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Seasonal fluctuations of Sabatieria punctata (Nematoda)
in a silty-sand station off the Belgian coast.

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Abstract

The life cycle of *S. punctata*, the dominant nematode species in the meiobenthos off Zeebrugge (Belgian coast) was studied over a three year period. Juveniles occur throughout the year and reproduction is considered to be nearly continuous. A more active reproductive period occurs in spring from March till May, and in autumn (Sep-Oct). Density varies between 45 (Feb 83) and 2083 (Nov 83) ind./10 cm²; relative abundance varies between 10.8% (Jun 85) and 98.6% (Mar 83).

S. punctata contributed for about 75% to the production of the whole community estimated as 22 g DW/m². Y. The yearly P/B=16.91 in 1983 for *S. punctata* (P/B=20 for the whole nematode community (Vranken et al., in press).

Introduction

Sabatieria punctata (Kreis, 1924) is one of the most dominant nematode species in silty and silty-sand sediments of the sublittoral area of the northern hemisphere (Lorenzen, 1974; Juariu, 1975; Herman et al., 1985 for ecological data). The species has been considered cosmopolit (North Sea and adjacent regions; English Channel, E- and W-coast of the USA, Brazil, Argentina, Falkland Island, Black Sea, Svalbard, Mediterranean, Antarctica, Auckland Islands).

Identification problems are very large for *S. punctata* and many different types have been described in the past as separate species (see Platt, 1985 for a revision). However, as the intraspecific variation within the *S. punctata* population of the Belgian coast is quite large, Vinck (1986) decided to synonymize closely related species with the original description of *S. punctata*. Only one closely related species has been retained as valid, i.e. *S. pulchra*, the brackish water "Sabatieria" of the northern hemisphere. A nematode community off the Belgian coast dominated by *S. punctata* has been followed with monthly intervals during 1983-1985. Other seasonal samplings were carried out in 1977-1979.

Material and Methods

Station 11860 (51°22'38"N, 03°18'41"E) was sampled every month in the period 1983-1985. Meiobfauna was collected by subsampling a Van Veen grab (sampling area: 0.10 m²) or a modified Reineck-box (sampling area: 170 cm²) before summer 1984. From October 1984 on, meiobfauna was sampled using a box-corer (sampling area: 0.25 m²) from the Belgian Oceanographic Research Vessel "Belgica".

Each meiobfauna sample was immediately subsampled with four plastic funnels (surface: 10.2 cm²); two for faunistic analysis (fixed with 4% hot (70°C) formaldehyde), one for sedimentological analysis and one was kept for chemical analysis (heavy metals during 1983, Braeckman et al., 1984).

Sediment analysis was carried out as described in previous papers (Heip et al., 1979).

Animals were extracted by decanting the sediment a few times (on a 58 µm sieve); afterwards they were centrifuged with 50% Ludox and fresh water (method described by Heip et al., 1985). Animals, coloured with Rose Bengal, were counted under a stereoscopic microscope; the first 200 nematodes were identified to species level with a Leitz Diavert (reversed) microscope. Males, females and juveniles were counted. Juveniles were measured from each month (body length and maximum body width) because it is difficult to distinguish different juvenile stages under the reversed microscope (it is not even easy with oil immersion under a normal microscope).

Results

Environmental characteristics

Sediment

The median grain size (mm), silt clay fraction and the sorting coefficient (σ) are determined for the period 1977-1983. In 1984-1985, the sediment analysis from only a few sampling dates was carried out. Table 1 shows the different sediment characteristics. Note that the median and the sorting coefficient of the last two years are only determined for the sand fraction and therefore not comparable with the earlier data. Only the silt-clay amount is comparable.

The amount of silt-clay in 1983-1985 is higher than in the earlier years. In 1983, monthly samples were analysed and in that year the median of the grain size is different between winter (Dec-Apr) and summer (May-Nov).

Temperature

Bottom temperature was measured each month (1983-1985); values are given in Table 2.

Others

Salinity, pH and Ω_{at} at the bottom were measured only in 1983.

