

Population dynamics of *Dipolaimelloides brucei*, a nematode associated with the salt marsh plant *Spartina anglica**

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ABSTRACT: The halophyte *Spartina anglica*, which occurs abundantly in the lower parts of Western European salt marshes, contains large amounts of standing dead plant material year round, supporting a rich faunal community. The population dynamics of *Dipolaimelloides brucei*, one of the dominant nematode species present on *S. anglica*, was studied in relation to the decomposition stage of the plant material. *S. anglica* vegetations are regularly flooded at high tide, reducing the nematode population density on the plant material as nematodes are flushed from the plants. The extent of population reduction by flooding was studied in a laboratory experiment using litter of 2 different decomposition stages. *D. brucei* was present throughout the year on all types of plant material, including live green plant parts. The population densities were highest on the older plant material, reaching 1000 to 2000 ind. g⁻¹ in late summer and autumn. In the laboratory the rate of removal by flooding was 4.4 times higher on brown leaves than on yellow leaves, while the birth rates were almost identical. As a result the population on yellow leaves increased at a much higher rate than on brown leaves and reached much higher densities. The total number and biomass of *D. brucei* formed in the *S. anglica* vegetation were calculated, assuming that the birth rate of the species depended only on temperature, to be 9 million ind. m⁻² yr⁻¹ accounting for 114 mg C m⁻². The total amount of carbon ingested by *D. brucei* as bacterial biomass accounted for 7.5% of the total bacterial biomass produced. The dominant bacterivorous nematodes together may remove over 20% of the total bacterial biomass.

KEY WORDS: Decomposition · Flooding · Nematodes · Population dynamics

INTRODUCTION

In the lower zone of Western European salt marshes, *Spartina anglica* can form extensive monospecific vegetations. On these sites relatively large amounts of standing dead plant material is found year round (Wolff et al. 1979, Groenendijk 1984). Export of plant-derived detritus from European coastal salt marshes is probably insignificant (Hemminga et al. 1992, 1993). The major part of the dead plant material, therefore, will decompose at the production site. Decomposing

leaves remain attached to standing stems for a prolonged period (Newell et al. 1989). Dead plant material of different stages of senescence and decay can be found in the canopy; senescent and dead leaves attached to the still green culms and old, dead culms with barely any leaves are simultaneously present.

Decomposition is largely a microbial process, but is influenced by the faunal community, which may consist of macro-, meio- and microfaunal species (Swift et al. 1979). In salt marshes especially, nematodes are abundantly present on decomposing *Spartina anglica* litter (Buth & de Wolf 1985, Hemminga & Buth 1991). *Dipolaimelloides brucei* is one of the dominant nematode species present on living and dead *S. anglica* leaves (Hopper 1970, Warwick 1981, Bouwman et al. 1984). *D. brucei* is scarcely found in the surrounding sediment, indicating that *D. brucei* is narrowly asso-

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ciated with *S. anglica* litter (Bouwman et al. 1984). In a previous study, we found that *D. brucei* can stimulate bacterial decomposition of *S. anglica* leaves under laboratory conditions (Alkemade et al. 1992). The effect of *D. brucei* on the decomposition of *S. anglica* is expected to depend on nematode population density and on the total number of nematodes formed, including the individuals lost due to death, flooding, etc. The study of population growth and of population density is therefore considered important to assess the potentially stimulating effects of the nematodes under field conditions.

The population density of *Diplolaimelloides brucei* probably depends on at least 3 factors. Firstly, since *D. brucei* is a bacterivorous nematode (Romeyn & Bouwman 1983, Nicholas 1984), the population density is expected to depend on the bacterial biomass production. Secondly, the population growth rate of *D. brucei* depends on temperature (Warwick 1981) and population growth will therefore fluctuate seasonally. Thirdly, flooding by seawater is expected to remove nematodes and thus will decrease population densities (cf. Fleeger et al. 1984).

