently the most popular diversity index among marine biologists. The index is more biased towards the species richness component of diversity than many other popular indices. Since it is dominance (the reciprocal of evenness) which appears to be more relevant in the context of pollution, Simpson's index is preferred, because it weights species by their abundance (Platt *et al.*, 1984).

Gray (1979) has shown that statistically significant changes in diversity indices are associated with only very gross changes in community structure; therefore, the value of using a diversity index in a monitoring context must be questioned.

Lambshhead *et al.* (1983) offered a criterion for comparing diversity based on the pattern of dominance of all species in a sample. The method is applied by plotting the % cumulative abundance of species: the so-called 'k-dominance' curves. This method can reveal that some assemblages cannot be compared in terms of diversity or equitability (when the curves intersect): the intrinsic diversity indices are unreliable under these circumstances. The k-dominance curves provide an easily visualized picture of diversity.

2.5.2 Species-abundance distributions

Species-abundance curves can only be drawn if the sample is large and contains many species ($S > 30$) (see Heip *et al.*, 1988b).

The relative abundances of species can be described in 'statistical models', which make assumptions about the probability distributions of the numbers of the species within the community. Heip *et al.* (1988b) discussed the use of several such models. Notable among these are the logarithmic normal (log normal) and log series statistical models of species frequency distributions,

which have been found to describe data from natural communities of harpacticoid copepods (Gray, 1978; Castel, 1980; Hicks, 1977; Hockin and Ollason, 1981; Hockin, 1982) and nematodes (Shaw *et al.*, 1983; Platt and Lamshead, 1985).

Gray and Mirza (1979) and Gray (1979, 1981) proposed that unperturbed communities can be identified by the fit of the log normal model to the observed species frequency distribution, while perturbed communities suffering from pollution are fitted by the log series model.

However, other authors (e.g., Kempton and Taylor, 1976) suggest the fit of a log series distribution for stable communities, and a log normal distribution for unstable communities.

Caswell (1976) derived the log series species distribution through application of a neutral model, i.e., a model in which the species abundances are governed entirely by stochastic processes such as immigration, emigration, birth and death, and not by competition, predation or other specific biotic interactions (see Heip *et al.*, 1988b). To date, effort has been mainly concentrated on the fitting of models to field data; the parameter estimates of these models have not been widely used in further analysis. Comparisons of different distributions by means of subsequent statistical testing are the only useful characteristics of these models.

2.5.3 Examples

COPEPODA

Marcotte and Coull (1974) examined the changes in species composition, diversity, and survival strategy of the subtidal harpacticoid community in response to organic enrichment in the North Adriatic. In winter, the copepods numerically dominated the most polluted stations; copepod diversity decreased in response to increased organic enrichment. The harpacticoids nearest the pollution source were dominated by *Tisbe* sp. in winter, and by *Bulbamphiascus imus* in summer. The material was collected from the top 10 cm of the bottom and sieved on a 0.125 mm mesh. Coull and Wells (1981) examined the intertidal meiofauna of muddy substrates in a polluted system, a nearby unpolluted system, and a healthy system in Australian waters. Sampling was confined to superficial sediments above the redox discontinuity layer (ranging from < 1 to 1-2 cm) and the material was sieved on a 0.044 mm mesh. Copepods dominated over nematodes in the first two systems; there was an extremely high percentage of oligochaetes in the polluted system (up to 78%). Copepod diversity was lowest in the polluted area. The healthy system showed a dominance of nematodes, a high abundance of *Echinoderes* aff. *coulli* (Kinorhyncha), and the highest species diversity of all taxonomic groups.

Hockin (1983) examined the effects of organic enrichment on a harpacticoid community on an estuarine intertidal beach (in Great Britain), by means of field experiments. The pollutant used was a suitable nutrient source for the sediment-dwelling microfauna upon which many of the copepods feed. The increased supply of organic matter resulted in an increase in the species richness, a decrease in the dominance diversity and no change in the number of individuals and, by inference, the biomass. It was observed that the log series model adequately fitted most data sets, while the log normal only fitted data drawn from the community inhabiting the organically enriched sediments.

Heip *et al.* (1984) recorded that *Microarthridion littorale* was the dominant copepod in the polluted eastern area of Belgian coastal waters, accounting for 94%, on average, of all harpacticoids. The impoverishment of the harpacticoid fauna from west to east (from less to more polluted) was also reflected in the average diversity, which decreased from $H' = 0.87$ bits/individual in the west to 0.43 bits/individual in the east, and in the observation that 14 out of 15 stations in the west yielded harpacticoids, against 21 out of 30 in the east.

