

THE PRODUCTIVITY OF MARINE NEMATODES

Guido Vranken & Carlo Heip

Marine Biology Section, Zoology Institute, State University of Gent, B-9000 Gent, Belgium

ABSTRACT

The productivity of marine nematodes was studied from laboratory experiments investigating the relationship between minimum generation time and temperature, the daily birth rate as calculated from life-tables taking fecundity and survivorship into account and the temperature regime in the field.

The life cycle of *Monbystera disjuncta* is described. Females produce about 200 eggs in agnotobiotic conditions over about 70 days: this represents 17 times their own body weight. The mean generation time is 20 days at 12°C and this species can produce 23 generations in the field each year. The maximum annual P/B is equal to 69. The annual P/B calculated from the birth rate is 60.

From similar studies on five other nematode species it is concluded that the life-cycle turnover is equal to three but the number of generations annually produced in the field varies from one to twenty. Annual P/B for the species studied and from literature data on other species lies between 4 and 69. The use of a single P/B value for nematodes is therefore invalid. Scaling with body weight is possible with the equation $\log P/B = -1.288 - 0.440 \log M_s$, where M_s is the weight at sexual maturity in kcal.

INTRODUCTION

Nematodes are the most abundant metazoans in marine sediments, with densities of several million animals per square meter of the sea floor in many shallow subtidal environments. This represents a biomass of around 0.2-0.5 g C·m⁻². Coastal sedimentary systems receive a carbon input in the order of 50-150 g C·m⁻²·an⁻¹, thus less than 1% of this amount shows up as nematode biomass. Though this may seem little, nematodes do far better than other meiofauna components, especially when the input is large (Heip *et al.* 1982); they represent more than 90% of the total meiofauna in many coastal sediments.

Whether nematodes are an important food to macrofauna or fish is still a matter of research today, but their role in stimulating bacterial productivity and thus mineralization of detritus, decomposition and nutrient regeneration has been well established (Tenore *et al.* 1977, Gerlach 1978, Tietjen 1980, Findlay & Tenore 1982). The rates of these processes in the sea are important in ecological models but largely unknown. One of the possible starting points to evaluate what nematodes may do in sediments is to examine the energy flow through nematode communities.

It is hardly possible to measure nematode respiration in the field or to calculate biomass production from an analysis of growth or mortality. Nearly all our knowledge of energy flow is based on laboratory experiments and extrapolation to the field is based on density and biomass of field populations. As an example of these calculations, consider the following: total ingestion (or consumption) is a constant $a \times$ assimilation (production + respiration) which is a constant $b \times$ production. Since production is a constant $c \times$ biomass, one ends up with the formula $I = a \cdot b \cdot c \cdot B$. There is no need to stress the uncertainty involved in this type of calculations.

Most studies on marine nematodes restrict their attention to the relationships between respiration or production and biomass. Since most nematodes, for which this is known, mature within a period of two to three weeks, and since reproduction is continuous and reproductive life is much longer than pre-adult life (Woombs & Laybourn-Parry 1984), generations in the field strongly overlap and individual cohorts cannot be distinguished. This makes the classical approach to production (Crisp 1971) inapplicable and our information is based nearly exclusively on laboratory studies. From one of the earliest of such studies, the work of Thun (1968) on the brackish water herbivore *Chromadorita tenuis*, Gerlach (1971) calculated the production/biomass ratio of the life cycle as three. Assuming that meiofauna species in general produce three generations per year in the field, Gerlach (1971) then obtained his classical figure $P/B = 9 \cdot \text{an}^{-1}$, which has since been universally used to estimate meiofauna and *a fortiori* nematode production.

A somewhat more sophisticated approach consists in calculating the annual P/B ratio from the empirical relationship between body weight at sexual maturity M_s and P/B (Banse & Mosher 1980). This relationship is described with a power law $P/B = aM_s^b$. For invertebrates living between 5 and 20°C $a = 0.65$ and $b = -0.37$ when M_s is in kcal. For nematodes and meiofauna in general, Banse & Mosher (1980) predicted that the line lies far below the general invertebrate line. This was however based on only one observation.

In this study we will show that the use of a life-cycle turnover of three, as proposed by Gerlach (1971) is indeed valid. When the number of generations produced in the field is known, we will then obtain an accurate figure of yearly production by multiplying this number by three. However, this will only in rare exceptions be possible. For small, rapidly reproducing species, laboratory studies have been performed that allow calculation of a maximum number of generations that may be produced when reproduction is continuous. These studies do show that the use of a single P/B ratio is invalid.

This research was supported through the Concerted Actions Oceanography of the Ministry of Scientific Policy of Belgium, grant 2.9007.82 from the Fund of Collective Fundamental Research of Belgium and through grants ENV-556-B and ENV-767-B of the CEC. The second author acknowledges a grant from the Belgian National Fund for Scientific Research (NFWO). Both authors are very grateful to Rudy Vanderhaeghen for invaluable help, and to Dr P. Herman for many discussions.

