

Correlation between nematode abundance and decomposition rate of *Spartina anglica* leaves

R. Alkemade*, A. Wielemaker, M. A. Hemminga

Netherlands Institute of Ecology – Centre for Estuarine and Coastal Ecology, Vierstraat 28, 4401 EA Yerseke, The Netherlands

ABSTRACT: Dead *Spartina anglica* leaves which are not washed away by the tides either decompose in the canopy as standing dead crop or decompose on the sediment surface. In the sediment, many nematode species are present which may colonize the *Spartina* litter. Some of these species may affect the decomposition of *Spartina* detritus. A field experiment was carried out to identify these nematode species. Small mesh containers were filled with green or aged *Spartina* leaves to obtain different decomposition rates. The containers were placed in the Stroodorpolder salt marsh (The Netherlands), in the Oosterschelde, a tidal inlet of the southern North Sea. After 3 mo the containers were collected and nematodes were counted and identified. The experiment was repeated in 4 subsequent seasons. Sixty nematode species were found in the containers; most species were found in all treatments. Total numbers of nematodes did not differ among treatments. Using multivariate analysis (RDA), however, we found differences of nematode community structure among treatments. Bacterivorous nematodes, particularly monhysterid species, prevailed in the containers with the highest decomposition rates. A positive correlation was found between decomposition rate and the numbers of *Diplolaimella dieven-gatensis* in spring, summer and autumn. The numbers of *Diplolaimelloides brucei*, *Monhystera parva*, *Desmolaimus zeelandicus* and *Theristus acer* showed positive correlations with decomposition rates in 1 or 2 of these seasons. In winter no significant correlations were found. Thus, of the 60 nematode species present in the litter the abundances of only 5 species seemed to be affected by decomposition rate of the litter. It is suggested that these nematode species react primarily to the increased microbial activity coinciding with higher decomposition rates. In addition, these species may further enhance microbial decomposition activity.

INTRODUCTION

Spartina anglica is a common halophyte of the lower zones of Western European salt marshes. Dead above-ground material of *S. anglica* which is not removed by the tides either decomposes in the canopy or on the sediment surface. Recent studies on the decomposition of *Spartina* material on the sediment surface showed that litter-associated nematodes are always found in high numbers (Montagna & Ruber 1980, Reice & Stiven 1983, Buth & de Wolf 1985, Hemminga & Buth 1991). A correlation between total nematode densities and decomposition rates, however, could not be established

(Reice & Stiven 1983, Buth & de Wolf 1985). In these studies nematodes were considered as 1 taxon, which masks possible differences among individual species with respect to their dependence on, or their role in, litter decomposition. The number of specimens of those species that feed on microbial decomposers is presumably determined by the decomposition rate, as at higher decomposition rates the microbial production will probably be higher, thus providing more food to microbial grazers.

In the present study, experiments were carried out to investigate changes in the nematode community in relation to changing decomposition rates of *Spartina anglica* leaf litter. An attempt was made to detect those nematode species, whose numbers correlated with decomposition rate.

Differences in decomposition rates were obtained by using leaf litter of different ages. Decomposition rate

* Present address: National Institute for Public Health and Environmental Protection, Laboratory LBG, PO Box 1, 3720 BA Bilthoven, The Netherlands

decreases during decomposition: the readily available substances, such as proteins and sugars, are lost first from the litter, leaving the more refractory components which decompose at much lower rates. Nematode densities are subject to conspicuous seasonal fluctuations (Buth & de Wolf 1985, Heip et al. 1985, Vincx 1989). Some species are found only in certain seasons. The experiments, therefore, were repeated in all 4 seasons.

Redundancy analysis (RDA) was used to evaluate the relation between nematode community structure and decomposition rates.

