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Food Dependence and Energetics of Freeliving Nematodes

II. Life History Parameters of *Caenorhabditis briggsae* (Nematoda) at Different Levels of Food Supply

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Summary. The food dependence of larval duration, fecundity and the intrinsic rate of natural increase follow a hyperbolic form, which can for the former be described by the Michaelis-Menten function.

Maximal larval duration at 20° C is 62 h, maximal fecundity is 153 eggs per female and r_{max} is 1.136 per day. The lower food threshold is 10^8 *E. coli* cells·ml^{-1} (=0.06 mg dry weight·ml^{-1}) for larval growth and $2 \cdot 10^8$ cells·ml^{-1} for reproduction and "r". 50% of maximal performances (K_s) are attained at $5 \cdot 10^8$ and $7.5 \cdot 10^8$ cells·ml^{-1} respectively.

Reproductive effort at dense food is highest immediately after maturation (e.g. 50% of the total eggs produced by a female are laid within 2 days after onset of egg production). At lower food densities the reproductive effort is delayed.

Larval mortality increases strongly below 10^9 cells·ml^{-1}.

The results reported sofar were obtained with *E. coli* cells which were harvested at the phase of decreasing population growth in batch cultures. With cells from the exponential and the stationary phase, performances are increased and decreased respectively. This is partly due to differences in bacterial biomass per unit cell, partly an expression of the change of nutritive value of bacterial cells with growth phases.

Introduction

Caenorhabditis briggsae has been widely used during the last thirty years for many types of biological research, e.g. for axenic cultivation, biochemical requirements, aging processes, behaviour a.o. (see Zuckerman 1980). In the present paper *C. briggsae* serves as a model for the effects of food concentrations on the life history and population parameters.

There is currently considerable discussion on the form and magnitude of temperature versus food dependence of population dynamics of invertebrates in the field. While temperature effects have been analysed in detail in many organisms, the influence of food concentration on larval developmental rates, mortality and reproductive patterns have so far received less attention.

The aim of the present study is to define the critical and optimal ranges of food supply, to clarify the limitations and the potential zones of occurrence of a saprophagous rhabditid in sediments of different trophic conditions and to quantify the effects of food availability on different life history and demographic parameters.

Methods

Preparation of Food Medium

A detailed description of the techniques employed for culturing *Caenorhabditis briggsae* at different concentrations of bacterial food has been given in the first part of this series of papers (Schiemer 1982a): The food medium – a sloppy agar-bacteria mixture – was prepared with 0.4% agar (without nutrients) and known densities of *E. coli* cells. The bacterial density was assessed photometrically. The bacterial cells were harvested by centrifugation and resuspended in the 0.4% agar by means of a manual glass homogenizer. The food medium prepared in this way ranged from $5 \cdot 10^7$ to $5 \cdot 10^{10}$ bacterial cells ml^{-1}. At higher bacterial densities (e.g. 10^{11} cells ml^{-1}) the mixtures became very patchy. Additionally, the medium at such concentrations is too opaque to allow observations on the developmental stage or egg numbers of the animals.

Size, weight and the nutritional state of bacterial cells change considerably during the population growth in batch cultures. Therefore, cells for preparing the food medium were harvested within a narrow range of bacterial population density. Most experiments on larval duration, reproductive pattern etc. were carried out with cells harvested at the end of the exponential growth phase, at cell densities of $1.3–1.6 \cdot 10^9$ cells·ml^{-1}. Additionally, a series of experiments on larval durations was carried out using *E. coli* cell harvested at two other phases of batch culture growth (see Fig. 3a and Table 2). Food concentrations are further referred to only as numbers in square brackets, e.g. [10^{10}].

Determination of the Dry Weight of E. coli Cells

Dry weight of *E. coli* cells was determined for different phases of the batch culture. Five ml portions of bacterial cultures were repeatedly washed by centrifugation and resuspension in distilled water. The final suspension was filtered through 0.2 µm Millipore filters and dried at 60° C to constant weight.

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Experimental Design for Determining Life History Parameters and Reproduction of C. briggsae

For the analysis of life history parameters at different food densities, animals of known age were obtained by transferring a number of reproducing females to a Nigon/2 solution and allowing them to lay eggs for a period of 1–2 h. Approximately 50 eggs were then transferred in drops of food medium of known bacterial density. These drops of a volume of 20–50 µl were kept on microscopic slides in wet chambers. The food medium in these experiments was renewed every second day (see Schiemer et al. 1980). The experimental population was controlled under the stereomicroscope at least once a day, but more frequently during the phase of maturation. Mortality and the onset of maturation within the population were recorded. The beginning of maturity was determined by the formation of the first egg – which could be easily observed as darkening of parts of the ovary under the stereomicroscope.

