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A COMPARATIVE STUDY OF THE LIFE STRATEGIES OF TWO BACTERIAL-FEEDING NEMATODES UNDER LABORATORY CONDITIONS. I. INFLUENCE OF CULTURE CONDITIONS ON SELECTED LIFE-HISTORY PARAMETERS OF *ACROBELOIDES NANUS* (DE MAN 1880) ANDERSON 1968 AND *DOLICHORHABDITIS DOLICHURA* (SCHNEIDER 1866) ANDRÁSSY 1983

ABSTRACT: Selected life-history parameters like age of maturity, fecundity, egg development time, pattern of growth and reproduction, longevity and intrinsic rate of natural increase (*r*) were compared for two bacterial-feeding nematode species in xenic (with a several bacterial species as food) and monoxenic (with a bacteria *Sporosarcina* sp. as a food organism) agar cultures at 20° C.

There were pronounced differences in the life-history patterns of the two species in both types of culture conditions. *D. dolichura* showed a higher growth and development rate than *A. nanus*. *D. dolichura* had a shorter pre-reproductive period, a shorter reproductive period but more intensive pattern of reproduction, a shorter total life span and a considerably greater *r* than *A. nanus*.

The differences in life-history traits of the two nematode species were discussed with reference to their adaptive significance for habitat properties. While *D. dolichura* represents short-lived habitats with temporarily high food supply, *A. nanus* can be found in habitats of various food abundance.

KEY WORDS: Life strategy, life-history parameters, bacterial-feeding nematodes, food conditions

1. INTRODUCTION

Life strategy of any particular species represents a compromise allocation of limited resources among different life-history traits. During the last three decades life-history parameters are broadly discussed with reference to their adaptive significance for various habitat properties (Stearns 1976, 1992, Calow 1977, Townsend and Calow 1981, Roff 1992). Life strategy theory is helpful in understanding the action of the natural selection as an optimising process leading to the evolution of the best possible traits (Stearns 1976, 1992).

Nematodes are a particularly good subject for comparative studies of life-history strategy because of their considerable ecological diversity. An expression of that diversity are diversified food preferences of nematodes. Bacterial-feeding nematodes considered in this study are among the primary grazers of bacteria in soil and thus they play an important role in processes of decomposition and mineralisation (Trofymow and Coleman 1982, Yeates and Coleman 1982, Ingham *et al.* 1985, Soh-

lenius *et al.* 1987, 1988, Griffiths 1989, 1990, 1994, Bouwman *et al.* 1993).

There are several laboratory experiments in which the effect of food conditions on different life history, energetic and population parameters of some bacterial-feeding species were studied (Sohlenius 1968, 1969a, 1969b, Yeates 1970, Popovici 1972, 1973, Sohlenius 1973a, b, c, Schiemer *et al.* 1980, Schiemer 1982a, b, Venette and Ferris 1998). The comparison of the results of these studies meets some difficulties because those experiments were conducted in different conditions (different bacteria species were used as a food; different densities of food were applied and/or different way of measurements was used). Furthermore, very rarely in those works the individual growth was associated with the growth of the whole population. That is why, until now there is only few information (Anderson and Coleman 1981, Schiemer 1983, Woombs and Laybourn-Parry 1984, 1985, Venette and Ferris 1998) on similarities and/or differences in life strategies of different bacterial-feeding species.

Thus, only experiments conducting under the same laboratory conditions allow us to get some comparable data concerning life strategy of chosen nematode species.

The aim of this work was to compare selected life-history traits of two bacterial-feeding nematodes *Acrobeloides nanus* (de Man 1880) Anderson 1968 (from the family Cephalobidae) and *Dolichorhabditis dolichura* (Schneider 1866) Andrássy 1983 (from the family Rhabditidae) in xenic and monoxenic agar cultures.

2. MATERIALS AND METHODS

2.1. BIOLOGY AND ECOLOGY OF THE EXPERIMENTAL ANIMALS

A. nanus is a cosmopolitan species, very common in soils but with distinct preferences to the plant rhizosphere (Ingham *et al.* 1985, Brussaard *et al.* 1990, Griffiths *et al.* 1991, 1992). It is a partenogenetic species (Goodey 1963, Anderson 1968). So far, *A. nanus* was the main subject in several laboratory studies (Anderson 1968, Popovici 1973, Sohlenius 1973a, 1973b, Wasilewska *et al.* 1975, Bird and Ryder 1993, Bird *et al.* 1993).

D. dolichura occurs in habitats with extremely high bacterial activity and high rate of decomposition and mineralization, for example in decayed parts of plants, in musty wood, in manure and earthworm casts (Janik 1962, Kozłowska 1962, Goodey 1963, Andrássy 1983). *D. dolichura* is a bisexual species and there are only a few studies until now in which that species has been investigated (Cayrol and Dreyfus 1975, Poinar and Hansen 1983).

2.2. EXTRACTION AND CULTURING OF *A. NANUS* AND *D. DOLICHURA*

Both species were extracted from the garden soil using the modified method of Baermann (Flegg and Hooper 1970).

A. nanus and *D. dolichura* were reared in Petri dishes with 2% bactoagar "Difco" using the method of Kozłowska and Mianowska (1971). An adaptation to laboratory conditions was obtained by rearing several successive progenies of each species. The experiments were carried out in xenic (with mixed unidentified bacteria as food) and monoxenic (with a bacteria *Sporosarcina* sp. as a food organism) agar cultures in the darkness at 20 ± 1°C.