Month/Year	Median Grain Size (mm)	Silt-Clay Fraction (%) < 62 um)	Sorting Coefficient (φ)
Jun 77	0.183	3.0	0.25
Sep 77	0.165	9.0	0.40
Mar 78	0.095	46.5	3.10
Apr 78	0.165	12.5	0.53
Sep 78	0.159	17.0	1.10
Dec 78	0.183	0.5	0.28
Apr 79	0.129	40.5	2.75
Jun 79	0.096	58.0	2.95
Sep 79	0.094	43.1	2.18
Jan 83	0.022	81.0	3.13
Feb 83	0.044	63.5	2.40
Mar 83	0.032	69.5	2.95
Apr 83	0.025	77.5	3.28
May 83	0.038	63.5	3.85
Jun 83	0.054	53.5	2.45
Jul 83	0.082	45.0	2.45
Sep 83	0.053	53.5	3.65
Oct 83	0.054	53.5	2.60
Nov 83	0.051	56.5	2.80
Dec 83	0.036	71.5	2.65
Apr 84	*0.153	57.7	*0.34
Oct 84	*0.156	35.0	*0.32
Apr 85 (0-5cm)	*0.158	66.4	*0.56
(> 5cm)	*0.114	70.5	*0.64

Table 1: Sediment characteristics from stations 11860 (median and sorting coefficient for 1984 and 1985 are determined on the sand fraction only; earlier data are determined and the total sediment fraction).

	1983			1984			1985		
	T	T	T	T	Sal.	pH	O ₂		
Jan	8.4	-	-	3.2	33.9	7.96	15.5		
Feb	5.5	6.8	0.5	30.6	8.26	-			
Mar	5.4	7.8	4.2	-	-	-			
Apr	7.5	7.6	7.8	32.8	8.51	9.3			
May	10.1	9.6	11.9	29.8	8.48	8.4			
Jun	12.3	12.3	15.2	-	-	5.5			
Jul	16.8	-	-	-	-	-			
Aug	-	-	17.5	32.9	8.53	8.1			
Sep	17.3	-	16.0	30.0	8.12	9.6			
Oct	15.3	14.8	-	-	-	-			
Nov	11.9	-	7.5	32.3	8.21	9.6			
Dec	9.5	10.0	-	-	-	-			

Table 2: Temperature (T in °C), Salinity (Sal in %), pH and ppm O₂ in station 11860.

Density of the whole nematode community

The mean density values of the whole nematode community is presented in Fig. 1. Differences between the two replica's of one sample are examined by means of a one way-anova (numbers were transformed to log10). Between sample (=months) variation is significantly higher than within sample variation ($F=4.966, df=26$ and $27, p<0.001$).

The mean density of the total community varies between 55 ind./10 cm² (Feb83) and 5610 ind./10 cm² (Jun85). Dates of minimum and maximum abundances together with the relative abundance of *Sabatieria punctata* in the community are given in Table 2.

The minimum numbers in the first half of the year (Jan-Jun) occur always in two periods.

Maximal values occur in Sep83, Nov83 and Oct84 in the second half of the year. A late maximum in 1985 was not observed but we probably missed it because two important autumn months were not sampled.

The relative abundance of *S. punctata* within the community ranges between 18-82% (Jun85) and 98.6% (Mar83). The species composition of the community is not discussed in this report (cfr. for 1983, Vincx & Heip, 1984). The very low relative abundance of *S. punctata* in Jun 85 is due to an explosive occurrence of juveniles of *Daptoema tenuispiculum*, a species which usually contributes a maximum of about 15-20% to the community.

Density of *Sabatieria punctata*

Between sample variance of the *S. punctata* population density (ad+juv) is significantly higher than within sample variance (between replica's) ($F=4.237, df=26$ and $27, p<0.001$). Therefore I did not use a running mean for the representation of the fluctuations during the three years; also, the sample intervals are quite large for population studies.