In this study we investigated the population dynamics of *Diplolaimelloides brucei* on standing live and dead plants of *Spartina anglica* in a salt marsh in the SW Netherlands. Monthly samples of above-ground *S. anglica*, consisting of visually distinguishable stages of decomposition, were collected and the nematode population associated with the plant material was analyzed. The population growth of *D. brucei* on *S. anglica* litter of different decomposition stages was also studied in laboratory experiments. A facility to simulate flooding was used to assess the influence of flooding on population densities present on the different litter types. Finally, an estimation of the proportion of the bacterial biomass consumed by *D. brucei* was made.

MATERIAL AND METHODS

Field study. Samples of *Spartina anglica* were collected in a salt marsh (called Rattekaai), situated in the Oosterschelde, a tidal inlet of the southern North Sea. The samples were taken in a 100 m² area near the edge of the salt marsh where *S. anglica* forms an almost monospecific vegetation. *Salicornia* sp. was also present in very low densities. The elevation of the site was 1.67 m above Dutch Ordnance Level (NAP).

Three paired randomly selected samples were collected monthly from 20 September 1990 to 15 August 1991. Small quadrats (0.04 m²) were harvested by cutting the plants at the sediment surface. The plant material was put into plastic bags and transported to

the laboratory where all samples were divided into 4 different categories: 'living green biomass'; 'greenish-yellow leaves', with the stem parts bearing these leaves; 'dead brown leaves', again with the stem parts bearing these leaves; and 'old stems', brown culms without any leaves. If the lower parts of the stems were covered by a layer of sediment, these parts were discarded, because nematode densities and species composition are highly influenced by this layer (Bouwman et al. 1984). One sample of a pair was dried at 70°C for 48 h in order to obtain dry weight estimates of the 4 different categories of plant material. The other sample was fixed in warm 4% formalin to preserve the nematodes.

Nematodes were extracted from the plant material by rinsing the samples with tap water over a household sieve (2 mm mesh). Nematodes and other particles passed through the sieve whereas the coarse plant material was retained. The plant material was dried and weighed. The suspension containing the nematodes was further processed using centrifugation as described in Alkemade et al. (1993). In each sample, the total number of nematodes was counted under a dissecting microscope. A total of 100 nematodes were identified and the number and biomass of *Diplolaimelloides brucei* were estimated in 1 of the 3 samples of each category collected each month.

Differences among total nematode densities and among densities of *Diplolaimelloides brucei* on the different categories of *Spartina anglica* material were evaluated by analysis of covariance. The relations between nematode densities, temperature and flooding frequency were evaluated by regression analysis. Densities were log-transformed prior to analysis. The monthly average air temperature measured at Vlissingen (data obtained from the Royal Dutch Meteorological Institute) and the flooding frequency between sampling days, derived from the high tide levels recorded at the nearby point of Marollegat (data obtained from the Ministry of Transport and Public Works, Tidal Waters Division), were used in the analysis.

Laboratory experiment. Two separate experiments with brown and yellow-greenish leaves were carried out in October/November 1991 and February/March 1992. Leaves were collected at the Rattekaai salt marsh. The leaves were washed with tap water and dried at air temperature. The leaf material was sterilized by gamma irradiation (2 Mrad) at a facility for food irradiation (Proefbedrijf voor Voedselbestraling Wageningen).

The leaves were cut into 3 cm long fragments and put into small nylon bags with 1 mm mesh. Each bag received ca 0.5 g DW. The bags were soaked in sterile, filtered seawater for about 2 h. All bags were inocu-

lated with 100 μl of a microbial assemblage. This assemblage was obtained by rinsing *Spartina anglica* plant material originating from the Rattekaai salt marsh with sterile seawater and filtering the water over a 1.2 μm filter. Specimens of *Diplolaimelloides brucei* obtained from cultures (see Alkemade et al. 1992) were also added to each bag. The initial nematode population density was determined after 2 d of incubation.

