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Influence of Temperature on the Reproductive Potential of *Oncholaimus oxyuris* (Nematoda: Oncholaimidae)

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Abstract

The large nematode *Oncholaimus oxyuris* Ditlevsen, 1911 is a dominant predator in a shallow polyhaline brackish-water pond in Belgium. The reproductive potential of this species was calculated as the intrinsic rate of natural increase $r = 1/D \ln pN_e$, in which D is the generation time, p is the percentage of females, and N_e is the number of eggs per female. The generation time varies between 570 days at 5°C and 101 days at 25°C and is the main factor in the determination of r. The relationship between r and temperature is nearly linear and is given by $r = 0.0013\ T - 0.0042$. The reproductive potential of *O. oxyuris* is much lower than would be predicted from body size; this, and the dominance of males in the population, is discussed in the light of the evolution of stable predator-prey systems.

Introduction

Free-living nematodes are the most numerous metazoans in the marine benthos and even their impact on the plankton must be important, at least in the shallow waters above the continental shelves, as they play a role in nutrient regeneration and the availability of detritus to higher levels in the food chain (Tenore *et al.*, 1977). Yet, little is known about the dynamics of marine nematode populations and only few authors have calculated their reproductive potential or their turnover.

In this study, we choose to investigate the influence of temperature on the reproductive potential of the large species *Oncholaimus oxyuris* Ditlevsen, 1911, mainly for two reasons: firstly, most studies till now have been made on small, rapidly reproducing species, and secondly, this species is an important predator, yet at times it may become the dominant species in the community where we studied it, posing some interesting problems on the resilience of this community.

The reproductive potential can be characterized by the intrinsic rate of natural increase, r, in the equation of an exponentially increasing population without mortality, $N_t = N_0 e^{rt}$; or in a life table as the solution of the equation $1 = \Sigma\ e^{-rx}\ l_x m_x$, in which l_x is the proportion of females surviving until age x, and m_x is the number of female progeny per female of age x. When D represents the generation time, $r = 1/D \ln R_0$, in which R_0 is the net reproductive rate, equal to N_D/N_0 for our purpose or to $\Sigma\ l_x m_x$ in life table notation. When p is the percentage of females in the population and N_e the number of eggs per female, $N_D/N_0 = pN_e$, from which

$$r = 1/D \ln pN_e\ . \qquad (1)$$

May (1976) showed that r as calculated by Eq. (1) is a good approximation of r as calculated from a life table in the case of many arthropods, and Caughley and Bird (1971) proposed the (over-restrictive) condition $r < 0.1$, which is satisfied for *Oncholaimus oxyuris*. Heip and Smol (1976) used Eq. (1) to calculate the reproductive potential of two harpacticoid copepods, and found no large difference between values obtained in this way and life table values.

Materials and Methods

The nematodes used in this study were obtained from a shallow brackish-water pond in northern Belgium, which has been described in other papers (e.g. Heip, 1976). *Oncholaimus oxyuris* Ditlevsen, 1911 was cultured on bacto-agar 0.6% in water from the habitat with a salinity between 18 and 23‰. The older juveniles

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and adults were fed on the small nematode *Panagrellus redivivus*. Cultures of the prey were fractionated in different size classes and only the appropriate size class was offered to a particular culture of *O. oxyuris*, depending on the growth phase of that culture. As the prey is a very fast-growing species, it was necessary to remove excess prey as they tended to overgrow the *O. oxyuris* cultures. Cultures containing only the two smallest size classes thrived on the bacteria and the algae growing on the agar.

The Petri-dishes used in the experiments were put in a water-tight vessel which was placed in a water bath adjusted to the required temperature by cooling with a kryothermat Haake KT-32 and heating with a thermostat Buhler TH2 with stirrer. In this way, water temperatures in the baths were maintained constant to within 0.5 C°.

All cultures were started with adults from the field, and were controlled at least every 3 days and mostly every 2 days. When contamination was observed, the nematodes were immediately transferred to a new medium.

