Oceanogr. Mar. Biol. Ann. Rev., 1985, **23**, 399–489
Margaret Barnes, Ed.
Aberdeen University Press

THE ECOLOGY OF MARINE NEMATODES

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INTRODUCTION

Nematodes are probably the most abundant metazoans in the biosphere and of very great importance to man. As parasites of man they are responsible for disease in hundreds of millions of people and an estimated eight billion nematodes are enjoying food, warmth and shelter in human intestines today; *Ascaris lumbricoides* is, after the viruses responsible for diarrhoeal disease, the second most infectious organism in the world, about a quarter of the world's population being infected (Ash, Crompton & Keymer, 1984).

Plant-parasitic nematodes cause considerable damage to crops and many species are vectors of soil-borne viruses. Today, plant nematology is one of the most vital fields in agricultural research and is studied in many university departments over the world, yet fifty years ago only a few pioneers were engaged in the study of plant-parasitic nematodes and were convinced of the economic importance of these worms.

Whereas the importance of parasitic nematodes has now been recognized for many decades, this is not the case for the free-living species, especially those of aquatic environments. They remain relatively unstudied, despite the fact that they are extremely abundant, often numbering millions per m^2 in soils and sediments, and that they occur in a range of habitats which is unsurpassed by any other metazoan group, being absent only from the oceanic plankton.

Free-living nematodes are small and inconspicuous and have very rarely attracted amateur naturalists. They tend to live in environments such as intertidal muds that are not particularly appealing to many people. Many species are difficult to maintain in the laboratory and the taxonomic literature has been very scattered until quite recently, making determination of nematodes a frightening affair and putting ecologists in the embarrassing position of studying animals they could not even name. Yet, other fields have recently been attracted to nematodes, and species such as the small soil-dwelling *Caenorhabditis* have become very popular model organisms in molecular biology, genetics (Brenner, 1974), and even gerontology (Vanfleteren, 1978), where methods have been developed that greatly surpass the degree of sophistication reached in most ecological work. The lack of interest for a group that is as dominant in sediments as copepods are in the plankton seems no longer justified on methodological grounds.

It is also unjustified on ecological grounds. Nematodes are important in the ecology of the seas and they are interesting. Of course, they are small or even

very small (down to 100 μm adult size) and structurally simple, basically consisting of two concentric tubes. In general most species are slender, with only a few tenths of μm diameter, but a considerable variation in habitus exists. As Platt & Warwick (1980) observed, not all nematodes look alike, many species of fine sediments are short while in coarse sands species are either very small or very elongate and thin. They are inconspicuous; many older papers do not even mention the occurrence of nematodes in sediments as nearly all specimens disappeared through the sieves that were used. Even today, when sieves of around 50 μm mesh size are universally used, estimates of nematode abundance are biased since many of the small species and juveniles of the bigger ones will be lost while processing the sample.

Despite their similar basic morphology nematodes occupy very different rôles and trophic positions in sediments. Many species feed on bacteria, on algae or on both, they eat detritus and possibly dissolved organic matter, and a considerable number are predators, feeding on other nematodes, oligochaetes, polychaetes, *etc.* This diveristy in feeding is reflected in species diversity; the number of nematode species in most habitats is much higher than that of any other metazoan group. As an example, a recent review counted a total of 735 nematode species in the North Sea (Heip, Herman & Vincx, 1983) and it is not uncommon to obtain 50 species or even more in a single 10 cm^2 core, often many congenerous, a situation that should be appealing to the theoretical ecologist trying to explain community structure in terms of predation or competition.

That nematodes are important in the energy flow through sediments has often been inferred from their numerical abundance. Yet, reliable data are scarce. In this paper we shall try to evaluate the existing literature, both the rather extensive literature describing the main structural features of nematode communities in the sea, and the far fewer papers on functional relationships and their possible use in pollution studies.

METHODOLOGY

General problems concerning benthic sampling have been treated in a number of publications (Holme & McIntyre, 1971; Elliott, 1971). For meiofauna the handbook edited by Hulings & Gray (1971) is still useful and it is in the process of revision.

SAMPLING

The most efficient sampling of nematodes from sediments is by hand-coring. The diameter of the cores used depends on the problem, but in general cores with an internal diameter of 3–4 cm are most efficient. In deeper water the different types of box-corers are to be preferred to grabs. An ideal corer should penetrate the sediment without a shock wave and as slowly as possible. We refer to the IBP-Handbook on Marine Benthos for further discussion.

THE NUMBER OF SAMPLES

The number of samples and sample size required depends on the problem being studied. Variability in nematode density appears to be mostly on a scale

of a few centimetres (see p. 434) and again on a scale of many km or even more, depending on substratum heterogeneity. Intermediate scales have surprisingly low variability. If the problem consists of studying small-scale horizontal distribution, what we might call the intrinsic spatial pattern of nematode populations, obviously the largest amount of the smallest possible samples is required, with the important restriction that sample size must be large compared with the individuals being sampled. When the problem consists, as is usually the case, in obtaining an estimate of nematode density, there may be two alternative solutions. The first is to destroy all small-scale variability in the sample and take a sample as big as possible, mix it thoroughly and, if necessary, take subsamples. We have tested this many times in our laboratory and found it satisfactory. If the intrinsic pattern is not destroyed, aggregation will require that the sample size is as small as possible and the number of samples taken as large as possible. This is so because most statistical analyses are robust when they are based on a large number of error degrees of freedom (Green, 1979). When mean density is estimated from simple random sampling the error degrees of freedom is $n-1$, with n the number of samples. If sampling is done t times at each of s stations, the error degrees of freedom is $st(n-1)$. It therefore pays to sample more stations more frequently: as an example, the error degrees of freedom are the same when five stations are sampled twice (*e.g.* in a year) with three replicates or when one station is sampled once with 21 replicates. Green (1979) proposes three replicates per treatment combination (station-time) as a good round number in the absence of other information.

If a relationship between the variance s^2 and the mean $\bar{x}$ such as Taylor's power law exist ($s^2 = a\bar{x}^b$), some powerful generalizations can be made (Green, 1979). The required precision, as a percentage of the mean, can then be estimated as:

$$D^2 = an^{1-b}T_n^{b-2}$$

in which T_n is the cumulative number of individuals in sample n, *i.e.* the number of individuals in samples 1 plus 2 plus . . . plus n. When, as is often the case, $b = 2$, $D^2 = an$, and $n = a/D^2$; a can be evaluated from the fact that, if $b = 2$, $s^2 = a\bar{x}^2$ and $a = v^2$, in which v is the coefficient of variation $s/\bar{x}$. Taking the value obtained by Delmotte (1975) in a study of 49 samples covering a 7×7 grid of $0{\cdot}4 \times 0{\cdot}4$ m one gets $a = 0{\cdot}15$. If the desired precision is 10% of the mean (confidence intervals approximately 20% of the mean), the number of samples required is 15. For a precision of 20%, four samples are required; three replicates give a precision of 22%, two replicates 27%.

EXTRACTION TECHNIQUES

The extraction of nematodes from sediments is easy when the sediment is a sand with low amounts of detritus or silt-clay. Simple decantation on a sieve is often satisfactory, although more elaborate apparatus has been developed (Hulings & Gray, 1971). The maximum sieve size to be used is 50 μm, although juveniles and even adults of many species will not be retained by such a sieve and sieves of 20 μm have been used. Such small mesh sizes can only be used for very clean sands, and a 38 μm standard sieve seems a good compromise.

The extraction from muds or detritus (after the sand has been removed by decantation or other methods) is done most efficiently by using Ludox,

although sugar can be used instead (Heip, Smol & Hautekiet, 1974). The method developed in our laboratory consists in the following procedure:

1. Rinse the sample thoroughly with tap water, to prevent flocculation of Ludox, over a sieve of 38 μm.
2. Bring the sample from the sieve in a centrifugation tube as large as available.
3. Add a small amount of kaolin, enough to cover the sample completely.
4. First centrifugation at 1800 g in water for 10 min.
5. Remove the supernatant.
6. Add Ludox HS 40%, which is half diluted, to at least five times the volume of sediment and again centrifuge at 1800 g for 10 minutes. The supernatant is passed through a sieve of 38 μm. The centrifugation is repeated three times.

It has been shown by Heip (1974) that the number of nematodes collected after successive centrifugations is a constant proportion. When N_1 and N_2 are the numbers found in the first and second supernatant, then the total number in the sample is given by

$$N_t = \frac{(N_1^2/N_2)-1}{(N_1/N_2)-1}.$$

When the procedure can be standardized and the constant factor $a = N_1/N_2$ has been shown to be indeed constant, even one centrifugation permits a good estimate of the total number in the sample since:

$$N_t = \frac{aN_1-1}{a-1}.$$

FIXATION

Samples have to be fixed with 4–7% neutralized formalin. Both cold and warm fixation (70 °C) have been used. Many workers in the field fix marine nematodes with formalin in tap water.

MICROSCOPICAL EXAMINATION AND DETERMINATION

After fixation, animals must be transferred to anhydrous glycerol. Specimens are transferred from formalin to glycerol through a series of ethanol-glycerol solutions to prevent the animals from collapsing (Seinhorst, 1959; De Grisse, unpubl.).

When in glycerol, animals may be mounted on glass slides. Many nematologists use Cobb-slides (Cobb, 1917) which permit examination from both sides as the animals are mounted between two cover glasses together with glass rods that prevent flattening of the nematode. If permanent slides are to be made, the cover glass may be sealed with Glyceel, Clearseal or Bioseal.

In toto preparations are usually satisfactory for species identification. A good quality microscope with a 100× oil immersion lens is required and interference-contrast equipment is useful, especially for microscope photography.

Comprehensive guides for identification of nematodes have been available

for ten years; the most important are: the Bremerhaven *Checklist of Aquatic Nematodes I & II* (Gerlach & Riemann, 1973/1974); *An Illustrated Guide to Marine Nematodes* (Tarjan, 1980); and *Free-living Marine Nematodes. I. British Enoplids* (Platt & Warwick, 1983) (Parts II and III are in preparation). A review of the important systematic literature is given in Heip, Vincx, Smol & Vranken (1982).

ISOLATION TECHNIQUES AND MAINTENANCE IN THE LABORATORY

The different techniques used in the cultivation of marine nematodes have been reviewed by Kinne (1977). Pioneering work in the field of cultivation is that of Chitwood & Murphy (1964) and von Thun (1966, 1968). These early workers started to use agar as a maintenance medium. Von Thun (1966, 1968) developed and successfully used a modified Killian agar for the cultivation of six species (listed in Table VIII, p. 444). Von Thun's medium was used later by Gerlach & Schrage (1971, 1972) for life-cycle studies.

The use of fungal mats has been popular for some time in Florida (Meyers, Feder & Tsue, 1963, 1964; Hopper & Meyers, 1966a,b, 1967a; Meyers & Hopper, 1966, 1967). These mats were used either for trapping or for culturing. Two fungi (*Dendryphiella arenaria* and *Halosphaeria mediosetigera*) were particularly appropriate, both forming a compact mat that proved to be a good substratum on which to culture both nematodes and food organisms.

With the publications by Tietjen *et al.* (1970) and Lee *et al.* (1970) the first successful attempts to culture both the nematodes and their food in controlled conditions were made. Especially Erdschreiber-3 medium proved a good basis for culturing several chromadorids. Techniques were presented for aseptical working with nematodes and for establishing monoxenic (see Dougherty, 1960, for terminology) cultures of *Rhabditis marina** with the bacterial strain *Pseudomonas* sp. From such monoxenic cultures, Tietjen & Lee (1975) produced an axenic medium for *Rhabditis marina*, based on Grace's insect medium, with marine salt mixture and sheep blood.

The same techniques were used for many studies on life-cycles of marine nematodes (Tietjen & Lee, 1972, 1973, 1977a,b), on studies of feeding behaviour using tracer techniques, and on studies of trophic interactions (Alongi & Tietjen, 1980). When algae were used as food the nematodes were cultured in Erdschreiber medium, with bacteria as food the basic medium was autoclaved sea water with cereal.

Hopper, Fell & Cefalu (1973) and Warwick (1981a) used corn meal agar. Heip, Smol & Absillis (1978) used bacto-agar (DIFCO) and Vranken, Thielemans, Heip & Vandycke (1981), Geraert, Reuse, Van Brussel & Vranken (1981) and Vranken, Vincx & Thielemans (1982) cultured on bacto-agar (DIFCO) enriched with Vlasblom-medium (containing glycine) and silicate. Romeyn, Bouwman & Admiraal (1983) and Bouwman (1983) used a very similar medium for *Eudiplogaster pararmatus* and several Aufwuchs species, among which was the Ghent stock of *Monhystera microphthalma.*

Several other species were established on agar as substrate. Trotter &

*Andrássy (1983) transferred *Rhabditis marina* to *Pellioditus marina* (Bastian, 1865) n. comb. Andrássy, 1983.

Webster (1984) did feeding experiments with three species using bacto-agar (DIFCO) with bacteria and diatoms, grown separately on standard media, as substance. Jensen (1982) cultured *Chromadorita tenuis* on a brackish water agar-bottom enriched with a modified Erdschreiber medium after Hällfors. Findlay (1982a) and Findlay & Tenore (1982) established the nematode, *Diplolaimella chitwoodi*, in monoxenic cultures, maintained on Gerber's mixed cereal (Pablum).

Gnotobiotic culturing methods were developed by Vranken, Van Brussel, Vanderhaeghen & Heip (1984a), *i.e.* a completely chemically-defined medium based on artificial sea water enriched with amino acids, modified Provasoli-Walne nutrient medium and a sterol mixture was established and the nematodes were cultured monoxenically on an *Alteromonas haloplanktis* strain.

Most species cultured up to now are members of Aufwuchs communities and thrive well on agar. Other species, such as the typical mud-dwelling *Sabatieria* and *Daptonema*, or typical sand-dwellers from the open sea have not yet been cultured on agar. The methods existing at present do not permit permanent cultivation of many of the most important marine species.

NEMATODE ASSOCIATIONS

ESTUARIES AND BRACKISH WATER

It has been known for many decades that benthic communities in brackish water have fewer species than either marine or freshwater communities (Remane, 1933). This is also true for nematodes. A species-salinity curve was constructed by Gerlach (1953, 1954) from comparable sediments in brackish waters along the German coast. This curve (Fig. 1) shows a minimum number of species between 3–7‰ *S*. Freshwater species penetrate into brackish water to a maximum of 10‰ *S* and marine species can invade, in relatively high densities, the oligohaline area to 0·5‰ *S*. Bilio (1966) listed 60, 59, 2 and 4 meiofauna species (with nematodes dominant) in eu-, poly-, meso- and oligohaline water, respectively.

Brackish-water nematodes have been divided into six groups according to salinity by Gerlach (1953) and this was later followed and adapted by Bilio (1966), Skoolmun & Gerlach (1971), Warwick (1971), Brenning (1973), and Van Damme *et al.* (1980). However, such groupings appear to be artificial and differ from place to place; different environmental factors may interact, the most important being type of sediment. Warwick (1971) even found an increasing number of species in the Exe estuary, U.K., with decreasing salinity but increasing grain size.

A list of the dominant brackish-water and marine nematodes invading brackish water is given in Table I. From the 155 species listed, only 18 are restricted to brackish water. The salinity boundaries are found in the systematic literature not reviewed here.

Whether true brackish-water nematode species exist is still a matter of debate. Meyl (1954, 1955) described nematode assemblages from inland saline waters in Braunschweig, West Germany, and found no marine species although the salinity was high enough. Paetzold (1955, 1958) described similar

assemblages in saline waters near Aseleben, West Germany. The species that occur in these habitats are well adapted, not only to low or high salinities, but especially to fluctuations. During dry weather, when salinity may become very high, some species survived 123°/₀₀ *S* (*Monhystera multisetosa, Theristus flevensis, Diplolaimelloides oschei, Tripyloides marinus, Paracyatholaimus intermedius*, and *Oncholaimus oxyuris*) whereas *Chromadora nudicapitata* was found surviving in up to 84·5°/₀₀ *S*.

Several estuaries around the North Sea have been well investigated. Riemann (1966) described the nematode communities along the Elbe in Germany and tried to classify them according to the Venice system of salinity. The polyhaline region of the Elbe is distinguished from the mesohaline zone by the presence of Desmodoridae. A series of species extend from the polyhaline zone into a salinity of 10°/₀₀ so that the boundary between α- and β-mesohaline zones can be found biologically. These species, however, have different salinity ranges in other estuaries. In the tidal freshwater region of the Elbe, the most abundant species is *Daptonema setosum*, whereas in the upper brackish-water regions an assemblage with *Axonolaimus spinosus* and *Theristus meyli* is characteristic. In areas with intermediate salinities the distribution of species is regulated by the variable degrees of sand movement.

Warwick (1971) described six different habitats along the Exe estuary by a combination of salinity, grain size, and degree of water retention. In muddy sediments, nematodes are small, with short setae. They are mainly deposit-

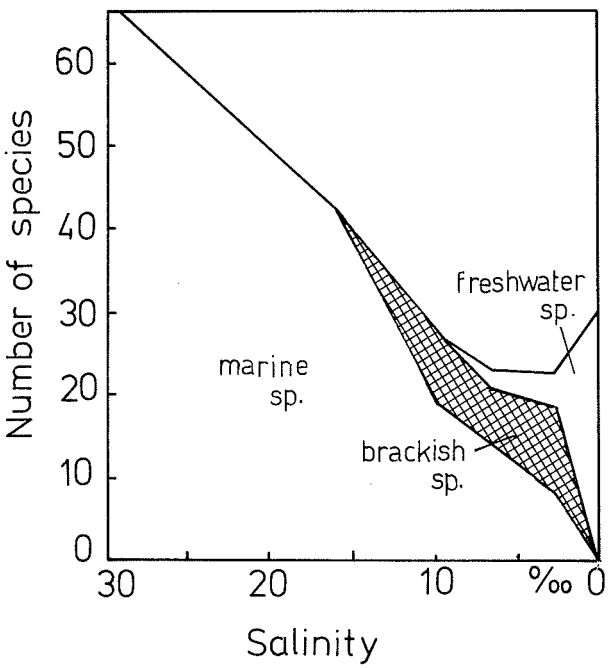

Fig. 1.—Species-salinity curve from comparable sediments in brackish waters along the German Bight (after Gerlach, 1954).

TABLE I

Salinity tolerances of brackish-water nematodes: except when otherwise mentioned, the tolerance is from sea water (35°/₀₀ S) at the upper level to the noted salinity value on the lower level; freshwater species are not included; reference numbers are given in parentheses. 1. Gerlach (1953): Kiel Bay, North Sea coast (W. Germany). 2. Meyl (1954, 1955): salt marsh (W. Germany). 3. Capstick (1959): Blyth estuary (U.K.). 4. Riemann (1966): Elbe estuary (W. Germany). 5. Bilio (1966): North Sea. 6. Skoolmun & Gerlach (1971): Weser estuary (W. Germany). 7. Warwick (1971): Exe estuary (U.K.). 8. Brenning (1973): Baltic coast (E. Germany). 9. Lasserre, Renaud-Mornant & Castel (1975): saline reservoirs (France). 10. Riemann (1975): Columbia (S. America). 11. Elmgren (1978): Baltic Sea. 12. Möller, Brenning & Arlt (1976): Baltic Sea (E. Germany). 13. Warwick & Price (1979): Lynher estuary (U.K.). 14. Van Damme et al. *(1980): Western Scheldt estuary (The Netherlands). 15. Jensen (1981a): Baltic Sea (Finland). 16. Bouwman (1983): Wadden Sea–Ems estuary (The Netherlands). 17. Schiemer, Jensen & Riemann (1983): N. Baltic Sea. 18. Jensen (1984): Baltic Sea (Finland). 19. Smol (unpubl.): Dievengat (Belgium)*

Species	°/₀₀ Salinity	Reference
Adoncholaimus fuscus	0·5	(3, 4, 7)
„ *thalassophygas*	0·5	(1, 2, 3, 4, 5, 6, 7, 8, 12, 16, 17, 18, 19)
Aegialoalaimus elegans	26·5	(13)
Anoplostoma viviparum	0·5	(1, 3, 5, 6, 7, 8, 12, 13, 16, 18, 19)
Antomicron elegans	2·1	(3, 14)
Aponema torosus	26·0	(13)
Ascolaimus elongatus	0·5	(1, 5, 6, 7, 8, 14, 17, 19)
Atrochromadora microlaima	0·5	(7, 13, 16)
Axonolaimus paraspinosus	0·9	(1, 3, 7, 8, 13)
„ *spinosus*	0·5	(1, 4, 6, 7, 8, 12, 16, 17, 18)
„ *typicus*	24·5	(3, 5)
„ sp. (aff. *spinosus*)	0·5	(18)
Bathylaimus assimilis	5·3	(1, 6, 7, 8)
„ *filicaudatus*	30·5	(3)
„ *longisetosus*	0·5	(1, 8)
„ *stenolaimus*	5·3	(7)
„ *tenuicaudatus*	0·5	(8)
Calomicrolaimus honestus	0·5	(1, 7, 8, 11, 13)
Calyptronema maxweberi	0·5	(4, 5, 7, 14, 19)
Camacolaimus barbatus	5·3	(7)
Campylaimus inaequalis	26·5	(13)
Choanolaimus psammophilus	0·5	(4)
Chromadora nudicapitata	17·0	(1, 8)
„ sp. (aff. *nudicapitata*)	17·0	(18)
Chromadorina erythropthalma	11·0 → 1·0	(18)
„ *germanica*	9·0	(9)
„ *microlaima*	24·0	(1, 3, 8)
„ sp. (aff. *germanica*)	24·0 → 9·0	(18)
„ sp. (aff. *viridis*)	5·0	(17)
Chromadorita fennica	15·0 → 4·0	(17, 18)
„ *guidoschneideri*	25·0 → 2·0	(1, 4, 5, 8, 18)
„ *nana*	2·0	(12)

Chomardorita tentabunda	26·0 → 0·5	(1, 4, 6, 8, 13, 17)
„ *tenuis*	25·0 → 4·0	(1, 8, 18)
Cyatholaimus punctatus	10·0	(1, 8)
Daptonema leptogastrelloides	0·5	(17)
„ *normandicum*	5·3	(1, 6, 7, 8, 13)
„ *oxycerca*	0·9	(1, 7, 8, 12, 13, 18)
„ *procerum*	26·0 → 11·0	(8, 13, 19)
„ *setosum*	0·5	(1, 2, 3, 4, 5, 6, 7, 8, 9, 12, 13, 14, 16, 17, 18, 19)
„ *tenuispiculum*	30·5	(3)
„ *trabeculosum*	26·0 → 0·5	(1, 4, 6, 8, 18, 19)
„ sp. (aff. *biggi*)	0·5	(17)
Desmodora communis	5·3	(7)
Desmolaimus fennicus	0·9	(7)
„ *zeelandicus*	0·5	(1, 8, 11, 12, 18, 19)
Desmoscolex falcatus	26·0	(13)
Dichromadora cephalata	0·5	(1, 7, 8, 13, 19)
„ *geophila*	0·5	(1, 2, 5, 8, 16, 17, 18)
„ *hyalocheile*	18·0	(1, 8)
Diplolaimelloides altherri	22·0	(2)
„ *islandicus*	0·5	(5)
„ *oschei*	27·5	(2)
Eleutherolaimus stenosoma	0·5	(1, 5, 6, 8, 11, 13, 16, 19)
„ sp. (aff. *stenosoma*)	0·5	(17)
Enoploides caspersi	18·0 → 0·5	(4)
„ *labiatus*	10·0	(1, 8, 16)
„ *spiculohamatus*	5·3	(6, 7)
Enoplolaimus balgensis	18·0 → 0·5	(1, 8, 17)
„ *litoralis*	2·1	(14)
„ *propinquus*	2·1	(1, 6, 8, 14)
„ *vulgaris*	0·5	(4)
Enoplus brevis	12·0	(1, 3, 5, 6, 8, 18)
„ *schulzi*	5·3	(7)
Eurystomina terricola	5·3	(7)
Halalaimus gracilis	7·5	(3, 5, 6, 8, 13, 14)
Halichoanolaimus robustus	11·0	(3, 8, 19)
Hypodontolaimus balticus	0·5	(1, 3, 5, 8, 13, 18, 19)
„ *geophilus*	0·5	(4, 7)
„ *inaequalis*	15·0	(16)
„ *setosus*	0·5	(6, 11, 16, 17)
Leptolaimus elegans	0·5	(8, 11, 17)
„ *limicolus*	11·0	(13, 19)
„ *papilliger*	0·5	(1, 5, 7, 8, 10, 11, 12, 14, 16, 17, 19)
„ *setiger*	22·0	(3)
Metachromadora remanei	5·3	(7)
„ *suecica*	12·0	(1, 6, 8)
„ *vivipara*	0·9	(3, 7, 13)
Metalinhomoeus filiformis	11·0	(19)
Metaparoncholaimus sp. (aff. *campylocercus*)	0·5	(4)
Microlaimus globiceps	0·5	(1, 2, 4, 5, 8, 11, 16, 17, 18, 19)
„ *marinus*	2·1	(14)
„ *robustidens*	5·4	(7)
Molgolaimus demani	24·5	(3, 13)
Monhystera disjuncta	0·5	(18)
„ *microphthalma*	25·0 → 11·0	(5, 19)
„ *parva*	0·5	(5, 8, 12, 13, 19)
„ *paramacramphis*	22·0	(2)
„ sp. (aff. *filiformis*)	0·5	(18)
„ sp. (aff. *parasimplex*)	3·5 → 2·0	(17)

TABLE I—*continued*

Species	‰ Salinity	Reference
Monhystrella parelegantula	11·0	(2, 19)
Monoposthia costata	25·0	(3)
„ *mirabilis*	24·0	(1, 8, 16)
Nemanema cylindraticaudatum	10·0	(1, 8)
Neochromadora izhorica	18·0 → 0·5	(1, 4, 8, 17, 18)
„ *poecilosoma*	8·6	(1, 8, 13, 16, 18)
„ *poecilosomoides*	18·0	(9)
„ *trichophora*	24·0	(16)
Odontophora armata	12·0	(3, 6)
„ *rectangula*	24·0	(16)
„ *setosa*	5·0	(1, 7, 8, 13, 16)
Oncholaimus brachycercus	5·0	(1, 6, 7, 8)
„ *conicauda*	18·0 → 10·0	(1, 8, 17)
„ *oxyuris*	0·5	(1, 2, 5, 8, 19)
Oxystomina elongata	11·0	(3, 13, 19)
„ *unguiculata*	31·0	(3)
Paracanthonchus caecus	0·5	(1, 3, 5, 8, 11, 16, 18, 19)
„ *bothnicus*	18·0 → 0·5	(17, 18)
„ *elongatus*	25·0	(3)
„ *sabulicolus*	24·0	(16)
„ *tyrrhenicus*	5·0	(7)
„ sp. (aff. *bothnicus*)	18·0 → 0·5	(18)
Paracyatholaimus intermedius	30·0 → 0·5	(1, 2, 4, 5, 6, 7, 8, 12)
„ *proximus*	0·5	(1, 4, 5, 6, 8, 16)
„ *ternus*	0·5	(10)
„ *truncatus*	0·5	(10)
Paralinhomoeus lepturus	11·0	(3, 19)
Pomponema sedecima	24·0	(16)
Praeacanthonchus punctatus	0·9	(7, 13)
Prochromadorella longicaudata	24·0	(15)
Ptycholaimellus ponticus	0·5	(1, 3, 5, 6, 7, 8, 9, 13, 18)
Quadricoma scanica	26·0	(13)
Sabatieria longispinosa	24·0	(16)
„ *pulchra*	0·5	(11, 13, 15, 16, 18, 19)
„ *punctata*	0·5	(1, 8)
„ *vulgaris*	0·9	(6, 7, 15)
Setoplectus riemanni	0·5	(10)
Sigmophoranema rufum	18·0	(1, 8)
Southernia zosterae	26·0	(1, 8, 13)
Sphaerolaimus balticus	22·0	(3, 8, 12, 16, 18)
„ *gracilis*	0·5	(3, 4, 5, 17, 19)
„ *hirsutus*	0·9	(3, 6, 7, 13)
Spilophorella paradoxa	2·1	(3, 14)
Spirinia parasitifera	22·0	(3)
Syringolaimus striaticaudatus	10·0	(5)
Terschellingia communis	0·9	(7, 13)
„ *longicaudata*	0·9	(7, 9, 13)
Thalassoalaimus tardus	22·0	(3, 13)
Theristus acer	5·3	(1, 3, 5, 7, 8, 12, 13, 18, 19)
„ *blandicor*	7·5	(6, 14)
„ *ensifer*	18·0	(5)
„ *flevensis*	0·5	(1, 2, 4, 5, 8, 10, 12, 17, 18)
„ *metaflevensis*	0·5	(10)
„ *meyli*	0·5	(4)

Theristus pertenuis	11·0	(5, 6, 8, 19)
„ *scanicus*	0·5	(4, 6, 17)
Trefusia conica	0·5	(10)
„ *longicauda*	5·3	(6, 7)
Trichotheristus mirabilis	2·1	(14)
Tripyla cornuta	18·0 → 0·5	(1, 4, 8)
Tripyloides amazonicus	0·5	(10)
„ *gracilis*	5·3	(7, 13)
„ *marinus*	0·5	(1, 3, 4, 5, 6, 8, 12, 14, 17)
„ sp. (aff. *marinus*)	0·5	(18)
Tubolaimoides tenuicaudatus	12·0	(6)
Viscosia rustica	24·0	(16)
„ *viscosa*	0·9	(1, 3, 6, 7, 8, 13, 14, 16, 19)

feeders. In sandy bottoms, species are longer with long setae and heavily ornamented cuticles. Epistratum-feeders and predators are numerous. Gourbault (1981) examined the nematodes in silt deposits along the Morlaix river bed (France). Species composition is primarily influenced by grain-size characteristics and secondarily by the range of the estuarine conditions (*e.g.* salinity ranges between 20–34‰). Most of the species are true marine, polyhaline species (and are, therefore, not included in Table I); the Comesomatidae (28%) and Linhomoeidae (27%) are the most abundant families.

