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Predator–prey interaction in soil food web: functional response, size-dependent foraging efficiency, and the influence of soil texture

Abstract In a series of laboratory experiments, we presented carnivorous *Macrobiotus richtersi* (Tardigrada, Macrobiotidae) with nematode prey to assess their importance as predator. We investigated consumption rate for (a) different prey densities (10–400 prey individuals), (b) different prey biomasses (22–80 ng), (c) different prey species (*Pelodera teres*, Rhabditidae, versus *Acrobeloides nanus*, Cephalobidae) and (d) different environments (2-D agar surface versus 3-D sand fractions of three different textures). *M. richtersi* consumed up to 4.6 μg nematode prey in 4 h, that is, 43% of the tardigrade's body mass. Predation rate was positively correlated with prey density. The optimal prey in the present investigation was the biggest prey because it yielded the highest biomass uptake per time. In addition, the size of *M. richtersi* played an important role in consumption rate. Bacterivorous nematodes reacted differently to attack. Even in a water film on stiff agar where nematode agility was limited, a vigorous undulation reaction of *P. teres* led to a measurable reduction in consumption rate. *A. nanus*, in contrast, showed little response to attack. Microcosm experiments with sands of different particle size demonstrated that *M. richtersi* is able to chase and consume small bacterivorous nematodes in a 3-D soil matrix. However, consumption rate in sand microcosms was significantly reduced compared with pure agar. The sand matrix improved nematode agility and possibly provided small pores as refuge for the nematodes. The lowest consumption rate was observed in fine sand. Effects of predatory tardigrades on nematode numbers in the field are discussed.

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Introduction

With densities of over one million individuals per square meter, nematodes are the most numerous metazoan soil inhabitants (Parmelee 1995). Their activities affect microbial activity (Traunspurger et al. 1997), rates of litter decomposition (Sohlenius 1980; Anderson 1995), nutrient cycling (Coleman et al. 1984; de Ruiter et al. 1993), and plant growth (Philips et al. 2003). Many predators exploit the nematode pool. As regulatory forces (Wasilewska 2000), these predators may have a top-down influence on nematode species composition and population dynamics (Mikola and Setälä 1998a; Laakso and Setälä 1999) and thus indirectly affect nutrient cycling (Bouwman et al. 1996) and overall ecosystem performance (Koehler 1997). Terrestrial nematodes are fed upon by predatory nematodes (Yeates 1969; Small and Grootaert 1983; Walter et al. 1986; Small 1987; Bilgrami 1992, 1993; Khan et al. 1995; Yeates and Wardle 1996), earthworms (Hyvönen et al. 1994; Ilieva-Makulec and Makulec 2002), various arthropods (Murphy and Doncaster 1957; Martikainen and Huhta 1990; Hyvönen and Persson 1996; Huhta et al. 1998), and fungi (Bouwman et al. 1996). Even amoeboid and testate protozoa may attack nematodes (Doncaster and Hooper 1961; Yeates and Foissner 1995).

However, despite the suggested abundance of predators of nematodes and their considered importance in ecosystem processes, our knowledge on predator–nematode systems and predation rates is scarce (Traunspurger 2002). Often, accidental observations are all the evidence we have about a predator–prey interaction, and quantitative estimates of the predation intensity are rare (Moens et al. 1999, 2000; Schmid-Araya and Schmid 2000; Beier et al. 2004). This lack of information is particularly evident for the soil food web. Feeding habits of soil inhabitants are highly diverse and non-specific, resulting in remarkably complex food-web entities (Moore and de Ruiter 1997;

Gange and Brown 2002). To construct a complete food web and to predict ecosystem processes, it is essential to learn both the types of interactions between food-web components (Bengtsson et al. 1995; Wardle 1995) and their strength (Scheu 2002).

In the present investigation, we focused on the tardigrade *Macrobiotus richtersi* as a predator of nematodes. The first detailed observations on a tardigrade (*Macrobiotus* sp. and *Hypsibius microps*) feeding on nematodes were recorded by Doncaster and Hooper (1961) and Sayre (1969). Later, tardigrade predation of nematodes was documented and described by Hallas and Yeates (1972). However, these studies only include observations that are not experimentally quantified. In the present study, we investigated simple predator–prey interactions in an artificial system where we could directly watch and measure feeding parameters and then tested the validity of our results under more natural conditions in microcosms. A series of laboratory experiments was used to (1) measure per capita feeding rate in relation to prey density (functional response), (2) investigate the impact of the prey species (behaviour) and the influence of the predator–prey size ratio on attack rate, handling time and consumption, and (3) test the effect of different soil textures on feeding rate.

