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Predation rates and prey selectivity in two predacious estuarine nematode species

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ABSTRACT: *Enoploides longispiculosus* and *Adoncholaimus fuscus* are representatives of nematode genera prominent in sediments of the North Sea and adjacent estuaries. Both are predatory nematodes, although predation is facultative in the latter. The present study investigates functional responses and prey selectivity in both species through the use of controlled laboratory experiments. Both predators had strongly prey density-dependent predation rates. A maximal predation rate of 4 monhysterid prey nematodes per predator per 24 h was found in *E. longispiculosus* at prey densities of 200 ind. per petri dish and higher; no such maximal predation rate was found for *A. fuscus*, indicating that this species was prey-limited at all prey densities tested. Predation rates were strongly affected by temperature, with a Q_{10} close to 2 between 10 and 20°C. Incubation in the light resulted in a similar decrease in predation rate compared to dark incubations, as did a temperature decrease from 20 to 10°C. *E. longispiculosus* exhibited a clear preference for some nematode prey over others. An encounter probability model indicated that preferences could not be explained by encounter rates. Strike rates were low (<10 %) in *E. longispiculosus*, and exceptionally low (<<1 %) in *A. fuscus*, indicating that many encounters did not result in attack, or that a portion of the attacks did not result in prey capture. The observed predation rates cannot be supported by prey nematode standing stock and production at the 2 sampling sites used in this study, where *E. longispiculosus* dominates the nematode community in abundance and, especially, biomass. *A. fuscus* may mainly derive food from feeding modes other than predation; *E. longispiculosus* may be prey-limited in its natural habitat. Since this nematode also feeds on other metazoans, it may also impact temporary meiofauna. The high predation rates and prey selectivity of predacious nematodes may be important structuring factors to meiofaunal communities.

KEY WORDS: Nematodes · Predation · Prey selectivity · Encounter probability · Top-down control

INTRODUCTION

Over the past 3 decades, considerable evidence has demonstrated the importance of meiofauna in the marine and estuarine benthos. Despite their small biomass contribution compared to macrofauna, their relatively high metabolic rates render them potentially important in marine benthic energetics (Gerlach 1971, Fenchel 1978, Coull & Bell 1979, Kuipers et al. 1981, Heip et al. 1985, Vranken et al. 1986). The direct food-web links of nematodes, i.e. their food intake and their role as prey to macrobenthic infauna and epi- and hyperbenthic predators, however, remain poorly quantified. From the limited available information, nematodes would appear to be capable of grazing significant amounts of bacteria and microalgae (Montagna 1995). However, the diets of free-living aquatic nematodes also include other small metazoans and protozoans (Moens & Vincx 1997).

To date, quantification of predation rates by marine or brackish water nematodes on metazoan prey has been restricted to 1 study using a single prey species at a single density (Moens et al. 1999). The potential

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impact of predatory nematodes on meiobenthic communities, therefore, is unknown, and estimates of carbon flow to (via predation on grazer nematodes) and through (via macrofaunal predation on large nematodes) this particular feeding guild have only been based on indirect calculations from field-abundance data assuming literature-proposed conversion factors (Kennedy 1994). The importance of meiofauna as an energy sink, whereby a major part of the carbon is internally recycled and mainly heat and nutrients are released (Kuipers et al. 1981), or, alternatively, as a transit of primary food sources up the trophic ladder (Chardy & Dauvin 1992), thus remains an open question. Furthermore, the potential predatory impact of permanent meiofauna on temporary meiofauna has been poorly documented.

This paper presents predation rates on nematode prey in a predatory (*Enoploides longispiculosus*) and a facultatively predatory (*Adoncholaimus fuscus*) nematode, sensu Moens & Vincx (1997). It describes a functional response, and demonstrates that predation may be selective among different nematode prey. Data are further analysed by use of a model predicting predator-prey encounter rates. The potential impact of predators on populations of other nematodes and of temporary meiofauna is discussed.

