THE LIFE CYCLE OF *ONCHOLAIMUS OXYURIS* (NEMATODA) IN ITS HABITAT

by

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ABSTRACT

The life cycle of the dominant predatory brackish-water nematode *Oncholaimus oxyuris* was studied over a four year period. Reproduction is similar throughout the years and is coupled to yearly temperature oscillations. Density fluctuations are characterized by annual bimodal curves for all age-classes, with an important peak in spring. Juveniles predominate in the population. Males are present all over the year ; they mature earlier than females and live longer. The presence of females is restricted to distinct periods. The sex-ratio is 45 : 55 in favour of males.

Oncholaimus oxyuris has either two generations annually or three generations in two years. It is both a K-selected and a semelparous species, which maintains a high density and a low reproductive potential in its habitat.

INTRODUCTION

This study contributes to the knowledge of the ecology of the benthic communities of a brackish-water pool, the 'Dievengat', in Belgium. In previous work, special emphasis has been placed on members of the meiofauna, such as Copepoda (Heip, 1969, 1971, 1972, 1973, 1974, 1975, 1979, 1980; Heip & Engels, 1977; Smol & Heip, 1974; Heip & Smol, 1976), Ostracoda (Heip, 1976; Vranken, 1976), Hydrozoa (Heip & Smol, 1975; Herman, 1978) and on some macrobenthic species, such as *Hydrobia ventrosa* (Herman, 1976) and *Nereis diversicolor* (Heip & Herman, 1979). This is the first report on nematodes from that habitat. Data on nematode populations from a four years survey are presented.

Although free-living nematodes are the dominant meiofauna group in benthic communities, studies on their population dynamics are rare (Warwick & Buchanan, 1970, 1971; Lorenzen, 1974; Juario, 1975 and Warwick & Price, 1979). However, in none of these studies populations were followed for more than one year.

Only with the aid of long-term studies at the species and community level, the reaction of species towards environmental changes and their levels of density and production can be evaluated. Indeed, year-to-year fluctuations appear to be very important so that next to nothing can be said on these parameters from a one year study (Heip, 1980).

In this paper we concentrate on a member of the Enoplida : *Oncholaimus oxyuris* Ditlevsen, 1911, because it belongs to the first five dominant nematode species, and it is even more important in terms of biomass, as its individual weight

is more than ten times that of most other species and it therefore makes up the largest part in the total biomass over the year.

MATERIAL AND METHODS

The area of investigation is a polyhaline brackish water pool in the southern part of the natural park 'Het Zwin', situated in the extreme corner of north-western Belgium.

The pool has a surface of $\pm$ 1.5 ha and a maximum depth of 50 cm. Because it is shallow, temperature and salinity fluctuate considerably : temperature : 0.6-30° C and salinity : 8 °/oo-40 °/oo. Temperature was recorded continuously with the aid of a Ryan D-30 recorder with a precision of 1° C and was measured fortnightly with a thermometer with a precision of 0.1° C. Salinity was calculated from chlorinity determined with Mohr's method as follows : S = 1.80655 Cl. The area is partly surrounded by reed beds (*Phragmites communis*), which enrich the pond with large amounts of detritus every year. The sediment consists of well sorted fine sand underlying a 2-3 mm layer of detritus.

The benthic fauna is characterized by : microfauna : Protozoa (not studied); meiofauna : Nematoda $(1 \times 10^6 \text{-} 9 \times 10^6/\text{m}^2)$, Copepoda $(100{,}000\text{-}1 \times 10^6/\text{m}^2)$, Ostracoda $(100{,}000\text{-}1.2 \times 10^6/\text{m}^2)$, Hydrozoa (*Protohydra leuckarti* with 1,500-38,000 specimens/m²) and an unknown number of the other groups; macrofauna is dominated by *Nereis diversicolor* (Polychaeta), *Hydrobia ventrosa* (Gastropoda), *Cerastoderma glaucum* (Bivalvia) and *Pomatoschistus microps* (Pisces).

Three random, replicate samples were taken with a glass corer (internal diameter : 3 cm) to a depth of 10 cm in the sediment. Water depth at the sampling station is approximately 10 cm. The regular fortnightly sampling program started in September, 1973 and is still being continued. For nematodes only samples with even numbers were investigated providing an interval of approximately one month. The samples were fixed in the laboratory : two with 4 % formalin at 60° C and one with 70 % ethanol (for Crustacea). Replicate cores proved to be alike in density and species composition (Govaert, 1979) and only one sample was studied in detail. The samples were elutriated using the method described by Barnett (1968). After removal of the sand fraction, the nematodes were extracted from the detritus by the sugar centrifugation method as described by Heip *et al.* (1974). From September 1977 onwards, this extraction method was adjusted for Ludox instead of sugar. In order to facilitate counting, the animals were stained with rose Bengale. About 200 nematodes were taken randomly from a counting chambre, using a table of random digits, and transferred to glycerin for microscopical examination, following the method of De Grisse (1965).