MATERIAL AND METHODS

Leaf material. Green leaves of *Spartina anglica* were collected in the Stroodorpepolder salt marsh (The Netherlands) in January 1988. This marsh is situated in the Oosterschelde, a tidal inlet of the southern North Sea. Immediately after harvesting, the leaves were washed and cut into fragments of 2 cm. To obtain leaf litter of progressive decomposition stages, the material was split into 3 portions. One part was immediately dried at 50°C (48 h) and stored. The other portions were aged for 2.5 and 5 mo by putting the leaf fragments into a bag of nylon gauze (2 mm mesh) and, in the laboratory, placing them in a tank on sediment originating from the Stroodorpepolder salt marsh. The sediment was flooded each day (3 h) with water from the Oosterschelde. The ambient temperature ranged from 15 to 25°C; the temperature of the flooding water ranged from 15 to 20°C. After 2.5 and 5 mo part of the leaf material was removed and dried at 50°C for 48 h. A sample of leaf material was used for determining the initial contents of carbon, nitrogen and phosphate.

Experimental design. Mesh containers were filled with 5 g dry weight (DW) of 1 of the 3 types of plant material. In addition, inert fragmented plastic drinking straws were used in control treatments. The containers used were permeable, consisting of 2 cm segments of perspex cylinders with a diameter of 7 cm, closed at both ends with 0.8 mm mesh gauze.

Four subsequent experiments were conducted at the same site in the Stroodorpepolder salt marsh. The site (10 m²) was situated near the edge of the marsh, where *Spartina anglica* forms a monospecific stand. In each experiment the mesh containers were laid out in 5 randomized blocks, each block in a row parallel to the marsh edge. Within the rows 1 container of each treatment was placed in random order on the sediment surface. The distance between the rows and between the containers within a row was 0.5 m. The containers were anchored by 2 wire wickets to the marsh sediment to prevent them from being washed away at high tide. The experiments started on 15 March, 20 June,

19 September and 20 December 1988. On these dates sediment samples were also collected to compare the number of nematodes in the upper sediment layer with the number found in the containers. The field exposure time of the containers was 3 mo. Containers with 5 mo aged leaves were included only in the summer, autumn and winter experiments.

Decomposition rate and chemical analyses. After retrieval of the mesh containers a small sample of the detritus was washed with tap water and dried for chemical analysis. The remaining part of the detritus was fixed with warm formalin at a final concentration of 4 to 5%. After at least 7 d the detritus was rinsed with tap water over a household sieve (mesh 1.5 to 2 mm) to separate the leaf material from the sediment and nematodes. The leaf material was retained on the sieve, whereas nematodes and sediment passed through. The leaf material was dried and weighed.

Decomposition rates were calculated as the loss of dry weight of leaf material from the mesh containers and expressed as g weight loss per 100 d, using a negative exponential relation for extrapolation (cf. Swift et al. 1979). Carbon and nitrogen content of the samples were analyzed with a Carlo Erba CN-analyzer, type 1500 A. Phosphate content was determined colorimetrically.

Nematodes. Nematodes were extracted using an Oostenbrink elutriator (Fricke 1979, 's Jacob & van Bezooijen 1986). The nematodes were recovered by passing the suspension with nematodes (see above) through a series of four 45 µm mesh sieves. The debris retained on the sieves was collected in 250 ml centrifugation tubes with tap water. After centrifugation (5 min at 3000 rpm) (1800 × g) the supernatant was discarded and the nematodes in the pellet were extracted by 2 repeated centrifugation steps (1 min at 3000 rpm) (1800 × g) with a MgSO₄ solution (specific gravity 1.28).

Nematodes were counted and 250 individuals were identified to species level using an inverted microscope.

Statistical analysis. Seasonal and treatment differences of losses of weight, nitrogen, carbon and phosphate and the total numbers of nematodes were evaluated using analysis of variance. Redundancy analysis (RDA) was used to evaluate the relation between the nematode community structure and the decomposition rate of the leaf material. RDA is the canonical form of principal component analysis (Jongman et al. 1987). Linearity between environmental gradients and species abundances is assumed for RDA. Since the experiments were carried out on a limited surface area, the environmental gradients were expected to be small. If gradients are small, the assumption for linearity is not very stringent (ter Braak & Prentice 1988, van der Meer 1990). A log(x+1) transformation was used in

order to stabilize variances. The log transformation implies that the assumption of linearity between environmental variables and species abundances must hold for the linearity between the variables and log-numbers. Decomposition rate was included as the only independent variable. Corrections for seasonal effects and effects which may arise from the row-position of the mesh container in the field were made by taking them as covariables in the computer program CANOCO (ter Braak 1990). The result of the RDA then only describes the variation explained by decomposition rate and the variation due to error terms. A Monte Carlo permutation test was carried out to test the significance of decomposition rate as the explaining variable. The species found to be correlated with decomposition rate were analyzed in more detail by regression of the numbers per individual species on the decomposition rate.