MATERIALS AND METHODS

Sampling and collection of predatory nematodes. Non-quantitative bulk samples were taken at 2 stations in the Schelde Estuary (SW Netherlands), i.e. (1) Stn 4 on the Molenplaat, and (2) a station at an intertidal flat adjacent to the Paulina salt marsh, by collecting roughly the upper 1 cm of sediment. A brief site description for both stations has been given elsewhere (Moens et al. 1999). Living nematodes were extracted by decantation over a 63 µm mesh sieve after vigorous shaking of the sediment with habitat water. They were subsequently stored for 1 to 4 d under a shallow water cover with some sediment and with prey nematodes from their habitat at 4°C in the dark prior to experiments. They were acclimated for 2 h at the experimental temperature before the start of any experiment (during this period several *Enoploides longispiculosus* captured prey) and selected on the basis of size and activity.

At Molenplaat Stn 4, quantitative samples were taken in June 1996 and June 1997 during low-tide exposure using 3.6 cm internal diameter Perspex cores. These cores were vertically subdivided on site into 0.5 and 1 cm slices for the upper 2 cm and the 2 to 8 cm horizon, respectively. Samples were preserved with 4% formaldehyde and used for nematode community analysis at the species level (Steyaert et al. unpubl. data).

Predation rates of *Enoploides longispiculosus* and *Adoncholaimus fuscus* on a monhysterid nematode. The monhysterid nematode *Diplolaimelloides meyli* was isolated from decaying *Spartina townsendii* leaves and cultivated synxenically with bacteria from its habitat, as described in Moens & Vincx (1998). Nematodes collected from such cultures were washed with sucrose in a final concentration of 40% to remove most adhering microbiota (modified after Sulston & Brenner 1974), rinsed 4 times in artificial seawater (ASW), and eventually resuspended in it. The density of the nematode suspension was approximately 400 *D. meyli* ml^{-1}. Dilutions were prepared in ASW to yield densities of ca 400 (300 to 415), 125 (100 to 135), 50 (30 to 51), and 25 (20 to 25) ind. ml^{-1} (the latter only in experiments with *Adoncholaimus fuscus*). One millilitre aliquots of such *D. meyli* suspensions were spread onto 0.5% bacto-agar layers (12 ml of agar in a 9 cm diam. petri dish) and allowed to stand under a laminar flowhood until the water of the inoculum had largely evaporated. On an areal basis, the prey densities used in our experiments were an order of magnitude lower than typical field densities. On a volume basis, however, they were well within the scope of densities found in the predators' natural habitat (see 'Discussion'). The number of *D. meyli* in each replicate was counted twice and, if deviant, the average of both counts was used as the best approximation of the exact number. Fifteen adults and fourth-stage juveniles (J4) of *E. longispiculosus* or *A. fuscus* were then added. Petri dishes were incubated at 20°C in the dark. Controls consisted of similar *D. meyli* incubations without predators. Three replicate incubations with each predator and 2 controls were counted for each prey density. Prey nematode numbers were counted after 24 and 72 h. A Leitz Dialux inverted microscope and a Wild M5 binocular were used for observations. Prey consumption was calculated as the difference between prey numbers remaining in the control and in the experimental incubations. The edges, walls and lids of the petri dishes were checked to ensure that no prey had escaped from the agar layers. No such prey evasion was noted in our experiments. Natural mortality was easily detectable, since decay times of dead nematodes were considerably longer than the incubation times of our experiments. Occasional findings of heavily damaged prey specimens were treated as removed prey, since we sometimes observed that predators captured but only partially ate prey.

The numbers of prey removed were converted to biomass using an average of 0.45 µg wet weight for *Diplolaimelloides meyli*, i.e. approximately 0.052 µg C, assuming a C content of 11.5% (i.e. between 10.6%

[Sikora et al. 1977] and 12.4% [Jensen 1984]). Nematode biomass was calculated, using Andrassy's (1956) formula, from length and width measurements performed via image-analysis on a Quantimet 500+ system.

Differences in prey-removal rates between different prey densities were examined with a 2-way ANOVA in which prey density and predator presence/absence were crossed (Peterson & Renaud 1989). Counts were $\log_{10}$-transformed to meet the assumptions of normality and homoscedasticity.

Influence of temperature and light on predation rates. Agar layers were prepared as in the previous experiment, but other prey densities were used. The prey (50 *Diplolaimelloides meyli*) were handpicked from stock cultures, rinsed twice in ASW, and subsequently inoculated; 15 predators were added as in the previous experiment. Three replicates and 2 controls were incubated at each of 2 temperatures (10 and 20°C); the experiment was performed in the light as well as in the dark. Predation rates were determined after 24 h. This experiment was run with *Enoploides longispiculosus* only.

