A re-evaluation of marine nematode productivity

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Key-words : 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 ~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) : $\log T_{min} = 2.202-0.0461t + 0.627 \log W$. When multiplied by the constant biomass turnover per generation $(P/B)_{gen} = 3$, 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 ± 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 *Pelliodítis 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 (°C) and adult female body weight W (in µg wet weight) for all species from temperate areas (maximum temperature lower than 22° C) for which reliable data exist (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 :

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

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

As an example eq. (1) was used to determine the annual production of a subtidal community from a muddy sediment (median grain size 45 µm) 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, Chromadora heterostomata, 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, Paracanthonchus 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 of species 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 vulgaris* 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 nematode 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.

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
Monhystera denticulata	1
Monhystera parva	2
Monhystera disjuncta	1,2
Diplolaimella spec. 1	2
Diplolaimelloides bruciei	1
Theristus pertenuis	1
Chromadora nudicapitata	1,2
Neochromadora poecilosomoides	Vranken, 1985
Paracanthonchus caecus	2
Chromadorita tenuis	Jensen, 1983
Eudiplogaster pararmatus	1
Oncholaimus oxyuris	1

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