

Specific Production of Free-Living Marine Nematodes

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ABSTRACT: Using the data available on generation time, life span, and number of eggs for marine nematodes, the daily specific production has been calculated. For approximate estimations of the specific production (C) for nematodes in natural populations as a function of water temperature (T°) the following equation is proposed: $C = 0.08 T^{0.96}$.

INTRODUCTION

Production in animal populations has received detailed attention in 'Marine Ecology', Volume IV (Greze, 1978). For solving a number of ecological problems we concentrate here on the productivity of communities which inhabit different biotopes. Since it is impossible to study the production of all species of a community, it is important to formulate regular quantitative relations between 'common' biological variables and population production. For this purpose, it is extremely important to ascertain the laws governing the value of daily specific production $C = P/B$, where P = daily production, B = average biomass for some 'typical' species and groups under different environmental conditions (Zaika, 1972, 1974).

In this report the results of analysis of specific production values are presented for free-living marine nematodes – one of the main groups of meiobenthos animals.

METHOD OF ESTIMATION AND INITIAL DATA

The specific production of nematodes may be estimated on the basis of biological literature data (for review consult Kinne, 1977, pp. 691–709). There are different possibilities of calculation. Proceeding from the character of the data available the method of analyzing potential population growth is considered to be the best one.

For this method we use data on generation time (τ_0 = time between identical stages in two successive

generations), average duration of life (τ_m) and general number of eggs deposited by the female (N_{ov}).

The data presented for τ_0 , τ_m and N_{ov} by different authors are summarized in Table 1. Whether this 'sample' is representative for mass species of marine nematodes from different regions of the World Ocean remains unknown. We suggest that size variety among mass meiobenthic nematodes and, hence, the variability of τ_0 , τ_m , N_{ov} , is not larger than that of the species studied.

Figure 1 presents the size distribution of Black Sea nematodes (data from Vodyanitsky, 1968). Note that 85 % of the species have sizes between 0.5 and 5 mm. About the same limits pertain to mass species of nematodes in the Weser Estuary (Skoolmun and Gerlach, 1971).

SCHEME OF C CALCULATION

The general basis of the method employed, as well as a number of assumptions have been accounted for by Zaika (1972). One point must be stressed here: some investigators consider production calculations incorrect unless rates of elimination are included. Gerlach (1972) considered possible C values of marine nematodes, based on hypothetical daily mortality rates as a function of age. However, it is not necessary to take into account elimination rates in our method of C calculation.

The method is based on the following fact: providing the rate of new biomass formation is proportionate to population number, the specific production equals the

Table 1. Development and reproduction of marine nematodes under experimental conditions