Before onset of reproduction a number of animals were transferred into new food medium of the same concentration and kept individually throughout the reproductive period. After maturation females were transferred daily into new food medium. The number of eggs produced during the foregoing 24 h period could be determined from the old food drops. This procedure permitted examination of the egg production rates throughout the reproductive phase of single animals. The females were observed individually until their death in order to obtain a complete set of data on life expectancy and mortality pattern at different food levels.

The transfer of eggs and hatched animals was performed with capillary "breaking" pipettes as used in the Cartesian diver technique (see Klekowski 1971).

All the experiments were carried out at 20° C ± 0.2° C.

Results

Duration of Different Developmental Stages of C. briggsae at Different Levels of Food Supply

The *egg development time* of the species at 20° C is 13 h, and is independent of the food condition at which the egg-producing females were grown. However, the development time of deposited eggs is variable due to the fact that embryonic development can occur within the oviduct. The time an egg spends there depends on the egg production rates of the female, e.g. females with high rates retain the eggs for shorter periods and thus egg development time appears to be prolonged and vice versa. In a few cases hatching of eggs within the oviduct of the mother, e.g. viviparity, was observed. The eggs of intensively reproducing females are usually laid in the 1- or 2-cell stage.

Larval duration is highly dependent on the food conditions at which animals are grown. The experiments were designed to test both the effect of cell density and the effect of the nutritive value of *E. coli* cells harvested at different growth phases of batch cultures. At bacterial densities of $[5 \cdot 10^8]$ and below, growth is usually retarded in a part of the experimental populations. In such a case animals can continue to live for several days but die before attaining maturity. At $[2 \cdot 10^8]$ the percentage of such animals is high and at $[10^8]$ only sundry individuals reach the reproductive phase. Because of this higher larval mortality at lower food

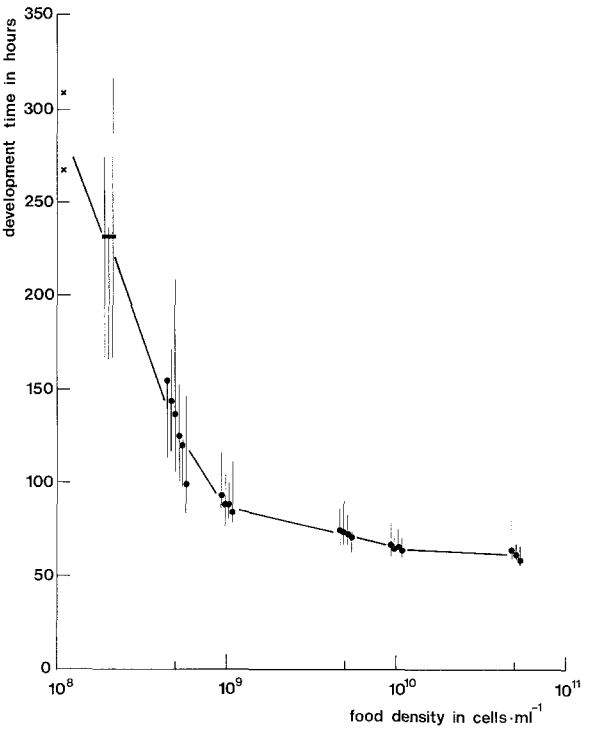

Fig. 1. Relationship between larval development time and food concentration. Bacteria used as food were harvested at the end of the expontial growth phase of batch cultures (see Fig. 3a). Full circles represent the mean, the vertical bars the range in larval development time of groups of 20–100 nematodes. In experiments where beginning or end of maturation within such groups were not exactly determined the vertical bars are omittted. For $[2 \cdot 10^8]$ the average larval duration was calculated from values of individual animals (horizontal bar). Asteriscs indicate the larval duration of sundry individuals reaching maturity at $[10^8]$

concentrations the "mean" larval duration within individual experiments is difficult to define. For higher food concentrations, from $[5 \cdot 10^8]$ upwards, it was taken as the period at which 50% of the surviving population had started reproduction. For $[2 \cdot 10^8]$ the mean larval duration was calculated on the basis of individual duration times. Figure 1 and Table 1 summarize the results of experiments with bacterial cells which had been harvested at the end of the exponential growth phase of batch cultures (see Fig. 3 and Table 2). Over a gradient of food densities ranging from $[2 \cdot 10^8]$ to $[5 \cdot 10^{10}]$ cells $\cdot$ ml^{-1} the mean larval duration decreases from 232.5 to 62.2 hours. Figure 1 demonstrates that the strongest dependence occurs at low densities above the limiting level ($[10^8]$). The relationship between food concentration and the larval development rate, expressed as the inverse value of larval duration ($d = 1/D$), is adequately described by the Michaelis-Menten equation

$$d = d_{max} \cdot S/K_s + S$$

where d, d_{max} = actual and maximal development rate; S = food concentration; K_s = food concentration at the development rate $d_{max}/2$.