Materials and methods

Predator and prey source

Both the tardigrade (*M. richtersi*) and the bacterivorous nematodes (*Pelodera teres*, *Acrobeloides nanus*) were recovered from young soils of the afforested coal-mining areas at Berzdorf (near Goerlitz, East Germany) in May 1999 (see Hohberg 2003) and cultured in the laboratory. Nematodes were cultured on *Escherichia coli* in LB agar (0.33%), whereas tardigrades were reared in a water film on pure agar (2%) and were fed on *P. teres* and *A. nanus*. For adult tardigrades (M2), females without mature oocytes and with a body length of 550–650 μm were chosen (Table 1). Juvenile tardigrades (M1) with a body length of 300–380 μm were chosen. *P. teres* (P) and *A. nanus* (A) were graded into size classes by letting them actively pass through nylon nets (Hydrobios, Kiel, Germany) with mesh sizes of 10 and 5 μm (Table 1). Smallest worms passing through the 5-μm net were graded into size class 1 (P1, A1); individuals passing through 10- but not through 5-μm meshes were assigned to size class 2 (P2, A2). The body lengths

and widths of 100 individuals of each prey class were measured under an inverted microscope after killing them by warm formaldehyde. Mean tardigrade and nematode biomasses were calculated using the formula $m=l(d/2)^2 (3.14)(1.04 \times 10^{-6})$ (Hallas and Yeates 1972) for tardigrade biomass and $m=l[d^2/(1.6 \times 10^6)]$ (Andrássy 1956) for nematode biomass, where l is body length, d is body width (both in micrometers), and m is individual fresh weight (in micrograms).

Experimental procedures

An arena of 0.79 cm^2 was bordered by a piece of silicone hose (Ø, 1 cm; 0.5 cm long), which was lowered into a thin film of hot agar (2%) within a petri dish, forming a ring of silicone with agar at the bottom. Living nematodes were then counted accurately into the arena with a micropipette. Water was cautiously added or removed to achieve a water film approximately 1 mm thick. A single predator that had been starved for 3 days was added to each arena. The experiment started when the predator touched ground (agar) and began to walk or feed. At the end of the experiment, the predator was removed and the remaining nematodes were transferred to a petri dish and recounted. In recounting, we distinguished between uninjured, pierced, and partially sucked prey individuals. The last were treated as 0.5 of nematodes that had been totally consumed.

First experiments on experimental conditions

In order to determine optimal exposure time for functional-response experiments we presented 250 individuals of A1 to a starved predator M1 and continuously observed consumption during 4 h of exposure ($N=3$). In a second experiment we determined the optimal temperature (resulting in highest feeding rate) for feeding experiments: we presented 50 individuals of A1 to M1 at 10, 15, or 20°C and measured consumption after 4 h of exposure ($N=4$).

Functional-response experiments

We investigated the consumption rate of adult *M. richtersi* (M2) in dependence of prey class and density by offering four different prey classes, A1, A2, P1, and P2, and 11 different prey densities, 10, 25, 50, 75, 100, 150, 200, 250,

Table 1 Predator and prey size classes

Abbreviation	Species	Phylum	Classification	Mean body length (μm)	Mean body width (μm)	Mean fresh weight (μg)
M1	*M. richtersi*	Tardigrada	Predator	300–380	82	1.9
M2	*M. richtersi*	Tardigrada	Predator	550–650	150	10.7
P1	*P. teres*	Nematoda	Prey	200–290	12	0.022
P2	*P. teres*	Nematoda	Prey	300–380	17	0.063
A1	*A. nanus*	Nematoda	Prey	180–240	14	0.028
A2	*A. nanus*	Nematoda	Prey	270–330	20	0.080

300, 350, or 400 individuals per arena ($N=8$ for each combination of prey class and prey density). The experiments were conducted in the dark at 20°C for 4 h. In order to examine the influence of predator age (size) on functional response, juvenile *M. richtersi* (M1) were also tested with P1 in densities of 10, 25, 50, 75, 100, 150, 200, 250, or 300 individuals ($N=8$ for each prey density).