2.3. EXPERIMENTAL DESIGN IN XENIC CULTURES

The nematode life cycle was studied when females were individually cultured on small glass dishes with 2 ml of 1% sterile nutrient agar "Difco". Each dish was placed into Petri plate to avoid evaporation. To be sure that the females used in the experiments were approximately of the same age, several reproducing females were taken from the stock cultures, put into sterile water for two hours and were allowed to lay eggs. It was assumed that the females developed from those eggs belonged to the same age cohort. The females were transferred (with a fine needle) daily until dead to new dishes leaving the eggs on the old ones and allowing them further development. All eggs, juvenile and adults were counted. In this way the progeny of 22 *A. nanus* females (i.e. about 3280 individuals) and 15 *D. dolichura* females (about 4200 individuals) were analysed.

To estimate individual production values of the studied species an additional experiment was conducted in which the growth of 10 females from each species was observed.

Every day about 15–20 individuals were taken and their length and width were measured under the microscope. Estimations of body weight started after the egg hatching and finished when the maximal size of individuals was reached. For calculating the nematode weight the method of Andrássy (1956) was used

$$w = \frac{W^2 \times L}{16 \times 10^5} \quad (1)$$

where:

w – body weight in μg fresh weight ,

W – body width in μm,

L – body length in μm.

Values of total production were estimated as summed values for body growth and egg production. The equation formula of Petrusewicz (1967) was used in the calculations:

$$P = P_g + P_r, \quad (2)$$

Where:

P – total production,

P_g – production derived from the body growth,

P_r – production derived from the reproduction.

The weight of newly laid eggs was defined in the same way as in Klekowski *et al.* 1974 i.e. using the formula for the volume of an ellipsoid and according to Andrássy (1956) assuming a specific gravity of 1.084.

Production values were converted to energy units assuming dry weight to be 20% of fresh weight (Yeates 1979) and 1 mg dry weight to represent 23 J (Nicholas and Stewart 1978).

On the basis of the data concerning the survival of eggs and juveniles as well as the fecundity of females life tables of the two species were constructed (Ilieva-Makulec 1997). Using the data included in those tables and taking into account general considerations outlined by several authors (Stearns 1976, 1992, Pianka 1981, Singh and Sharma 1995, Krebs 1997) R_0, T, r were calculated, where:

R_0 – the net reproductive rate i.e. the total reproduction of an average female during her lifetime

$$R_0 = \sum_{\alpha}^{\omega} m_x \, l_x \quad (3)$$

where:

x – age of individuals in days

l_x – age specific survival – the proportion of individuals still alive at age x

m_x – age specific fecundity – mean number of female offspring produced per female in the age interval (x),

α – the age at which females start egg production (age at maturity),

ω – the age at which females finish reproduction.

T – mean generation time i.e. the average age in days at which females lay their eggs

An approximate estimation of T was obtained by the equation:

$$T \approx \sum_{\alpha}^{\omega} x l_x m_x \, / R_0 \quad (4)$$

r – intrinsic rate of natural increase (Malthusian parameter) – a measure of population growth rate for a population with a stable age-distribution and growing exponentially in non-limiting conditions.

For an initial estimate of r the following equation was used:

$$r \approx \log_e R_0/T \quad (5)$$

The exact value of r was obtained by solving the equation of Lotka-Euler by iteration, using the initial estimate of r as a starting value:

$$1 = \sum e^{-rx} l_x m_x \quad (6)$$

Then the exact value of T was calculated according to:

$$T \approx \log_e R_0/r \quad (7)$$

Two other parameters were also calculated:

λ – finite capacity for increase – it shows how many times the population increases per unit time

$$\lambda = \text{antilog}_e r \quad (8)$$

DT – doubling time – time taken by a species to double its population

$$DT = \log_e 2/r \quad (9)$$

2.4. EXPERIMENTAL DESIGN IN MONOXENIC CULTURES

For surface sterilisation of nematodes a mixture of two antibiotics penicillin and

streptomycin (25 mg ml^{-1} of each antibiotic) was applied.

Bacteria *Sporosarcina* sp. used as a food organism in the experiments were isolated from the stock nematode cultures. It is a Gram-positive, motile, strictly aerobic, 1.2–2.5 μm in size (Claus and Fahmy 1986). Bacterial densities were measured photometrically at 595 nm (Schiemer 1982a).

Experimental females were taken from monoxenic cultures with an initial level of *Sporosarcina* sp. of 8 10^8 colony-forming-units (cfu) ml^{-1} and left for two hours in sterile water to lay eggs. Then the eggs were put into glass dishes with 2 ml agar-bacteria mixture with 0.6% agar (without nutrients in order to stop bacterial growth) and a density of *Sporosarcina* sp. 8 10^8 cfu ml^{-1}. The nematodes were transferred (with a fine needle) (every three days before maturing and daily after that) until dead to new dishes (with the agar-bacteria mixture of the above density) leaving the eggs on the old ones and allowing them further development. All eggs, juvenile and adults were counted. In this way, the same life-history parameters as in the xenic experiment were analysed for the offspring of 18 *A. nanus* females (about 940 ind.) and 19 *D. dolichura* females (about 760 ind.).

2.5. STATISTICAL ANALYSIS

Student t-test was applied to test significance of differences between means of all studied life-history parameters.

3. RESULTS

3.1. FECUNDITY, EGG DEVELOPMENT TIME, AGE AND SIZE AT MATURITY, PATTERNS OF GROWTH, REPRODUCTION AND SURVIVAL

Both species had a greater fecundity in xenic compared to monoxenic cultures (Table 1).

In xenic cultures *D. dolichura* females produced two times more eggs than females of *A. nanus* about 280 and 149, respectively. In monoxenic cultures the two species had a similar total fecundity (Table 1).

It was found that the egg development time of both studied species did not depend on culture conditions. In both, xenic and monoxenic cultures the eggs of *A. nanus* hatched slower (in 3 days after they were laid) than the eggs of *D. dolichura* (just next day after they were laid) (Table 1).