Van Damme *et al.* (1984) examined the influence of pollution on the harpacticoid copepods of two North Sea estuaries, the Western Scheldt estuary and the Ems Dollard estuary. The Western Scheldt estuary is more loaded with heavy metals (Zn, Cu, Pb) than the Ems Dollard estuary; in particular, copper is continuously present at concentrations which, according to bioassays, would severely affect egg production and larval development of planktonic copepods. The remarkable scarcity of harpacticoid life on the nutrient-rich mudflats of the Western Scheldt is probably due to heavy metal pollution. In the Western Scheldt, two distinct copepod assemblages occur, a mesobenthic assemblage (small, interstitially living grazers, e.g., *Kliopsillus constrictus*, *Paramesochra* sp. A, and *Paraleptastacus espinulatus*) and an endo-epibenthic assemblage (large, burrowing or epibenthic detritus-feeders, e.g., *Canuella perplexa*, *Pseudobradia* spp. and *Tachidius discipes*). In the Ems Dollard estuary, the copepods all belong to the endo-epibenthic assemblage and are found in the pure as well as in the muddy sands.

Keller (1984, 1985, 1986) described the copepod community which was influenced by a sewage outfall off Marseille, France. As was the case with the nematode communities, the copepods could be divided into two main groups: (1) near to the outfall, the community was dominated by the copepod species *Darcythompsonia faviliensis* (which had not previously been reported in marine environments); (2) the second community (from 400 to 4000 m from the outfall) was characterised by the dominance of *Bulbamphiascus imus*, a cosmopolitan species relatively tolerant to pollution. Both species diversity and Motomura's constant (calculated from the log linear model) increased from the outfall to the offshore zone. (Nematodes showed the same trend: see below).

Gee *et al.* (1985) studied the effects of organic enrichment on meiofaunal abundance and community structure in mesocosms containing sublittoral soft sediments. Harpacticoid copepods increased significantly in abundance in the treatment boxes, and showed a general trend towards increased dominance and decreased diversity with increasing levels of organic enrichment. However, in the low-dose treatment, there was also an increase in the number of species present.

Moore and Pearson (1986) examined the impact of sewage sludge dumping on the copepod community of a subtidal muddy deposit off the Scottish coast. Three groups of species were recognized, each characteristic of the different levels of sludge loading. The first group, in the centre of the dumping ground, consisted of only one species (*Bulbamphiascus imus*), which was overwhelmingly dominant there. The second group included those species which were virtually absent from the centre of the dumping ground, but become dominant in the moderately enriched sediments on either side (e.g., *Amphiascoides debilis*, *Typhlamphiascus lamellifer*, *Paramphiascoides hyperborea*). A third group of species only began to appear towards the ends of the transect (e.g., *Pseudameira furcata*, *Pseudameira* sp., *Amphiascoides subdebilis*).

Bodin (1988) examined changes in the meiofauna of three beaches between 1978 and 1984, following pollution by the 'Amoco Cadiz' oil spill. The hydrocarbons exerted a toxic effect on the meiofauna only during the first weeks. Thereafter, the major pollution came from excess organic matter that induced oxygen impoverishment in the environment. Among harpacticoid copepods, 'test' species and groups (sensitive, tolerant, opportunistic, etc.) could be distinguished, which represented bioindicators of an imbalance caused by perturbations due to excess organic matter.

Hockin (1983) concluded that the use of copepods as indicators of environmental quality was presently problematic. The response of natural communities seemed to be dependent both upon the load of organic matter and the composition of the community with respect to the ratio of bacterial- and algal- feeding species. Increased bacterial productivity alone (on organically

enriched beaches) may cause increased diversity of the copepod fauna, because of the increase in density as well as in diversity of typically bacterial-feeding species.

Along a putative pollution gradient in two Norwegian fjords, data on copepod distributions provided a better means to discriminate between sites than data on nematodes (Heip *et al.*, 1988a).

NEMATODA

The species distribution of the nematodes has been more extensively studied, because they have proved to be sensitive biological indicators of pollution. Nematodes are very diverse taxonomically and occur everywhere, usually in large numbers which often exceed those of other taxa by an order of magnitude or more (Platt, 1984; Heip *et al.*, 1985).

A decrease in nematode density after contamination with hydrocarbons has been demonstrated in the sediments of several beaches (Wormald, 1976; Giere, 1979; Boucher, 1980), but not in all cases (Green *et al.*, 1974), and not in sublittoral sands (Elmgren *et al.*, 1980; Elmgren *et al.*, 1983; Boucher, 1980, 1981). An obvious decrease in nematode abundance after an oil spill has often been followed by 'explosive development' of a few opportunistic species within one year (Wormald, 1976; Giere, 1979). However, after the 'Amoco Cadiz' oil spill, no such 'explosive development' occurred on the beaches (Boucher, 1980, 1981).

After an oil spill at La Coruña (northern Spain), *Enoplolaimus littoralis* became extremely dominant; many specimens had ingested oil droplets covered with bacteria. In the intestine of *Bathylaimus* sp. and *Tripyloides* sp., oil particles surrounded by clouds of bacteria were found (Giere, 1979).