MATERIAL AND METHODS

The species studied were isolated from the Sluice Dock of Ostend, a marine lagoon near the Belgian coast of the North Sea and from the Dievengat, a poly-mesohaline brackish water pond in a polder in northern Belgium. The bacterial feeders *Diplolaimella dievengatensis* (previously misidentified as *Monhystera microphthalma* (Jacobs & Vranken, in press)), *Monhystera disjuncta* and *Monhystrella parelegantula* were cultured in 0.4% brackish water bacto-agar (DIFCO) enriched with Vlasblom medium and silicate (Vranken *et al.* 1984). The diatom-feeders *Chromadora nudicapitata*, *Monhystera parva* and *Paracanthochus caecus* were grown on 0.4% modified brackish water Killian agar (Thun 1966). The food of the herbivorous species consisted of an unidentified bacterial mixture supplemented with the following diatom mixture: *Navicula peregrina*, *Nitzschia ovalis*, *Cocconeis scutellum*, *Cyclotella* sp. and *Melosira* sp., and the green alga *Dunaliella salina*. The bacteria which served as food for the bacterivorous species were grown simultaneously in the same Petri dishes as the nematodes. The bacterial feeders were kept in the dark and the herbivorous species were grown under continuous light.

The minimum generation time T_{\min} was determined as the time between identical stages in two successive generations (the time between a gravid female in the mother generation and a gravid female in the daughter generation).

The intrinsic rate of natural increase r_m and the net reproductiveity R_0 (the multiplication rate per generation) were calculated from observations on the age-specific fecundity m_x and survival l_x , using standard demographic equations:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad \text{and} \quad \sum_{x=0}^{\infty} e^{-r_m x} l_x m_x = 1.$$

The birth rate was calculated with the method described in Nisbet & Gurney (1982) assuming that mortality within each age group is exponential.

RESULTS

Influence of temperature

Temperature has a profound influence on the minimum generation time T_{\min} in all species studied, with Q_{10} values in the lower temperature interval ranging between 2.6 in *Paracanthochus caecus* and 7.6 in *Chromadora nudicapitata* (Sluice Dock population). Developmental acceleration is higher in the lower temperature range in all species. The optimum temperature, defined as the temperature at which the highest development rate is realized (Taylor 1981), is higher than 20°C in all species. In *Monhystrella parelegantula* it is higher than 30°C. The basal temperature, below which development stops, ranges between 10°C in *Diplolaimella dievengatensis* and *Monhystrella parelegantula* and below zero degrees in *Monhystera disjuncta*.

Table 1. Minimum generation time T_{min} of females of different nematode species. n is the number of females studied. SD: Sluice Dock population; D: Dievangat population.

Species	Salinity ‰S	Temp. °C	$T_{min} \pm SD$	n
<i>Diplolaimella dievangatensis</i>	20	15	27.9 ± 5.7	123
		20	10.2 ± 1.2	113
		25	7.8 ± 2.5	174
		30	6.6 ± 1.7	137
<i>Monhystrella parelegantula</i>	30	15	54.3 ± 7.3	39
		20	18.1 ± 2.9	275
		25	7.9 ± 0.9	539
		30	6.3 ± 0.9	467
		35	5.3 ± 0.9	550
<i>Monhystera parva</i>	30	8	50.6 ± 6.7	87
		12	19.6 ± 4.7	238
		17	12.7 ± 2.0	152
		22	8.8 ± 1.6	229
<i>Monhystera disjuncta</i>	30	3	52.3 ± 8.4	287
		8	18.6 ± 3.9	56
		12	17.2 ± 4.5	662
		15	11.8 ± 2.1	241
		17	10.9 ± 2.4	226
		20	9.3 ± 2.2	291
<i>Chromadora nudicapitata</i> (SD)	30	3	153.6 ± 18.7	22
		8	76.9 ± 7.6	95
		12	24.7 ± 3.0	127
		17	17.3 ± 2.4	323
		22	9.7 ± 1.0	148
<i>Chromadora nudicapitata</i> (D)	20	5	84.5 ± 8.3	52
		10	52.5 ± 4.0	96
		15	24.9 ± 2.8	64
		20	14.0 ± 1.4	108
		25	16.9 ± 1.7	44
<i>Paracanthonchus caecus</i>	20	10	131.9 ± 16.0	93
		15	65.7 ± 3.6	82
		20	51.1 ± 5.6	66
		25	41.9 ± 4.2	92

The relationship between temperature T and development time T_{min} (days) can be represented by an allometric relationship $T_{min} = aT^b$. The coefficients of this equation for the different species are given in Table 2. a can be considered as the development time at 1°C and b is a measure of the temperature dependency of

Table 2. Values of a and b of the allometric relationship $T_{\min} = aT^b$ between development time T_{\min} (days) and temperature T ($^{\circ}\text{C}$). r^2 is the coefficient of determination. T_m and T_0 are the optimum and basal temperature ($^{\circ}\text{C}$). $D(t)$ is the number of juvenile periods realized in the field. SD: Sluice Dock population; D: Dievengat population.