The following events were observed: the increase of the number of eggs in the uterus; the deposition of the egg-masses and the number of eggs in each egg-mass; the appearance of the first juveniles; the disappearance of the egg-mass; the appearance of the other juvenile stages and the new adults; copulation and subsequent development and deposition of egg-masses in the new generation. All observations were performed under a dissecting microscope or under an inverted microscope using special observation chambers (Maertens, 1975). As we had no morphometric data, the 4 juvenile stages were distinguished according to a set of criteria based on appearance, length and width of the nematodes; distinction between large juveniles and females without eggs in the uterus was difficult.

Results

The difference between values of the reproductive potential for *Ocholaimus oxyuris* obtained by $r = 1/D \ln pN_e$ (Eq. 1) and by life table calculations was tested for different schemes of survival. The difference was always small, not exceeding 10%, and mostly in the order of 1 to 5% when mortality was not too large (not larger than 30% during juvenile development). Mortality is only known from cultures and might be higher there than in the field; values of r obtained from Eq. (1) will always be higher than life table values, because juvenile mortality is not included in the former. This could be remedied by calculating $r = 1/D \ln pdN_e$ with d the proportion of individuals surviving till adulthood; values calculated in this way are indeed closer to life table values based on the same mortality. However, as it is doubtful whether mortality in cultures is a good estimate of mortality in the field, we preferred not to include this factor at all.

Table 1. *Oncholaimus oxyuris*. Duration of different life-cycle stages at 5 different temperatures. Mean and standard error of n observations. Development times of eggs inside the uterus, U, and in the egg-mass, E, of juveniles, J, and the maturation time, M, and generation time, D (all in days) are shown. $U = D - (E+J+M)$. We did not succeed in culturing throughout entire life cycle at 5° and 10°C

Stage	Temperature				
	5°C	10°C	15°C	20°C	25°C
E	84.7±8.0 $n=3$	36.3±1.6 $n=9$	16.9±0.6 $n=31$	11.3±1.1 $n=24$	9.0±0.3 $n=29$
$E+J$	-	-	98.0±2.1 $n=4$	71.3±5.2 $n=6$	65.8±3.5 $n=12$
$E+J+M$	-	-	122.3±4.6 $n=6$	98.2±3.5 $n=5$	82.8±4.5 $n=12$
D	-	-	152.5±4.3 $n=4$	113.9±1.4 $n=9$	101.7±2.9 $n=24$

In order to calculate the intrinsic rate of natural increase, the values of generation time, D, sex ratio, p, and number of eggs per female, N_e, are required. To calculate generation time we divided the life-cycle of *Oncholaimus oxyuris* into the following events: at a certain moment a mature female starts producing eggs which accumulate in the uterus and, after a time U, she deposits an egg mass. Embryological development then continues outside the body and, after a time E, the first juveniles appear. They moult four times and become adult after a time J. After a maturation time, M, the female starts producing eggs and completes the life cycle. The generation time, D, is thus equal to $D = U + E + J + M$.

The values of these life-cycle stages are given in Table 1. We did not succeed in culturing the nematodes throughout an entire life cycle at 5° and 10°C, in spite of the fact that problems of culture contamination were greater at higher temperatures. In order to obtain an estimate of generation time at these lower temperatures, we had to rely on indirect calculations. They were performed using the duration of the different life-cycle stages relative to the duration of egg development, which is known at all temperatures, and linear extrapolation of the values obtained at the three high-

Table 2. *Oncholaimus oxyuris*. Duration (days) of different life-cycle stages as obtained from the relative duration of these stages at higher temperatures and the duration of extra-uterine egg development. Lettering as in Table 1

Stage	Temperature				
	5°C	10°C	15°C	20°C	25°C
U	127	60	31	22	19
E	85	36	17	11	9
J	272	144	80	62	56
M	86	45	25	19	17
D	570	285	153	114	101

Table 3. *Oncholaimus oxyuris*. Number of eggs accumulated in the uterus per day (N_e'), number of eggs produced by a female (N_e), number of eggs per egg-mass (N_e'') and number of egg-masses produced per female (N_m) at 5 different temperatures. Means and standard errors of *n* observations