After the 'Amoco Cadiz' spill, nematode diversity in the sublittoral sands in Morlaix Bay decreased significantly, and most obviously 9 to 12 months after the accident happened (Boucher, 1980). This was due, on the one hand, to an increase of *Anticoma ecotronis*, *Sabatieria celtica*, *Paracyatholaimus occultus* and *Calomicrolaimus monstrosus*, species normally abundant in silty sands and, on the other hand, to a decrease of *Ixonema sordidum*, *Monoposthia mirabilis*, *Rhynchonema ceramotos*, *Chromadorita mucrocaudata*, *Xyala striata*, *Viscosia franzii* and *Rhynchonema megamphidum*, species normally dominant in clean sands.

Renaud-Mornant *et al.* (1981) also examined the same polluted area and found that the mortality 10 days after the oil input was not significant. After one month, density decreased: mortality occurred especially in the surface sand layers while, in the deeper layers, meiofauna was found to be in the process of spring reproduction. After six months, nematodes became extremely dominant and accounted for 90% of the meiofauna.

Gourbault (1984) examined the nematodes from the Bay of Morlaix Channel over a period of two years after the 'Amoco Cadiz' oil spill. A change of species composition was observed, with diversity decreasing in the upper part of the Channel. (Species typical of sediments two years after the spill were: *Sabatieria pulchra*, *Terschellingia longicaudata* and *Aponema torosus*.)

Gourbault and Lecordier (1984) and Gourbault (1987) found that the nematode assemblage data from the Bay of Morlaix Channel could not be fitted with the usual abundance distribution models (log normal, log series, log linear). The Pareto law ($y=ax..$), used in some economic studies when dealing with partitioning of resources, was found to be more meaningful in this case. The nematode assemblages from the Morlaix estuary were regularly monitored at three

sites from October 1978 (half a year after the 'Amoco Cadiz' oil spill) to November 1984. It was concluded that by 1984 the fauna had recovered at all sites to a situation similar to that prevailing in October 1978.

Field monitoring studies of the effects of heavy metal pollution have been conducted by Lorenzen (1974), Tietjen (1977, 1980) and Heip *et al.* (1984), and laboratory studies by Howell (1982, 1983, 1984).

Lorenzen (1974) found no short-term effects on the nematode fauna in a region of the German Bight of the North Sea subjected to industrial waste disposal. (The waste contained 10% sulphuric acid and 14% ferrous sulphate.)

Tietjen (1977) found that heavy metals did not affect nematode populations in Long Island sublittoral muds, although a slight decrease in diversity was evident. Tietjen (1980) examined the nematodes from the New York Bight Apex, a sandy sediment area with high levels of heavy metals and organic carbon. High concentrations of the contaminants in medium sands resulted in lowered abundance of the nematode families which normally live in this kind of sediment, namely Chromadoridae, Desmodoridae and Monoposthiidae. Other species, such as *Sabatieria pulchra*, which are normally associated with finer sediments, increased in abundance. This species is adapted to living in conditions of low dissolved oxygen concentration and/or high organic content.

In Belgian coastal waters, influenced by the impact of the polluted Western Scheldt estuary, Heip *et al.* (1984) found that nematode species richness was significantly correlated with the heavy metal content. Closest to the mouth of the Western Scheldt, the only meiofaunal component which survived in high densities consisted of non-selective deposit-feeding nematodes, albeit with few species per station (*Sabatieria punctata*, *Daptonema tenuispiculum*, *Metalinhomoeus* n.sp. and *Ascolaimus elongatus*). A combination of trophic diversity (expressed in a trophic index: see Heip *et al.*, *op. cit.*) and species richness provided a good indication of the influence of pollution along the Belgian coast. The impoverishment of the nematode community along a gradient of increasing pollution from west to east could be explained by the gradual elimination of species, as stress increased. Trends in harpacticoid copepods could also be explained in the same way.

Huys *et al.* (1984) and Smol *et al.* (1986) examined the effects of dumping waste from TiO₂ manufacture on the meiofauna in the Southern Bight of the North Sea. The copepod communities were most diverse outside the dumping area; the samples from the dumping area were characterized by low diversities and high densities of nematodes. A comparison of data on the nematode communities with an interval of ten years between sampling (corresponding with the period before and during dumping, respectively) revealed that a change in nematode composition had occurred. However, the seasonal variability of the communities in this type of sediment is not known; therefore, further research is necessary before a proper interpretation of these results can be made.