In estuaries with semidiurnal tides, the interstitial salinity is rather constant and nematodes can burrow down, whereas in areas where salinity changes are irregular and unpredictable the only possible adaptation is a broad physiological tolerance. Brackish-water pools or salt marshes will have a lower number of species than estuaries. Bouwman (1983) thinks that the number of nematode species in an estuary is probably close to 200 (compare with 735 for the North Sea). The maximum number of species in inland brackish waters is about 50 (Gerlach, 1953; Meyl, 1954, 1955; Brenning, 1973; Smol, unpubl.).

In his study of the Ems estuary and the Wadden Sea (The Netherlands) Bouwman (1983) examined the occurrence of associations in relation to the conditions offered by particular habitats. Sublittoral marine and estuarine muds are dominated by members of the same genera (*e.g. Sabatieria, Spirinia, Terschellingia, Odontophora,* and *Desmolaimus*). Tidal flats differ from subtidal estuarine sediments in having a dense stock of microphytobenthos at the surface. A considerable part of the nematode community from the upper sediment layers in the Ems estuary is made up by diatom-feeders. Most of these species are not found in sublittoral marine sediments (*Atrochromadora microlaima, Dichromadora geophila, Hypodontolaimus balticus, Ptycholaimellus ponticus, Chromadorita guidoschneideri, Chromadora nudicapitata, Eudiplogaster pararmatus, Daptonema* aff. *normandicum, D. oxycerca, D. setosum, D. trabeculosum, D. xyaliforme, Paracyatholaimus proximus,* and *Praecanthonchus punctatus*). Bouwman thinks that the preference of these species for diatoms, as food and their tolerance to reduce salinities are two of the main differences between nematodes from sublittoral sediments and those from tidal estuarine sediments. The amount of diatom-feeders in sublittoral

sediments, however, may be very important; Tietjen (1969) found epigrowth-feeders (mainly Desmodoridae) dominant with maximum abundance in spring and summer in four subtidal stations in two estuaries in New England. The distribution of marine nematodes in near-coast fresh water (0·5‰ *S*) was examined by Riemann (1975). Contrary to observations from the macrofauna, the abundance of the meiofauna and especially nematodes was not influenced by the latitudinal position of the habitats.

Table II summarizes data on density and biomass of nematode assemblages in brackish-water habitats. Most of the studies are from intertidal or shallow subtidal stations in estuaries or from salt marshes in the United States of America, where *Spartina alterniflora* is abundant.

Especially sheltered, muddy regions have an extremely high abundance of meiofauna, with nematodes always the dominant taxon. 16 300 ind.·10 cm^{-2} were counted in a *Spartina* salt marsh in Georgia (Teal & Wieser, 1966) and a record figure of 22 860 ind.·10 cm^{-2} was found on a mud-flat in the Lynher estuary, U.K. (Warwick & Price, 1979). Van Damme *et al.* (1980) studied the meiofauna of the Western Scheldt estuary in The Netherlands along five transects over a one-year period. The highest densities of nematodes (up to 17 500 ind.·10 cm^{-2}) were found in summer in sediments with a small grain size ($\pm$0·105 mm) and a relatively high organic content. The decrease of annual mean density from the sea to the inner part of this polluted estuary is shown in Figure 2. Biomass values follow the same trend. Diversity is relatively low in the eu- to polyhaline zones ($H = 2{\cdot}27 - 2{\cdot}44$), reaches a peak in the poly- to mesohaline zones ($H = 3{\cdot}01$) and declines to $H = 1{\cdot}63$ in the meso- to oligohaline zones (all values in bits/ind.). The relatively low diversity in the sandy sediment at the mouth of the estuary may be explained through high turbulence and periodical re-working of the sediment, a phenomenon that also occurs in the nearby Eastern Scheldt mouth (Heip *et al.*, 1979). A decrease of diversity with increasing environmental fluctuations has also been observed by Ott (1972b) on an intertidal sand-flat.

Schiemer, Jensen & Riemann (1983) examined the subtidal (>80 m depth) nematodes from the northern part of the Baltic (Bothnian Bay, salinity only 2–3·5‰), where the meiofauna is the dominant constituent of the benthic fauna in density as well as in biomass (Elmgren, 1978). The composition of the fauna is similar to the situation along the German coast described by Gerlach (1953). Diversity is relatively low, with 5–18 species present, $H = 1{\cdot}9$–$3{\cdot}3$ bits/ind. The area is quite uniform in species composition and similarity between stations is high.

The abundance of epiphytic nematodes in brackish water has been discussed by Jensen (1984) who compared benthic and epiphytic nematodes from several brackish-water areas in Finland and other European brackish waters. In winter, when the submerged vegetation in this area is destroyed and incorporated in the sediments as detritus, epiphytic nematodes stay within the sediment. In spring, the epiphytes leave the bottom and colonize the newly grown submerged macrophytes. The abundance of Chromadoridae appears to be related to three conditions: salinity, explaining large-scale horizontal distribution, and substratum and oxygen, which determine vertical distribution. *Chromadorita tenuis* inhabits all types of submerged vegetation; its salinity preference is 4–25‰. The four other *Chromadorita* species are benthic and have different types of locomotion: *C. tentabunda* jumps from sand grain

TABLE II

Nematode densities (ind.·10 cm^{-2}), biomass (mg dry wt·10 cm^{-2}) from estuarine and brackish-water areas: salinity values °/$_{oo}$, sediment characteristics and species composition (Sp. comp., — not given in text, + given in text) also included

Reference	Locality	Sediment	Salinity	Density	Biomass	Sp. comp.
Rees, 1940	Bristol Channel (U.K.)	mudflat	brackish	1000–10 000	—	—
Smidt, 1951	Danish Wadden Sea	mud/sand	?	223	0·03–0·43	—
Capstick, 1959	Blyth estuary (U.K.)	mud/sand	31–33	625–2210	—	+
			25–32	750–1880	—	+
			22–30	228–715	—	+
Teal & Wieser, 1966	Georgia (U.S.A.)	mud/sand	?	46–16 300	0·05–2·43	+
Muus, 1967	Danish estuaries lagoons	?	5–18	300–1400	—	—
Tietjen, 1969	New England estuaries (U.S.A.)	mud/sand	26–31	1000–4811	3·3–8·0	+
Skoolmun & Gerlach, 1971	Weser estuary (W. Germany)	sand	12–26	8–107	—	+
Nixon & Oviatt, 1973	New England (U.S.A.)	mud	20–25	1600–10 000	0·2–1·0	—
Lasserre *et al.*, 1975	Arcachon (France)	mud	3–40	200–12 600	0·1–10·4	+
Möller *et al.*, 1976	Baltic Sea (E. Germany)	sand	5–6	245–423	—	+
Arlt, 1977	Greifswalder Bodden (E. Germany)	sand–sandy mud	5–9	105–1559	—	—
Saad & Arlt, 1977	Tigris & Euphrates estuary (Arabian Gulf)	mud	fresh	71	—	—
			mixed	24	—	—
			marine	636	—	—
Dye & Furstenberg, 1978	Swartskop estuary (S. Africa)	sand	0–43	960–1380	0·1–0·4	—
Warwick & Price, 1979	Lynher estuary (U.K.)	mud	26	800–22 860	1·4–3·4	+
Van Damme *et al.*, 1980	Western Scheldt estuary (The Netherlands)	mud/sand	2–32	160–17 500	0·03–4·58	+
Coull & Wells, 1981	Wellington estuary (New Zealand)	mud	5–34	22–444	—	—
Sikora & Sikora, 1982	S. Carolina (U.S.A.)	mud	high-intertidal	4400	—	—
			mid-intertidal	3600	—	—
			low-intertidal	2300	—	—
			subtidal	1900	—	—
Bouwman, 1983	Ems estuary (The Netherlands)	mud/sand	3–32	40–10 000	—	+
Montagna *et al.*, 1983	S. Carolina (U.S.A.)	mud/sand	22–36	270–304	—	—
Schiemer *et al.*, 1983	N. Baltic Sea	mud/sand	2–3·5	?	?	+
Ellison, 1984	Cornwall (U.K.)	mud	33–35	1100	—	—
Jensen, 1984	Baltic Sea (Finland)	mud	18–30	1200–1500	—	+

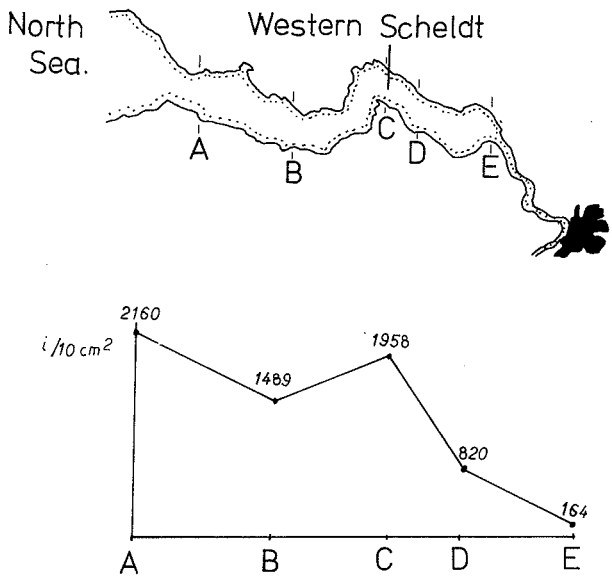

Fig. 2.—Annual mean density of nematodes communities in the Western Scheldt estuary, along 5 transects A–E (after Van Damme *et al.*, 1980).

to sand grain (*e.g.* Riemann, 1980) whereas *C. fennica*, an oligo- to mesohaline species, glides through the sediments like a snake. *C. leuckarti* is a freshwater species and *C. guidoschneideri* occurs mostly in sandy bottoms and does not enter oligohaline waters.

MARINE SANDY BEACHES

The intertidal environment of marine beaches has a particular brackish-water fauna which lives in the coastal subsoil water. This environment is a transition zone between sublittoral, truely marine bottoms and the continental subterranean waters with their phreatic freshwater fauna.

The different types of sandy beaches have been classified by McLachlan (1980) in relation to exposure. He distinguishes four types.

(1) Very sheltered beaches, with virtually no wave action, reduced layers close to the surface, abundant macrofauna burrows; this type of beach is to some extent modified and stabilized by the fauna.
(2) Sheltered beaches, with little wave action; the reduced layer is present and there are some macrofaunal burrows.
(3) Exposed beaches subject to moderate to heavy wave action; the reduced layer, if present, is deep and there are usually no macrofaunal burrows.
(4) Very exposed beaches subject to heavy wave action; there is no reduced layer and macrofauna consists solely of burrowers.

Table III summarizes the references on marine sandy beaches. When we compare density values in this table with those from muddy substrata (Table

TABLE III

Nematode densities (ind.·10 cm^{-2}) and biomass (mg dry wt·10 cm^{-2}) from marine sandy beaches: habitat characteristics (e.g. *grain size*), *distribution depth (cm) and species composition (Sp. comp., — not given in text, + given in text) also included*

Reference	Locality	Habitat	Density	Biomass	Depth	Sp. comp.
Smidt, 1951	Danish Wadden Sea	'hard' sand	10–1050	–	?	–
		'soft' sand	31–367	–	?	–
Renaud-Debyser & Salvat, 1963	Atlantic coast	279–343 μm	83–591	–	20	–
	Channel (France)	174–211 μm	19–389	–	20	–
Jansson, 1967, 1968	Baltic Sea	180–320 μm	1–169	–	11	–
	North Sea					
Renaud-Mornant & Serène, 1967	Malaya	exposed	8170	–	20	–
McIntyre, 1968	S.E. India	'soft bottom'	2233	–	?	–
Boaden & Platt, 1971	N. Ireland	205–228 μm	570	–	12	+
Gray & Rieger, 1971	Yorkshire (U.K.)	sheltered	827	–	10	+
		exposed	38–71	–	10	+
Harris, 1972	Cornwall (U.K.)	exposed	109–1062	–	50	–
Ott, 1972a	N. Carolina (U.S.A.)	fine sand	500–1100	–	30	+
McIntyre & Murison, 1973	W. Coast Scotland	210–279	371–1449	–	40	+
Platt, 1977a	N. Ireland	sheltered; 125–196 μm	200–3300	–	5 (95% of the fauna)	+
Munro *et al.*, 1978	W. Coast Scotland	sand: 208 μm	168–1905	–	–	–
	S.W. Coast India	sand: 175 μm	127–524	–	105	–
Fricke *et al.*, 1981	S. Africa	196–337 μm	±5000	–	30	+
McLachlan *et al.*, 1981	S. Africa	–	7000	0·8	?	–
Sharma & Webster, 1983	W. Canada	234 μm	230–670	–	6	+
		813 μm	36–160	–	6	+

II), it can easily be seen that densities in silty or fine sand (1000–5000 ind. $\cdot 10\ cm^{-2}$) are lower than in muds and that the lowest densities of nematodes are found in very exposed beaches, down to 100 ind.$\cdot 10\ cm^{-2}$. Along the beach, the highest densities are often found near M.T.L. which, on an average beach, is the place where the water table comes closest to the surface (McIntyre, 1969; Ganapati & Rao, 1968; Ott, 1972b; McIntyre & Murison, 1973). McLachlan, Wooldridge & Dye (1981) observed a shift in dominance between nematodes and harpacticoids when grain size increases, the percentage of both groups being correlated with the grain size. The shift occurs at about 330 μm, in coarser beaches harpacticoids dominate. An extreme example is a very coarse (1200 μm) tideless beach in Sweden, where only one nematode species was collected (Jansson, 1968).

Although nematodes tend to increase in density in finer sediments, diversity is higher in coarser sediments. In sediments finer than about 120 μm a true interstitial fauna is lacking and a poorer burrowing fauna remains. A true interstitial fauna exists in sediments between 125 and 500 μm grain size (Wieser, 1959; McIntyre & Murison, 1973), and sorting of the sediment is another important factor determining the available interstitial space.

Nematodes, like most other meiofaunal taxa, may penetrate very deep into coarse sandy beaches (Table III). Meiofaunal zonation is essentially three-dimensional here (McLachlan, 1977). Factors responsible for this distribution are desiccation during low tide and dissolved oxygen in the interstitial water. McLachlan (1980) made a scheme for an average beach in South Africa (Fig. 3) and recognized four strata in the sediment.

(1) A dry sand stratum near the top of the shore, wetted only at high tide; meiofauna consists mainly of nematodes.

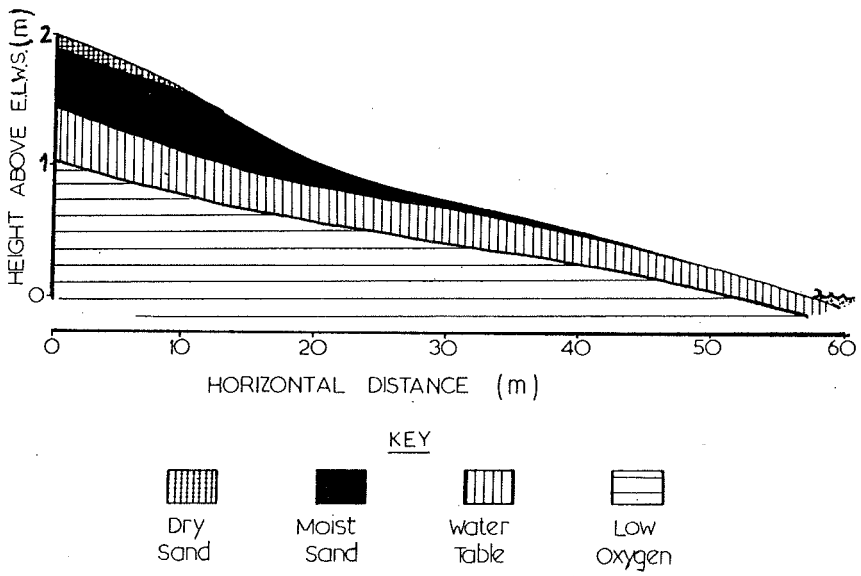

Fig. 3.—Diagrammatic representation of meiofauna strata on East Cape high energy beaches (after McLachlan, 1980).

(2) A moist sand stratum, under the dry sand and down to the permanent water table; a numerous and diverse meiofauna exists, dominated by crustaceans.
(3) The water table stratum, where lower oxygen tensions prevail; meiofauna occurs in moderate numbers and nematodes and crustaceans dominate.
(4) A low oxygen stratum, under the water table stratum, with low numbers of meiofauna and nematodes dominant.

This zonation is not static and shows tidal rhythms with the macrofauna moving upshore and the meiofauna towards the surface at higher tidal levels when the tide comes in (McLachlan, Winter & Botha, 1977).

The distribution of the meiofauna from such a model beach in South Africa is shown in Figure 4 (after McLachlan *et al.*, 1981). Meiofauna is abundant up to a considerable depth into the sand, penetrating below the permanent water

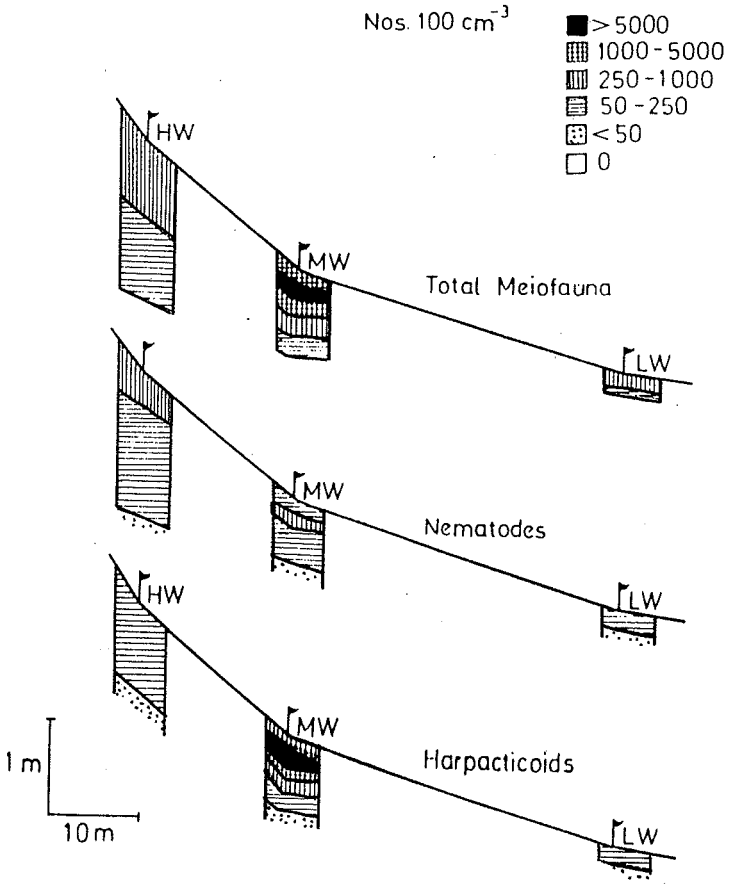

Fig. 4.—Distribution of total meiofauna and dominant taxa on Struisbaai beach (after McLachlan, Wooldridge & Dye, 1981).

table. Maximum densities occur just below the surface near mid-water and numbers generally drop more rapidly towards low water than towards high water. The dry sand stratum, the upper layer above high water neaps (HWN) harbours mostly small nematodes, adapted to live in water films around the sand grains. In the moist sand stratum, the fauna is more diverse, with harpacticoids extremely abundant. In the water table stratum larger nematodes become important and abundance drops. Below this level, nematodes are the dominant group.

In these studies from South Africa, nematode species composition is only partially known. Fricke & Fleming (1983) found the following genera: *Desmodora, Paramonhystera, Oncholaimellus, Bathylaimus, Trissonchulus,* and *Nudora.*

An extensive study of species composition from an intertidal sandy beach on the island of Sylt (North Sea) over one year has been made by Blome (1983). Densities vary between 67 and 366 ind.·100 cm^{-3}. The beach profile was divided in different regions. Dominant species which show a preference for a particular region are noted in Figure 5. The middle to upper regions of the beach slope show the greatest density and the damp sand zone is preferred. *Leptolaimus ampullaceus* and *Enoploides spiculohamatus* are important here, and also on the sand-flat before the beach slope. Over the whole shore, the dominant species is *Viscosia franzii* (27·4%), followed by *Microlaimus nanus* (8%), *Metepsilonema emersum* (6·4%), and *Paracanthonchus longus* (6·1%). The beach slope is poorer in nematode species than the sand-flat. The slope-living species

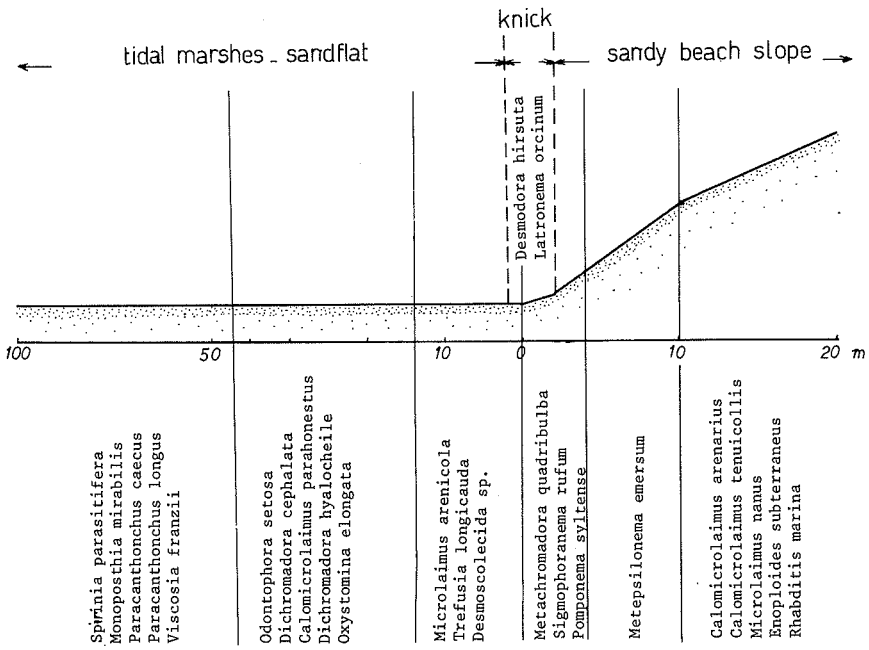

Fig. 5.—Species composition on a beach profile near the Isle of Sylt (after Blome, 1983).

show vertical migration, moving deeper into the sediment at lower temperatures. *Enoplolaimus litoralis* follows horizontal fluctuations of the high-water level over the year.

The intertidal meiofauna from exposed to sheltered beaches along the coast of North Carolina, U.S.A., close to *Spartina* marshes, has been studied by Ott (1972a). He distinguished four associations along a transect from high to low water.

(1) The upper centimetre of the high intertidal: the dominant species of this as well as the following association is *Metachromadora obesa.* Characteristic are *Microlaimus dimorphus* and *Desmolaimus zeelandicus.* Diversity is intermediate, 3·99 bits/ind.
(2) The upper centimetre from mid-tidal level to low tide: characteristic are *Cytolaimium exile, Terschellingia brevicauda, T. longicaudata, Eubostrichus parasitiferus, Gomphionema typicum, Synonchiella hopperi, Chromaspirina parma, Paradesmodora sinuosa, Camacolaimus prytherri, Pomponema hastatum, P. macrospirale, Xyzzors iubatus,* and *Nannolaimoides decoratus.* Diversity is high, 4·76 bits/ind.
(3) The deep fauna at high tidal levels: this fauna is dominated by a *Theristus* species and has the lowest diversity, 1·83 bits/ind.
(4) The deep fauna at lower tidal levels: the largest faunal unit; characteristic are *Axonolaimus paraponticus, Ptycholaimellus pandispiculatus* and *Chromadorina minor.* Diversity is highest here, 5·11 bits/ind.

These faunal assemblages are affected by temperature, salinity, pore water content and redox potential and variations in these factors (Ott, 1972b). The deeper layers of the sediment are not inhabited by a depauperate surface fauna but by a fauna of its own, containing the overall dominant *Metachromadora obesa,* penetrating often deepest into the sediment, and species such as *Cytolaimium exile,* confined to the deeper layers and which is tolerant of low oxygen levels.

In these beaches closely related species, mainly of the genera *Ptycholaimellus, Microlaimus, Theristus, Pomponema,* and *Terschellingia,* cooccur (Ott, 1972a). Within the first four genera, differences in the size of trophic structures (*e.g.* size of teeth in the mouth cavity) exist, so that food partitioning seems to be important. The distribution of the two *Terschellingia* species suggests actual competition for the same resources. *T. brevicauda* is limited to the mid-tidal region and out-competes in this area the closely related species *T. longicaudata,* a species that occurs under a wider range of conditions.

Hulings & Gray (1976) examined the interstitial sandy beach meiofauna from Mediterranean coasts. They found that meiofaunal abundance is controlled by waves, tide, and current action, which also control sorting in tidal beaches. In most atidal beaches, biological interactions such as competition and predation, were thought to control meiofaunal abundance, although no evidence for this was given.

A sheltered intertidal, fine-particle sand-flat in Northern Ireland was examined at three sites by Platt (1977a). The number of nematodes was generally lower than in intertidal muds, but higher than in coarse beaches (*cf.* Table III). Densities are influenced by sediment composition and the amount and nature of the available food. The number of species recorded ranges from 51 to 71 per station. Important species of this sand-flat are: *Spirinia*

parasitifera, Neochromadora poecilosoma, Daptonema setosum, Microlaimus zosterae, Theristus pertenuis, Chromadorita tentabunda, Monoposthia mirabilis, Pomponema sedecima, and *Spirinia laevis.* This species assemblage is found in many shallow subtidal areas over the northern hemisphere.

EPIPHYTIC NEMATODES

When macrophytes are present in the littoral zone, an enormous increase in food availability, habitat complexity, and shelter for the fauna is created. The structure and shape of the plants is important as are the presence of epiphytes (hydrozoans, bryozoans, small algae *etc.*), sediment and detritus caught by the plant.

In a comparison between phytal nematodes of Chile and the Plymouth region of England, Wieser (1951, 1959) could detect some common patterns. The same species appear to be common on different species of algae (Table IV) but dominance differs. The size of the nematodes is correlated with the general shape of the algae and the amount of detritus caught in the rhizoids. In foliaceaous algae from exposed coasts, small chromadorids dominate (62–68% in the Plymouth area, 68% in Chile). The most abundant species are closely related: *Chromadora nudicapitata* in England, *Chromadorina laeta* in Chile, and the fauna is in general more diverse than in other types of algae. In tuft-like algae from exposed coasts, a slight dominance of the large Enoploidea was found, although Chromadoroidea remained important. *Enoplus communis* has a dominance of 48% in the Plymouth area, *Oncholaimus longus* has the same dominance in Chile. Shrub-like algae have a similar fauna. In encrusting algae, small chromadorids are dominant whereas in the holdfasts of large brown algae, the enoploids are most abundant; the holes within the holdfasts provide shelter for large animals, even in an exposed environment.

In sheltered areas, the algae accumulate sediment and detritus and these

TABLE IV

Relative abundance (%) of dominant nematode species on different algae (after Wieser, 1951)

	Gelidium	*Ceramium*	*Fucus*	*Gigartina*	*Nitophyllum*
Anticoma limalis	7·0	0·2	9·2	1·2	2·0
Enoplus communis	28·7	10·0	27·6	20·4	11·3
Dolicholaimus marioni	7·6	–	0·2	1·2	–
Paracanthonchus caecus	9·5	–	0·2	1·5	–
Desmodora serpentulus	11·0	2·5	0·7	3·3	0·5
Chromadora nudicapitata	3·8	56·4	17·2	35·5	18·2
Chromadorina germanica	0·2	20·7	25·9	13·6	–
Prochromadorella paramucrodonta	–	–	0·5	0·3	7·8
Neochromadora poecilosomoides	–	–	+	+	24·0

plants have a richer nematode fauna. *Theristus* species are dominant, a consequence of the presence of sediment. In an earlier paper, Wieser (1954) used dominance of the family Monhysteridae as an indicator of the degree of sedimentation in littoral areas.

Nematodes living in the soft sediments in sea-grass beds (*Spartina, Thalassia, Zostera, Posidonia*) are not really epiphytic (Hopper & Meyers, 1967b). These habitats contain large amounts of detritus derived from the plants and contain a typical fauna. *Metoncholaimus scissus, Daptonema fistulatum, Spirinia parasitifera,* and *Gomphionema typicum* are the dominant benthic species in *Thalassia*-beds, whereas *Oncholaimus dujardinii, Chromadora macrolaimoides, Paracanthonchus platypus,* and *Chromadorina epidemos* were dominant inhabitants of the epiphytic algae on the *Thalassia* plants (Hopper & Meyers, 1967b) and did not occur except sporadically in the sediments.

The nematodes inhabiting holdfasts of kelp (*Laminaria*) are mostly epigrowth-feeders and omnivores (Moore, 1971). Species with short setae, a body length above 1·5 mm, smooth cuticle and visual perception mechanisms are dominant. Most species are large enoplids, such as *Enoplus communis, Anticoma acuminata, Thoracostoma coronatum, Phanoderma albidum,* and *Pontonema vulgaris.* Chromadoroidea, Axonolaimidae and Monhysteroidea are poorly represented. Nematodes with strongly ornamented cuticles are present in very finely branched algae (as in the interstitial environment).

There exists a large resemblance between nematodes from holdfasts of kelp in the North Sea and littoral nematodes from Chile. The large omnivorous nematodes exploit the niches normally occupied by deposit-feeders in exposed environments, whereas in more sheltered conditions the smaller deposit-feeders are able to exist in the holdfasts.

Warwick (1977) found that the nematode fauna of finer, softer weeds is different from that of coarse weeds, stiff in texture. In these stiff weeds the dominant species were *Enoplus communis, Oncholaimus dujardinii, Thoracostoma coronatum,* and *Anticoma acuminata,* whereas in fine weeds the dominant species are *Oncholaimus dujardinii, Theristus acer, Symplocostoma tenuicolle,* and *Enoplus communis.* The coarse rigid weeds have a much higher percentage of large nematodes (>6 mm length) and of species with visual mechanisms, particularly true ocelli. Predators and omnivores (Group 2B) and nematodes with smooth cuticles predominate in all weeds (Figs 6 and 7).