The good fit of the Michaelis-Menten function (see Fig. 2) is confirmed by the linearity of the relationship between the inverted values of food concentrations ($1/S$) and the larval development rate ($1/d = D$). The regression coefficient of the linear regression is 0.9678 ($n = 22$). The parameters of the Michaelis-Menten curve can be determined from

Table 1. Influence of food density on life history parameters of C. briggsae at 20° C. The total life span as calculated for low food densities (in brackets) is not including the mortality during the larval phase

	Food density in bacterial cells · ml^{-1}					
	2.10^8	5.10^8	10^9	5.10^9	10^{10}	5.10^{10}
Generation time (egg to egg) in hours	245.5	143.0	100.7	87.0	78.8	75.2
Larval development time in hours	232.5	130.0	87.7	74.0	65.8	62.2
Reproductive period in days (±SD)	4.4 (±2.7)	8.7 (±2.5)	10.3 (±2.0)	7.4 (±1.3)	8.4 (±2.1)	6.4 (±1.0)
Postreproductive period in days (±SD)	3.0 (±1.1)	2.7 (±1.6)	2.4 (±1.9)	–	4.2 (±3.1)	4.8 (±3.8)
Total life span in days	(17.6)	(17.4)	16.9	–	15.9	14.3
Fecundity, eggs per female (±SD)	13.1 (±16.2)	50.1 (±25.5)	83.1 (±32.8)	133.5 (±20.4)	144.7 (±17.6)	153.4 (±21.9)

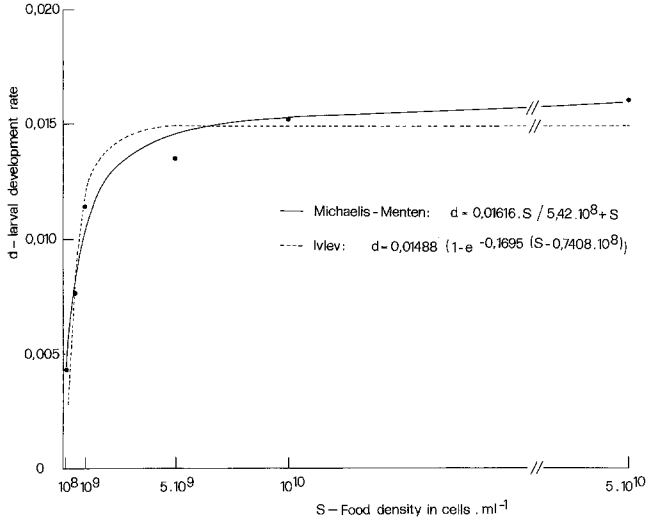

Fig. 2. Relationship between food concentration and larval development rates. The curves represent the Michaelis-Menten and Ivlev functions fitted to the data

this regression as

$$d_{max} = 0.01616$$
$$K = 5.42 \cdot 10^8.$$

The d_{max} of 0.01616 refers to a minimal larval duration of 61.9 hours which is only slightly below the minimal actual value attained, 62.2 h at $[5 \cdot 10^{10}]$. It is of interest to note that with decreasing food concentration the variability in larval duration increases distinctly. This holds good for the range of individual larval durations in single experiments as well as for the variation of mean larval durations in replicate experiments. The latter is associated with the technical problems in preparing the same quality food for replicate experiments in respect to bacterial numbers and their physiological conditions.

It is well established that bacterial cells change in size, chemical composition and membrane thickness during the population growth of batch cultures, and thus may differ in their nutritive value for bacterivorous species. To test this influence, the *E. coli* cells used for preparing the food medium were harvested at three growth stages (see Fig. 3A and Table 2). Larval duration are distinctly shorter using cells from the exponential growth phase than with cells from the intermediate or stationary phase. For example, at a food concentration of $[10^9]$ larval duration was 74 h, 87 h and 127 h respectively. The corresponding K_s-values are $2.8 \cdot 10^8$, $5.4 \cdot 10^8$ and $6.5 \cdot 10^8$ cells · ml^{-1}.