Shaw *et al.* (1983) and Lamshead *et al.* (1983) examined several methods for the analysis of monitoring data. (The results from surveys of littoral nematode assemblages in Strangford Lough, N. Ireland, provided the basis for much of this work; see Platt, 1977.) They found that the abundance of the most common species as a percentage of the total sample (i.e., the dominance index) was a good indicator of environmental stress. However, the work did not include measurement of any chemical pollutants for correlative purposes. The use of the dominance index is not suitable in every case study (Platt and Lamshead, 1985; Lamshead, 1986). Platt and Lamshead (1985) found that disagreement with predictions of a neutral model for the distribution of species abundances (Caswell, 1976) provided a method of detecting

disturbance or stress. They subjected 98 samples of marine benthic organisms to the neutral model analysis, with some conflicting results. Assemblages of marine organisms may be more (nematodes) or less (macrofauna) diverse when influenced by contaminants, compared with the normal situation. Where disturbance was known to have occurred, spatial or temporal variations in the degree of deviation from the predicted diversity were in accordance with a hypothesis of diversity based on a combination of the 'intermediate disturbance hypothesis' (Connell, 1978) and the 'general hypothesis of species diversity' (Huston, 1979). These state that an undisturbed assemblage of organisms would have a low diversity, due to competitive exclusion of some species, while at moderate levels of disturbance such competitive interactions are prevented, and the diversity rises as more species are able to co-exist. Further increases in the scale of disturbance result in a lowering of diversity, as certain species are eliminated as a result of 'catastrophic' effects.

Vitiello and Aissa (1985) described the nematode communities in polluted sediments of the lagoon of Tunisia; only three nematode species were characteristic of the organically polluted communities, namely *Terschellingia* n.sp., *Sabatieria pulchra* and *Penzencia flevensis*. The mean length of the nematodes was longer in the polluted area, where the predators among the nematodes were almost absent. In the non-polluted region, predators amounted to about 15% of the communities.

As was the case with copepods, the nematode communities near a sewage outfall off Marseille (France) were divided into two assemblages (Keller, 1986): (1) near the outfall, nematodes of the order Rhabditida occurred. These are generally abundant in polluted rivers, and the source of the populations off Marseille appeared to be sewage-derived; it was also known that a polluted stream was diverted into the sewer prior to discharge. Some marine nematodes known for their affinity to polluted sediments, such as *Metoncholaimus pristiurus*, *Sabatieria pulchra* and *Terschellingia* n.sp., were also present; (2) at distances of 400-4000 m from the outfall, sampling stations had different nematode assemblages consisting mainly of deposit-feeders, because of the presence of significant amounts of organic matter in the sediments. Moreover, two heavily influenced nematode associations were detected at the two most distant stations (1.8 km and 4 km from the outfall), one of them being composed of only mud-dwelling deposit-feeders. This showed that the whole study area was perturbed by the presence of the outfall. Keller (1986) concluded that, in general, both species diversity and Motomura's constant increased from the outfall to the offshore zone; this indicated a rise in the number of ecological niches available.

Hodda and Nicholas (1986) studied nematode diversity in mangrove mud-flats adjacent to the steel works and chemical factories in the Hunter River Estuary, Australia. Their results suggested that nematode diversity might not be a good universal indicator of marine pollution. The polluted areas were more diverse taxonomically, though seasonal variations in population density and other environmental factors complicated the comparison.

The most recent example of the problems with this approach to pollution monitoring is given by Lamshead (1986). He reported on an investigation into the effects of contamination, at a 'subcatastrophic' level, on some marine nematode assemblages of beaches in the Clyde Inland Sea area, Scotland. All stations were sampled once (in September 1978), and the median of the sand fraction varied from less than 150 μ m for the contaminated stations to more than 150 μ m for the uncontaminated stations. Results were consistent with the expectation that, at uncontaminated stations, diversity would be higher, density lower and feeding-type ratio in favour of the epistratum feeders. However, 'k-dominance' curves did not show significant differences between the uncontaminated and the contaminated stations.

Therefore, Lamshead (1986) and Lamshead and Paterson (1986) proposed a new method for the detection of sub-catastrophic contamination at the community level, which involved the application of numerical cladistics to ecological analysis. The presence of a species is coded as the derived character state, while absence is coded as primitive; this means that the outgroup consists of a theoretical station containing no species. All the species used in the analysis must be potentially capable of reaching (if not surviving in) any of the stations examined. This kind of cladistic analysis can only be applied to stations drawn from the same potential species pool. However, reduction in diversity and survival of only the most tolerant species is the only obvious effect of pollution so far detected; therefore, it is difficult to agree that species presence is a derived character, especially when the interest is in pollution effects. The establishment of 'homology' in ecological studies also has some problematic features; thus, the ontogenetic method as well as the outgroup comparison are highly speculative.

3 CONCLUSIONS

This review of the use of meiobenthos in studies of marine pollution has highlighted some of the difficulties and controversies surrounding the interpretation of observed changes. It is usually very hard to distinguish pollution-induced from natural changes as, in most cases, the pre-pollution status of the meiobenthic community and supporting environment is not well known. *A posteriori* studies of the effects of pollutants often involve the use of 'natural experiments', in which the density or species diversity of benthic organisms of a polluted area is compared with an environmentally similar area nearby, usually referred to as a 'comparison' or 'reference' area (see Eskin and Coull, 1984, for a review). Eskin and Coull (*op. cit.*) warned that great caution should be taken when reference areas are selected and compared with 'disturbed' areas; in such cases, a single factor (e.g., pollution) should not be interpreted as causative of observed differences in densities, or in the distribution of abundances. Regardless of the mechanisms controlling distribution, small- and medium- scale (mm-cm) spatial distribution of meiofauna appeared to be so variable and unpredictable that no *a priori* assumption about the similarity of meiofaunal populations at the two comparison sites could be made, despite the apparent visual similarity of the sediment sites. It was, therefore, concluded that larger samples, which obscured the patchy distribution of the meiofauna, were necessary for bio-monitoring purposes. In contrast, great stability and spatial predictability of harpacticoid copepods have been observed in other locations (Willems, in preparation), while a recent workshop demonstrated that the ability to discriminate between stations using meiofauna data was as good as, or better than, that using macrofauna data (Heip *et al.*, 1988a).