	Temperature				
	5°C	10°C	15°C	20°C	25°C
N_e'	0.20±0.04 (*n*=8)	0.38±0.05 (*n*=17)	0.93±0.07 (*n*=27)	1.49±0.09 (*n*=28)	1.73±0.09 (*n*=25)
N_e	13.5±13.4 (*n*=4)	18.5±6.0 (*n*=9)	34.3±10.9 (*n*=14)	35.6±7.4 (*n*=14)	36.8±8.3 (*n*=14)
N_e''	10.5±9.2 (*n*=4)	11.7±2.2 (*n*=15)	13.6±0.5 (*n*=34)	15.7±0.9 (*n*=32)	13.6±3.2 (*n*=38)
N_m	1.17	1.65	2.50	2.29	2.71

est temperatures to the lower range. The regressions of these relative durations upon temperature, as obtained from the observed values at 15°, 20° and 25°C are:

$$J/E = 0.151\ T + 2.543,$$
$$M/E = 0.045\ T + 0.797,$$
$$U/E = 0.031\ T + 1.347,$$
$$D/E = 0.228\ T + 5.573.$$

It is immediately obvious that estimates obtained from the summation of the 4 different life-cycle stages are very close to estimates from D/E directly, as $J/E + M/E + U/E = 0.227\ T + 4.597 = D/E - E/E$. This indicates that the linear approximation is good and that the error will depend mainly on the values of E at lower temperatures.

Values of the 4 life-cycle stages, obtained from these regressions at all temperatures, are given in Table 2, together with the generation time, D, obtained from this summation.

To obtain one expression relating generation time and temperature, the regression of D upon T, assuming a power law $D = aT^b$ was calculated as

$$D = 3350\ T^{-1.127}. \qquad (2)$$

This equation predicts a substantially lower value for D at 25°C than was observed, i.e., 94 instead of 101 days, and a substantially higher value at 15°C, 167 instead of 153 days. However, the impact of this difference on the final calculation of r is well within the error of measurement, as we will show.

The second parameter we have to know is the percentage of females in the adult population. There was no clear influence of temperature on p, measured as the percentage of females in the second generation, but it remains uncertain if this is true for the lower temperatures as well. In our calculations we used the average of all cultures, $p = 0.4$.

The last parameter required in the calculation of r is the number of eggs produced by a female. The rate of egg-production is a linear function of temperature: the number of eggs produced per day, N_e', measured by the increase of the number of eggs in the uterus, is given in Table 3. The regression of N_e' upon temperature is $N_e' = 0.083\ T - 0.315$. This equation predicts $N_e' = 0$ for $T =$ 3.7°C, which would be the temperature below which no reproduction occurs. The total number of eggs, N_e, produced by a female is also given in Table 3. There is a large variance in these data which might reflect variance in the culture conditions, some of which will be due to salinity differences. There is a clear sigmoid relationship with temperature, the total number of eggs reaches a plateau of 37 per female. The equation relating N_e and temperature is:

$$N_e = \frac{37}{1 + e^{2.345\ -\ 0.296\ T}}\ . \qquad (3)$$

As additional information, the number of eggs per egg-mass, N_e'', and the number of egg-masses deposited by a female are also given in Table 3. When eggs were deposited singly or in pairs they were assumed to belong to an egg-mass if they were laid on the same day. From Table 3 it is clear that there is no obvious influence of temperature on the number of eggs in an egg-mass but that the number of egg-masses produced by a female is lower at lower temperatures; the relationship is not linear, and not valid at higher temperatures where there appears to be no influence of temperature.