ANOVA and regression analyses were carried out with SYSTAT statistical package (Wilkinson 1990). RDA and the Monte Carlo permutation test were carried out with CANOCO 3.10 (ter Braak 1990).

RESULTS

After a few weeks of exposure in the field the leaf fragments were covered with a layer of sediment in most of the containers. Since the *Spartina* vegetation was flooded frequently during the course of the experiments, no desiccation of the sediment surface took place.

Decomposition rates

The decomposition rates of the 3 detrital types in the successive seasons are shown in Fig. 1. Statistically significant treatment and seasonal differences were observed ($p < 0.001$). In all seasons decomposition rates of fresh leaves were higher than those of the aged material (Tukey test; $p < 0.05$). The 2.5 mo aged leaves decomposed slightly faster than the 5 mo aged material, but only in summer was this difference significant (Tukey test; $p < 0.05$). The differences between the detrital types were most pronounced in the summer season. The decomposition rates of the fresh leaves showed the most conspicuous seasonal fluctuations, with the highest rates in summer and the lowest in winter.

With respect to the fresh leaf material and to the 2.5 mo aged material, differences in decomposition rates between the various seasons were nearly all significant (Tukey test; $p < 0.05$). Decomposition rates of the 5 mo aged material were not significantly different

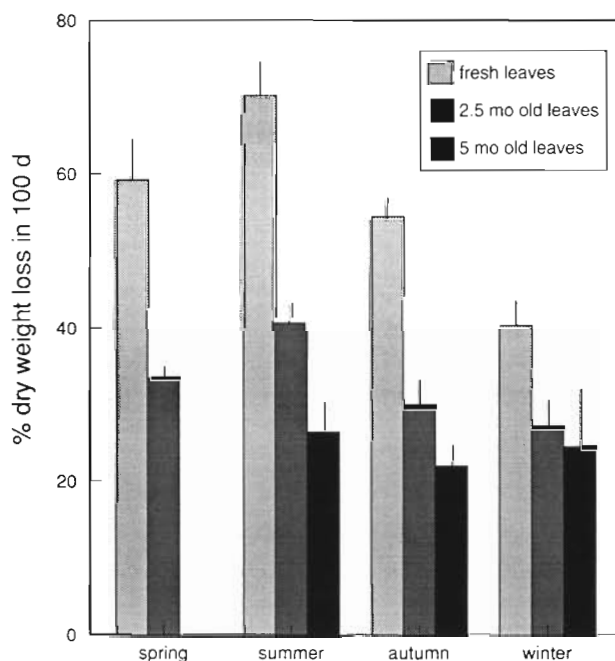


Fig. 1. *Spartina anglica*. Decomposition rates (% losses of dry weights of litter after 100 d). Means + SD (n = 5)

Table 1. Correlation coefficients between decomposition rates and nutrient losses; all coefficients are significant (Bonferroni $p < 0.001$)

	Decomposition rate	Carbon	Nitrogen
Carbon	0.986		
Nitrogen	0.930	0.943	
Phosphate	0.923	0.939	0.925

between seasons. No weight losses from the inert material were observed.

Carbon, nitrogen and phosphate losses yielded similar patterns, the losses of these nutrients were highly correlated with dry weight losses (Bonferroni $p < 0.001$; Table 1). Carbon, nitrogen and phosphate losses were highest in summer and lowest in winter. The losses of these nutrients were highest from fresh leaf material.