Species	Temperature (°C)	Egg number (average)	Average Generation time (days)	Average lifespan (days)	Source
<i>Adoncholaimus thalassophygas</i>	20-22	17	63	78	Gerlach and Schrage, 1971
<i>Acanthonchus cobbi</i>	-	-	29	-	"
<i>Chromadorita tenuis</i>	20-22	20	26	43	"
<i>Chromadora macrolaimoides</i>	25	-	22	45	Tietjen and Lee, 1973
<i>Desmodora scaldensis</i>	7	>6	~730	603	Gerlach and Schrage, 1971
<i>D. ocellata</i>	20-22	22	29	56	"
<i>D. ocellata</i>	30	-	6	-	Hopper et al., 1973
<i>D. ocellata</i>	24	-	11.5	-	"
<i>D. ocellata</i>	21	-	12	-	"
<i>D. ocellata</i>	18	-	43	-	"
<i>Diplolaimelloides oschei</i>	20-22	36	29	54	Gerlach and Schrage, 1971
<i>D. islandica</i>	20-22	22	31	50	"
<i>D. sp.</i>	30	-	4.5	-	Hopper et al., 1973
<i>D. sp.</i>	24	-	7	-	"
<i>D. sp.</i>	21	-	9.5	-	"
<i>D. sp.</i>	18	-	14	-	"
<i>D. sp.</i>	12	-	30	-	"
<i>Enoplus paralittoralis</i>	28	-	21	-	"
<i>E. paralittoralis</i>	24	-	22	-	"
<i>E. paralittoralis</i>	21	-	41	-	"
<i>Euchromadora gaulica</i>	-	-	35	-	Gerlach and Schrage, 1971
<i>Halichoanolaimus robustus</i>	7	-	> 730	855	Gerlach and Schrage, 1972
<i>Haliplectus dorsalis</i>	30	-	27	-	Hopper et al., 1973
<i>H. dorsalis</i>	24	-	34	-	"
<i>H. dorsalis</i>	21	-	70	-	"
<i>Monhystera disjuncta</i>	20-22	16	23	33	Gerlach and Schrage, 1971
<i>M. disjuncta</i>	17-22	37	13	61	"
<i>M. disjuncta</i>	13-15	-	15	-	"
<i>M. disjuncta</i>	9-12	-	17	-	"
<i>M. disjuncta</i>	7	-	22	-	"
<i>M. disjuncta</i>	0-2	-	77	-	"
<i>M. disjuncta</i>	1-1	-	135	-	"
<i>M. filicaudata</i>	20-25	8-20	24-35	-	"
<i>M. parelegantula</i>	-	-	30	-	"
<i>M. denticulata</i> (at 26‰)	25	18-23	10	34	Tietjen and Lee, 1972
<i>M. denticulata</i> "	15	18-24	18	53	"
<i>M. denticulata</i> "	5	10-17	180	330	"
<i>Oncholaimus brachycercus</i>	7	>6	180	610	Gerlach and Schrage, 1972
<i>O. oxyuris</i>	5	13.5	-	-	Heip et al., 1978
<i>O. oxyuris</i>	10	18.5	-	-	"
<i>O. oxyuris</i>	15	34.3	152	-	"
<i>O. oxyuris</i>	20	35.6	114	-	"
<i>O. oxyuris</i>	25	36.8	102	-	"
<i>Oncholaimus sp.</i>	30	-	20	-	Hopper et al., 1973
<i>O. sp.</i>	24	-	2.25	-	"
<i>O. sp.</i>	21	-	39	-	"
<i>O. sp.</i>	18	-	86	-	"
<i>Rhabditis marina</i>	33	-	1.5	-	"
<i>R. marina</i>	24	-	2.25	-	"
<i>R. marina</i>	21	-	2.5	-	"
<i>R. marina</i>	18	-	4	-	"
<i>R. marina</i>	12	-	8	-	"
<i>Theristus pertenuis</i>	17-22	-	23	-	Gerlach and Schrage, 1971
<i>T. pertenuis</i>	13-15	-	41	-	"
<i>T. pertenuis</i>	9-12	-	47	-	"
<i>T. pertenuis</i>	7	-	71	-	"

reproduction coefficient reflecting the numerical increase in the absence of elimination. Hence, the C value must be estimated as the specific rate of potential growth, not as 'intrinsic rate of increase', actually observed in the presence of elimination.

The specific production is calculated as

$$C = \frac{\log N_2 - \log N_1}{t_2 - t_1} \quad (1)$$

where N_1 and N_2 = numbers of individuals at times t_1 and t_2 ; N_2 is estimated either by geometrical progression of potential population growth or experimentally, providing it is possible to neglect elimination.

However, if calculation according to equation (1) is based on a real N_2 in the presence of elimination, we obtain an underestimation of the C value. This is why C must be calculated without elimination.

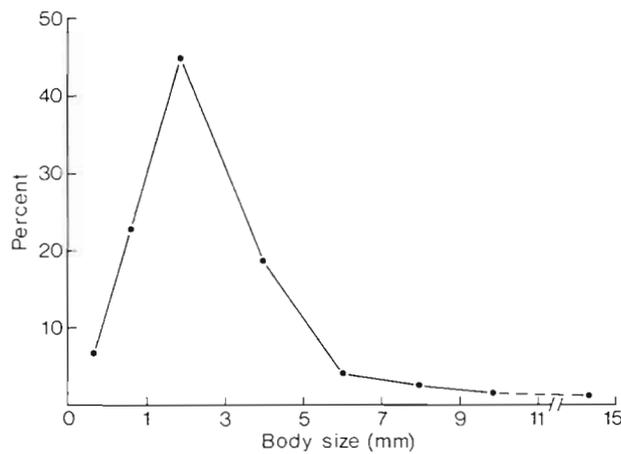


Fig. 1. Size distribution of Black Sea nematodes

In general, the specific production is completely defined by the reproductive potential, individual growth rate, and age structure of a population. The production value (but not C !) depends on the biomass present. Elimination influences the number and biomass levels and therefore production. It influences the specific production only if changes in age-structure are caused.