Functional responses were fitted to Rogers (1972) random predator equation that considers prey exploitation during an experiment: $N_e=N_0[1-e^{-a(T-N_eT_h)}]$, where N_e is the number of prey consumed, T is the total time prey was exposed to predation (240 min), N_0 is the initial prey density, a is the attack coefficient, and T_h is the handling time. The equation was transformed to Rogers' linearisation, $\ln[(N_0-N_e)/N_0]=aT_hN_e-aT$, and solved for the parameters a and T_h by means of linear regression (SPSS) for each prey class separately.

Furthermore, handling time T_h was determined in direct observations for adult tardigrades feeding on prey *A. nanus* of various body lengths. Handling time T_h was the time in seconds that the predator was occupied in attacking, overwhelming, and consuming one single prey individual.

Microcosm experiments

To investigate the influence of soil texture on consumption rate, experiments were carried out in microcosms of 0.79 cm² without substrate (A) and with three different sand fractions: coarse sand (CS), medium sand (MS), and fine sand (FS). A layer (5 mm) of sterilised sand grains (autoclaved at 120°C for 20 min) in three different particle size classes (CS, 0.50–0.63 mm; MS, 0.25–0.32 mm; and FS, 0.10–0.16 mm) was added to three of four microcosms ($N=6$). We then added 200 individuals of P1 (22 ng) and water until a film of water (approximately 1 mm thick) remained at the sand surface. After 30 min, a single adult tardigrade (M2) was placed into the surface water film. Experiments were conducted at 20°C for 24 h. After 24 h, nematodes, sand, and tardigrade were transferred to a petri dish, the tardigrade was removed, and nematodes were killed by adding hot water (60°C). Dead nematodes were carefully washed off the sand and counted as described above (see functional-response experiments). To evaluate the number of prey individuals lost during washing, controls without predator ($N=6$) were conducted for each substrate type.

The mean predation rate, $P_{200}=1-(R_p/R_c)$, was calculated for each substrate type (A, CS, MS, FS), where R_p is the mean recovery with predator present and R_c is the mean recovery in controls without predator. To examine whether the predator was significantly feeding on nematode prey, a Mann–Whitney U test (SPSS) was performed for each texture. Finally, the influence of texture on consumption rate was tested with a two-way ANOVA (SPSS) after log transformation of the data (R). The two factors were predator (present or absent) and substrate type (FS, MS, or CS). The interaction term then tested whether the influence of the predator presence on recoveries is consistent over the different grain sizes, i.e. whether the consumption rate depends on soil texture.

Results

Direct observation of predator–prey interaction for 4 h revealed that even tardigrades of the same age, size, and history differed in feeding behaviour. Some individuals of *M. richtersi* started feeding instantly and consumed nematodes rapidly one after the other. Then they had a rest for a variable time. Others were much slower but continued feeding for some hours. Mean consumption increased from 38.2 nematodes after 1 h to 62.3 nematodes after 4 h (initial prey density, 250 A1). At the same time, the standard deviation decreased from 32.5 to 19.6 prey individuals. After 4 h, waste (fragments of dead nematodes and tardigrade faeces) began to accumulate on the agar surface and then stuck to tardigrade legs and claws, inhibiting locomotion. Thus, 4 h was an appropriate exposure time for functional-response experiments. Tests revealed that the temperature had significant influence on feeding rate: mean consumption ($\pm$SD) was 9.3$\pm$5.7 at 10°C, 14.8$\pm$4.9 at 15°C, and 23.5$\pm$6.0 at 20°C (initial prey density, 50 A1). Thus, we performed functional response and substrate experiments at 20°C where tardigrade activity and consumption rate were highest.

