# PROCEEDINGS OF THE FOURTH INTERNATIONAL CONGRESS OF NEMATOLOGY, 8–13 JUNE 2002, TENERIFE, SPAIN

*R. Cook and D.J. Hunt (Editors)*

NEMATOLOGY MONOGRAPHS AND PERSPECTIVES

VOLUME 2

BRILL
LEIDEN - BOSTON
2004

*Nematology Monographs & Perspectives*, 2004, Vol. 2, 529-545

# Use of carbon and energy sources by nematodes

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**Summary** – The ubiquity and abundance of nematodes in soils and aquatic sediments interest ecologists seeking models for fluxes of matter and energy. However, the complete spectrum of roles and the quantitative importance of nematodes in soils and aquatic sediments remain poorly documented. Feeding type classifications of nematodes usually rely strongly on buccal morphology, but there are many unresolved questions on food sources and feeding rates. Here we comment on the much used feeding type classification of Yeates *et al.* (1993a), which, pending minor modifications, we still consider valid. However, we argue against the use of the separate category, omnivores. We also advocate the use of this terrestrial nematode-based scheme in aquatic nematology, including marine nematodes. A potentially major shortcoming of feeding type classifications is that they attribute guild- rather than species-specific functions to nematodes. This conflicts with evidence of high feeding selectivity and flexibility. Nematode species diversity at small spatial scales thus provides an intriguing system for studies on the functional implications of diversity and of species redundancy. Finally, to relate laboratory-derived feeding rates to population growth rates under natural conditions, we address the effects of external influences on nematode activity in soils, and stress the need for a better understanding of nematode functional responses.

The ubiquity and abundance of nematodes in soils and aquatic sediments interest ecologists seeking models for fluxes of carbon, nitrogen, phosphorus, *etc.* However, the complete spectrum of roles

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and the quantitative importance of nematodes in soils and aquatic sediments remain poorly documented. Feeding types of nematodes are usually inferred from buccal morphology but there are many unresolved questions on food sources and feeding rates, which affect the accuracy with which nematodes can be included in flux models.

Any estimate of worldwide nematode species diversity is at present speculative, but some authors predict astounding species numbers (Lambshead, 1993). Assessing diversity at smaller scales increases the relative diversity of small species (Fenchel, 1993), emphasizing that studies into the functional role of diversity should particularly focus on meio- and micro-sized organisms. High diversity is often attributed to a high level of niche specialisation with food as an important driving factor, but functional redundancy does occur and may be facilitated by patchy population dynamics (Ettema *et al.*, 2000). Nematode species diversity thus provides an intriguing system for studies on the links between biodiversity and ecosystem functioning.

## Food and energy sources for nematodes

All nematodes are heterotrophs, relying on energy fixed through primary production. Nematodes that directly utilise living autotrophic biomass are 'grazers' – although this term is also frequently applied to feeding on (heterotrophic) bacteria – and belong to 'grazing foodwebs', whereas foodwebs based on dead organic matter may be referred to as 'detritus foodwebs' (Petersen & Luxton, 1982). Food provides heterotrophic organisms with both energy and material. Unlike energy, material can flow in closed cycles, and it is these fluxes (especially of carbon, nitrogen and phosphorus) that generally are the prime focus of system models and 'budget' studies of animals.

In deep-sea sediments, all benthic consumers ultimately depend on sedimentation of dead (phyto)plankton. Estuarine tidal flats usually have high microphytobenthos production rates. In one tidal flat nematode community, 95% of the individuals were capable of grazing on diatoms (Bouwman *et al.*, 1984a) although this is probably an exception. Grazing and detritus foodwebs are however, rarely so well separated (Ruess & Ferris, 2004). Since initial organic matter inputs into grazer and decomposer webs may differ substantially with respect to quality and elemental ratios, feeding at different trophic levels, or from different webs, may help to overcome temporary deficiencies in any single trophic channel.

