Nematologica 29 (1983): 468-477, E. J. Brill, Leiden

CALCULATION OF THE INTRINSIC RATE OF NATURAL INCREASE, r_m, WITH *RHABDITIS MARINA* BASTIAN 1865 (NEMATODA)

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The life-cycle of *Rhabditis marina* Bastian 1865 was studied at 25°C and $20^0/_{00}$ salinity. The following demographic parameters were computed from life-table data: the intrinsic rate of natural increase $(r_m) = 0.914$ day; net reproductivity $(R_o) = 400$; minimum generation time $(T_{min}) = 4.5$ days; cohort generation time $(T_c) = 7.2$ days; mean generation time $(T) = 6.6$ days; and the age of an adult female when a median egg is deposited $(\underline{T}) = 6.1$ days. Several approximate equations used to estimate r_m were compared with these life-table calculations. Some give erroneous estimations and should be used with extreme caution. For iteroparous organisms (including most free-living nematodes), T_{min} only gives an indication of the development time and is therefore unsuitable for describing 'mean generation time'.

Key words: life-table, net reproductivity, development time, generation time, life cycles.

Rhabditis marina Bastian 1865 is a cosmopolitan species that is both euryhaline and eurythermal (Tietjen *et al.*, 1970; Hopper *et al.*, 1973). It has been collected in great numbers from seaweeds stranded between tides in the upper littoral zone (Inglis and Coles, 1961; Sudhaus, 1974) and from decaying mangrove leaves (Hopper *et al.*, 1973). Sudhaus (1974) illustrates its distribution in Europe, differentiating northern and southern subspecies. Feeding of this species has been studied, both gnotobiotically (Tietjen *et al.*, 1970; Tietjen and Lee, 1977a) and axenically (Tietjen and Lee, 1975). Although *R. marina* has been studied very intensively, no life table data are available.

This paper discusses the instrinsic rate of natural increase 'r_m' as originally defined by Lotka for a population with a stable age-distribution and growing in an unlimited environment. It is calculated from:

$$\sum_{x=0}^{\text{max age}} e^{-r_m x}\, l_x m_x = 1 \qquad (1)$$

requiring knowledge of age-specific survival (l_x) and age-specific fecundity (m_x). Traditionally these are summarized in life tables (see Mertz (1970) and Southwood (1978) for a lucid discussion of concepts). However, some confusion has arisen about r_m because many authors (Tietjen and Lee, 1977b; Alongi and Tietjen, 1980; Romeyn *et al.*, 1983) use r_m as the actual rate of increase in any environment whether or not the population has a stable age distribution:

$$dN/dt = r_m N \qquad (2)$$

where t is time and N the number of individuals. In the following we shall use r_m as the increase defined by equation (1).

Several approximate methods for the calculation of r_m have been used:

a. The capacity of increase (Laughlin, 1965):

$$r_c = (\ln R_0)/T_c \qquad (3)$$

where R_0 is the net reproductivity,

$$R_0 = \sum_{x=0}^{\text{max age}} l_x m_x \qquad (4)$$

$$T_c = (1/R_0) \sum_{x=0}^{\text{max age}} x l_x m_x \qquad (5)$$

b. the formulae used by Heip *et al.* (1978) for the predatory nematode *Oncholaimus oxyuris*:

$$r_m = (1/T_{min}) \ln (p\, N_e) \qquad (6)$$

where T_{min} is the minimum generation time (= time between two identical stages of successive generations), p the proportion of females in the adult population and N_e the *total* number of eggs produced by an average female (fertility);

c. the estimations used by Grootaert (1976) for the saprophagous nematode *Mesodiplogaster lheritieri*, Grootaert and Jacques (1979) for the predatory nematode *Butlerius degrissei* and Grootaert and Small (1982) for the predatory nematode *Labronema vulvapapillatum*:

$$r_m = \ln (p\, N_e^*)/T_{min} \qquad (7)$$

where N_e^* is the *daily* egg-production.