The number of prey consumed increased curvilinearly with prey density. The more prey individuals that were presented to the predator, the shorter was the searching time, until searching time was small compared with handling time and a plateau was reached (Fig. 1). Consumption rates at different prey densities are best described by Holling's type II functional response (Holling 1959). Consumption rate N_e depended on individual prey size (Fig. 1). The highest one was measured for the smallest prey P1 (Fig. 1a): adult *M. richtersi* ingested up to 105 individuals of P1 in 4 h (N_e maximum consumption, Table 2). With increasing prey size, handling time increased and, consequently, the number of prey individuals consumed decreased. The maximum uptake of biomass by adult *M. richtersi*, on the other hand, increased with increasing prey size (Fig. 2). In terms of biomass uptake, the optimal prey in the present investigation was the largest nematode A2 (80 ng): up to 4.64 µg biomass, that is, 43% of its own body mass, was consumed by the predator within 4 h (Fig. 2, Table 2). Even though being much smaller (18% of the adult biomass), juvenile tardigrades consumed up to 56 prey individuals (P1) in 4 h, that is, 1.23 µg or 65% of their own mass (Table 2).

Apart from body-size relationships between predator and prey, the type of prey also affected consumption rate and biomass uptake. In contrast to *A. nanus* that showed little response to attack, *P. teres* responded with vigorous undulation. Several times we observed that a predator lost its prey in consequence of the active movements of *P. teres*. This observation was confirmed by actual consumption rates. Firstly, *P. teres* P2 was consumed at a rather lower rate than the bigger prey *A. nanus* (A2; Table 2).

Fig. 1 Functional responses of *M. richtersi* to the densities (N_0) of different prey classes ($N=8$). N_e is the number of prey consumed within 4 h. **a**–**d** Adult predator M2 feeding on **a** P1 (22 ng), **b** A1 (28 ng), **c** P2 (63 ng), and **d** A2 (80 ng). **e** Juvenile predator M1 feeding on P1. Predicted curves were obtained by separately fitting the data of each prey class to Rogers' (1972) equation, $N_e = N_0 \left[1 - e^{-a(T - N_e T_h)}\right]$, by means of linear regression
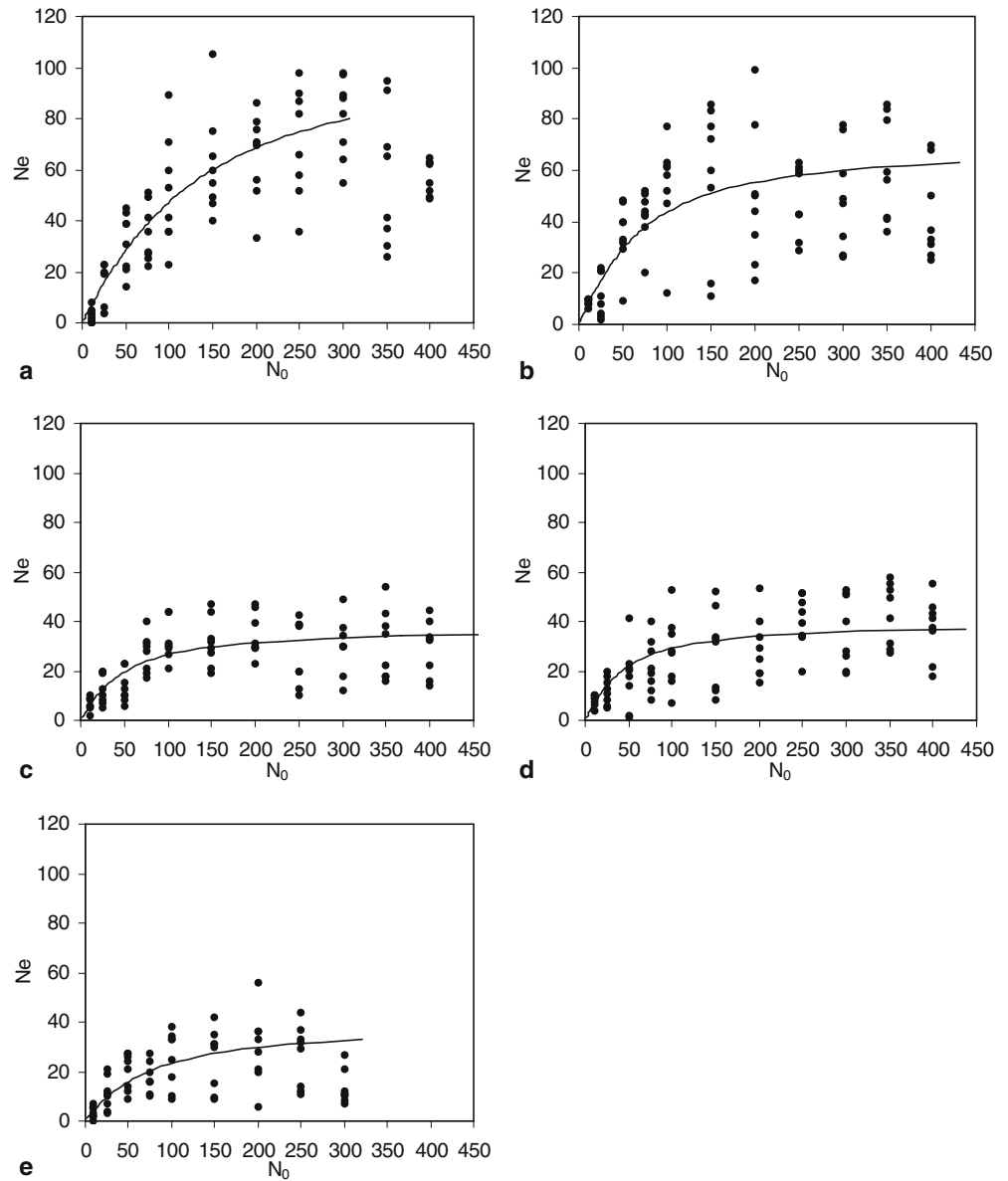
Secondly, high densities of *P. teres* (P1) seem to have confused the predator, leading to a decreased consumption rate (Fig. 1a).