Prey selectivity in *Enoploides longispiculosus* and *Adoncholaimus fuscus*. Two experiments aimed at elucidating potential prey selectivity were performed. In a first test, a mixed inoculum of 50 *Diplolaimelloides meyli* and 50 *Monhystera* sp. was offered as prey to 15 predators. Numbers of prey removed were determined after 24 and 48 h. There were 3 replicates per predatory species and 3 controls.

In a second experiment (with *Enoploides longispiculosus* only), 10 predators were inoculated on agar layers to which 100 individuals each of the following prey species were added: *Monhystera* sp., *Pellioditis marina*, *Chromadora nudicapitata*, and *Diplolaimella dievengatensis*. The total number of prey was thus 400 per replicate. All prey nematodes were obtained by manual transfer from monospecific, agnotobiotic cultures (Moens & Vincx 1998). Three replicates and 2 controls were incubated at 20°C in the dark and counted after 24 h.

Statistical analysis of feeding-preference experiments is fraught with difficulty, particularly in relation to the dependence of predation rates on 1 prey species on those on the other prey species (Peterson & Renaud 1989). For the first of our preference experiments, this problem was overcome by comparing differences between the numbers of the 2 prey species remaining at any given time in an experimental series with the corresponding differences in the control series (Peterson & Renaud 1989). These differences were analysed by Student's *t*-tests (if the results of several predators are to be compared, 1-way ANOVA can be used). No data transformation was needed to meet the assumptions of normality and homoscedasticity.

In the second preference experiment, however, predators faced 4 prey options, and the differences between all possible pairs of prey species were interdependent. We have therefore analysed the untransformed counts with a replicated *G*-test for goodness of fit (Sokal & Rohlf 1995). The null hypothesis was that predation rates would not differ among different prey species; the ratio of prey captured would be 1:1:1:1. Heterogeneity G (G_H) (with [no. of replicates – 1] × [no. of prey species – 1] degrees of freedom) was calculated to assess heterogeneity among replicate incubations. Pooled G (G_P) (with no. of prey species –1 degrees of freedom) tested the goodness of fit for the pooled data over all experimental replicates, and G_T, the sum of G_H and G_P (with [no. of replicates – 1] × [no. of prey species – 1] degrees of freedom) tested whether the data as a whole fitted the expected distribution. The same *G*-test procedure was used for pairwise comparisons, at an α-level of 0.005 in order to control the experimentwise α (there were 6 *a posteriori* pairwise comparisons). To include the variability in the controls, both analyses have used a hypothetical set of 6 replicates, 3 of which were obtained by subtracting the higher of 2 control values from the experimental counts, the other 3 by subtracting the lower of the control values.

Analysis of predation rates and prey selectivity using encounter probabilities. The derivation of the encounter probability in 2 dimensions (the agar layers used were thin, and most of the prey and predators remained on the agar surface) closely follows the 3-dimensional model of Gerritsen & Strickler (1977). We assume that the predator is a moving point with velocity v and encounter radius R. The prey has a density per unit surface H. Prey items have velocity u. If the speeds u and v are constant but the directions are independent random variables, define θ as the angle between v and u, and $w = v - u$ as the relative velocity of prey to predator. The relative speed of prey and predator is $w = \sqrt{u^2 + v^2 - 2uv\cos\theta}$. There are $\frac{H\mathrm{d}\theta}{2\pi}$ prey items per unit surface with a relative angle of direction in the range $\mathrm{d}\theta$. The number of prey with an angle in $\mathrm{d}\theta$ entering the encounter circle per unit time is $\frac{H\mathrm{d}\theta}{2\pi}$. The total number of encounters per unit time, z, is the integral over $\mathrm{d}\theta$:

$$z = \frac{RH}{\pi}\int_0^{2\pi}\sqrt{u^2 + v^2 - 2uv\cos\theta}\cdot\mathrm{d}\theta$$

This integral cannot be solved exactly. We approximated its solution by the binomial expansion of the power series $(1+x)^m$. Neglecting terms of order 6 and higher, this yields:

$$z = \frac{RH}{\pi}\sqrt{u^2+v^2}\left(2\pi - \frac{1}{2\pi}k^2 - \frac{15}{512\pi}k^4\right)$$

where

$$k = \frac{-2uv}{u^2+v^2}$$

Motility of the nematodes on the agar was determined under a binocular microscope by drawing and subsequently measuring the path followed by at least 5 nematodes per species over a 5 min interval. Average motility per species was used in our calculations. The observational radius of a predator was considered to be directly proportional to the probing radius of the head, and taken as one-eighth of the total body length, i.e. 0.3 mm in *Enoploides longispiculosus* and 0.7 mm in *Adoncholaimus fuscus*.