The proportion of survived eggs was higher in monoxenic cultures than in xenic and it was characteristic for the two species (Table 1).

In xenic cultures the proportion of survived eggs was higher for *A.nanus*, whereas in monoxenic cultures – for *D. dolichura* (Table 1).

When juveniles of *A. nanus* were taken into consideration, it was found that they survived better in xenic than in monoxenic cultures. Juveniles of *D. dolichura* found better conditions for surviving in monoxenic than in xenic cultures (Table 1).

The comparison of the two species revealed that in xenic cultures the proportion of juveniles survived was higher for *A. nanus*, whereas in monoxenic cultures – for *D. dolichura* (Table 1).

Irrespective of culture conditions, *A. nanus* had an age at maturity of 11 days. *D. dolichura* matured only 5 days after eggs were laid in xenic cultures, but that species needed 3 days more for maturing in monoxenic cultures (Table 1).

In both types of culture conditions juveniles of *D. dolichura* developed faster and matured significantly earlier than those of *A. nanus* (Table 1).

The period of egg production for the both species was longer in xenic cultures than in monoxenic (Table 1).

In both cultures *A. nanus* females laid eggs for a longer period than those of *D. dolichura* (Table 1).

The ratio of duration of the pre-reproductive to the reproductive period was 1:2 in *A. nanus* and 1:3.4 in *D. dolichura* xenic cultures. In monoxenic conditions that ratio was lower 1:1.5 and 1:1 for *A. nanus* and *D. dolichura*, respectively. So, *D. dolichura* spent relatively more time for reproduction in xenic conditions, whereas the opposite situation was observed in monoxenic cultures.

In xenic cultures reproductive effort of *A. nanus* females was distributed in a more or less uniform way in the course of the whole reproductive period (Fig. 1A). The reproductive curve of that species was more extended and showed some fluctuations. Under the same culture conditions *D. dolichura* attained a maximal egg reproduction 6 days after the beginning of the reproductive period (Fig. 1A).

Table 1. Life history traits (mean ±S.D.) of *A.nanus* and *D.dolichura* in xenic and monoxenic cultures. Minimal and maximal values are given in brackets

Traits	Xenic cultures (X)			Monoxenic cultures (M)			*A.n*	*D.d*
	A. nanus	*P*	*D. dolichura*	*A. nanus*	*P*	*D. dolichura*	X/M	X/M
Fecundity (eggs female^{-1})	149±93.38 (3–316)	**	280±167.30 (26–583)	52±27.52 (11–113)	n.s.	40±15.99 (16–76)	***	***
Egg development time (days)	3	*	1	3	*	1	n.s.	n.s.
Survival of eggs (%)	84.25±10.88 (65.63–100.00)	**	76.03±2.16 (75.74–76.92)	89.82±2.25 (83.33–96.10)	***	92.33±1.01 (90.63–94.44)	*	***
Survival of juveniles (%)	92.91±6.05 (80.00–100.00)	***	80.49±1.29 (75.78–81.29)	75.37±2.16 (70.00–80.00)	*	98.21±1.77 (94.12–100.00)	***	***
Age at maturity (days)	11.45±0.92 (10–14)	*	5.17±0.63 (4–8)	10.57±1.68 (8–12)	**	7.58±2.09 (5–12)	n.s.	***
Reproductive period (days)	23±12.44 (1–38)	n.s.	17±7.41 (3–25)	16±4.36 (3–21)	***	9±3.24 (2–13)	*	***
Rate of reproduction (eggs female^{-1} day^{-1})	6.1±1.67 (2.4–8.1)	**	13.9±6.67 (2.9–25.3)	2.7±1.70 (0.6–6.0)	n.s.	2.6±1.69 (0.7–7.0)	***	***
Post reproductive period (days)	1.41±1.05 (0–5)	*	3.47±4.22 (1–14)	2.94±2.82 (1–12)	*	6.63±5.05 (1–18)	***	***
Total life span (days)	35±12.88 (12–50)	*	25±9.14 (9–44)	30±4.67 (15–35)	**	24±4.90 (11–32)	n.s.	n.s.

Significant differences :* – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$; n.s. – non significant

In monoxenic cultures *A. nanus* females laid the highest number of eggs 6 days after the beginning of the reproduction. In the case of *D. dolichura*, the rate of reproduction was the highest immediately after the onset of reproduction (Fig. 1B).

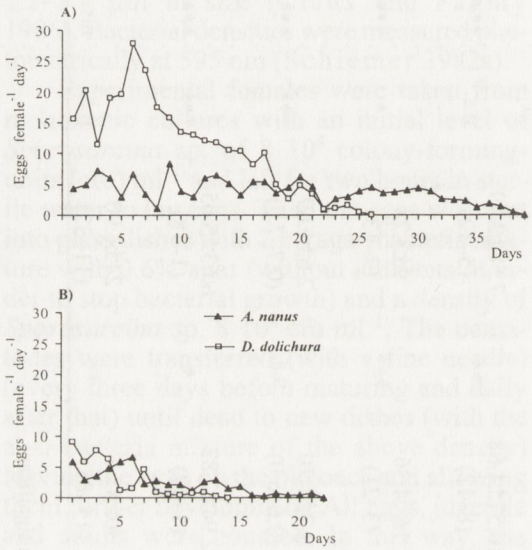

Fig. 1. Egg production of *A. nanus* and *D. dolichura* in xenic (A) and monoxenic (B) agar cultures

The comparison of cumulated egg production also showed a distinct delay in reproductive effort in *A. nanus*. In both types of cultures *D. dolichura* produced 50% of the total number of eggs about two times faster than *A. nanus* (Fig. 2A, B)