Now we come to the limitations of the method of C calculation. The method under discussion is precise enough when the age structure is constant, i. e. with mortality distributions according to age. It permits to ignore the population structure and to consider all individuals to be conventionally identical. Hence it is necessary to use the method of C calculation over rather long periods of time, i.e. at $(t_2 - t_1) \geq \tau_0$.

Indeed, in the case of large long-lived animals with seasonal reproduction the calculation of C with Equation (1) over short periods is meaningless: in one season adults with growth rates close to 0 may predominate while in another one population may consist

mainly of quick growing juveniles. But if we consider periods not shorter than τ_0 , the method discussed will yield satisfactory specific-production estimation - average values for the whole period.

The precision of the method increases with decreasing of animal sizes τ_m and τ_0 . Thus far, this method has only been used for bacteria and unicellular organisms. However, it is suitable also for metazoans as nematodes.

In order to obtain a geometrical progression of potential growth values for a population, Gerlach (1972) used the following initial data: $\tau_0 = 26$ days, $\tau_m = 34$ days, $N_{ov} = 20$; male : female ratio = 1. Hence a pair of nematodes will yield 22 offspring in 26 days; 220, in 52 days; 2200, in 78 days.

Using Equation (1) for such population growth rate we obtain $C = 0.09$. For a precise estimation of the average C value over the whole year it is necessary to know the characteristics of seasonal τ_0 changes, taking N_{ov} as invariable.

Gerlach (1972) assumed that nematodes produce 12 generations per year; assuming further a certain mortality rate as a function of age and making use of growth curves for calculation, he obtained a yearly turnover rate of 26, corresponding to an average annual C of 0.07. Taking into account the fact that the water temperature near Helgoland exceeds 15 °C only during 2.5 months each year and the data of Table 1 concerning the influence of temperature on τ_0 , the results obtained by Gerlach may be considered realistic, even though his C estimates are too complex.

According to Table 1, $N_{ov} = 20$ can be taken as average value for all nematodes. The fact that $\tau_m > \tau_0$ is not significant for C calculations, since the presence or absence of individuals of previous generations does not affect the calculation. Hence, for further calculations Equation (1) may be simplified taking $t_2 - t_1 = \tau_0$ and assuming for meiobenthic nematodes the following law of potential numerical growth: 2-20-200-2000 . . ., with the step τ_0 , so that

$$C = \frac{2.3}{\tau_0} \quad (2)$$

SPECIFIC PRODUCTION OF NEMATODES AS A FUNCTION OF TEMPERATURE

We must distinguish at least between 2 master factors which influence τ_0 and N_{ov} of all poikilothermal animals: temperature and nutrition. Both may become limiting factors in any part of the distributional area of a species. Other factors such as salinity undergo appreciable fluctuations only in some marine biotopes, while such factors as population density or predation

rate cannot influence the characteristics discussed in marine nematodes.

Table 1 shows that the influence of temperature was studied for a number of species. Specific-production values obtained from such data might be a little higher than in the sea, since natural food conditions are usually not as favourable as in experiments. We have calculated specific-production values, using Equation (1), excluding data obtained at extremely high temperatures (Hopper et al., 1973).

Our results are listed in Table 2. The variability of the C values is, at some temperature intervals, high; this is not surprising, since the investigations were conducted both with nematodes of the North Sea and a mangrove belt. The extremely high C values for *Rhabditis marina* are of great interest; they are just as high as those of rotifers and infusorians (Zaika, 1972). *R. marina* clearly falls out of the general range and hence was excluded from calculations. In addition it seems that while developing so quickly *R. marina* might not attain $N_{ov} = 20$. The average C values from Table 2 may be used for estimating nematode production in natural communities. *R. marina* is of non-marine origin, but we do not consider this fact as a reason for the peculiarities mentioned. The dependence of average C values on temperature is presented graphically in Figure 2. In order to determine the equation for describing these empirical dependences, it was previously established that the points characterizing the thermal dependence of τ_0 of different species, lie on straight lines in logarithmic coordinates. This means that the dependencies can be represented as

$$\tau_0 = aT^b \quad (3)$$

where T = temperature; a and b = constants.