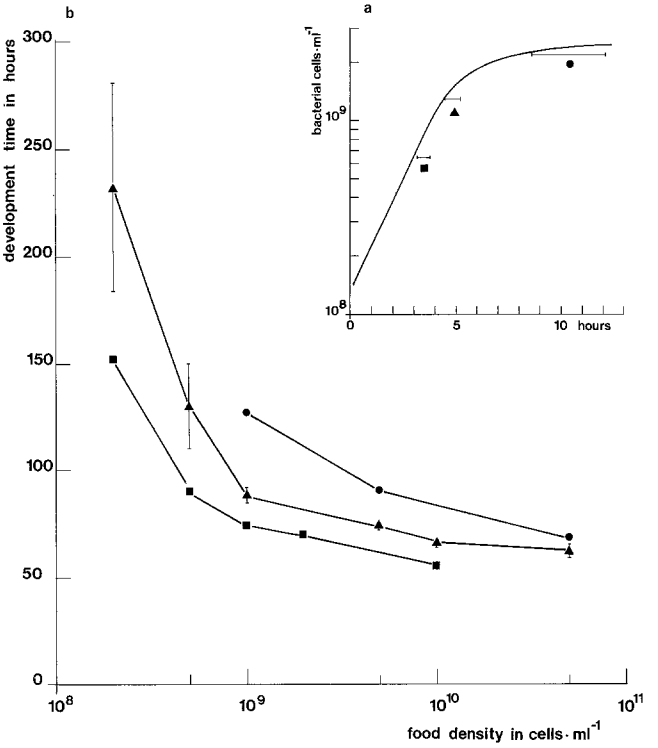

Fig. 3. a Population growth curve of *E. coli* in batch cultures grown at 30° C. The three growth phases at which cells were harvested as food are indicated by horizontal bars. The symbols refer to Fig. 3b. **b** Relationship between average larval development time and food concentration using *E. coli* cells harvested at three different growth phases (see Fig. 3a). Vertical bars = standard deviations of the mean duration in a series of experiments

Table 2. Cell weights of Escherichia coli obtained at different growth phases of batch cultures (population densities in bacterial cells · ml^{-1}). See Fig. 3A

		g dry weight · cell^{-1}
Exponential phase	($9.2 \cdot 10^8$ cells/ml)	8.65 (±0.68 S.C.) · 10^{-13}
Intermediate phase	($1.4 \cdot 10^9$ cells/ml)	6.06 (±0.71 S.D.) · 10^{-13}
Stationary phase	($2.2 \cdot 10^9$ cells/ml)	5.43 (±0.88 S.D.) · 10^{-13}

The number of replicate experiments with food cells from the exponential and stationary stage was too small for a good resolution of the maximal larval development rate to be obtained from a Michaelis-Menten function. These differences are to some extent an expression of decreasing

cell weights in the course of the bacterial growth phase (Table 2). To outrule this effect, the food densities can be expressed as bacterial biomass. This procedure reduces the differences especially between the exponential and the intermediary phase. However, a distinct difference in larval duration remains for the various food types, showing that the nutritive value of *E. coli* per unit weight diminishes with the age of the cells (e.g. a larval development time of roughly 100 hours is achieved at a density of $[5 \cdot 10^8]$, $[10^9]$ and $[5 \cdot 10^9]$ of food of decreasing quality. In terms of biomass this densities represent 0.4, 0.6 and 2.7 mg dry weight ml^{-1} respectively).

The *duration of the reproductive phase* is restricted to a period of maximally 15 days. At high food densities, most of the eggs are laid shortly after maturation and reproduction ceases within 8–10 days. At lower food levels fecundity is lower but the reproductive phase is slightly more extended.

After cessation of egg production, females continue to live for a few days before they die. At high food concentration ($[10^{10}]$, $[5 \cdot 10^{10}]$) this postreproductive phase extends on an average for 4–5 days (range 0–8 days), at lower food densities only for 2–3 days. This shorter postreproductive phase coincides with the slightly prolonged reproductive period (see above).

The *total life span* is similar at all food concentrations. The mean life expectancy ranges from 14–17 days at the different food densities. The data given in Table 1 indicate a slightly decreasing life expectancy with increasing food density. The differences are, however, statistically not significant.

The Effect of Food Density on the Reproduction Pattern and the Total Fecundity

Figure 4 shows the reproductive pattern at different food densities. At high food concentrations, maximal numbers of eggs are laid during the first three days after onset of reproduction, with a peak occurring at the second day. After this initial phase of high fecundity, egg production decreases abruptly. At lower food levels the reproductive curve is flatter and more extended. This change in pattern is further evaluated in Fig. 5, where cumulated egg production versus time is expressed in percentages of total fecundity. This comparison of the time pattern independent of absolute differences in fecundity, shows a distinct delay in reproductive effort (Christiansen and Fenchel 1977) at lower food densities. For example, at $[5 \cdot 10^{10}]$, over 50% of the reproductive effort of a female occur during the first two days after maturation, while at lower food densities $[10^9]$ 50% of total fecundity is attained only after 4 days. At food densities of $[5 \cdot 10^8]$ and below the average reproductive pattern is greatly influenced by mortality (see below) and is difficulat to compare in this respect. The shift in reproductive effort is of significance for population growth rates since the impact of reproduction at an earlier stage of maturity is stronger than at a later stage (e.g. Cole 1954).