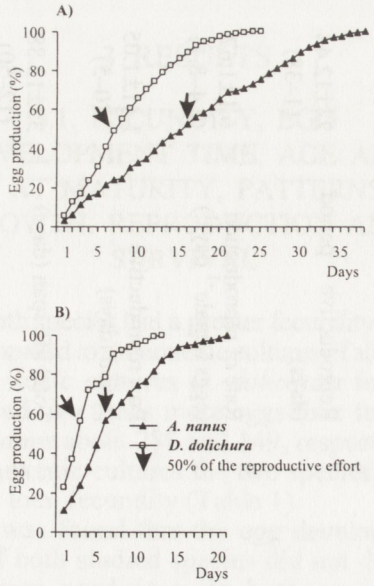

Fig. 2. Cumulated egg production of *A. nanus* and *D. dolichura* in xenic (A) and monoxenic (B) cultures

The number of eggs produced per day by females of both studied species was higher in xenic than in monoxenic cultures (Table 1).

In xenic cultures *D. dolichura* showed higher rate of egg production than *A. nanus*. In monoxenic cultures the number of eggs laid daily by *A. nanus* and *D. dolichura* was similar (Table 1).

It was found that the post reproductive period of both species in xenic was shorter than in monoxenic cultures (Table 1).

In both, xenic and monoxenic cultures *A. nanus* females died in a shorter period after the egg laying was finished than females of *D. dolichura* (Table 1).

The total longevity of studied nematodes did not depend on the type of a culture (Table 1). *A. nanus* lived longer (30–35 days) than *D. dolichura* (24–25 days) under both culture conditions (Table 1).

Figure 3 shows that the pattern of survival of the studied species was similar under both culture conditions. In both species in their monoxenic cultures a high rate of surviving was observed for a longer period than in xenic cultures. In monoxenic cultures when the last *A. nanus* female finished the egg production activity, about 50% of total number of females were still alive. At the same time in xenic cultures only 13% alive females were noticed. In the case of *D. dolichura*, 71 and 33 % alive females were found at the end of reproduction in monoxenic and xenic cultures, respectively (Fig. 3A, B).

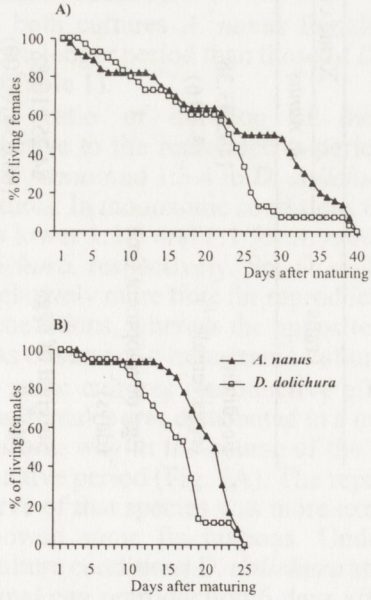

Fig. 3. Survivorship curves of *A. nanus* and *D. dolichura* females in xenic (A) and monoxenic (B) cultures

In xenic cultures *A. nanus* spent in reproduction about 58% of its total life span and almost 96% of its time as an adult, whereas for *D. dolichura* the same parameters had following values – 64 and 85 %, respectively.

In monoxenic cultures values of the above parameters were lower – for the *A. nanus* 53 and 84% and for *D. dolichura* 38 and 56%.

3.2. POPULATION GROWTH PARAMETERS

In both types of cultures generation time for *A. nanus* was longer than that for *D. dolichura* (Table 2). Culture conditions had no effect on the *A. nanus* intrinsic rate of natural increase and the *r* values for that species were similar in xenic and monoxenic cultures – 0.26 ind^{-1}. d^{-1} and 0.23 $ind.^{-1}$ d^{-1}, respectively (Table 2). *D. dolichura* had higher values of *r* in xenic (0.62 $ind.^{-1}$ d^{-1}) than in monoxenic cultures (0.36 $ind.^{-1}$ d^{-1}) (Table 2).

The finite rate of natural increase indicated that *D. dolichura* population would multiply 1.86 or 1.44 times per day and it would take about 1 or 2 days to double the population, respectively in xenic and monoxenic cultures (Table 2). *A. nanus* population would multiply slower than *D. dolichura*, about 1.30 times per day and it would take 3 days for that species to double the population in both types of cultures (Table 2).

3.3. INDIVIDUAL GROWTH PARAMETERS

The two species have 6 development stages: eggs, four juvenile stages: J1, J2, J3, J4 and an adult form. In the course of growth four moultings were observed. The high rate of growth of the two species at 20° C and the way of observation (in 24 hours intervals) did not allow for observation of the exact moments of the successive moultings. In both types of cultures the studied species continued their growth for some time even after they have matured (Fig. 4).

In both, xenic and monoxenic cultures, the mean body weight of *A. nanus* increased 9 times in the course of the growth from newly hatched juveniles to matured adults (Fig. 4A, B). The body weight of matured *D. dolichura* was 19 and 21 times higher then the weight of J1 in xenic and monoxenic cultures respectively (Fig. 4A, B). If we take into account also the fact that *D. dolichura* matured faster, the above results showed the higher growth rate of that species in comparison to *A. nanus* in both cultures. In xenic cultures, for example, the growth rate of *A. nanus* was 0.03 μg f.w. day^{-1} (in the period from J1 to a matured adult). That value was only 19.7% of the daily growth rate of *D. dolichura* (0.152 μg f.w. day^{-1}) (Fig. 4A).

In monoxenic cultures the both species grew slowly. Growth rate of *A. nanus* was 0.023 μg f.w. day^{-1} and that was about 31% of the growth rate of *D. dolichura* (0.075 μg f.w. day^{-1}) (Fig. 4B).