In general, density is not much affected by pollution, whereas diversity seems to decrease. Pollution is often accompanied by changes in habitat characteristics; both the lethal effect of a pollutant or the change in sediment texture may be responsible for the observed changes. It is known that some nematode species are resistant to high levels of pollution and anaerobiosis. However, the effect of, e.g., heavy metals on nematode population dynamics can only be studied in the laboratory. Despite their significant role in marine sediments, only a few experimental studies into the effects of pollution have been conducted (see Heip *et al.*, 1985, for a review). It is concluded that knowledge of the ecotoxicology of meiobenthos is still very poor, and that much more work remains to be done.

4 REFERENCES FOR PART D

- Aissa, P., and Vitiello, P. 1984. Impact de la pollution et de la variabilité des conditions ambiantes sur la densité du méiobenthos de la lagune de Tunis. *Rev. Fac. Sc. Tunis*, **3**: 155-177.

- Amjad, B., and Gray, J.S. 1983. Use of the nematode-copepod ratio as an index of organic pollution. *Mar. Pollut. Bull.*, **14**: 178-181.
- Bodin, P. 1979. Catalogue des nouveaux copépodes harpacticoides marins. *Mém. Mus. Nat. Hist. Nat. Paris, Sér. A, Zool.*, **104**: 1-228.
- Bodin, P. 1988. Results of ecological monitoring of three beaches polluted by the 'Amoco Cadiz' oil spill: development of meiofauna from 1978 to 1984. *Mar. Ecol. Prog. Ser.*, **42**: 105-123.
- Boucher, G. 1980. Impact of Amoco Cadiz oil spill on intertidal and sublittoral meiofauna. *Mar. Pollut. Bull.*, **11**: 95-101.
- Boucher, G. 1981. Effets sur long terme des hydrocarbures de l'Amoco Cadiz sur la structure des communautés de nématodes libres des sables fins sublittoraux. *Actes Coll. Internat. COB Brest, CNEXO Ed., Paris*, 539-549.
- Brinkhurst, R.O., and Jamieson, B.G.M. 1971. *Aquatic oligochaeta of the world*. Oliver & Boyd, Edinburgh.
- Castel, J. 1980. Descriptions des peuplements de copépodes méiobenthiques dans un système lagunaire du Bassin d'Arcachon. Utilisations des modèles de distributions d'abondance. *Cah. Biol. mar.*, **21**: 73-89.
- Caswell, H.H. 1976. Community structure: a neutral model analysis. *Ecol. Monogr.*, **46**: 327-354.
- Coates, K., and Ellis, D.V. 1980. Enchytraeid oligochaetes as marine pollution indicators. *Mar. Pollut. Bull.*, **11**: 171-174.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science, N.Y.*, **199**: 1302-1310.
- Coull, B.C., Hicks, G.R.F., and Wells, J.B. 1981. Nematode/copepod ratios for monitoring pollution: a rebuttal. *Mar. Pollut. Bull.*, **12**: 378-381.
- Coull, B.C., and Palmer, M.A. 1984. Field experimentation in meiofaunal ecology. *Hydrobiologia*, **118**: 1-19.
- Coull, B.C., and Wells, J.B.J. 1981. Density of mud-dwelling meiobenthos from three sites in the Wellington region. *New. Zeal. Jour. Mar. Freshw. Res.*, **15**: 411-415.
- Elmgren, R., Vargo, G.A., Grassle, J.F., Grassle, J.P., Heinle, D.R., Langlois, G., and Vargo, S.L. 1980. Trophic interactions in experimental marine ecosystems perturbed by oil, pp. 779-800. *In* *Microcosms in ecological research*. Ed. by J.P. Giesy. DOE Symposium Series, 52, CONF 781101, NTIS, Washington, D.C.
- Elmgren, R., Hansson, S., Larsson, U., Sundelin B., and Boehm, P.D. 1983. The 'Tsesis' oil spill: acute and long-term impact on the benthos. *Mar. Biol.*, **73**: 51-65.
- Eskin, R.A., and Coull, B.C. 1984. *A priori* determination of valid control sites: an example using marine meiobenthic nematodes. *Mar. Environ. Res.*, **12**: 161-172.