RESULTS

Predation rate of *Enoploides longispiculosus* and *Adoncholaimus fuscus* on a monhysterid nematode

The daily *per capita* removal of prey by both predators is depicted in Fig. 1. *Enoploides longispiculosus* captured approximately 4, 2, and 1 *Diplolaimelloides meyli* during the first 24 h at prey densities of 400, 100, and 50 ind. per petri dish. Assuming that predation rates during the second and third day were equal, each *E. longispiculosus* consumed on average 4, <1, and <0.5 *D. meyli* d^{-1} over the next 48 h. In other words, at the highest initial prey density, predation rates remained constant over the entire 72 h incubation, while they decreased by more than 50% at the lower 2 prey densities. A consumption of 4 prey corresponded to 0.21 µg C, which is just under one-third of the predator's own body weight (0.75 µg C).

Over the first 24 h, *Adoncholaimus fuscus* consumed on average 5.5, 2, 0.5, and 0 prey at respective initial densities of 400, 100, 50, and 25 ind. per petri dish. Over the next 48 h, the corresponding daily averages were approximately 2, 0.6, 0.5, and just under 0.5. At an initial prey number of 50, separate counts after 48 and 72 h revealed that during the second and third day each predator consumed just under 1 and 0.25 *Diplolaimelloides meyli*, respectively. Apparently, none of the initial prey densities supported a constant feeding rate in this nematode. The highest daily prey ingestion observed equalled 0.29 µg C, accounting for a mere 5% of the predator's body mass.

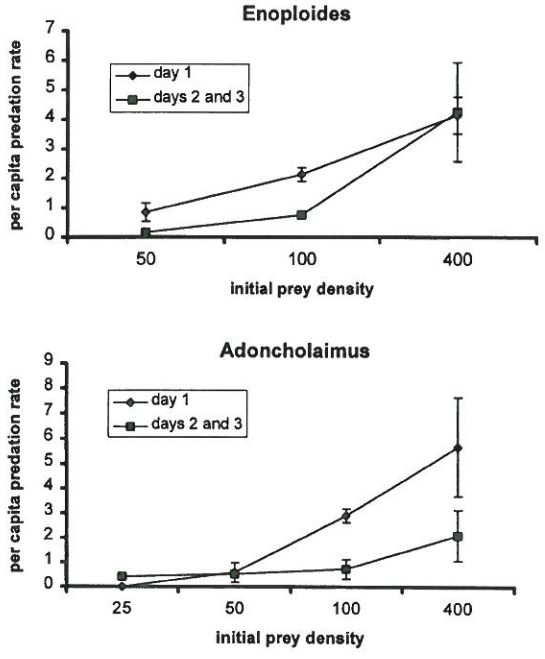

Fig. 1. *Enoploides longispiculosus* (upper panel) and *Adoncholaimus fuscus* (lower panel). Per capita predation rates (ind. predator^{-1}) on the prey nematode *Diplolaimelloides meyli* under laboratory conditions (see 'Materials and methods' for details) over a 3 d period at different initial prey densities (number of individuals). Values are means ±1 SD of 3 replicate incubations

Influence of temperature and light on predation rates of *Enoploides longispiculosus*

Enoploides longispiculosus caught approximately twice as many prey at 20°C than at 10°C (2 ± 0.2 vs 1.1 ± 0.3 prey predator^{-1} 24 h^{-1}). The Q_{10} in this temperature interval was 1.87, close to the Q_{10} for respiration (1.83; Moens et al. 1999). Incubation in the light instead of in the dark had an effect similar to a temperature decrease of 10°C; i.e. the predation rate in the dark at 10°C nearly equalled that in the light at 20°C (0.8 ± 0.1 prey predator^{-1} 24 h^{-1}).