A total of 20 bags were placed in a 1 l glass jar and transferred to an incubator (20°C). Flooding was simulated 4 times a week by pumping filtered and autoclaved Oosterschelde seawater into the glass jar. The jar was filled within 30 min at a rate of 15 ml min⁻¹. The water remained 2 h in the jar before it was pumped back into a bottle. The water in the bottle was renewed 2 times a week. Nematode numbers were counted in a 10 ml sample of the water that was removed from the bottle. Two replicate jars were prepared for each experiment. Once a week 2 bags were removed from each jar. One bag was dried and weighed to determine weight loss. The other bag was fixed in warm formalin (4%) and the number of nematodes determined. The experiments lasted 42 d.

The population density on the *Spartina anglica* material was assumed to be determined by the rate of removal of nematodes from the litter and the population growth rate. An exponential growth model with a constant rate of removal by flooding was adopted to describe the population dynamics of *Diplolaimelloides brucei*. It was assumed that birth rate minus death rate remained constant during the experiment, resulting in a net growth rate. Furthermore, it was assumed that the rate of removal by flooding was the only source of disappearance apart from death. The model can be described by the following equation:

$$N_t = N_0 e^{(\beta - \alpha)t} \quad (1)$$

where N_t = number of nematodes present on the *S. anglica* detritus at time t ; N_0 = number of nematodes present at the start of the experiment; β = growth rate; and α = rate of nematodes flushing due to flooding. The flooding parameter can be estimated independently of β by using the number of nematodes flushed away and the number of nematodes present on the leaves. As the days on which the bags were removed from the jar did not coincide with the days on which the flushing took place, the number of nematodes present on the leaves at the moment of flushing was calculated by linear interpolation between the sampling days. α was found by linear regression of the number of nematodes flushed away per unit time on the number of nematodes present on the *S. anglica* leaves. It was assumed that the errors in the observations had a Poisson distribution, as the data were counts. The parameters were

estimated using maximum likelihood estimation (McCullagh & Nelder 1989). Using the calculated values for α , the growth rate β was then calculated by non-linear regression of the exponential growth equation (Eq. 1). Again the errors were assumed to have a Poisson distribution and maximum likelihood estimation was used to estimate the parameters. Subsequently, the total numbers developed during the course of the experiments were estimated by integrating growth β over time:

$$P = \int_0^T \beta N dt \quad (2)$$

where P = the total number of nematodes; and T = the last day of the experiment.

The regression analyses were carried out using SYSTAT 5.0 (Wilkinson 1990) and the total number of nematodes formed was calculated by numerical integration using SENECA 1.5 (De Hoop et al. 1992).

RESULTS

Field study

Green biomass of *Spartina anglica* showed a clear seasonal pattern (Fig. 1). In August a maximum of 850 g DW m⁻² of green biomass was reached. Green *S. anglica* leaves were found year round, but in winter months only a very low biomass was observed. Yellow leaves were also found in most of the samples. The peak amount of 200 g DW m⁻² of yellow leaves was found in January. Older plant material of the categories 'brown' and 'old stems' were found throughout the year in relatively constant amounts. The total dead biomass, consisting of the categories 'yellow', 'brown'

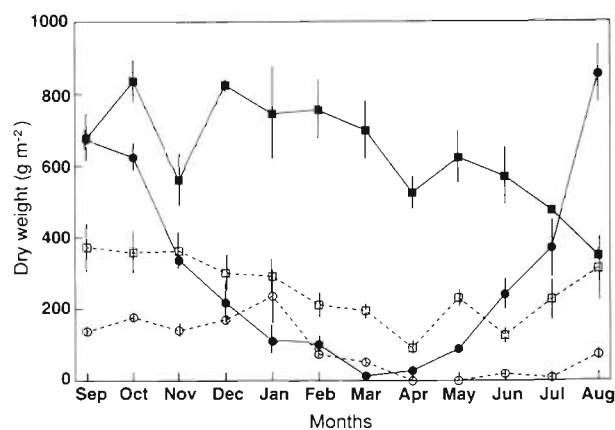


Fig. 1. *Spartina anglica*. Dry weights (g m⁻², mean \pm SE, n = 3) of 4 categories of standing plant material in the salt marsh. (●) Living green biomass; (○) yellow leaves; (■) brown leaves; (□) old stems

and 'old stems', exceeded the biomass of the green plant parts in every month except August.