Nematodes

The total number of nematodes found in the mesh containers showed clear seasonal fluctuations (Table 2). The highest numbers were found in summer, whereas the lowest numbers were present in autumn. The numbers found in the mesh containers were in the

Table 2. Total number of nematodes found in the mesh containers in the various treatments and seasons and in the same volume of surrounding sediment. -: not sampled

	Fresh	2.5 mo old	6 mo old	Control	Sediment
Spring	22 700	12 700	–	14 200	19 400
Summer	46 900	34 900	27 800	41 300	28 700
Autumn	9 900	9 400	9 200	9 500	20 300
Winter	21 200	13 100	15 300	18 200	11 300

same range as the numbers found in the upper layer of the surrounding sediment. No statistical differences were found between the treatments. Sixty nematode species were found in the mesh containers (Table 3). Most species are known from intertidal estuaries of the southern North Sea (Bouwman 1983, Vincx 1986). The majority of these species are known to feed on a variety of food sources. Carnivorous and omnivorous species are represented by *Enoplus communis* and *Adoncholaimus fuscus*. Herbivores are represented by members of the family Chromadoridae. Bacterivorous species are represented by some members of the family Monhysteridae. Selective deposit feeders, with a

very small buccal cavity, are represented by the *Halalaimus* species and by *Oxystomina* sp.

RDA analysis was carried out on the whole species assemblage. The relation between the log number of the most dominant species and the decomposition rate showed a linear pattern, therefore we could use and interpret RDA without restriction. Fig. 2A, B shows the RDA ordination diagrams obtained for the mesh containers and for the species respectively. The arrows indicate the direction of increasing decomposition rates. The first ordination axis, explained by the decomposition rate, accounted for 6.9% of the total variance. The Monte Carlo permutation test showed that, in spite of this small percentage of explained variance, the nematode community changed significantly with changing decomposition rate (F -ratio = 5.08, $p < 0.01$).

In Fig. 2A the different treatments were ordered along the first axis in such a way that the control treatments appear on the left hand side and the fresh leaf treatments appear on the right hand side. In Fig. 2B the ordination diagram of the species is shown. The posi-

Table 3. Species of nematodes found in the litter containers, with abbreviations as used in Fig. 2B

Species	Abbreviation	Species	Abbreviation
<i>Enoplus communis</i>	Enop comm	<i>Metochromadora vivipara</i>	Meta vivi
<i>Anoplostoma viviparum</i>	Anop vivi	<i>Microlaimus globiceps</i>	Micr glob
<i>Anticoma acuminata</i>	Anti acum	<i>Microlaimus</i> sp.	Micr sp
<i>Dolicholaimus marioni</i>	Doli mari	<i>Nudora bipapillata</i>	Nudo bipa
<i>Halalaimus gracilis</i>	Hala grac	<i>Monoposthia costata</i>	Mono cost
<i>Halalaimus longicaudatus</i>	Hala long	<i>Leptolaimus mixtus</i>	Lept mixt
<i>Oxystomina elongata</i>	Oxys elon	<i>Leptolaimus</i> sp.	Lept sp
<i>Adoncholaimus fuscus</i>	Adon fusc	<i>Aegialolaimus</i> sp.	Aegi sp
<i>Viscosia viscosa</i>	Visc visc	<i>Quadracoma scanica</i>	Quad scan
<i>Calyptronema maxweberi</i>	Caly maxw	<i>Diplolaimella dievengatensis</i>	Dipl diev
<i>Bathylaimus australis</i>	Bath aust	<i>Diplolaimelloides brucei</i>	Dipl bruc
<i>Tripylloides marinus</i>	Trip mari	<i>Monhystera disjuncta</i>	Monh disj
<i>Atrochromadora microlaima</i>	Atro micr	<i>Monhystera parva</i>	Monh parv
<i>Chromadora nudicapitata</i>	Chro nudi	<i>Monhystera</i> sp.	Monh sp
<i>Chromadorina</i> sp.	Chro ina	<i>Daptonema</i> sp. 1	Dapt sp1
<i>Chromadorita</i> sp.	Chro ita	<i>Daptonema</i> sp. 2	Dapt sp2
<i>Dichromadora geophila</i>	Dich geop	<i>Daptonema</i> sp. 3	Dapt sp3
<i>Dichromadora scandula</i>	Dich scan	<i>Daptonema</i> sp. 4	Dapt sp4
<i>Hypodontolaimus inaequalis</i>	Hypo inae	<i>Daptonema</i> sp. 5	Dapt sp5
<i>Hypodontolaimus</i> sp.	Hypo sp	<i>Theristus acer</i>	Ther acer
<i>Neochromadora</i> sp.	Neoc sp	<i>Theristus pertenuis</i>	Ther pert
<i>Neochromadora poecilosoma</i>	Neoc poec	<i>Trichotheristus</i> sp.	Tric sp
<i>Prochromadorella paramucrodonta</i>	Proc para	<i>Sphaerolaimus</i> sp.	Spha sp
<i>Ptycholaimellus ponticus</i>	Ptyc pont	<i>Desmolaimus zeelandicus</i>	Desm zeel
<i>Spilophorella paradoxa</i>	Spil para	<i>Metalinhomoeus bififormis</i>	Meta bifo
<i>Paracantonchus caecus</i>	Para caec	<i>Paralinhomoeus</i> sp.	Para linh
<i>Praeacantonchus</i> sp.	Prae sp	<i>Ascolaimus</i> sp.	Asco sp
<i>Sabatieria</i> sp.	Saba sp	<i>Axonolaimus typicus</i>	Axon typi
<i>Desmodora communis</i>	Desm comm	<i>Pellioditis marina</i>	Pell mari
<i>Metochromadora remanei</i>	Meta rema		