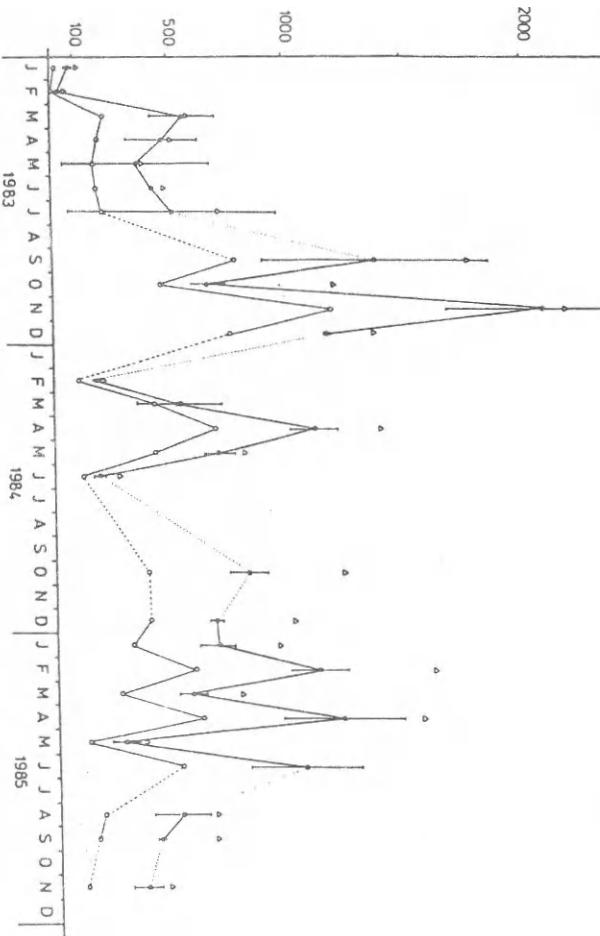
Fig. 1 shows the fluctuation of the total density over the three years. Because *S. punctata* is the dominant species of the community, the pattern is similar to the density pattern of the whole community.

A maximum density peak is present in Mar83, Sep83, Nov83, Apr84, Oct84, Feb85, Apr85 and Jun85. An absolute maximum is found in Nov83 (2033 ind./10 cm²). Lowest density value occurs in Feb83 (45 ind./10 cm²); in Oct83, Feb84, Jun84, Jan85, May85, May85 and Aug to Nov85 only about 100 ind./10 cm² were present.

Neither the maximum, nor the minimum values are preceded by an important increase or decrease in temperature (cfr. Table 2).



Fig. 1. Density (ind./10cm²) of the nematode community (Δ), of S.punctata (ad + juv.) (\bullet ; \pm SE) and of S.punctata (juv.○) over three years (ad + juv.) in station 11860.



Adults

The population consists for 30.4% to 70.7% of adults, represented by juveniles (cfr. Fig. 1); values vary between 29.3% and 69.6%.

Mean densities of juveniles over three years are given in Table 4. The density pattern of the juveniles follows the increase and decrease in total density (cfr. Fig. 1).

Three size classes of juveniles (JUVI: less than 700 μm ; JUVII: between 700-1100 μm and JUVIII: more than 1100 μm) are distinguished (cfr. Jurria, 1975). The detailed composition of the population (relative abundance of JUVI, JUVII, JUVIII, Δ and ○) is presented in Fig. 2.

The smallest juveniles were absent in Jan83, Feb83, Mar83, May83 and Jun83. They account for 20-30% of the juveniles in Mar83, Apr83, Oct83, Jun84, Oct84, Aug85 and Sep85. The largest juveniles account for 40% or more of the juveniles in Jan83, Feb83, May83, Jul83, Nov83, Feb85, Mar85, May85 and Jun85. These maxima are about one to two months after the max of the smallest juveniles. The maximum density of the smallest juveniles is 152 ind./10cm² (Oct83); the max. density of the largest juveniles is 479 ind./10 cm² (Nov83).

In the following table the periods are noted when the increase in relative abundance of one of the three juvenile classes exceeds or equals 10% in comparison with the previous date.