Distinction was made between males, gravid and non-gravid females and juveniles. Because it is difficult to distinguish the different stages, juveniles from samples covering one year (Oct. 1976-Sept. 1977) were measured.

In order to eliminate the high frequency 'noise' in the data, due to aggregation, sampling and measurement errors, which obscure underlying patterns, we used the running mean of three successive sample values with weights 0.23, 0.54, 0.23 together with the sample values. In this way random fluctuations are evened out to a certain extent. Sample values are represented in tables and figures respectively as 'S' and '+;' and smoothed or trendline values as 'T.L.' and '●'.

RESULTS

Density of the population over four years is plotted in Figs. 1 and 2.

Total numbers

Total numbers are represented each year by a bimodal curve with two peaks of maximum abundance : one in summer and one in winter. Data of minimum and maximum abundance are given in Table I.

There is a good agreement between the years of the dates and values of minimum abundance. Minima occurred during late February or March with rather constant densities between 40×10^3 and 50×10^3 individuals per m². However exceptionally high values were noted in February, 1975. A second minimum occurred in August.

TABLE I

Dates and numbers of minimum and maximum abundance of the different age-classes

	Minimum numbers $\times$ 10^3/m²			Maximum numbers $\times$ 10^3/m²		
	Date	S	T.L.	Date	S	T.L.
Total numbers	21 Mar 74	41	65	24 Jan 74	403	248
	09 Jul 74	40	120	28 Nov 74	1049	608
	27 Feb 75	152	236	24 Apr 75	790	574
	13 Aug 75	48	113	04 Oct 75	212	191
	25 Mar 76	42	86	29 Jan 76	260	188
	12 Aug 76	99	179	09 Sep 76	354	247
	23 Mar 77	48	72	02 Dec 76	317	243
	10 Aug 77	57	81	14 Jun 77	292	206
Juveniles	27 Dec 73	50	137	24 Jan 74	317	193
	13 Jun 74	0	16	28 Nov 74	958	554
	27 Feb 75	128	206	24 Apr 75	617	412
	20 Jun 75	42	64	09 Oct 75	168	152
	03 Dec 75	59	73	29 Jan 76	208	155
	22 Apr 76	61	41	09 Sep 76	342	228
	04 Nov 76	103	128	02 Dec 76	226	175
	21 Apr 77	33	20	13 Jul 77	153	131

	Minimum numbers × 10³/m²			Maximum numbers × 10³/m²		
	Date	S	T.L.	Date	S	T.L.
Adults				24 Jan 74	86	55
	22 Feb 74	0	20	18 Apr 74	139	89
	08 Aug 74	27	21	28 Nov 74	91	54
	27 Feb 75	24	30	22 May 75	273	226
	13 Aug 75	16	33	09 Oct 75	44	39
	03 Dec 75	12	12	20 May 76	154	112
	12 Aug 76	0	06	02 Dec 76	91	67
	24 Feb 77	24	25	14 Jun 77	138	88
Males				24 Jan 74	86	55
	22 Feb 74	0	11	16 May 74	62	52
	09 Jul 74	0	14	28 Nov 74	91	49
	27 Feb 75	16	20	22 May 75	159	119
	13 Aug 75	0	17	09 Oct 75	44	34
	03 Dec 75	12	06	20 May 76	88	71
	12 Aug 76	0	06	02 Dec 76	91	66
	24 Feb 77	24	24	14 Jun 77	108	58
	10 Aug 77	0	04			

The time of occurrence and value of the maximum peaks are less constant. Winter maxima occur from January to April and summer maxima from June to November. We consider the months April and November as exceptionally late since both phenomena were recorded in the same year. Maximum densities differ widely in different years, from 140×10^3 to 1050×10^3 individuals per m².

Mean abundance for the total population per year is given in Table II.

Juveniles

On the average, 70 % of the total population is represented by juveniles (see Fig. 3). Of course, this makes the graphs of the density of the juveniles and of the total density rather similar (see Fig. 1).

Mean densities of the juveniles over the four years are given in Table II. Data of minimum and maximum abundance are given in Table I. The highest value recorded was 958×10^3/m², on 28 November 1974, when 91 % of the population were

TABLE II

*Mean abundance in 10^3 individuals per m^2 per year $(n = 13)$
for the different age-classes*