Species	a	b	r^2	T_m	T_0	$D(t)$
<i>Diplolaimella dievengatensis</i>	4679	-1.96	0.75	28	10	10
<i>Monhystrella parelegantula</i>	208053	-3.11	0.94	35	10	6
<i>Monhystera parva</i>	1755	-1.74	0.97	22	5	16
<i>Monhystera disjuncta</i>	118	-0.84	0.90	21	<0	23
<i>Chromadora nudicapitata</i> (SD)	1167	-1.49	0.92	22	0-3	13
<i>Chromadora nudicapitata</i> (D)	607	-1.16	0.90	24.5	0-3	10
<i>Paracanthochnus caecus</i>	2357	-1.28	0.89	25	5	3.5

development time (Heip *et al.* 1985). a and b were calculated from the mean of several experiments (Fig. 1a).

Water temperature in the Dievengat and the Sluice Dock can be described with a simple sinus function of time t . The equations are:

$$T(t) = 11.2 + 8.3 \sin(t - 117) \text{ Dievengat (Heip \& Smol 1976a)}$$

$$T(t) = 11.5 + 8.5 \sin(t - 120) \text{ Sluice Dock (Podamo 1976)}$$

Combining the coefficients of the power equation a and b with the sinusoid temperature functions we obtain the daily development rate $R = 1/T_{\min}$ as a function of time. Integrating R over a period of one year we find the maximum annual number of generations. In the species studied this varies between 3.5 and 23 (Table 2), corresponding to yearly P/B ratios of between 10 and 69.

The life cycle of Monhystera disjuncta

The life cycle of *Monhystera disjuncta* is shown in Fig. 1. The eggs are deposited in the first cell stage. At 12°C the embryonic period lasts 3.5 days ($\text{SD} = 1.2$; $n = 956$). The females become gravid 17.2 days ($\text{SD} = 4.5$; $n = 662$) after egg deposition. Somatic growth during the juvenile stage is exponential (Fig. 1d) and thus equal to the daily P/B (Herman *et al.* 1984). This juvenile growth rate is 0.37 per day at 17°C . At 12°C a single female produces about 218 eggs ($\text{SE} = 31.9$; $n = 9$) in agnotobiotic conditions. In monoxenic cultures, which are less representative for natural conditions, females of *Monhystera disjuncta* are able to produce 400-500 eggs when fed on the bacterium *Alteromonas haloplanktis*. Freshly deposited eggs have a wet weight of 23 ng; since an adult female weighs about $0.3 \mu\text{g}$ wet weight, she produces about 17 times her own body weight during her reproductive life.

Reproduction occurs over about 70 days. During the first 40 days females produce, at a constant rate, 5.1 eggs per day (95% C.I. = 0.4). During the last 30 days, fecundity drops to 1 egg per day (Fig. 1b). Hatching success is 96%

MONHYSTERA DISJUNCTA

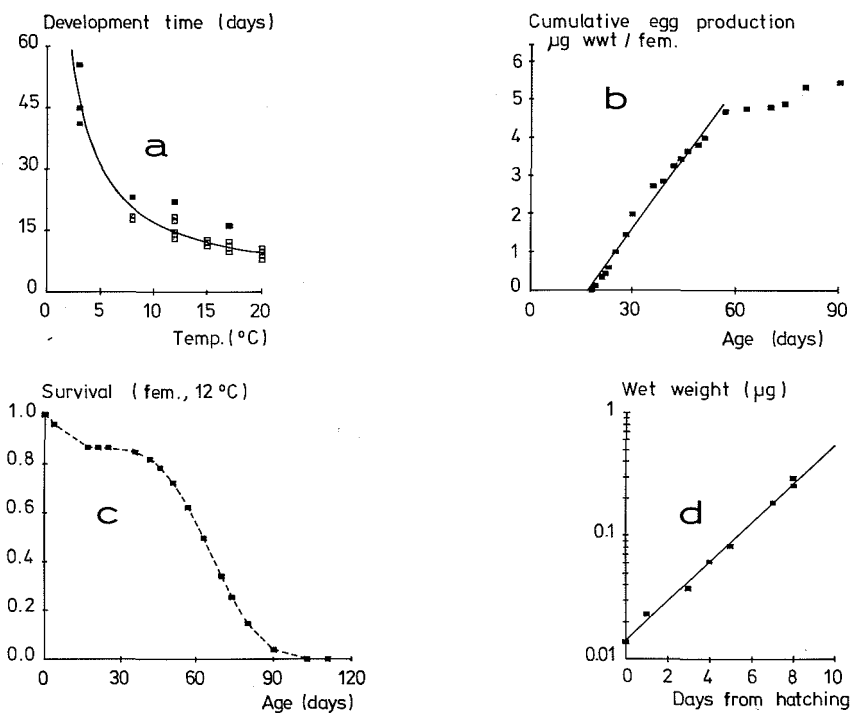


Fig. 1. *Monhyстера disjuncta*: life cycle at 30%S; a: relationship between female development time (T_{min}) and temperature (°C); b: cumulative egg production (μg wet weight) per female at 12°C; c: survival of females at 12°C, time zero: moment of egg deposition; d: juvenile somatic growth at 17°C.