In this way, highest abundances are noted in following periods:

month	minimum %Saba	month	maximum %Saba
Feb83	55	Mar83	582
May83	389	Sept83	98.6
Oct83	1208	Nov83	1774
Feb84	202	Apr84	78.8
Jun84	278	Oct84	2186
Jan85	954	Feb85	95.6
Mar85	796	Apr85	202
May85	368	Jun85	88.7
Nov85	475		1400
			1224
			69.8
			1622
			69.8
			1570
			79.8
			5610
			18.8
			77.8

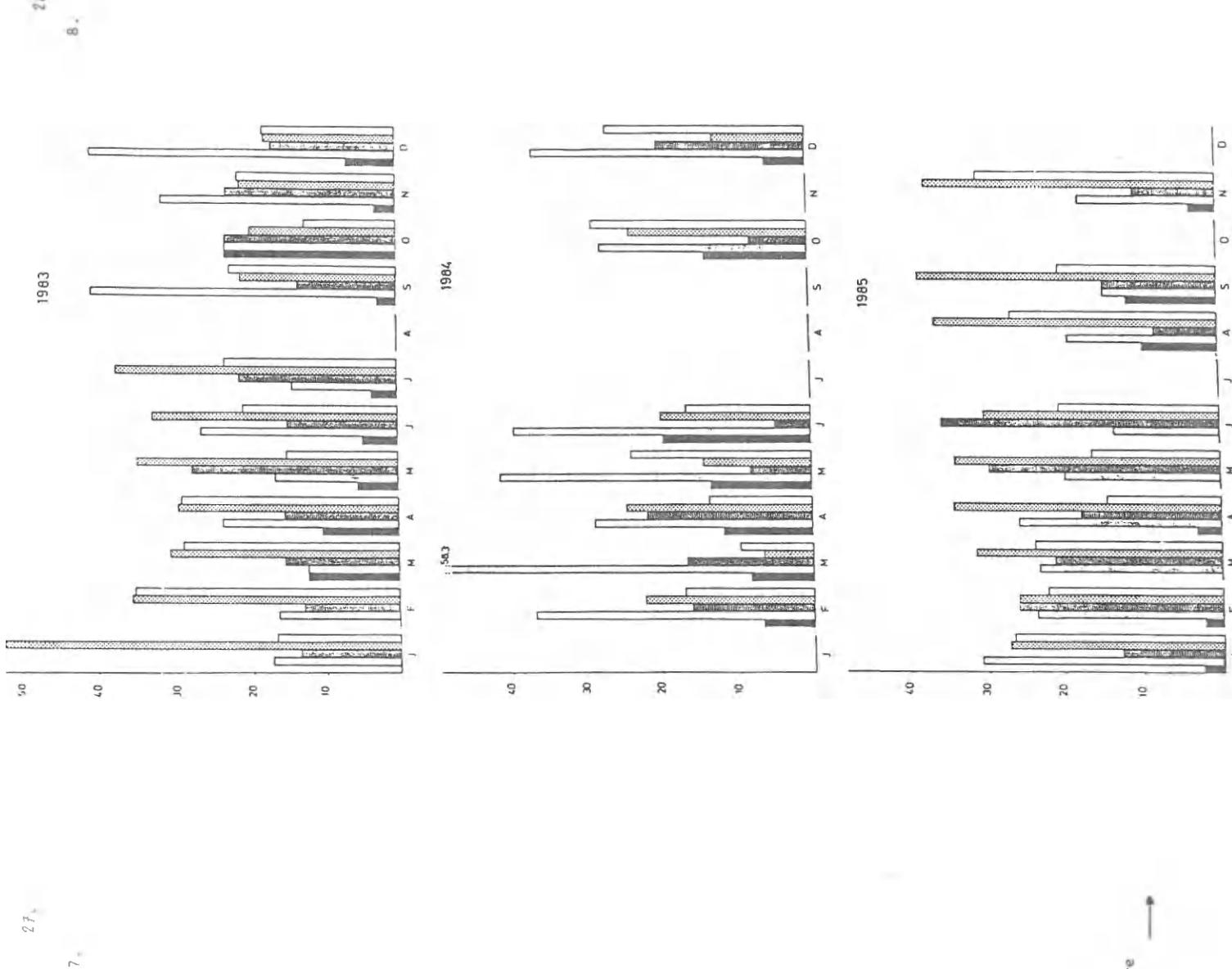
Table 3: Dates and numbers of minimum and maximum density values (ind./10cm²) for the nematode community and relative abundance of S.punctata (%Saba) within the community.