MATERIAL AND METHODS

Rhabditis marina was obtained from the "Dievengat" a polyhaline brackish water pool, situated near the Nature Reserve "het Zwin" in north-western Belgium. Following the method described by Vranken *et al.* (1982), *R. marina* was cultivated in a 0.8% bacto-agar, made with water from the Dievengat (20‰ salinity) enriched with 1% Vlasblom-medium (Vranken *et al.*, 1982) and 0.5-1.0% $Na_2SiO_3.9H_2O$ (0.053 M stock solution). Unidentified bacteria, supplied in excess, served as food-supply. Salinity during the experiments was measured with a refractometer. The experiments were carried out in the dark with animals adapted to room temperature. The development of 47 eggs was followed at 25°C and 20‰ salinity.

For the study of the life-cycle parameters the cultures were checked once or twice daily. At each observation the adult females were transferred into new culture dishes.

Age-specific fecundity m_x, was determined from egg-counts using the following expression: $m_x = Ne_{(x)}p$, with $Ne_{(x)}$ the number of eggs laid at age x, p the proportion of females in the adult population (0.65). The age-specific survival l_x was observed directly while transferring adult females into new cultures. The observations on l_x were stopped when egg-laying ceased. During the females' egg production period young males were always present in the cultures.

RESULTS

All 47 eggs hatched between 0.5 day and 1 day after laying, the individuals started reproducing between day 4 and day 5, the females (n = 29) immediately they became adult, and no mortality occurred during embryonic and post-embryonic development (i.e. all 47 individuals matured). The cumulative egg production per female (n = 10) is given in figure 1.

Egg production ceased after approximately 6 days. On that day the first female died and two other females died on day seven. Assuming, 1) equal

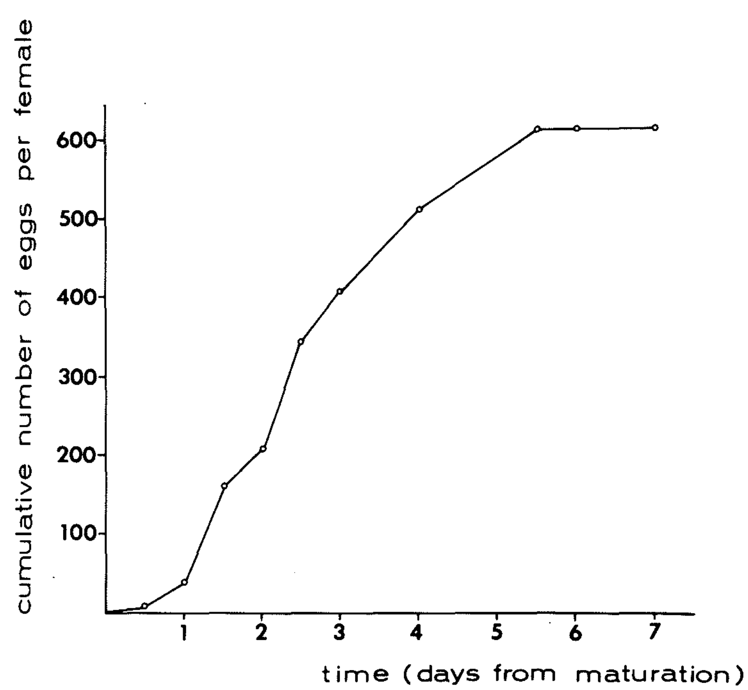

Fig. 1. *R. marina*: Cumulative egg-production per female at 25°C and $20^0/_{00}$ salinity (mean of 10 females).

TABLE I

Rhabditis marina: *life table and fertility table combined in $l_x m_x$ (= U_x) figures assuming no mortality and 65% females in the adult population. The third column xU_x shows the weighting of each age by its total realized female offspring number. For a nongrowing population ($R_0 = 1$), the sum of these products equals the cohort generation time, T_c*

x (pivotal age, in days)	U_x	xU_x
5	26.0	130.0
6	108.6	651.6
7	130.0	910.0
8	69.6	556.8
9	43.6	392.4
10	22.1	221.0
	$R_0 = \sum_{0}^{10} U_x = 399.9$	$\sum_{0}^{10} xU_x = 2861.8$

viability of the eggs produced at different ages, 2) no mortality before and during egg production (our observations) and 3) 65% females in the adult population (Tietjen *et al.*, 1970), we can calculate for each age-interval the $l_x m_x$ (= U_x) figure (Table 1), being the expressions necessary to solve equation (1). The results of the computations from our results for *R. marina*, cultured at 25°C and $20^{0}/_{00}$ salinity are listed in table 2. This table also shows the results of the calculations when an additional mortality of 50% ($l_x = 0.5$), completely localized in the immature stages, is considered (Tietjen *et al.*, 1970). This mortality reduces the net reproductivity R_0, with 50% ($R_0 = 0.5 \sum m_x$, see table 2), and r_m with 12% (from 0.914 day^{-1} to 0.801 day^{-1}). The post-reproductive mortality pattern is irrelevant to these computations.