($n = 2937$) and mortality during juvenile development is 10% ($n = 2816$). Total mortality in the pre-adult phase is thus 14%. In the fertile life-cycle period, mortality is nearly zero (Fig. 1c). Survival (l_x) during the adult female stage can be described with a Weibull function (Pinder *et al.* 1978):

$$l_x = l_0 e^{-(x/(53.94))^{3.71}}$$

Mean longevity of adult females at 12°C is 49 days and mean total longevity is 66 days. The mean life expectancy e_x for first-day adult females is 46 days.

At 12°C a population with a stable age-distribution has the following composition: 47% eggs, 48% juveniles, and 5% adults. A modal egg weighs 20 ng wet weight, a hatchling 14 ng, an average juvenile 47 ng, and an adult somewhat less than 300 ng. On a weight basis, 21% of the population consists of eggs, 51% of juveniles and 28% of adults. 73% of the adult population consists of females.

The birth rate of the population is 0.18 per day (Table 3) at 12°C. A female has a net reproductiveity of 120 female eggs. Table 4 shows the population energetics

Table 3. Life history characteristics of free-living nematodes at a fixed salinity (S) and temperature (T); R_0 : net reproductiveity; r_m : intrinsic rate of natural increase (day^{-1}); $F_{(0)}^*$: birth rate (day^{-1}); P/B per T_{\min} : life-cycle turnover during one generation; p.a.m.: pre-adult mortality.

Species	S(‰)	T(°C)	R_0	r_m	$F_{(0)}^*$	P/B per T_{\min}	p.a.m. (%)	Authors
<i>Diplolaimella dievengatensis</i>	20	20	65	0.238	0.257	2.6	12	this study
<i>Monhystrella parelegantula</i>	30	30	37	0.307	0.347	2.2	5	this study
<i>Monhystera disjuncta</i>	30	12	123	0.171	0.181	3.1	14	this study
<i>Monhystera parva</i>	30	12	76	0.156	0.156	3.1	1.5	this study
<i>Chromadora nudicapitata</i>	30	12	246	0.135	0.135	3.3	1	this study
<i>Pellioiditis marina</i>	20	25	400	0.914	0.914	4.1	0	Vranken & Heip 1983

Table 4. *Monhystera disjuncta*. Weight-specific productivity (population level) at 12°C and 30‰S. The data are given in $\text{joule} \cdot \text{joule}^{-1} \cdot \text{day}^{-1}$; sP: total weight-specific productivity; sF: weight-specific fecundity; sG(A): weight-specific somatic growth of adults; sG(J): weight-specific somatic growth of juveniles; sE: weight-specific growth rate in the embryonic stage; contribution (%) of specific reproductive production (A) when hatchlings, (B) when deposited eggs are considered as reproductive units.

sP	sG(A)	sG(J)	sE	sF	A	B
0.176	negligible	0.108	-0.026	0.094	39%	53%

(Herman *et al.* 1984). In the stable age-distribution adult, somatic growth is negligible. In the embryonic stage production is negative because freshly deposited eggs are heavier than hatchlings. Gonad output accounts for 53% of the total production; when hatchlings are considered as the reproductive units, somatic growth is 61% and gonad output is reduced to 39% of the total P/B. Summation of the weight-specific production realized in the different life stages results in a value of 0.176 for the daily P/B, very close to the birth rate (0.181 per day).

Annual P/B and the life history of other species

From similar observations (Vranken 1985) we estimated net reproductiveity R_0 and birth rate of five other nematode species. These values are given in Table 3. Net reproductiveity ranges between 37 in the parthenogenetic species *Monhystrella parelegantula* and 246 in the most productive dioecious species *Chromadora nudicapitata*. When the pre-adult mortality is low, the birth rate approximately equals

Table 5. Annual P/B of free-living brackish water nematodes.

Species	Mean temperature, annual growth period (°C)	Duration, growth period (days)	Birth rate (J·J ⁻¹ ·day ⁻¹)	Annual P/B
<i>Diplolaimella dievengatensis</i>	16.0	196	0.135	26
<i>Monhystrella parelegantula</i>	16.0	200	0.108	22
<i>Monhystera disjuncta</i>	11.5	365	0.173	63
<i>Chromadora nudicapitata</i>	11.5	365	0.129	47
<i>Monhystera parva</i>	14.0	270	0.194	52
<i>Oncholaimus oxyuris</i> *	11.2	365	~0.010	~3.7

*Data after Heip *et al.* 1978.

the intrinsic rate of natural increase, but in some species the bias in using r_m is rather large, between 6% in *Monhystera disjuncta* and 13% in *Monhystrella parelegantula*.

Multiplication of the daily birth rate by the minimum generation time T_{\min} yields the turnover per generation. This ranges between 2.2 in *Monhystrella parelegantula* and 3.3 in *Chromadora nudicapitata*. *Pellioiditis marina*, an inhabitant of decaying seaweeds on the beach, has a P/B per T_{\min} of 4.1, the highest value found. The mean value of the life-cycle P/B is 3.1 (SE = 0.26) with *Pellioiditis marina* included or 2.9 (SE = 0.20) without.

Daily birth rate can be used to calculate the annual P/B when the duration of the growth period, when the species is reproducing, is known. We estimated this duration from the basal temperature (Table 2). Multiplication of the birth rate at the average temperature during the growth period with its duration gives the annual P/B. The annual P/B calculated in this way varies between 4 and 60 (Table 5).