Age-class	Period	S		T.L.	
		$\bar{x}$	$\pm$ s.e.	$\bar{x}$	$\pm$ s.e.
Total numbers	Oct. 73 — Sept. 74	172	43	177	25
	Oct. 74 — Sept. 75	319	80	321	25
	Oct. 75 — Sept. 76	61	24	157	13
	Oct. 76 — Sept. 77	132	24	136	17
Juveniles	Oct. 73 — Sept. 74	131	39	134	29
	Oct. 74 — Sept. 75	244	75	246	40
	Oct. 75 — Sept. 76	122	25	117	15
	Oct. 76 — Sept. 77	88	18	92	14
Adults	Oct. 73 — Sept. 74	43	12	44	7
	Oct. 74 — Sept. 75	75	22	75	18
	Oct. 75 — Sept. 76	38	11	38	8
	Oct. 76 — Sept. 77	43	11	42	7
Males	Oct. 73 — Sept. 74	29	7	30	4
	Oct. 74 — Sept. 75	43	14	43	9
	Oct. 75 — Sept. 76	29	8	30	6
	Oct. 76 — Sept. 77	34	9	33	5

TABLE III

*Periods with less than 50 % juveniles in the population,
and dates and values of minimum abundance*

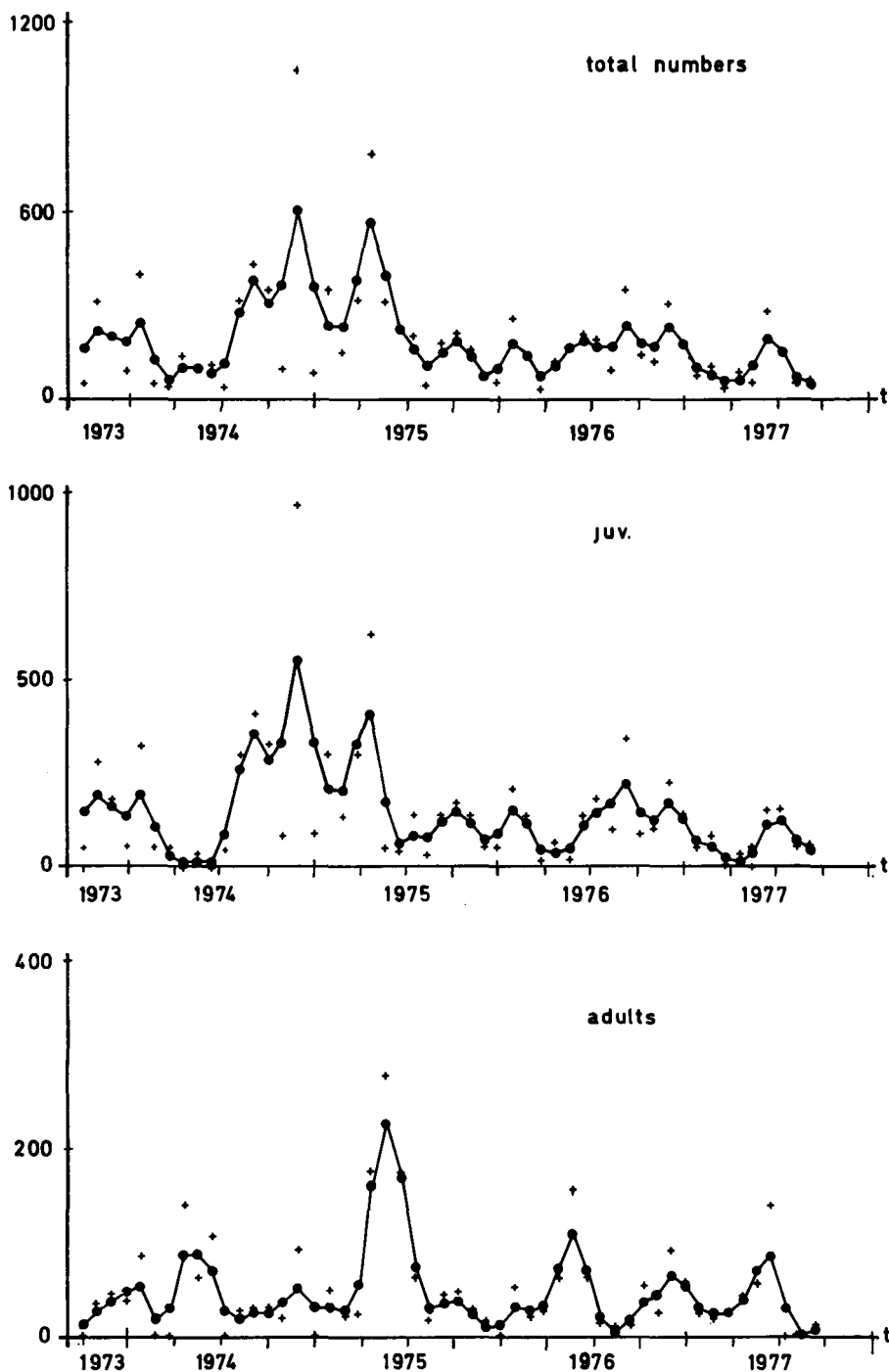| Period	Date	Numbers $\times 10^3/m^2$	
		S	T.L.
April — June 74	18 Apr 74	0	16
May — June 75	22 May 75	14	44
March — May 76	20 May 76	13	32
March — May 77	17 May 77	0	36