The nematodes from the thalli of the brown algae *Sargassum confusum* have been studied by Kito (1980) in northern Japan. Nematodes were second in abundance after harpacticoids. Four families accounted for 98% of all nematodes: Monhysteridae (60·2%), Chromadoridae (26·2%), Axonolaimidae (9·5%) and Cyatholaimidae (2·1%). Four dominant species accounted for 80–90%: *Monhystera refringens, Chromadora nudicapitata, C. heterostomata,* and *Araeolaimus elegans.*

Two pairs of closely related species occurred: *Monhystera refringens* and *M. disjuncta* and *Chromadora nudicapitata* and *C. heterostomata.* The two monhysterids had differences in food preference: *M. disjuncta* takes fine, soft material while *M. refringens* also eats pennate diatoms. The two *Chromadora* species have asynchronous reproductive activity. It is also interesting to note that one of the species in each species pair has visual sensory means while the other has not (*Monhystera refringens* and *Chromadora nudicapitata* have).

The same two *Monhystera* species, *M. disjuncta* and *M. refringens*, together with *Prochromadorella neapolitana*, comprised 91–99% of the nematode fauna from the kelp *Macrocystis integrifolia* in western Canada (Trotter & Webster, 1983).

From these data it appears that nematode communities from marine algae are similar world-wide, and many species appear to be true cosmopolitans, occurring independently of the exact species of algae.

Submerged macrophytes from the Baltic (*e.g. Pomatogeton*, *Cladophora*, *Pilayella*) and European brackish waters also harbour a typical nematode assemblage. *Adoncholaimus thalassophygas*, *Axonolaimus spinosus*, *Chromadora* aff. *nudicapitata*, *Chromadorina* aff. *germanica*, *Chromadorita tenuis*, *Diplogaster rivalis* (freshwater), *Koernia fictor* (freshwater), *Prochromadora orleji* (freshwater), *Punctodora ratzeburgensis*, *Theristus acer*, and *Tripyloides* aff. *marinus* are the most important species, and occur independent of the precise nature of the plant (Jensen, 1984). These species are only rarely reported from the well-investigated Baltic and appear to inhabit the plants as long as possible. Most of these species were much more easily cultivated than benthic species (Jensen, 1982, 1984) and appear to be opportunists.

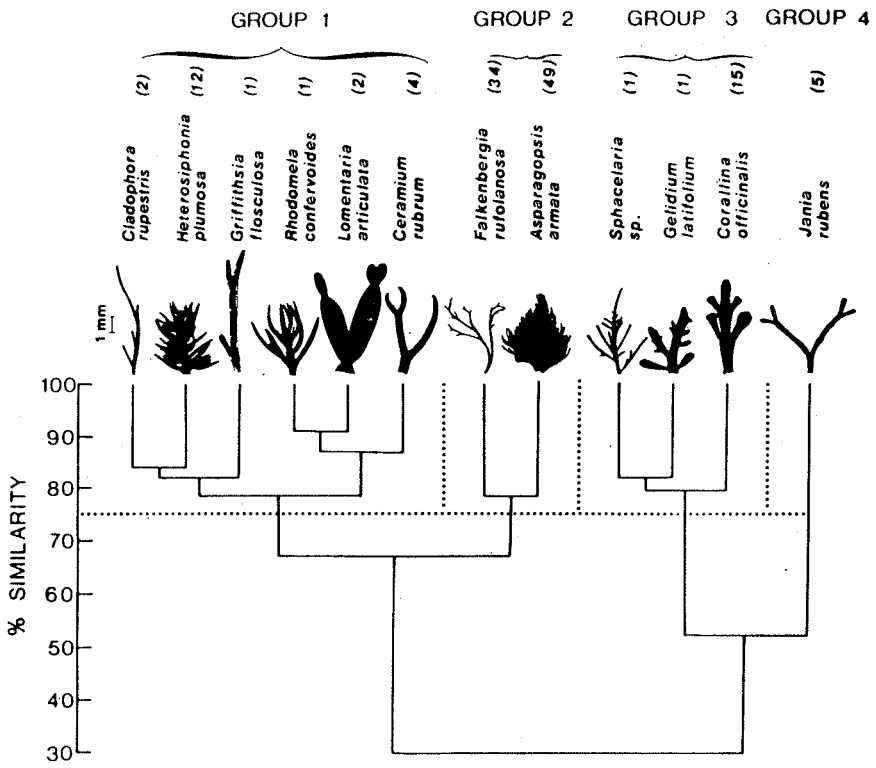

Fig. 6.—Dendrograms of faunal affinities between weed types, showing four weed groups defined at the 75% similarity level: number of samples used in analysis bracketed; after Warwick (1977).

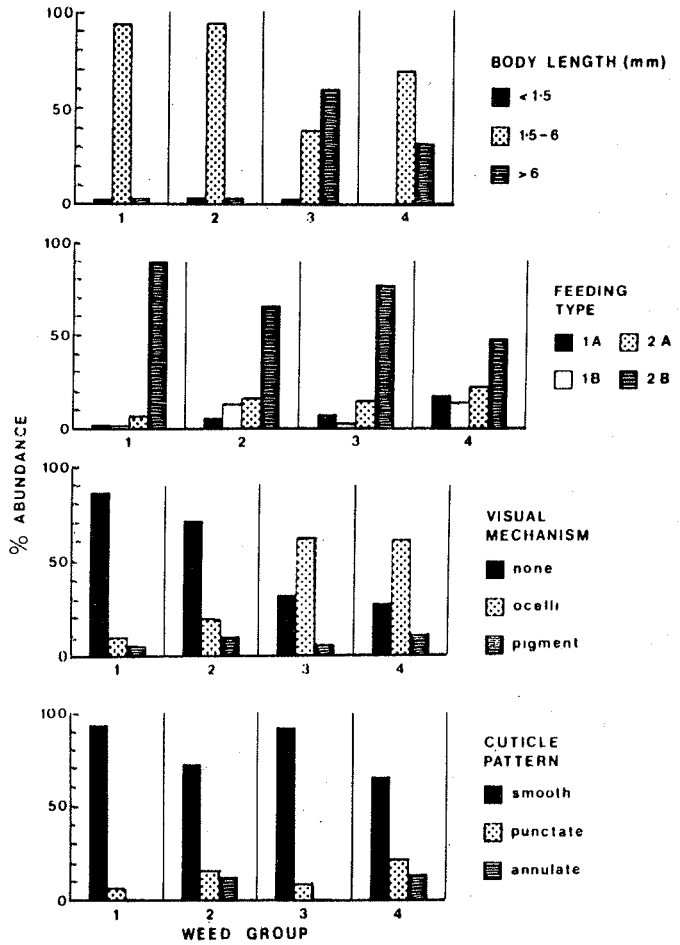

Fig. 7.—Distribution of physiognomic characters as defined by Wieser (1959), based on percentage of specimens in each weed group (after Warwick, 1977).

SHALLOW MARINE SUBTIDAL AREA

Most studies on nematodes of shallow subtidal environments deal with describing different communities occurring in different habitats, mostly characterized by sediment composition. McIntyre (1969) summarized the quantitative aspects of marine subtidal meiofauna (with nematodes, of course, very abundant); later, Heip, Herman & Vincx (1983) reviewed the state of knowledge of the subtidal meiofauna of the North Sea.

Wieser (1960a) examined the meiofauna from Buzzards Bay (U.S.A.), and was the first to deal with the community concept in marine nematodes. An *Odontophora–Leptonemella* community from sandy habitats and a *Terschellingia longicaudata–Trachydemus mainensis* (Kinorhynch) community from a silty habitat were described. In the 'silty community' one species

dominated, whereas in the 'sandy community' three or four equally dominant species were present. The sandy stations represent a more heterogeneous habitat than the silty station. The existence of numerous microhabitats within a more general environment can be inferred from the distribution of closely related species. More species, and a more even distribution of feeding-types, will be present in a habitat with a larger number of niches; silt-clay content, sorting efficiency, and median grain size determine the heterogeneity of the sediment. In all later studies, these concepts were examined in more detail.

Herman, Vincx & Heip (1985) found that nematodes appear to be more sensitive to slight changes in sediment composition than either macrofauna or harpacticoids. In the Southern Bight of the North Sea (a grid described by Govaere, Van Damme, Heip & De Coninck, 1980), six zones can be distinguished on the basis of nematode families; these zones could also be found using the properties of the sediment. Based on macrofauna and harpacticoids, Govaere *et al.* (1980) recognized only three zones. That the meiofauna is more sensitive to changes in sediment composition than the macrofauna, is also found by Warwick & Buchanan (1970).

Coastal muds are characterized by a few dominant genera which all belong to the families Comesomatidae, Linhomoeidae, Xyalidae, Spiriniidae, and Sphaerolaimidae. This assemblage seems to occur world-wide, indicating the existence of parallel communities.

The Mediterranean muds are characterized by a homogeneous set of species with Comesomatidae (mainly *Sabatieria proabyssalis*, *S. vulgaris*, *S. granulosa*, and *Dorylaimopsis mediterranea*) and Sphaerolaimidae (*Sphaerolaimus dispar*) very abundant (Schuurmans Stekhoven, 1950; Boucher, 1972; Vitiello, 1974). The infralittoral area (2–6 m) has 16 characteristic species; mainly Linhomoeidae (31%) and Spiriniidae (29%) with dominant species *Terschellingia longicaudata* and *Spirinia parasitifera*, respectively. The first species is more abundant in more sandy regions while the second species is more abundant in more silty areas, with vegetal detritus. The deeper stations (25–90 m) have a higher degree of silt and are dominated by Comesomatidae (64%), with *Sabatieria proabyssalis* and *S. vulgaris* most important. Sphaerolaimidae are the second important family.

The muddy sediments along the Northumberland coast in the North Sea (U.K.) (Warwick & Buchanan, 1970, 1971) are characterized by *Dorylaimopsis punctata*, *Leptolaimus elegans*, and *Sabatieria celtica*. *Dorylaimopsis punctata* and *Sabatieria celtica* are also dominant in the mud samples of the Fladen Ground and Loch Nevis (McIntyre, 1961).

Sabatieria is the dominant genus in the muddy habitats of Liverpool Bay (Ward, 1973), with *Odontophora*, *Neochromadora*, and *Dichromadora* also important in the muddy sands and muddy coarse bottoms. The relative abundance of characteristic genera seems to be influenced by small differences in sediment granulometry.

The muds in the German Bight of the North Sea are characterized by *Sabatieria pulchra*, *Terschellingia longicaudata* and *Desmolaimus*, aff. *bulbulus* (Lorenzen, 1974; Juario, 1975), whereas in the Southern Bight of the North Sea, *Sabatieria breviseta*, *S. vulgaris*, *Daptonema tenuispiculum*, and *Monhystera disjuncta* are the characteristic species of the polluted muddy subtidal stations along the Belgian coast (Heip, Herman & Vincx, 1984).

North American subtidal muddy areas are generally characterized by the

same genera (Tietjen, 1977). *Sabatieria pulchra, Terschellingia communis, Tripyloides gracilis,* and *Spirinia parasitifera* are the dominant species in the muds and muddy sands of Long Island Sound (U.S.A.). Those species showed very reduced abundances in sands, where *Tripyloides gracilis* was absent. *Sabatieria pulchra* is also dominant in medium sands which are contaminated by heavy metals (Tietjen, 1980a). The species which are normally very abundant in silt tolerate 'stressed' sands better than the 'typical' sand species.

With progressive increase in grain size (and decrease in silt-clay content), the numbers of Chromadoridae, Desmodoridae, Xyalidae, Axonolaimidae, and Enoplidae become increasingly abundant. Araeolaimida and Monhysterida are typical for fine sands with a small amount of silt.

The existence of parallel communities (at a species level) is not so obvious in sandy habitats as in silty ones. The fine and very fine sands along the Northumberland coast are characterized by *Odontophora longisetosa* (Warwick & Buchanan, 1970), *Mesacanthion* sp., and *Sabatieria hilarula.* In Liverpool Bay (Ward, 1973), where only genera are discussed, the sandy substrata are characterized by *Desmodora, Neochromadora, Microlaimus,* and *Richtersia.* In a fine sandy area of the German Bight of the North Sea, the following species have a relative abundance $>5\%$: *Sabatieria celtica, Daptonema leviculum,* and *Richtersia inaequalis.* The silty sands have high abundances of *Sabatieria pulchra, Molgolaimus turgofrons, Sabatieria celtica,* and *Longicyatholaimus complexus.* Lorenzen (1974) found also an increasing number of chromadorid species in the transition from mud to sand (*e.g. Prochromadorella ditlevseni, Dichromadora cucullata*). A very fine sand station (with $\pm 25\%$ silt) in the German Bight was studied in detail by Juario (1975). *Molgolaimus turgofrons* is the most abundant nematode, followed by *Sabatieria pulchra, Aponema torosus, Calomicrolaimus honestus, Marylinia complexa, Sabatieria celtica, Metalinhomoeus* aff. *typicus, Daptonema flagellicauda, D. longissimecaudatum, Prochromadorella ditlevseni,* and *Leptolaimus venustus.* These species make up for 75% of the total number of nematodes. Juario (1975) also compared different stations in the German Bight and distinguished the following nematode communities in sandy areas: a fine sand community dominated by *Sabatieria celtica, Metadesmolaimus heteroclitus,* and *Paracanthonchus caecus*; a silty sand community dominated by *Molgolaimus turgofrons, Sabatieria pulchra,* and *Aponema torosus.* In clean sand stations in the Southern Bight of the North Sea, mostly Chromadoridae such as *Chromadorita mucrocaudata, Neochromadora munita, N. paramunita, Ptycholaimellus ponticus,* and *Dichromadora cucullata,* and Desmodoridae species such as *Desmodora schulzi, Microlaimus* (several spp.), *Chromaspirina parapontica,* and *C. pellita* dominate the community (Jensen, 1974; Vincx, unpubl. results).

The sand community in Long Island Sound (Tietjen, 1977) is also characterized by low species dominance and high species diversity. It seems that more species are endemic to sands than to muds. *Theristus flevensis, Paralinhomoeus* sp., and *Theristus rusticus* were the most abundant species. The number of species per family increased in the progression muds → muddy sands → sands. In the Comesomatidae, for example, the number of species increased from one in muds to ten in medium-coarse sands, despite the fact that the relative abundance of the family decreased from an overwhelming 42% to only 10% in sands. The spatial distribution of species in the New York

Bight Apex (Tietjen, 1980a) agreed with previous findings. In silty sands especially *Sabatieria pulchra* and *Terschellingia* are dominant; in medium sands, the Comesomatidae were also important and the family is represented by more species.

Nichols (1980) examined the nematode community in sandy stations off the coast of Peru. The three species, *Tricoma* sp., *Latronema piraticum*, and *Choanolaimus* sp. that dominate the community, have a short, stout annulated body, especially adapted to the large interstitial spaces present. Ward (1975) found that the range of nematode lengths is greater in more heterogeneous sediments. Nematodes with very ornate cuticular ornamentation tended to be associated with coarser, silt-free sediments; it is suggested that this may be correlated both with their mode of locomotion and with the need for mechanical protection in unstable substrata.

A fine sand station in the Bay of Morlaix (English Channel) was examined by Boucher (1980a) during an annual cycle. The following species are important: *Richtersia kreisi*, *Calomicrolaimus monstrosus*, *Chromaspirina renaudae*, *Daptonema divertens*, *Actinonema celtica*, *Prochromadorella ditlevseni*, and *Dichromadora cucullata*.

Subtidal, very coarse sands, in a high energy environment were studied by Willems *et al.* (1982). The high abundance of Draconematoidea and Epsilonematidae is similar to the abundance of those taxa in beaches under strong hydrodynamical stress. No dominance of any feeding type indicates perhaps that this biotope is very heterogeneous and that nematodes occupy many niches. Wieser (1959) described genera confined to coarse sand; *e.g. Trefusia*, *Latronema*, *Campylaimus*, *Oxyonchus*, *Pomponema*, *Nudora*, *Bathylaimus*, and *Xyala*. The same genera are found in the fine sands of the sublittoral sandbank of the Belgian coast.

The occurrence of closely related nematode species with and without evidence of competition has been noted by Wieser (1960a), Ott (1972a), Boucher (1972, 1980a), and Juario (1975). It seems that microhabitats within a more general habitat will be occupied by closely related species or, conversely, if closely related species are found within one well-defined habitat, the segregation of the habitat into microhabitats is to be expected. Wieser (1960a) found two *Odontophora* species, *O. pugilator* and *O. papusi*, equally abundant in a sample area of 10 cm^2. The structure of the buccal plates of these two species is different which may reflect the adaptation to different food sources. Boucher (1972) proposed a competitive displacement of some species of *Sabatieria* in terms of vertical distribution. Juario (1975) found three very closely related dominant species in the upper 2 cm of sandy sediment: *Molgolaimus turgofrons*, *Aponema torosus*, and *Calomicrolaimus honestus*. These three species have the same structure of buccal cavity. It does not seem that these species are competing for limited food sources as they do coexist. Perhaps they actually feed on different kinds of food. Boucher (1980a) found five species of *Microlaimus s.l.* dominant in the same community.

Table V gives density and biomass values of some shallow subtidal areas. Muds and fine sands, with a large amount of silt, are the richest habitats in terms of nematode density; coarse sands and gravels have especially low density values, comparable with exposed sandy beaches. In most subtidal environments, nematodes represent 90–100% of the total meiofauna numbers and 50–100% of the total meiofauna biomass.

TABLE V

Nematode densities (ind.·10 cm^{-2}), biomass (mg dry wt·10 cm^{-2}) from shallow marine subtidal areas: sediment characteristics and species composition (Sp. comp., – not given in text, + given in text) also included

Reference	Locality	Sediment	Density	Biomass	Sp. comp
Wieser, 1960a	Buzzards Bay (U.S.A.)	silt–sand	1690–1860	0·1–0·6	+
McIntyre, 1964	N. North Sea	silt	1845	0·7–0·8	–
	W. Scotland coast	silt	853	0·7–1·6	–
Guille & Soyer, 1968	Mediterranean	silt	79	0·1–0·8	–
Stripp, 1969	German Bight of the North Sea	silt	788–884	0·8–3·1	–
Warwick & Buchanan, 1970	Northumberland coast (U.K.)	very fine sand	185	–	+
		fine sand	815	–	+
		silt	713	0·3–0·7	+
Soyer, 1971	Mediterranean	silt	400	1·0–1·4	–
Boucher, 1972	Mediterranean	silt	3665	3·8	+
McIntyre & Murison, 1973	Firemore Bay (U.K.)	fine sand	960–2765	0·5	–
Ward, 1973	Liverpool Bay (U.K.)	mud, sand	290–565	–	+
de Bovée & Soyer, 1974	Mediterranean	mud	4279	–	–
Lorenzen, 1974	German Bight of the North Sea	fine sand	530	–	+
		silty sand	2350	–	+
		silt	920	–	+
Juario, 1975	German Bight of the North Sea	very fine silty sand	3047–5261	0·6–1·3	+
Gray, 1976	River Tees estuary (U.K.)		393–1904	0·1–3·1	–
de Bovée & Soyer, 1977	Kerguelen Islands	mud/sand	138–3599	–	–
Tietjen, 1977	Long Island Sound (U.S.A.)	mud	530–2710	–	+
		muddy sand	560–1450	–	+
		fine sand	370–1650	–	+
		med. coarse sand	110–5010	–	+
Ito, 1978	Ishikari Bay (N. Japan)	sand	103–525	–	–
Heip *et al.*, 1979	North Sea	mud, sand	1650	1·0	–
Boucher, 1980a	Bay of Morlaix (France)	fine sand	1446–3432	–	+
Govaere *et al.*, 1980	North Sea	coast zone	1178	–	+
		transition zone	1423	–	+
		open sea zone	998	–	+
Nichols, 1980	E. Pacific (Peru)	sand	150–220	0·1–1·0	+
Tietjen, 1980a	New York Bight Apex (U.S.A.)	sand	221–1381	–	+
Willems *et al.*, 1982	North Sea	sand	58–1095	–	+

The correlation between sediment composition and trophic structure of the community has been studied by Wieser (1953, 1959), Hopper & Meyers (1967b), Tietjen (1969), Warwick & Buchanan (1970), Coull (1970), Boucher (1972, 1974, 1980a), Vitiello (1974), and Juario (1975). In general, they state that muddy sediments are dominated by non-selective deposit-feeders (50–60%) and that sandy bottoms are dominated by epistratum-feeders (50–60%); in most biotopes, selective deposit-feeders and omnivorous predators are numerically less important. A large number of selective deposit-feeders were found by Boucher (1980a) in sublittoral fine sand of the Bay of Morlaix (with important species of the Stilbonematidae) and by Willems *et al.* (1982) (mostly Epsilonematidae and Draconematoidea).

Warwick & Buchanan (1970), Heip & Decraemer (1974) and Juario (1975) found a correlation between diversity and sedimentological characteristics (silt-clay fraction and median grain size of the sand fraction). Tietjen (1977) found two basic faunistic units: a mud unit characterized by high species dominance, low species diversity (Shannon-Wiener diversity index, H', 1·00–2·00 bits/ind.) and low species endemism. The sand unit is characterized by low species dominance, high species diversity (H', 2·34–3·10 bits/ind.) and high species endemism. Same trends are found in medium and silty sands in the New York Bight Apex (Tietjen, 1980a). Willems *et al.* (1982) found very high diversities in the nematode communities in a sandbank in the Southern Bight of the North Sea (Brillouin diversity index, H, 3·30–4·60 bits/ind.); a high number of microhabitats may explain this high diversity.

DEEP SEA

Prior to 1960, no information was available on the abundance of meiofauna in the deep sea. Wieser (1960a), without having reliable data, postulated a decrease in meiofauna abundance with depth in a constant ratio to the already known decrease in macrofauna abundance. From that moment on, some effort has been made to gather quantitative data on the abundance of meiofauna in general and nematodes in particular. Table VI gives the density of nematode communities for the different deep-sea regions investigated. Densities range from a few to 1500 ind.·10 cm^{-2} and generally decrease with increasing depth. An extremely high density of 4000 ind.·10 cm^{-2} is found in the northeastern Atlantic near the Faeroes (Thiel, 1971).

Thiel (1979) discussed the abundance of meiofauna in the different deep-sea regions. In poor as well as in rich areas nematodes comprise between 85–95% of the meiofauna, when Foraminifera are excluded. Meiofauna densities are roughly three orders of magnitude higher and decrease slower with depth than macrofauna densities. The meiofauna gains in importance with increasing depth, community structure changes to smaller life forms (see also Thiel, 1975).

Contrary to Thiel's suggestions, Shirayama (1983) found in the western Pacific, that the rate of decrease in macrobenthic biomass was not significantly higher than that of meiobenthos. The size structure of the meiobenthic community (and nematode assemblages) examined by Shirayama (1983) was expressed by three indices: median size, sorting, and skewness. The correlation between median size of the nematodes and water depth was positive, which was thought to be related to the predominance of adults, a characteristic feature of deep-sea communities. The age structure of nematode communities

TABLE VI

Nematode densities (ind.·10 cm^{-2}), biomass (mg dwt·10 cm^{-2}) in deep sea communities, including species composition (Sp. comp., – not given in text, + given in text) and water depth (m)

Reference	Locality	Depth	Density	Biomass	Sp. comp.
Wigley & McIntyre, 1964	W. Atlantic, off New England	40–567	50–924	0·06–0·51	–
Thiel, 1971	N.E. Atlantic (Faroës)	290–2500	26–3999	0·08–1·78	–
Tietjen, 1971, 1976	W. Atlantic, N. Carolina (U.S.A.)	600–2500	32–140	–	+
Thiel, 1972a	N.E. Atlantic	250–2250	–	0·10–0·20	–
	North Sea (Spitsbergen)	750–3000	–	0·32–1·30	–
	W. Mediterranean	2500	600	–	–
Thiel, 1972b	N.E. Atlantic, Iberian deep sea	5271–5340	80–278	0·06–0·18	–
Dinet, 1973	S.E. Atlantic	1440–5170	294–961	–	–
Rachor, 1975	N.E. Atlantic	838–5510	6–187	0·001–0·023	–
Vitiello, 1976	W. Mediterranean	320–580	–	–	+
Coull *et al.*, 1977	W. Atlantic (N. Carolina, U.S.A.)	400	51–353	–	–
		800	280–942	–	–
		4000	4–60	–	–
Dinet & Vivier, 1977, 1979	Bay Biscayne	1920–4725	81–487	–	+
Vivier, 1978	W. Mediterranean	168–580	72–441	0·005–0·105	+
Dinet, 1979	N.E. Atlantic (Norwegian Sea)	2465–3709	9–1127	–	–
Shirayama, 1983	W. Pacific	2090–8260	31–1195	0·009–0·145	–
Soetaert, 1983	W. Mediterranean	175–1605	91–403	0·006–0·07	+
Rutgers *et al.*, 1984	Ibernian deep sea	4000–4800	101–989	0·008–0·028	–
Tietjen, 1984	Venezuela Basin	3517–5054	36–94	0·030–0·088	+

has only been studied by Vivier (1978) and Soetaert (1983) both in a Mediterranean transect from 168–580 m and from 175–1605 m, respectively. Vivier (1978) found between 43–65% juveniles and Soetaert (1983) found 48–61% juveniles in September. From these data it seems incorrect to assume that deep-sea nematode communities have a low frequency of juveniles, as hypothesized by Shirayama (1983).

The median size of nematodes is not controlled by the size of the interstitial space in the deeper clayey bottoms. In silty, shallow subtidal and intertidal environments, nematodes are longer than in coarse sandy sediments (*cf.* above). Soetaert (1983) found an opposite trend in the size structure of the nematode assemblage in relation to depth; nematodes are larger (5 times) in shallower areas (175 m) than in the deeper stations (from 305–1605 m). These last stations are more similar in species composition. On the basis of sediment granulometry, two station groups could be recognized, from 175–540 m and from 805–1605 m. It is obvious that sediment composition alone in this region is not responsible for the distribution of nematode species.

Only five studies from deep-sea environments are available in which species composition (mostly at generic level) and diversity of the nematode community are discussed: Tietjen (1976) in the Western Atlantic off North Carolina; Vivier (1978) in the Mediterranean off Marseilles; Dinet & Vivier (1979) from the Bay of Biscay (eastern Atlantic), Soetaert (1983) in the Mediterranean off Corsica, and Tietjen (1984) from the Venezuela Basin.

Tietjen (1976) recognized on a transect from 50–2500 m, four habitats. The upper sandy sediments (quartz-algal sands from 50–100 m and foraminiferan sands from 250–500 m) contain 35 and 17 species, respectively, mainly members of the Enoplidae, Ceramonematidae, Chromadoridae and Desmodoridae. The transition zone (500–800 m) consists of sandy silt with little species endemism. The lower part (800–2500 m) consists of clayey-silts with the highest number of stenotopic species, mainly members of the Leptosomatidae, Oxystominidae, Axonolaimidae, Leptolaimidae, Linhomoeidae, Siphonolaimidae, Sphaerolaimidae, and Comesomatidae.

Sabatieria stekhoveni, *S. conicauda*, *Sphaerolaimus uncinatus*, *Sabatieria pisinna*, *Acantholaimus spinicauda*, and *Sphaerolaimus paragracilis* are the dominant species of the nematode associations in the bathyal mud off Marseilles (Mediterranean), mostly members of the Chromadoridae, Comesomatidae, Sphaerolaimidae, and Monhysteridae (Vivier, 1978). Dinet & Vivier (1979) found the same families dominant in the Bay of Biscay, together with Oxystominidae, Desmoscolecidae, Microlaimidae, and Axonolaimidae. The following families are dominant in the deep sea off Corsica (Soetaert, 1983) (ordered in decreasing degree of abundance): Comesomatidae (mainly *Sabatieria*), Monhysteridae *s.l.*, Chromadoridae (mainly *Acantholaimus*, *Dichromadora*), Oxystominidae (mainly *Halalaimus* and *Oxystomina*), Selachinematidae (mainly *Richtersia*), and Leptolaimidae (mainly *Leptolaimus*) have an abundance of more than 5%. The 175 m sample is characterized by genera lacking in the deeper stations: *Odontophora*, *Spirinia*, and *Eubostrichus*.

The availability of food is very important for explaining the quantitative distribution of nematodes (and meiofauna in general) in the deep sea. Dinet (1979) found that proteins are correlated with meiofaunal densities while the organic matter is used by meiofauna; more precise analyses of the organic

compounds in sediments are necessary for a better understanding of the energy pathways in the abyssal environment. The energy flow most probably goes through bacteria and different other microorganisms as recently pointed out by Burnett (1973) (*i.e.* amoeba, sarcodines, sporozoans). Organic matter is recycled in the food web and partitioned in surface waters. It reaches the deep-sea bottom mostly in a refractory stage and as small-sized particles. The decreasing density of organisms limits resources for predators; only 6–16% of omnivorous predators are found in the Mediterranean communities (Soetaert, 1983). Deposit-feeding is predominant (35–56%); species with very small buccal cavities (mainly selective deposit-feeders) are important in the deep-sea environment (16–35%), contrary to most shallow subtidal silty areas. The occurrence of deep-sea nematodes without mouth or gut (Hope, 1977) suggests a direct assimilation of the dissolved organic matter.

Shirayama (1984) found close correlations between density of nematodes and factors of food conditions, *e.g.* surface productivity and organic carbon content of the sediment, but the calcium carbonate content of the sediment had the strongest influence on meiobenthic density. Besides indicating a large sedimentation rate, a high $CaCO_3$-content may increase interstitial space. Diversity in deep-sea clayey-silts is significantly higher than diversity in shallow-water clayey-silts. Environmental predictability is probably important in regulating diversity. The increasing diversity with depth is also confirmed by Dinet (1977) down to 4000 m, by Vivier (1978), by Soetaert (1983), and by Tietjen (1984). Tietjen (1984) found in an extensive investigation of the nematodes in the Venezuela Basin that the abundances of the nematodes are directly related to depth and geographic position; the distribution of the trophic types is similar to that found in many coastal regions. Even so, sediment heterogeneity and organic content are important in governing species diversity.

The deep sea is a rather stable environment. Waste disposal and mining for mineral resources have started recently; large-scale industrial operations could disturb this fragile ecosystem rather drastically. A better knowledge and understanding of the deep-sea ecosystems is urgently needed.