Table 2. Population growth parameters of *A. nanus* and *D. dolichura* in xenic and monoxenic agar cultures

Parameter	Xenic cultures		Monoxenic cultures	
	A. nanus	*D. dolichura*	*A. nanus*	*D. dolichura*
Net reproductive rate (R_0) (number of females produced in each generation)	116.78	171.53	35.29	36.3
Intrinsic rate of natural increase (r $ind.^{-1}$ day^{-1})	0.259	0.622	0.234	0.363
Mean generation time (T) (average age in days at which females lay their eggs)	18.4	8.3	15.2	9.9
Finite rate of natural increase (λ) (days)	1.295	1.863	1.264	1.438
Doubling time (DT) (days)	2.681	1.114	2.962	1.909

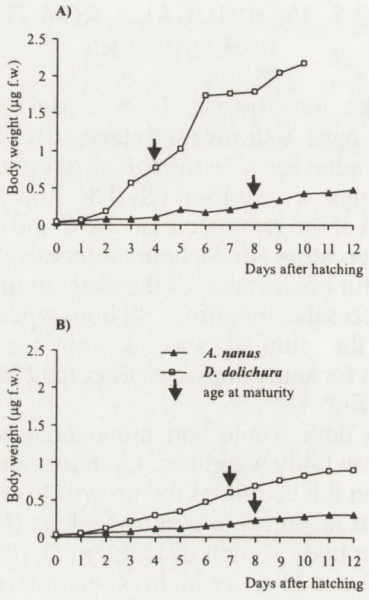

Fig. 4. Individual growth curves of *A. nanus* and *D. dolichura* in xenic (A) and monoxenic (B) cultures

It was interesting to find out that the both species started to reproduce at a lower mean body weight in monoxenic than in xenic cultures (for *A. nanus* 0.230 and 0.270 µg and for *D. dolichura* 0.600 and 0.760 µg) (Fig. 4).

It was found that the weight of eggs of both studied species did not depend on culture conditions (Table 3). In both cultures, eggs of *D. dolichura* were heavier than the eggs of *A. nanus*.

Juveniles (J1+J2) and J3 of *A. nanus* had a similar body weight in both cultures ($P > 0.05$) (Table 3). Both, J4 and adults of *A. nanus* had significantly higher ($P < 0.05$) weight in xenic than in monoxenic (Table 3). In the case of *D. dolichura* the weight of juveniles did not depend on culture type and only adults *D. dolichura* were significantly heavier in xenic than in monoxenic cultures ($P < 0.05$) (Table 3).

The comparison of the two species showed that only their J1+J2 forms had a similar mean body weight. All other stages of *D. dolichura* were heavier in comparison to the same stages of *A. nanus* ($P < 0.05$) (Table 3).

3.4. INDIVIDUAL PRODUCTION CURVES

In both species a distinct increase in production rates was observed during the reproductive period (Figs 5 and 6). In both species, production values for the individuals of the same age were different in xenic and monoxenic cultures

Total production value of *A. nanus* and *D. dolichura* in monoxenic cultures represented only 42 and 22% respectively of their total production in xenic cultures. (Figs 5 and 6).

The comparison of the species showed that in xenic cultures total production of *A. nanus* presented only 25% of the production of *D. dolichura* whereas in monoxenic cultures the production of *A. nanus* was al-

Table 3. Body weight (µg f.w.) of all development stages (mean values ± S.D.) of *A. nanus* and *D. dolichura* in xenic and monoxenic cultures. Maximal and minimal values are given in brackets.

Development stage	Xenic cultures		Monoxenic cultures	
	A. nanus	*D. dolichura*	*A. nanus*	*D. dolichura*
Eggs	0.01±0.001	0.02±0.004	0.01±0.001	0.02±0.002
Juveniles J1 + J2	0.060±0.02 (0.02–0.09)	0.053±0.02 (0.02–0.10)	0.050±0.02 (0.01–0.08)	0.039±0.02 (0.01–0.09)
J3	0.125±0.02 (0.10–0.16)	0.186±0.04 (0.11–0.27)	0.116±0.02 (0.09–0.14)	0.158±0.06 (0.10–0.25)
J4	0.201±0.02 (0.17–0.23)	0.395±0.08 (0.28–0.65)	0.165±0.01 (0.15–0.18)	0.424±0.08 (0.30–0.53)
Adults	0.366±0.03 (0.25–0.61)	1.636±0.62 (0.75–3.56)	0.292±0.09 (0.19–0.51)	0.737±0.16 (0.56–1.12)

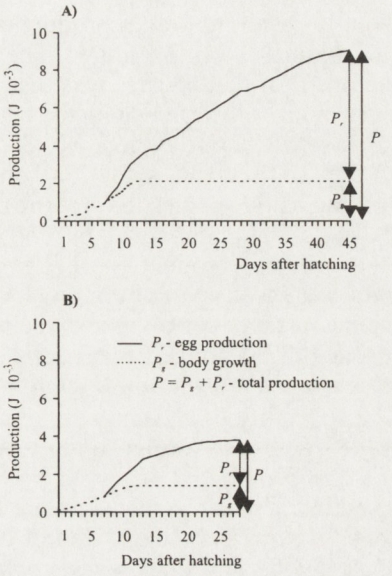

Fig. 5. Individual production curves (energy content) of *A. nanus* (from newly hatched juveniles till the end of reproduction) in xenic (A) and monoxenic agar cultures (B)

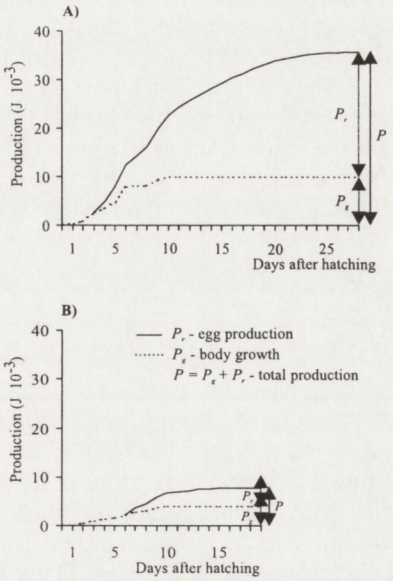

Fig. 6. Individual production curves (energy content) of *D. dolichura* (from newly hatched juveniles till the end of reproduction) in xenic (A) and monoxenic agar cultures (B)

most half (49%) of the production of *D. dolichura* (Figs 5 and 6).