O. OXYURIS

Fig. 1. — Density of the ~~Oncholaimus oxyuris~~ population over four years.
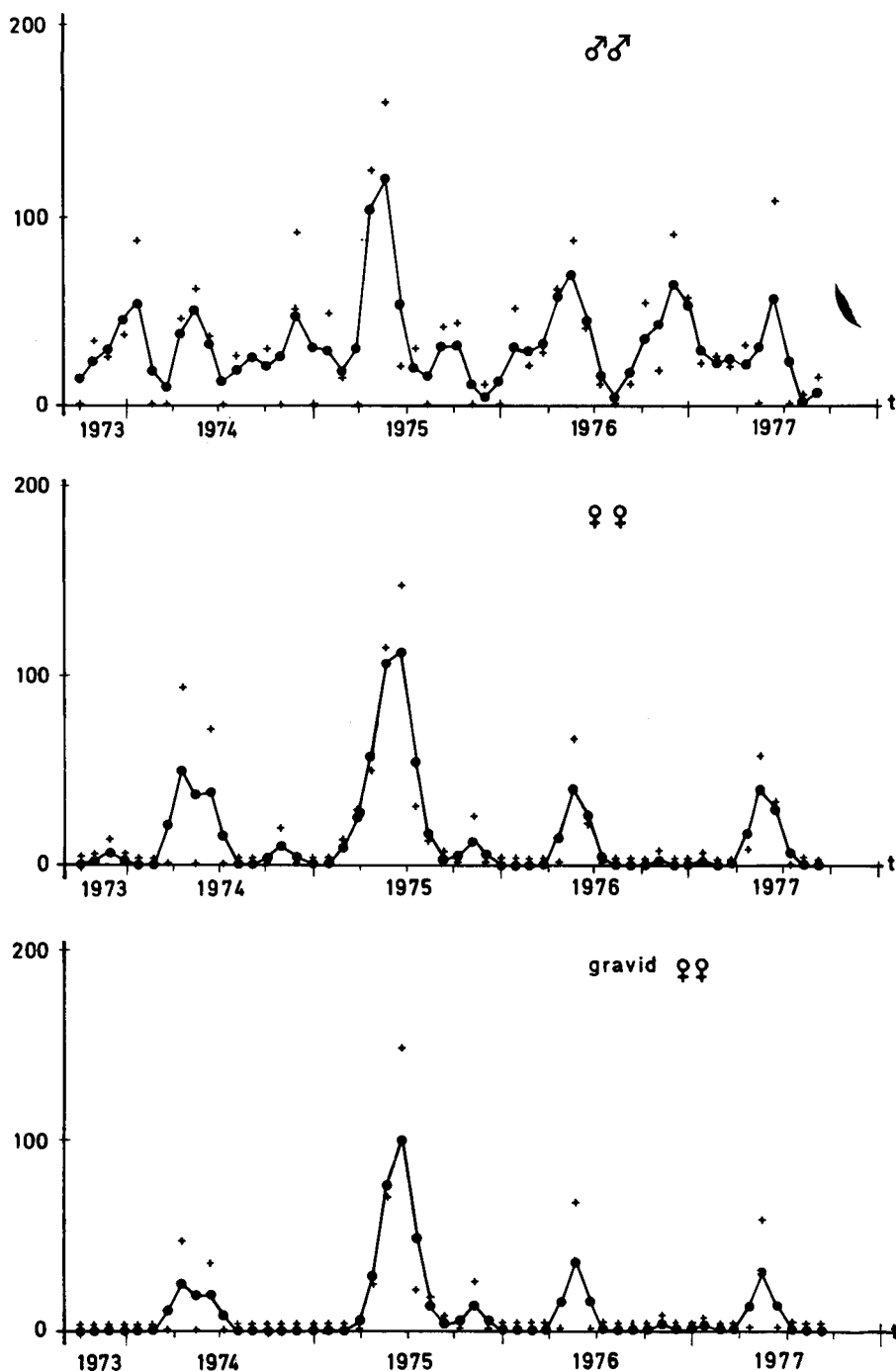
O. OXYURIS