SPATIAL DISTRIBUTION

VERTICAL DISTRIBUTION IN THE SEDIMENT

The vertical distribution of meiofauna in general and nematodes in particular in sediments has attracted much attention since the development of the sulphide system concept (Fenchel & Riedl, 1970). As originally defined, this sulphide system is the anaerobic environment typically established under a cover of oxidized aerobic sediments; it occurs world-wide except along surf-stressed beaches and has been postulated to be the environment where early metazoan evolution took place. This sulphide biome or thiobios, as it was subsequently renamed by Boaden & Platt (1971) is bounded at its top by the redox discontinuity layer where oxidized processes become replaced by reducing processes. The RPD layer is sharply defined in protected beaches and occurs there to within a few mm of the sediment surface. Values of the redox potential drop from $+400$ mV to -50 and -250 mV. The lower limits of the sulphide system can reach metres down and correspond to the deeper burial

stage, defined by the termination of bacterial activity and accumulation of poisonous compounds, close to the H_2O/H_2 fence where partial pressure of H_2 reaches 1 atm (Fenchel & Riedl, 1970).

The Metazoa in this system are represented nearly exclusively by the Platyhelminthes (Turbellaria and Gnathostomulida) and the Aschelminthes (mainly Nematoda, although some Gastrotricha and Rotatoria occur). Nematodes extend farthest down into the sulphide system and often have population densities of 1000 ind.·10 cm^{-2} in the system.

This concept of thiobios has recently come under discussion since Reise & Ax (1979) demonstrated that most of the so-called thiobiotic meiofauna occurred consistently in greater numbers near oxygen islands in the anaerobic environment. These oxygen islands are formed around the burrows of macrofaunal animals, such as large polychaetes, nemertines, and amphipods on tidal flats or large decapods in deeper water.

The paper of Reise & Ax (1979) can serve to demonstrate the typical vertical distribution of nematodes on intertidal sand-flats. On this *Arenicola*-flat the colour of the sediment changes abruptly from brown (due to hydrous ferric oxides) in the upper layers to black (due to the presence of FeS) at a depth of 5 mm in summer and 20 mm in autumn. At greater depths, the sediment colour changes again to grey, due to pyrite sulphur FeS_2. In summer, away from the *Arenicola*-burrows about 66% of the meiofauna (82% without the nematodes) occurred above 6 to 8 mm depth. All meiofauna, except for a few nematodes, in the black zone were restricted to its upper fringe and did not occur below 50 mm depth. In autumn the sand turned black at a depth of 17 mm and nematode abundance was highest at 2–3 cm depth.

In the vicinity of the *Arenicola*-burrows the vertical distribution of the meiofauna changed entirely (Fig. 8). Alongside the burrows meiofaunal abundance was much higher than in the surrounding sediments and nematodes, in particular, were ten times more abundant. At 5–15 cm depth away from burrows, the average abundance of nematodes was only 39·10 cm^{-3}.

In salt marshes in Louisiana, nematodes occur in greatest density in the upper 2 cm of the sediment (Sikora & Sikora, 1982), and disappear nearly completely below 6 cm. Oxygen is completely (?) absent below 0·5 cm. Sikora & Sikora (1982) make a good point when remarking that below a redox potential of +350 mV there is no free oxygen, and that the dark zone in many sediments is the zone (125 mV) where ferric iron is reduced to ferrous iron, not the dividing line between oxic and anoxic sediments.

That nematodes do occur in greatest numbers close to the surface has been demonstrated in many studies, but in shallow waters there are often subsurface maxima as well. Tietjen (1969) demonstrated clear seasonal changes in fine shallow subtidal sands, where in spring most individuals were concentrated in the top centimetre whereas they occurred deeper in autumn, despite the fact that the RPD layer did not change position. Only in coarse sands do nematodes remain most abundant in the top layer. Skoolmun & Gerlach (1971) also found relatively high numbers of nematodes in the deeper layers of intertidal fine sands in the Weser estuary in Germany, especially in winter when most nematodes occurred in the 5–8 cm layer (sample depth was 8 cm). Even in spring, when maximum density was reached, still 20% of the nematodes was found beneath 5 cm depth.

Seasonal changes in vertical distribution were also observed by Platt

(1977b) on a fine sand beach in Northern Ireland. In this situation, the RPD layer changed position and the seasonal variation of penetration depth of the nematodes was correlated with this. In Platt's study, species were distinguished. Fifty-three percent of them were virtually restricted to the top centimetre while another 40% had their maximum abundance there but penetrated deeper. Only 7% of the species had their maximum abundance below the top centimetre layer. There was also a change in feeding types, the surface layer comprising about 30% epigrowth-feeders whereas the next centimetre only had 17% epigrowth-feeders, this percentage increasing again in deeper layers with a corresponding decrease in deposit-feeders. The deeper occurring genera were *Microlaimus*, *Monoposthia*, *Paracanthonchus* and *Pomponema* whereas the surface epigrowth-feeders were mainly Chromadoridae, and it may be that the feeding behaviour of these groups are different.

The nematode fauna of the intertidal area studied by Reise & Ax (1979) was analysed by Blome (unpubl.) who found that of 70 species present, 31 were found in the oxic surface sediments, 29 were mainly there but extended into the suboxic zone and only 8 species were found exclusively in the black suboxic sediment layers. In another study (Blome, 1983) on the island of Sylt, clear seasonal changes in vertical distribution were observed with deeper penetration in winter. *Theristus pertenuis*, where it was most abundant, had maximum densities in the 5 to 10-cm layer and in the 10 to 15-cm layer its abundance was nearly ten times higher than at the sediment surface. *Paracanthonchus caecus* had the same vertical extension at the same station in October and occurred consistently with large numbers even below 20 cm in

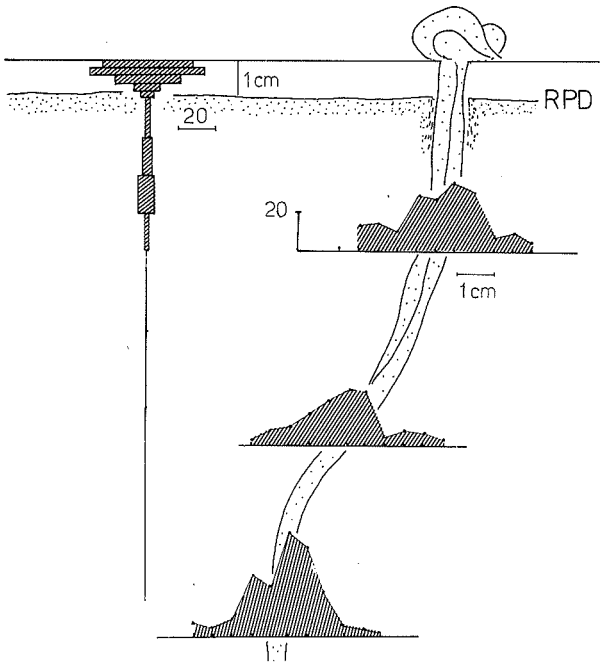

Fig. 8.—Distribution of meiofauna in the vicinity of *Arenicola*-burrows: scale bar is 20 ind.·1 cm^{-3}; data are from Reise & Ax (1979).

January. *Odontophora setosa* was even completely absent from the top 5 cm in that month.

Blome's (1983) paper clearly demonstrates the deep penetration of certain nematode species on intertidal sand-flats, but for nematodes in general this has been known for a long time; *e.g.* McLachlan (1977) reports nematodes 140 cm deep in the sand. Even in shallow subtidal sands the penetration depth may be high. McLachlan, Winter & Botha (1977) used long cores along four transects from 5 to 30 m depth in medium to fine sands off Algoa Bay, South Africa, and found meiofauna abundant to at least 35 cm down in the sediment. Oxygen was present at this depth (about 7% saturation) because in this area wave energy is important. In a stagnant marine lake in the Netherlands, Heip, Willems & Goossens (1975) found nematodes to at least 25 cm depth in a sandy station, but here also oxygen was present. In 1977 and 1978 the RPD layer, however, moved up from −20 cm to −2 cm with a concurrent compression of the nematodes in the surface layer, although significant numbers remained present in the deeper layers (Willems, Sharma, Heip & Sandee, in press).

In deeper waters, penetration of nematodes into the sediment diminishes. In mud stations off the Belgian coast, 93–99% of the nematodes were found in the upper 4 cm, but in a sandy station penetration was much deeper and maximum density was found between 6 and 10 cm (Heip *et al.*, 1979). Boucher (1980a) found most nematodes in the surface layers of a subtidal (−19 m) fine sand in Brittany in spring (59% in the upper 2 cm) and summer (51%), but in autumn and winter nematodes migrated down; only 42% was present in the upper 2 cm in autumn, only 13% in winter. In spring and summer, subsurface secondary maxima were found around 5–10 cm depth. Seven out of the 17 dominant species showed seasonal variations in their depth distribution; six out of 40 species were restricted to the deeper layers.

At depths around 100 m in the North Sea, nematodes remain important to at least 10 cm depth in the sediment (Heip *et al.*, 1979; Faubel, Hartwig & Thiel, 1983). The same is true in deep-sea sediments. Coull *et al.* (1977) found nematodes evenly distributed through the first 6 cm at 400 m depth, with a surface maximum at 800 m depth and a subsurface maximum between 2–3 cm at 4000 m depth. Vivier (1978) found Araeolaimidae, Desmodorida, and Desmoscolecida living in the surface layers, together with Enoplida (especially Oxystominidae), Chromadoridae, Cyatholaimidae, and Choanolaimidae. The Comesomatidae were present in all layers of the fluid red muds studied (168–580 m).

The vertical distribution of nematodes in twelve bathyal to hadal stations in the western Pacific was studied by Shirayama (1984). Meiofauna was most abundant in the top centimetre and declined exponentially with depth in the sediment. At seven stations no organisms were found beneath 12 cm, but at one station nematodes together with rhizopods were found as deep as 30 cm. A surface maximum for meiofauna was also found by Soetaert (1983) in five stations from 350–1600 m in the Mediterranean and by Rutgers van der Loeff & Lavaleye (1984) in the Iberian Deep Sea.

VERTICAL MIGRATION AND HORIZONTAL DISPERSAL

Tidally induced vertical and horizontal displacements have been observed by Rieger & Ott (1971) in the Adriatic Sea near Venice. Four nematode species

showed clear changes in distribution over a tidal cycle. *Daptonema leviculum* migrated upwards at high tide and downwards at low tide while *Microlaimus criminalis* had just the opposite behaviour. Two other monohysteroid species (*Theristus pictus* and *Daptonema curvispiculum*) are periodically concentrated and dispersed again by the shifting sands, moving towards the high water line during flood.

Gerlach (1977b) summarizes the few data existing on meiofauna dispersal. Drifting materials, such as driftwood, coconuts, ice and algae may transport meiofauna over long distances. The ballast of sailing vessels mainly consisted of heavy material such as stones and sand, and much material was transported in this way across the oceans.

Nematodes are frequently found in plankton samples in shallow waters (Gerlach, 1977b; Hagerman & Rieger, 1981). Sibert (1981) found nematodes in the water column to be most abundant just above the sediment–water interface; at 5 cm they were two to five times more abundant than at 30 cm above the bottom. Chandler & Fleeger (1983) found that nematodes colonize defaunated sediments either *via* the water column or *via* the sediment, but that even after 29 days their densities were less than in the surrounding sediment.

That nematodes can swim has been observed in cultures (*e.g.*, Jensen, 1981b) but it must be much more common in the field than is generally thought. Gerlach (1977b) cites Schneider who found many females of the nematode *Tripyla* in the gut of the pelagic plankton-feeding fish *Coregonus* and postulates that ripe females of this nematode swim up into the water column to spawn. Quite the opposite happens in the viviparous species *Anoplostoma viviparum*, where ripe females migrate down in the sediment to the anoxic layers before spawning; then the hatched juveniles migrate to the flocculent layer and are dispersed by water currents (Surey-Gent, 1981).

Colonization by nematodes after disturbances may take anything from hours to years, depending on the environment and the kind of disturbance. Sherman & Coull (1980) disturbed a 9 m^2 area of intertidal mud-flat by hand-turning. Total nematode density was restored after only one tidal cycle. Two *Ptycholaimellus* species had significant lower densities the night after the disturbance was created, which may indicate migration. Re-population was thus very quick and may have occurred mainly by advection *via* the flocculent layer. Other recolonization rates reported for meiofauna are much lower, of the order of months (Coull, 1969) and even years (Pequegnat, 1975; Rogers, 1976).

A particular example of a natural disturbance are the pits created by stingrays (*Dasyatis sabina*) in shallow subtidal sands at night. These pits have been studied by Sherman, Reidenauer, Thistle & Meeter (1983) who found reduced nematode densities until three days after the formation of the pit. No single species seemed to exploit the disturbance better than others during recolonization, which was ascribed to the fact that nematodes lack sufficient dispersal capability to arrive quickly at newly opened space, although 48 h after the pits had been made re-population was effective.

By studying the recolonization of tube-caps of the polychaete *Diopatra cuprea*, Bell & Coen (1982) found rapid recolonization by nematodes through the water column and *via* the sediments.

SPATIAL PATTERN

The small-scale spatial distribution or pattern of populations has received considerable attention since space has been recognized as one of the important niche dimensions along which species segregate (*e.g.* Schoener, 1974). In general, three types of pattern are distinguished: regular, random, and aggregated. In benthos studies, as in much terrestrial work, only the two-dimensional horizontal plane is considered. To discriminate these types many authors use the variance/mean ratio $s^2/\bar{x}$ or some measure derived from it such as $(n-1)s^2/\bar{x}$, distributed as χ^2, or the index of clumping $s^2/\bar{x}-1$ (David & Moore, 1954). Discrimination is based on the fact that a Poisson distribution, describing the occurrence of rare, random events, is completely determined by only one parameter since $s^2 = \bar{x}$. When for a given species $s^2/\bar{x} = 1$, its spatial pattern is considered random; when $s^2/\bar{x} > 1$, the pattern is aggregated. Based on such measures nematodes have generally been found to be aggregated (Vitiello, 1968; Gray & Rieger, 1971; Arlt, 1973; Gerlach, 1977a).

There are, however, some problems with this approach. Basically, spatial pattern is a property of populations, not of communities or taxocenes. Other statistical distributions, such as the binomial and normal, also describe the occurrence of random events but without the restriction that the event (presence or absence) must be rare. Empirically it has been found that the variance is often a function of the mean, as in Taylor's power law $s^2 = a\bar{x}^b$ (Taylor, 1961). Since b is often near to two, the variance/mean ratio is often a linear function of the mean $s^2/\bar{x} = a\bar{x}$ and the coefficient of variation $s/\bar{x}$ is often constant (Heip, 1975), at least for $\bar{x}$ large enough. For these reasons the $s^2/\bar{x}$ ratio is of only limited usefulness.

Detailed studies of spatial patterns of marine nematodes are rare. Olsson & Eriksson (1974) studied horizontal distribution of the meiofauna from the Swedish west coast at a depth of 22 m on a clayey bottom. A contiguous grid with cells of 9·3 cm^2 surface was used for subsampling a box corer on deck. For nematodes two adjacent patches with high density were observed on a scale of about 10 cm. The coefficient of variation $s/\bar{x}$ was 0·515 and the number of samples required to detect a 20% difference in means with 95% confidence was estimated as seven. Findlay (1981) studied a mud and a sand station using four different core sizes to sample approximately the same surface area. There was a marked influence of core size but nematodes were only slightly aggregated with the highest values of the index used (Green's index of dispersion $(s^2/\bar{x}-1)/(N-1)$ with N the total number of individuals) at a core size of 5 cm^2 in the mud station and the sand station in February, but no aggregation at all in the sand station in September. These data relate to the total density of the nematode taxocene and the significance of the weak departure from randomness at 5 cm^2 core size is unclear.

Samples taken at the sand site in February with drinking straws were re-analysed in a second paper (Findlay, 1982b). Eighty-one drinking straws in a 9×9 array were taken covering an area of 0·02 m^2 (15×15 cm). From these densities a contour map was drawn which was then sampled by simulation with three different core sizes. Each sampling scheme had the same efficiency for estimating the original abundance, indicating that sampling scale has a negligible effect on abundance estimates. Larger scale sampling schemes tended, however, to obscure the heterogeneity of the distribution. Larger

numbers of smaller cores gave a better resolution of the pattern and Findlay (1982b) concludes that roughly fifty 0·5 to 1·0-cm^2 cores is a reasonable optimum sampling scheme for intra-community research on spatial pattern.

Hogue & Miller (1981) also studied total nematode density but in a system with macroscopic heterogeneity, a sand-flat with ripples. Using autocorrelation they demonstrated that a significant periodicity in density existed at the wavelength of the ripple crests. This is unexpected, since organic material concentrates in the troughs, but it was thought that this material is buried, after drying, by the moving sediments so that after several tidal cycles it would be under the crests. Of course this requires that ripples would move over distances equal to half the wave length. Also, samples were taken at low tide and the pattern may change over a tidal cycle, and only to 4 cm depth, and the nematodes may have been deeper.

In a study of sandy sediments on the coast of Oregon, U.S.A., Hogue (1982) took 72 straw samples in two parallel transects 3 cm apart from a box corer at a station with water depth 28 m. Neighbouring samples were correlated over distances of approximately 2–3 cm and there was no periodicity in density flucuations, *i.e.* aggregations were not spaced at constant intervals. The two transects were also correlated, so that the physical dimensions of patches of high density were estimated to be about 3 cm in size.

Using 1·9 cm cores, the pattern of 21 dominant species of the same site was also studied. For all species, the index of dispersion indicated aggregation in May, but in January only five out of eleven superficially occurring species were aggregated, although total density had a very high value for the index of dispersion. Another interesting result of Hogue's (1982) study was that the dominant species were not correlated spatially, they occurred independently. This, and the predominantly random distribution of nematodes in winter, points to biological factors such as food availability and reproductive processes as the most likely cause for small-scale patchiness in marine nematodes (Hogue, 1982).

Similar conclusions were reached by Delmotte (1975) in a study of a 10-cm deep brackish water pond in Belgium. He studied spatial pattern of nematodes from a 7 × 7 grid of 0·8-cm^2 cores, each core 5 cm apart, in summer. All species were aggregated and their frequency distribution could, but for two species, be fitted with the negative binomial distribution. Most species were distributed independently, and juveniles tended to co-occur with adults of the same species.

These few existing studies on small-scale horizontal distribution tend to agree that patches exist on a scale of centimetres and that species tend to be distributed independently. The consequence is that a large number of small samples are required to study spatial pattern but also that a small number of large samples may give good estimates of density. If indeed patch size would be as small as 2–3 cm one can expect that 6 cm diameter cores will already be reliable for this purpose.

LARGER HORIZONTAL SCALES

The studies of Delmotte (1975), Findlay (1981, 1982b), and Hogue (1982) indicate that important variability exists on the scale of a few centimetres. Variability on a larger scale seems to be much less important, except when

strong gradients exist, as on beaches (Platt, 1977b; Blome, 1983). Again Hogue's (1982) study is very illustrative of this point. He compared the data from three cores taken within three quadrants (10 cm scale) of a box corer (25 cm scale) at three stations 30 m apart. Only about one-quarter of the total variance was due to between-boxes differences and this difference was even only 9% when species living in the first 5 cm of the sediment were considered. For these species, 67% of the variance occurred within quadrants (10 cm scale) and 24% between quadrants (25 cm scale).

When six stations were compared (km scale), it was found that only 40% of the variance was due to between-station differences, even though two distinct communities could be discerned. The same was found by Heip *et al.* (1979) for eighteen stations covering an area of nearly 1000 km^2 in the Southern Bight of the North Sea.

Variability on a scale larger than the nematode patches may, however, exist when environmental gradients exist or where disturbance is common. Powell, Bright, Woods & Gitting (1983) studied the meiofauna from a very interesting and uncommon system, the East Flower Garden Brine Seep. This consists of a brine seep at 72 m depth in the Gulf of Mexico. The brine, rich in sulphide, flows by gravity into a basin located about 60 m from the bank's edge into a brine lake. The overflow from that lake flows into a 96-m deep canyon. Nematodes were absent from the brine lake and occurred only in low abundance in most stations: between 2–75·10 cm^{-2} in the stations closest to the brine lake where sulphide concentrations were in the range of 60–80 μg-at.$\cdot l^{-1}$. Then a big peak occurred, together with an even bigger and remarkable peak in the density of gnathostomulids, at a station where sulphide remained high and oxygen was even lower than in the previous station of the brine seep. At stations further from the brine lake, nematode density dropped again despite the fact that oxygen levels increased and sulphide decreased. Why this is so was not explained, although an abundant bacterial growth at this interface between 'thiobiotic' and 'oxybiotic' conditions is to be expected.

LIFE CYCLES

SEASONAL CYCLES

Yearly fluctuations in nematode density and/or species composition have been studied by a number of authors but sampling is in most cases with a low temporal resolution and in some cases not really quantitative. Data exist for the Baltic (Arlt, 1973; Arlt & Holtfreter, 1975; Möller, Brenning & Arlt, 1976), the Swedish west coast (Nyholm & Olsson, 1973), intertidal or brackish water areas along the North Sea (Skoolmun & Gerlach, 1971; Smol, Heip & Govaert, 1980; Bouwman, Romeyn & Admiraal, in press), subtidal areas of the North Sea (Warwick & Buchanan, 1971; Lorenzen, 1974; Juario, 1975), intertidal (Harris, 1972), and subtidal (Boucher, 1980a) areas of the English Channel, the Scottish west coast (McIntyre & Murison, 1973), the western Mediterranean (Soyer, 1971; de Bovée & Soyer, 1974); estuaries (Tietjen, 1969), salt marshes (Coull & Bell, 1979), and sea-grass communities (Hopper & Meyers, 1967b) along the U.S. east coast and some information from the Canadian west coast (Sharma & Webster, 1983).

Skoolmun & Gerlach (1971) studied an intertidal sand-flat in the Weser estuary in Germany. Total density of nematodes, which was very low overall, had a clear peak in May–June and another high value in October. The dominant species had different density patterns: *Hypodontolaimus setosus* had a peak in summer, *Tripyloides marinus*, *Sabatieria vulgaris*, and *Chromadorita tentabunda* had a peak in winter or spring. Two *Theristus* species and *Enoploides spiculohamatus* had several peaks over the year whereas *Viscosia viscosa* and *Oncholaimus brachycercus* had two abundance peaks and may have two generations annually.

Another oncholaimid, *O. oxyuris*, has been studied over several years in a brackish water pond in Belgium (Smol *et al.*, 1980). This species has either two generations annually or two generations in three years, in a strange pattern in which overwintering juveniles belong to two different generations. Large juveniles become adult in spring and produce a second generation in late summer whose offspring overwinter as small juveniles. Small overwintering juveniles become adult in summer and their offspring overwinters as large juveniles.

The Ems-Dollard estuary, on the Dutch–German border, has been studied by Bouwman *et al.* (1983). The Dollard receives a heavy load of organic matter in autumn. Maximum abundance in two stations on a transect near the outfall reached a peak in June, whereas maximum abundance in the third station, further from the outfall, was reached in August. In the first station, closest to the outfall, a second peak was reached in September. Maximum density reached was highest in the intermediate station (close to 19×10^6 ind.$\cdot$m^{-2}) and lowest in the far station (close to 10×10^6 ind.$\cdot$m^{-2}), but the number of species was highest there (between 12 and 20 compared with between 6 and 10). The whole transect had 27 species, with only two dominants near the outfall: *Eudiplogaster pararmatus* and *Dichromadora geophila*, whereas the far station was dominated by *Sabatieria pulchra*, *Ptycholaimellus ponticus*, and *Leptolaimus papilliger*. Similarity between samples from different months was almost as high as between replicates, but significant changes in the nematode community structure took place in spring at the three stations. At this time the density of all the dominant species increased.

Eudiplogaster pararmatus appeared to reproduce all through the year, gravid females and juveniles being always present. *Dichromadora geophila*, however, had only juveniles from April to August and they had a conspicuous peak in May, so that reproduction appears to be restricted to a short period in spring. *Ptycholaimellus ponticus* started reproduction in spring and continued to reproduce during the whole summer. *Leptolaimus papilliger* seemed to reproduce continuously, although more gravid females were present in summer. *Sabatieria pulchra* also had continuous reproduction and juveniles dominated in all seasons. Spring and summer peaks in nematode density in intertidal habitats have also been found by Harris (1972) in a beach in Cornwall, but Schmidt (1969) observed no distinct peaks in Sylt (Germany).

A very thorough analysis of nematode fluctuations on a flatfish nursery ground on the Scottish west coast (McIntyre & Murison, 1973) from monthly samples over seven years taken near M.L.W.N. shows that on average there is a peak in June and another in August. Lowest densities were reached in January, and the average February value was slightly higher than the

subsequent March value, but whether a third peak occurs in late winter is uncertain. Statistically, the winter values are lower than the densities from May onwards. At 6 m depth subtidally on the same beach annual fluctuations were much smaller, with a peak in July and another one in January.

Temperature and food are the most obvious factors explaining these density changes. As nematodes belong to different feeding types, one expects changes correlated with the availability of different food items. This has been observed in two shallow estuaries in New England by Tietjen (1969). In these estuaries again one or two annual peaks in density were observed, a spring peak in April–May and a summer peak in July–August. The spring peak was due to an increase in epigrowth-feeders, mostly *Nudora lineata*, *Tripyloides gracilis*, *Spirinia parasitifera*, *Monoposthia costata*, two *Chromadora*, and six *Hypodontolaimus* species. All these species declined rapidly after the summer, maybe due to predation by juvenile polychaetes. A summer increase for *Hypodontolaimus* sp. and *Spirinia parasitifera* was also observed by Hopper & Meyers (1967b) for sea-grass beds in Florida and Wieser & Kanwisher (1961) found increased numbers of *S. parasitifera* in June when compared with November in a salt marsh near Woods Hole.

Deposit-feeders and omnivorous predators did not exhibit such marked seasonal variations in density, but deposit-feeders tended to reach maximum numbers in fall (autumn), winter or early spring, due to the incorporation of dead *Zostera* leaves and other vegetation into the sediment. This incorporation coincided with peaks of *Paralinhomoeus*, *Theristus*, *Paramonhystera*, and *Sabatieria*. Oncholaimids were the dominant omnivorous predators and their seasonal distribution closely followed that of the deposit-feeders.

The seasonal cycles of nematodes on algae have been studied by Warwick (1977) for red algae on the Scilly Isles, by Kito (1982) for the fauna on *Sargassum confusum*, and by Trotter & Webster (1983) for the fauna on *Macrocystis integrifolia*. On this last algae, only three species of nematodes accounted for more than 90% of the fauna. They occurred in all months, but *Prochromadorella neapolitana* peaked in summer, when epiphytic diatoms were abundant, and *Monhystera refringens* peaked from July till October; *M. disjuncta* was relatively common throughout the year. All species occurred in greatest abundance on the lower and middle blades of *Macrocystis* in the deep end of the kelp bed.

The nematodes from *Sargassum confusum* show two peaks in population density, one in September and one in May. Three out of four dominant species had both peaks, whereas *Chromadora heterostomata* had only the spring peak. Gravid females and juveniles occurred in all months, except for *C. heterostomata* which was absent from August to October. Of the five most abundant nematodes from algae on the Scilly Isles (Warwick, 1977), *Oncholaimus dujardinii* has peak dominance in spring and early summer, and then makes up for nearly 80% of the total nematode density, *Theristus acer* has a similar though somewhat more irregular pattern, while *Symplocostoma tenuicolle*, *Euchromadora striata*, and *Cyatholaimus gracilis* have peaks in late summer and winter. These peaks, however, relate to relative dominance; absolute densities in the algae are not known.

The reproductive cycle of *Leptosomatum bacillatum*, a nematode living in sponges, was studied at Texel, The Netherlands, by Bongers (1983), where it lives in *Halichondria panicea*. It has an annual life cycle with small juveniles

appearing in July and growing slowly over the winter, the first becoming adult near March.

Whereas spring and summer peaks appear to be common in intertidal and shallow subtidal areas on an annual basis, little is known on long-term temporal variability. Two density peaks were found in two subsequent years by Harris (1972) at the same time of the year but with different heights. McIntyre & Murison (1973) compared mean spring densities over seven years and found differences of about 5:1, the minimum value being 328 ind.·10 cm^{-2} in 1970 and the maximum value 1767 ind.·10 cm^{-2} in 1969. Coull & Bell (1979) describe the density fluctuations from monthly samples from 1972 to 1977 in a shallow subtidal muddy creek, and demonstrated important variations from year to year: from 1972 to 1974 maximum densities were around 700–800 ind.·10 cm^{-2}, from 1975 to 1976 two years with maximum densities around 3500 ind.·10 cm^{-2} followed, while in 1977 maximum density was around 1500 ind.·10 cm^{-2}.

Whereas seasonal and annual variation in nematode density are important in intertidal or shallow subtidal estuarine areas, this is much less the case for subtidal marine areas. Here nematode populations appear to be much more stable. In the German Bight, two studies exist (Lorenzen, 1974; Juario, 1975). In a fine sand station in a TiO_2 dumping ground a summer maximum around August and a spring maximum around May were found and an exceptionally high value in December, but summer densities were statistically not different from winter densities. Dominance of most nematode species did not change appreciably over the year but some species had higher dominance in summer (*Daptonema leviculum*, *Metadesmolaimus heteroclitus*, and *Axonolaimus helgolandicus*). Juveniles made up 50% of the community over the whole year, but for several species an increase in reproduction could be established; *A. helgolandicus*, *Metadesmolaimus heteroclitus*, *Mesacanthion diplechma*, *Paracyatholaimus pentodon* and *Paracanthonchus caecus* all had a maxima in reproductive activity in spring. *Mesacanthion diplechma* only occurred in June to July as mature adults and probably has only one generation annually. This is a large species and related to *Enoplus communis*, which also has only one generation annually (Wieser & Kanwisher, 1960). The other species all had adults and juveniles present throughout the year.

The station studied by Juario (1975) at 35-m depth in the German Bight of the North Sea had maximum nematode densities in April and August, but winter values were not significantly different from summer values and there was no change in the relative abundance of feeding types. The most abundant species, *Molgolaimus turgofrons*, had continuous reproduction throughout the year, and this was also true for all 11 dominant species. Juveniles were found in high densities all over the year. Species composition of the nematode assemblage remained very stable.