The handling time T_h (Rogers 1972) calculated from functional-response regression curves highly differs from that evaluated in direct observations for different prey sizes of *A. nanus* (Table 2). In direct observations, we measured

Table 2 Parameters of consumption [maximum consumption, mean consumption at high prey densities ($N_0 = 300$), and observed handling time T_h (mean±1 SE, $N_{A1} = 344$, $N_{A2} = 82$)] for different predator and prey size classes

Predator		Prey		Max. consumption		Mean consumption		Observed	Calculated (Rogers' equation)		
Abbreviation	µg	Abbreviation	ng	N_e	M (%)	N_e	M (%)	T_h (s)	T_h (s)	a	R^2
M2	10.7	P1	22	105	22	80.5	17	–	132	0.0047	0.8207
M2	10.7	A1	28	99	26	49.6	13	18.6±1.7	205	0.0064	0.4358
M2	10.7	P2	63	54	32	30.0	18	–	385	0.0044	0.6500
M2	10.7	A2	80	58	43	36.0	27	80.8±4.5	362	0.0054	0.6171
M1	1.9	P1	22	56	65	14.8	17	–	362	0.0027	0.6371

In addition, we calculated handling time T_h and attack rate a according to Rogers' random predator equation $N_e = N_0 \left[1 - e^{-a(T - N_e T_h)}\right]$
R^2 sum of squares, N_e prey numbers consumed, N_0 initial prey density, M consumed prey mass relative to predator's individual body mass

Fig. 2 Nematode biomass consumed by a single adult *M. richtersi* (M2) to the densities (N_0) of four different prey classes P1, A1, P2, and A2 within 4 h (mean±SE, N=8)
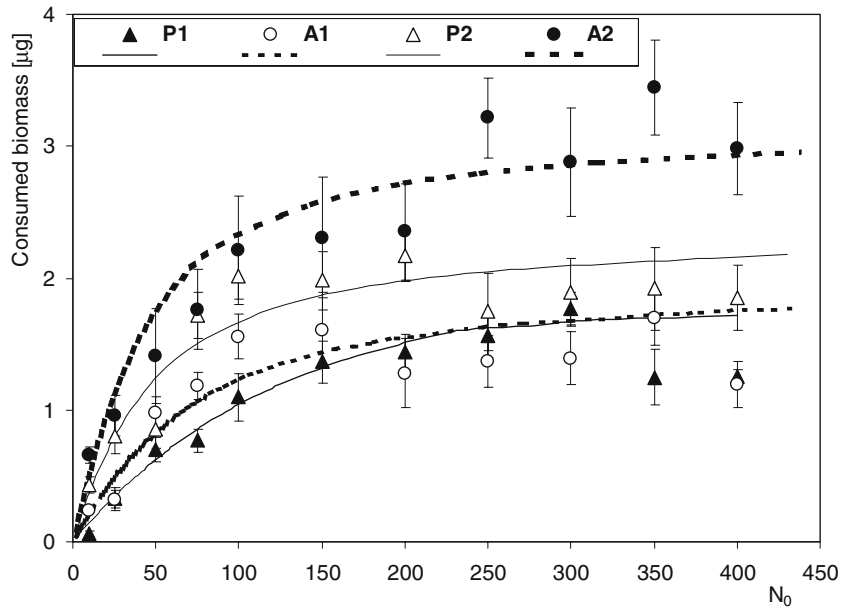
only the time the predator was occupied in actually overwhelming prey and feeding. Thus, the difference between the observed and the calculated values is the time the predator is occupied in digestion.