Fig. 2. — Density of the males, females and gravid females of *Oncholaimus oxyuris* over four years.
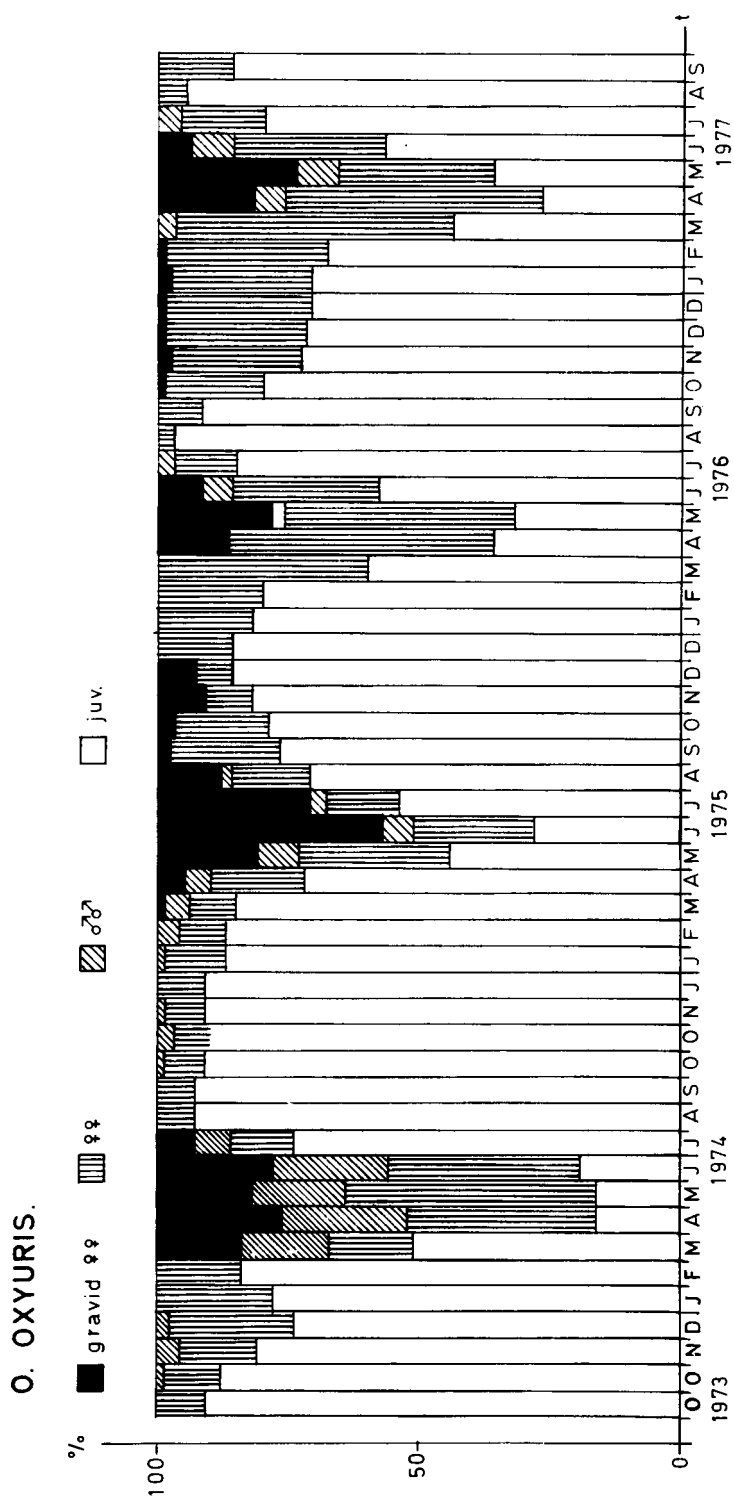
Fig. 3. — Composition of the *Oncholaimus oxyuris* population over four years.

juveniles. Lowest densities of juveniles occur each year during spring, from March till June; in the same period their part in the population is reduced to below 50 % (Table III). During this period low numbers of juveniles are found as most of them moult into adults. In winter we notice a second but less distinct period of low abundance, with the percentage of juveniles in the population remaining above 50 %.

Adults

The number of adults is represented by a distinct bimodal curve with one main peak in the spring and a smaller one in autumn-winter, always preceding the increase of the juveniles.

Data of minimum and maximum abundance and the corresponding densities are given in Table I. Minimum values are around 10×10^3 individuals/m² and are found in winter, from December to February and in late summer, from August to October. Maxima vary from 140×10^3 to 280×10^3 individuals/m² in the main reproductive period and from 40×10^3 to 100×10^3 individuals/m² in autumn-winter.

The numbers start to increase and decrease at approximately the same time each year. From March onward the number of adults gradually increases until late April-early June. A second minimum is reached in August, due to the mortality of the females. From April until June females represent more than 50 % of the population. This percentage drops to a minimum of less than 10 % in August 1974, 1976 and 1977; however in 1975, the percentage of females decreases more slowly with a minimum of 14 % in December.

The density of the different age classes within the adult population is shown in Fig. 2. The relative composition of the population is shown in Fig. 3.

Mean abundance of the adults over the four years is given in Table II.

Males

Males are found throughout the year with an average abundance of 34×10^3 individuals/m². Their density fluctuates following a bimodal curve characterized by peaks of high abundance in spring and autumn-winter.

Data of minimum and maximum abundance are presented in Table I.