The total nematode densities, all species included, expressed as numbers per g dry weight (DW) of plant material, are shown in Fig. 2A. The numbers found on brown and old material were usually higher than on yellow and green leaves and showed little seasonal variation. The numbers fluctuated between 1000 and 4000 ind. g⁻¹ DW. The numbers of nematodes on green and yellow plant parts were usually much lower, but showed a sharp peak in March and June, respectively. The total numbers per m² of *Spartina anglica* vegetation fluctuated from about 1 million in spring and summer to 2 to 3 million in autumn (Fig. 2B).

Diplolaimelloides brucei was found in all samples. Densities differed significantly between the various litter categories ($p < 0.05$). For this test we assumed that the observations from the different sampling dates were replicates. On the brown plant parts and the old

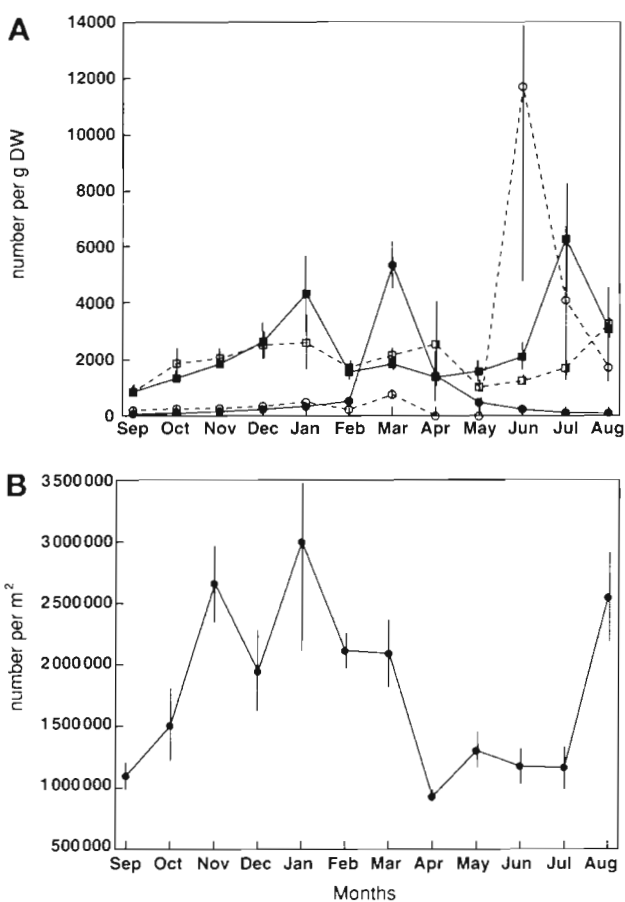


Fig. 2. Nematodes living on *Spartina anglica*. (A) Densities (ind. g⁻¹ DW) of all species of nematodes on 4 categories of standing plant material: (●) living green biomass; (○) yellow leaves; (■) brown leaves; (□) old stems. (B) Total number of nematodes (ind. m⁻²) on aboveground plant parts. Means \pm SE, $n = 3$

stems, population densities were usually higher than on the green and yellow plant parts (Tukey's test, $p < 0.05$). Population density on the green leaves was usually lower than 100 ind. g⁻¹ DW, but a much higher density was found in the March sample (Fig. 3). On yellow leaves the population density was usually about 100 ind. g⁻¹ DW, but higher population densities were found in the summer reaching a maximum of more than 2000 ind. g⁻¹ DW in July. On brown plant parts, population densities were highest in summer (July and August), and reached densities of 1400 ind. g⁻¹ DW; in the other seasons the numbers of *D. brucei* were much lower. On old stems a similar pattern was observed; the highest numbers were found in summer. In Fig. 4 the relative abundance of *D. brucei* is shown. In September 1990 and in August 1991 the relative abundance of *D. brucei* was 38 and 45% respectively (Fig. 4). In the winter months *D. brucei* did not dominate: less than 12% of the total number were of this species in December 1990, January and February 1991. On average, *D. brucei* formed 20% of the total nematode community on the *Spartina anglica* plants.