Sand did not hinder tardigrade activity, but allowed tardigrades to intrude into the pore system where they moved quickly between sand grains. We were able to observe their agility through an inverted light microscope when a tardigrade reached the bottom of the sand layer. In all four microcosm systems (no sand, coarse sand, medium sand, and fine sand), tardigrades were able to successfully capture nematodes (Fig. 3). Predation rates over 24 h of exposure, however, were highest on pure agar (P_{200}=89.9%). Considering different sand treatments (coarse, medium, and fine sand), the effect of predation on the number of nematodes recounted significantly depended on grain size (ANOVA: two-way interactions Predator × Substrate, P=0.009, F=5.522). Calculated predation rate (P_{200}) decreased with decreasing sand particle size (Fig. 3). In ad-

dition, the recovery rate (Fig. 3, white columns) varied among different sand sizes. It was highest when nematode and sand grain were of equal size (medium sand). Larger sand grains easily covered nematode bodies. Smaller sand grains were, due to their small mass, difficult to separate from nematodes in the washing treatment.

Discussion

Predatory tardigrades and nematodes compose the highest trophic level within water-filled soil pores (Wardle 1995). Several field studies (Hallas and Yeates 1972; Sohlenius 1979; Yeates and Wardle 1996) suggested that tardigrades may reduce nematode numbers. Field data, however, are very difficult to interpret because there are many factors influencing the numbers of soil organisms, e.g. climatic or nutritional changes. The present investigations for the first time quantified tardigrade–nematode feeding interactions,

Fig. 3 Microcosm experiments. The effect of the soil texture and of the predator *M. richtersi* on the recounts of prey individuals P1 after 24 h of experimental procedure (N=6, mean±1 SE, initial prey number of 200 individuals). P is the calculated predation rate and p is the probability with which the assumption "there was no significant consumption" is agreed (U test)
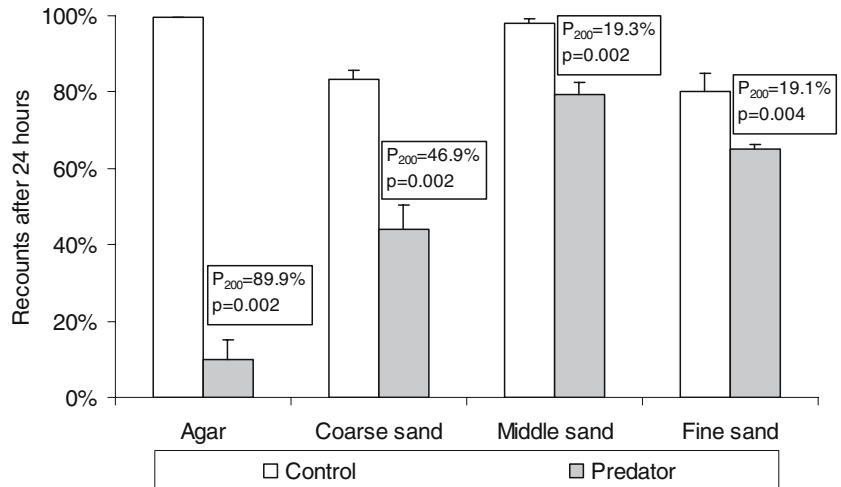
using simple functional-response experiments, where the actual feeding was directly observed and counted, as well as more naturally conditioned microcosm experiments. These experiments revealed that a tardigrade, *M. richtersi*, effectively reduced the number and biomass of nematodes. In our functional-response experiments, the adult tardigrade consumed up to 4.6 μg nematode biomass, corresponding to 43% of the tardigrade body mass, within 4 h.