JuvI: Mar83 - Apr83	JuvII: Apr83 - Jun83	JuvIII: May83
Oct83	Sept83	Oct83 - Nov83
Apr84 - Jun84	Dec83 - Mar84	(Apr84)
Oct84	May84 - Jun84	Dec84 - Jun85
Apr85 ($\Delta = 62\%$)	(Dec84 - Apr85)	(Dec84 - Jun85)
Aug85 - Sep85		

Table 4. Composition of the *Sabatieria punctata* population over three years (mean values per month).
 (N = ind./10 cm², relative abundance (%) and sex ratio (♀/♂)).

Month	N (Juv.)	% (Juv.)	N (♀)	% (♀)	N (♂)	% (♂)	N tot.	♀/♂
Jan 83	27	30.6	47	52.6	15	16.8	B9	3.13
Feb 83	12	29.3	15	35.5	14	35.2	41	1.07
Mar 83	227	40.3	173	30.7	163	29.0	563	1.06
Apr 83	200	41.4	142	29.6	140	29.1	482	1.01
May 83	180	50.0	125	34.8	55	15.2	360	2.27
Jun 83	191	46.4	141	32.6	91	21.0	433	1.55
Jul 83	205	39.6	193	37.3	119	23.1	517	1.62
Sep 83	787	56.4	294	21.1	314	22.5	1395	0.94
Oct 83	455	69.6	130	19.9	69	10.6	654	1.88
Nov 83	1157	57.5	440	21.2	445	21.4	2CB2	0.99
Dec 83	753	64.1	210	17.9	211	18.0	1174	0.99
Feb 84	107	59.9	41	23.1	31	17.0	179	1.32
Mar 84	435	83.3	35	6.8	52	9.9	522	0.67
Apr 84	639	62.2	271	24.2	154	13.7	1124	1.76
May 84	434	61.9	121	14.4	166	23.7	701	0.61
Jun 84	124	64.0	38	19.7	32	16.3	194	1.19
Oct 84	395	4B.1	193	23.5	234	28.4	922	0.82
Dec 84	398	61.3	80	12.3	172	26.4	650	0.47
Jan 85	322	46.3	188	27.1	185	26.6	695	1.02
Feb 85	589	51.9	295	26.0	252	22.2	1136	1.17
Mar 85	260	44.5	185	31.6	140	23.9	585	1.32
Apr 85	626	50.8	428	34.8	178	14.4	1231	2.40
May 85	141	49.4	97	34.2	47	16.4	285	2.06
Jun 85	525	49.2	323	30.3	219	20.5	1067	1.47
Aug 85	194	36.9	192	36.5	140	26.6	526	1.37
Sep 85	179	40.9	169	38.7	89	20.4	437	1.90
Nov 85	116	31.6	137	37.5	112	30.9	365	1.22

Fig. 2. Age structure of *S. punctata* over three years in station 11860. Five age classes were distinguished; from the left to the right in each month: JuvI, JuvII, JuvIII, ♀ and ♂.



The mean body length of all the juveniles over three years is shown in Fig. 3. The differences between the mean values of juvenile body length per month are significantly different, ($F=2.432$, $df=26$ and $481, p<0.001$). An a posteriori contrast test (LSD) shows that the juveniles of Oct83, Feb84, Oct83, May84, Jun84, Apr83, Mar84, Apr84, Aug85, Sep85, Jan85 and Nov85 are significantly smaller than in the other months (arranged in decreasing order of difference) at the 5% level.

The numbers (and relative abundance) of the smallest size class of juveniles increase two times per year: the first time in spring (March, Apr, May) and a second time in autumn (Oct83, Aug85, Sep85); only in spring 1984 is the increase in small juveniles not limited to one or two months but seems to continue to a maximum value of smallest juveniles in June84; no summer data of 1984 are available but Oct84 has a fairly large amount of small juveniles too.