The ratio of P_g (body growth) to P_r (egg production) in xenic cultures was 1 to 3.17 for *A. nanus* and 1 to 2.58 for *D. dolichura*, and in monoxenic cultures 1 to 1.68 for *A. nanus* and 1.12 to 1 for *D. dolichura* (Figs 5 and 6). Hence, the both species allocated more energy in production process (growth and reproductive investment) in xenic than in monoxenic cultures.In both cultures *A.nanus* was the species which allocated more energy in reproduction than *D. dolichura* (Figs 5 and 6)

4. DISCUSSION

The obtained results showed that *A. nanus* and *D. dolichura* responded to the culture conditions in which they were grown. Distinct differences in some life-history traits were observed. In monoxenic cultures (with only one bacterial species) both species grew more slowly and had an earlier reproduction effort, a shorter reproductive period and a lower rate of reproduction than in xenic cultures (a mixture of different bacterial species). In consequence, the total fecundity of studied species was significantly lower in monoxenic than in xenic conditions. Similar trend i. e. an decrease of the egg numbers with a decrease of food supply were observed by Sohlenius (1969a) in *Mesodiplogaster biformis* while Sohlenius (1973a) in *A. nanus* found that the total egg numbers did not depend on food conditions.

Both species started to reproduce at a lower mean body weight in monoxenic than in xenic cultures. Similar phenomena observed Schiemer *et al.* (1980) when they studied the growth rate of *Plectus palustris* at different food concentrations. So, not only the quantity of food but also food diversity (in the present study) can change evidently the growth and reproductive pattern of nematodes. According to Schiemer *et al.* (1980) the ability of *P. palustris* to produce smaller primiparous females at lower food densities is a strategy for shortening juvenile duration and cutting down the metabolic costs required to attain sexual maturity. It seems that such a strategy is particularly important for *D. dolichura* in monoxenic cultures where age at maturity of that species was significantly longer then in xenic cultures.

In xenic cultures both species had longer reproductive but shorter post reproductive period than in monoxenic cultures. This is in line with Parry's finding (1981) that high and low reproductive effort is correlated respectively, with high and low adult mortality rates. Similar relation between the above two processes observed Schiemer (1982b) in

Caenorhabditis briggsae and Schiemer *et al.* (1980) in *P. palustris*.

Some life-history parameters of *A. nanus* and *D. dolichura* such as egg weight, egg development time and total longevity did not depend on culture conditions and they had the same or similar values in both types of cultures. The same egg weight at different food densities was observed also in *P. palustris* by Schiemer *et al.* (1980), while eggs of *C. briggsae* grown at lower food densities were smaller than those grown at high densities (Schiemer 1982b). Similar to my species, the egg hatching time of *C. briggsae* (Schiemer 1982b) as well as the longevity of the species in that study and also in *P. palustris* (Schiemer *et al.* 1980) did not differ in cultures with different food concentrations. In the other study Sohlenius (1969a) found that *M. biformis* longevity was shorter when food supply decreased.

Apart from the high similarity in the reaction of both studied species to the change in food culture conditions, significant differences in the values of their life-history traits were found. In both types of cultures *D. dolichura* showed higher growth and development rate than *A. nanus*. *D. dolichura* had a shorter pre-reproductive period, shorter reproductive period but more intensive pattern of reproduction and a shorter total life span than *A. nanus*.

A comparison of nematode life-history data in the literature reveals that life-history pattern of *D. dolichura* in the present study is common among nematode species of families Rhabditidae and Diplogasteridae, while life cycle of *A. nanus* is similar to that of species of Cephalobidae and Panagrolaimidae.

Reproduction pattern of *D. dolichura* in both types of cultures with a fast increase, reaching the egg peak at the beggining of the reproductive period and a sharp decrease after the maximum was reported also for *M. biformis* (Sohlenius 1969a), *C. briggsae* (Zuckerman *et al.* 1971, Schiemer 1982b), *Mesodiplogaster lheritieri* (Anderson and Coleman 1981), *Diplogasteritus nudicapitatus*, *Paroigolaimella bernensis* and *Rhabditis curvicaudata* (Woombs and Laybourn-Parry 1984). That common feature in egg production i.e. a decrease in the egg numbers with the age of females Woombs and Laybourn-Parry (1984) explained by the death of reproductive cells in the older nematodes.

Totally different was reproduction pattern of *A. nanus* in xenic cultures. The reproduction effort of that species was distributed in a more or less uniform way in the course of the whole reproductive period. My data confirmed the Sohlenius's (1973a) observations on the same species. Schiemer *et al.* (1980) found that under constant food conditions the daily egg production of *P. palustris* gradually increased up to a maximal level and remained constant even up to six weeks. Mianowska (1976) noticed two peaks of egg production in *Panagrolaimus rigidus*.

The fecundity of *A. nanus* in xenic cultures (148 eggs) was similar to the fecundity of *P. rigidus* (154 eggs) observed by Greet (1978) and somewhat higher than the fecundity of *P. rigidus* (111 eggs) found by Mianowska (1976) and *Acrobeles complexus* (118 eggs) studied by Thomas (1965). In xenic cultures, *Cephalobus litoralis* (Saeed *et al.* 1988) had much higher number of eggs (200–300) than *A. nanus*.