The relationship between birth rate and temperature was studied in *Monhystera disjuncta* and *Diplolaimella dievengatensis*. For the first species a Q_{10} value of 3.3 was found for the interval 3-12°C. For *D. dievengatensis* the Q_{10} equals 4.2 in the 15-25°C interval. Vranken (1985) has also demonstrated that for similarly sized nematodes the birth rate (or daily P/B) is a linear function of temperature.

DISCUSSION

The important conclusions concerning the life history of marine and brackish water nematodes from our results are:

- a. Fecundity of marine nematodes may be much higher than 20 eggs (Gerlach 1971, Zaika & Makarova 1979); in some species fecundity can reach values as high as 400-500 eggs per female.

- b. The intrinsic rate of natural increase r_m at the optimum temperature is in all species studied higher than 0.2 per day, a value considered high for nematodes (Banse 1982).
- c. The number of generations realized in the field is, except for the slowly developing chromadorid *Paracanthochus caecus*, higher than three in all species studied by us.
- d. The biomass turnover per generation is close to three.
- e. There is no validity in assuming an annual P/B of nine for nematodes as a whole (and, *a fortiori*, for meiofauna as a whole).

Since the life-cycle turnover is close to three, a value also found in the field for meiobenthic crustaceans (Herman *et al.* 1984) and already predicted by Waters (1969), the only parameter to be estimated is the number of generations produced in the field per year in order to obtain a good estimate of the annual P/B. Our estimates, based on the development rate and the dependency on temperature, are maximum numbers since it is supposed that nematode reproduction in the field is continuous when temperature exceeds the basal temperature. However, there are indications that this assumption is not completely unjustified: in many nematode communities juveniles dominate all over the year and gravid females of many species occur at all seasons (see Heip *et al.* 1985 for a review).

The key factor in the field is probably food availability. Schiemer (1982) has shown how variations in food density significantly influence development rate of *Caenorhabditis briggsae*. At a level of 2×10^8 cells \cdot ml $^{-1}$ the development time of this species is ten days, at 5×10^{10} cells \cdot ml $^{-1}$ it is only three days. A similar reduction in development time at two food levels was found in *Plectus palustris*, where it was reduced from 18.5 to 12.5 days between suboptimal and optimal food levels (Schiemer *et al.* 1980). The threshold food densities where assimilation equals respiration are 0.025 mg dry weight per ml for *Plectus palustris* and 0.1 mg dry weight for the very productive *C. briggsae* (Schiemer 1983). Heip *et al.* (1985) compared published rates of bacterial production in shallow subtidal habitats with these figures and proposed that nematode productivity is not limited by food supply in coastal waters, where bacterial densities up to 8×10^9 cells per ml occur (Fallon *et al.* 1983). However, for marine nematodes no information about optimum food levels exists, and estimates of bacterial production are currently being questioned (Peter M.J. Herman, pers. comm.).

For the long-lived, relatively *K*-selected species there is good agreement between the number of generations realized in the field and predictions from laboratory cultures. *Oncholaimus oxyuris* has one or two generations per year in the Dievenгат (Smol *et al.* 1980) and this number was predicted from laboratory experiments (Heip *et al.* 1978). This also holds for three other species: *Adoncholaimus thalassophygas* cultured by Thun (1968) and observed in the Kiel Canal (Schütz 1966); *Oncholaimus brachycercus* cultured by Gerlach & Schrage (1972) and observed in

the Weser estuary (Skoolmun & Gerlach 1971), and *Anticomma limalis*, observed in Kiel by Schütz (1966), assuming its life cycle is similar to that of *Anticomma pellucida*. All these species produce only 1-2 generations annually.

Banse & Mosher (1980) hypothesized that the annual P/B ratio for meiofauna is low. To investigate this hypothesis we calculated annual P/B for all species on which reliable data on development have been published (data in Heip *et al.* 1985, and Vranken & Heip 1985). The annual P/B ranges from 1.5 in the large enoplid *Pontonema vulgare* to 69 for the fast-developing *Monhystera disjuncta*. The geometric mean is 16.4 (95% C.I. = 11.0-24.5). To compare with the equation presented by Banse & Mosher (1980) we calculated a linear least squares regression considering weight as the independent variable, assuming dry weight being 25% of wet weight and a calorie content of 5 kcal per g dry weight. A model II design being more appropriate, we also calculated the coefficients of a GM-regression analysis (Table 6). There is a highly significant correlation between log P/B and log M_s of $r = -0.91$. The equation is:

$$\log P/B = -1.288 - 0.440 \log M_s$$

However, this log-log relationship is not recommended as a tool for estimating annual P/B from weight because back-transformation to the linear scale can result into serious bias.

Table 6. Regression coefficients of P/B on M_s (kcal): $P/B = aM_s^b$; n = number of observations; C.I. = 95% confidence interval; r = correlation coefficient.