Prey selectivity in *Enoploides longispiculosus* and *Adoncholaimus fuscus*

Fig. 2 shows the change in prey numbers over a 2 d period in the presence and absence of predators. Approximately 92 and 100% of *Monhystera* sp. and of *Diplolaimelloides meyli*, respectively, were recovered in the controls without predators. *Adoncholaimus fuscus* caught no net prey over the first 24 h, but removed on average 0.33 and 0.37 *Monhystera* sp. and *D. meyli*, respectively, over the next 24 h. Although the average number of prey remaining in the *A. fuscus* treatments after 48 h was lower for *Monhystera* sp. than for *D. meyli*, there was no significant preference for either

prey ($p \gg 0.05$). An average of 0.67 *Monhystera* sp. and of 0.39 *D. meyli* were removed per predator by *Enoploides longispiculosus* over the first 24 h (Fig. 2). Over the next 24 h, the respective values were 0.36 and 0.73, again without significant differences between the 2 prey species ($p \gg 0.05$).

In the second preference experiment, *Enoploides longispiculosus* exhibited a distinct preference for some prey species over others: each predator removed on average 3.5, 2.3, 1.2 and 1.1 specimens of *Monhystera* sp., *Pellioditis marina*, *Chromadora nudicapitata*, and *Diplolaimella dievengatensis*, respectively. No net predation on the latter species was noted in 1 of 3 replicates, while the remaining 2 replicates averaged a consumption of nearly 2 prey predator^{-1}, i.e. intermediate between *P. marina* and *C. nudicapitata*. The prey ranked in decreasing order of attractiveness as: *Monhystera* sp. > *P. marina* > *D. dievengatensis* ≅ *C. nudicapitata*. The results of the *G*-tests for goodness of fit showed that replicates were heterogeneous ($p < 0.001$). Nevertheless, the experimentwise and all pairwise pooled G_Ps and G_Ts were highly significant ($p < 0.001$), except for the differences between *P. marina* and *C. nudicapitata* and between *C. nudicapitata* and *D. dievengatensis* ($p > 0.05$) There was no evidence of a selection of larger prey, since prey species ranked in the following biomass order: *P. marina* (0.15) > *C. nudicapitata* (0.054) > *Monhystera* sp. (0.047) > *D. dievengatensis* (0.032) (data in µg C ind.$^{-1}$). Predation in this experiment accounted for 0.53 µg C predator^{-1} d^{-1}, i.e. 81.5% of the predator's own body weight (0.65 µg C ind.$^{-1}$ compared to 0.75 in all other experiments). The higher predation rate in this compared to other experiments probably reflects predator age: J4 juveniles and young adults in this preference experiment versus mostly adults in other experiments. The biomass contributions of *Monhystera* sp., *P. marina*, *C. nudicapitata* and *D. dievengatensis*, in the ration of *E. longispiculosus* were 0.141, 0.299, 0.054 and 0.032, µg C, or 26.8, 56.8, 10.3, and 6.1%, respectively.

Table 1. Motility of predatory and prey nematodes used in the present experiments. Values are means ± 1 SD of at least 5 observations. (P): predatory nematode

Species	Motility (mm min^{-1}) Average	SD
Enoploides longispiculosus (P)	5.15	1.96
Adoncholaimus fuscus (P)	9.35	2.27
Monhystera sp.	1.72	1.06
Diplolaimelloides meyli	6.09	4.06
Pellioditis marina	7.3	1.54
Chromadora nudicapitata	5.55	2.05
Diplolaimella dievengatensis	2.37	1.49