The intrinsic rate of natural increase, $r = 1/D \ln pN_e$ can now be calculated as a function of temperature from Eqs. (2) and (3) and the constant value $p = 0.4$ as:

$$r = \frac{1}{3530\ T^{-1.127}} \ln \frac{14.8}{1 + e^{2.345\ -\ 0.296\ T}}\ . \qquad (4)$$

Values from r, as calculated from Eq. (4), are given in Table 4. It is clear that the relationship between reproductive potential and temperature is nearly

Table 4. *Oncholaimus oxyuris*. Values of intrinsic rate of natural increase, r, as calculated from Eq. (4), and corresponding doubling times, t_2, at 5 different temperatures

	Temperature				
	5°C	10°C	15°C	20°C	25°C
r per day	0.0026	0.0086	0.0154	0.0220	0.0286
t_2 (days)	267	81	45	32	24

linear. When considered as such, the following regression is obtained:

$$r = 0.0013, T - 0.0042. \tag{5}$$

Two values are of particular interest: for T = 11.2°C, the mean annual temperature of the habitat, r = 0.0104, corresponding with a doubling time of 67 days. For r = 0, T = 3.2, and this is close to the value obtained from the rate of egg-production.

In order to estimate the error introduced by assuming a power relationship between D and T valid over the whole temperature range, we calculated the regression between r and T, calculating r from the observed values of D at the three highest temperatures and the calculated values at 5° and 10°C. This regression is $r = 0.0013\ T - 0.0035$, yielding an expected value of r = 0.0106 per day at the annual average temperature of T = 11.2°C. This is nearly the same value as obtained from Eq. (5). Although there is a slowing down of development rate at lower temperatures relative to the power relationship, its magnitude is too small to require more complicated empirical relationships describing the dependence of generation time on temperature.

A rough estimate of annual production is possible by observing that the $P{:}B$ ratio for a population with continuous exponential growth equals the exponential growth rate, G, independent of the mortality model (Allen, 1971). With a stable age distribution $G \approx r$, and assuming the production of one generation annually, $P{:}B \approx rD = 2.4$. This is the potential value; actual values will be considerably less. These have to be deduced from information on *Oncholaimus oxyuris* populations in the field combined with the values obtained in this study.

Discussion

The large predatory nematode *Oncholaimus oxyuris* has a long life cycle relative to its weight (3.5 µg dry weight for an average adult). The reproductive potential is low, and a yearly average of r = 0.0104 per day, corresponding with a doubling time of t_2 = 67 days, has been found. The generation time at the annual average temperature is 232 days, and we may conclude that the *O. oxyuris* population inhabiting this shallow brackish-water pond produces only one generation annually. With continuous reproduction, the average annual temperature required to produce two generations would be 13.9°C.

There are only few studies on the influence of temperature on life cycles of marine nematodes (Tietjen *et al.*, 1970; Gerlach and Schrage, 1971, 1972; Tietjen and Lee, 1972, 1977; Hopper *et al.*, 1973), and all of these clearly demonstrate the importance of this environmental factor. We can compare our values of D with those obtained by Gerlach and Schrage (1972) for *Oncholaimus brachycercus* from Helgoland: this species requires 399 days to complete its life cycle at 7°C. At this temperature, the generation time calculated from Eq. (2) would be 394 days for *O. oxyuris*, which is in very good agreement. Details of the development of *O. brachycercus* are also quite similar to what we observed for *O. oxyuris*, e.g. the relatively long duration of maturation. On the other hand, Hopper *et al.* (1973), studying *Oncholaimus* sp. from decaying mangrove leaves in Florida, found a generation time of only 39 days at 21°C and 86 days at 18°C; the corresponding times for *O. oxyuris* at these temperatures would be 114 and 136 days, i.e., much longer.

Tietjen and Lee (1972) measured the influence of salinity on generation time of the salt-marsh species *Monhystera denticulata*. In this species, the generation time was 11 days at 25°C and 26‰ S, but 20 days at 25°C and 13‰ S and 17 days at 25°C and 39‰ S. At lower temperatures, the influence of salinity was also large: at 15°C the generation time was 18 days at 26‰ S, but 36 days at 13‰ S and 34 days at 39‰ S. The influence of salinity seemed to disappear at 5°C. This pronounced effect of salinity was not investigated in our study, but salinity in our cultures fluctuated only between 18 and 23‰ S, and the additional variance due to salinity differences will be small compared with the variance due to temperature differences. Tietjen and Lee (1972) observed no difference in the number of eggs produced by *M. denticulata* at 15° and 25°C, but this number was lower at 5°C, exactly as we found for *Oncholaimus oxyuris*. Survival and sex-ratio did not change with temperature.