Model	n	a	C.I. for a	b	C.I. for b	r
I	30	0.05	0.02-0.15	-0.44	(±0.08)	-0.91**
II (GM-regression)	30	0.03	—	-0.48	(±0.08)	-0.91**

** : $P < 0.01$.

Weight-dependency of P/B is not significantly different from the value of 0.37 calculated by Banse & Mosher (1980) for invertebrates. The proportionality coefficient however is ten times smaller for nematodes. It is not easy to explain this. Herman *et al.* (1983) pointed out that there is no obvious reason why P/B ratios have to be correlated with body weight. Body weight depends on an interaction of a whole set of life history characteristics: food availability, length of pre-reproductive life, reproductive strategy, vulnerability to predation etc. The main factor determining P/B is development rate. In nematodes, development rate is correlated with body weight and temperature (Heip *et al.* 1985), so a correlation between P/B and M_s may be expected.

The reason for the low meiofauna P/B (low relative to their size) is, according to Banse & Mosher (1980) related to the fact that the meiofauna constitutes an independent food web, with low predation pressure and low mortality. Recent observations do not substantiate this: Pihl (1985) showed that several dominant

fish and crustaceans such as *Pomatoschistus microps*, *P. minutus*, *Pleuronectes platessa* and *Crangon crangon* mainly prey upon the meiofauna and calculated that up to 60% of the harpacticoids and 90% of the ostracods are consumed by these species. Hoffman *et al.* (1984) noted a ten-fold increase in nematode abundance when the fiddler crab *Uca pugnax* was eliminated from experimental enclosures. On the other hand, data for three harpacticoids confirm Banse & Mosher's hypothesis: the most productive species, *Tachidius discipes*, is indeed most vulnerable to predation (Herman *et al.* 1984, Heip & Smol 1976b).

The low P/B ratio of nematodes is certainly not a consequence of a low production efficiency ($P/P+R$). Banse (1979) summarized the data for 15 temperate invertebrate species and found values between 13 and 55%. Production efficiencies for meiobenthic crustaceans vary between 36% for the ostracod *Cyprideis torosa* and 43% for *Tachidius discipes* (Herman & Heip 1985). For nematodes, published values range from 38% for the freshwater species *Pelodera* sp. (Marchant & Nicholas 1974) up to values as high as 80-90% (Schiemer *et al.* 1980, Warwick 1981, Tietjen 1980, and Schiemer 1983). High nematode efficiencies have been considered as artefacts by Herman *et al.* (1984), but it is clear that production efficiency in nematodes is certainly not lower than for other invertebrates.

However, assimilation efficiency may be lower. Woombs & Laybourn-Parry (1985) give figures between 5 and 15%, with rare maxima of 20% for polysaprobic species. Species studied by Tietjen (1980) absorbed food with an efficiency between 6 and 26%. Food density may be important: *Plectus palustris* assimilated energy with an efficiency of 12% at high food levels but of 52% at low levels (Schiemer *et al.* 1980). In other invertebrates assimilation appears to be higher: 25-78% for the rotifer *Brachionus calyciflorus* (Winberg 1971), 79% for the cladoceran *Daphnia pulex* fed on green and blue-green algae (Arnold 1971), between 40 and 85% for the zoea and megalopa stages of *Menippe mercenaria* fed on *Artemia salina* (Kinne 1977). Other organisms, such as the ascidian *Pyura stolonifera* (Klumpp 1984), the bivalve *Mercenaria mercenaria* (Bricelj *et al.* 1984), the deposit-feeding gastropod *Hydrobia totteni* and the bivalve *Nucula annulata* (Lopez & Cheng 1983) and the mussel *Mytilus edulis* (Hawkins *et al.* 1985) also have higher assimilation efficiencies. The lower assimilation efficiency of nematodes has been ascribed to a high defaecation rate (Woombs & Laybourn-Parry 1985). The retention time of food in the gut is short and digestive enzymes, which may be present in low concentrations (Deutsch 1978), have a limited time to act. Whether low assimilation is related to low production is not clear, however.