Nearly the same features have been observed by Warwick & Buchanan (1971) at an 80-m deep station off the Northumberland coast in the North Sea; there were no significant changes in population structure (juveniles being always dominant), species composition, density and biomass of the nematodes during the year. Boucher (1980a) again came to the same conclusions for the nematodes in a 19-m deep fine sand in the Bay of Morlaix in Brittany. Density variations over one year were not significant when either the four seasons or summer–winter were compared. Only three species out of 67 had significant

seasonal fluctuations: *Prochromadorella ditlevseni*, *Actinonema celtica*, and *Theristus bastiani*. Juveniles again were abundant in all seasons and formed a constant proportion of the population. Gravid females were, in general, more abundant in spring and maturing females more in autumn.

In the deeper waters of the North Sea, however, Faubel, Hartwig & Thiel (1983) found peaks in nematode density in March at one station (134 m) and in December when all stations were averaged. In this area bottom water temperature is highest in December due to the influx of Atlantic water.

In the western Mediterranean seasonal changes in density have been studied by Soyer (1971) and de Bovée & Soyer (1974). At a 35-m deep station, there was a clear summer peak in August in 1964 but it was much retarded, in October, in 1965, and earlier, in July, in 1966. This was related to water temperature and the persistence of warm water masses in the area. These seasonal changes disappeared in deeper water; from 75 m to 550 m the average abundance was the same in the four seasons.

LABORATORY STUDIES

Most laboratory studies on life cycles of marine nematodes have focused on the effect of temperature and/or salinity on development. In these studies either embryonic development or generation time have been used with different meanings, which makes comparison difficult. For example, generation time was measured as the time between first egg deposition in successive generations (Gerlach & Schrage, 1971; Tietjen & Lee, 1972, 1973; Warwick, 1981a); as the time between the appearance of gravid females in successive generations (Vranken, Thielemans, Heip & Vandycke, 1981); the experiment sometimes starts with gravid females or eggs and runs until either the first gravid female or egg is detected or until 50% of the daughters become gravid or 50% of the eggs hatch. In any case, all these definitions are only approximations of the mean generation time, and for fast-developing, iteroparous species these time periods are approximations of the development time or minimum generation time T_{min} (Vranken & Heip, 1983). In the rest of this paper we will, unless otherwise stated, only refer to minimum generation time or development time T_{min}.

Development times of marine nematodes may vary between a few days for the rhabditids and several months for the large oncholaimids. In the earlier papers, generation times of approximately one month have been reported for several monhysterids and chromadorids (Chitwood & Murphy, 1964; Hopper & Meyers, 1966a; Tietjen, 1967; von Thun, 1968). We now know that some of these species have been grown suboptimally, resulting in too long generation times; *e.g.* for *Monhystera disjuncta*, Chitwood & Murphy (1964) found T_{min} = 30 days at 22 °C, whereas Gerlach & Schrage (1971) found T_{min} = 12 days at 17–22 °C.

The effect of body weight

An important generalization relating development time with body mass of the species states that small species will have short life cycles, large species mature later and have longer life cycles. This has been shown true for many animal groups (Fenchel, 1974; Steele & Steele, 1975; McLaren, 1966). For the

meiofauna, especially for nematodes and harpacticoids, an inverse relationship between P/B and adult body weight was postulated by Banse & Mosher (1980) and demonstrated by Heip, Herman & Coomans (1982). When life-cycle turnover is constant, this relationship may be reduced to a relationship between the annual number of generations and body weight, and it is then evident that a relationship between development time and body weight should exist. One complication arises because reproductive activity is limited by temperature: at the low end of the range the basal temperature or biological zero T_0, below which no reproduction occurs and at the other, the upper temperature limit (see Wieser, 1975).

In general, a direct relationship between development time and biomass (weight) is to be expected. We have checked this using all published data on generation time and added unpublished results from Vranken and co-workers. The relationship between minimum generation time T_{min} at 20 °C and biomass (dry weight) is given in Figure 9. The different corrections made are

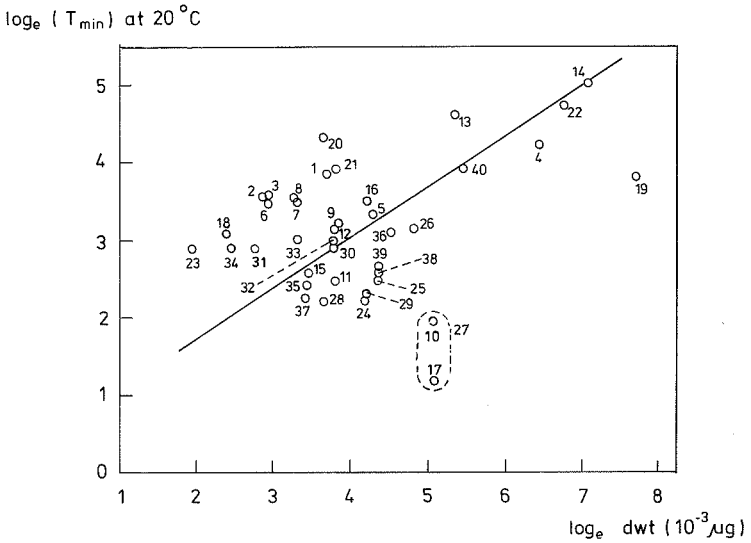

Fig. 9.—Relationship between T_{min} at 20 °C and dry weight at the moment of maturation: corrections to 20 °C were made, using Krogh's normal curve or by equation $T_{min} = aT^b$; code numbers of the species are listed in Tables VII and VIII; 30 is *Chromadorina germanica*; 31, 32, 33, and 34 are consecutively *Monhystera* sp.; *Atrochromadora denticulata*, *Monhystera parva* and *M. multisetosa* (Garcia, 1982); dry weight is 15% of wet weight, which was estimated with Andrássy's formula using a combination of the smallest length and width of a data-set; most morphometric data are from the original experimental papers; the others are from De Coninck & Schuurmans Stekhoven (1933) for 22, 35, 37, and 40; Schuurmans Stekhoven (1935) for 3; Chitwood (1951) for 18; Gerlach (1951) for 21; Timm (1952) for 15; Hopper & Meyers (1967b) for 16 and 30; Lorenzen (1969) for 20; Boucher (1976) for 36; Platt & Warwick (1983) for 19; Herman, Vranken & Heip (1984) for 28; from growth curves (Vranken, pers. obs.) for 23, 27, 29, and 38.

summarized beneath the figure, the coded species in Tables VII and VIII. There exists a weak but significant correlation ($r = 0{\cdot}338$, $0{\cdot}05 > P > 0{\cdot}01$; $n = 40$) between body weight and generation time. There is, however, substantial scatter around the line, calculated by GM-regression (model II, Sokal & Rohlf, 1981) as $\log_e T_{min}$ (days) $= 0{\cdot}430 + 0{\cdot}651 \log_e$ dry wt (10^{-3} μg) (95% CI slope = 0·450–0·853). Part of this scatter can be attributed to the following factors: (a) suboptimal cultivation, resulting in an over-estimate of T_{min} (species 1, 2, 3, 9, and 33); (b) differences in acceleration rate and basal temperature between species inhabiting different climates (species 18, 19, 20 *versus* the others); and (c) the nature of the temperature response of extreme opportunists (species 10, 17, 23, and 27).

To illustrate: *Monhystrella parelegantula* (23) has a very high basal temperature $T_0 = 14$ °C, hence the effective temperature for this species at 20 °C is only 6 °C. Such an increase is not high enough to arrive at $T_{min} = 5{\cdot}5$ days, as predicted by the general equation, even though the species has a very high $-b = 3{\cdot}11$.

The warm-water species cultivated by Hopper, Fell & Cefalu (1973) also have very high basal temperatures (around 12–15 °C) and also a high $-b > 2$, but the effective temperature of 20 °C is too low, so that they are positioned above the general line in the case of *Diplolaimella ocellata* and *Haliplectus dorsalis*. *Enoplus paralittoralis* is, however, under the line, although it has a high basal temperature as well (12·0 °C) and was not found reproducing below 18 °C in laboratory conditions. That above the basal temperature, warm-water species may develop faster than cold-water species is demonstrated in two cases for which we have data: *Diplolaimella ocellata* and *Rhabditis marina* populations of warm water develop faster at a comparable effective temperature than the same species in cold water. *R. marina* is in both cases below the general line, which is expected since it is known that saprobic nematodes such as the rhabditids are extremely fast developers (Tomlinson & Rothstein, 1962; Grootaert, 1976; Schiemer, 1982b). We excluded this species from our calculations since it can hardly be called typical for the marine environment, being a representative of terrestrial forms which happen to tolerate salt water (it occurs mainly in rotting seaweed high on the beach) (Sudhaus, 1974).

When this and species (1, 2, 3, 9, 10, 17, 18, 19, 20, 23, 27, and 33) are excluded from our calculation we obtain a correlation coefficient $r = 0{\cdot}681$ ($P < 0{\cdot}01$, $n = 28$) between development time and body weight. A similar analysis (Fig. 10) on embryonic development time resulted in a correlation coefficient of $r = 0{\cdot}524$ ($P < 0{\cdot}01$, $n = 30$) for all data and of $r = 0{\cdot}599$ ($P < 0{\cdot}01$, $n = 28$) with *R. marina* excluded. As the correlation found between embryonic development time and biomass is not significantly different from the correlation found between generation time and biomass, prolongation in post-embryonic development due to suboptimal cultivation cannot be proved statistically.

Influence of temperature

Temperature has a profound effect on minimum generation time T_{min} in all nematodes studied (Gerlach & Schrage, 1971; Tietjen & Lee, 1972; Hopper, Fell & Cefalu, 1973; Bergholz & Brenning, 1978; Heip, Smol & Absillis, 1978; Warwick, 1981a; Garcia, 1982; Vranken, Herman & Heip, unpubl.). At high

TABLE VII

Mean embryonic duration (E_{min}) and minimum generation time (T_{min}) of free-living brackish-water nematodes in laboratory conditions: ( ), species code number; SD, standard deviation; N_e, number of eggs studied; N, number of females studied; +, sampled from the Dievengat (Knokke, Belgium); + +, sampled from the Sluice Dock (Ostend, Belgium); Medium I, bacto-agar (DIFCO) + 1% Vlasbom-medium + 0·5 − 1% $Na_2SiO_3 \cdot 9H_2O$ (concentration in stock-solution is 15 $g \cdot l^{-1}$); Medium II, bacto-agar (DIFCO) enriched with phosphorus modified Walne-medium (5 parts) and ES medium of Provasoli (1 part) and 0·5–1% $Na_2SiO_3 \cdot 9H_2O$ (15 $g \cdot l^{-1}$) (for constitution see Vranken et al., *1984a); Medium III, modified Killian-nutrient agar after von Thun (1966)*

Species	Medium	Salinity (‰)	Temp. (°C)	E_{min} (days)	T_{min} (days)	Authority (unpubl.)
Monhystrella parelegantula^{++} (23)	I	30	20	3·8 (SD = 0·75; N_e = 181)	18·1 (SD = 2·87; N = 275)	Vranken
Monhystera parva^{+} (37)	II/III	20	20	2·7 (SD = 0·76; N_e = 163)	11·5 (SD = 1·41; N = 75)	Vranken
Monhystera parva^{++} (35)	III	30	22	3·7 (SD = 1·09; N_e = 53)	8·8 (SD = 1·64; N = 229)	Vranken & Coppieters
Chromadora nudicapitata^{++} (38)	III	30	22	3·3 (SD = 1·17; N_e = 313)	9·7 (SD = 0·96; N = 148)	Vranken & Dua
Chromadora nudicapitata^{+} (39)	II	20	20	—	14·0 (SD = 1·40; N = 108)	Van Brussel & Vranken
Neochromadora poecilosomoides^{++} (36)	II/III	30	20	5·3 (SD = 1·57; N_e = 204)	21·7 (SD = 4·10; N = 115)	Vranken
Paracanthonchus caecus^{+} (40)	II	20	20	—	51·1 (SD = 4·8; N = 66)	Van Brussel & Vranken

TABLE VIII

Life history of free-living marine nematodes: a, number of eggs in the uterus; b, after this time-period approximately 60% of the females died; c, generation time from ♀♂ to ♀♂, data between brackets are the shortest minimum and the longest maximum; d, only 1 individual has been studied; e, only 2 individuals have been studied; f, maximum number of eggs produced; g, generation time measured as the time elapsed between first egg-depositions; h, Sudhaus' population of R. marina *(Kiel, FRG) is viviparous, therefore this figure = postembryonic development time; i, data read from Bergholz & Brenning's fig. 3; j, generation time* (T_{min}) *calculated as* $T_{min} = (0{\cdot}228T + 5{\cdot}573) \times E_{min}$, *with* T = *temperature* (°C) *and* E_{min} = *embryonic development time (days); k, daily egg-production·female*$^{-1}$, *read from Warwick's Figs 2 and 3; l, number of juveniles·female*$^{-1}$ (E. paramatus *is viviparous) at unspecified temperature; m, generation of* M. disjuncta *cultivated monoxenically on* Alteromonas haloplanktis (ISC_2); *n, mean fecundity (= potential capability of a nematode to produce eggs) of 12 ♀♀ (3 °C) and 9 ♀♀ (12 and 17 °C); *, mean adult longevity, or time at which 50% of the adult females studied, died, mean total longevity can be obtained by adding* T_{min} *of the corresponding temperature, N = 106 at 17 °C; N = 125 at 12 °C and N = 105 at 3 °C; N, number of females studied during the generation time experiments; SD, standard deviation; SE, standard error; ♂, male; ♀, female*

Species (Code no.)	Salinity (‰)	Temp. (°C)	Egg number (average and/or min., max.)	Average min. generation time (days) (min.–max.)	Average life span (days)	Reference
Diplolaimella schneideri (1)	Sea water	20–24	—	40	—	Chitwood & Murphy, 1964
Monhystera disjuncta (2)	Sea water	20–24	—	30	—	"
Acanthonchus cobbi	Sea water	—	—	29	—	Hopper & Meyers, 1966a
Euchromadora gaulica	Sea water	—	—	35 (30–40)	—	"
Monhystrella parelegantula	Sea water	—	—	30	—	"
Monhystera filicaudata (3)	Estuarine	20–25	8–20[a]	29·5 (24–35)	—	Tietjen, 1967
Adoncholaimus thalassophygas (4)	15	20–22	17 (14–22)	63 (55–72)	78	von Thun, 1968
Chromadorita tenuis (5)	15	20–22	20 (16–28)	26 (19–34)	43	"
Diplolaimella ocellata (6)	15	20–22	22 (12–26)	29 (22–39)	56	"
Diplolaimelloides oschei (7)	20	20–22	36 (24–42)	29 (23–35)	54	"
Diplolaimelloides islandica (8)	15	20–22	22 (16–25)	31 (24–39)	50	"
Monhystera disjuncta (9)	5	20–22	16 (14–20)	23 (18–28)	33	"
Rhabditis marina (10)	25	25	85 (70–100)	4·5–5	♀♀: ±10[b] ♂♂: up to 19	Tietjen *et al.*, 1970

Monhystera disjuncta (11)	32	26	—	no juvenile growth	—	Gerlach & Schrage, 1971
	32	17–22	37	12 (8–15)[c]	61[d]	,,
	32	13–15	—	15 (9–20)[c]	—	,,
	32	9–12	—	17 (13–24)[c]		,,
	32	7	—	22 (14–32)[c]		,,
	32	0–2	—	78 (77–81)	—	,,
	32	(−1)–(+1)	—	131 (128–134)[c]	—	,,
Theristus pertenuis (12)	32	17–22	—	23 (19–26)[c]	—	,,
	32	13–15	—	42 (35–47)[c]	—	,,
	32	9–12	—	47 (37–54)[c]	—	,,
	32	7	at least 30	72 (61–90)[c]	208[d]	,,
Oncholaimus brachycercus (13)	32	7	6[f]	399	♀♀ (541 & 610)[c] ♂: 580[d]	Gerlach & Schrage, 1972
Desmodora scaldensis (14)	32	7	8[f]	603	♀: >800[d] ♂: >750[d]	,,
Halichoanolaimus robustus (A)	32	7	—	>20 months	at least 855	,,
Monhystera denticulata (15)	13	5	8–19	197 (173–204)[g]	at least 330	Tietjen & Lee, 1972b
	13	15	12–21	36 (30–41)[g]	69	,,
	13	25	16–22	20 (18–24)[g]	37	,,
	26	5	10–17	180 (163–196)[g]	at least 330	,,
	26	15	18–24	18 (15–20)[g]	53	,,
	26	25	18–23	10 (8–12)[g]	34	,,
	39	15	15–23	34 (27–38)[g]	57	,,
	39	25	15–23	17 (15–22)[g]	29	,,
Chromadora macrolaimoides (16)	26	25	10 (9–18)	22 (18–25)[g]	45 (35–54)	Tietjen & Lee, 1973
Rhabditis marina (17)	15	35	—	1·75 (1·5–2)[g]	—	Hopper *et al.*, 1973
(at present called *Pellioditis marina* (Bastian, 1865) Andrássy, 1983 n. comb.)		33	—	1·5 (1–1·5)[g]	—	,,
		30	—	2 (1–2)[g]	—	,,
		24	—	2·25 (2–3)[g]	—	,,
		21	—	2·5 (2–3)[g]	—	,,
		18	—	4 (2–6)	—	,,
		12	—	8 (6–9)	—	,,
Diplolaimelloides sp.	15	37	—	7 (7–8)	—	,,
		35	—	4 (3–5)	—	,,
		33	—	4 (4)	—	,,
		30	—	4·5 (4–5)	—	,,
		24	—	7 (6–8)	—	,,
		21	—	9·5 (8–10)	—	,,
		18	—	14 (13–15)	—	,,
		12	—	30 (24–35)	—	,,

TABLE VIII—*continued*

Species (Code no.)	Salinity (‰)	Temp. (°C)	Egg number (average and/or min., max.)	Average min. generation time (days) (min.–max.)	Average life span (days)	Reference
Diplolaimella ocellata (18)	15	35	—	8 (7–11)	—	Hopper *et al.*, 1973
		33	—	6·5 (5–10)	—	"
		30	—	6 (5–7)	—	"
		24	—	11·5 (8–16)	—	"
		21	—	12 (10–14)	—	"
		18	—	43 (33–60)	—	"
Enoplus paralittoralis (19)	15	31	—	27 (27)	—	"
		28	—	21 (21)	—	"
		24	—	22 (19–24)	—	"
		21	—	41 (27–59)	—	"
Oncholaimus sp.	15	33	—	23 (16–34)	—	"
		30	—	20 (17–28)	—	"
		24	—	29 (25–40)	—	"
		21	—	39 (31–44)	—	"
		18	—	86 (80–94)	—	"
Haliplectus dorsalis (20)	15	35	—	35 (28–42)	—	"
		33	—	26 (26)	—	"
		30	—	27 (21–31)	—	"
		24	—	34 (30–37)	—	"
		21	—	70 (60–74)	—	"
		18	—	112 (109–114)	—	"
Rhabditis marina		room T	128 (70–260)	3–4[h]	—	Sudhaus, 1974
Rhabditis marina (B)	5	5	17[i]	57 (49–64)	—	Bergholz & Brenning, 1978
		9	27[i]	48 (42–57)	—	"
		16	31[i]	30 (24–39)	—	"
		25	43[i]	20 (14–25)	—	"

Prochromadora orleji (21)	5	5	7[i]	112	—	"
		9	5[i]	87	—	"
		16	13[i]	54	—	"
		25	14[i]	46	—	"
Oncholaimus oxyuris (22)	18–23	5	13·5 (SE = 13·4)	570[j]	—	Heip *et al.*, 1978
		10	18·5 (SE = 6·0)	285[j]	—	"
		15	34·3 (SE = 10·9)	153 (SE = 4·3)	—	"
		20	35·6 (SE = 7·4)	114 (SE = 1·4)	—	"
		25	36·8 (SE = 8·3)	102 (SE = 2·9)	—	"
Monhystrella parelegantula (23)	30	25	—	8·9 (SE = 0·04; N = 539)	—	Vranken *et al.*, 1981
Diplolaimelloides bruciei (24)	26	5	—	—	—	Warwick, 1981a
		10	0·7[k]	>64	—	"
		15	3·7[k]	13·5	—	"
		20	4·9[k]	9	—	"
		25	5·2[k]	7·5	—	"
		30	7·1[k]	5·5	—	"
	1·75	20	1·2[k]	—	—	"
	8·95	20	2·3[k]	13	—	"
	17·5	20	2·6[k]	10·2	—	"
	26	20	4·9[k]	9	—	"
	35	20	2·9[k]	12·5	—	"
Chromadora nudicapitata (25)	?	15	8	19	28	Warwick, 1981b
		20	50	13	19	"
Eudiplogaster pararmatus (26)	5	12	8–10[l]	45	—	Romeyn *et al.*, 1983
		21		21		
Rhabditis marina (27)	20	25	600	4·5 (4–5; N = 47)	—	Vranken & Heip, 1983
Monhystera disjuncta (28)	30	17	—	♀♀: 10·9 (SD = 2·36; N = 226)	—	Vranken *et al.*, 1984a
		17	—	♂♂: 11·0 (SD = 2·68; N = 90)	—	"
Monhystera microphthalma (29)	20	20	—	♀♀: 10·2 (SD = 1·20; N = 113)	—	"
		20	—	♂♂: 11·2 (SD = 1·61; N = 107)	—	"
Monhystera disjuncta	30	17	—	♀♀: 8·8 (SD = 0·96; N = 209)[m]	—	"
		17	—	♂♂: 8·6 (SD = 0·87; N = 140)[m]	—	"
Monhystera disjuncta	30	3	180[n] (SE = 18·5)	♀♀: 52·3 (SD = 8·41; N = 287) ♀♀: 123*	—	Vranken *et al.*, unpubl.
		12	218[n] (SE = 31·9)	♀♀: 17·2 (SD = 4·53; N = 662) ♀♀: 49*	—	"
		17	187[n] (SE = 10·4)	♀♀: 10·9 (SD = 2·36; N = 226) ♀♀: 38*	—	"
		20	—	♀♀: 9·3 (SD = 2·21; N = 291)	—	"

temperatures T_{min} may be as low as 1·5 days (*R. marina* at 33 °C; Hopper, Fell & Cefalu, 1973) whereas at low temperatures development time may be more than 100 days (Gerlach & Schrage, 1971; Tietjen & Lee, 1972). Some species are adapted to low temperatures, *e.g. Monhystera disjuncta* develops at 0 °C and reproduces at 3 °C (Vranken, Herman & Heip, unpubl.). Extremely long generation times have been reported for *Desmodora scaldensis* and *Oncholaimus brachycercus*; at 7 °C the former species needs 566 days to reach sexual maturity, the latter approximately 300 days (Gerlach & Schrage, 1972), whereas *Halichoanolaimus robustus* could not even complete its life cycle within a period of 20 months. Some of these experiments, however, may have been in suboptimal conditions because the authors did not observe the nematodes feeding.

For many species development is more temperature-dependent in the lower temperature range than near the optimum. This is illustrated in Table IX, which shows Q_{10} values for different temperature intervals. As an example, *Monhystera disjuncta* has a $Q_{10} = 7$ in the interval 0–10·5 °C and a $Q_{10} = 1{\cdot}5$ in the interval 10·5–19·5 °C (Gerlach & Schrage, 1971). Most species show this higher response, but some have a more or less constant Q_{10}: *Theristus pertenuis* (Gerlach & Schrage, 1971), *Rhabditis marina* (Tietjen *et al.*, 1970; Bergholz & Brenning, 1978), and *Prochromadora orleji* (Bergholz & Brenning, 1978).

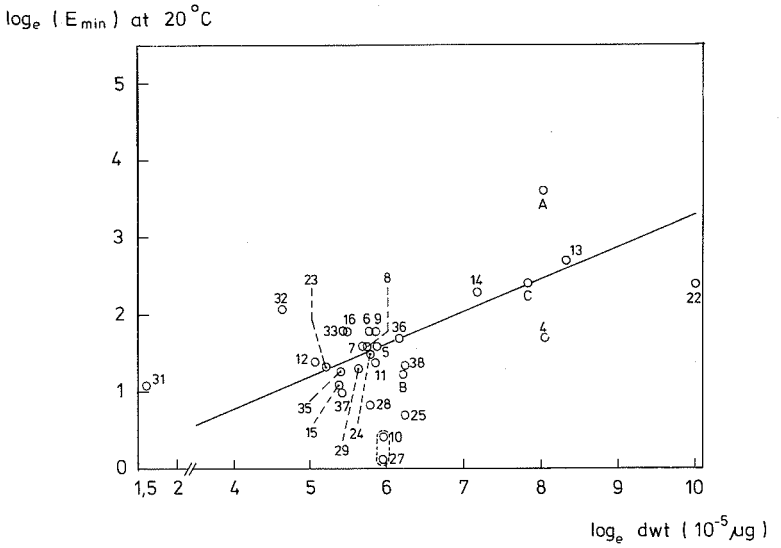

Fig. 10.—Relationship between embryonic development (E_{min}) at 20 °C and dry weight of the eggs (15% of wet weight): the weight of the cylindriform eggs was estimated by using Andrássy's (1956) formula, that of globular eggs was calculated by multiplying the volume (sphere) by the density 1·08 proposed by Andrássy (1956); morphometric data not quoted in the original experimental publications are from Ditlevsen (1911) for 22; Meyl (1954b) for 12; Man (1889), Rachor (1969), and Belogurova (1978) for 13; Luc & De Coninck (1959) for 14; Smol (unpubl.) for A; Vincx (unpubl.) for C = *Anticoma pellucida*; Vranken (unpubl.) for 23, 28, 29, 35, 36, 37, and 38.

Development rate reaches a maximum near some optimum temperature beyond which generation time is prolonged. This is the typical response for most meiofauna (Vernberg & Coull, 1981). The optimum temperature is near to 33 °C for the warm-water species cultivated by Hopper, Fell & Cefalu (1973) and near to 20 °C for *Chromadora nudicapitata* at 20°/$_{oo}$ *S* (Heip *et al.*, 1985). To describe the relationship between temperature and development time the power equation $D = aT^b$ has been used by Heip, Smol & Absillis (1978) for *Oncholaimus oxyuris*, by Warwick (1981a) for *Diplolaimelloides bruciei* and by Heip *et al.* (1982) for reviewing the available information on life cycles. Heip *et al.* (1982) obtained a modal value of $b = -1{\cdot}8$, which is considerably higher than the *b*-values obtained for other groups such as calanoids and harpacticoids.

In Figure 11 all *b*-values for the nematode species cultivated up to now are compiled, with some omissions when the cultivation method was judged to be inadequate, and some of the unpublished data obtained by Vranken and co-

TABLE IX

Temperature coefficient, $Q_{10} = (v_1/v_2)^{10/(T_1 - T_2)}$, *calculated from development rates* $v = 1/T_{min}$ *of free-living marine nematodes, for different temperature intervals (figures in parentheses): temperature, T, is in °C and* $T_1 < T_2$

Species	(°/$_{oo}$)	Q_{10} (temperature interval)		Reference
Monhystera disjuncta	32	6·99 (0–10·5)	1·47 (10·5–19·5)	Gerlach & Schrage, 1971
Theristus pertenuis	32	2·16 (7–14)	2·99 (14–19·5)	Gerlach & Schrage, 1971
Monhystera denticulata	13	5·47 (5–15)	1·80 (15–25)	Tietjen & Lee, 1972
	26	10·00 (5–15)	1·80 (15–25)	Tietjen & Lee, 1972
	39	—	2·00 (15–25)	Tietjen & Lee, 1972
Rhabditis marina	15	3·64 (12–21)	1·28 (21–30)	Hopper *et al.*, 1973
Diplolaimella sp.	15	3·59 (12–21)	2·29 (21–30)	Hopper *et al.*, 1973
Rhabditis marina	5	1·79 (5–16)	1·57 (16–25)	Bergholz & Brenning, 1978
Prochromadora orleji	5	1·94 (5–16)	1·20 (16–25)	Bergholz & Brenning, 1978
Oncholaimus oxyuris	18–23	3·73 (5–15)	1·50 (15–25)	Heip *et al.*, 1978
Diplolaimelloides bruciei	26	>7·11 (5–15)	1·64 (15–25)	Warwick, 1981a
Monhystera disjuncta	30	3·44 (3–12)	2·16 (12–20)	Vranken *et al.*, unpubl.

workers. The *b*-values are highly heterogeneous ($F = 7{\cdot}27$; d.f. = 18, 48; $P < 0{\cdot}001$), so that the use of a single *b*-value for marine nematodes is invalid on statistical grounds (see Zaika & Makarova, 1979). The bars around the *b*-values indicate 95% comparison intervals (Gabriel's *T*-method in Sokal & Rohlf, 1981), when intervals do not overlap the *b*'s are significantly different. Some interesting features emerge from this figure. *Monhystera disjuncta*, a truly marine species, has a much lower *b*-value than the other species, most of which are estuarine or brackish-water forms. At the other extreme we find the tropical species cultured by Hopper, Fell & Cefalu (1973). These have statistically higher *b*-values than those inhabiting temperate regions. The monhysterids, with the exception of *Monhystrella parelegantula*, have intermediate *b*-values, between $-2{\cdot}01$ for *Monhystera microphthalma* at $30^{\circ}/_{\circ\circ}$ *S* and $-1{\cdot}67$ for the same species at $11^{\circ}/_{\circ\circ}$ *S*. *Monhystrella parelegantula* occupies a peculiar position; the influence of temperature on development time is as strong as for the warm-water species. *M. parelegantula* is a brackish-water species with a wide salinity tolerance and one of the dominant species in inland salinas in Germany (Meyl, 1954a; Paetzold, 1955, 1958). Its basal temperature $T_0 = 14$ °C and a high developmental acceleration is necessary to achieve a high productivity and, therefore, survival in the temporary habitats where it lives (Vranken *et al.*, 1981). Temperature appears to have little effect on *Monhystera disjuncta*; as mentioned, it reproduces at 3 °C and was found in Antarctica (Viglierchio, 1974). *Rhabditis marina* has an intermediate *b*-value

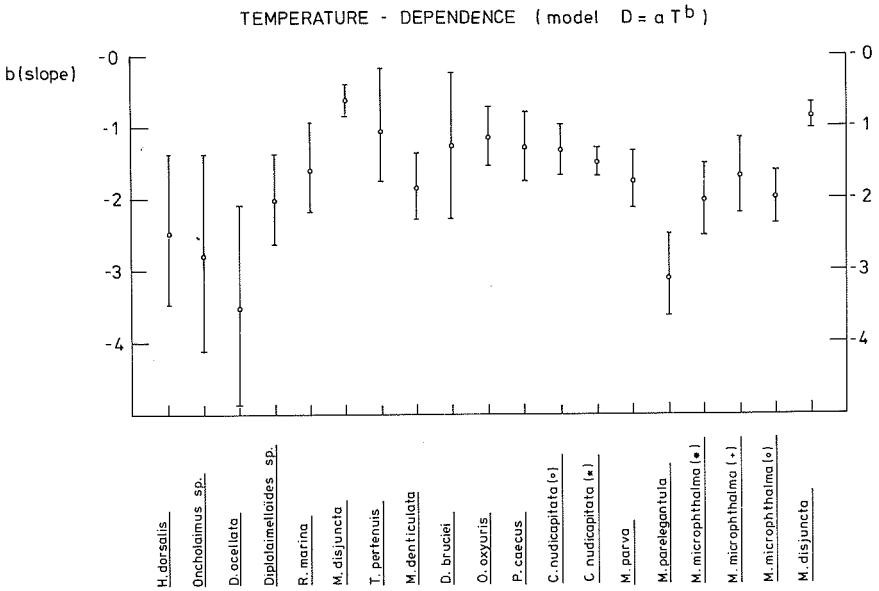

Fig. 11.—Values of *b* in the equation $T_{min} = aT^b$, with T_{min} = minimum generation time and T = temperature (°C): sources are quoted in Table XI; for *R. marina*, the *b*-value obtained from the data of Hopper, Fell & Cefalu (1973) is shown; (+) = $11^{\circ}/_{\circ\circ}$ *S*, (○) = $20^{\circ}/_{\circ\circ}$ *S*; (*) = $30^{\circ}/_{\circ\circ}$ *S*; *b*-values for *P. caecus* and *C. nudicapitata* are from Heip *et al.* (1985); the unquoted data are unpublished results from Vranken and co-workers.