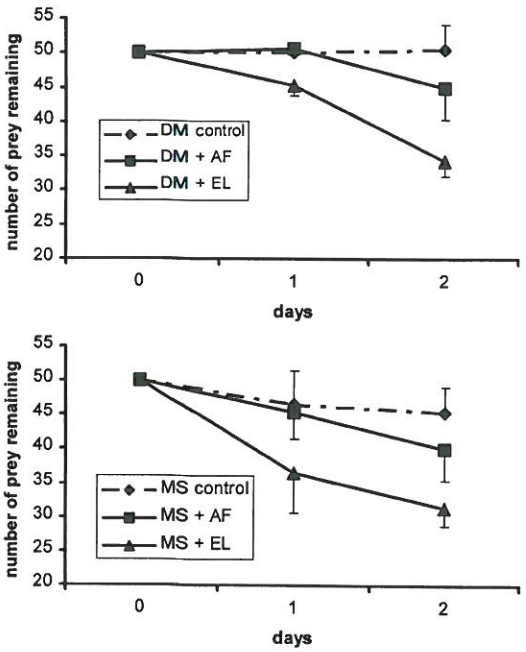

Fig. 2. Change in prey numbers (*Diplolaimelloides meyli* and *Monhystera* sp. as prey species) over a 2 d incubation with 2 prey species offered simultaneously to the predatory nematodes *Enoploides longispiculosus* or *Adoncholaimus fuscus*. Upper panel: *D. meyli*; lower panel: *Monhystera* sp. DM control = *D. meyli* without predators; MS control = *Monhystera* sp. without predators; + AF = with *A. fuscus* as the predator; + EL = with *E. longispiculosus* as the predator. Values are means and 1 SD of 3 replicates per treatment

The encounter-rate model predicted only a minor effect of prey motility in determining feeding preferences. Using the motility rates in Table 1, the number of predator-prey encounters involving *Enoploides longispiculosus* over a 24 h period varied from 42 with *Diplolaimella dievengatensis* as prey to 59 with *Pellioditis marina* as prey. The most frequently caught prey, *Monhystera* sp., yielded only 43 encounters, so the observed preference for this species did not result from a disproportionately high encounter probability.

DISCUSSION

Both predatory nematode species showed a marked functional response: *Enoploides longispiculosus* fed at a constant rate (4 prey predator^{-1} d^{-1}) when prey densities exceeded 200 ind. per petri dish, while catching only half and a quarter of this amount of prey at 100 and 50 ind. per petri dish, respectively. The fact that predation rate remained constant over a 3 d incubation implies that satiation did not occur. At lower prey densities, predation rates were proportional to prey avail-

ability. For *Adoncholaimus fuscus*, however, none of the prey densities in our experiments yielded a constant predation rate. Since *A. fuscus* moved actively through the agar and 1 complete generation of this species has been reared on agar media (Moens & Vincx 1998), it is unlikely that the reduced feeding activity from Day 1 onwards resulted from an unfavourable environment or substrate rather than from an insufficient prey density. Therefore, none of the tested prey densities supported a maximal predation rate. Further experiments should elucidate whether predation rates in *A. fuscus*, like those in *E. longispiculosus*, attain a plateau at higher prey densities.

These predation rates can be translated to the 3 dimensions of a sediment through reference to the encounter-probability function for a 3-dimensional sphere as given by Gerritsen & Strickler (1977), where $z = \pi R^2 H/3 \cdot [(u^2+3v^2)/v]$. This, however, requires information on strike rates. In the absence of data on attack rates (i.e. the proportion of predator-prey encounters resulting in an attempt to capture prey [Bilgrami & Jairajpuri 1989]), strike rates were defined as the ratio of prey captured to the number of encounters. Using the motility rates in Table 1, strike rates in *Adoncholaimus fuscus* were far below 1% at all prey densities. *Diplolaimelloides meyli* was not an unsuitable prey, since it was one of the most frequently captured species in multi-species microcosms (Moens unpubl. obs.) The low strike rates in *A. fuscus* are therefore indicative of low predatory efficiency. It has been demonstrated elsewhere that oncholaimid nematodes preferentially feed in organically enriched microhabitats, probably utilizing a mix of particulate and dissolved compounds, and that predation is merely a facultative strategy (Lopez et al. 1979, Moens et al. 1999). It is surprising, though, that in an environment devoid of other food, *A. fuscus* did not increase its predation efficiency. Observations on juvenile *Adoncholaimus* sp. starved for several days suggest that such an increased predation efficiency may, however, occur in the longer term (Moens et al. 1999). Similarly, starved mononchids, terrestrial predatory nematodes, showed a higher attraction to prey compared to recently fed individuals (Bilgrami & Jairajpuri 1988).

Strike rates in *Enoploides longispiculosus* in experiments with *Diplolaimelloides meyli* as the sole prey were also rather low, ranging from 2 (at 400 prey per petri dish) to 4% (at 50 prey per petri dish). It is difficult to interpret prey limitation in combination with low strike rates. Prey handling time in the predators used here was less than 15 min, and hence did not significantly impact strike rates. Obviously, not every predator-prey encounter results in an attack, and not every attack results in prey capture. Prey nematodes may have escape mechanisms that can either depress encounter rates or result in a discrepancy between attack rate (i.e. the number of times a predator-prey encounter results in an attempt to catch prey) and strike rate (i.e. the number of times a predator-prey encounter results in consumption of the prey) (Bilgrami & Jairajpuri 1989, Bilgrami 1992). Predation efficiency may be different in the agar medium compared to sediment, although contrary to the situation in water, neither predator had difficulties catching prey on agar (Moens et al. 1999). Finally, predators may need yet unknown specific stimuli in order to attack encountered prey.