Although males are rare in late winter and in summer with densities of 10×10^3 individuals/m², they show a tenfold increase in spring and again in early winter. A maximum value of 160×10^3 individuals/m² is attained on 22 May 1975. As there is good agreement between the dates of minimum and maximum abundance in different years, it is possible to predict low numbers in February and August and high numbers in late May-early July. The time of maximum abundance in winter is more variable, being in January 1974, November 1974, October 1975 and December 1976.

Males constitute a large part of the adult population, with a mean value of 75 %. This percentage is at a minimum from April to June, the main reproductive period, with values decreasing to 55 %. Minima that are not as well defined occur in October-November, the second reproductive period, with values around 80 %. During the rest of the year they represent ± 100 % of the adult population. Mean abundance (in 10^3 individuals/m²) of males over the four years is given in Table II.

Females

A well-defined cycle is found representing the numbers of females, characterized by a main peak of high abundance during spring with numbers varying from 60×10^3

to 150×10^3 individuals/m². Females appear again during winter but in much lower numbers. During the rest of the year females are absent, providing a mean sex-ratio of 1 : 4 over the whole year. Females are abundant from March to June as indicated in Table I.

When adult females are present, at least 50 % and often 100 % of them are gravid (Fig. 3), providing (except for 1974) a nearly identical picture of the numbers of females and the numbers of gravid females (see Fig. 2). The number of gravid and non gravid females starts to increase at about the same time every year and maxima were found at comparable dates : 18 April 1974, 20 June 1975, 20 May 1976 and 17 May 1977. It is likely that the main reproductive period falls in the months of March, April, May and June. At this time gravid females are found in densities of about 50×10^3 individuals/m², with maximum numbers in 1975 : 150×10^3 individuals/m².

In this period the sex ratio approaches 1 : 1. In autumn gravid females appear for the second time, but in fewer numbers, when the juveniles of the first cohort reach adulthood and start reproducing. However, this second peak was not recorded in 1974, probably due to low density. In 1976, temperature in summer was exceptionally high, and the water temperature remained above 20° C for more than two months, reaching values close to 30° C; a second cohort could therefore moult into adults and gravid females appeared again in winter, with the same low numbers as in autumn, indicating that only a small part of the juveniles had enough time to mature.

Juveniles of the lowest size class (500-1000 μm) are abundant in May-June. In winter most of the juveniles belong to the size class 2500-3500 μm, the fourth juvenile stage. Nevertheless a few small juveniles of the size-class 1000-1500 μm are also present and this may indicate a second generation born in the autumn.

Characteristics of the increase and decrease

The increase and decrease can be described by the general exponential equation $N_t = N_0 e^{rt}$, where N_t = the numbers at time t, N_0 = the numbers at t_0, and r = the rate of increase or decrease.

In Table IV the value of r is given for different periods of increase and decrease for each class. Numbers could be fitted by the equation, with goodness of fit, expressed as r^2, larger than 0,80 in all cases. For the same period and age class, there are few differences in the values of r from year to year. Also, the mean values over the four years for the different classes of males, adults and juveniles are quite similar and vary between 0,015 and 0,021 per day. The females are exceptional with high values ranging from 0,030-0,052 for increase and — 0,019 to — 0,048 for mortality.

There is a good correlation between the rate of decrease and the mean water temperature at the time of sampling in the case of the ♂♂ : $r = 0,932$ ($n = 4$), the adults : $r = 0,904$ ($n = 5$) and the juveniles : $r = 0,706$ ($n = 8$). For the ♀♀ a good correlation was found $r = 0,954$ ($n = 4$) with the mean temperature measured by the recorder. However, no significant correlation was noted for the rate of increase.

<div align="center">DISCUSSION</div>

The life cycle

Oncholaimus oxyuris occurs in very high densities in the Dievengat, with a grand mean of 171,000 ind./m² over all samples and peak total values up to

608,000 ind./m² (trendline value of 28 November 1974). Although it is a predator, it is also one of the dominant species in the habitat.

Juveniles and males are found throughout the year, whereas females are absent in winter. On average, the total population consists of 70 % juveniles and the adult population of 75 % males. A similar high proportion of juveniles has been found by Meyers et al. (1970) for *Metoncholaimus scissus*, but the extraordinary high proportion of males seems to be rather unique.

With a remarkable constancy the number of juveniles declines from a peak in winter to a minimum in early (March) to late (June) spring, when the number of adults consequently starts to increase exponentially. On reaching adulthood the individuals mate and most females are gravid in early to late spring, when also the sex-ratio tends to become equal. The first juveniles resulting from reproduction in spring appear in April and their number increases until September-November. After reproduction in spring, females are absent in August-September and males attain their lowest overall density in this same period.

Males appear earlier than females and they also live longer, so that the sex-ratio over the whole period of main reproduction is 40 : 60 in favour of males, a value which was also found in laboratory experiments (Heip et al., 1978).