DISCUSSION

The calculations are based on data obtained from a small cohort ($n = 47$), and the observations were terminated after an egg laying period of seven days. Additional egg production could therefore have been possible, but from figure 1 it appears that the curve depicting the cumulative number of eggs produced per female flattens and reaches a plateau. The observation of an egg laying period of three days for *R. marina* (Tietjen *et al.*, 1970) strengthens our assumption. However, if additional egg laying occurred, although most improbable, it would not influence r_m as calculated from equation (1) greatly, as R_o is high (Lewontin, 1965; Snell, 1978) and because reproduction after age T (see further) contributes relatively little to r_m (King, 1982).

A mean number of 600 eggs per female is the most ever observed for a free-living brackish water nematode. Tietjen *et al.* (1970) noted that individuals of the same species produced 70-100 eggs, whereas Sudhaus (1974) found a maximum of 260 offspring, with a mean of 128 for an ovoviviparous population.

Because our observations were made on a small cohort we used the proportion of females in the adult population (♀ = 0.65) given by Tietjen *et al.* (1970), and included a mortality-correction until maturity given by the same authors. This resulted in a 50% reduction of the net reproductivity, R_0 (table 2). It also illustrates that halving R_0, when R_0 is high, does not cause a similar decrease in r_m.

As one can see from table 2, r_c is an under-estimation of r_m. Bergmans (1981) illustrated this effect using data on the harpacticoid copepod *Tisbe furcata*. Bergmans (1983) pointed out that r_c can only be used as an approximation of r_m when either $R_0 \approx 1$ or the organism under study is semelparous (i.e. breeding only once in its life-span). For *R. marina*, an iteroparous (i.e. breeding more than once in its life-span) nematode producing offspring (eggs) continuously, r_c results in an under-estimation of 8% (calculated as $(r_m - r_c)/r_c$ (May, 1976)). Bergmans (1983) reports that for several *Tisbe* species the bias introduced with equation (3) ranges from 8 to 29%.

Approximate methods applied to nematodes

1. For *Oncholaimus oxyuris* Heip *et al.* (1978) used equation (6). When $r_m < 0.1$, this will give reasonably good approximations of r_m. [E.g., using their values at 25°C (± 3 egg-masses per female, the first produced on day 101 and thereafter one every seventh day, 12.3 eggs per egg-mass, a sex-ratio of 40% females and no mortality) we obtained an $r_m = 0.0250$ day^{-1} from life-table calculations and an $r_m = 0.0266$ day^{-1} with equation (6). For convenience during calculations we simplified the observations on egg-deposition and used 3 egg-masses each of 12.3 eggs instead of the reported 2.71 egg-masses with 13.6 eggs, both yielding ± 36.9 eggs per female.] This equation (6) results in an overestimation of 6.4%.

2. Values of r_m obtained by applying equation (6) will be higher than life table values because juvenile mortality is not included in the former. This has already been noted by Heip *et al.* (1978). These authors therefore proposed

$$r_m = (1/T_{min}) \ln (pl^* N_e) \qquad (8)$$

with l^* the proportion of juveniles surviving till adulthood. After correcting for l^*, equation (8) still results in over-estimations (Table 3) because l^* is only a partial correction. The more serious bias in equation (8) is in using the minimum generation time (T_{min}) for iteroparous organisms with a long reproductive period relative to their life-span. In this case T_{min} is not the proper weighting factor. It provides only good estimations of the generation time for semelparous individuals and organisms reproducing by fission (see

TABLE II

Life history parameters of different nematode species at different temperatures, Temp. (° C). All parameters related to generation time are in days (d); the capacity for increase, r_c and the intrinsic rate of natural increase, r_m are given in reciprocal days (d^{-1})