## Feeding type classifications: an attempt at structuring nematode feeding chaos

Links between buccal morphology and (presumed) feeding habits have long appealed to nematologists trying to understand the different trophic relations and roles of nematodes. Many feeding type classifications for soil nematodes have been proposed. Yeates *et al.* (1993a) condensed available information into a comprehensive grouping of soil nematodes by their feeding habits, and listed documented or presumed food sources by genus. Here, we briefly describe and comment on those feeding groups.

### 1. PLANT FEEDERS

Except for those species piercing microalgae, lichens or mosses, plant feeders use vascular plant tissue and fluids as their main energy source, utilising a tylenchoid stomatostylet or dorylaimid odontostyle. Six (Yeates *et al.*, 1993a) or seven (Bongers & Bongers, 1998) subgroups are generally distinguished. The food sources of the delicate-speared Tylenchidae and Psilenchidae remain largely enigmatic. Since they often occur in high densities in the rhizosphere, without apparent negative effects on plants, and since direct feeding on plant cells has not been adequately documented, they have sometimes been classified separately as plant-associated nematodes (Yeates *et al.*, 1993b; Yeates, 1999).

### 2. HYPHAL FEEDERS

Hyphal feeders also feed by means of a stomatostylet or odontostyle. They include both obligate hyphal feeders and the alternate life cycles of some parasites of invertebrates. Feeding on yeasts or fungal spores may be included here if cells are pierced, not ingested.

### 3. BACTERIAL FEEDERS

Bacterial feeders generally ingest bacterial cells whole although, especially in forms with a broad stoma, bacteria may not be the only food. Slender diatoms were readily ingested by the brackish-water monhysterid *Diplolaimelloides meyli* (Moens & Vincx, 1997), and a variety of unicellular algae by *Pellioditis marina* (Bouwman *et al.*, 1984b). Elliott *et al.* (1980) observed soil texture-dependent trophic-level switching in *Mesodiplogaster*: where soil pores became too small for access to the bacteria, adult *Mesodiplogaster* switched to predation on amoebae. (Facultative) feeding on amoebae and other protozoa may be a more general phenomenon among bacterivorous soil (Bonkowski, pers. comm.) and aquatic nematodes (Moens & Vincx, 1997; Olafsson, pers. comm.).

## 4. SUBSTRATE INGESTION

Substrate ingestion is in the widest sense applicable to all feeding behaviours where some substrate is swallowed concomitantly with 'prey', but is restricted here to a foraging behaviour where ingestion of the substrate itself appears to be the purpose. Good examples are the ingestion of agar covered with a bacterial lawn by *Diplenteron colobocercus* (Yeates, 1998), and the seemingly random collection of sediment particles by *Metoncholaimus scissus* (Meyers & Hopper, 1966). Although it is unclear whether the substrate itself, the microbial epigrowth or both are utilised, this behaviour is distinct from any other listed feeding habit. Aquatic nematologists confusingly use the term (non-selective) deposit-feeders for a seemingly random ingestion of suitably sized and shaped particles (see below), often including substrate (Wieser, 1953; Jensen, 1987; Moens & Vincx, 1997). Many dominant groups in marine and estuarine muds (especially Xyalidae and Comesomatidae) are such presumed 'deposit-feeders'. Gut volume is an important factor determining whether or not deposit-feeding is energetically favourable (Taghon *et al.*, 1978); it is doubtful whether this is true in average-sized nematodes. Apart perhaps from the random behaviour reported for *Metoncholaimus*, deposit-feeding as in several macrofauna is probably not a common strategy in nematodes.

