# COLLECTED PAPERS

ON

# MEIOFAUNA DYNAMICS AND ENERGY FLOW

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# The Life-Cycle of *Cyprideis torosa* (Crustacea, Ostracoda)*

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**Summary.** The life-cycle of the dominant brackish water ostracod *Cyprideis torosa* (Jones, 1850) has been studied during 4 years. The species has only one generation anually. Reproduction is fairly similar throughout the years and appears to be tuned in to temperature. The number of adults has one peak every year and can be described by two exponential functions, one for the increase and one for the decrease. Mortality is very similar every year and approximately constant for months. *Cyprideis torosa* is on top of the food chain: regulation of numbers is probably not external and may be a function of the past of the habitat. A model is described which permits the evaluation of the duration of development from field data only. Predicted values are in good agreement with observed values.

## Introduction

*Cyprideis torosa* (Jones 1850) [= *C. littoralis* (Brady 1868)] is a dominant species of the meiobenthos in brackish water areas throughout Europe; it occurs in North America, Asia, and Africa as well. The distribution of the species has been reviewed by Vesper (1972). *Cyprideis torosa* is a holeuryhaline and strongly eurythermic species, but its main distribution is on soft sediments of shallow brackish water habitats where large amounts of organic detritus are present. Hartmann (cit. Vesper, 1972) has observed that the entire sediment seems to consist of this species at times, while Redeke (1936) has found that the valves constitute a characteristic component of the sediment of the former Zuiderzee (now IJsselmeer) in the Netherlands. Remane (1941) defined the benthic biocoenosis of shallow brackish bays (Stillwasserbuchten) as the *Cyprideis-Manayunkia* community, herewith clearly stressing the importance of the species in these biotopes.

Information on the life-cycle of meiobenthic organisms is still scarce and only slowly accumulating. The life-cycle of ostracods in particular has been studied

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only on a few occasions. The important studies concerning brackish water and benthic marine species are those of Elofson (1941), Hagerman (1966, 1968, 1969), Theisen (1966), and Muus (1967). All these authors worked in Scandinavian waters and all have given information on *C. torosa* but their material was insufficient to permit detailed analysis. Because of the importance of this species in large areas and in view of the scarcity of data on meiobenthos we have followed the changes in numbers of a population of *C. torosa* for nearly seven years.

As Watt (1970) observed, ecology is remarkably short of long runs of data. If one wishes to study patterns of fluctuations over long periods of time in order to assess the relative impact of density-dependent and density-independent factors on the population dynamics of a species one needs data of a type which are not frequently collected.

The number of factors which influence the number of individuals in a population is probably very large. As it is impossible to solve systems of $n$ equations with more than $n$ unknowns it appears that a very large number of years is required to discern between the influence of factors following a yearly cycle. The number of relevant factors may be substantially smaller than the total number of influences, but it still appears improbable that one or two years of investigation will suffice to prove anything about regulation of numbers in a population which inhabits an environment where yearly cycling factors prevail.

In the habitat I examined, the number of possible regulating factors will be smaller than in other habitats: it is well known that the number of species is smaller in brackish water habitats than in either fresh water or the sea. Moreover, the habitat in question, a pond in a polder, is very recent, originating from 1872 when the polder was diked, and the number of species is consequently still lower than in comparable habitats. Careful analysis has revealed the presence of only two molluscs, three polychaetes, six higher crustaceans (of which two were only found once), one insect larva and three fishes (of which one very rare). Numbers of meiobenthic species are somewhat higher, with about twenty species of nematodes (Smol, personal communication), eleven species of copepods and four species of ostracods (Heip, 1971). The polyp *Protohydra leuckarti* is also present.

## Material and Methods

Samples were collected fortnightly from August 1968 till now (February 1976) with the exception of a 6-month period from August 1969 till November 1969. The series is still being continued, giving values of population density and composition for nearly 8 years. This paper reports the analysis of 4 years (August 1968 till December 1972).

Three samples were taken with a glass tube covering a surface area of 6 $cm^2$ to a depth of 5 cm. It had been proven that ostracods do not descend into the anaerobic layers of the sediment, which extend below 1 or 2 cm from the surface. The sediment which is sampled covers the bottom of a very shallow brackish water pond, called Dievengat and situated in northern Belgium. The sediment is a fine sand (median grain size 0.223 mm), well sorted and covered with large amounts of detritus, derived from reed beds (*Phragmites communis*) at the border. Depth at the sampling station is approximately 10 cm.