Regression analyses showed that the log-transformed nematode densities were not related to the flooding frequency ($p > 0.5$ for all categories of plant parts). The log-numbers of nematodes on yellow and on brown leaves were highly correlated with the mean monthly temperature ($p < 0.01$). On green plant parts and old stems no correlation was found between the nematode densities and the temperature ($p = 0.67$ and 0.19 , respectively).

Laboratory study

During the experiments the weight of *Spartina anglica* leaves in the litter bags decreased gradually.

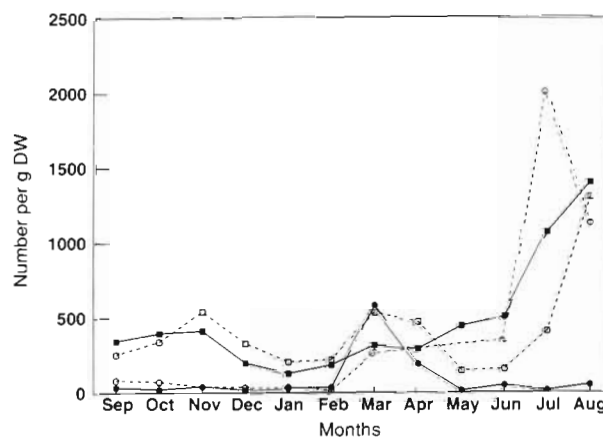


Fig. 3. *Diplolaimelloides brucei* living on *Spartina anglica*. Densities on 4 categories of standing plant material: (●) Living green biomass; (○) yellow leaves; (■) brown leaves; (□) old stems

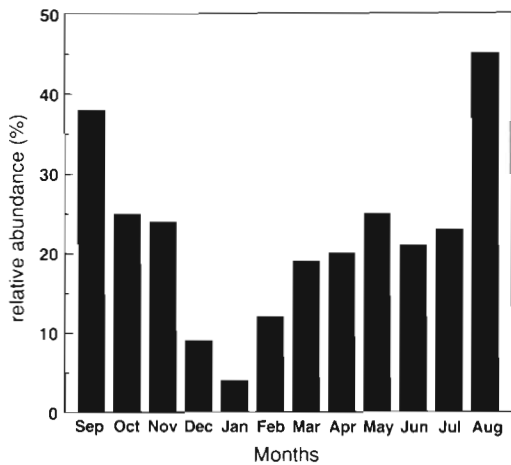


Fig. 4. *Diplolaimelloides brucei* living on *Spartina anglica*. Abundances relative to the total nematode community present

The weight losses from the yellow leaves were higher than from the brown leaves. After 42 d the yellow leaves lost, on average, 32% of the initial weight, whereas the brown leaves lost < 10%.

The initial nematode population on the yellow leaves was smaller than on the brown leaves. At the first sampling date, 2 d after inoculation, 25 ind. g⁻¹ DW were found on the yellow leaves and 300 ind. g⁻¹ DW on the brown leaves. These figures were used in the calculation of the population growth parameters. Conspicuously more nematodes were flushed away from the brown leaves, relative to the numbers in the litter bags, than from the yellow leaves. In Fig. 5, the numbers flushed away during 1 flushing time are plotted against the numbers present on the leaves. The flooding parameter α was 4.4 times higher on brown leaves than on