## 5. CARNIVORES

Many nematodes are carnivores, feeding on a variety of invertebrate metazoa. Buccal adaptations include teeth, stylet and mandibles, although ingestion of nematode prey by nematodes with 'unarmed' buccal cavities has been observed (*e.g.*, *Daptonema*, Moens & Vincx, 1997). Prey may either be sucked empty after piercing/tearing, or ingested whole, depending in part on buccal cavity size (Small, 1987). Ingestion of large prey requires special adaptations of the buccal cavity and pharynx. Many oncholaimids and mononchids are capable of both ingestion and piercing but, especially ingestion, may be limited by prey size (Borgonie *et al.*, 1995c). Predation may be the principal feeding strategy (*e.g.*, *Seinura, Labronema, Enoploides, Sphaerolaimus*) or a facultative one (*e.g.*, many Oncholaimidae). The ability of *Mononchus, Diplenteron* and other predators to thrive on bacterial food suggests predation in these nematodes to be facultative. In some aquatic sediments, predacious nematodes may switch between protozoan (category 6) and metazoan prey depending on availability, and have a significant impact on both types of prey populations (Hamels *et al.*, 2001). Unfortunately, most assessments of predation rates and prey selectivity are from artificial media and with prey offered in excess. In soils and sediments, both these factors depend at least partly on encounter probabilities, which are a function of both prey and predator mobility (Moens *et al.*, 2000), and of the availability of suitable prey refuges. Next to predation on living organisms, 'scavenging' of dead prey, as frequently observed in oncholaimid nematodes, may be important (see Moens and Vincx (1997) for review).

### 6. UNICELLULAR EUCARYOTE FEEDERS

Unicellular eucaryote feeders utilise diatoms, other microalgae, yeasts, fungal spores, flagellates, ciliates and/or other protozoa. Many aquatic nematodes with 'unarmed' but fairly spacious mouth openings belong in this feeding group. As in carnivores, cells may be ingested whole or perforated (pierced). Jensen (1982) and Moens and Vincx (1997) described 'cracking' of diatom cells, mostly by chromadorid nematodes. Size and shape of food particles greatly affect feeding success: nematodes have often been observed to suck particles onto the mouth opening but release them because they are too large to be ingested (Moens & Vincx, 1997). However, stoma dimensions do not always accurately reflect the size range of ingestable particles: the ingestion of algal cells much larger than the stoma diameter in *Alaimus* was interpreted as evidence of food cells being compressed prior to ingestion (Mulk & Coomans, 1979), while ingestion of 24 × 220 $\mu$m diatoms by a *Theristus* sp. with a 10 $\mu$m stoma is enabled by significant expansion of the buccal cavity (Boucher, 1973). Apparent substrate ingestion (category 4) by aquatic nematodes may be incidental to feeding on unicellular organisms.

### 7. ANIMAL PARASITES

Free-living stages of animal parasites may contribute to soil processes and should then be included under the appropriate category. If, however, they are ensheathed or otherwise inactive they are placed here as a separate group.

### 8. OMNIVORES

The term omnivore has usually been restricted in soil nematology to some dorylaims (Ferris & Ferris, 1989) while in aquatic nematology it has mostly been applied to oncholaimids. We do not support this restricted use of the term. In ecological theory, an 'omnivore' is an organism which feeds at more than one trophic level. Hence, bacterial-feeding nematodes that also prey on protozoa, substrate ingesters that utilise both bacteria and microalgae, facultative predators feeding on nematode prey as well as on bacteria, are omnivores. Perhaps the only true food-source specialists are herbivores and fungivores, most other nematodes essentially being omnivores with a food range constrained by their feeding structures. Further, many nematodes shift partly or wholly from feeding on one trophic level to another during development (see, for example, Yeates (1987a, b) and Hellwig-Armonies *et al.* (1991)): these are life-history omnivores. Ecological theory often attributes a key role to omnivory in determining food web stability, principally because it increases connectance. While a high level of omnivory appears a common attribute of food webs (Polis & Strong, 1996), its consequences on system functioning are not well understood (Griffiths *et al.*, 2004).

Nematologists have previously been advised to attempt to allocate the foods used by 'omnivorous' dorylaims proportionally to the appropriate other categories (Yeates, 1998) and, despite the difficulties, we support that view. While careful observations and analyses of nematode species are needed, in several ecological studies both 'omnivores' and predators have shown similar matches with food-web parameters (Mikola *et al.*, 2001; Yeates *et al.*, 2003).