The samples were fixed with alcohol 70% or Formalin 4‰, brough to and elutriated in the laboratory, using the method described by Barnett (1968). In this method the sample is put on a horizontal trough, 90 cm lang and 2 cm wide. Tapwater is allowed to run over the sample for about

**Table 1.** Length of the larval stages and the adults of *C. torosa*. Mean length and standard error from *n* observations

| Stage | Mean length | *n* |
|---|---|---|
| I | 0.132 ± .005 mm | 9 |
| II | 0.167 ± .002 mm | 10 |
| III | 0.208 ± .004 mm | 9 |
| IV | 0.267 ± .002 mm | 50 |
| V | 0.328 ± .001 mm | 90 |
| VI | 0.415 ± .001 mm | 117 |
| VII | 0.555 ± .003 mm | 74 |
| VIII | 0.741 ± .003 mm | 130 |
| ♀♀ | 0.966 ± .005 mm | 95 |
| ♂♂ | 1.028 ± .008 mm | 15 |

30 min. The sand is periodically stirred with the aid of a siphon. Although it allows only small samples to be treated, this method is superior to other elutriation methods for ostracods, which pose problems because of their heaviness.

After elutriation and separation from the detritus the animals were counted. Distinction was made between the sexes, females carrying or not carrying eggs and the eight larval stages. Because it proved to be difficult to separate the first three larval stages under the dissecting microscope they were counted together. The distinction between the larvae was made by grouping them according to their size; this is possible because increases in size occur during moults and differences between individuals belonging to the same stage are much smaller than differences between the mean size of the stages (Table 1).

Several physico-chemical parameters were measured at the same time: temperature was recorded continuously with the aid of a Ryan D-30 recorder with a precision of 1° C and measured fortnightly with a thermometer with a precision of 0.1° C. Salinity was calculated from chlorinity determined with Mohr's method by using Knudsen's formula $S = 1.805\ Cl + 0.03$. Oxygen in the water was measured with Winkler's method. Several other parameters which were recorded, e.g. nutrients and chlorophyll, will not be discussed here.

In order to smooth the curves of density changes the value obtained from the middle of three samples succeeding in time was replaced by the running average of the three sample values. This allowed for the processing of only one sample when density was low and but two samples when numbers were changing rapidly. Knowledge of the spatial pattern of this species (Heip, 1976) and the application of an exponential model for the temporal pattern made it possible to prove that the running average gives better estimates of density at a particular date than the sample value at that date (Heip, 1973). This substitution is only valid within a certain range of the value of $r$, the rate of change of the exponential function $N_t = N_0 e^{rt}$. Values obtained in this study all fall in this range. However, by using the running average the peak density is underestimated when it is a maximum and overestimated when it is a minimum. Therefore, in the case of peaks we used sample values.

To describe the temporal pattern of density we used the simplest model available, i.e. the exponential function $N_t = N_0 e^{rt}$, in which $N_t$ is the number at time $t$, $N_0$ the number at the beginning and $r$ the rate of change (positive or negative) observed during the period of time $t$. $r$ and time must be in the same units, which were days in our study. The exponential function was calculated by regression of numbers against time for each period of continuous increase or decrease. Numerous calculations showed that there was very little difference between the value of $r$ as calculated from the running average or from the sample values, estimates being generally somewhat lower when using the former.

The use of the exponential function calculated by regression of numbers against time permits inference on the date at which density changes reverse direction, i.e. the date of minimum or maximum abundance. When the first change is described by $N_1 e^{r_1 t_1}$ and the second by $N_2 e^{r_2 t_2}$, the intersection, most easily calculated from the logarithms of the numbers, is given by $\ln N_1 + r_1 t_1 = \ln N_2 + r_2 \Delta t$, from which $\ln (N_1/N_2) = r_2 \Delta t - r_1 t_1 = r_2 \Delta t - r_1 (t_2 + \Delta t)$ and:

$$\Delta t = \frac{\ln (N_1/N_2) + r_1 t_2}{r_2 - r_1}$$

in which $t_1$ is the time between $N_1$ and the intersection, $t_2$ is the time between $N_1$ and $N_2$ and $\Delta t$ is the time to add to or to substract from $t_2$ in order to find the time at intersection.

It was thought unnecessary to reproduce the extensive tables used in the calculations. They are available from the author on request.

## Results

### *The Adults*

The number of adults (Fig. 1) has one peak every year, with the exception of 1969 when a secondary peak occurred in February. The percentage of adults lies between 10 and 40% throughout the year (Fig. 2) and the majority of them are females at all times (Fig. 1). Numbers vary between a minimum of 20,000 to 40,000 individuals per $m^2$ and a maximum which differs widely in different years.