Species	Temp. (°C)	R_0	$r_c(d^{-1})$	$r_m(d^{-1})$	T_c(d)	T (d)	$\bar{T}$ (d)	T_{min}(d)	Juvenile mortality (%)	Authors
R. marina	25	200	0.740	0.801	7.2	6.6	6.2	4.5	50	Present study*
	25	400	0.837	0.914	7.2	6.6	6.1	4.5	0	Present study
M. lheritieri	25	265	1.015	1.447	5.5	3.9	3.2	2.3	0	Grootaert (1976)
L. vulvapapillatum	25	167	0.061	0.084	83	61	49	36	40	Grootaert & Small (1982)
	28	155	0.077	0.099	65	51	43	31	40	idem

* Present life-history observations using the mortality-figure given by Tietjen *et al.* (1970).

King (1982) for detailed figures). For iteroparous organisms, on the contrary, T_{min} measures only development time. Because most free-living nematodes reproduce continuously during a given period, more realistic parameters of the generation time are given by the following definitions: 1) the mean generation time (Andrewartha and Birch, 1954):

$$T = (\ln R_0)/r_m \tag{9}$$

2) the mean age of mothers in cohort at birth of female offspring or the cohort generation time (Dublin and Lotka, 1925 cited in Krebs, 1978):

$$T_c = (1/R_0) \sum_{x=0}^{\text{max age}} x l_x m_x \tag{5}$$

and 3) the age of the mother of an average newborn in an exponentially growing population (Leslie, 1966):

$$\bar{T} = \sum_{x=0}^{\text{max age}} x e^{-r_m x} l_x m_x \tag{10}$$

However, there remain some difficulties and neither definition can be used for all purposes (Mertz, 1970). The mean generation time (T) refers to that period of time necessary for a population growing at a constant rate r_m, to increase by the factor R_0 (Mertz, 1970; Ricklefs, 1973):

$$R_0 = e^{r_m T} \tag{11}$$

However, equation (9) is not defined when $R_0 = 1$ and $r_m = 0$ (stationary population i.e. a population holding steady in size). The cohort generation time (T_c), is a direct measure of the time-interval between the distributions of births of successive generations (Laughlin, 1965; Leslie, 1966). Therefore T_c has a clear biological meaning and the relationship between T_c and the mean time of the distribution of the nth generation births ($\bar{t}_n$) for all $n > 1$ is given by:

$$\bar{t}_n = \bar{t}_1 + (n - 1)T_c \tag{12}$$

with $\bar{t}_1$ the mean of the distribution of time at birth of the first generation (Leslie, 1966). T_c gives good approximations of T when either successive generations do not overlap or when the population is composed largely of individuals of the same age (Ricklefs, 1973). By contrast when generations do overlap T_c over-estimates T, because the progeny number R_0 is attained in a shorter time: R_0 ($= e^{r_m T}$) $<$ R_c ($= e^{r_m T_c}$) (Laughlin, 1965).

Leslie (1966) preferred equation (10) which he considered to be the most meaningful definition: "this period of time ($\bar{T}$) is directly related to the rate ($1/\bar{T}$) at which, after a certain point (A), the mean generation number ($\bar{n}_t$) increases per unit of time (t) in a population with a number of overlapping generations''. Leslie also noted that the weak point in his definition is the poorly defined point (A) for which the following equation holds:

$$\bar{n}_t = A + (1/\bar{T})t \tag{13}$$

For a stationary population ($R_0 = 1$, $r_m = 0$), $\bar{T} = T_c$.

Pielou (1977) found it meaningful to calculate all three parameters related to mean generation time. Obviously, it is very important to state which generation time is being referred to.

TABLE III

Comparison of different estimations of the intrinsic rate of natural increase, r_m (see text for definition), at different temperatures, Temp. (°C). The unit in each case is in d^{-1}, except in equation 7, where it is in d^{-1} ln (d^{-1}). Data for M. lheritieri *and* L. vulvapapillatum *were obtained from figures given by Grootaert (1976) and Grootaert and Small (1982)*

Species	Temp. (°C)	Eq. (1)	Eq. (3)	Eq. (6)	Eq. (7)	Eq. (8)	Juvenile mortality (%)
R. marina	25	0.801	0.740	1.331	0.952	1.177	50
	25	0.914	0.837	1.331	0.952	1.331	0
M. lheritieri	25	1.447	1.015	2.427	1.496	2.427	0
L. vulvapapillatum	25	0.084	0.061	0.156	0.025	0.142	40
	28	0.099	0.077	0.179	0.040	0.163	40