From September onwards the first born juveniles reach adulthood and most females become gravid. This second reproductive period in autumn is less important than the main reproductive period in spring, the sex-ratio does not exceed 20 : 80 in favor of the males. Nevertheless, a distinct upward change in the number of juveniles is apparent and produces a second peak in winter.

The overwintering population thus consists mainly of males and small juveniles from the autumn generation and large fourth-stage juveniles from the spring generation which did not succeed in reaching adulthood before winter. In the next spring, these large juveniles are the first to become adult and the juveniles of the autumn generation follow them near the end of the spring reproductive period.

Summarizing, we find a reproductive period in spring extending from March till June; the first juveniles then produced are able to complete their life cycle before winter, whereas the later juveniles have to overwinter to attain adulthood in next spring. The juveniles becoming adult before winter are able to reproduce so that the overwintering juveniles belong to two generations, but their offspring is produced during the same main reproductive period in the next spring. Whether these generations remain distinct, i.e. whether juveniles produced later in spring are always and only the offspring of overwintering small juveniles, is not clear. We may thus have either two generations, one in spring and one in autumn; or more complicated, we have an alternation of two generations in one year and one in the next in the following way : overwintering small juveniles produce an adult generation late during the main reproductive period in spring. The offspring of that generation overwinters as large juveniles, which attain adulthood early next spring and produce another generation in next autumn; the offspring of that generation again overwinters as small juveniles. In this case we have three generations in two years.

That this plausible though slightly complicated scheme may nevertheless represent the most exact picture of the life cycle of *Oncholaimus oxyuris* is somewhat substantiated by the laboratory experiments (Heip et al., 1978). These authors suggested one generation annually for *O. oxyuris* at the mean annual temperature of the habitat of 11.2° C, and predicted two generations for a mean annual tem-

TABLE IV

Rate of increase and decrease, r, at different periods for each class, compared with the duration $\triangle T$ and mean water temperature measured at sampling days, t_s, and by continuous recorder t_R

	Increase									
	ΔT days	t_s °C	t_R °C	Period	r	ΔT days	t_s °C	t_R °C	Period	r
Males	112	7.9	5.7	04.10.73-24.01.73	0.014	84	9.1	9.5	27.02.75-22.05.75	0.026
	142	14.8	11.9	09.07.74-28.11.74	0.005	142	8.4	8.1	30.12.75-20.05.76	0.011
	112	14.9	11.9	12.08.76-02.12.76	0.022	83	13.2	12.9	23.03.77-14.06.77	0.017
mean	12.7				0.015	11.0				0.021
Females						141	19.3	10.1	30.01.75-20.06.75	0.030
						112	11.1	10.6	24.02.77-17.05.77	0.052
mean						10.8				0.041
Adults	112	7.9	5.7	04.10.73-24.01.74	0.014	83	11.3	11.4	22.02.74-16.05.74	0.025
	112	12.9	10.4	08.08.74-28.11.74	0.012	112	9.1	9.5	27.02.75-22.05.75	0.027
	112	14.9	11.9	12.08.76-02.12.76	0.023	169	7.7	7.6	03.12.75-20.05.76	0.014
						110	14.7	11.6	24.02.77-14.06.77	0.016
mean	10..6				0.016	10.4				0.021
Juveniles	168	15.9	12.9	13.06.74-28.11.74	0.019					
	111	21.2	17.4	20.06.75-09.10.75	0.008					
	140	20.0	18.2	22.04.76-09.09.76	0.015					
	83	17.4	15.5	21.04.77-13.07.77	0.026					
mean	17.3				0.017					
Total population	168	16.7	13.9	13.06.74-28.11.74	0.010					
	168	18.5	16.9	25.03.76-09.09.76	0.005					
	83	13.1	—	23.03.77-14.06.77	0.013					
mean	15.8				0.009					

			Decrease						
ΔT days	t_s oC	t_R oC	Period	r	ΔT days	t_s oC	t_R oC	Period	r
91	6.4	5.6	28.11.74-27.02.75	— 0.016	83	21.5	19.2	22.05.75-13.09.75	— 0.028
140	7.1	8.0	02.12.76-21.04.77	— 0.009	84	20.9	20.0	20.05.76-12.08.76	— 0.033
	6.8			— 0.013		20.4			— 0.031
					82	19.2	16.8	18.04.74-09.07.74	— 0.019
					83	23.2	19.1	20.06.75-11.09.75	— 0.044
						19.6			— 0.032
91	6.4	5.6	28.11.74-27.02.75	— 0.034	84	20.9	16.8	16.05.74-08.08.74	— 0.017
84	5.6	6.0	02.12.76-24.02.77	— 0.039	83	21.5	19.2	22.05.75-13.08.75	— 0.026
					84	20.9	20.0	20.05.76-12.08.76	— 0.016
	5.9			— 0.036		19.9			— 0.020
91	6.4	5.6	28.11.74-27.12.75	— 0.017	140	11.6	11.4	24.01.74-13.06.74	— 0.022
					84	6.8	6.8	29.01.76-22.04.76	— 0.020
					224	10.0	8.7	09.09.76-21.04.77	— 0.011
						9.2			— 0.018
111	19.9	17.6	24.04.75-11.09.75	— 0.015	91	6.4	5.7	28.11.74-27.02.75	— 0.011
86	17.9	—	14.06.77-09.09.77	— 0.015	111	6.1	—	02.12.76-23.03.77	— 0.011
	18.5			— 0.015		6.1			— 0.011