describe the relation between the number of specimens and weight losses. Only in spring is the regression coefficient significantly different from zero. In each season, however, the highest numbers were found in the mesh containers with the highest weight losses, i.e. the fresh leaf treatment.

Desmolaimus zeelandicus occurred in almost all samples. The regression coefficients are significantly different from zero in summer and autumn, but not in spring and winter (Fig. 3D). The slopes of the regression lines in summer and autumn were less steep than the slopes found for the species of the family Monhysteridae. From the calculated slopes it can be estimated that in summer and autumn 1.5 to 1.6 more specimens occurred with an increased weight loss of 1 g in 100 d.

Theristus acer occurred only in spring and in summer in more than 50% of the containers. In the winter *T. acer* was almost absent. The regression coefficient, fitted for the summer data, is significantly different from zero, and is intermediate between the slopes found for the monhysterids and for *Desmolaimus zeelandicus* (Fig. 3E). From the regression equation it can be derived that in summer 2.9 times more specimens occurred with an increased weight loss of 1 g in 100 d. In autumn the slope is also significantly different from zero and is very close to the figure found in summer. However, *T. acer* occurred in only 7 of the 20 mesh containers.

DISCUSSION

The decomposition rates found in this study ranged from 25 to 85% weight losses after 100 d and are in the range found for *Spartina* spp. in the literature. Montagna & Ruber (1980) summarized decomposition rates from 6 studies on the decomposition of *S. alterniflora* which covered different seasons. The weight losses after 100 d in these studies ranged from 25 to 90%, and our data fall within this range. Hemminga & Buth (1991) reviewed studies on decomposition of salt marsh halophytes in the Netherlands. They calculated mean decomposition rates for *S. anglica* leaves ranging from 0.25 to 0.45% d⁻¹ over a period of 6 mo. Assuming negative exponential decay, this would result in weight losses of 22 to 36% after 100 d.