By using the exponential function to describe the two density movements each year it is possible to obtain an estimate of the rate of change $r$ and the date of minimum and maximum abundance. Values of these parameters are given in Table 2. As can be seen from this table there is good agreement between the dates of minimum abundance in the different years; the number of adults starts to rise in the beginning of April (earliest date: 5 April 1971, latest date: 15 April 1972). The time at which maximum abundance is attained differs much more widely, being at the end of July in 1970 and at the beginning of August in 1971, but much later, at the end of October, in 1972. In 1969, the peak falls in the missing period. Interpolation between the rising curve from April 1969 onwards and the falling curve from December 1969 onwards gives 7 September 1969 as the date of maximum abundance with an improbably high figure of 744,000 individuals per $m^2$ as maximum density. It seems more likely that in autumn 1969, as in the spring of the same year, there occurred a second peak in the number of adults.

In Table 2 the rate of increase is compared with the duration of the increase and the mean temperature of the water during the increase. There is a perfect correlation ($r=1$) between the rate of increase and the mean temperature during the increase. The relationship is given by $r=-0.114+0.0080\,T$ or $r=-0.097+0.0064\,T_s$, in which $T$ is the mean temperature as measured by the recorder and $T_s$ is the mean temperature measured fortnightly with a thermometer. $r=0$ for $T=14.2$ °C and $T_s=15.2$ °C. Mean temperature must be higher than these values to permit development. The correlation between duration of increase and temperature is not significant; neither appears there to be a significant correlation between the duration and the rate of increase ($r=-0.786$), but the by far longest duration in 1972 corresponds to the by far smallest rate of increase, whereas the difference in the other two years appears to be insignificant.

The value of $r$ during the exponential decrease of density from the peak to the minimum abundance in April is a measure of adult mortality $r=-d$. These values are given in Table 3, from which it is clear that they are very similar in different years.

I also made a comparison between the sexes which showed little difference. The mean values of four years are given in Table 4. The sex-ratio, defined here

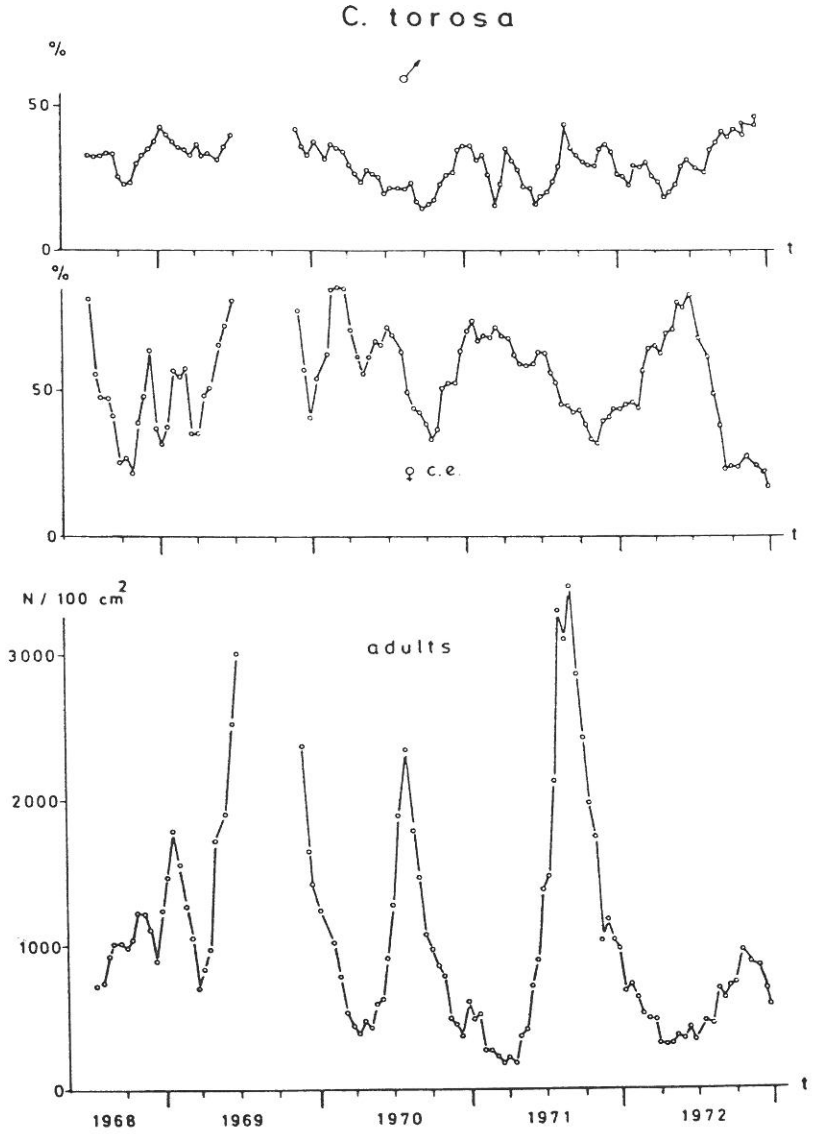


**Fig. 1.** *Cyprideis torosa*: numbers per 100 cm², percentage of females carrying eggs on the total number of females and percentage of males on the total number of adults

as the percentage of males in the adult population, yields information on periods when moulting from stage VIII to adults occurs (Fig. 1). Migration and patchiness are disregarded in this case. Heip (1976) has shown that there is a significant correlation between the numbers of males and females in samples from different locations, hereby ruling out spatial differences as a consistent source of sex-ratio changes. Differential migration is very improbable since there are no signs that migration occurs in this species at all.