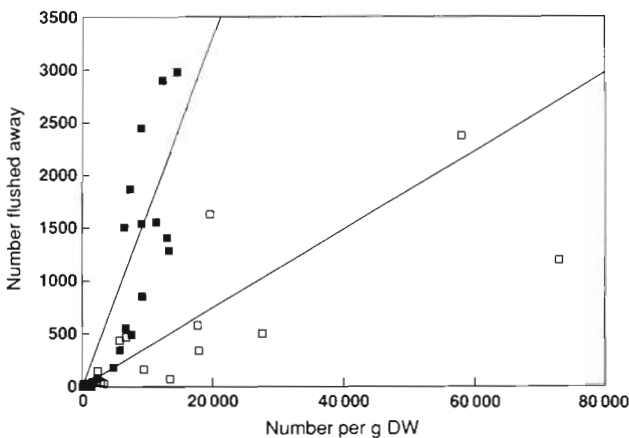


Fig. 5. *Diplolaimelloides brucei* living on *Spartina anglica*. Numbers flushed away from yellow (\square) and brown (\blacksquare) leaves plotted against the number present on decomposing leaves

yellow leaves, 0.164 and 0.037 per flushing time respectively. Apparently α depended largely on litter type. These figures and the initial population densities were used to calculate the birth rate β . Since the flooding parameter α was calculated as a rate per flushing time and flushing occurred 4 times a week, these parameters had to be transformed to rates per day by dividing the parameters by 1.75. In Fig. 6 the growth curves of the populations on yellow and on brown leaves are shown. The prolonged initial phase of population growth on yellow leaves is due to the lower initial population density. At the end of the experiment much higher densities were reached on yellow leaves than on brown leaves. The calculated birth rates in both populations were almost identical: 0.206 (\pm 0.008, 95% CL) on yellow leaves and 0.197 (\pm 0.01, 95% CL) on brown leaves. The calculated total number of nematodes formed was 55 800 on yellow leaves and 42 000 on brown leaves. The difference between these 2 numbers was low in comparison with the population densities present at the end of the experiment, ca 56 000 on yellow leaves and ca 11 500 on brown leaves.

DISCUSSION

The *Spartina anglica* vegetation in the Rattekaai salt marsh contains a large proportion of dead plant material. More dead plant material was found than green, live plant material almost year round. Nematodes were present throughout the year on green plant parts as well as on senescent and decaying plant parts. The highest numbers of nematodes per m² were found during the autumn and winter, coinciding with the highest amounts of dead plant material present on the salt marsh. The total numbers of nematodes ranged

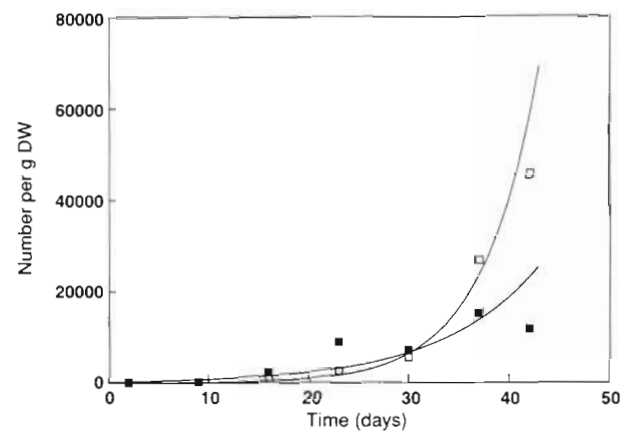


Fig. 6. *Diplolaimelloides brucei* living on *Spartina anglica*. Population growth on yellow (\square) and brown (\blacksquare) leaves. Fitted lines are exponential growth curves

from 1×10^6 to 3×10^6 m^{-2} . These numbers are of the same magnitude as the numbers found in salt marsh and estuarine sediments; the total number in the sediment supporting *S. anglica* vegetation varied from 2 to 10 million $ind. m^{-2}$ (Alkemade et al. 1993), and in coastal sediments usually densities between 1 and 20 million $ind. m^{-2}$ are observed (e.g. Teal & Wieser 1966, Warwick & Price 1979, Heip et al. 1985). Thus, the nematode community living on the standing dead plant parts forms a substantial part of the total salt marsh nematofauna.

