

A re-evaluation of marine nematode productivity

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Keywords: nematodes, meiobenthos, production, P/B, generation time

Abstract

Nematodes are the most abundant multicellular animals in marine sediments but their role in the benthos has not been properly quantified yet. In nearly all energy-flow budgets of marine systems their annual production P is given as about nine times their mean biomass B and their part in the total energy-flow is consequently estimated as anywhere between 3 and 30% of the total (carbon) input in the benthic system. Our laboratory experiments demonstrate that nematode productivity is much higher than $P/B \sim 9$ per year and may reach values of over 60 for bacterial grazers. To obtain more reliable estimates for field populations we propose a regression equation relating egg-to-egg development time T_{\min} to temperature (t) and adult female weight (W in μg wet weight): $\log T_{\min} = 2.202 - 0.0461 t + 0.627 \log W$. When multiplied by the constant biomass turnover per generation $(P/B)_{\text{gen}} = 3$, development rate $1/T_{\min}$ is a good predictor of daily P/B . This method was applied to two series of field data. A rather stable community from a sublittoral mud in the North Sea had an annual $P/B = 20$. A less stable Aufwuchs community from *Sargassum* in Japan had an annual $P/B = 58$.

Density of marine nematodes is in the order of $10^5 - 10^6$ ind. per m^2 , their biomass usually ranges between 0.1 and 1 g dry weight per m^2 (Heip *et al.*, 1985). There is experimental evidence that they stimulate mineralisation of organic matter (Findlay & Tenore, 1982) and nutrient regeneration (Tietjen, 1980) by grazing on bacteria. They cycle an important proportion of the sediment pool of some heavy metals (e.g. Cd) (Frithsen, 1984). They are eaten by small crustaceans (Gerlach & Schrage, 1969; Feller, 1984) and fish (Lasserre *et al.*, 1976), thus forming a link between bacterial production and higher trophic levels. The rates of these processes are largely unknown. These rates may be estimated from energy flow through the populations (Crisp, 1971). An important part of the energy intake is channeled into biomass production. Production estimates of nematode populations in the sea do not exist: many species reproduce continuously throughout the year and the logistics of

sampling subtidal sediments also prohibit the use of the classical methods in production studies (analysis of growth or mortality of cohorts in the field). Nearly the whole literature on benthic productivity uses an annual P/B around nine (McIntyre, 1969; Gerlach, 1971; Warwick & Price, 1979) as representing the annual biomass turnover of marine nematodes and even meiofauna in general. Gerlach's estimate $P/B = 9$ is based on a study of one brackish-water species in the laboratory with a biomass turnover of three per generation. Three generations per year is an average for the few long-lived meiofauna species for which the life-cycle was known at the time. Warwick & Price (1979) calculated $P/B = 8.7$ from respiration measurements and the relationship between respiration and production proposed by McNeil & Lawton (1970).

A production in each generation of three times the average biomass is a valid figure for the several copepods, ostracods and nematodes where it has

been verified (Heip *et al.*, 1982; Herman *et al.*, 1984). Field data for nematodes do not exist. Since the birth rate of a population in the stable age distribution is equal to its daily P/B (Zaika, 1973) we constructed life tables for four species of nematodes cultured in our laboratory (Vranken, 1985). The average value obtained from these experiments was $P/B = 2.98 \pm 0.13$ ($n = 7$) per T_{min} . From these experiments it also became clear that fecundity of nematodes is much higher than previously thought. In a recent review (Zaika & Makarova, 1979) an average fecundity of twenty eggs per female was proposed. However, a single female of *Monhystera disjuncta* in agnotobiotic conditions (Dougherty, 1960) produces over 200 eggs during the 70 days that her productive adult life lasts, which represents more than fifteen times her own body weight (Vranken, 1985). When fed in monoxenic cultures on an optimal diet the figure rises to over 500 eggs. These eggs develop into adults within two weeks. The rhabditid *Pellioiditis marina* has an even higher reproductive potential, producing over 600 eggs per female which mature in less than five days (Vranken & Heip, 1983).

For most marine nematodes studied the average duration of egg-to-egg development is in the order of two to three weeks at the annual mean temperature in the habitat. This indicates maximum annual P/B ratios in the order of 50 to 70. For the best studied species, *Monhystera disjuncta*, the yearly P/B was estimated as 69 from three times the number of generations produced in the field calculated from development time and temperature (Vranken & Heip, 1985) and as 66 from the daily birth rate, which is a linear function of temperature in all species studied (Vranken & Heip, 1985). These figures are almost an order of magnitude higher than assumed in the literature.

In order to better assess the productivity of marine nematodes in the sea we calculated a multiple linear regression between duration of egg-to-egg development T_{min} and temperature t ($^{\circ}C$) and adult female body weight W (in μg wet weight) for all species from temperate areas (maximum temperature lower than $22^{\circ}C$) for which reliable data exists (Table 1). The resulting equation (1) has a temperature coefficient corresponding to a $Q_{10} = 2.95$ and a very steep dependence on body weight, indicating that the spectrum of biomass in a nematode community will strongly influence its production:

Table 1. List of species used to calculate the relationship of T_{min} versus temperature and body weight; data coded 1 are compiled by Heip *et al.* (1985); others, labeled 2 are from Vranken & Heip (in press).