The longevity of *A. nanus* in xenic cultures (35 days) was similar to that of *P. rigidus* (37.8 days) observed by Mianowska (1976) but much shorter than the longevity *A. complexus* (6 months) found by Thomas (1965).

The age at maturity of *A. nanus* (11 days) in my experiments was the same as the age at maturity of *Acrobeloides buetschlii* (Nicholas 1962) and similar to that of *P. rigidus* (14.6 days) in the study of Mianowska (1976).

My results are in line with Sohlenius's finding (1968, 1969a, b) that high growth and reproduction rate is characteristic for many species of Rhabditidae. For example, development time of *D. dolichura* in xenic cultures (5 days) was similar to that of *Rhabditis terricola*, *Diplogaster nudicapitatus* and *Pelodera teres* in the studies of Sohlenius. Venette and Ferris (1998) also found that species of Rhabditidae developed faster than nematodes from Cephalobidae.

The reproductive period of *D. dolichura* (17 days) in xenic cultures was longer than that period of *D. nudicapitatus* (13 days) and *R. curvicaudata* (7 days) (Woombs and Laybourn-Parry 1984). Fecundity of *D. dolichura* (280 eggs) was similar to the fecundity of *D. nudicapitatus* (243 eggs) but much higher than the fecundity of *R. curvicaudata* (113 eggs).

The longevity of *D. dolichura* (25 days) was evidently shorter than the total life span

of *Rhabditis oxycerca* (100–150 days) (Kämpfe and Schmidt 1966).

It seems interesting to compare life history traits of *A. nanus* and *D. dolichura* in the cultures with *Sporosarcina* sp. (monoxenic) with the data concerning the same or other closer nematode species but in the cultures with other bacterial species. As it is know from the literature (Sohlenius 1968, Cayrol and Dreyfus 1975, Wasilewska *et al.* 1975, Andrew and Nicholas 1976, Marinari, Palmisano and Turchetti 1976, Anderson and Coleman 1981, Grewal 1991) and as my preliminary results showed, not all bacteria species are a suitable food source for nematodes. Cayrol and Dreyfus (1975) found that each bacterial-feeding species is associated with a typical for it bacterial complex. Some bacteria provide the nematode with an abundant food and favour a fast development and dense populations ("favourable" bacteria). Others provide only a poor food and are not favourable for the nematode development ("tolerant" bacteria). Lastly, there are some "unfavourable" bacteria in the presence of which no nematode growth can be observed. These bacteria are unable to provide any nutritions factors and nematodes die in their presence.

A. nanus had the same age at maturity (11 days) in cultures with *Sporosarcina* sp. (in the present study) and with *Escherichia coli* (Sohlenius 1973a). The same development time for *Acrobeloides* sp. in cultures with *Pseudomonas cepacia* was noticed also by Anderson and Coleman (1981).

Fecundity of *A. nanus* in the present experiments was similar to fecundity of the same species grown on *E. coli* (Sohlenius 1973a) and to fecundity of *Acrobeloides* sp. grown on *P. cepacia* (Anderson and Coleman 1981). The length of reproductive period of *Acrobeloides* was the same in the cultures with *P. cepacia* and *Sporosarcina* sp. (16 days) and much shorter in cultures with *E. coli* (7 days).

A. nanus from the present monoxenic experiments had a shorter reproductive period, shorter longevity and lower fecundity in comparison with *Cephalobus persegnis* grown with *E. coli* (Popovici 1972).

Life-history parameters of *D. dolichura* (such as fecundity, age at maturity, length of the reproductive period and longevity) in cultures with the density of *Sporosarcina* sp. 810^8 cfu ml^{-1} was similar to the same parameters of *C. briggsae* grown at similar density of *E. coli* (Schiemer 1982b).

My results concerning fecundity of *D. dolichura* were in line with the results of Anderson and Coleman (1981) and Sohlenius (1969a) in their studies respectively on *M. lheritieri* grown with *P. cepacia* (47 eggs) and on *M. biformis* with *E. coli* (42 eggs). *D. dolichura* lived longer than *M. lheritieri* and *M. biformis* (respectively: 24, 11 and 8).

The intrinsic rate of natural increase (r) is a useful parameter for comparing reproductive capacities among different species and under different conditions (Singh and Sharma 1995). Furthermore the estimation of r allows a quantitative comparison of life strategy between species (Allan 1976). The comparison of my results with published by other authors estimates of r shows that species of Rhabditidae and Diplogasteridae have higher r than other bacterial-feeding nematodes. For example the values of r for *C. briggsae* (Schiemer 1982b), *Rhabditis marina* (Vranken and Heip 1983), *M. lheritieri* (Anderson and Coleman 1981) and *D. dolichura* in xenic and monoxenic cultures were respectively 1.14, 0.91, 0.88, 0.62 and 0.36 ind.$^{-1}$ day^{-1}.

Species of Cephalobidae and Plectidae have lower r – 0.34 ind.$^{-1}$ day^{-1} for *Acrobeloides* sp. (Anderson and Coleman 1981), 0.28 for *P. palustris* (Schiemer 1983), 0.14 for *Chiloplacus* (Procter 1984) and 0.26 and 0.23 for *A. nanus* in xenic and monoxenic cultures.

The obtained results are in agreement with life-history theory, that the age at maturity, length of reproductive period and the number of offspring have significant influence on r (Stearns 1976). The lower values of r estimated for *A. nanus* than those for *D. dolichura* in my experiments could be explained mainly by longer age at maturity of the former species.