REFERENCES

- Arnold, D.E., 1971. Ingestion, assimilation, survival, and reproduction by *Daphnia pulex* fed seven species of blue-green algae. – *Limnol. Oceanogr.* 16: 906-920.
- Banse, K., 1979. On weight dependence of net growth efficiency and specific respiration rates among field populations of invertebrates. – *Oecologia (Berlin)* 38: 111-126.
- Banse, K., 1982. Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. – *Mar. Ecol. Progr. Ser.* 9: 281-297.
- Banse, K. & S. Mosher, 1980. Adult body mass and annual production/biomass relationships of field populations. – *Ecol. Monogr.* 50: 355-379.
- Bricelj, V.M., A.E. Bass & G.R. Lopez, 1984. Absorption and gut passage time of microalgae in a suspension feeder: an evaluation of the ^{51}Cr : ^{14}C twin tracer technique. – *Mar. Ecol. Progr. Ser.* 17: 57-63.
- Crisp, D.J., 1971. Energy flow measurements. – In N.A. Holme & A.D. McIntyre (eds): *IBP Handbook 16: Methods for the study of marine benthos*, pp. 197-279. Blackwell Sci. Publ., Oxford.
- Deutsch, A., 1978. Gut ultrastructure and digestive physiology of two marine nematodes, *Chromadorina germanica* (Bütschli, 1874) and *Diplolaimella* sp. – *Biol. Bull.* 155: 317-335.
- Fallon, R.D., S.Y. Newell & S.C. Hopkinson, 1983. Bacterial production in marine sediments: will cell-specific measures agree with whole-system metabolism? – *Mar. Ecol. Progr. Ser.* 11: 119-127.
- Findlay, S.E.G. & K.R. Tenore, 1982. Effect of a free-living marine nematode (*Diplolaimella chitwoodi*) on detrital carbon mineralization. – *Mar. Ecol. Progr. Ser.* 8: 161-166.
- Gerlach, S.A., 1971. On the importance of marine meiofauna for benthos communities. – *Oecologia (Berlin)* 6: 176-190.
- Gerlach, S.A., 1978. Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. – *Oecologia (Berlin)* 33: 55-69.
- Gerlach, S.A. & M. Schrage, 1972. Life cycles at low temperatures in some freeliving marine nematodes. – *Veröff. Inst. Meeresforsch. Bremerh.* 14: 5-11.
- Hawkins, A.J.S., P.N. Salkeld, B.L. Bayne, E. Gnaiger & D.M. Lowe, 1985. Feeding and resource allocation in the mussel *Mytilus edulis*: evidence for time-averaged optimization. – *Mar. Ecol. Progr. Ser.* 20: 273-287.
- Heip, C., P.M.J. Herman & A. Coomans, 1982. The productivity of marine meiobenthos. – *Acad. Anal.* 44: 1-20.
- Heip, C. & N. Smol, 1976a. Influence of temperature on the reproductive potential of two brackish-water harpacticoids (Crustacea, Copepoda). – *Mar. Biol.* 35: 327-334.
- Heip, C. & N. Smol, 1976b. On the importance of *Protohydra leuckarti* as a predator of meiobenthic populations. – In G. Persoone & E. Jaspers (eds): *Proc. 10th Europ. Symp. Mar. Biol.*, Vol. 2: Population dynamics, pp. 285-296. Universa Press, Wetteren, Belgium.
- Heip, C., N. Smol & V. Absillis, 1978. Influence of temperature on the reproductive potential of *Oncholaimus oxyuris* (Nematoda: Oncholaimidae). – *Mar. Biol.* 45: 255-260.
- Heip, C., M. Vincx & G. Vranken, 1985. The ecology of marine nematodes. – *Oceanogr. mar. Biol. Ann. Rev.* 23: 399-489.
- Herman, P.M.J. & C. Heip, 1985. Secondary production of the harpacticoid copepod *Paranycho-campius nanus* in a brackish-water habitat. – *Limnol. Oceanogr.* 30: 1060-1066.
- Herman, P.M.J., C. Heip & B. Guillemijn, 1984. Production of *Tachidius discipes* Giesbrecht 1881 (Copepoda: Harpacticoida). – *Mar. Ecol. Progr. Ser.* 17: 271-278.
- Herman, P.M.J., C. Heip & G. Vranken, 1983. The production of *Cyprideis torosa* Jones 1850 (Crustacea: Ostracoda). – *Oecologia (Berlin)* 58: 326-331.
- Herman, P.M.J., G. Vranken & C. Heip, 1984. Problems in meiofauna energy-flow studies. – *Hydrobiologia* 118: 21-28.