Species	Reference
<i>Monhystera denticulata</i>	1
<i>Monhystera parva</i>	2
<i>Monhystera disjuncta</i>	1, 2
<i>Diplolaimella spec. 1</i>	2
<i>Diplolaimelloides brucei</i>	1
<i>Theristus pertenuis</i>	1
<i>Chromadora nudicapitata</i>	1, 2
<i>Neochromadora poecilosomoides</i>	Vranken, 1985
<i>Paracanthochus caecus</i>	2
<i>Chromadorita tenuis</i>	Jensen, 1983
<i>Eudiplogaster pararmatus</i>	1
<i>Oncholaimus oxyuris</i>	1

$$\log T_{min} = 2.202 - 0.0461 t + 0.627 \log W \quad (1)$$

$$(R^2 = 0.88; F(2,46) = 173; n = 49)$$

As an example eq. (1) was used to determine the annual production of a subtidal community from a muddy sediment (median grain size $45 \mu m$) off the Belgian coast in the North Sea (Vincx & Heip, 1984) and from an Aufwuchs community on *Sargassum confusum* in Japan (Kito, 1982). The North Sea station is polluted and characterized by a low diversity community dominated by *Sabatieria punctata* (av. 84.5%) and *Daptonema tenuispiculum* (av. 8.4%). The biomass structure (males, females and juveniles) was determined each month. The average biomass was $1.10 g$ ww per m^2 . The P/B was calculated for each month as $1/T_{min} \times D \times 3$, with D the number of days in the month. Total production so calculated amounted to $22.2 g$ ww per m^2 per year and the annual P/B of this community is $P/B = 20$. The Aufwuchs community from *Sargassum* showed a marked seasonality with maximum numbers in Spring and Summer and virtually disappeared in Winter. *Monhystera refringens*, *Chromadora nudicapitata*, *Araeolaimus elegans* and *Theristus acer* were the five dominant species. The average biomass of this community, again determined from monthly samples, was $157 mg$ ww per m^2 , its annual production $9144 mg$ ww per m^2 . The annual $P/B = 58$. The calculation proposed here still has speculative aspects. These include two extrapolations: 1) laboratory rates are used to estimate development

rates in the field; and 2) data based on a limited number of species are extrapolated to all species in a community. Our equation is based on all the reliable data available in the literature and includes 15 populations belonging to 12 species. For *Oncholaimus oxyuris*, *Eudiplogaster pararmatus* and *Chromadora nudicapitata* we dispose of data on growth rates in the field and in laboratory conditions (Heip *et al.*, 1978; Smol *et al.*, 1980; Romeyn *et al.*, 1983; Vranken, 1985). These show a good agreement between development rates realized in the field, and those predicted from laboratory experiments. Although very limited, this data set suggests that our first extrapolation may be valid.

The second extrapolation, from the limited set of cultured species to all species in a community, is the most far-reaching assumption in our method. Three species (*Oncholaimus oxyuris*, *Paracanthochus caecus* and *Eudiplogaster pararmatus*), possess either low fecundity or slow development rates and may be considered relatively 'conservative' species. The majority of our data are from opportunistic species able to realize high population growth rates (Heip *et al.*, 1985). This of course, reflects a quite 'natural' selection by experimental nematologists. Nematode-communities in the field, especially of subtidal sediments, are often dominated by more conservative species. Due to the inclusion of many opportunistic species, our equation may overestimate the productivity of these communities. Unless more dominant species from marine communities are cultured, we cannot assess the importance of this factor. In any case, in our data set the more 'conservative' species did not deviate in a systematic way from the pattern shown by the other species. Body weight may well be a good predictor of the strategy of a particular species.

In a similar approach to the one adapted here, Vranken & Heip (1985) showed a relationship between egg weight and embryonic development time at 20°C. This relationship predicted the embryonic development time of *Sabatieria punctata* from the sluice dock of Ostend (Belgium), which was not included in the data-set, exactly (prediction: 9.87 d, experimental: 9.92 d). Unfortunately we were not able to maintain the cultures long enough to determine generation times.

Our regression equation is a new tool to estimate nematode production indirectly, requiring only knowledge of the biomass spectrum of the nema-

tode community in the field and of the annual temperature regime of the habitat. Other methods to determine productivity of field populations, indirectly have been reviewed by Heip *et al.* (1985).

In our opinion, the use of a single P/B value for nematodes, and a fortiori for the meiofauna as a whole is invalid. Nematode productivity, especially that of members of 'Aufwuchs' communities may be much higher than previously thought. Nematodes are a significant component in the energy flow in shallow-water marine ecosystems.

Acknowledgements

This paper results from research under contracts from the Ministry of Scientific Policy (Concerted Actions Oceanography), the Fund for Collective Fundamental Research (grant 2.9007.82) and the Commission of the European Communities (grants ENV-556-B and ENV-767-B).