The net reproductive rate and the intrinsic rate of natural increase are the most widely used fitness measures in life-history theory (Kozłowski 1993). The fact that values of r for *A. nanus* were similar in xenic and monoxenic cultures shows greater compensation of development of this species to food conditions than does *D. dolichura*. This compensation of *A. nanus* may be explained by the occurrence of the species in habitats different in regard to their food supply. *A. nanus* tolerates a wide range of food condi-

tions and can even occur in sites with very low bacterial densities (Sohlenius 1973b, 1993, Bååth *et al.* 1978). The reproductive strategy of *A. nanus* reveals its less habitat dependency. The delayed maturity and prolonged period of reproduction of *A. nanus* increase the probability for that species to live on until more favourable food conditions occur.

In the opposite, the distinct difference in the values of *r* for *D. dolichura* in both types of cultures reveals the lower adaptive capabilities of this species. Life-history traits of *D. dolichura* such as the fast growth and development, early reproduction effort and high fecundity can be related to the typical saprobic habitats in which dense populations of Rhabditidae species occur (Sohlenius 1969b, 1973c, Wasilewska 1974, Yeates 1981, Schiemer 1983, Kozłowska 1986, Dmowska and Kozłowska 1988, Weiss and Larink 1991, Ettema and Bongers 1993). So, the reproductive strategy of *D. dolichura* is directed to a fast utilization of temporarily favourable conditions of these habitats.

The obtained results show the pronounced differences in life-history parameters of the two studied bacterial-feeding nematodes *A. nanus* and *D. dolichura*. My data are in line with Bongers (1990), who categorised nematodes into five classes along a continuum from "colonizers" to "persisters" basing upon known and assumed life-history characteristics of nematodes. In his classification nematodes from Rhabditidae with distinct characteristics of *r*-strategists are assigned to class1 while Cephalobidae to class 2.

The observed differences in the life-history traits of *A. nanus* and *D. dolichura* will undoubtedly influence their population development and in consequence will define the role of the two nematode species in the soil ecosystem.

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5. SUMMARY

Bacterial-feeding nematodes considered in this study are among the primary grazers of bacteria in soil and thus they play an important role in processes of decomposition and mineralisation. There are several laboratory experiments in which the effect of food conditions on different life history, energetic and population parameters of some bacterial-feeding species were studied. The comparison of the results of these studies meets some difficulties because those experiments were conducted in different conditions (different bacteria species were used as a food; different densities of food were applied and/or different way of measurements was used). Furthermore, very rarely in those works the individual growth was associated with the growth of the whole population. That is why, until now there is only few information on similarities and/or differences in life strategies of different bacterial-feeding species.

Selected life-history parameters like age of maturity, fecundity, egg development time, pattern of growth and reproduction, longevity and intrinsic rate of natural increase (*r*) were compared for two bacterial-feeding nematode species *Acrobeloides nanus* (de Man 1880) Anderson 1968 (from the family Cephalobidae) and *Dolichorhabditis dolichura* (Schneider 1866) Andrássy 1983 (from the family Rhabditidae).

The experiments were carried out in xenic (with mixed unidentified bacteria as food) and monoxenic (with a bacteria *Sporosarcina* sp. as a food organism) agar cultures in the darkness at 20 ± 1°C.

The obtained results showed that *A. nanus* and *D. dolichura* responded to the culture conditions in which they were grown. In monoxenic cultures both species grew more slowly and had an earlier reproduction effort, a shorter reproductive period and a lower rate of reproduction than in xenic cultures (Table 1, Figs 1, 2, 4, 5 and 6). In consequence, the total fecundity of studied species was significantly lower in monoxenic than in xenic conditions (Table 1). Both species started to reproduce at a lower mean body weight in monoxenic than in xenic cultures (Fig. 4). That strategy for shortening juvenile duration and in that way cutting down the metabolic costs required to attain maturity was particularly important for *D. dolichura* in monoxenic cultures where age at maturity of that species was significantly longer then in xenic cultures. Some life-history parameters of *A. nanus* and *D. dolichura* such as egg weight, egg development time and total longevity did not depend on culture conditions and they had the same or similar values in both types of cultures (Tables 1 and 3, Fig. 3)

There were pronounced differences in the life-history patterns between the two species in both types of culture conditions. *D. dolichura* showed a higher growth and development rate than *A. nanus*. *D. dolichura* had a shorter pre-reproductive period, a shorter reproductive period but more intensive pattern of reproduction, a shorter total life span and a considerably greater *r* than *A. nanus* (Tables 1 and 2, Figs 1–6).

Life-history traits of *D. dolichura* such as the fast growth and development, early reproduction effort and high fecundity can be related to the typical saprobic habitats in which dense populations of

Rhabditidae species occur. So, the reproductive strategy of *D. dolichura* is directed to a fast utilization of temporarily favourable conditions of these habitats.

In the opposite the reproductive strategy of *A. nanus* reveals its less habitat dependency. It is known that *A. nanus* tolerates a wide range of food conditions and can even occur in sites with very low bacterial densities. The delayed maturity and prolonged period of reproduction of *A. nanus* increase the probability for thist species to live on until more favourable food conditions occur.

The obtained results show the pronounced differences in life-history parameters of the two studied bacterial-feeding nematodes *A. nanus* and *D. dolichura*. My data are in line with Bongers (1990), who categorised nematodes into five classes along a continuum from "colonizers" to "persisters" basing upon known and assumed life-history characteristics of nematodes. In his classification nematodes from Rhabditidae with distinct characteristics of *r*-strategists are assigned to class1 while Cephalobidae to class 2.

The observed differences in the life-history traits of *A. nanus* and *D. dolichura* will undoubtedly influence their population development and in consequence will define the role of the two nematode species in the soil ecosystem.

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