The bacterivorous nematode *Diplolaimelloides brucei* is one of the dominant species present on the above-ground plant parts, representing up to 50% of the nematodes in late summer and autumn. Bouwman et al. (1984) found similar percentages for *D. brucei* on *Spartina anglica* vegetation in the northeastern part of The Netherlands. The numbers of *D. brucei* found in the field were much lower than the densities observed under laboratory conditions, which possibly is due to the more moderate conditions in the laboratory. In the field, temperature fluctuates much more than in the laboratory and usually does not reach values over 20°C. Flooding is irregular and probably often more vigorous than in the laboratory experiment, causing higher losses of nematodes from the population.

In the laboratory experiment the population dynamics of *Diplolaimelloides brucei* could be described by an exponential growth model, consisting of 2 components: a constant growth rate and a constant rate of loss of nematodes as a result of flushing. The results showed that the birth rates were almost identical on both leaf types (0.206 and 0.197 on yellow and brown leaves respectively) and were close to the value of 0.21 d^{-1} found by Warwick (1981) for the rate of population increase of the same species at 20°C. The pre-

sent values are also consistent with our earlier estimate of 0.22 d^{-1} (Alkemade et al. 1992). The growth of the nematode population on the different leaf types was mainly affected by flooding. On brown leaves the proportion of nematodes flushed away relative to the population density present on the leaves was 4.4 times higher than on the yellow leaves. This may be caused by the fact that the surface properties of the leaf litter alters with age. During decomposition the leaves disintegrate to tangles of long shreds (Newell et al. 1989). At the beginning of the experiments both leaf types had clear surface structures consisting of longitudinal grooves. Nematodes may be relatively protected against the risk of being flushed away in these grooves. The brown leaves lost this surface structure within a few weeks. As a result, nematodes may lose their 'grip' and consequently are flushed away during high tide. The structure of the yellow leaves, in contrast, remained much more intact during the experiment, which may have enabled the nematode population to reach relatively high densities.

The disappearance of large numbers of nematodes from disintegrating leaves is not necessarily a loss to the population. Some of these nematodes may reach other *Spartina anglica* sites. We observed that *Diplolaimelloides brucei* remained in suspension for several hours, sufficiently long to migrate within a salt marsh during high tide.

In the field the numbers of *Diplolaimelloides brucei* were usually highest on the older plant litter of the categories 'brown' and 'old stems'. Only in late summer did the numbers found on yellow leaves exceed the numbers on brown leaves and old stems. During the first phases of decomposition the population density apparently increases from the low numbers found on yellow leaves to the high numbers found on brown

Table 1. *Diplolaimelloides brucei*. Estimation of monthly production. For calculation of C production, a nematode C content of 10.6% of wet weight was assumed (Heip et al. 1985)

Month	Mean temperature (°C)	Growth rate (d^{-1})	Density ($ind. m^{-2}$)	Mean wet wt ($\mu g ind.^{-1}$)	Production	
					$ind. m^{-2}$	$mq C m^{-2}$
Sep 90	14.7	0.13	303 700	0.144	1 184 400	18.1
Oct 90	13.1	0.11	221 800	0.156	722 100	11.9
Nov 90	7.8	0.04	390 700	0.130	439 700	6.1
Dec 90	5.1	0.001	136 300	0.126	5 500	0.1
Jan 91	4.1	0.0	102 100	0.130	0	0.0
Feb 91	0.5	0.0	163 100	0.117	0	0.0
Mar 91	8.1	0.04	231 600	0.222	288 600	6.8
Apr 91	8.8	0.05	153 100	0.184	233 900	4.6
May 91	10.0	0.07	177 500	0.184	356 800	7.0
Jun 91	13.1	0.11	207 700	0.133	676 200	9.5
Jul 91	18.2	0.18	247 800	0.118	1 314 700	16.4
Aug 91	18.8	0.18	662 200	0.086	3 673 700	33.5
Total					8 895 600	114.0

leaves. Probably, as discussed above, the numbers decrease again as the leaves gradually lose their surface structure. In the laboratory experiments the nematode population reached much higher densities on the (initially) yellow leaves than on brown leaves, since the yellow leaves had changed into 'brown' leaves at the end of the experiment, whereas the initially brown leaves lost their leaf-surface structure in the course of the experiment, resulting in large losses during flooding. On the stems the changes in population density are probably slower, since the stems disintegrate at a much slower rate.