Peter Herman and Carlo Heip acknowledge a grant from the Belgian National Fund for Scientific Research NFWO. The authors wish to thank Dr. R. M. Warwick for his valuable comments on the manuscript.

References

- Crisp, D. J., 1971. Energy flow measurements. In: N. A. Holme & A. D. McIntyre (eds), *Methods for the study of marine benthos*, IBP Handbook 16. Blackwell Sci. Publ., Oxford & Edinburgh: 197–279.
- Dougherty, E. C., 1960. Cultivation of Aschelminthes, especially rhabditid nematodes. In: J. N. Sasser & W. R. Jenkins (eds), *Nematology. Fundamentals and recent advances, with emphasis on plant parasitic forms*. Chapel Hill, Univ. Nth. Carolina Press: 297–318.
- Feller, R. J., 1984. Serological tracers of meiofaunal food webs. *Hydrobiologia* 118: 119–125.
- 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.
- Frithsen, J. B., 1984. Metal incorporation by benthic fauna: relationships to sediment inventory. *Estuar. coast. shelf Sci.* 19: 523–539.
- Gerlach, S. A., 1971. On the importance of marine meiofauna for benthos communities. *Oecologia (Berl.)* 6: 176–190.
- Gerlach, S. A. & M. Schrage, 1969. Freilebenden Nematoden als Nahrung der Sandgernele *Crangon crangon*. Experimentelle Untersuchungen über die Bedeutung der Meiofauna als Nahrung für das marine Makrobenthos. *Oecologia (Berl.)* 2: 362–375.

- 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., P. M. J. Herman & A. Coomans, 1982. The productivity of marine benthos. *Acad. Anal.* 44: 1–20.
- Heip, C., M. Vincx & G. Vranken, 1985. The ecology of marine nematodes. *Oceanogr. Mar. Biol. annu. Rev.* 23: 399–489.
- Herman, P. M. J., G. Vranken & C. Heip, 1984. Problems in meiofauna energy-flow studies. *Hydrobiologia* 118: 21–28.
- Jensen, P., 1983. Life history of the free-living marine nematode *Chromadorita tenuis* (Nematoda: Chromadorida). *Nematologica* 29: 335–345.
- Kito, K., 1982. Phytal marine nematode assemblages on *Sargassum confusum* Agardh, with reference to the structure and seasonal fluctuations. *J. Fac. Sci. Hokkaido Univ., VI, Zool.* 23: 143–161.
- Lasserre, P., J. Renaud-Mornant & J. Castel, 1976. Metabolic activities of meiofaunal communities in a semi-enclosed lagoon. Possibilities of trophic competition between meiofauna and mugilid fish. In: G. Persoone & E. Jaspers (eds), *Population dynamics, Proc. 10th eur. Symp. Mar. Biol.*, vol. 2. Universa Press, Wetteren: 393–414.
- McIntyre, A. D., 1969. Ecology of marine meiobenthos. *Biol. Rev.* 44: 245–290.
- McNeil, S. & J. H. Lawton, 1970. Annual production and respiration in animal populations. *Nature* 225: 472–474.
- Romeyn, K., L. A. Bouwman & W. Admiraal, 1983. Ecology and cultivation of the herbivorous brackish-water nematode *Eudiplogaster pararmatus*. *Mar. Ecol. Progr. Ser.* 12: 145–153.
- Smol, N., C. Heip & M. Govaert, 1980. The life cycle of *Oncholaimus oxyuris* (Nematoda) in its habitat. *Annls. Soc. r. Zool. Belg.* 110: 87–103.
- Tietjen, J. H., 1980. Microbial meiofaunal interrelationships: a review. In: *Microbiology, 1980, VIII Conf. am. Soc. Microbiol. on Ecology*. Am. Soc. Microbiol., Washington D.C., USA: 335–338.
- Vincx, M. & C. Heip, 1984. Composition and seasonal fluctuations of the nematode community in a silty station off the Belgian coast. *Concerted Actions Oceanography. Report to the Ministry of Scientific Policy, Brussels, Belgium*: 87–100.
- Vranken, G., 1985. Een autoecologische studie van brakwater-nematoden in laboratoriumomstandigheden (in Dutch). Ph.D. Thesis, State Univ. Gent, 281 + 203 pp.
- 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*. Belg. Comm. Oceanol. & belg. Centr. Oceanogr., Brussels, Belgium: 267–278.
- Vranken, G. & C. Heip. The productivity of marine nematodes. *Ophelia* (in press).
- Warwick, R. M. & R. Price, 1979. Ecological and metabolic studies on free-living nematodes from an estuarine mudflat. *Estuar. coast. mar. Sci.* 9: 257–271.
- Zaika, V. E., 1973. Specific production of aquatic invertebrates. Halsted Press, J. Wiley & Sons, N.Y., 154 pp.
- Zaika, V. E., & N. P. Makarova, 1979. Specific production of freelifving marine nematodes. *Mar. Ecol. Progr. Ser.* 1: 153–158.