The relationship between total fecundity and food density in the medium is similar to that obtained for larval developmental rates (Fig. 6). The lowest food density at which reproduction was observed was $[2 \cdot 10^8]$. The mean fecundity was 13.1 eggs (range 0–62, $n=11$) per female.

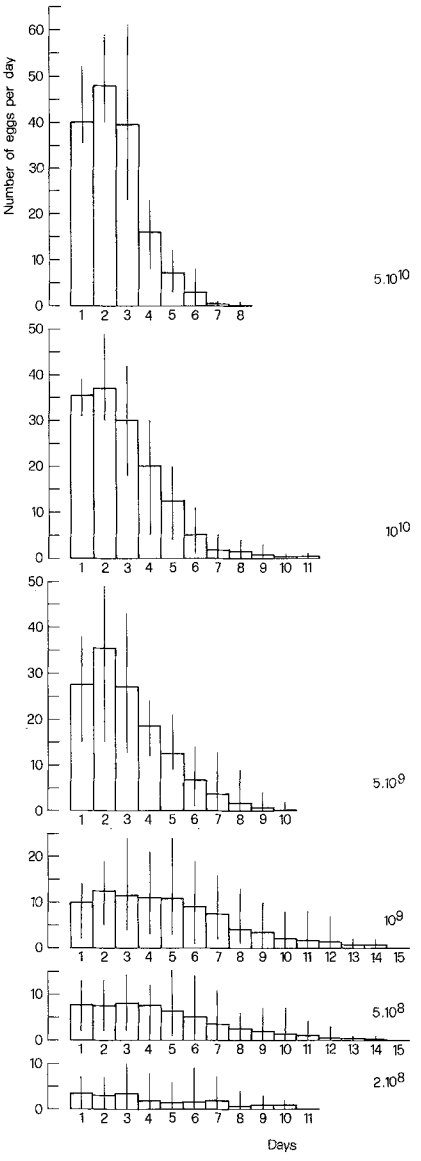

Fig. 4. Reproductive pattern at different food concentrations. Daily egg production from maturation to the end of the reproductive phase. Means (columns) and range (vertical bars) of 10–18 individually cultured females

Maximal fecundity ($\bar{x}=153$, range = 122–187, $n=14$) was obtained at $[5 \cdot 10^{10}]$.

Mortality

Egg mortality under the experimental conditions described is practically zero. Larval mortality shows a distinct pattern of food dependency (Fig. 7): At food densities of $[10^9]$ and above larval mortality approaches zero. Losses which occurred in the larval stage are considered to have been the result of experimental handling. Below $[10^9]$ mortality rates increased drastically with increasing food density and approaches 100% at $[10^8]$. Adult mortality: Survivorship curves of adults at different food densities (Fig. 8) are based on 15–17 animals; $[10^9]$ is representative for survivorship at higher food densities; mortality is low throughout the whole reproductive phase and increases strongly thereafter. At lower food densities survivorship curves decline more gradually from the beginning of the reproductive phase.

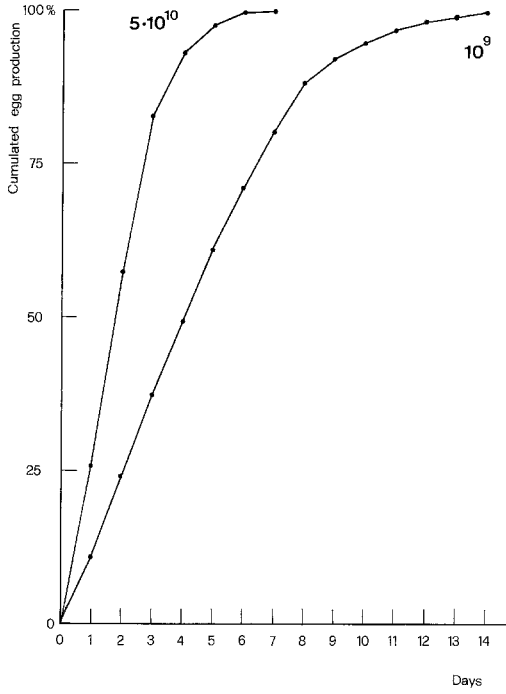

Fig. 5. Reproductive pattern at two food concentrations expressed in a cumulative form