- Frithsen, J.B., Elmgren, R., and Rudnick, D.T. 1985. Responses of benthic meiofauna to long-term, low-level additions of No. 2 fuel oil. *Mar. Ecol. Prog. Ser.*, **23**: 1-14.
- Gee, J.M., Warwick, R.M., Shaaning, M., Berge, J.A., and Ambrose, W.G. Jr. 1985. Effects of organic enrichment on meiofaunal abundance and community structure in sublittoral soft sediments. *J. exp. mar. Biol. Ecol.*, **91**: 247-262.
- Gerlach, S.A., and Riemann, F. 1973. The Bremerhaven checklist of aquatic nematodes: a catalogue of Nematoda Adenophorea excluding the Dorylaimida. Part 1. *Veröff. Inst. Meeresforsch. Bremerh. Suppl.* **4**: 1-404.
- Gerlach, S.A., and Riemann, F. 1974. The Bremerhaven checklist of aquatic nematodes: a catalogue of Nematoda Adenophorea, excluding the Dorylaimida. Part 2. *Veröff. Inst. Meeresforsch. Bremerh. Suppl.* **4**: 405-754.
- Giere, O. 1979. The impact of oil pollution on intertidal meiofauna. Field studies after the La Coruña spill, May 1976. *Cah. Biol. mar.*, **20**: 231-251.
- Gourbault, N. 1984. Fluctuation des peuplements de nématodes du chenal de la Baie de Morlaix. I. Résultats à moyen terme, après pollution par les hydrocarbures. *Cah. Biol. mar.*, **25**: 169-180.
- Gourbault, N. 1987. Long-term monitoring of marine nematode assemblages in the Morlaix Estuary (France) following the Amoco Cadiz oil spill. *Estuar. coast Shelf Sci.*, **24**: 657-670.
- Gourbault, N., and Lecordier, N. 1984. Application de la loi de Paréto aux structures des peuplements de nématodes de la Baie de Morlaix. *Cah. Biol. mar.*, **25**: 343-352.
- Gray, J.S. 1971. The effects of pollution on sand meiofauna communities. *Thalassia Jugosl.*, **7**: 79-86.
- Gray, J.S. 1978. The structure of meiofauna communities. *Sarsia*, **64**: 265-272.
- Gray, J.S. 1979. Pollution-induced changes in populations. *Phil. Trans. R. Soc. Lond. B.*, **286**: 545-562.
- Gray, J.S. 1981. The ecology of marine sediments: an introduction to the structure and function of benthic communities. Cambridge University Press, Cambridge. 185pp.
- Gray, J.S., Boesch, D., Heip, C., Jones, A.M., Lassig, J., Vanderhorst, R., and Wolfe, D. 1980. The role of ecology in marine pollution monitoring. Ecology Panel report. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, **179**: 237-252.
- Gray, J.S., and Mirza, F.B. 1979. A possible method for the detection of pollution-induced disturbance on marine benthic communities. *Mar. Pollut. Bull.*, **10**: 142-146.
- Green, D.R., Baudez, C., Gretney, W.T., and Wono, C.S. 1974. The Alert Bay oil spill: a one-year study of the recovery of a contaminated bay. *Pacific mar. Sci. Rep.*, **74** (9).
- Heip, C. 1980. Meiobenthos as a tool in the assessment of marine environmental quality. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, **179**: 182-187.

- Heip, C., Herman, R., and Vincx, M. 1984. Variability and productivity of meiobenthos in the Southern Bight of the North Sea. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, **183**: 51-56.
- Heip, C., Vincx, M., and Vranken, G. 1985. The ecology of marine nematodes. *Oceanogr. Mar. Biol. Ann. Rev.*, **23**: 399-489.
- Heip, C., Warwick, R.M., Carr, M.R., Herman, P.M.J., Huys, R., Smol, N., and Van Holsbeke, K. 1988a. An analysis of community attributes of the benthic meiofauna of Frierfjord/Langesundfjord. *Mar. Ecol. Prog. Ser.*, **46**: 171-180.
- Heip, C., Herman, P.M.J., and Soetaert, K. 1988b. Data processing, evaluation and analysis, pp. 197-231. *In* Introduction to the study of meiofauna. Ed. by R.P. Higgins and H. Thiel. Smithsonian Institution Press, Washington and London.
- Herman, R., Vincx, M., and Heip, C. 1985. Meiofauna of the Belgian coastal waters: spatial and temporal variability and productivity, pp. 65-80. *In* Concerted Actions Oceanography. Final Report, Vol. 3. Ministry of Science Policy, Brussels, Belgium.
- Hicks, G.R.F. 1977. Observations on substrate preference of marine phytal harpacticoids (copepoda). *Hydrobiologia*, **56**: 7-9.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**: 427-432.
- Hockin, D.C. 1982. The harpacticoid copepod fauna of the River Ythan and its estuary, Aberdeenshire, Scotland. *J. mar. biol. Ass. UK.*, **62**: 729-736.
- Hockin, D.C. 1983. The effects of organic enrichment upon a community of meiobenthic harpacticoid copepods. *Mar. Environ. Res.*, **10**: 45-58.
- Hockin, D.C., and Ollason, J.G. 1981. The colonisation of artificially isolated volumes of intertidal estuarine sand by harpacticoid copepods. *J. exp. mar. Biol. Ecol.*, **53**: 9-29.
- Hodda, M., and Nicholas, W.L. 1985. Meiofauna associated with mangroves in the Hunter River Estuary and Fullerton Cove, South-eastern Australia. *Aust. J. Mar. Freshw. Res.*, **36**: 41-50.
- Hodda, M., and Nicholas, W.L. 1986. Temporal changes in littoral meiofauna from the Hunter River Estuary. *Aust. J. Mar. Freshw. Res.*, **37**: 729-741.
- Howell, R. 1982. Levels of heavy metal pollutants in two species of marine nematodes. *Mar. Pollut. Bull.*, **13**: 396-398.
- Howell, R. 1983. Heavy metals in marine nematodes: uptake, tissue distribution and loss of copper and zinc. *Mar. Pollut. Bull.*, **14**: 263-268.
- Howell, R. 1984. Acute toxicity of heavy metals to two species of marine nematodes. *Mar. Environ. Res.*, **11**: 153-161.
- Huston, M.M. 1979. A general hypothesis of species diversity. *Amer. Natur.*, **113**: 81-101.