Substituting the motility of *Enoploides longispiculosus* for u and that of *Diplolaimelloides meyli* for v in the encounter-probability function for a 3-dimensional sphere (see above), the encounter rate becomes $3.07 \cdot H$ (d^{-1}), where H = the number of individuals per cm^3. With a strike rate of 4% and a predation rate of 4 prey $predator^{-1}$ d^{-1}, and assuming comparable strike rates in agar and in sediment, a predator would need an extant prey density of 33 ind. cm^{-3}, corresponding to 330 prey nematodes 10 cm^{-2} if all prey nematodes were restricted to a 1 cm thick sediment horizon. Since the strike rate at sufficient prey density was closer to 2%, the prey density would have to be twice as high. Densities of 330 to 660 prey nematodes 10 cm^{-2} in the upper 1 cm of sediment are realistic for fine-sand, estuarine, intertidal sediments. A similar calculation for the predator-prey combination *Adoncholaimus fuscus-Diplolaimelloides meyli*, assuming a strike rate of 0.4% and a predation rate of 5.5 prey $predator^{-1}$ d^{-1}, results in 580 prey 10 cm^{-2} if all prey are contained within a 1 cm thick horizon.

While the foregoing suggests that *Enoploides longispiculosus* feeds at rates sustainable by extant prey densities, its potential impact on prey abundance is striking. When feeding at a rate of 0.4% prey $predator^{-1}$ d^{-1}, 15 *E. longispiculosus* removed approximately half the *Diplolaimelloides meyli* stock at the highest initial densities in 3 d. Assuming that (1) all nematodes were equally available as prey, and (2) predation rates on *D. meyli* were representative of rates on other nematodes, (adult) *E. longispiculosus* would reduce prey abundance by 50% within 3 d even when it comprised less than 5% of total nematode numbers. At Molenplaat Stn 4, *E. longispiculosus* comprised 75% of total nematode numbers in the upper 1.5 cm.

Neglecting the observed predation rates, but assuming that *Enoploides longispiculosus* (1) produces 1 generation annually (see e.g. Wieser & Kanwisher 1960, Lorenzen 1974, Malakhov 1974, Smol et al. 1980, for information on other enoplid nematodes with 1 generation annually in their natural habitat), (2) has a production to biomass ratio of 3 per generation, as for other aquatic nematodes (Gerlach 1971), (3) has a

production efficiency of 75% (Moens et al. 1999), and (4) has an assimilation efficiency of 60% (Marchant & Nicholas 1974), the prey nematode community at Stn 4 as it was in June 1996 and 1997 (Steyaert unpubl. data) would need an annual P/B of 8.44 to balance the production of the *E. longispiculosus* standing stock. This value is nearly identical to that of a nematode community of a tidal flat in the Lynher Estuary, where the most abundant predatory species averaged less than 1% of total nematode numbers (Warwick & Price 1979). These estimates of C requirements for *E. longispiculosus* are conservative, since (1) the above value for assimilation efficiency is the highest reported for aquatic nematodes, and also influences the production efficiency of 75%, and (2) other enoplid nematodes, including *E. spiculohamatus*, produce 2 to 3 generations annually in their natural habitat (Schütz 1966, Skoolmun & Gerlach 1971).