(−1·59). It has a short development time in its lower temperature range and its acceleration rate is limited. The remaining species, mainly chromadorids and *Oncholaimus oxyuris*, have smaller (statistically not significant) *b*-values than the monhysterids and much smaller *b*-values than the warm-water species. Some relationship between temperature-dependency and geographic occurrence appears to exist. The warm-water species have the highest *b*-values.

Some precaution, however, is necessary when comparing *b*-values of different species. This is because the power equation as a temperature model is a simplification of Bělehrádek's function, $T_{min} = a(T - T_0)^b$, with T_0 the basal temperature. In the power equation T_0 is fixed at zero degree Celsius. Therefore, if Bělehrádek's function is the underlying temperature model, it is to be expected that *b* obtained in the power equation highly correlates with T_0. This makes comparison of the *b*-values (power equation), without knowledge of T_0 somewhat difficult. Nevertheless when regressing T_{min} against the effective temperature, extreme opportunists tend to have the higher *b*-values (Vranken, unpubl.).

Influence of salinity

Only a few studies (Tietjen & Lee, 1972, 1973; Warwick, 1981a) report on the combined effect of temperature and salinity on generation time. In *Monhystera denticulata*, generation time was almost doubled by decreasing and by increasing the optimum salinity of 26°/₀₀ *S* by 13°/₀₀ *S*, both at 15 and 25 °C. At 5 °C, development rates were nearly equal at 13°/₀₀ *S* and 26°/₀₀ *S*. For *Chromadorina germanica*, population growth, measured as *r*, was maximal at 26°/₀₀ *S* and, within the optimum temperature range of 20–30 °C, a drop to 13°/₀₀ *S* caused a doubling of the generation time. Outside the optimum temperature range, the difference increased. Tietjen & Lee (1977a) concluded that both species are better adapted to the middle and upper regions of their salinity tolerance range than to the lower part. Mortality, however, was higher at high salinity than at low salinity.

Croll & Viglierchio (1969) claim that *Deontostoma californicum* is able to osmoregulate in hypertonic solutions but not in hypotonic solutions. These results have been questioned by Wright & Newall (1976, 1980) who report on the osmoregulation of *Enoplus communis* and *E. brevis*; especially the latter, brackish-water dwelling species, is able to regulate its body volume in both hyper- and hypotonic solutions. As calcium is required to maintain the normal permeability of membranes, the single salt solutions used by Croll & Viglierchio (1969) and Viglierchio (1974) cause artifacts. Evidence for active osmoregulation in nematodes is absent (Wright & Newall, 1980).

That generation time increases with salinity has been shown for *Diplolaimelloides bruciei* by Warwick (1981a) at both sides of the optimum of 26°/₀₀ *S* for this species; Vranken & Van Brussel (unpubl.) found the same effect for *Monhystera microphthalma* on both sides of the optimum 20°/₀₀ *S*, although the slope (*b*) did not change.

The number of annual generations

A further step in many papers dealing with the influence of temperature and salinity on development is to estimate the number of generations the

population would produce in the field given comparable situations would exist. As many nematodes have continuous reproduction it is often impossible to obtain this information from field studies.

For a number of chromadorid and monhysterid species estimates obtained from laboratory experiments exist. The following annual numbers of generations have been calculated: 1·6 for *Oncholaimus oxyuris* in the Dievengat, a brackish-water pond in Belgium (Heip, Smol & Absillis, 1978); 5 to 5·5 generations for *Monhystrella parelegantula* in the Sluice Dock of Ostend, Belgium (Vranken *et al.*, 1981); 5 generations for *Prochromadora orleji* in the Barther Bodden, G.D.R. (Bergholz & Brenning, 1978); a maximum of 7 and probably nearer to 5 generations for *Theristus pertenuis* (Gerlach & Schrage, 1971); 10 generations for *Rhabditis marina* in the Barther Bodden, G.D.R. (Bergholz & Brenning, 1978); 13 generations for *Chromadorina germanica* in North Sea Harbor, New York (Tietjen & Lee, 1972); an average of 15 and a maximum of 21 for *Monhystera denticulata* in North Sea Harbor, New York (Tietjen & Lee, 1972); 17 generations for *Diplolaimelloides bruciei* in the Lynher estuary (calculated by Heip, Herman & Coomans, 1982, from Warwick, 1981a); and a maximum of 17 and a mean of 12 generations for *Monhystera disjuncta* in the North Sea (Gerlach & Schrage, 1971).

In fact, all these calculations over-estimate the mean annual number of generations. Nematodes cultured in the laboratory immediately start reproduction and reproduce continuously over a relatively long time in comparison with their pre-reproductive life. The time elapsed between two identical stages in two successive generations 'egg to egg' or 'female to female', roughly equals development time and the time necessary to produce the median egg has to be added to obtain a good estimate of mean generation time (Laughlin, 1965). The above calculations are valid estimations of the number of juvenile periods realized each year (see Taylor, 1981, for a definition).

As most species cultivated belong to the group of fast-growing nematodes it remains premature to speculate upon a model minimum generation number of nematodes in the field. Moreover, the data in many papers in this field are sometimes difficult to interpret and calculations erroneous. Important information that is often withheld is replication of the experiment, mortality in cultures, the number of individuals studied; even such basic statistics as the standard error or deviation are not always found in the paper.

Reproductive potential

The intrinsic rate of natural increase r_m (also called Malthusian parameter and the innate capacity for increase) is the actual rate of increase when the population has attained a stable age distribution, in the absence of competition or predation. When this stable age distribution is not reached, every actual rate of increase will depend on age structure of the population; therefore, only r_m is a good measure of the capacity of the species to increase when conditions are favourable and only r_m should be used in interspecies comparisons.

Three features of the life history are of paramount importance in determining reproductive potential: development rate, fecundity and longevity. We have shown how generation time is dependent on temperature and salinity. Food is of obvious importance, but there are no data for marine nematodes.

For the soil-dwelling *Caenorhabditis briggsae* development time increased three times at food densities two orders of magnitude higher (Schiemer, 1982b), and food quality was also important.

Temperature has an important effect on fecundity. The number of eggs produced per female is often higher at higher temperatures (Tietjen & Lee, 1972; Bergholz & Brenning, 1978; Heip, Smol & Absillis, 1978; Warwick, 1981a). For two species, *Oncholaimus oxyuris* and *Diplolaimelloides bruciei*, a linear relationship between daily egg production and temperature has been demonstrated (Table X). Similarly, in *Monhystera microphthalma* daily egg production increased from 2·4 eggs·fem.$^{-1}$·day^{-1} at 15 °C to 12·8 eggs·fem.$^{-1}$·day^{-1} at 25 °C (Vranken, unpubl.). At 30 °C the species still produced 11·7 eggs·day^{-1}. These data also indicate that the effect of temperature is dependent on species; *M. microphthalma* is very temperature-dependent, *Diplolaimelloides bruciei* intermediate and *Oncholaimus oxyuris* is only little affected.

Most literature on longevity is casual. Many authors do not even mention how it was measured and often a very small number of individuals is followed, producing results that have no basis for generalization. Again, temperature has a profound influence on longevity, and Tietjen & Lee (1972) report for *Monhystera denticulata* 330 days at 3 °C compared with 30–40 days at 25 °C. In *M. disjuncta*, mean longevity of adult females decreased from 175 days at 3 °C to 49 days at 17 °C (Vranken, Herman & Heip, unpubl.).

Temperature, salinity, and food thus have a profound influence on the reproductive potential (Table XI) (Tietjen & Lee, 1977a; Heip, Smol & Absillis, 1978; Alongi & Tietjen, 1980; Warwick, 1981a; Vranken *et al.*, 1984a). In four species, a linear increase of r_m with temperature has been observed (Table XII), with a large slope for *Diplolaimelloides bruciei*, *Chromadorina germanica* and *Monhystera microphthalma* and a small slope for the large *Oncholaimus oxyuris*. Beyond a certain optimum temperature, the reproductive potential is depressed (Tietjen & Lee, 1977a). As for temperature, there exists a salinity optimum with depression of the reproductive potential at both higher and lower salinities (Tietjen & Lee, 1977a; Warwick, 1981a; Romeyn, Bouwman & Admiraal, 1983). The importance of food has been demonstrated by Alongi & Tietjen (1980): *r*-values ranging between 0 and 0·12 have been reported from *Chromadorina germanica* and *Diplolaimella* sp. grown on different diets; with *Monhystera disjuncta* the range was somewhat smaller. On the other hand, Findlay (1982a) found that the carrying capacity K was a straightforward function of ration and type of detritus given to *Diplolaimella chitwoodi*.

TABLE X

Relation between daily egg-production and temperature

Species	*a*	*b*	R^2	Reference
Oncholaimus oxyuris	−0·3050	0·0834	0·9727	Heip *et al.*, 1978
Diplolaimelloides bruciei	−1·429	0·286	0·951	Warwick, 1981a

TABLE XI

Reproductive potential, r (per day) of free-living marine nematodes as a function of temperature, salinity and food: a, r-values read from original figure

Species	Temperature (°C)	Salinity (‰)	Food	r (per day)	Reference
Chromadorina germanica[a]	13	26	*Chlorococcum* sp. and *Cylindrotheca closterium*	0·038	Tietjen & Lee, 1977a
	17·7	26	„	0·116	„
	21	26	„	0·164	„
	23	26	„	0·179	„
	30	26	„	0·185	„
	33	26	„	0·075	„
	19·5	39	„	0·115	„
	24·8	39	„	0·164	„
	30	39	„	0·137	„
	31·2	39	„	0·070	„
	19·5	13	„	0·051	„
	26	13	„	0·120	„
	30	13	„	0·078	„
Oncholaimus oxyuris	5	18–23	*Panagrellus redivivus* and bacteria, algae	0·003	Heip, Smol & Absillis, 1978
	10	18–23	„	0·009	„
	15	18–23	„	0·015	„
	20	18–23	„	0·022	„
	25	18–23	„	0·029	„
Chromadorina germanica	23	26	*Pseudomonas* sp. 1	0·064	Alongi & Tietjen, 1980
	23	26	*Pseudomonas* sp. 2	0·058	„
	23	26	*Dunaliella* sp.	0	„
	23	26	*Nitzschia* sp.	0·007	„
	23	26	*Cylindrotheca closterium*	0·118	„
Diplolaimella punicea	23	26	*Pseudomonas* sp. 1	0·096	Alongi & Tietjen, 1980
	23	26	*Pseudomonas* sp. 2	0·086	„
	23	26	*Dunaliella* sp.	0·117	„
	23	26	*Nitzschia* sp.	0	„
	23	26	*Cylindrotheca closterium*	0	„

Monhystera disjuncta	23	26	*Pseudomonas* sp. 1	0·099	Alongi & Tietjen, 1980
	23	26	*Pseudomonas* sp. 2	0·093	"
	23	26	*Dunaliella* sp.	0·098	"
	23	26	*Nitzschia* sp.	0	"
	23	26	*Cylindrotheca closterium*	0	"
Diplolaimelloides bruciei	10	26	Bacteria (unidentified)	0·034	Warwick, 1981a
	15	26	"	0·172	"
	20	26	"	0·231	"
	25	26	"	0·244	"
	30	26	"	0·311	"
	20	1·75	"	0·056	"
	20	8·95	"	0·107	"
	20	17·5	"	0·118	"
	20	26	"	0·231	"
	20	35	"	0·135	"
Diplolaimella chitwoodi	20	25	Detritus from *Ulva fasciata*	0·280	Findlay, 1982a
	20	25	Pablum (mixed cereal)	0·230	"
	20	25	Detritus from *Gracilaria foliifera*	0·280	"
	20	25	Detritus from *Spartina alterniflora* (S-13)	0·093	"
	20	25	Detritus from *Spartina alterniflora* (S-1)	0·302	"
	20	25	Detritus from *Thalassia testudinum*	0	"
Eudiplogaster pararmatus[a]	17	0·5	*Navicula salinarum*	0·052	Romeyn *et al.*, 1983
	17	2·5	"	0·060	"
	17	5	"	0·057	"
	17	10	"	0·028	"
	17	20	"	0·008	"
Rhabditis marina	25	20	Bacteria	0·914	Vranken & Heip, 1983
Monhystera microphthalma	15	20	Bacteria	0·102	Vranken *et al.*, 1984a
	20	20	"	0·277	"
	25	20	"	0·268	"
	30	20	"	0·350	"
Monhystera disjuncta	3	30	Bacteria	0·102	Vranken *et al.*, 1984a
	12	30	"	0·121	"
	18	30	"	0·131	"

Banse (1982) studied the relationship between r_m and body weight for small metazoans, including nematodes. The optimal growth rates of meiobenthic nematodes were markedly lower than those of other nematodes (including *Caenorhabditis briggsae* and *Plectus palustris*) and other small invertebrates. Banse predicted an allometric relationship between r_m and wet weight, with an exponent "well below $-0{\cdot}25$". On the other hand, we have the general value of this exponent $-0{\cdot}274$ calculated by Fenchel (1974) for heterotherm metazoans. To re-examine the case for nematodes, we have re-calculated this expression using all literature data on r (Table XIII) (not r_m because most values published are only approximations of r_m for reasons given above). Only the figures for *Diplolaimelloides bruciei* (Warwick, 1981a), *Chromadora nudicapitata* (calculated by us from data in Warwick, 1981b), *Caenorhabditis briggsae* (Schiemer, 1982b), and *Rhabditis marina* (Vranken & Heip, in press) are real r_m values. The values quoted from von Thun (1968) relate to capacities for increase r_c (Laughlin, 1965) and are under-estimations, the more so since in recent years it has become clear that marine nematodes may produce a much higher number of eggs than previously assumed. *Monhystera denticulata* produces 60 eggs in a life time according to Tietjen & Lee (1972) whereas *M. disjuncta* lays approximately 200 eggs (Vranken, Herman & Heip, unpubl.); *Rhabditis marina* produces 600 eggs per female in only six days (Vranken & Heip, 1983), and a single observation of 800 eggs per female for this species exists (Vanderhaeghen, pers. comm.). For these reasons we excluded the values from von Thun (1968); the rhabditids were excluded for the same reasons as given previously (see p. 442), although some of the monhysterids also have high r-values: *Monhystera microphthalma*, $r = 0{\cdot}350 \cdot \text{day}^{-1}$ at 30 °C and $20‰$ S and *M. disjuncta*, $r = 0{\cdot}260 \cdot \text{day}^{-1}$ at 15 °C and $30‰$ S (Vranken, unpubl.).

There are also some problems with the other literature data, but we calculated nevertheless a linear least square regression line (model I) through

TABLE XII

Relation between the intrinsic rate of natural increase and temperature: CI, 95% confidence interval

Species	a	b	R^2	Reference
Oncholaimus oxyuris	−0·0042	0·0013 (CI:0·00005)	0·9996	Heip *et al.*, 1978
Diplolaimelloides bruciei	−0·067	0·0134 (CI:0·0042)	0·953	Warwick, 1981a
Chromadorina germanica	−0·1453	0·0144 (CI:0·0051)	0·988	Tietjen & Lee, 1977a
Monhystera microphthalma	−0·0815	0·0147 (CI:0·0217)	0·8196	Vranken *et al.*, 1984a (*logistic function*)
Monhystera microphthalma	−0·1018	0·0146 (CI:0·0157)	0·896	Vranken *et al.*, 1984a (*exponential*)

TABLE XIII

Relation between r-value and biomass: a, r-value computed as r_c (Laughlin, 1965); b, obtained by graphic interpretation; c, corrected to 20 °C assuming a linear relationship between r_m and temperature (Heip, 1977) with $r_m = 0$ at 0 °C; d, real r_m calculated with Lotka's formula

Species	r·day^{-1} at 20 °C	Wet weight (μg)	Reference
Adoncholaimus thallasophygas[a]	0·032	9·8	von Thun, 1968
Chromadorita tenuis[a]	0·072	1·3	von Thun, 1968
Diplolaimella ocellata[a]	0·068	0·2	von Thun, 1968
Diplolaimelloides oschei[a]	0·085	0·2	von Thun, 1968
Diplolaimelloides islandica[a]	0·068	0·2	von Thun, 1968
Monhystera disjuncta[a]	0·076	0·85	von Thun, 1968
Chromadorina germanica[b]	0·15	0·28	Tietjen & Lee, 1977a
Oncholaimus oxyuris	0·022	20	Heip *et al.*, 1978
Diplolaimella punicea[c]	0·118	1·13	Alongi & Tietjen, 1980
Monhystera disjuncta[c]	0·116	1·76	Alongi & Tietjen, 1980
Plectus palustris	0·28	1·5	Schiemer *et al.*, 1980
Diplolaimella chitwoodi	0·27	0·67	Findlay, 1982a
Diplolaimelloides bruciei	0·231	0·45	Warwick, 1981a
Caenorhabditis briggsae[d]	1·136	0·50	Schiemer, 1982b
Eudiplogaster pararmatus[c]	0·071	1·1	Romeyn *et al.*, 1983
Rhabditis marina [c]	0·731	1·1	Vranken & Heip, 1983
Monhystera microphthalma	0·277	0·6	Vranken *et al.*, 1984a
Monhystera disjuncta	0·116	0·32	Vranken, unpubl.
Chromadora nudicapitata[d]	0·209	0·71	Warwick, 1981b
Mesodiplogaster lheritieri[c]	1·158	7·3	Grootaert, 1976
Labronema vulvapapillatum[c]	0·067	10·7	Grootaert & Small, 1982

the existing data, which resulted in the following equation: $\log_e r_m = -1{\cdot}959$ (SE = 0·154) − 0·429 (SE = 0·122) $\log_e$ wet wt, WW (μg) ($F = 12{\cdot}4$, d.f. = 1, 10; $0{\cdot}005 < P < 0{\cdot}01$). This shows that weight-dependency of r_m in marine nematodes is about 1·6 times higher than calculated by Fenchel (1974) (although the values are statistically not different). A high correlation, $r = -0{\cdot}74$, exists between body weight and reproductive potential, large nematodes have a lower reproductive potential than small nematodes. The equation demonstrates that indeed the reprodutive potential of nematodes is lower than that of similarly sized heterothermic animals. Only the rhabditids realize approximately the r right for their size, the large *Oncholaimus oxyuris* has r about 20 times too low.

Calculation of the intrinsic rate of natural increase

As mentioned, the calculations above suffer from the fact that the literature data are not very precise. The exact calculation of r_m requires the construction of an age-specific fecundity (m_x) and survival (l_x) table from which r_m can be

TABLE XIV

Life-history parameters of Rhabditis marina *and* Chromadora nudicapitata*: all parameters related to generation time (T_c, T, $\bar{T}$ and T_{min}) are in days (d); the capacity of increase r_c and the intrinsic rate of natural increase, r_m, are in reciprocal days (day^{-1}); R_0 is the net reproductivity* (i.e. *the multiplication rate per generation*)

	Species	
	Rhabditis marina	*Chromadora nudicapitata*
Temp. (°C)	25	20
R_0	400	26
r_c	0·837	0·205
r_m	0·914	0·209
T_c	7·2	15·9
T	6·6	15·5
$\bar{T}$	6·1	15·1
T_{min}	4·5	12·5
Reference	Vranken & Heip, 1983	Warwick, 1981b

calculated with Lotka's formula:

$$\sum_{0}^{\infty} e^{-r_m x} l_x m_x = 1$$

with x the pivotal age of the different age groups (Ricklefs, 1973; Krebs, 1978). r_m can also be calculated from growth experiments when the initial population structure is the stable age distribution, *i.e.* when all the different age groups occur in the appropriate proportions (see Krebs, 1978, for the calculation of the stable age distribution). Then r_m can be calculated from $r_m = 1/t \ln N_t/N_0$, provided the stable age distribution is maintained (no heterogeneity around the regression line).

There exist only two life tables for two brackish water nematodes: *Rhabditis marina* (Vranken & Heip, in press) and a graphic one for *Chromadora nudicapitata* (Warwick, 1981b). They are shown in Table XIV, where several measures of generation time are calculated (see Pielou, 1977; Southwood, 1978). These parameters all give substantially longer values than the minimum generation time or development time T_{min}.

ENERGY FLOW

FEEDING

Much of the literature on feeding and indeed general ecology of marine nematodes is based on a paper by Wieser (1953) who classified nematodes in

feeding types according to the morphology of their buccal cavity. Indeed, although the organization of free-living nematodes is quite uniform, a great diversity in buccal structures exists which bears on ecological relationships and the niche of the species.

Wieser made a division into four feeding types in two groups; Group 1 contains those species in which the buccal cavity is unarmed, Group 2 species have an armed buccal cavity. Type 1A (Fig. 12) contains those species where there is no real buccal cavity, although some species where it is small are included. These species supposedly pick up small food particles, such as bacteria, selectively. Type 1B (Fig. 12) contains those species in which the unarmed buccal cavity is wide and they supposedly feed non-selectively on deposits. Type 2A (Fig. 12) contains species which are presumably herbivorous.

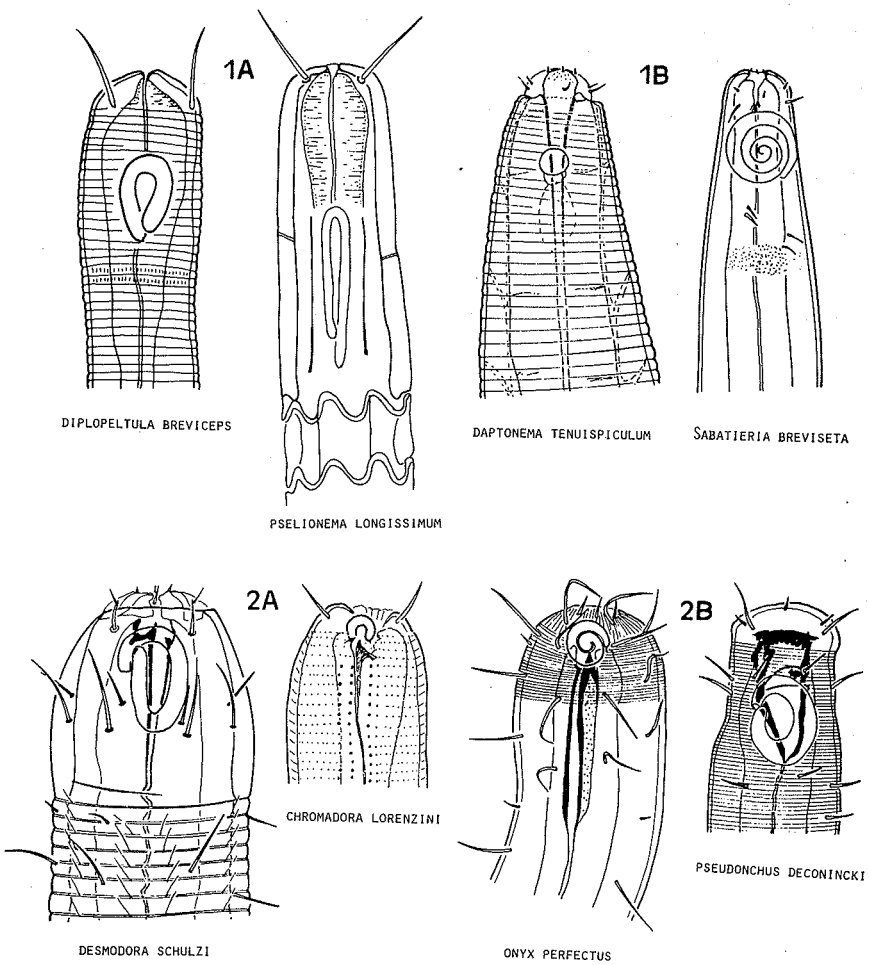

Fig. 12.—Heads of some marine nematode species arranged per feeding type (see text p. 459): note *C. lorenzini* should read *C. lorenzeni*.

Type 2B species (Fig. 12) have wide buccal cavities and glands opening on teeth, and they are supposedly carnivores or omnivores. This rather simple scheme has been used over and over again and has obtained the status of a paradigma in marine nematology. Wieser (1953) himself, however, warned against such over-simplications: ". . . [das Man] ein Einteilung mit ökologischer Zielsetzung niemals ausschlieslich auf morphologischen Fakten aufbauen kann." When writing in 1953, Wieser remarked that there were no observations on solid particles in the guts of 1A animals, but that diatoms had often been observed in 1B and 2A animals. Since then anecdotal observations on the gut contents of nematodes have been numerous; most earlier data were summarized by von Thun (1968). The scheme itself has often been discussed but seldom questioned and only since Romeyn & Bouwman (1983) has some original contribution appeared. They considered oesophageal pumping rates as relevant to the problem. Non-selective deposit-feeders, such as *Monhystera* and *Diplolaimelloides*, that have very small sensory organs and a very small buccal cavity, exhibit continuous pumping activity of the pharynx and food intake is purely passive. When the buccal cavity is somewhat wider, as in *Monhystera disjuncta*, diatoms may be ingested as well as smaller particles. Selective feeders have well-developed sensory organs and pumping of the pharynx is not continuous. Here two routes are open: either the nematode ingests the food particle wholly or it attacks it first by breaking it using its buccal armature and then sucking out the contents. This breaking may be achieved by either piercing or cracking the cell wall.

Jensen (1982) has described how *Chromadorita tenuis* attacks the diatom *Nitzschia* sp. (Fig. 13). The nematode brings one end of the diatom into the buccal cavity and then breaks open the girdle causing the two valves to

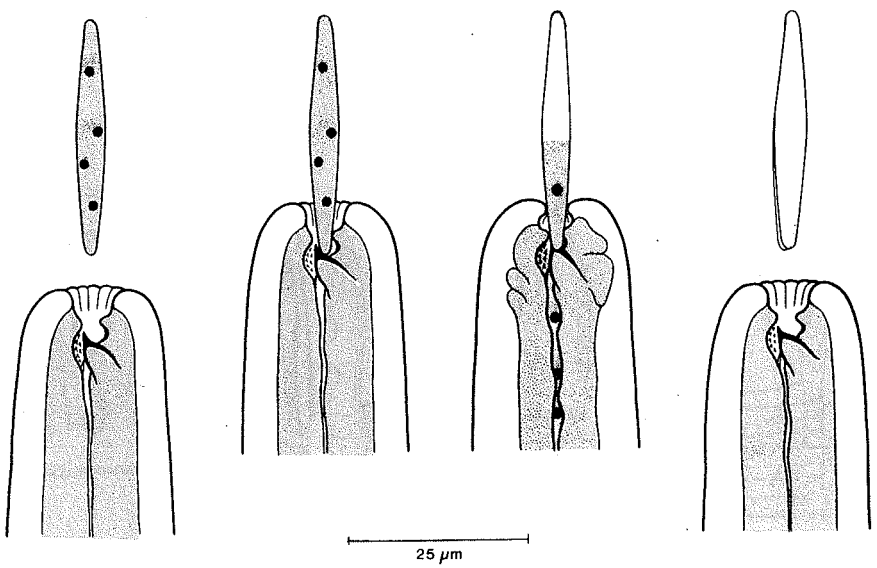

Fig. 13.—*Chromadorita tenuis*: sequence of events when the nematode feeds on the diatom *Nitzschia* sp.; after Jensen (1982).

separate, after which it sucks out the content by one or two pumping movements of the oesophagus. The gut never contained fragments of frustules of *Nitzschia*.

A disadvantage of the Wieser scheme is that it confines nematode species to a single trophic status. Non-selective feeders are in a sense omnivores; although the particle size of the food is restricted, it may include bacteria, non-living aggregates, small flagellates *etc.* Many selective feeders, either with an unarmed or armed buccal cavity, seem to be diatom-feeders, but diatoms are only numerous in shallow sediments and very little is known about the feeding of the abundant deep-sea nematodes.