For describing the dependence between development times of poikilothermal animals and temperature, usually the Beleradek equation is used (Corkett

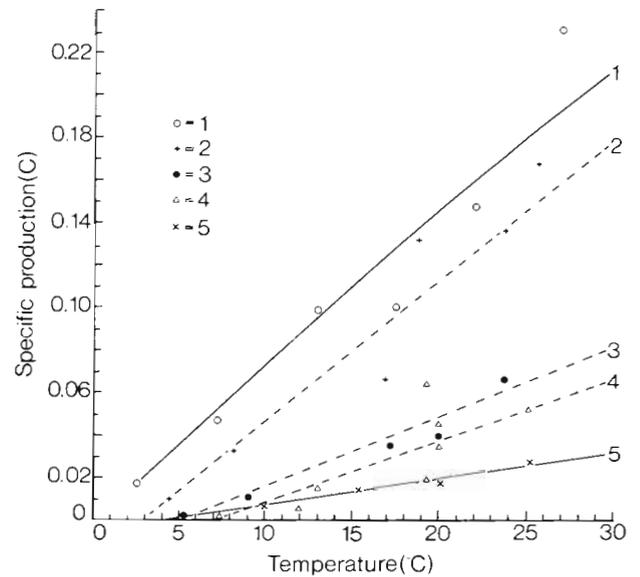


Fig. 2. Dependence of average C values (day^{-1}) on temperature. 1: average for marine nematodes; 2: *Acartia clausi*; 3: *Calanipeda aquae-dulcis*; 4: *Orchestia bottae* (2–4 crustaceans, from Zaika, 1972); 5: *Oncholaimus oxyuris* (from Heip et al., 1978). Curve 1 based on the Equation (5); Curves 2–5 eyefitted

and McLaren, 1970). The only difference between Equation (2) and the Beleradek equation is that the curve passes through the original coordinate.

Substituting τ_0 in Equation (2) in accordance with (3) we get

$$C = \frac{2.3}{a} \cdot T^{-b} \quad (4)$$

From the average data of Table 2, using the least square method, we find the numerical values of a and b in Equation (4):

$$C = 0.08 T^{0.96} \quad (5)$$

The corresponding curve is shown in Figure 2. Com-

Table 2. Specific production of nematodes at different temperatures

Species	Temperature (°C)					
	0–5	5–10	10–15	15–20	20–25	25–30
<i>Diplolaimella ocellata</i>	–	–	–	0.05	0.20	0.38
<i>Diplolaimelloides</i> sp.	–	–	0.08	0.16	0.28	0.50
<i>Enoplus paralittoralis</i>	–	–	–	–	0.08	0.11
<i>Haliplectus dorsalis</i>	–	–	–	0.02	0.05	0.08
<i>Monhystera disjuncta</i>	0.03	0.10	0.14	0.18	–	–
<i>M. denticulata</i>	0.01	0.01	0.13	0.13	0.23	0.23
<i>Rhabditis marina</i>	–	–	0.29	0.57	0.97	1.15
<i>Theristus pertenuis</i>	–	0.03	0.06	0.10	–	–
<i>Oncholaimus</i> sp.	–	–	–	0.03	0.07	0.11
Average C (excluding <i>R. marina</i>)	0.02	0.05	0.10	0.10	0.15	0.23
C limits (excluding <i>R. marina</i>)	0.01–0.03	0.01–0.10	0.06–0.14	0.02–0.18	0.05–0.28	0.08–0.50

paring equations (5) and (4) we obtain $a = 287$; and for (3) we have

$$\tau_o = 287 T^{-0.96} \quad (6)$$

Equation (5) and Figure 2 allow to estimate approximately the production of marine nematodes. It is necessary to know the nematodes' biomass and the water temperature. Presumably the pattern of this dependence is not random as are the same kind of C and temperature relations established earlier for some marine crustaceans (Zaika, 1972). The corresponding data are shown in Figure 2.