- Hoffman, J.A., J. Katz & M.D. Bertness, 1984. Fiddler crab deposit feeding and meiofaunal abundance in saltmarsh habitats. – J. exp. mar. Biol. Ecol. 82: 161-174.
- Jacobs, L.J. & G. Vranken. Description of *Diplolaimella dievengatensis* n. sp. (Nematoda, Monhysteridae), an aquatic nematode of the Belgian coast. – Nematologica, in press.
- Kinne, O., 1977. Cultivation of animals: research cultivation. – In O. Kinne (ed.): Marine Ecology, vol. III, Cultivation, part 2, pp. 579-1293. Wiley & Sons, Chichester.
- Klumpp, D.W., 1984. Nutritional ecology of the ascidian *Pyura stolonifera*: influence of body size, food quantity and quality on filter-feeding, respiration, assimilation efficiency and energy balance. – Mar. Ecol. Progr. Ser. 19: 269-284.
- Lopez, G.R. & I.J. Cheng, 1983. Synoptic measurements of ingestion rate, ingestion selectivity, and absorption efficiency of natural foods in the deposit-feeding molluscs *Nucula annulata* (Bivalvia) and *Hydrobia totteni* (Gastropoda). – Mar. Ecol. Progr. Ser. 11: 55-62.
- Marchant, R. & W.L. Nicholas, 1974. An energy budget for the free-living nematode *Pelodera* (Rhabditidae). – Oecologia (Berlin): 237-252.
- Nisbet, R.M. & W.S.C. Gurney, 1982. Modelling fluctuating populations. – John Wiley & Sons, New York. 379 pp.
- Pihl, L., 1985. Food selection and consumption of mobile epibenthic fauna in shallow marine areas. – Mar. Ecol. Progr. Ser. 22: 169-179.
- Pinder, J.E. III, J.G. Wiener & M.H. Smith, 1978. The Weibull distribution: a new method for summarizing survivorship data. – Ecology 59: 175-179.
- Podamo, J., 1976. Ecometabolism of a shallow marine lagoon at Ostend (Belgium). V. General discussion. – In G. Persoone & E. Jaspers (eds): Proc. 10th Europ. Symp. Mar. Biol., Vol. 2: Population dynamics, pp. 549-562. Universa Press, Wetteren, Belgium.
- Schiemer, F., 1982. Food dependence and energetics of free-living nematodes. II. Life history parameters of *Caenorhabditis briggsae* (Nematoda) at different levels of food-supply. – Oecologia (Berlin) 54: 122-128.
- Schiemer, F., 1983. Comparative aspects of food dependence and energetics of freelifing nematodes. – Oikos 41: 32-42.
- Schiemer, F., A. Duncan & R.Z. Klekowski, 1980. A bioenergetic study of a benthic nematode, *Plectus palustris* De Man 1880, throughout its life-cycle. II. Growth, fecundity and energy budgets at different densities of bacterial food and general ecological considerations. – Oecologia (Berlin) 44: 205-212.
- Schütz, L., 1966. Ökologische Untersuchungen über die benthos-fauna im Nordostseekanal. II. Autökologie der vagilen und hemi-sessilen Arten im Bewuchs der Pfähle: Mikro- und Mesofauna. – Int. Revue ges. Hydrobiol. 51: 633-685.
- Skoolmun, P. & S.A. Gerlach, 1971. Jahreszeitliche Fluktuationen der Nematodenfauna im Gezeitenbereich des Weser-Ästuars (Deutsche Bucht). – Veröff. Inst. Meeresforsch. Bremerh. 13: 119-138.
- Smol, N., C. Heip & M. Govaert, 1980. The life-cycle of *Oncholaimus oxyuris* (Nematoda) in its habitat. – Anns Soc. r. zool. Belg. 110: 87-103.
- Taylor, F., 1981. Ecology and evolution of physiological time in insects. – Am. Nat. 117: 1-23.
- Tenore, K.R., J.H. Tietjen & J.J. Lee, 1977. Effect of meiofauna on incorporation of aged eelgrass, *Zostera marina*, detritus by the polychaete *Nephtys incisa*. – J. Fish. Res. Bd Can. 34: 563-567.
- Thun, W. von, 1966. Eine methode zur Kultivierung der Mikrofauna. – Veröff. Inst. Meeresforsch. Bremerh. 2: 277-280.
- Thun, W. von, 1968. Autökologische Untersuchungen an freilebenden Nematoden des Brackwassers. – Ph.D. thesis, University of Kiel. 72 pp.
- Tietjen, J.H., 1980. Microbial-meiofaunal interrelationships: a review. – In Microbiology 1980. VIII Conf. Amer. Soc. Microbiol. on Ecology, Feb. 7-10, 1979, Clearwater Beach, Florida, pp. 7-10. Amer. Soc. Microbiol. Washington DC, USA.

- Vranken, G., 1985. Een autoecologische studie van brakwaternematoden in laboratoriumomstandigheden. – Ph. D. thesis, State University of Ghent. 281 + 203 pp. (In Dutch.)
- Vranken, G. & C. Heip, 1983. Calculation of the intrinsic rate of natural increase, r_m , with *Rhabditis marina* Bastian, 1865 (Nematoda). – *Nematologica* 29: 468-477.
- Vranken, G. & C. Heip, 1985. Aspects of the life-cycle of free-living marine nematodes. – In R. Van Grieken & R. Wollast (eds): Progress in Belgian oceanographic research, pp. 267-278. Belg. Comm. Oceanol. & Belg. Centr. Oceanogr., Brussels, Belgium.
- Vranken, G., D. Van Brussel, R. Vanderhaeghen & C. Heip, 1984. Research on the development of a standardized ecotoxicological test on marine nematodes. I. Culturing conditions and criteria for two monhysterids, *Monhystera disjuncta* and *Monhystera microphthalmia*. – In G. Persoone, E. Jaspers & C. Claus (eds): Ecotoxicological testing for the marine environment, pp. 159-184. State Univ. Ghent and Inst. Mar. Scient. Res., Bredene, Belgium.
- Warwick, R.M., 1981. The influence of temperature and salinity on energy partitioning in the marine nematode *Diplolaimelloides brucei*. – *Oecologia* (Berlin) 51: 318-325.
- Waters, T.F., 1969. The turnover ratio in production ecology of freshwater invertebrates. – *Am. Nat.* 103: 173-185.
- Winberg, G.G., 1971. Methods for the estimation of production of aquatic animals. – Academic Press, London and New York. 175 pp.
- Woombs, M. & J. Laybourn-Parry, 1984. Growth, reproduction and longevity in nematodes from sewage treatment plants. – *Oecologia* (Berlin) 64: 168-172.
- Woombs, M. & J. Laybourn-Parry, 1985. Energy partitioning in three species of nematodes from polysaprobic environments. – *Oecologia* (Berlin) 65: 289-295.
- Zaika, V.E. & N.P. Makarova, 1979. Specific production of free-living marine nematodes. – *Mar. Ecol. Progr. Ser.* 1: 153-158.