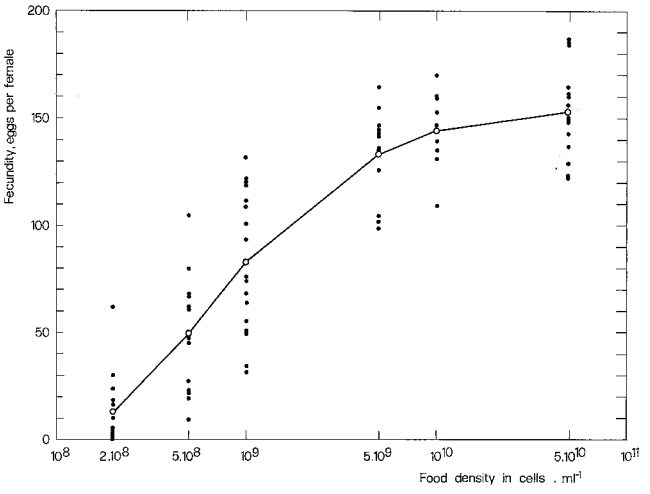

Fig. 6. Total fecundity of females cultured at different food concentrations. Values for individual females (full circles) and arithmetic means (open circles)

In respect to the population growth rates it is of significance that at high food densities ($>10^9$) mortality rates are high only after the termination of the reproductive phase.

Population Parameters

Life history tables including the "age specific survivorship" ("l_x") and the age specific fecundity ("b_x") (see Table 3) can be used for a calculation of the "intrinsic rate of natural increase" ("r"), the net reproductive rate (the total reproduction of an average female during her lifetime; $R_0 = \Sigma l_x \cdot b_x$) and the "mean generation time" ("T", the average age in days at which females lay their eggs).

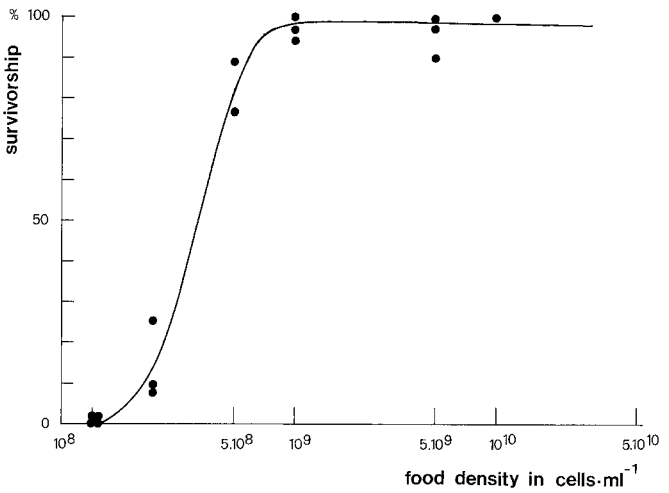

Fig. 7. Survivorship during the larval period at different food concentrations

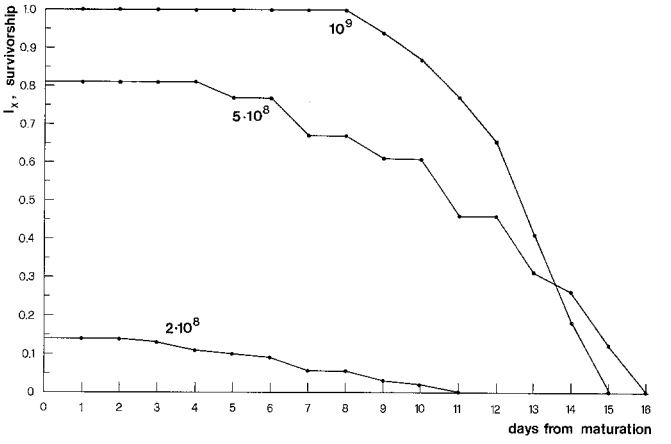

Fig. 8. Survivorship curves of females cultured at different food concentrations from maturation onward

An initial estimate of "r" is obtained by the equation:

$r = \ln R_0/T$

where "T" is approximated by

$T = \Sigma x \cdot l_x \cdot b_x / R_0$ (x = age in days).

The exact value of "r" is obtained by solving the equation

$1 = \Sigma e^{-rx} \cdot l_x b_x \cdot dx$

by iteration, using the initial estimate of "r" as starting value. The general considerations on which the calculations of population parameters are based, have been outlined by Andrawartha and Birch 1954: Slobodkin 1963; Pianka 1974; Ricklefs 1973 a.o.