OTHER APPROACHES TO SPECIFIC-PRODUCTION ESTIMATION

There exists an empirical dependence between the daily specific production and life span; this statement is based on data obtained from the different animal species (rotifers to fishes; Zaika, 1972, Fig. 30). Comparing the data of Table 1 with the dependence, it may be seen that in the temperature interval 15 °–25 °C, the average value τ_m of the nematode species studied is 33–78 days; that corresponds to a C of 0.06–0.15. At low temperatures, τ_m can be about one year and the corresponding C would be about 0.01.

Finally, it is possible to use an individuals' growth data for estimating its specific production.

The daily specific rate of linear growth, averaged for the period from hatching to maturation, has been calculated for two species of nematodes according to the growth curve (Tietjen and Lee, 1972, 1973) employing the equation

$$q_l = \frac{\log l_2 - \log l_1}{t_2 - t_1} \quad (7)$$

where q_l = daily specific rate of linear growth; l_1 and l_2 = body length at times t_1 and t_2 . We obtain the following q_l values

	25 °C	15 °C
<i>Monhystera denticulata</i> :	0.19	0.14
<i>Chromadora macrolaimoides</i> :	0.15	–

The weight-length dependence is

$$w = ml^3 \quad (8)$$

where w = individual weight; m = constant.

For the specific rate of weight growth (q_w) we have

$$q_w = \frac{\log w_2 - \log w_1}{t_2 - t_1} \quad (9)$$

Substituting w in Equation (9) in accordance with (8) we obtain:

$$q_w = 3q_l \quad (10)$$

Equation (10) is adequate for calculating specific rates of weight growth from linear growth data. Wher-

ever in Equation (8) the power at w differs from 3, it is sufficient to use in Equation (10) the corresponding value instead of 3.

Employing Equation (10) for the species discussed at temperatures between 15 ° and 25 °C we get:

$$q_w = 0.42 - 0.57$$

Gerlach (1972) used the curve of weight growth for calculating turnover rate in *Chromadora tenuis*. Using his growth data for the period from the hatching to maturation, Equation (9) gives

$$q_w = 0.38$$

Thus for three species of marine nematodes we now have average daily specific rates of weight growth for the period of active development. For estimating the specific production it is necessary to know also the age structure of the population concerned – in this case the ratio juvenile to adult biomass. If 20 % of the general biomass consists of actively growing individuals, the specific production of that population is 0.08–0.12 (at 15 °–25 °C).

Finally, it was shown by Zaika (1972) that the intrinsic rate of increase r provides a minimal estimation of the average specific production rate. Data on r values for *Oncholaimus oxyuris* at different temperatures are available (Heip et al., 1978). It is interesting that the relationship between r and temperature is nearly linear. Assuming $C \approx r$ we have for *O. oxyuris* the same kind of curve, as for other nematodes and crustaceans (Fig. 2). These data were not included in calculations of average C values for nematodes, since *O. oxyuris* has large dimensions and a long generation time.

After completion of the present manuscript the authors, thanks to assistance from Prof. Kinne, got an opportunity to acquaint themselves with the paper by Tietjen and Lee (1977), containing data on r and τ_o for *Chromadorina germanica* at different temperatures. Estimating C according to the expression $C \approx r$ and Equation (2) for *C. germanica*, we obtain similar values. From comparing C dependence on temperature for *C. germanica* with Curve 1 in Figure 2, it follows that, in the temperature range 17 °–23 °C, the C values are practically identical – although, in general, the curve obtained for *C. germanica* has a different slope. The data by Tietjen and Lee (1977) suggest that the nematodes' reaction signals close-to-lethal temperatures. Such cases should probably be excluded from analysing general dependencies similar to those expressed by Equations (5) and (6).

The results of our analysis indicate high average specific production rates of marine nematodes, and allow to estimate very quickly nematods productions in different marine biotopes, using data on biomass, age structure and water temperature. The methods of C

calculation discussed allow to conduct a more profound analysis of the production process in this important group of meiobenthos animals (Gerlach, 1971; Juario, 1975), providing the corresponding data are at hand.

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