An example of a 2B species is *Oncholaimus oxyuris*. Older juveniles and adults were fed with another nematode, *Panagrellus silusiae*, in cultures by Heip, Smol & Absillis (1978). It also behaves as a scavenger feeding on dead *Hydrobia ulvae*, moving into the shells of the gastropod. Juveniles and adults also concentrate around the tracks made by the polychaete *Nereis diversicolor*, where organic matter is concentrated and there is a dense growth of microorganisms. Besides a scavenger and bacterivore, it is a predator and adults, especially females, attack in small groups of 2–4 individuals oligochaetes several times longer than themselves. They pierce through the body wall and move into the body of their victim (Vranken, pers. obs.).

Bacteria and algae

Feeding of nematodes in cultures has been very important in obtaining more reliable information on their food requirements. Many species can be cultured on bacteria and on algae. Tietjen & Lee (1973) tested 20 species of algae as food for *Chromadora macrolaimoides* but only 11 were ingested in sufficient quantities and only five were able to sustain growth for many generations. Only two sustained growth indefinitely. That nematodes may be highly selective was also demonstrated in other experiments by Lee, Tietjen, Mastropolo & Rubin (1977) who offered pure cultures of different algal species to nematodes in the field and to selected nematode species in the laboratory in so-called cafeteria experiments (see also Trotter & Webster, 1984). Both these experiments again clearly demonstrated that selective recruitment to patches of particular algae took place.

For bacteria the same selectivity holds. Three species of bacteria out of sixteen tested were not taken up at all in an experiment by Tietjen & Lee (1973). Vranken *et al.* (1984a) report how of 11 species tested only one permitted optimal growth of a *Monhystera* species.

The few data existing on meiofauna grazing on microflora have been summarized by Tietjen (1980a). These studies indicate that the consumption of bacteria and algae is in the order of 0·1 to 10 μg dry wt·animal^{-1}·day^{-1}. For three nematode species ingestion varied from 14×10^{-2} μg C·day^{-1} (*M. disjuncta*), 40×10^{-2} μg C·day^{-1} (*Chromadorina germanica*), and 60×10^{-2} μg C·day^{-1} (*Rhabditis marina*). The ingestion rate of the diatom-feeder *Eudiplogaster pararmatus* was studied by Admiraal, Bouwman, Hoekstra & Romeyn (1983) by radioactive labelling of diatoms. Six or seven diatoms were taken each hour, amounting to a total daily carbon intake of 0·17 μg C. Each nematode, with a carbon content of 0·10 μg C, thus ingests about double its body carbon each day.

The effects of nematodes grazing on bacteria and algae have also been evaluated by Tietjen (1980b) and Admiraal *et al.* (1983). Direct effects on bacterial or algal biomass are difficult to estimate: a nematode community with a standing stock of 0·3 g $C \cdot m^{-2}$ would consume about 0·6 g $C \cdot m^{-2} \cdot day^{-1}$, or about 220 g $C \cdot m^{-2} \cdot yr^{-1}$. This is a very large figure compared with the annual C-input into most benthic systems. Admiraal *et al.* (1983) concluded that herbivorous nematodes are unable to decrease algal populations on tidal flats in The Netherlands. These benthic diatoms had a maximum production of nearly 2 g $C \cdot m^{-2} \cdot day^{-1}$ of which at most 100 mg C was grazed by the meiofauna. This estimate may be too low, since daily carbon intake by nematodes was estimated as 0·17 μg C. A standing stock of 1×10^6 herbivorous nematodes would thus consume 170 mg $C \cdot day^{-1}$.

The effects of nematodes on bacterial dynamics were measured by direct heat flow measurements by Pamatmat & Findlay (1983). When food was absent, sand with 7000 nematodes showed barely detectable heat production. When bacteria were added, heat production started to increase after 6 hours from a basic level of 0·1 $mJ \cdot s^{-1}$ to a peak of 0·7 $mJ \cdot s^{-1}$ 7 hours later. Then heat production levelled off again to a slightly higher level than the production with bacteria alone. The peak level of 0·7 $mJ \cdot s^{-1}$ was also reached without nematodes, but four hours earlier. Nematodes thus seem to affect bacterial population growth by prolonging the lag phase and by reducing the total amount of energy flow, although some inhibition may have been due to metabolites excreted by the nematodes.

Indirect effects of grazing have been summarized by Tietjen (1980b). Burrowing may induce advection of nutrients and oxygen within the sediments (Cantelmo, 1978, cited in Tietjen, 1980b). Tietjen (1980b) provides evidence that meiofauna may contribute to nutrient regeneration; the addition of nematodes to experimental flasks in which algae were grown axenically provoked significant increases in the levels of orthophosphate in the absence of bacteria. The secretion of mucus by producing slime trails may attract and sustain bacterial growth (Riemann & Schrage, 1978; Warwick, 1981b).

When fresh sediments are observed through a stereo-microscope nematodes can be seen gliding along an intricate network of thread-like burrows reinforced by mucus secretions (Cullen, 1973). This mucus may trap organic particles and adsorb macromolecules and thus act as substrate for the growth of microorganisms (Riemann & Schrage, 1978). This mucus-trap hypothesis has been considered as a gardening mechanism by Gerlach (1978), and this has been confirmed by Warwick (1981b) who found that the trails of *Praecanthonchus punctatus* induced the growth of very dense monospecific populations of the non-motile phase of the flagellate *Tetraselmis*. The presence of the nematode induced the formation of these non-motile cells; in cultures without nematodes all the cells remained motile. It is possible that such mechanisms are widespread but nothing is known of their occurrence in nature. More commonly observed is the growth of algae and bacteria on the body wall or within the cuticular ornamentation of the nematode itself.

Of particular interest is the occurrence of mouthless and gutless nematodes in anoxic or microxic environments. Hope (1977), Hope & Murphy (1969), and Vitiello (1970) described the occurrence of bacteria-like structures in deep-sea nematodes. Ott, Rieger, Rieger & Enderes (1982) describe the mouthless and gutless nematode *Astomonema jenneri* from polychaete tubes of an intertidal

mud-flat in North Carolina. These animals contained two types of micro-organisms in the rudiment of the gut and they occurred in near anoxic or microxic sediments rich in organic matter and hydrogen sulphide.

Detritus

The utilization of detritus by nematodes has been only rarely studied. The input of higher plants and macroalgae is an important carbon source in coastal systems. The subsequent mineralization of this detritus is predominantly a bacterial process and the impact of nematodes grazing on bacteria has been postulated to exert an effect on mineralization rates in the benthos (Johannes, 1965). This has been studied by Findlay & Tenore (1982) who investigated the rates of carbon mineralization in the presence or absence of the nematode *Diplolaimella chitwoodi*. They looked at detritus derived from a vascular plant, *Spartina*, and a red algae, *Gracilaria*. In controls without nematodes the mineralization rate amounted to 25 μg C·h^{-1}, with less than 6% of the initial dry weight being mineralized in one week. With ten nematodes ·10 cm^{-2} the maximum mineralization rate was doubled and with 50 to 1500 nematodes·10 cm^{-2} it was more than three times higher, and 9–10% of the initial dry weight was mineralized within one week. This increase in mineralization rate occurred independent of particle size. *Spartina*-detritus appeared to be more difficult to attack and, although the increase in mineralization rate in the presence of nematodes was about 50%, the amount mineralized after one week was not much different without and with nematodes present (4·8 and 5·8%, respectively). The effect of nematodes on mineralization rates thus seems to be significant, but nematodes only account for 4% of this mineralization directly. Apparently their main action is to increase bacterial metabolism. The impact of this on the benthic system could vary: for directly available detritus, such as derived from seaweeds, increased mineralization would decrease overall production of the system. For more refractory detritus the effect of nematodes may be to enhance production.

Detritus as a food source has been studied for the same species *Diplolaimella chitwoodi* by Findlay (1982a). The detritus was either dead *Spartina* or *Thalassia* from the field or *Gracilaria*, *Ulva*, and *Spartina* from cultures, and was inoculated with mixed cereals containing bacteria. Two population parameters were tested, the rate of increase r and the carrying capacity K. The rate of increase of the nematode proved to be less dependent on detritus quality, but the carrying capacity K is a straightforward function of detrital type and ration and nitrogen input was a good predictor of K. Findlay (1982a) hypothesized that systems receiving pulses of directly available detritus should exhibit population fluctuations closely tied to the rate of food supply. Conversely, systems receiving pulses of not directly available detritus should exhibit fewer sporadic fluctuations. Many detritus systems are nitrogen-limited and nitrogen input seems to be the best measure of food available to the benthos.

Uptake of dissolved organic matter

Uptake of dissolved organic matter has been reported for two oncholaimids, *Pontonema vulgaris* (Chia & Warwick, 1969) and *Adoncholaimus thalasso-*

phygas (Lopez, Riemann & Schrage, 1979). *A. thalassophygas* consistently failed to incorporate labelled microorganisms and consistently succeeded in incorporating labelled glucose. It was suggested that hatched juveniles feed primarily on dissolved organic matter released by microbial activity and that adults retain this ability but supplement their diet by scavenging and predation. *Rhabditis marina*, however, neither absorbed dissolved organic matter through its body wall nor did it ingest this material through the gut (Tietjen & Lee, 1975). Uptake of the label occurred when particulate material (small latex spheres) was added to the culture, but high levels of organic matter were used in this experiment.

PRODUCTION

There does not exist a single estimate of the production of a marine nematode in the field. Studies on the energy flow through nematode populations (Faubel, Hartwig & Thiel, 1983; Heip *et al.*, 1984; Witte & Zijlstra, 1984) are based on indirect estimations of production either by respiration or by using an annual production/biomass ratio $P/B = 9$ as proposed by Gerlach (1971). This estimate is based on the life cycle of the herbivore *Chromadorita tenuis* as studied in cultures by von Thun (1968). The wet weight of an adult varies between 0·8 and 1·3 μg. Eggs, with a weight of 25 ng, are deposited singly over 5–11 days, with an average total of 20. The embryos develop in 4–5 days and the adult stage is reached after another 12–15 days, at 20–22 °C. Five days later the first eggs are deposited. With a mortality scheme holding the population constant, the average standing stock is 3·3 μg wet weight and production is 9·8 μg. The life-cycle turnover is thus three. The same calculation was done for *Monhystera disjuncta*, with a life-cycle turnover rate of 2·2 and a daily egg production of 2–3 eggs during 8 days.

M. disjuncta has been studied extensively in our laboratory by one of us (G.V.) and its productivity was discussed by Herman, Vranken & Heip (1984). For this species complete life-tables were determined and the intrinsic rate of natural increase r_m, the stable age distribution at exponential growth, the birth rate, and several measures of generation time are known. When a stable age distribution is reached, $P/B = b$, the birth rate (Zaika, 1973). For *M. disjuncta* $P/B = 0{\cdot}18 \cdot \text{day}^{-1}$ or $65 \cdot \text{yr}^{-1}$.

The egg production of *M. disjuncta* in our cultures is very much higher than has been previously observed. Eggs are laid at a nearly constant rate of $5{\cdot}1 \cdot \text{day}^{-1}$ until, after 40 days, senescence starts rather abruptly. So, more than 200 eggs per female are produced. Another species, *Rhabditis marina*, lays between 300–800 eggs (Vanderhaeghen, pers. comm.) in cultures. These figures relate to optimum conditions, but they demonstrate that the productivity of those nematodes that have been successfully cultivated in the laboratory is very high indeed. If this high productivity is realized in the field, it is difficult to see from the existing field data. It seems that, in order to obtain the best possible estimates of actual production of nematodes in the field one may follow one of two ways: either measure the number of generations actually produced and use a life-cycle turnover of three, as this appears to be a good constant figure (Herman, Vranken & Heip, 1984); or use the adult body weight and predict production from Banse & Mosher's (1980) regression equation relating body weight and annual P/B.

The first approach requires knowledge of the annual number of generations in the field. For many species, especially smaller ones, it has been shown that production is nearly continuous and juveniles occur throughout the year (see p. 437). Only for a few, large species are generation times known and they appear to be very long, from less than one to two generations per year (Wieser & Kanwisher, 1961, for *Enoplus communis*; Smol, Heip & Govaert, 1980, for *Oncholaimus oxyuris*; and Gerlach & Schrage, 1972, for *O. brachycercus*). Indirect estimates for the annual number of generations are often based on development time in the laboratory and should be treated with caution. Several authors (Tietjen & Lee, 1973) postulate about 10–15 generations annually for species such as *Chromadorina germanica* and *Monhystera disjuncta*.

The available data have been summarized by Zaika & Makarova (1979). They calculated daily production rates C (or specific production) based on the fact that $P/B = b$, the birth rate. To evaluate the birth rate a life-table has to be constructed and to equate the birth rate with the rate of increase, as the authors do, seems hazardous. From the available literature the equation, $C = 0{\cdot}008\ T^{0{\cdot}96}$ was found. At $T = 10$ °C, specific production would thus be $0{\cdot}07{\cdot}\text{day}^{-1}$ or $27{\cdot}\text{yr}^{-1}$.

Another indirect approach to calculate production has been used by Warwick & Price (1979). They used the empirical relationship between production and respiration of short-lived poikilotherm animals proposed by McNeil & Lawton (1970), $\log P = 0{\cdot}8262 \log R - 0{\cdot}0948$ (in $\text{kcal}{\cdot}\text{m}^{-2}{\cdot}\text{yr}^{-1}$). By measuring the respiration of 16 species they arrived at a value of $P/B = 8{\cdot}4$, surprisingly close to a value of $P/B = 8{\cdot}7$ calculated by accepting a net growth efficiency of $P/P+R = 0{\cdot}38$, as found by Marchant & Nicholas (1974) for the freshwater nematode *Pelodera*.

RESPIRATION

Respiration of individual or batches of nematodes has been measured as oxygen consumption using electrodes (Atkinson, 1973) or cartesian diver respirometry (Lasserre, 1976). Respiration is most commonly expressed in nl $O_2{\cdot}\text{h}^{-1}$ per individual or unit body weight or volume (in nl) and described in a power relation $R = aV^b$. As in other poikilotherms $b = 0{\cdot}75$ on average, although Atkinson (1975) suggested a somewhat higher value $b = 0{\cdot}79$ and Zeuthen (1953) even believed that metabolism of nematodes is weight-independent. This is certainly not true but it is interesting to note that Laybourn (1979) found a varying value of b according to temperature in the freshwater nematode *Anonchus*, with b approaching one at temperatures of 20–25 °C.

The value of a is considered to be an indication of metabolic intensity (Schiemer & Duncan, 1974); it represents the repiration of a weight or volume unit nematode and is thus not identical to respiration per unit weight, a confusion often found in the literature. As an example, a nematode with dry weight 0·3 μg and a respiration of 0·6 nl $O_2{\cdot}\text{h}^{-1}{\cdot}\text{ind.}^{-1}$ has a weight-specific respiration of 2 nl $O_2{\cdot}\text{h}^{-1}{\cdot}\mu\text{g}^{-1}$ and a metabolic intensity of 1·48 nl $O_2{\cdot}\text{h}^{-1}{\cdot}\mu\text{g}^{-1}$.

The literature on nematode respiration prior to 1979 has been reviewed by Warwick & Price (1979), who added many new data (Table XV). The value of b

TABLE XV

Nematode respiration rates at 20 °C, denoted by log a' values: n = number of determinations; after Warwick & Price (1979); S Dep, *selective deposit-feeders;* Non S Dep, *non-selective deposit-feeders;* Epig, *epigrowth-feeders;* Pred/omn, *predators and omnivores;* S, *saltmarsh;* M, *mudflat;* A, *algae;* FS, *fine sand (anaerobic);* Ter, *terrestrial;* FW, *freshwater; 1, Wieser & Kanwisher (1961); 2, Teal & Wieser (1966); 3, Wieser* et al. *(1974); 4, Scheimer & Duncan (1974); 5, Warwick & Price (1979)*

Species	Log *a'*	*n*	Feeding group	Habitat	Reference no.
Oncholaimus campylocercoides	0·386	6	Pred/omn	S	2
Oncholaimus paralangrunensis	0·378	5	Pred/omn	S	2
Axonolaimus spinosus	0·370	3	Non S Dep	S	2
Panagrolaimus rigidus	0·361	40	Non S Dep	Ter	4
Tripyloides gracilis	0·343	10	Non S Dep	S	2
Metoncholaimus pristiurus	0·334	13	Pred/omn	S	2
Bathylaimus 'kanwisheri'	0·328	1	Non S Dep	S	2
Viscosia viscosa	0·188	55	Pred/omn	M	5
Bolbellia tenuidens	0·183	2	Pred/omn	S	2
Enoplus communis	0·128	80	Pred/omn	A	4
Mesotheristus setosus	0·113	16	Non S Dep	S	2
Axonolaimus spinosus	0·105	6	Non S Dep	S	1
Odontophora 'papusi'	0·057	5	Non S Dep	S	2
Aphelenchus avenae	0·053	22	Plant parasite		4
Sphaerolaimus hirsutus	0·027	38	Pred/omn	M	5
Theristus 1	0·019	12	Non S Dep	S	1
Axonolaimus paraspinosus	0·002	26	Non S Dep	M	5
Innocuonema tentabundum	−0·012	5	Epig	M	5
Halichoanolaimus dolichurus	−0·030	4	Pred/omn	S	2
Anticoma litoris	−0·042	6	S Dep	S	2
Mesotheristus setosus	−0·047	40	Non S Dep	M	5
Paracanthonchus caecus	−0·048	7	Epig	S	2
Mesotheristus erectus	−0·062	8	Non S Dep	S	1
Ptycholaimellus ponticus	−0·081	5	Epig	M	5
Praeacanthonchus punctatus	−0·091	17	Epig	M	5
Odontophora setosa	−0·092	2	Non S Dep	M	5
Sphaerolaimus balticus	−0·112	5	Pred/omn	M	5
Sphaerolaimus 2	−0·121	6	Pred/omn	S	1
Dichromadora cephalata	−0·133	5	Epig	M	5
Atrochromadora microlaima	−0·142	5	Epig	M	5
Cylindrotheristus normandicus	−0·150	5	Non S Dep	M	5
Mesotheristus erectus	−0·154	16	Non S Dep	FS	3
Terschellingia longicaudata	−0·170	4	S Dep	M	5
Terschellingia sp.	−0·188	1	S Dep	S	2
Sabatieria pulchra	−0·197	1	Non S Dep	M	5

Odontophora setosoides	−0·199	4	Non S Dep	S	1
Spirinia parasitifera	−0·203	6	S Dep	S	2
Theristus 3	−0·204	3	Non S Dep	S	1
Hypodontolaimus 1	−0·204	4	Epig	S	1
Hypodontolaimus geophilus	−0·218	3	Epig	S	1
Tobrilus gracilis	−0·261	30	Non S Dep	FW	4
Terschellingia communis	−0·277	4	S Dep	M	5
Sphaerolaimus 1	−0·278	5	Pred/omn	S	1
Metachromadora vivipara	−0·424	24	Epig	M	5
Trefusia schiemeri	−0·448	6	S Dep	FS	3
Spirinia hamata	−0·600	5	Epig	S	1
Nannolaimoides decoratus	−0·885	10	Epig	FS	3
Spirinia gnaigeri	−1·081	5	S Dep	FS	3

was assumed constant ($b = 0{\cdot}75$) and all data were re-calculated using this value. The conversion factors used are those of Wieser (1960a), who estimated density equal to 1·13 and a dry weight/wet weight relationship of 0·25. An animal 1 mm in length and 35 μm wide all over has a volume of 1 nl, a wet weight of 1·13 μg, and a dry weight of 0·28 μg. To translate metabolic intensity log *a*, based on volume, to dry weight, 0·41 has to be subtracted from the values given by Warwick & Price (1979).

The values of metabolic intensity on a volume basis vary between 0·386 for *Oncholaimus campylocercoides* and −1·081 for *Spirinia gnaigeri, i.e.* from 2·43 nl $O_2 \cdot h^{-1} \cdot nl^{-1}$ and 0·08 nl $O_2 \cdot h^{-1} \cdot nl^{-1}$. The distribution of log *a* values is given in Figure 14. Most species have a log *a* value between −0·24 and −0·03. When transformed to respiration per unit body weight, two groups can be found (Fig. 15): one with a respiration between 0·14 and 0·43 nl $O_2 \cdot h^{-1} \cdot \mu g$ dry wt^{-1} and one with a repiration between 0·86 and 1·00 nl $O_2 \cdot h^{-1} \cdot \mu g$ dry wt^{-1}. The mean respiration for all nematodes is 0·412 nl $O_2 \cdot h^{-1} \cdot \mu g$ dry wt^{-1}. Fast respiring species include two *Oncholaimus* species, *Axonolaimus spinosus*, and *Tripyloides gracilis*. The slowest respirers are *Spirinia hamata, S. gnaigeri*, and *Nannolaimoides decoratus*.

According to feeding types metabolic intensity differs although no significant difference exists between types 1A and 2A and between 1B and 2B (Table XVI). The average per species is −0·081, the average over the four feeding types is −0·121. This corresponds to a metabolic intensity of 0·76 nl $O_2 \cdot h^{-1} \cdot nl^{-1}$ or 0·69 nl $O_2 \cdot h^{-1} \cdot \mu g$ wet wt^{-1}. To obtain log respiration 0.75 log *V* (or *W*) has to be added to log *a*. For a nematode with a body weight between 0·5 and 1·5 μg wet wt, total respiration would be between 0·41 and 0·94 nl $O_2 \cdot h^{-1} \cdot ind.^{-1}$ or between 10–22 nl $O_2 \cdot day^{-1} \cdot ind.^{-1}$ and 3·6–8·2 μl $O_2 \cdot yr^{-1} \cdot ind.^{-1}$. All these values hold at 20 °C.

From this value an estimate of total community respiration would be between 7·2 and 5·5 litres $O_2 \cdot yr^{-1}$ per g wet wt. Wieser & Kanwisher (1961), Teal & Wieser (1966), and Warwick & Price (1979) calculated total community respiration of nematodes at 20 °C and arrived at a similar figure of 6·0 l $O_2 \cdot m^{-2} \cdot yr^{-1}$ per g wet weight. A correction for field temperatures is necessary when applying this figure but the available information suggests that it could

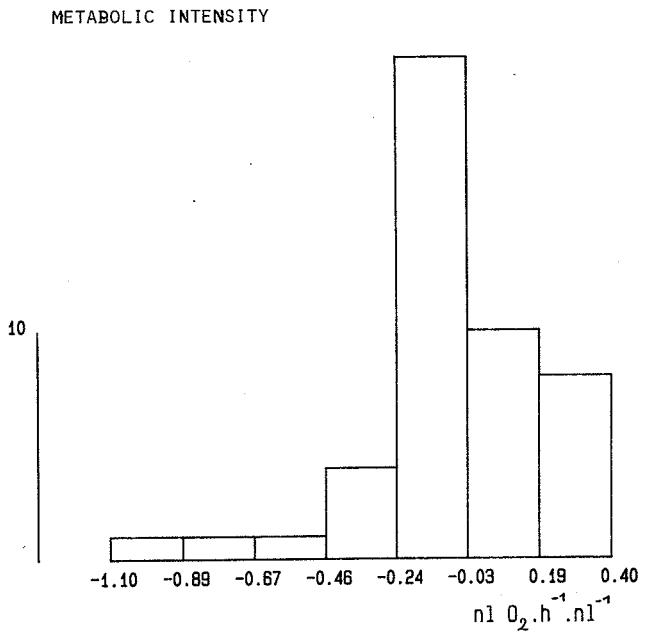

Fig. 14.—Values of metabolic intensity on a volume basis: distribution of log *a*-values.

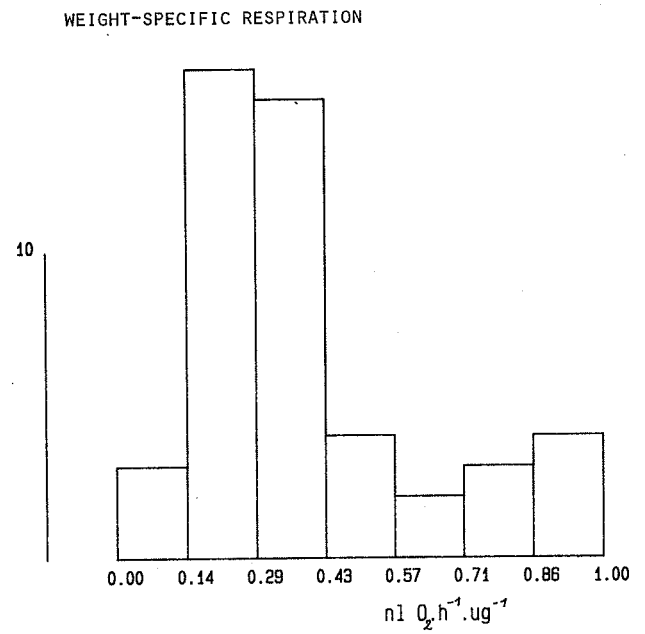

Fig. 15.—Values of metabolic intensity on a volume basis: distribution of weight-specific respiration.

TABLE XVI

Metabolic intensity of feeding types in marine nematodes: values of log a in nl $O_2 \cdot h^{-1} \cdot nl^{-1} \pm SE$ based on n species

	log *a*	*n*	*V* (nl)	Wet wt (μg)	Dry wt (μg)
Selective deposit-feeders	−0·344 ± 0·095	7	0·45	0·50	0·13
Non-selective deposit-feeders	0·018 ± 0·059	18	1·04	1·14	0·28
Epistratum-feeders	−0·258 ± 0·076	11	0·55	0·61	0·15
Predators and omnivores	0·101 ± 0·076	11	1·26	1·38	0·34

be used for making approximate budgets when original respiration data are not available (Warwick & Price, 1979). It must be borne in mind, however, that all data are from intertidal habitats and extrapolation to other biotopes seems risky.

The effect of temperature on respiration has been studied by Price & Warwick (1980) for *Sphaerolaimus hirsutus* and by Wieser & Schiemer (1977) for *Trefusia schiemeri* and *Trichotheristus floridianus*. Q_{10} values of 1·17 were found for *Sphaerolaimus hirsutus* between 5° and 25 °C and about 2 for *Trefusia schiemeri*. For *Sphaerolaimus hirsutus*. respiration is related to temperature as $\log R = 0{\cdot}180 + 0{\cdot}0069\ T$, with R in nl $O_2 \cdot h^{-1} \cdot$ind.$^{-1}$. Price & Warwick (1980) tentatively proposed that animals living in habitats where food supply is stable should have a low Q_{10}, around 1, whereas animals living in habitats with a variable food supply may have a higher Q_{10} of around 2. Too few data exist at present to see if this generalization really holds.

Conversion factors

To convert respiration into other units some difficulties exist. Sikora, Sikora, Erckenbrecker & Coull (1977) determined some conversion factors for marine nematodes which are summarized in Table XVII. To convert oxygen consumption to carbon metabolized most often 1 l O_2 is considered equivalent to 0·4 g C. This conversion factor depends on assumptions concerning the respiratory quotient $RQ = \Delta CO_2/\Delta O_2$. For the respiration of fats $RQ = 0{\cdot}71$, for proteins $RQ = 0{\cdot}71$ and for carbohydrates $RQ = 1$. With an $RQ = 0{\cdot}71$, the conversion factor would be $8{\cdot}4/22{\cdot}4 = 0{\cdot}375$, when carbohydrates dominate the food the conversion would be 0·535. When fermentation or anaerobic respiration is predominant, the respiratory quotient would be larger than 1 and the use of a conversion factor 1 l O_2 = 0·4 g C would no longer be justified.

Anaerobic respiration

Many benthic animal species have evolved very efficient anaerobic pathways yielding as much net energy as aerobic respiration (Pamamat, 1980). Howarth

TABLE XVII

Conversion factors for energy budgets in marine nematodes

Factors				Reference
Wet weight in μg = volume in nl × 1·13				
Wet weight	100%			
Dry weight	25%	100%		Wieser, 1960a
Ash-free dry weight	20%	80%	1 μg	Sikora *et al.*, 1977
Carbon	10·6%	42%	0·53 μg	Sikora *et al.*, 1977
Calorific equivalent			6·12 mcal	Sikora *et al.*, 1977
Calorific equivalent			25·58 mJ	

& Teal (1980) state that in salt marshes sulphate reduction is many times more important in the degradation of organic matter than oxygen respiration and denitrification combined. Microbial production is as high as in aerobic sediments and nematodes are the most important grazers of this production.

Although these anaerobic pathways are certainly very important in many environments, little information on nematodes is available (Wieser, Ott, Schiemer & Gnaiger, 1974).

EXCRETION

Nothing is known about excretion in marine nematodes. For terrestrial nematodes Wright & Newall (1976) found that nitrogen excretion is dependent on body size with $b = 0{\cdot}75$, and a nematode of 1 μg wet wt would excrete 1·92 μmol $N{\cdot}h^{-1}{\cdot}g^{-1}$. In mammals, 1 g of nitrogen excreted corresponds to 5·94 l O_2 respired.

In a soil microcosm significantly more N was mineralized, as ammonium, in the presence of nematodes than with bacteria alone (Coleman *et al.*, 1977). Soil nematodes have high C:N ratios (8:1 to 12:1) in comparison with bacteria (3:1 to 4:1) and thus must release N as a waste product (Anderson *et al.*, 1983). If the same is true in marine systems, the impact of nematodes on the nitrogen cycle may be correspondingly more important than on the carbon cycle.

ENERGY FLOW THROUGH NEMATODES

The energy flow through nematode populations can be written as $C = P + R + U + F$ (Crisp, 1971), in which all terms must be written in the same units, and where C is consumption or ingestion, P is production and can be divided into production due to growth and gonad output, R is respiration, and U and F are soluble and particulate waste products, respectively. A first trial to establish a carbon budget was that of Tietjen (1980b) for females of three species (Table XVIII). As this budget was termed preliminary, we shall not discuss it in detail and shall only use it to clarify some problems. First, assimilation efficiency seems to be low, and much lower for *Chromadorina germanica*, a herbivore,

TABLE XVIII

A carbon budget for females of three nematode species (from Tietjen, 1980b): all values in ng C·day^{-1}

	Chromadorina germanica	*Monhystera disjuncta*	*Rhabditis marina*
Consumption *C*	400	144	600
Assimilation *A*	25	26	155
Respiration *R*	5·3	5·3	5·3
Production *P'*	19·5	21	150
Growth *P*	6·7	5	54
Egg production *G*	12·8	16	96
Efficiencies (%)			
A/C	6·2	18·3	25·8
P'/A	78·7	79·8	96·5
P/A	26·8	19·2	34·8

than for bacterial feeders. As herbivores often do not, however, ingest the cells wholly, this may be an under-estimate. The second point is that production efficiency is very high, and that most of the energy is channelled into egg production.