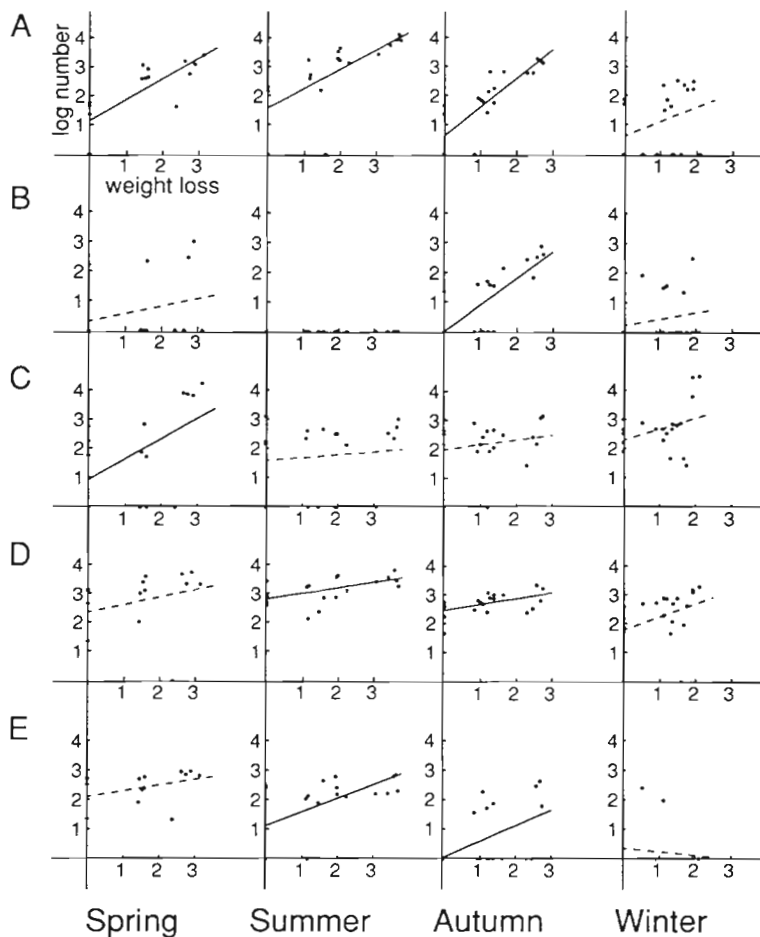


Fig. 3. Plots of the log number of specimens against the decomposition rates. (A) *Diplolaimella dievengatensis*; (B) *Diplolaimelloides brucei*; (C) *Monhystera parva*; (D) *Desmolaimus zeelandicus*; (E) *Theristus acer*. Horizontal axis denotes dry weight losses (g per mesh container), vertical axis denotes the log number of nematodes per mesh container. Lines are linear regression lines. Broken lines indicate non-significant regression coefficients

Obviously the wide range in our study is a result of the separation into different quality classes and the influence of different seasons. In the studies reviewed by Hemminga & Buth (1991) samples of a mixture of quality types were used; other studies were performed in only 1 season.

A wide range of nematode species occurred in the mesh containers. The abundances of most of these species were not correlated with decomposition rate, they occurred in equal densities in treatments with decomposing material and in the control treatments. Apparently, the decomposing material forms only a living space for them. Our observations that the numbers of individuals of these species numerically dominate the total nematode fauna in the litter are consistent with the results of Montagna & Ruber (1980) and Buth & de Wolf (1985), who found that the total number

of nematodes in halophyte litter was dependent on the available space expressed as the amount of litter and not on the age of the decomposing detritus.

The RDA analysis showed that of the many species present in the litter, the number of specimens of only a few species were positively correlated with decomposition rate. These species were found in high numbers in the treatments with the highest decomposition rates, occurred in lower numbers in the treatments with aged leaf material and were practically absent in the control treatments. To date such a direct relation between decomposition rate and nematode numbers has not been found in field experiments. Three of the associated species, *Diplolaimella dievengatensis*, *Diplolaimeloides brucei* and *Monhystera parva*, are members of the family Monhysteridae. *Desmolaimus zeelandicus* belongs to the family Linhomoeidae and *Theristus acer* is a member of the family Xyalidae. Members of the family Monhysteridae are considered non-selective deposit feeders (Wieser 1959) and are always found on locations with high organic inputs (Riemann 1968, Lamshead 1986) or otherwise disturbed locations (Bongers et al. 1991). *D. brucei* is mostly found in association with *Spartina* debris (Warwick 1981, Bouwman et al. 1984). Bouwman et al. (1984) stated that the non-selective feeding behaviour is efficient if the concentration of food (bacteria) is high and not mixed with non-edible particles of the same size. The decomposing *Spartina* detritus in the mesh containers probably provides high concentrations of bacteria and consequently offers a favourable environment to non-selective deposit feeders. The relation between decomposition rate and the numbers of the 5 above-mentioned species depended on the species and on the season. In winter the numbers of the 5 species did not increase significantly with decomposition rates, but *D. dievengatensis* had significant regression coefficients in spring, summer and autumn, *D. zeelandicus* and *T. acer* in summer and autumn, while *D. brucei* and *M. parva* increased significantly with decomposition rate in autumn and spring respectively.