Encounter rate and consequently consumption rate were positively related to prey density. Like the majority of non-filter feeding predators (Jeschke et al. 2004), the tardigrade's consumption followed a curvilinear type II functional-response curve (Holling 1959). In addition to prey density, the body-size relationship between predator and prey highly influenced the feeding rate. Small prey led to high encounter rate, high attack rate, high capture success, short handling time, and consequently to a high consumption rate (Pastorok 1981; Manly and Jamieson 1999; Wahlström et al. 2000; Cogni et al. 2002).

McKee et al. (1997) and Beier et al. (2004) demonstrated for a triclad predator (*Dugesia*) preying on nematodes that there may be a maximum size of prey accessible to the predator where larger prey are not attacked. In the present investigation, all prey types presented were voluntarily consumed by the tardigrade. A limiting prey size was not experienced. The maximum feeding rate, however, decreased with increasing prey size. Still, the optimal prey of the present investigation was the biggest prey (A2) leading to the highest biomass uptake for the tardigrade.

Nematode species may react differently to predator attack as we observed in the functional-response experiments. Furthermore, in addition to temperature, prey density, and prey size, prey behaviour did influence the consumption rate. Even swimming in a water film on stiff agar, where nematode locomotion is limited, *P. teres* (Rhabditidae) responded vigorously to attack. *A. nanus* (Cephalobidae), on the other hand, showed little response. As a result, *P. teres* was consumed to a lower rate than expected due to its body size. Above all, at high densities, the active undulation of *P. teres* seemed to confuse the predator. Consequently, consumption rate of *P. teres* declined at high prey densities. Also, Grootaert et al. (1977) and Bilgrami (1992, 1993), studying predatory nematodes feeding on several bacterivorous nematode genera, reported of the very pronounced 'escape response' of rhabditid nematodes (e.g. *Rhabditis* and *Pelodera* spp.). They found that the escape response often provided resistance against predation. We suggest that for the tardigrade the vigorous escape behaviour of *P. teres* increased handling time rather than reducing success rate. This is confirmed by the fact that the behaviour's greatest effect was at high prey densities; an influence on the success rate would be noticeable at low prey densities (Jeschke and Tollrian 2000). In our experiments on stiff agar, the prey's escape seldom saved the prey from dying because individual prey often first detected the predator after being pierced. Doncaster and Hooper (1961) suggested that predatory tardigrades may inject a toxic secretion into the nematode. Recent scanning electron microscopy of the buccopharyngeal apparatus of *Echiniscus sigismundi* re-

vealed that tardigrade stylets may be hollow, with openings both at the basal part and at the stylet tips. Thus, enzymes or toxins could indeed be injected through the piercing stylets into the food organism (Eibye-Jacobsen 2001). However, a pierced cuticle alone may immobilise and lead to subsequent death of the nematode, as piercing results in a loss of hydrostatic pressure, affects locomotion, and may permit invasion of pathogenic microorganisms (Bilgrami 1992).

Antipredation adaptations, such as vigorous escape movements, toxic or unfavourable secretions, or even a relatively thick, annulated cuticle are found in many bacterial-feeding nematode species (Small and Grootaert 1983). Their presence is presumably attributable to strong top-down effects of top predators, particularly nematodes and tardigrades (Wardle 1995).

Microcosm experiments revealed that *M. richtersi* is able to detect and consume small nematodes within a 3-D soil matrix. However, the sand matrix clearly reduced predation rates compared with those on stiff agar. We suggest two reasons for this reduction. Firstly, the 3-D soil system allows enhanced nematode agility and an improved ability to escape and defend. Nematode locomotion in soil is directly affected by the water content and the size of soil particles (Freckman 1988; Hunt et al. 2001). The average diameter of soil particles that allows for optimum movement is about one third of the worm's length (Wallace 1958; Nicholas 1975), 70–100 μm in case of *P. teres* (P1), which is close to the particle size of fine sand (100–160 μm), where we recorded lowest predation rates. Secondly, soil pores differ in size and smaller pores may serve as places of refuge where an adult predatory tardigrade is not able to intrude. Beier et al. (2004) demonstrated in microcosm experiments with fine sands and gravel that sediment offers a physically complex refuge for nematode prey and may effectively increase predator (*Dugesia gonocephala*) search and handling time by reducing the opportunity of visual, mechanical, or chemical detection of prey organisms. Spatial heterogeneity (Wardle 1995; Keeling et al. 2000) and prey refuges may have a stabilising effect on predator–prey dynamics (Murdoch and Oaten 1975; Sih 1987; González-Olivares and Ramos-Jiliberto 2003).