## Feeding type classifications and the placement of aquatic nematodes

Freshwater nematologists are confronted with a nematode assemblage of mixed aquatic and terrestrial origins. They generally draw upon terrestrial feeding type schemes. Marine and brackish-water nematologists usually apply the feeding type classification of Wieser (1953), distinguishing between nematodes without (group 1) and with (group 2) a 'buccal armature' (teeth, onchia, jaws, *etc.*). Within the former, Wieser further discriminated between selective (1A) and non-selective (2A) deposit-feeders, based on the assumption that smaller buccal cavities are more adapted to a selective foraging strategy where particles are ingested one-by-one. Within group 2, distinction was made between epistrate-feeders and predators/omnivores. The size and structure of the buccal armature and the presence and prominence of a muscular pharygeal bulb were often used to assign nematodes to either feeding type. Variations to this scheme can be found in Romeyn and Bouwman (1983), Jensen (1987) and Moens and Vincx (1997). In contrast to the generic list in Yeates *et al.* (1993a), backed by at least some empirical evidence, Wieser's (1953) list relies mainly on the predictive power of buccal morphology, and was found to suffer some shortcomings when tested against observations of actual feeding behaviour of estuarine nematodes (Moens & Vincx, 1997).

In our opinion, there are no compelling reasons to use different feeding groups for terrestrial and aquatic nematodes. Aquatic nematodes fit well into the scheme of Yeates *et al.* (1993a) as modified here, and (dis)similarities between aquatic and terrestrial communities will be more obvious when common trophic groupings are used (Table 1). An important feature of the Yeates *et al.* (1993a) and current scheme is that nematodes can be assigned to more than one trophic type at the same time. Many nematode species have flexible feeding strategies and acknowledging their trophic versatility will enhance the accuracy of model construction and hypothesis testing.

All feeding type classifications mentioned here group nematodes on the basis of food source and/or feeding habit. While the two are often strongly linked, they are not necessarily synonymous. For instance, substrate ingesters form a group based on feeding habit, whereas bacterial feeders do so on the basis of food source. Many substrate ingesters may in fact derive a significant part of their nutrition from bacteria. Hence, assignment to feeding categories still remains prone to some subjectivity. Insofar as groupings are based on food source, nematode feeding types are typical alpha or resource guilds (Wilson, 1999). They are not necessarily functional groups (although they have often been named so), as this term implies that they share

**Table 1.** *Overview of the translations of the feeding types introduced by Wieser (1953) and Moens and Vincx (1997) to those proposed in the present study. Feeding types in italic are, based on current knowledge, considered of subordinate importance.*

| Wieser (1953) | Moens & Vincx (1997) | This study |
|---|---|---|
| 1A selective deposit-feeders | microvores | 3 bacterial feeders |
| 1B non-selective deposit-feeders | deposit-feeders | 6 unicellular eukaryote feeders<br>*3 bacterial feeders*<br>*4 substrate ingesters* |
| 1B non-selective deposit-feeders | ciliate feeders | 6 unicellular eukaryote feeders<br>*3 bacterial feeders* |
| 2A epistrate-feeders | epistrate-feeders | 6 unicellular eukaryote feeders<br>*3 bacterial feeders* |
| 2B omnivores/ predators | predators | 5 carnivores<br>6 unicellular eukaryote feeders[1] |
| 2B omnivores/ predators | facultative predators | 5 carnivores[2]<br>4 substrate ingesters |

[1] The assignment of (omnivores/)predators to feeding type 6 (unicellular eukaryote feeders) is so far based on a single species in which predation on ciliates was shown to be important (Hamels *et al.*, 2001).

[2] Incidences of scavenging on foraminifers have also been reported (Moens & Vincx, 1997).

both food and predators. We currently have insufficient information on selective feeding in nematodes to assess levels of food specialisation, and vulnerability to predators may also differ substantially among nematode species sharing a resource. In many cases, functional guilds are best constructed using a mix of resource, autecological and other relevant ecological information on (groups of) nematodes, and defined in relation to a specific process/function. Examples are the scheme of Bongers and Bongers (1998) based on feeding type and response dynamics (c-p scores), or the structure, enrichment and channel indices (Ferris *et al.*, 2001).