The lack of correlation between the abundances of the majority of the nematode species and decomposition rate, as we found in our study, is probably because many of these species feed on microalgae or diatoms or they are omnivorous or carnivorous species, whereas the microbial organisms directly involved in halophyte decomposition are fungi and bacteria (Newell et al. 1989). The positive correlation between the abundance of the 5 microbivorous species and the decomposition rate of *Spartina anglica* leaves is probably caused by increased microbial biomass production. Higher decomposition rates imply a higher microbial activity and probably also a higher microbial biomass production. This increased availability of food for the

microbivorous nematodes allows higher nematode population densities (cf. Findlay 1982).

The populations of microbivorous species of nematodes on halophyte litter may not only react to changing rates of decomposition, they may also, in turn, influence these rates. Several studies showed that in the presence of bacterivorous nematodes of the family Monhysteridae, higher weight losses of detritus occurred (Findlay & Tenore 1982, Rieper-Kirchner 1989, Alkemade et al. 1992). This stimulatory effect of nematodes probably depends on the population density (Tietjen & Alongi 1990, Alkemade et al. 1992). If under field conditions nematode species are able to stimulate decomposition of *Spartina* leaves then the most likely candidates are those whose numbers correlate with decomposition rate, as were identified in our study. Further investigation on the role of nematodes in decomposition processes should be focused on these decomposition-associated species. The most pronounced effects of these nematode species on decomposition rates may be expected on plant material in the first stages of decomposition in the warmer seasons (spring to autumn), since under these circumstances the highest numbers were found. As the time of year in which the correlation between numbers and decomposition rate was found varied between species, it is possible that these species exert their effect on litter decomposition in different seasons.

Acknowledgements. The authors thank Dr P. M. J. Herman for statistical advice, Prof. Dr Ir. A. F. van der Wal for fruitful discussions and critical reading of the manuscript and Dr M. Vincx for help with the identification of the nematodes. Communication no. 653 of the Centre for Estuarine and Coastal Ecology.

LITERATURE CITED

- Alkemade, R., Wielemaker, A., Hemminga, M. (1992). Stimulation of decomposition of *Spartina anglica* leaves by the bacterivorous marine nematode *Diplolaimeloides brucei* (Monhysteridae). *J. exp. mar. Biol. Ecol.* 159: 267-278
- Bongers, T., Alkemade, R., Yeates, G. W. (1991). Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the Maturity Index. *Mar. Ecol. Prog. Ser.* 76: 135-142
- Bouwman, L. A. (1983). A survey of nematodes from the Ems estuary. Part II. Species assemblages and associations. *Zool. Jb. (Abt. Syst. Ökol. Geogr. Tiere)* 110: 345-376
- Bouwman, L. A., Romeyn, K., Kremer, D. R., van Es, F. B. (1984). Occurrence and feeding biology of some nematode species in Aufwuchscommunities. *Cah. Biol. mar.* 25: 287-303
- Buth, G. J. C., de Wolf, L. (1985). Decomposition of *Spartina anglica*, *Elytrigia pungens* and *Halimione portulacoides* in a Dutch salt marsh in association with faunal and habitat influences. *Vegetatio* 62: 337-335
- Findlay, S. E. G. (1982). Effect of detrital nutritional quality on