The increase of the relative abundance of the smallest juveniles coincides with a decrease in total numbers of the population; i.e. the increase of the relative abundance of the juvenile classes may be partly due to mortality of adults too. This probably occurs in Oct83, Feb84, Aug85 and Sep85. These periods may be considered as periods where a more distinct change of generations takes place. However, it is not possible from these data to predict the exact number of generations per year. Moreover, the interpretation is even more uncertain when we compare with the seasonal data from 1977-1979. The total nematode density, relative abundance of S.punctata within the community and the age structure of S.punctata are given in Table 4. The low relative abundances in March 78 and June 79 are due to a very high number of Daptonema tenuispiculum (comparable with Jun85).

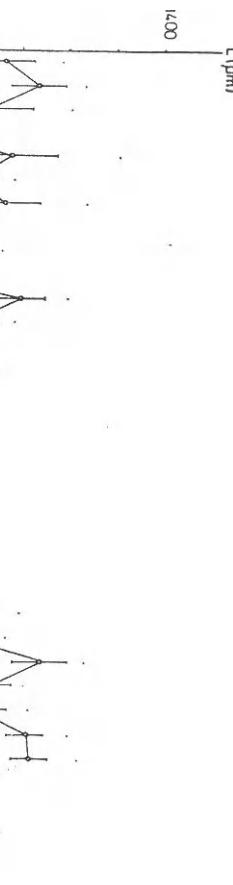


Table 5. Total nematode density (ind./ 10 cm^2 ; relative abundance of Sabatieria punctata in the community and age structure (n Juv, % Juv and % for the period 1977-1979.

Dens. Nem.	% Sabata	Juv	% Juv	% Juv
Jun 77	45	84.4	23.7	50.0
Mar 78	2065	8.0	50.0	37.5
Apr 78	3817	93.0	49.5	30.1
Jun 78	1910	71.0	56.3	25.4
Dec 78	655	74.0	51.4	24.3
Apr 79	2250	91.0	57.5	26.3
Jun 79	721	13.5	16.7	50.0
Sep 79	1439	52.2	32.5	29.2
				33.3

J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1983 1984 1985

Fig. 3. Mean body length of the juveniles of S.punctata over three years in station 11860 (including SE and 95% confidence intervals).

Table 6. Vertical distribution pattern of the age structure of *Sabatieria punctata* in station 11860. (N = number of specimens examined).

	Feb 1985			Mar 1985		
	Juv (%)	♀ (%)	♂ (%)	Juv (%)	♀ (%)	♂ (%)
0- 1 cm	87.5	-	12.5	100.0	-	10.2
1- 2 cm	75.6	17.0	7.4	67.8	22.0	10.2
2- 3 cm	55.6	23.0	21.4	45.3	29.2	25.5
3- 4 cm	38.5	35.6	25.9	32.3	39.9	27.8
4- 6 cm	55.8	23.1	21.1	44.0	36.0	20.0
6- 8 cm	16.7	55.6	27.7	0	71.4	28.6
8-10 cm	-	-	-	60.0	-	40.0

Vertical distribution in the sediment

The vertical profile of Feb85 and Mar85 is examined in order to see if there is an optimum zone for the different age classes. Density changes are given in Fig.4 for the whole *S.punctata* population. Highest density occurs in the 3-4 cm layer with a rather abrupt decrease beneath 6 cm (Feb85). In Mar, max. density occurs in the 2-3cm layer. Abundance of *S.punctata* varies from 12.2% at the surface level (where the other species *Aescolaimus elongatus* and *Daptionema tenuispiculum* are abundant) to 100% from 6 cm on in Feb and from 4 cm on in Mar85.

The pattern (relative abundance of Juv, ♀ and ♂) is given in Table 6. Juveniles as well as adults are present from the surface to 6-8 cm in both Feb and Mar85. Juveniles are more dominant in the upper layers; females are more dominant in the deeper layers.

We do not possess measurements of environmental parameters of the vertical profile from this period.