The results of these computations are given in Table 4. The relationships between food concentration and "r" resembles that between food dependency of larval development rates and total fecundity. Threshold food concentrations are between [10^8] and [$2 \cdot 10^8$] (Fig. 9). Starting with a single mature female the "r" values obtained imply a theoretical population increase ($N_t = N_0 e^{rt}$) during a period of 10 days to 1.6 at [$2 \cdot 10^8$], 685 at [10^9], 35,000 at [10^{10}] and 86,000 at [$5 \cdot 10^{10}$]. The "r" values obtained at high bacterial densities (e.g. "r" = 1.136 at [$5 \cdot 10^{10}$]) are among the highest recorded for animals of this size range.

Table 3. Life table data (b_x = fecundity – number of eggs per female per day; l_x = survivorship) at different food densities (bacterial cells · ml^{-1}). The duration of the prereproductive period (in days) is given in brackets. Age in days from maturation onward

Age in days	$2 \cdot 10^8$ (10.2)		$5 \cdot 10^8$ (6.0)		10^9 (4.2)		$5 \cdot 10^9$ (3.6)		10^{10} (3.3)		$5 \cdot 10^{10}$ (3.1)	
	b_x	l_x	b_x	l_x	b_x	l_x	b_x	l_x	b_x	l_x	b_x	l_x
Prerepr. period	0	0.14	0	0.82	0	1.0	0	1.0	0	1.0	0	1.0
1	3.3	0.14	7.7	0.82	10.1	1.0	27.5	1.0	35.4	1.0	39.9	1.0
2	2.9	0.13	7.6	0.82	12.3	1.0	35.5	1.0	36.9	1.0	47.9	1.0
3	2.3	0.11	8.1	0.82	11.5	1.0	26.9	1.0	30.0	1.0	39.4	1.0
4	1.7	0.10	7.4	0.82	10.9	1.0	18.5	1.0	20.2	1.0	15.9	1.0
5	1.4	0.09	6.3	0.77	10.8	1.0	12.5	1.0	12.5	1.0	7.2	1.0
6	1.6	0.06	5.1	0.77	8.9	1.0	6.7	1.0	5.2	1.0	2.8	1.0
7	1.8	0.06	3.5	0.67	7.6	1.0	3.7	0.92	1.7	1.0	0.4	0.93
8	0.7	0.03	2.5	0.67	7.8	1.0	1.7	0.92	1.4	1.0	0.1	0.86
9	1.0	0.03	1.9	0.61	3.5	0.94	0.8	0.92	0.8	1.0	0	0.8
10	1.0	0.02	1.2	0.61	2.2	0.82	0.2	0.92	0.4	0.9	0	–
11	0	0	0.9	0.46	1.8	0.76	0	–	0.4	0.8	0	–
12			0.3	0.46	1.4	0.65	0	–	0	0.4	0	–
13			0.3	0.31	0.7	0.41	0	–	0	0.4		
14			0.2	0.26	0.7	0.18			0	0.2		
15			0	0.13	0	0			0	0		
16			0	0								

Table 4. Relationship between population parameters R_0, T, "r" (see text) and food concentration (in cells · ml^{-1})

	$2 \cdot 10^8$	$5 \cdot 10^8$	10^9	$5 \cdot 10^9$	10^{10}	$5 \cdot 10^{10}$
R_0	1.8	40.4	87.7	133.5	144.8	153.6
T	12.78	8.58	6.85	5.21	4.76	4.43
"r"	0.048	0.431	0.653	0.939	1.046	1.136

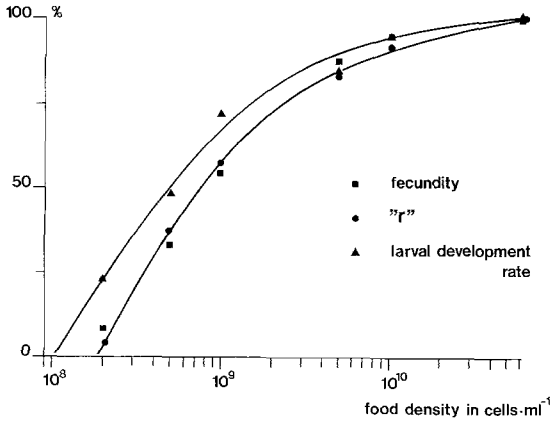

Fig. 9. Food dependence of larval development rate, fecundity and "r", expressed in percent of the maximal performances

Discussion

Food supply is a key factor for determining species associations, production and decomposition processes in benthic environments. The present paper attempts to analyse the effect of food supply on life history and population parameters for a representative species of saprophagous nematodes. Besides ciliates, these play an important role in regulating bacterial processes in situations of organic enrichment as well in terrestrial as in aquatic ecosystems. The present paper concentrates on two relevant aspects,

a) the pattern of food dependence on different life history and population parameters, and

b) the threshold value for the species in respect to food supply.