- population dynamics of a marine nematode (*Diplolaimella chitwoodi*). Mar. Biol. 68: 223–227
- Findlay, S., Tenore, K. R. (1982). Effect of a free-living marine nematode (*Diplolaimella chitwoodi*) on detrital carbon mineralization. Mar. Ecol. Prog. Ser. 8: 161–166
- Fricke, A. H. (1979). Meiofauna extraction efficiency by a modified Oostenbrink apparatus. Helgoländer wiss. Meeresunters. 32: 436–443
- Heip, C., Vincx, M., Vranken, G. (1985). The ecology of marine nematodes. Oceanog. mar. Biol. A. Rev. 23: 399–489
- Hemminga, M. A., Buth, G. J. C. (1991). Decomposition in salt marsh ecosystems of the S. W. Netherlands: the effects of biotic and abiotic factors. Vegetatio 92: 73–83
- Jongman, R. H. G., ter Braak, C. J. F., van Tongeren, O. F. R. (1987). Data analysis in community and landscape ecology. PUDOC, Wageningen
- Lambshhead, P. J. D. (1986). Sub-catastrophic sewage and industrial waste contamination as revealed by marine nematode faunal analysis. Mar. Ecol. Prog. Ser. 29: 247–260
- Montagna, P. A., Ruber, E. (1980). Decomposition of *Spartina alterniflora* in different seasons and habitats of a Northern Massachusetts salt marsh, and a comparison with other Atlantic regions. Estuaries 3: 61–64
- Newell, S. Y., Fallon, R. D., Miller, J. D. (1989). Decomposition and microbial dynamics for standing, naturally positioned leaves of the salt-marsh grass *Spartina alterniflora*. Mar. Biol. 101: 471–481
- Reice, S. E., Stiven, A. E. (1983). Environmental patchiness, litter decomposition and associated faunal patterns in a *Spartina alterniflora* marsh. Estuar. coast. Shelf Sci. 16: 559–571
- Riemann, F. (1968). Nematoden aus dem Strandanwurf. Veröff. Inst. Meeresforsch. Bremerhaven 11: 25–35
- Rieper-Kirchner, M. (1989). Microbial degradation of North Sea macroalgae: field and laboratory observations. Botanica mar. 32: 241–252
- 's Jacob, J. J., van Bezooijen, J. (1986). Manual for practical work in nematology. Agricultural University, Wageningen
- Swift, M. J., Heal, O. W., Anderson, J. M. (1979). Decomposition in terrestrial ecosystems. Blackwell Scientific Publications, Oxford
- ter Braak, C. J. F. (1990). CANOCO 3.10. Agricultural Mathematics Group, Wageningen
- ter Braak, C. J. F., Prentice, I. C. (1988). A theory of gradient analysis. Adv. ecol. Res. 18: 271–317
- Tietjen, J. H., Alongi, D. M. (1990). Population growth and effects of nematodes on nutrient regeneration and bacteria associated with mangrove detritus from northeastern Queensland (Australia). Mar. Ecol. Prog. Ser. 68: 169–179
- van der Meer, J. (1990). Exploring macrobenthos-environment relationship by canonical correlation analysis. J. exp. mar. Biol. Ecol. 148: 105–120
- Vincx, M. (1986). Free-living marine nematodes from the southern bight of the North Sea. Ph.D. thesis, State University of Ghent, Ghent
- Vincx, M. (1989). Seasonal fluctuations and production of nematode communities in the Belgian coastal zone of the North Sea. Verhandelingen van het symposium 'invertebraten van België' State University of Ghent, Ghent, p. 57–66
- Warwick, R. M. (1981). The influence of temperature and salinity on energy partitioning in the marine nematode *Diplolaimelloides brucei*. Oecologia 51: 318–325
- Wieser, W. (1959). Free-living nematodes. IV. General part. Reports of the Lund University expedition 1948–1949. Acta Univ. lund. (Sect. 2) 55(5): 68–85
- Wilkinson, L. (1990). SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL

This article was submitted to the editor

Manuscript first received: February 12, 1993

Revised version accepted: July 2, 1993