With the data available it is possible to make an estimate of the total number and biomass of *Diplolaimelloides brucei* formed on a *Spartina anglica* vegetation and of the bacterial biomass consumed by the nematodes. The total amount of *S. anglica* detritus formed approximately equals the total yearly production of the macrophyte. The peak above-ground living biomass can be considered as a rough estimate of the yearly production of *S. anglica* (De Leeuw et al. 1991). The peak above-ground living biomass at the Rattakaai salt marsh occurred in August, being 850 g DW m⁻², equivalent to ± 340 g C m⁻². The nematode production depends on the number of nematodes present at the sampling time and the growth rate of the nematodes (Heip et al. 1982):

$$P = \sum r_i N_i \quad (3)$$

where P = production, r_i = arithmetic growth rate; and N_i the number of nematodes in the i th sampling interval. Warwick (1981) showed that the growth rate depended on temperature and derived a linear regression formula for the relation between the birth rate and the temperature. Using this formula the average monthly growth rate of every month was calculated from the mean monthly temperatures. In Table 1 the mean monthly temperature, the calculated growth rates, the total number of *D. brucei* m⁻² and the estimated daily total number of nematodes formed are shown. An estimate of the total number of *D. brucei* formed during the year was obtained by summing the daily production of new nematodes, and was approximately 8.89 million ind. m⁻² yr⁻¹.

The mean biomass per individual was calculated each sampling day (Table 1). The total biomass production, calculated from these figures, was approximately 1.07 g wet weight, equivalent to 114 mg C m⁻², which represents only a small fraction of the *Spartina anglica* production. The amount of bacteria ingested by the nematodes is much higher than the biomass produced, since a large amount of bacterial C ingested by the nematodes is lost by defecation, excretion and respiration. The fraction of the bacterial C ingested which is transferred to biomass of *Diplolaimelloides*

brucei is not known. Herman & Vranken (1988) gave estimates of the assimilation efficiency and the production efficiency of the related species *Monhystera disjuncta*. When we assume that the efficiency of *D. brucei* is similar to that of *M. disjuncta*, the fraction of bacterial C transferred into nematode biomass can be considered as the product of the assimilation efficiency and the production efficiency, and equals approximately 0.15. Thus, to form 114 mg C of nematode biomass, 760 mg C m⁻² of bacterial biomass is needed.

If *Spartina anglica* carbon is transformed into bacterial biomass with an efficiency of 10%, the maximum total bacterial biomass formed is equal to 34 g C m⁻² yr⁻¹. This figure, however, is unrealistically high, since only a part of the *S. anglica* detritus is decomposed by bacteria. Another part is decomposed by fungi or is removed from the salt marsh by the tides. Padgett et al. (1985) estimated that about 30% of *S. alterniflora* leaves were decomposed by bacteria. The total bacterial biomass formed may be equivalent to 10 g C m⁻² yr⁻¹. Thus the bacterial biomass ingested by *Diplolaimelloides brucei* may account for 7.5% of the total bacterial biomass formed during decomposition of *S. anglica* litter. *D. brucei* was not the only bacterivorous nematode present on *S. anglica* leaves. The numbers of *Monhystera disjuncta* and *Pellioiditis marina* were of the same order as the numbers of *D. brucei*. If equal growth is assumed for the 3 bacterivorous nematodes, the ingested proportion of bacterial biomass may be over 20%.

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