- Huys, R., Vincx, M., Herman, R., and Heip, C. 1984. Het meiobenthos van de dumpingszone van titaandioxide-afval in de Nederlandse kustwateren. Report of the Marine Biology Section, State University of Gent. 102pp.
- Keller, M. 1984. Effets du déversement en mer du grand collecteur de biologie l'agglomération Marseillaise sur les populations méiobenthiques. C. R. Acad. Sc. Paris, T. 299, serie III, **19**: 765-768.
- Keller, M. 1985. Distribution quantitative de la méiofaune dans l'aire d'épandage de l'Egout de Marseille. Mar. Biol., **89**: 293-302.
- Keller, M. 1986. Structure des peuplements méiobenthiques dans le secteur pollué par le rejet en mer de l'Egout de Marseille. Ann. Inst. oceanogr., Paris, **62**: 13-36.
- Kempton, R.A., and Taylor, L.R. 1976. Models and statistics for species diversity. Nature, **262**: 818-820.
- Lamshead, P.J.D. 1984. The nematode/copepod ratio, some anomalous results from the Firth of Clyde. Mar. Pollut. Bull., **15**: 256-259.
- Lamshead, P.J.D. 1986. Sub-catastrophic sewage and industrial waste contamination as revealed by marine nematode faunal analysis. Mar. Ecol. Prog. Ser., **29**: 247-260.
- Lamshead, P.J.D., and Paterson, G.L.J. 1986. Ecological cladistics - an investigation of numerical cladistics as a method for analysing ecological data. J. Nat. Hist., **20**: 895-909.
- Lamshead, P.J.D., Platt, H.M., and Shaw, K.M. 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. J. Nat. Hist., **17**: 859-874.
- Lorenzen, S. 1974. Die Nematodenfauna der sublitoralen Region der Deutschen Bucht, insbesondere im Titan-Abwassergebiet bei Helgoland. Veröff. Inst. Meeresforsch. Bremerh., **14**: 305-327.
- Lorenzen, S. 1981. Entwurf eines phylogenetischen Systems der freilebenden Nematoden. Veröff. Inst. Meeresforsch. Bremerh., suppl. 7, 1-449.
- Marcotte, B.M., and Coull, B.C. 1974. Pollution, diversity and meiobenthic communities in the North Adriatic (Bay of Piran, Yugoslavia). Vie et Milieu, **24** (2B): 281-300.
- Margalef, R. 1975. Assessment of the effects on plankton, pp. 301-306. *In* Marine pollution and marine waste disposal. Ed. by E.A. Pearson, and E. de Frangipane. Pergamon Press, Oxford.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta, **1**: 493-509.
- Moore, C.G., Murison, D.J., Mohd Long, S., and Mills, D.J.D. 1987. The impact of oily discharges on the meiobenthos of the North Sea. Phil. Trans. R. Soc. Lond. B, **316**: 525-543.
- Moore, C.G., and Pearson, T.H. 1986. Response of a marine benthic copepod assemblage to organic enrichment. Proc. 2nd. Int. Conf. Cop., Syllogeus no. 58, 369-373.