Warwick (1981a) studied production efficiency of the monhysterid *Diplolaimelloides bruciei*, and the influence of temperature and salinity on this. Daily *P/B* was measured as the rate of increase *r* (instead of the birth rate, giving a slight under-estimation) and respiration was also expressed in units of body weight. *r* was a rather complex function of temperature which was linearized as $r = -0{\cdot}067 + 0{\cdot}0134\ T$. *r* was highest at 26‰ *S* and about twice higher than at both higher and lower salinities. Respiration increased exponentially with temperature between 5° and 25 °C as $\log R = -0{\cdot}7238 + 0{\cdot}05957\ T$. Fecundity, expressed as the number of eggs produced daily by a female, was also a linear function of temperature $f = -1{\cdot}429 + 0{\cdot}286\ T$. The proportion of adults in the population was independent of temperature (13·6%) and the sex-ratio was in favour of males (65·6%). From these figures the biomass of eggs produced per unit biomass of the entire population was calculated as $Pr = -0{\cdot}00826 + 0{\cdot}00165\ T$.

The linear relationship between *r* and temperature, or between production and temperature, was also found for *Chromadorina germanica* (Tietjen & Lee, 1977a) and *Oncholaimus oxyuris* (Heip, Smol & Absillis, 1978). Whereas the slope is similar for *Chromadorina germanica* and *Diplolaimelloides bruciei* (0·0145 and 0·0134, respectively), it is about ten times lower for *Oncholaimus oxyuris* (0·0013).

The energy budget for *Diplolaimelloides bruciei* is given in Table XIX, with the same symbols as for Table XVIII. The same features are apparent as in Tietjen's (1980b) estimates. Production efficiency is very high, between 0·7 and 0·9 between 10 and 30 °C. In females, all of this production is due to eggs and

TABLE XIX

Energy budget for Diplolaimelloides bruciei *(total population): values in J* $(J^{-1} \cdot day^{-1})$ *(after Warwick, 1981b)*

	Temperature (°C)		
	5	15	25
P growth (*P*)	0	0·151	0·214
P eggs (*G*)	0	0·021	0·030
P total (*P'*)	0	0·172	0·244
R	0·007	0·026	0·101
$P'/(P'+R)$ (%)	0	87	71
$P/(P+R)$ (%)	0	45	45
$G/(G+R)$ (females)	0	90	77

efficiencies were again very high. Taking into account that females represent only a small fraction of the population, growth efficiency must, however, also be very high in the juveniles. Reproductive effort, $G/(G+R)$, is in the order of 77–90%, and was calculated from the ratio of egg volume on female volume. It may be (Herman, Vranken & Heip, 1984) that the energy content of eggs is much lower than that of adults, since the weight of neonates is often much lower than the egg weight and considerable respiration may occur during the egg stage.

A detailed analysis was done by Schiemer (1982a,b; 1983) on the freshwater species *Plectus palustris* and the soil-dwelling *Caenorhabditis briggsae*, a small and extremely rapid developing species. The weight of an adult female is about 0·4–0·5 μg wet wt. The respiration rate of this species depends on food concentration: at a density of 5×10^7 cells·ml^{-1}, oxygen consumption was 1·23 nl·h^{-1}·μg^{-1}, at a food level of 10^8 cells·ml^{-1} oxygen consumption was 1·64 and at higher food concentrations oxygen consumption remained equal, between 3·2 and 3·7 nl O_2·h^{-1}·μg^{-1}. Production of the species and the P/R ratio vary throughout its life cycle and the P/R ratio is also dependent on food concentration; it varies from 0·62 at 5×10^8 cells·ml^{-1} to 1·77 at 10^{10} cells·ml^{-1}. Over the whole life cycle, from hatching until the end of the reproductive stage, the total amount of energy assimilated is more than double at 10^{10} cells·ml^{-1} than at 5×10^8 cells·ml^{-1} (Table XX).

In general, respiration increases linearly with food supply but production increases hyperbolically. This is probably not due to an increased intake of food only, as ingestion appears to be proportional to food availability (Nicholas, Grassia & Viswanathan, 1973), but to a decrease in assimilation efficiency.

The comparison between these two species yields some interesting results (Schiemer, 1983). Over its whole life cycle, *Plectus palustris* has $P = 161$ mJ and $R = 33$ mJ, so that production efficiency is 83%. In the shorter living *Caenorhabditis briggsae* $P = 170$ mJ and $R = 100$ mJ, production efficiency

TABLE XX

Energy budgets for Caenorhabditis briggsae *at three food concentrations: values in* $\mu J \cdot 10\ h^{-1}$ *(after Schiemer, 1982b)*

	Food concentration (cells/ml)		
	5×10^8	10^9	10^{10}
P growth (%)	11·6	10·2	10·0
P eggs (%)	36·6	43·0	53·0
P total (%)	48·2	53·2	63·0
R (%)	51·8	46·8	37·0
$A = P + R$ ($\mu J \cdot 10\ h^{-1}$)	11·9	19·3	27·2

thus being only 63%, which is still very high. Reproduction accounts for 84% of total production in *C. briggsae*, for 94% in *Plectus palustris*, values that are again astonishingly high.

Whether this enormous productivity is realized in the field depends strongly on food availability. The dependence of assimilation on food concentration can be described by a Michaelis–Menten equation. The food concentration at which assimilation was half its maximum was 0·75 mg dry wt·ml^{-1} for *Caenorhabditis briggsae* and 0·10 mg dry wt·ml^{-1} for *Plectus palustris*. The threshold at which $A = R$ and $P = 0$ was about 0·1 mg dry wt·ml^{-1} for *Caenorhabditis briggsae* and 0·025 mg dry wt·ml^{-1} for *Plectus palustris*.

Oligotrophic lakes have bacterial biomass lower than 0·01 mg dry wt·ml^{-1}, whereas in eutrophic lakes this is between 0·02 and 1 mg dry wt·ml^{-1}.

Joint (1978) showed numbers on an intertidal mud-flat from 1×10^6 to 1×10^9 cells·g^{-1} wet sediment, or about twice these values for the amounts per ml of interstitial water. These densities represent anything from threshold conditions to abundant food supply and much more study is necessary.

Fallon, Newell & Hopkinson (1983) found bacterial densities between 0·97 $\times 10^9$ cells·ml^{-1} wet sediment in subtidal stations 15 km offshore and 8·1 $\times 10^9$ cells·ml^{-1} wet sediment in a salt marsh. Production, as measured by thymidine uptake, was 36·5 g C·m^{-2}·yr^{-1} 15 km offshore and 296 g C·m^{-2}·yr^{-1} 250 m offshore. There is still much uncertainty in these figures and more study is needed; as marine nematodes are, however, less productive than *Caenorhabditis briggsae*, bacterial production in the shallow areas of the sea may be of the order of magnitude at which nematode production is not seriously limited.

The apparently very high production efficiencies have not been taken into account in existing estimates of carbon flow through nematode populations.

We shall revise here the estimates given by Heip, Herman & Coomans (1982) and Heip, Herman & Vincx (1984). These authors discuss two contrasting situations in the Belgian coastal waters of the Southern Bight of the North Sea. One is a linear sandbank in a highly dynamic environment (the Kwintebank), the other a series of stations in shallow, polluted waters with a

high input of organic material. Production estimates were based on respiration, amounting to 2·3 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ in coastal waters and 1·06 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ on the Kwintebank. When assuming that production efficiency is 80%, then production in the coastal waters would be 9·2 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ since food is probably not limiting there. Since assimilation efficiency is again low, around 20% for bacterivores, the total consumption of bacteria by these nematodes would amount to 57 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$, a very significant part of the total input into the benthos. Conversely, when assuming that each nematode eats about double its weight per day (see p. 461), the total consumption would be 1·4 g dry $wt{\cdot}m^{-2}{\cdot}dry^{-1}$ or 511 g dry $wt{\cdot}m^{-2}{\cdot}yr^{-1}$ or about 200 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$. This figure is even higher.

Much more study is necessary before such figures can be more than order of magnitude indications; but as such they show that nematodes are very important components of benthic systems. This has also been shown by Warwick & Price (1979) for the Lynher estuary, where respiration plus production of nematodes is minimum 29·7 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ and consumption, assuming that a nematode eats about double its body weight each day, would amount to an astonishing 600 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$.

That the extrapolation of general regression equations may yield contrasting results is shown in the study of Witte & Zijlstra (1984) on an intertidal flat in the Wadden Sea. Nematodes number on average 2117 ind.·10 cm^{-2} with an average standing stock of 0·60 g dry $wt{\cdot}m^{-2}$. Respiration and production were estimated using some general equations. For respiration Banse's (1982) regression between biomass and respiration for larger invertebrates was used, $R = 5{\cdot}4\ W^{0{\cdot}75}$ at 20 °C. This yields a value of 2·08 nl $O_2{\cdot}h^{-1}{\cdot}ind.^{-1}$, compared with the value of 0·75 nl $O_2{\cdot}h^{-1}{\cdot}ind.^{-1}$ we calculated from the data in Warwick & Price (1979). For the nematodes total this would amount to 7·5 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$. In Witte & Zijlstra's further calculations a P/B-ratio of 8·5 for nematodes (also based on a figure of Warwick & Price, 1979) gives a nematode production of 5·1 g dry $wt{\cdot}m^{-2}{\cdot}yr^{-1}$ or 2·14 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$. Total assimilation thus calculated is 9·6 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$. If we assume a production efficiency of 80%, total assimilation would be 37·5 or 13·5 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ and total consumption would be 180 or 67 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ (depending on which respiration estimate is used). These discrepancies strongly indicate the need for more research in this area and caution against the use of general equations which may not be at all applicable to nematodes.

POLLUTION STUDIES

FIELD STUDIES

The influence of pollution on nematodes has received little attention until the last few years. Oil pollution in intertidal and shallow subtidal areas has been studied most intensively. A decrease in nematode density after contamination with hydrocarbons has been demonstrated on several beaches (Wormald, 1976; Giere, 1979; Boucher, 1980b), but not on others (Green, Bauden, Gretney & Wono, 1974) and not in sublittoral sands (Elmgren, Hansson & Sundelin, 1980; Elmgren *et al.*, 1983; Boucher, 1980b). An obvious decrease in nematode abundance after an oil spill has often been followed by explosive development

of some few opportunistic species within one year (Wormald, 1976; Giere, 1979). After the Amoco Cadiz spill (Boucher, 1980b), however, there was no such explosive development on the beaches.

After an oil spill in La Coruña (northern Spain), *Enoplolaimus litoralis* became extremely dominant; many specimens had ingested oil droplets covered with bacteria. In the intestine of *Bathylaimus* sp. and *Tripyloides* sp., oil particles were found surrounded by clouds of bacteria (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, 1980b). This was due, on the one hand, to an increase of *Anticoma ecotronis, Sabatieria celtica, Paracyatholaimus occultus,* and *Calomicrolaimus montrosus,* 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, Gourbault, de Panafieu & Helléouet (1981) also examined the same polluted area (mainly Roscoff Beach and Bay of Morlaix) and found that mortality 10 days after the oil input was not important. After one month, density decreased; mortality was especially important in the surface sand layers while in the deeper layers meiofauna was found in the process of spring reproduction. After six months, nematodes became extremely dominant and accounted for 90% of the meiofauna.

In the Adriatic Sea, the density and distribution of sublittoral meiofauna is not influenced by raw domestic sewage (Vidakovic, 1983). The effects of heavy metal pollution have been studied by Lorenzen (1974), Tietjen (1977, 1980a) and by Heip *et al.* (1984) in monitoring field studies and in the laboratory by Howell (1982a,b, 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 (containing 10% H_2SO_4 and 14% $FeSO_4$).

Tietjen (1977) found that heavy metals (expressed in mg l^{-1} by weight of the total heavy metal concentration; *i.e.* Cd, Cr, Cu, Hg, Mn, Pb, Zn) did not affect nematode populations in Long Island sublittoral muds, although a slight decrease in diversity was obvious. Tietjen (1980a) examined the nematodes from the New York Bight Apex, a sandy sediment area with high heavy metal content and organic carbon loads. The amounts of heavy metal contamination were between 3·0–302·0 mg $Cr{\cdot}l^{-1}$; 3·0–361·0 mg $Cu{\cdot}l^{-1}$; 3·0–47·0 mg $Ni{\cdot}l^{-1}$; 8·5–141·5 mg $Pb{\cdot}l^{-1}$; 7·5–580·0 mg $Zn{\cdot}l^{-1}$. High concentrations of the contaminants in medium sands may result in lowered abundance of the nematode families which normally live in this kind of sediment: Chromadoridae, Desmodoridae, and Monoposthiidae. Other species, such as *Sabatieria pulchra,* which are normally associated with finer sediments, increase in abundance. This species is already adapted for living under low dissolved oxygen concentration and/or high organic content (it lives mostly in muddy sediments).

Heip *et al.* (1984) examined the composition and density of the meiofauna of the Belgian coastal waters (North Sea). The impact of the Western Scheldt river, a highly polluted stream, is reflected in a decrease in diversity on all taxonomic levels. In the coastal zone, nematodes are dominant and represent

more than 90% of the meiofauna on all stations; they are the only animal group that survives in normal or even greater abundance, albeit with lower diversity. Nematode richness (number of species) is significantly correlated with heavy metal content (*e.g.* 2–20 mg $Cu \cdot l^{-1}$; 4–17 mg $Mn \cdot l^{-1}$; 15–124 mg $Pb \cdot l^{-1}$; 41–154 mg $Zn \cdot l^{-1}$). In the highly polluted part of the Belgian coast (most close to the mouth of the Western Scheldt) only non-selective deposit-feeders are the meiofaunal component which survive in high density, but with few species per station (2–5): *S. breviseta, S. vulgaris, Daptonema tenuispiculum, Metalinhomoeus* n. sp., and *Ascolaimus elongatus.*

A matter of debate in the last few years has been the use of nematodes (and meiofauna in general) as a possible tool for detecting pollution. Marine nematodes have been suggested as possible pollution indicators as they possess some characteristics such as a short life-span and high diversity which makes them potentially useful in ecological monitoring (Heip, 1980). Three tools are commonly used with meiofauna as pollution indicators: (1) the nematode:copepod ratio; (2) the log-normal distribution of individuals over species; and (3) diversity indices or graphical methods (*k*-dominance curve).

Raffaelli & Mason (1981) indicate that copepods may be more sensitive to environmental stress than nematodes, so that a high nematode:copepod ratio may be indicative of polluted situations. The ratio of nematodes to copepods increases also with decreasing particle size, but ratios from polluted sites were always extremely high and it is proposed that the ratio is a tool for monitoring organic pollution of sandy beaches. Ratios from clean beaches were low and always less than 100, even for muddy sites; all intertidal sites (fine as well as coarse) with ratios exceeding 100 were polluted with organic material (sewage). An increase in the abundance of deposit-feeding nematodes (which profit from the organic material associated with the sewage) and a decrease in copepods which appear generally more sensitive to environmental stress (McIntyre, 1977) are the probable cause for the increase of the ratio. Some sublittoral ratios from unpolluted sites were high, but never approached the very high values characteristic of polluted intertidal sites. The sublittoral ratios also increased with depth. It is obvious that this ratio must be used with caution as this index is also largely affected by sediment granulometry. Coull, Hicks & Wells (1981) dispute that a single ratio is appropriate to describe the very complex meiofaunal community structure. Factors which enormously influence this ratio are horizontal distribution and seasonal variability.

Warwick (1981c) proposes refinement of the ratio based on the trophic dynamic aspects of the meiofauna. He assumed that food is the factor which limits energy flow through the nematode and copepod community; in that case, the total number of copepods should be proportional to the number of type 2A nematodes 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 (1981c) suggests that pollution might be indicated by ratios around 40 for fine sediments and 10 for sands. These values are considerably lower than the values of over 100 proposed by Raffaelli & Mason (1981). Vidakovic (1983) even found a totally opposite trend in the ratio of nematodes to copepods. In Adriatic sublittoral stations, which are constantly influenced by

sewage, the number of copepods increases more than the number of nematodes. This controversy indicates that one should be very careful when using the ratio between nematodes to copepods, without further information on the natural variability and the situation before pollution.

Gray & Mirza (1979) suggested an intrinsic probability-plotting method to detect pollution-induced disturbances. This method is based on the frequency distribution of species abundances; deviation from a log-normal distribution of individuals per species may indicate a disturbed or polluted assemblage. They propose the probability paper method of estimating goodness-of-fit to the log-normal distribution. This method has some restrictions; samples should be very large (to prevent effect of patchiness) and this may be problematic for marine nematodes.

Shaw, Lambshead & Platt (1983) and Lambshead, Platt & Shaw (1983) proposed another method for detecting differences among assemblages of marine benthic species (*e.g.* nematodes). Shaw *et al.* (1983) suggested that ranked species abundance curves (RSA-curves) are a sensitive tool in detecting disturbances in the community, as is the index *d* (*i.e.* the proportional abundance of the most abundant species). Where no single species shows overwhelming dominance, it is also interesting to consider the combined dominance of the two, three, . . . *k*, most abundant species (Lambshead *et al.*, 1983). By plotting *k*-dominance (% cumulative abundance) against *k* (species rank) in a so-called *k*-dominance curve, it is possible to 'describe' the diversity pattern of the community. When the *k*-dominance curves of two communities intersect, the communities are not comparable in terms of intrinsic diversity. For an extensive discussion of the last method, we refer to Lambshead *et al.* (1983). As an example of several methods used, we show the data of Platt (1977a), discussed by Shaw *et al.* (1983) and by Lambshead *et al.* (1983).

Figure 16 (A–D) compares the log-transformed species abundances (Gray & Mirza, 1979) from the nematode assemblages in Strangford Lough, Northern Ireland at high (H), mid (M) and low (L) tide level (Fig. 16 A and B) with the RSA curves and *k*-dominance curves of the same data (Fig. 16 C and D). The different kinds of presentation of the data all show the same trends in the nematode assemblages from high to low tide. The dominance curves have the advantage that only a minimum sample size of about 150 individuals is required. For transformation of the abundances, very large samples are necessary.

A combination of trophic diversity (expressed in a trophic index $\Sigma\theta^2$) (θ = percentage of each feeding type) and species richness, provides for the highly polluted Belgian coast a good indication of the influence of pollution (Heip *et al.*, 1984). The relation between the number of species and the trophic index is shown in Figure 17. When non-selective deposit-feeders dominate, the number of species is always low. On moderately polluted stations, type 1B is already the dominant group, but species number still drops when the heavy metal content of the sediment increases. The less polluted sandy stations are always more diverse, with trophic indices approaching 0·25. The high dominance of non-selective deposit-feeders is, however, also correlated with a high silt content. Effects of pollution and effects of sediment granulometry are very often difficult to distinguish.

This review of marine pollution monitoring studies using nematodes shows the difficulties and controversies in the interpretation of observed changes. It is

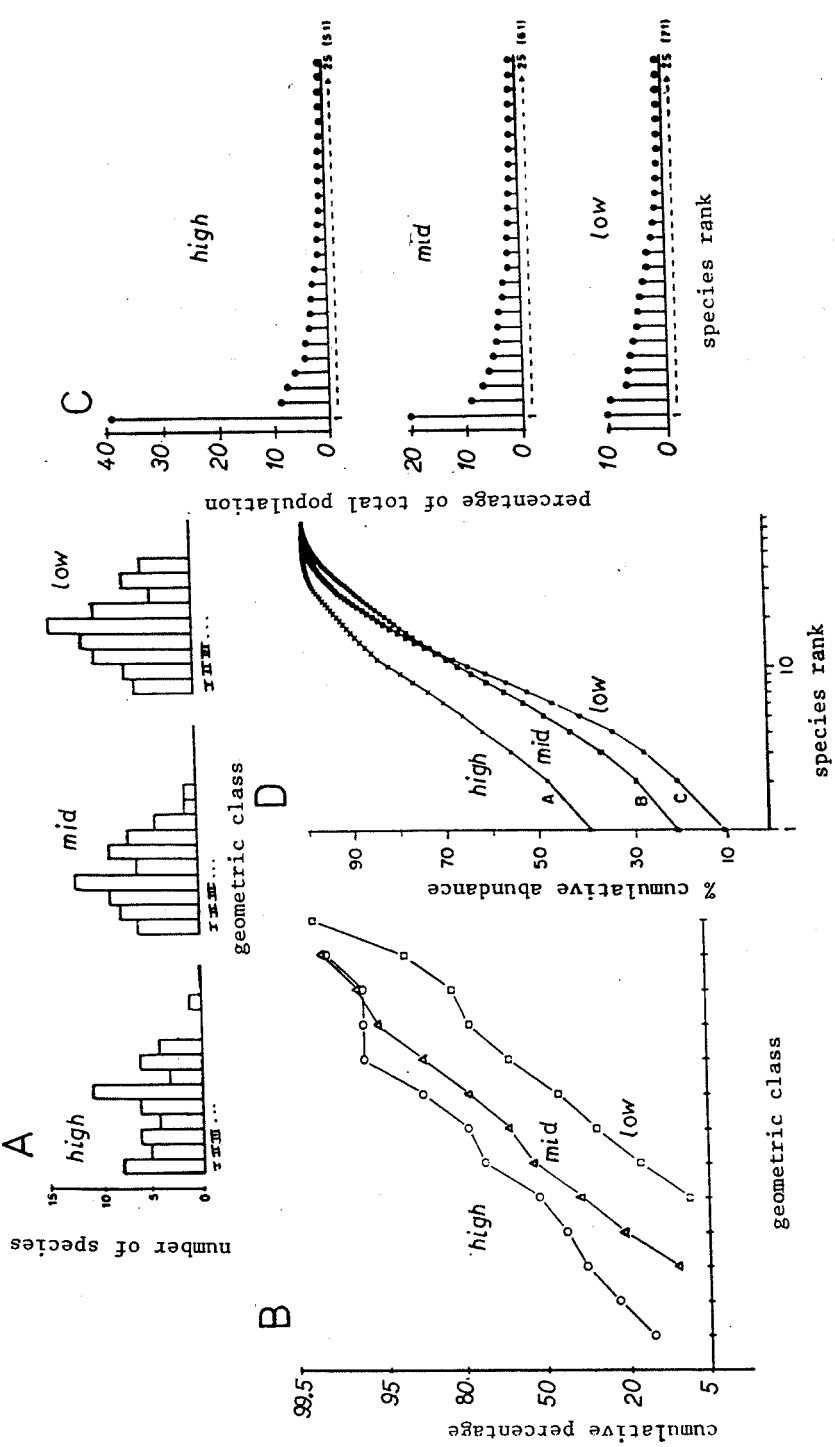

Fig. 16.—A, log-transformed species abundances from nematode assemblages at high, mid and low tide level in Strangford Lough, N. Ireland (after Platt, 1977a in Shaw, Lambshead & Platt, 1983). B, probability plot of the same data (Platt, 1977a): X-axis indicates × 2 geometric class; first point of each curve represents class I (*i.e.* the curves are staggered); after Shaw *et al.* (1983). C, RSA (rank species abundance) curve of the 25 most common species from Strangford Lough: data with the total number of species shown in parentheses; after Platt (1977a), Platt & Warwick (1980), and Shaw *et al.* (1983). D, *k*-dominance curves for the three nematode assemblages (same data from Platt, 1977a, in Lambshead *et al.*, 1983).

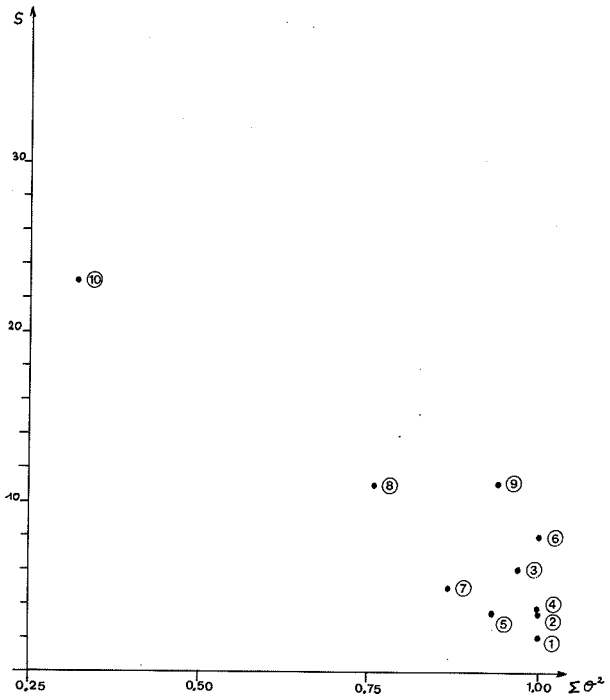

Fig. 17.—The relation between the number of species (S) and the trophic index ($\Sigma\theta^2$): number in circle indicates degree of heavy metal pollution, 1 highest → 10 lowest; after Heip, Herman & Vincx (1984).

very hard to distinguish pollution induced from natural changes, as in most cases the pre-pollution situation is not well known. Density in general is not much affected by pollution, whereas diversity generally seems to decrease. Pollution is often accompanied by general changes in sediment characteristics; the lethal effect of a pollutant or the change in habitat texture may be responsible for the observed changes. We know that some nematode species are resistant to high levels of pollution and anaerobiosis. The effect of *e.g.* heavy metals on nematode population dynamics, however, can only be studied in the laboratory.

LABORATORY STUDIES

Despite their ecological importance, and their significant rôle in all marine and brackish-water sediments, only a few experimental pollution studies, *e.g.* assays with nematodes as model organisms such as the traditional LC_{50} experiments, are available at the present time. As far as we know, only one paper, studying the acute toxicity of pollutants (heavy metals) to marine nematodes, has been published to date (Howell, 1984). From this study it appeared that the susceptibility to copper, lead, and mercury was higher than to zinc and cadmium, with both *Enoplus brevis* and *E. communis*, and that the

toxicity of all metals changed with exposure time. Furthermore, it was suggested that animals from polluted stations were less susceptible to the toxicants tested than those of unpolluted sites. Unfortunately, Howell (1984) did not mention whether he fed his animals during the experiments. If not, then interference caused by starvation may have been possible, particularly when exposure time was long. Vranken *et al.* (1984b) dealt with the acute toxicity of mercury to the nematode *Monhystera disjuncta* and the mortality response of the three different life-stages (eggs, juveniles, and adults) was monitored for three different mercury compounds (Hg_2Cl_2, $HgCl_2$, and CH_3HgCl). Mortality during the post-embryonic stages was the most sensitive index for acute stress and developmental inhibition could not be used as a toxicity-criterion for this particular metal. The organic mercury compound was much more toxic than the other two forms tested, but *M. disjuncta* was particularly insensitive to mercury when compared with other invertebrates.

Recently, Tietjen & Lee (1984) used a somewhat different experimental approach to measure the effect of wastes. Two nematodes, *Chromadorina germanica* and *Diplolaimella punicea* were grown in contaminated sediment taken from the field and a number of potential toxicants were measured in these sediments. The intrinsic rate of natural increase (but see p. 452) was used as an indicator of sediment quality. The worms grew better in low contaminated sediments and concentrations of 270 μg polychlorinated biphenyl (PCB)$\cdot l^{-1}$ and 8700 μg polynuclear aromatic hydrocarbon (PAH)$\cdot l^{-1}$ reduced population growth by 50%. Growth was consistently better when sediments were more diluted. With such approaches it remains difficult to pinpoint the most toxic compound and to determine non-toxic levels for individual contaminants.

A somewhat similar idea of experimentation is found in Cantelmo & Rao (1978a,b). These authors used aquaria containing sand and provided with a continuous supply of sea water, to study the effect of the biocide pentachlorophenol (PCP). They found that high concentrations of PCP caused a compositional shift in the nematode assemblages in such a way that epistratum-feeders, which are dominant in conditions of low stress, were outnumbered by selective deposit-feeders in conditions of high stress. An identical experimental set-up was used by Cantelmo, Tagatz & Rao (1979) to study the effect on meiofauna of barite ($BaSO_4$) a major constituent of drilling muds used in marine oil drilling operations. Some groups (Rotifera, Foraminifera, Hydrozoa, Turbellaria, Ostracoda, Polychaeta, and Bivalvia) were unaffected by barite, and a mixture of barite and sand, in some proportions, increased sediment heterogeneity, which resulted in increases in densities of the meiofauna. On the contrary, barite deposited on the surface of the sediment caused a significant reduction in meiofaunal density.

Howell (1982a) studied the occurrence of copper, zinc, lead, cadmium, and mercury in two enoplids, *Enoplus brevis* and *E. communis*, sampled from three estuaries on the northeastern coast of Britain. It was concluded that metal concentrations found in nematodes are in agreement with values reported for benthic organisms with comparable life histories, feeding behaviour and habitus. Howell (1982b) found that the acid mucopolysaccharide (mucus) secreted by the two enoplids (see above) possesses metal-binding properties; this mucus may play an important rôle in heavy metal uptake and loss. The uptake, loss, and tissue distribution of copper and zinc in the same two

enoplids was studied by Howell (1983) who suggested that surface adsorption is very important and that most likely the uptake of heavy metals from sea water is *via* the cuticle. Besides this route, uptake *via* the gut, pharynx, and other tissues (hypodermis, muscle layers, and reproductive structures) is significant. In another study (Howell & Smith, 1983) the existence of two heavy-metal binding proteins, binding copper and cadmium, was reported in *E. brevis*. One of the two was probably the collagen-like component of the cuticle. The identity of the other is not yet known.

This review of ecotoxicological work with free-living marine nematodes shows that our knowledge on this topic is very poor and that much more work remains to be done.

ACKNOWLEDGEMENTS

We are grateful to Prof. Dr A. Coomans and Dr P. Herman for a critical reading of parts of the manuscript. This research is supported by the Belgian National Fund for Scientific Research (N.F.W.O.) and the Ministry of Scientific Policy (Concerted Actions Oceanography). Part of this work was conducted under Contract No. ENV.566B of the Environmental Programme of the C.E.C.

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