There is only one other study on the reproductive potential of marine nematodes. Tietjen and Lee (1977) reported on the influence of temperature and salinity on the reproductive potential of

Chromadorina germanica. At 26‰ S the mean value of *r* for *C. germanica* over a 20°to 30°C temperature span was 0.12 per day; values from field populations of the closely related *C. macrolaimoides* were of the same magnitude and amounted to 0.15 per day. Both species reproduce rather rapidly and have more than 10 generations per year. Their reproductive potential is about five times higher than what we calculated for *Oncholaimus oxyuris* at these high temperatures.

Low Reproductive Rate of Meiofauna

The values of the intrinsic rate of natural increase found in this study are of general importance for several reasons. Fenchel (1974) studied the relationship between *r* and body weight and calculated three different linear equations with the same slope but with different intercepts for unicellular organisms, heterothermic metazoans and homoiothermic metazoans. For heterothermic metazoans the equation is $\log r = -1.6391 - 0.2738 \log W$, in which *r* is per day and *W* is the wet weight in g. An average value for the wet weight of an adult *Oncholaimus oxyuris* is 20 µg and, from this and Fenchel's equation, we would predict $r = 0.444$ per day; this is about forty times higher than the mean annual value actually found, and still fifteen times higher than the maximum value at the highest temperature. Although Fenchel (1974) gives some arguments why his regression equations would yield maximum values rather than average values for all species, it is clear that the large deviation reflects some real difference between the reproductive rate of this nematode and similarly sized heterothermic animals. In fact, the reproductive rate of *O. oxyuris* would be typical for an animal having a weight of 28 g! Whether lowered reproductive rates are typical of nematodes or even meiofauna in general is unclear at the moment, although some of the available evidence seems indeed to indicate this (Gerlach, 1971). Values of *r* for two harpacticoid copepods (Heip and Smol, 1976) are also lower than would be predicated from Fenchel's equation, but the difference is not as large as in the case of *O. oxyuris*. For the epibenthic harpacticoid *Tachidius discipes* the mean annual reproductive potential is $r = 0.098$ per day instead of the expected 0.537 per day assuming a wet weight of 10 µg; this is somewhat five times less. However, the appropriate value to compare with might be the maximum value in the case of *T. discipes*, as this species is not present during the whole year and only reproduces in late spring and early summer when water temperatures are higher. For $T = 20°C$, $r = 0.186$ per day in this species, i.e., about three times less than would be expected from body weight. The difference for *Paronychocamptus nanus*, another harpacticoid copepod, must be larger as this species has a smaller body weight and a smaller reproductive potential than *T. discipes*. These values at least suggest that meiofauna might reproduce slower than other similarly sized animals.

Dominance of Males

There is a second interesting feature in the life cycle of *Oncholaimus oxyuris* which has been discussed by Heip (1977): the sex-ratio in this species is in favor of males, both in culture conditions and in the field (where the dominance of males is even more pronounced, probably because males live longer). This is hard to explain, because natural selection would either produce equal sex-ratios or a predominance of females (Fisher, 1930); to our knowledge there is no model accounting for this unusual sex-ratio in favor of males (although in view of the current explosion in genecological models this might be remedied soon). Whatever the explanation, the consequences of this phenomenon for the population are clear: it can maintain a high density and yet lower its reproductive potential considerably. As *O. oxyuris* is a top predator in this community, yet at times the dominating nematode both in numbers and biomass, it appears that this community can only exist when a very low turnover of the predator is accompanied by a very high turnover of the prey populations. This could explain the enormous differences which exist in the generation times of marine nematodes which range from 2 days to more than 1 year. Moreover, a heavy predator pressure such as this should allow for a high diversity of the prey community (Paine, 1966), and the very high diversity of nematode guilds is a by now well established fact (Ott, 1972; Heip and Decraemer, 1974; Juario, 1975; De Bovée, 1975, and others).

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