The concept of habitable pore space can explain the distribution of predator and prey in soils (Yeates et al. 2002). If a considerably larger predator is present, a part of the prey population may live in soil pores inaccessible to their predators (Mikola and Setälä 1998b; Mikola and Sulkava 2001). The smallest *M. richtersi* that we observed successfully piercing and sucking on a living nematode was 220 μm long with a body diameter of just 50 μm. However, even this juvenile tardigrade is more than twice the diameter of the smallest nematode in the present investigation. Naturally, there will be soil pores too small even for this juvenile tardigrade to follow its nematode prey. However, Elliott et al. (1980) reported a situation in which a transfer agent (protozoa) made food (bacteria) better available to predators (nematodes) by entering soil pores inaccessible to nematodes, feeding on bacteria, and being later fed upon by nematodes.

From the results of our microcosm experiments where a realistic nematode biomass of about 560 mg m^{-2} was inoculated, some simple calculations can be made: In the fine sand microcosms, *M. richtersi* ingested about 19% of the 200 *P. teres* (P1) individuals in 24 h, i.e. 840 ng or about 8% of the tardigrade's body mass. For a mine spoil in which the tardigrade (*M. richtersi*) biomass made up 50% of the nematode biomass (Hohberg in preparation) this would mean that 4% of the nematode biomass could be consumed by tardigrades (*M. richtersi*) each day. However, the field data did not reveal any correlation between tardigrade and nematode abundances or biomasses (Hohberg in preparation). There are only few correlations of tardigrade and nematode densities published. Small (1987) stated a negative correlation of tardigrades and nematodes (*Acrobeloides*, *Alaimus*, and *Plectus* spp.) in humus and suggested that these nematode species were preyed upon by tardigrades. Hallas and Yeates (1972) demonstrated a significant correlation between the numbers of the tardigrade *M. harmsworthi* and the total numbers of nematodes in a Danish beech forest where tardigrade predators had a great impact on nematodes and predatory nematodes played a minor role (Yeates and Wardle 1996).

The 800 to 900 tardigrade species known from freshwater, marine, and terrestrial habitats probably include very different feeding types (Nelson and Marley 2000; Nelson 2002; Nelson and McInnes 2002). Thus, it would be misleading to extrapolate the feeding rates of *M. richtersi* to overall numbers of tardigrades extracted, for example, from a soil sample. Tardigrades may pierce and suck the contents of living cells (fungi, algae, yeasts) and tissue (animals, plant roots) or swallow whole cells (bacteria, protozoa) or entire animals (nematodes, rotifers). Determination of feeding habit according to the mouth-tube armature of nematodes is not reliable (Yeates et al. 1993; Traunspurger 2002) and is even more limited in tardigrades, which all possess stylets. By this criterion alone, all tardigrades should be able to feed on nematodes. However, we never observed J1 juveniles of *M. richtersi* feeding on nematode prey. Probably, with their delicate stylet they cannot pierce the nematode cuticle. Instead, we observed J1 juveniles of *M. richtersi* feeding on detritus, probably consuming bacteria, which, incidentally, makes them competitors of bacterivorous nematodes, their later prey. The same dual-feeding behaviour was reported for 'predatory' mononchid nematodes (Yeates 1987). This omnivorous capacity guarantees survival (Diehl and Feißel 2000) and demonstrates that in the soil food web actual feeding depends on life stage and on the type of food available (Bouwman et al. 1996).

Conclusions

This investigation revealed that tardigrades may be very effective predators of bacterivorous nematodes. Feeding rate depends on temperature, prey density, the individual body mass of prey and predator, the behavioural response

of prey to attack (which may differ considerably between nematode species), as well as on the structure of the environment. In microcosm experiments, we for the first time demonstrated and quantified that tardigrades actually reduced the numbers of small nematodes in a soil system by their feeding activity. We also found a significant positive correlation between the particle size and the consumption rate. Further investigations on the ecology and distribution of tardigrade species in soils are needed to reveal whether *M. richtersi* is exceptional or representative for soil tardigrades.

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