Production estimates of *S.punctata*

Production of *S.punctata* is calculated by the method developed by Vranken et al. (in press). This method is based on a regression equation relating egg-to-egg development time T_{min} to temperature (t) and adult female body wet weight (W in μg):

$$\log T_{min} = 2.202 - 0.0461t + 0.6271 \log W \quad (1)$$

The P/B was calculated for each month as $1/T_{min}Dx3$ (D =number of days per month).

Biomass structure (males, females and juveniles) is determined for each month and so the monthly production for the species is calculated. Total production for one year divided by the average biomass (W) gives the annual P/B for the species.

Dry weight of *S.punctata* is determined for 150 males, females and juveniles; dry weight is 15% of the wet weight and individual W are: males : 2.424 μg and juveniles 0.699 μg .

From equation (1) it is shown that the calculated T_{min} for *S.punctata* varies between 263.0 days at 0.5°C and 43.3 days at 17.5°C.

The annual P/B is not determined for 1984 because too many months (and even long periods) were not sampled.

1985 (Jan-Dec)

Total production : 16.61 g $\text{ww/m}^2/\text{year}$

Average biomass : 0.93 g ww/m^2

P/B : 16.91

Total production : 14.17 g $\text{ww/m}^2/\text{year}$

Average biomass : 1.00 g ww/m^2

P/B : 14.17

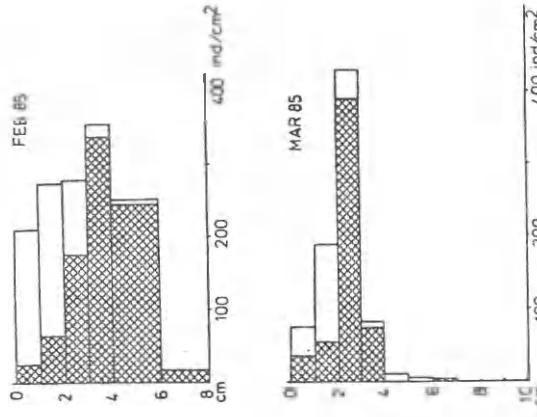


Fig. 4. Vertical density profile (mean density of two replicates) of the nematode community from two months in station 11860. Shaded area indicates the total mean density of *S. punctata*.

Discussion

Sabatieria punctata occurs in very high numbers in the silty sand station 11860 off Zeebrugge (Belgian coast) with a grand mean of 678 ind./10 cm² over three years and peak values up to 2186 ind./10 cm² (NuvB3) or a relative abundance of 98.6% (Mar85) in the whole community.

S. punctata is always very abundant in silty stations along the Belgian coast. Mean relative abundance of the species decreases generally from the west coast to the east coast. (cfr. Vinck et al., 1984).

In station 11860 it is obvious that the relative abundance of S. punctata (or the abundance of accompanying species) is determined by factors which are not quite understood at the moment (cfr. aberrant situation in JunB3).

The life cycle can be summarized as follows: juveniles occur throughout the year and reproduction is considered to be nearly continuous. Analysis of growth or mortality of cohorts in the field has not been possible for this population. A more active reproductive period occurs in spring from March till May. Juveniles from this period probably reach adulthood two to three months later. These adults probably produce juveniles in autumn (Sep-Oct) and adults of the older generation die at this moment (7). There is always a clear decrease in total density at that time and the decrease in adults is more pronounced than in the juveniles, cfr. Fig. 1). Difference between male and female development have not been found.

From regression equation (1) it is shown that the influence of temperature on the reproductive cycle is very important. Equation (1) is mainly determined by values for opportunistic species. The nematodes from sublittoral areas are probably more conservative species and the obtained result for the annual P/B may overestimate the productivity of these species (Vranken et al., in press). Vranken & Heip (1985) found a relationship between egg weight and embryonic development at 20°C. This relationship predicted the embryonic development time of S. punctata from the Sluice Dock of Ostend exactly (prediction: 9.87d; experimental: 9.92d). Generation time is about 3.5 times longer than embryonic development (Vranken, unpublished results) and from this a generation time of about 35 days is predicted for 20°C. A similar value is obtained calculating T_{min} from equation (1) for 20°C, i.e. 23.3d.

The annual P/B is 16.91 for 1983 and 14.17 for 1985. Vranken et al. (in press) calculated the annual P/B (1983) for the whole community: $P/B = 20$.