However, when only the experimentally obtained consumption data are considered, the picture changes completely. The prey nematode community at Stn 4 would now need an annual P/B more than 1 order of magnitude higher than the above value to meet the consumption of the extant *Enoploides longispiculosus* at average environmental temperatures. The vertical distribution of nematodes at Stn 4 on the Molenplaat shows a generally bimodal pattern. *E. longispiculosus* largely dominates the upper 2 cm, but is virtually absent below this depth, where the community is dominated mainly by deposit-feeding nematodes (Fig. 3). It is tempting to consider the subsurface peaks of the deposit-feeding meiofauna as resulting from predator control, but the hydrodynamic regime on this site is confounding to this interpretation. The presence of high predator densities in the upper sediment layers may be of significance in structuring permanent meiofauna communities as well as in the recruitment and survival of temporary meiofauna on this tidal flat. Permanent meiofauna has been suggested to potentially play a role in the settlement and survival of the temporary meiofauna, both by predation and competition (see e.g. Thorson 1966, Watzin 1983, 1985, Danovaro et al. 1995). Competition for space and resources is generally considered of prime importance (Zobrist & Coull 1992, Olafsson et al. 1994, Hunt & Scheibling 1997), but both indirect evidence and observations suggest that predation by permanent meiofauna (especially turbellarians and predatory nematodes) may also be significant (Staarup 1970, Watzin 1983, 1985). When added to the drift of permanent meiofauna being redistributed and deposited from elsewhere on the flat and from adjacent tidal flats, this 'mobile' meiofauna may constitute an important food for *E. longispiculosus*. It could tentatively be hypothesized that in the particular environment of Molenplaat Stn 4, the high numbers of

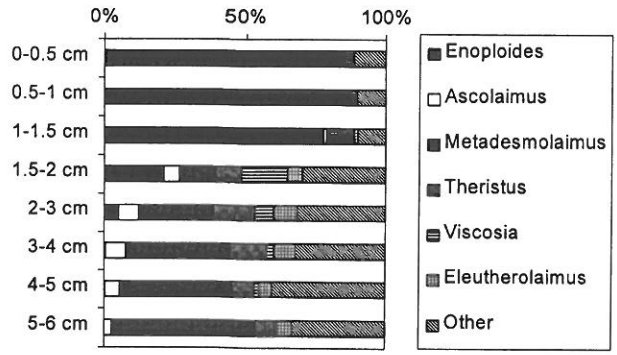

Fig. 3. Vertical distribution pattern of *Enoploides longispiculosus* and other abundant nematode genera at Stn 4 on the Molenplaat, Schelde Estuary, The Netherlands. Data are relative biomass contributions, and represent averages of at least 3 replicate sediment samples

E. longispiculosus may generally be prey-limited, but may benefit from episodes of higher prey abundance, e.g. during recruitment events of macrofauna larvae. Cannibalism, as observed among *E. longispiculosus* from the Molenplaat, could be interpreted as a further indication of prey-limitation (Moens et al. 1999). Alternatively, the possibility remains that *E. longispiculosus* does not feed exclusively on metazoan prey. Although the nematodes' reproductive effort is probably restricted to 1 or a few periods annually, a minimum generation time of just over 3 wk has been noted for a related nematode, *Enoplus paralittoralis* (Hopper et al. 1973). This suggests that enoplids such as *E. longispiculosus* may easily adapt to improving 'environmental' conditions, and we tentatively hypothesize that reproduction, maturation and high predation rates may be limited to such periods.

The prey selectivity observed for *Enoploides longispiculosus* probably did not result from differences in the activity of the different species used, encounter probabilities being lower for *Monhystera* sp. and *Diplolaimella dievengatensis* than for the other prey species. In contrast, strike rates of a freshwater predator, *Mononchus aquaticus*, were higher on less motile prey, because these have lower escape rates (Bilgrami et al. 1983). Since predator-prey encounter probability was not limiting to strike rate, the observed differences reflect a true feeding preference. Observations of *E. longispiculosus* attacking a variety of candidate prey from its natural habitat also suggest that some species are more readily attacked and/or captured than others, as found for several terrestrial and freshwater predatory nematodes (Bilgrami et al. 1983, Small & Grootaert 1983, Bilgrami & Jairajpuri 1989, Bilgrami 1992, but note a non-selective predation for *Mononchoides potohikus* reported by Yeates 1969). Relative

size differences between prey and predator may contribute to the observed selectivity, since larger prey may more readily escape predator attacks (see also Moens & Vincx 1997). In the present experiments, the largest of the different prey species offered, *Pellioditis marina*, was the only species of which individuals were sometimes observed escaping from predator attacks or found heavily damaged but not eaten. So far there is no evidence that *E. longispiculosus* may locate prey from a distance, as do some mononchid predators (Bilgrami & Jairajpuri 1988). The combination of high predation rates with significant prey selectivity suggests that predation among meiofauna may be an important structuring factor for meiofauna communities.

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