## Particulate *vs* dissolved food

Traditionally, nematode feeding groups take into account only particulate food sources, not dissolved ones. Uptake of dissolved organic matter (DOM) has been demonstrated in several aquatic nematodes (Chia & Warwick, 1969; Lopez *et al.*, 1979; Riemann *et al.*, 1990; Moens *et al.*, 1999b). While most studies have utilised highly labile DOM, Höss *et al.* (2001) have shown that refractory compounds (*e.g.*, fulvic acids) may also stimulate nematode growth and reproduction. A major methodological difficulty in assessing the potential contribution of DOM to nematode nutrition is separating direct from bacterial-mediated uptake processes. The most telling evidence for DOM-utilisation consists of axenic cultivation of several bacterial- and fungal-feeding nematodes. *Caenorhabditis elegans* can be sustained indefinitely axenically, although it typically has metabolic and reproductive rates at least one third lower than when fed bacterial food (Johnson, 1985). Höss *et al.* (2001) suggested that DOM adsorbs to (*e.g.*, bacterial) cells and is ingested and utilised in this way. The bacterivorous rhabditid *Pellioditis marina*, however, fails to assimilate radiolabelled DOM from liquid bacterial cultures, although carbon from bacterial cells is readily ingested and absorbed (Moens, unpubl.). On the other hand, bacterial and microalgal biofilms generally produce significant amounts of highly labile exopolysaccharides which may provide nematodes with an easily accessible pool of DOM (Decho & Lopez, 1992). It thus seems likely that DOM contributes to the nutrition of nematodes, but its significance remains to be established.

## 'Conflicts' between stoma morphology and feeding habit

Although it is clear that feeding habits are linked to stoma morphology, presumptive feeding strategies which are not backed by any empirical evidence may be misleading. Firstly, very similar stoma structures may be used for very different feeding behaviours. The diversity of food sources in aphelenchid nematodes provides a telling example: *Aphelenchoides* species may be hyphal feeders and/or ecto- or endoparasites of plants, while the genus *Seinura* is predacious. Differences in stylet dimensions and cephalic structure are functionally linked to much more subtle resource partitioning between stylet-bearing nematodes (Yeates, 1986; Wyss, 2002).

On the other hand, different morphologies may be used for very similar feeding behaviours. For example, stomatostylets or odontostyles may be used to pierce microalgae, but *Pareudiplogaster pararmatus* (Romeyn & Bouwman, 1983) and several Chromadoridae (Jensen, 1987; Moens & Vincx, 1997) pierce diatoms using a partly eversible tooth. Many soil bacterivorous nematodes ingest bacterial cells whole, but the range of differently sized and shaped buccal cavities, lips, appendages, *etc.* suggest many different strategies for obtaining this resource. Rhabditidae and Panagrolaimidae appear to have their pharynx in continuous pumping mode when sufficient food is available, while Cephalobidae generally have a narrower, muscular mouth and feed more intermittently, also at lower food availability. Both Cephalobidae and Wilsonematinae (Plectidae) combine complex cephalic structures with active sweeping motions during feeding. Wilsonematinae appear more specialised in sweeping bacteria off flat microsurfaces (De Ley & Coomans, 1997) while Cephalobidae seem more adept at collecting bacteria in three-dimensional microspaces (De Ley, unpubl.). Resource partitioning between different (bacterivorous) nematodes may not only be selection- and ingestion-dependent, but also linked to digestion. Borgonie *et al.* (1995a, b) described both biochemical and ultrastructural differences between intestinal cells from a range of rhabditid bacterivores. These may impact digestive efficiency and/or selectivity, although functional implications remain poorly understood.