Vranken et al. (in press) calculated an annual production of 22.2 g ww/m²·y (=1.33 g C/m²·y) and an average biomass of 10.9 g ww/m² (=0.66 g C/m²) for the nematodes in station 11860 for the period Jan83-Dec83. S. punctata contributed for about 75% to the production of the whole community. Ascolaimus elongatus (2.2 µg ww/ind.) and Daptoneema tenuispiculum (0.9 µg ww/ind.) are the other important species of the community.

For the period 1977-1979, Heip et al. (1984) calculated the production of the nematode communities for several coastal stations. The average biomass of the nematode community for this period equals 0.15 gC/m² which is two times higher than for 1983. For the period 1977-1979, only the high density months were sampled, and no information was available on the fluctuation of the biomass over the year. P/B=9 (Gerlach, 1971) was used to calculate the annual production and a value of 1.37 gC/m²·y was obtained. When we use the P/B=20, as determined by Vranken et al. (in press) for the nematode community in 1983, a value of 3 gC/m²·y is obtained for the period 1977-1979.

Billen & Somville (1985) discussed the flux of organic material to the sediment. In shallow coastal seas, such as the Belgian shelf, up to 50% of net primary production is deposited on the sediment. Faecal pellets and zooplankton corpses only make up a small fraction of this sedimentation flux. Phytoplanktonic cells and phytoplankton-derived detritus constitute the bulk of the organic matter deposited on the sediment. The local distribution of the flux of sedimenting organic material in the Belgian coastal zone can be explained on the basis of a hydrodynamical model of the tidal circulation. Some places (like the mud accumulation zone in front of Zeebrugge, with low energy and low bottom stress) appears to act as traps for organic material produced in the whole coastal zone (Adam et al., 1981). The annual amount of organic carbon deposition there has been estimated as 390 gC/m²/year, while the mean value for the Belgian coastal zone as a whole is only 160 gC/m²/year and is 70 gC/m²/year in the offshore area (for a review see Joris et al., 1982).

Heip et al. (1984) found that the nematodes from station 11860 have a lower production than the nematodes in the stations along the Belgian coast. The production of the nematodes is higher in the region off Ostend, which seems to contrast with the higher amount of organic C present off Zeebrugge. However, the east coast is more loaded with pollutants than the rest of the Belgian coast (Braeckman et al., 1984).

A review of the knowledge of the seasonal cycles of marine free-living nematodes is given in Heip et al. (1985). Temperature and food are the most obvious factors explaining the density changes in marine nematodes. Deposit-feeders (as is S. punctata) tend to reach maximum numbers in autumn, winter or early spring, due to the incorporation of primary production into the sediment. From several studies (Tietjen, 1969; Skoelmen & Gerlach, 1971; Smal et al., 1981; Bouwman, 1983) it is shown that spring and summer peaks in nematode densities are common in intertidal, shallow subtidal or brackish-water areas on an annual basis; however very few is known on long-term temporal variability.

Comparing overall community densities throughout the year, no significant differences in winter and summer values can be found in the sublittoral nematode communities studied so far (e.g. Lorenzen, 1974; Juario, 1975; Boucher, 1980). Only few species show significant

differences between seasons. In most cases, the species which show significant differences between summer and winter are those from which enough material (specimens) is examined.

Several authors examined the reproductivity of *S. punctata* in the field. Skoelmen & Gerlach (1971) found a density peak in winter or spring from *S. vulgaris* (=syn. with *S. punctata*) in an intertidal sand-flat in the Waser estuary in Germany. Juarij (1975) discussed the life cycle of *S. vulgaris* (=close to *S. punctata*) in the German Bight. The three juvenile size classes were encountered every month; egg deposition occurs regardless of season. The mean abundance as well as the number of juveniles in summer and winter do not differ significantly. Throughout the year, the population consists for more than 50% of juveniles except in sep (45-50%). Bouwman (1983) found no significant differences between seasons for *S. vulgaris* in the Ens-Dollard estuary; reproduction is continuous and juveniles dominated in all seasons.

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