- Parker, R.H. 1975. The study of benthic communities. Elsevier Oceanography Series No. 9, Elsevier, Amsterdam. 279pp.
- Pequegnat, W.E. 1975. Meiobenthos ecosystems as indicators of the effects of dredging, pp. 573-583. *In* Estuarine Research, 2: Geology and engineering. Ed. by L.E. Cronin. Academic Press, New York.
- Platt, H.M. 1977. Ecology of free-living marine nematodes from an intertidal sandflat in Strangford Lough, Northern Ireland. *Estuar. coast. Mar. Sci.*, 5: 685-693.
- Platt, H.M. 1984. Planners and pollution: afloat on a sea of ignorance. *New Scientist*, 22: 34-35.
- Platt, H.M., and Lamshead, P.J.D. 1985. Neutral model analysis of patterns of marine benthic species diversity. *Mar. Ecol. Prog. Ser.*, 24: 75-81.
- Platt, H.M., Shaw, K.M., and Lamshead, P.J.D. 1984. Nematode species abundance patterns and their use in the detection of environmental perturbations. *Hydrobiologia*, 118: 59-66.
- Platt, H.M., and Warwick, R.M. 1983. Free-living marine nematodes. Part I. British enoplids. *Synopses of the British fauna (new series)*, No. 28. Cambridge University Press, Cambridge. 307pp.
- Platt, H.M., and Warwick, R.M. 1988. Free-living marine nematodes. Part II. British chromadorids. *Synopses of the British fauna (new series)*, No. 38. E J Brill/Dr W Backhuys, Leiden. 502pp.
- Raffaelli, D.G. 1982. An assessment of the potential of major meiofauna groups for monitoring organic pollution. *Mar. Environ. Res.*, 7: 151-164.
- Raffaelli, D. 1987. The behaviour of the nematode/copepod ratio in organic pollution studies. *Mar. Environ. Res.*, 23: 135-152.
- Raffaelli, D.G., and Mason, C.F. 1981. Pollution monitoring with meiofauna, using the ratio of nematodes to copepods. *Mar. Pollut. Bull.*, 12: 158-163.
- Renaud-Mornant, J., Gourbault, N., De Panafieu, J.-B., and Hellequet, M.N. 1981. Effets de la pollution par hydrocarbures sur la méiofaune de la Baie de Morlaix. *Actes Internat. COB, Brest, CNEXO éd.*, Paris, 551-561.
- Shaw, K.M., Lamshead, P.J.D., and Platt, H.M. 1983. Detection of pollution-induced disturbance in marine benthic assemblages with special reference to nematodes. *Mar. Ecol. Prog. Ser.*, 11: 195-202.
- Shiells, G.M., and Anderson, K.J. 1985. Pollution monitoring using the nematode/copepod ratio: a practical application. *Mar. Pollut. Bull.*, 16: 62-68.
- Smol, N., Herman, R.L., and Heip, C. 1986. Studie via bodemfauna van een dumpingsgebied van titaandioxide-afval in de Nederlandse kustwateren. Report of the Marine Biology Section, State University of Gent. 102pp.
- Tarjan, A.C. 1980. An illustrated guide to the marine nematodes. *Inst. Food Agric. Sciences, University of Florida*, 1-135.

- Tietjen, J.H. 1977. Population distribution and 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.
- Van Damme, D., and Heip, C. 1977. Het meiobenthos in de Zuidelyke Noordsee. *In* Nationaal onderzoeks-en ontwikkelingsprogramma - Projekt Zee. Ed. by C.F. Nihoul and L.A.P. De Coninck. Ministry of Science Policy, Brussels, Belgium, **7**: 1-114.
- Van Damme, D., Heip, C., and Willems, K.A. 1984. Influence of pollution on the harpacticoid copepods of the two North Sea estuaries. *Hydrobiologia*, **112**: 143-160.
- Vidakovic, J. 1983. The influence of raw domestic sewage on density and distribution of meiofauna. *Mar. Pollut. Bull.*, **14**: 84-88.
- Vitiello, P., and Aissa, P. 1985. Structure des peuplements de nématodes en milieu lagunaire pollué. Actes du 110 Congrès nat. Soc. sav. Montpellier, Sciences, **2**: 115-126.
- Warwick, R.M. 1981. The nematode/copepod ratio and its use in pollution ecology. *Mar. Pollut. Bull.*, **12**: 329-333.
- Wells, J.B.J. 1971. The Harpacticoida (Crustacea: copepoda) of two beaches in south-east India. *J. Nat. Hist.*, **5**: 507-520.
- Wells, J.B.J. 1978. Keys to aid in the identification of marine harpacticoid copepods. Amendment Bull. No. 1. Zool. Publ. Victoria Univ., Wellington, No. 70. 11pp.
- Wells, J.B.J. 1979. Keys to aid in the identification of marine harpacticoid copepods. Amendment Bull. No. 2. Zool. Publ. Victoria Univ., Wellington, No. 73. 8pp.
- Wells, J.B.J. 1981. Keys to aid in the identification of marine harpacticoid copepods. Amendment Bull. No. 3. Zool. Publ. Victoria Univ., Wellington, No. 75. 13pp.
- Wormald, A.P. 1976. Effects of a spill of marine diesel oil on the meiofauna of a sandy beach at Picnic Bay, Hong Kong. *Environ. Pollut.*, **11**: 117-130.