## Feeding selectivity and intraguild diversity

Trophic groupings inevitably tend to treat all members of one group as if they draw upon the entire resource class. From the foregoing it is clear that feeding selectivity and flexibility may instead cause intraguild resource partitioning. Unfortunately, feeding selectivity and flexibility in free-living nematodes are generally poorly understood. Venette and Ferris (1998) demonstrated that not all bacteria are suitable food for bacterial-feeding nematodes and linked this, among other things, to cell size. Moens *et al.* (1999a) showed that four coexisting species of Monhysteridae all respond differently to the presence of different bacteria. Such response differences relate not only to the bacterial strains offered, but also to density, age, growth conditions and activity of the bacteria (see also Grewal and Wright (1992)). The importance of these subtle and highly specific response differences remains to be investigated in a natural environment, where nematodes are confronted with a much wider array of stimuli. While such responses are probably impossible to model in their full complexity, the implications for food web models are potentially very significant.

At the same time, the issue of selectivity and flexibility is central to the debate about functional implications of diversity, and of species redundancy within trophic levels. If selectivity tends to be very high and flexibility low, the level of intraguild species redundancy is likely to be low, and ecosystem functioning will be more diversity-dependent. In the opposite situation, a high level of species redundancy may be expected, and the often high intraguild diversity in nematodes becomes even more intriguing. Because nematode assemblages have a high diversity on a small spatial scale, and because many species are amenable to culture and laboratory experiments, they offer striking opportunities to test such general ecological concepts. Mikola and Setälä (1998) demonstrated that bacterial-feeding nematodes perform species- rather than guild-specific functions in soil food webs. Several other research initiatives along similar lines are underway.

## Environmental constraints on nematode feeding

Ekschmitt and Griffiths (1998) listed four major components of soil nematode activity patterns: habitat utilisation, tolerance range, response dynamics and functional contribution. Next to resource use, habitat utilisation also encompasses elements of substrate range, *e.g.*, texture and pore size. Available pore size, in conjunction with factors such as moisture, is of great significance to nematode feeding, as it may affect activity (and 'efficiency') of both consumer and resource (see, for example, Elliott *et al.* (1980)). Tolerance range refers to the ability of organisms to maintain activity under changing environmental conditions. Temperature preference/tolerance patterns are a classical example. Yeates *et al.* (2002) report population development of *Cephalobus* at soil matrix potentials close to wilting point. Previously field capacity was considered the optimum moisture for both motility and feeding in nematodes (Wallace, 1971). In addition, drought may increase concentrations of infochemicals (thus potentially influencing response patterns to available resources), which in turn may be modified by structural heterogeneity (Anderson *et al.*, 1997a, b).

Response dynamics basically refer to the capacity of organisms to react to a change in resource availability, and include among others functional responses to food availability. Foraging involves a variety of trade-offs, *e.g.*, between energy expenditure on feeding (ingestion and digestion) and on searching for the optimal feeding conditions. Other environmental variables aside, a nematode in a patchy environment almost constantly faces two options: maximising energy gains either by moving to a better feeding location or by foraging within a given patch. The choice between these options will depend on the nematode's functional response to a given type of food, and on the presence, suitability and detectability of alternative food sources.

Unfortunately, nematode functional responses have been poorly documented. Many bacterial-feeding nematodes need high threshold densities of bacteria to feed upon, and show fairly simple response dynamics (Nicholas *et al.*, 1973; Schiemer, 1983; Venette & Ferris, 1998; Moens & Vincx, 2000). Interestingly, ingestion and absorption (or assimilation) rates may show different food-density dependent patterns. Ingestion (Moens *et al.*, 1996) and absorption rates (Moens & Vincx, 2000) are a different function of bacterial density in *Pellioditis marina*, for instance, suggesting that absorption efficiencies are food-density dependent. Next to food quantity, quality may also impact these budget parameters. Future modelling exercises of the role of nematodes in energy and carbon fluxes would benefit greatly from budget studies using a broader range of both food sources and nematode trophic groups.

## Acknowledgements

The authors receive funding from the Flemish Fund for Scientific Research (FWO), where Tom Moens is a postdoctoral research fellow, from Ghent University *via* contract BOF 98-03, 12050398, and from the Marsden Fund of the Royal Society of New Zealand. Tom Moens is indebted to Howard Ferris and Gregor Yeates, convenors of the FICN-session on 'Food webs', for this forum. Howard Ferris made critical inputs to this paper.

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