3) Finally equation (7) (table 3) is erroneous. In this formula, used by Grootaert (1976), Grootaert and Jacques (1979) and Grootaert and Small (1982), r_m is expressed in day^{-1} ln day^{-1}, a unit difficult to interpret. The use of this equation consistently results in negative reproductive values (e.g. an imaginary nematode starts reproducing on day twenty, terminates its reproduction on day forty and dies on day forty-five. It deposits during the egg-producing period three eggs every two days, the sex-ratio in this hypothetical population is (1:1) and juvenile mortality is 5%. According to equation (7) a population possessing such life-history characteristics has a negative intrinsic rate of increase: $r_m \approx 1/20 \ln (0.5 \times 1.5) = -0.014 \text{ day}^{-1} \ln \text{day}^{-1}$, whereas life table calculations give an $r_m = 0.0932 \text{ day}^{-1}$, a birth rate $b = 0.0976 \text{ day}^{-1}$ and a death rate $d = 0.0044 \text{ day}^{-1}$). A similar situation has been reported for the nematode *Labronema vulvapapillatum* at 15°C. At this temperature the species produces 1.08 eggs day^{-1} during approximately 80 days, has a development time of 126 days and a sex-ratio of (1:1). Substituting these observations in equation (7) yields a reproductive value $r_m \approx 1/126 \ln (0.5 \times 1.08) = -0.005 \text{ day}^{-1} \ln \text{day}^{-1}$ instead of the given + 0.005.

4) Another point that needs some clarification, is that r_m can only be calculated properly when one possesses accurate estimations of l_x and m_x, extended over the complete reproductive period. It is therefore meaningless to calculate the reproductive potential from observations that cover only part of the total egg-laying period as did Grootaert and Jacques (1979). Observations should be made at least until the cumulative egg-production curve flattens before one calculates the intrinsic rate of natural increase.

Using the very detailed figures given by Grootaert (1976) and Grootaert and Small (1982) we have recalculated some life-history characteristics of *Mesodiplogaster lheritieri* and *Labronema vulvapapillatum* where indications of adult and juvenile mortality were available and where reasonable estimates of R_0 (l_x and m_x patterns) could be made.

Part of this research was conducted under contract N° ENV.556.B of the Environmental Program of the EEC. The second author acknowledges a grant from the Belgian National Fund for Scientific Research (N.F.W.O.). The authors thank Drs. M. Bergmans, G. W. Yeates and two anonymous reviewers for their comments and criticism on an earlier draft of this paper.

Note added in proof:
After submission of this paper the name of *Rhabditis marina* Bastian, 1865 was changed to *Pellioditis marina* (Bastian, 1865) Andrássy, 1983 n. comb.
ANDRÁSSY, I (1983). *A taxonomic review of the suborder Rhabditina* (*Nematoda*: *Secernentea*). Editions de l'Office de la Recherche Scientifique & Technique Outre-Mer, ORSTOM-Paris; 241 pp.

RÉSUMÉ

Calcul du taux intrinsèque d'accroissement naturel, r_m, chez Rhabditis marina (*Bastian, 1865*)

Le cycle biologique de *R. marina* a été étudié à 25°C et 20‰ salinité. Différents paramètres démographiques ont été obtenus à partir de la fécondité journalière et de la mortalité des adultes. Le taux intrinsèque d'accroissement naturel, r_m, égale 0.914 par jour et le taux net de reproduction, R_0, 400. Différents paramètres représentant la durée d'une génération ont été mesurés: la durée de developpement jusqu'à l'adulte, T_{min} est de 4,5 jours et celle d'une cohorte, T_c, est de 7,2 jours; la durée moyenne de développement d'une génération, T, est de 6,6 jours et l'âge d'une femelle à la ponte d'un oeuf median, $\bar{T}$, est de 6,1 jours.

Plusieurs méthodes approximatives pour déterminer r_m ont été comparées au calcul exact de r_m à partir de tables de mortalité et de fécondité. Pour des espèces itéropares, ce qui est le cas de la plupart des nématodes libres, T_{min}, represente seulement une estimation de la durée de développement.

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Accepted for publication: December 13, 1983.