Strong responses to food supply are expressed in life history parameters linked with production processes. The food dependence of the larval development rate ($1/D$), the fecundity per female and the "intrinsic rate of natural increase" are compared in Fig. 9 by transforming all curves to a percentage scale with the maximal values taken as 100%. This comparison demonstrates the hyperbolic nature of all 3 curves, with the strongest dependence in all cases at bacterial densities between 10^8 and 10^9 ml^{-1}. It was found that parameters linked directly to production processes, like larval development rate, reproduction rate and growth rate (see Schiemer 1982a) can be adequately described by the Michaelis-Menten function. For life history and population parameters of a compound nature, like fecundity (which includes a timing process) and "r" (which includes fecundity, generation time and mortality), the Michaelis-Menten function appears to be inadequate, despite a similar shape of the curve. The model has been successfully applied to describe the relationship of food supply and population growth patterns in microorganisms (see Caperon 1967) and ciliates (e.g. Proper and Garver 1966; Hamilton and Preslan 1970; Curds 1975; and Taylor 1978) and the larval duration in *Daphnia* (Hrbáčková and Hrbáček 1978).

Besides the overall similarity in the form of the relationship, there are distinct differences between larval development and adult reproduction both in the threshold and the K_s (i.e. the food density at which 50% of the maximal performance is achieved). K_s for the larval developmental rates was found to be $5.4 \cdot 10^8$ cells ml^{-1} while for fecundity and "r" the K_s lie between $8–9 \cdot 10^8$ cells ml^{-1}. A similar

shift occurs in the food threshold, given by the intercept of the curves in Fig. 19 with the x-axis: 10^8 cells ml^{-1} (0.06 mg bacterial dry weight ml^{-1}) for larval development and $2 \cdot 10^8$ cells ml^{-1} (0.12 mg d.wt.) for reproduction and "r". Higher thresholds and K_s-values of reproducing females compared to the larvae are of interest both from a bioenergetic and an ecological point of view. The higher threshold values in the reproductive phase are in contrast to the distinctly higher maximal assimilation rates per unit weight achieved during the egg production phase (Schiemer 1982a). The lower weight specific respiration rates during the reproductive phase and lack of difference in the mode of feeding between larvae and adults suggests that the displacement to higher thresholds may result from reduced assimilation performances of reproducing females at lower food availability. This reduced assimilation may be due to specific trophic requirements.

Both Lampert (1977) and Vidal (1980) observed a similar phenomenon, namely a shift in food threshold with increasing body size in herbivorous zooplankton species. This indicates that increasing food requirements during the course of the life cycle are of a more general nature and thus would merit a more detailed physiological analysis of their causes.

The observed pattern may, however, also be of adaptive significance: It indicates a strategy exposing the reproductive stages to higher risks, in terms of food supply, than the larval stages. The fact that reproduction occurs only at higher food concentrations than larvae can grow, can be interpreted as mechanism to minimize the risks for descendants, the eggs being laid only in situations of ample food supply. In combination with a short prereproductive phase the adaptive advantage of this characteristic may be high, particularly in unpredictable environments. A comparison of the food dependence of larval duration rates and larval mortality shows the proximity of the critical food concentrations for both processes. 50% larval survivorship occurs at a food concentration of approximately $3.5 \cdot 10^8$ cells ml^{-1} compared to the K_s of $5.2 \cdot 10^8$ for the larval development rate. *C. briggsae* could thus be termed a "reckless producer" (see Calow 1978) whose storage capacity for reserve material is likely to be low. This hypothesis also agrees with strong starvation effects on the respiratory metabolism (Schiemer 1982a).

The food threshold, as discussed above, is an ecologically important parameter, indicating its trophic limitations of a species. According to the experimental data no population growth can be expected below a bacterial density of $2 \cdot 10^8$ cells ml^{-1} (or 0.13 mg dwt ml^{-1}). These data confirm the result of a tentative analysis by Nicholas et al. (1973), who found low reproduction at $6.3 \cdot 10^8$ cells ml^{-1} and no population growth at $6.7 \cdot 10^7$ cells ml^{-1}. In comparing these experimentally obtained threshold values with food concentrations in the field, it has to be borne in mind that the nutritive value per unit cell under field conditions is probably lower. Our results give conclusive evidence that the trophic value per cell and per unit biomass are dependent highly on the growth phase of the bacterial cell. Assuming that bacteria in natural sediments are in a mixed state with respect to their nutritive condition and their age, thresholds in terms of bacterial biomass will be even higher than those experimentally determined.

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