perature of 13.9° C. As this is only slightly above the observed annual mean temperature, a mean generation time of 1.5 does seem possible. Skoolmun & Gerlach (1971) found one or two generations for the related species *O. brachycercus*, depending on temperature. In the North Sea only one generation is possible, but when annual temperature exceeds 13.5° C two generations are produced.

At this point it is interesting to point out the striking resemblance between the life cycle of *Oncholaimus oxyuris* and the totally unrelated ostracod *Cyprideis torosa*, which is also on top of a food chain but is a detritus feeder. In this animal as well the generations are split in two by the winter period and the overwintering population consists largely of (large) juveniles (Heip, 1976).

The rate of increase of the *Oncholaimus oxyuris* population is 0,009 ± 0,003 ($n = 3$) per day, a low value for such a small animal. However, calculations of the reproductive potential in laboratory conditions give a value of $r_m = 0,0163$ per day at the mean temperature during increase of 15,8° C. This is not much higher than the actual rate of increase. *O. oxyuris* therefore reproduces at a rate close to its maximum possible rate.

The cyclicity in the density of *O. oxyuris* will be further investigated, but it is already apparent that a large amount of constancy in the cycles is found. This again is similar to what has been found in other meiobenthic species, such as *Cyprideis torosa* (Heip, 1976) and several species of harpacticoid copepods (Heip, 1980). In all these species as in *Oncholaimus oxyuris*, density is characterized by the predominance of periodicities with a long period (low frequency), and it appears that this is due to coupling with temperature as an external oscillator with a very pronounced yearly component.

Reproductive biology

There is relatively little knowledge about the reproductive biology of meiobenthic nematodes. De Bovée (1975) noticed that males of *Dorylaimopsis mediterranea* have a shorter life-span than females. However, for *Oncholaimus oxyuris* and *Metoncholaimus scissus* (Meyers *et al.*, 1970) the reverse is true. Maturation in these species is followed by a single period of intense reproduction and rapid death thereafter. Gerlach & Schrage (1971) observed no further reproduction for *Oncholaimus brachycercus* after egg-deposition, although culture conditions might not have been suitable to study this problem. De Fonseca (1975) observed repeated copulations for *Oncholaimus oxyuris* when culture conditions changed suddenly, but the total number of offspring did not change; apparently only the first copulation is necessary (Absillis, 1975).

After moulting, the females of *Oncholaimus oxyuris* accumulate oocytes in the uterus, are fertilized, deposit a small number of egg-masses and die within a couple of days or weeks. *O. oxyuris* can thus be considered as a semelparous species (Gadgil & Bossert, 1970; Schaffer & Gadgil, 1975; Bell, 1980).

Females mature later than males and this can be related to their relatively higher biomass (Smol, unpublished results). More energy and time is required to produce this excess in somatic production; moreover, there is the production of an additional organ, which is absent in males (where, however, supplementary organs such as spicules and their associated muscles exist as well). This is the demanian system, which plays an important role as receptaculum seminis in reproduction (Rachor, 1969; Maertens & Coomans, 1979; Calcoen & Dekegel, 1979). Besides this reproduction of supplementary tissue, egg-deposition itself is an energy-consuming

process and the deleterious effects of reproduction on survival are clear. However, the fact that there is always a significantly higher number of eggs in the first egg-mass than in subsequent ones (De Fonseca, 1975; Absillis, 1975) reduces the influence of lower survival during reproduction on the number of offspring.

Females of *Oncholaimus oxyuris* produce a maximum of 37 eggs, a small number for a nematode. The species is also characterized by its big size, relative to other nematodes, its slow development and consequently long generation time, and the predominance of males in adult population. These characteristics certainly suggest that *O. oxyuris* has to be considered a relatively K-selected species, a statement that may seem to be contradictory to its semelparous reproduction. However, it should be recalled that the standing stock of this species in the community is extremely high so that the death of the (large) females results in the biomass remaining high but a lower reproductive potential. Of course, the next question is why such a high density should be selected for. We have no clear answer to this, but one possibility is competition for space with other predatory nematodes, such as *Viscosia viscosa* which is less abundant in the Dievengat. That maintaining a high density is one of the main reproductive strategies of this species is further demonstrated by the fact that when prey becomes rare cannibalism is quite frequent (De Fonseca, 1975). Large males may attack up to five smaller individuals in half an hour under these circumstances.

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