**Fig. 2.** *Cyprideis torosa*: percentage of juveniles in the population

**Table 2.** Characterisation of the period during which the number of adult *C. torosa* increased ($T$ = temperature recorded continuously; $T_s$ = temperature recorded for nightly while sampling)

| Year | Minimum (date of) | Maximum (date of) | Duration (days) | $r$ (per day) | $T$ | $T_s$ |
|---|---|---|---|---|---|---|
| 1969 | 9 Apr | – | – | .0153 | – | 16.5 |
| 1970 | 13 Apr | 27 Jul | 105 | .0161 | 16.2 | 17.7 |
| 1971 | 5 Apr | 7 Aug | 124 | .0243 | 17.2 | 19.0 |
| 1972 | 15 Apr | 24 Oct | 192 | .0058 | 14.9 | 16.1 |

**Table 3.** *C. torosa:* Rates of change in adult numbers during the annual period of decrease.

| Period | $-r$ (per day) |
|---|---|
| 1969–1970 | .0138 |
| 1970–1971 | .0095 |
| 1971–1972 | .0099 |
| 1972–1973 | .0098 |

**Table 4.** Life-cycle characteristics of females and males of *C. torosa*. Mean values of 4 years

| | Rate of increase $r$ (per day) | Rate of decrease $-r$ (per day) | Duration of increase (days) |
|---|---|---|---|
| ♀♀ | .0158 | .0105 | 135 |
| ♂♂ | .0163 | .0105 | 142 |

The percentage of males is clearly at a minimum on 20 Sep 68, 30 Sep 70, 17 Mar 71, 23 Jun 71, 2 Feb 72, 26 Apr 72, and 3 Aug 72. Less clear are minima on 12 Jun 69, 5 May 70, 1 Jul 70, 10 Nov 71, and 28 Sep 72. Although it is not always clear if these minima are real, the general pattern is fairly consistent over the years, changes in sex-ratio occurring three times a year. The first change occurs in Spring during the period of minimum abundance, the second change around July (somewhat later in 1972) during the increase when there are large numbers in the population, the third change in Autumn or in early Winter when numbers are decreasing.

Other information about periods of reproduction is given by the percentage of females carrying eggs (Fig. 1) in the female population. This percentage follows a clearly defined cycle, except for 1968–1969. The percentage of females carrying eggs is at a minimum in Autumn, the lowest point being on 18 Nov 68, 31 Dec 69, 14 Oct 70, 10 Nov 71, and 13 Sep 72 (in 1972–1973 the percentage starts to rise later than 7 Dec 72). There are much less well defined minima in February and April–May in most years. These minimum percentages are probably the consequence of egg-laying in late Winter, and of moulting in Spring. It is not always easy to distinguish between the possible causes of a decrease in the percentage of females carrying eggs. This may result from either the laying of eggs or from intense moulting resulting in many new adult females not carrying eggs at first. However, the relative increase of females carrying eggs after the deep Autumn minimum is certainly a consequence of the laying eggs, because there is no development at that time.

### *The Larvae*

Comparison between the results obtained before and after the 6-month period between August and November 1969 showed that the number of young larval stages I to IV had been seriously underestimated in the first sample. For this reason the analysis of larval numbers will be restricted to the samples from 9 Dec 69 anwards.

In Figure 3 the density of the eight larval stages is shown. As mentioned before, the difficulty of separating the three youngest stages obliged us to count them as one group. The four younger stages show one peak each year. Stage V is somewhat intermediate, showing one peak in 1971 but probably two in 1970 and 1972. The three older stages have more than one peak every year.

By using the same procedure for the larval stages as for the adults, i.e. calculation of the exponential regression of numbers against time, and calculation of the intersections between the regression curves, it is possible to obtain estimates of the dates of minimum and maximum abundance, the rates of increase and the duration of changes in population density.

The dates of minimum abundance of the larval stages are given in Table 5. The first young larvae appear at the end of March with remarkable constancy every year. Stage IV increases from mid-May onwards, stage V from the beginning of June, stage VI from mid-June, stage VII from near the end of June, and stage VIII from the beginning of July onwards.

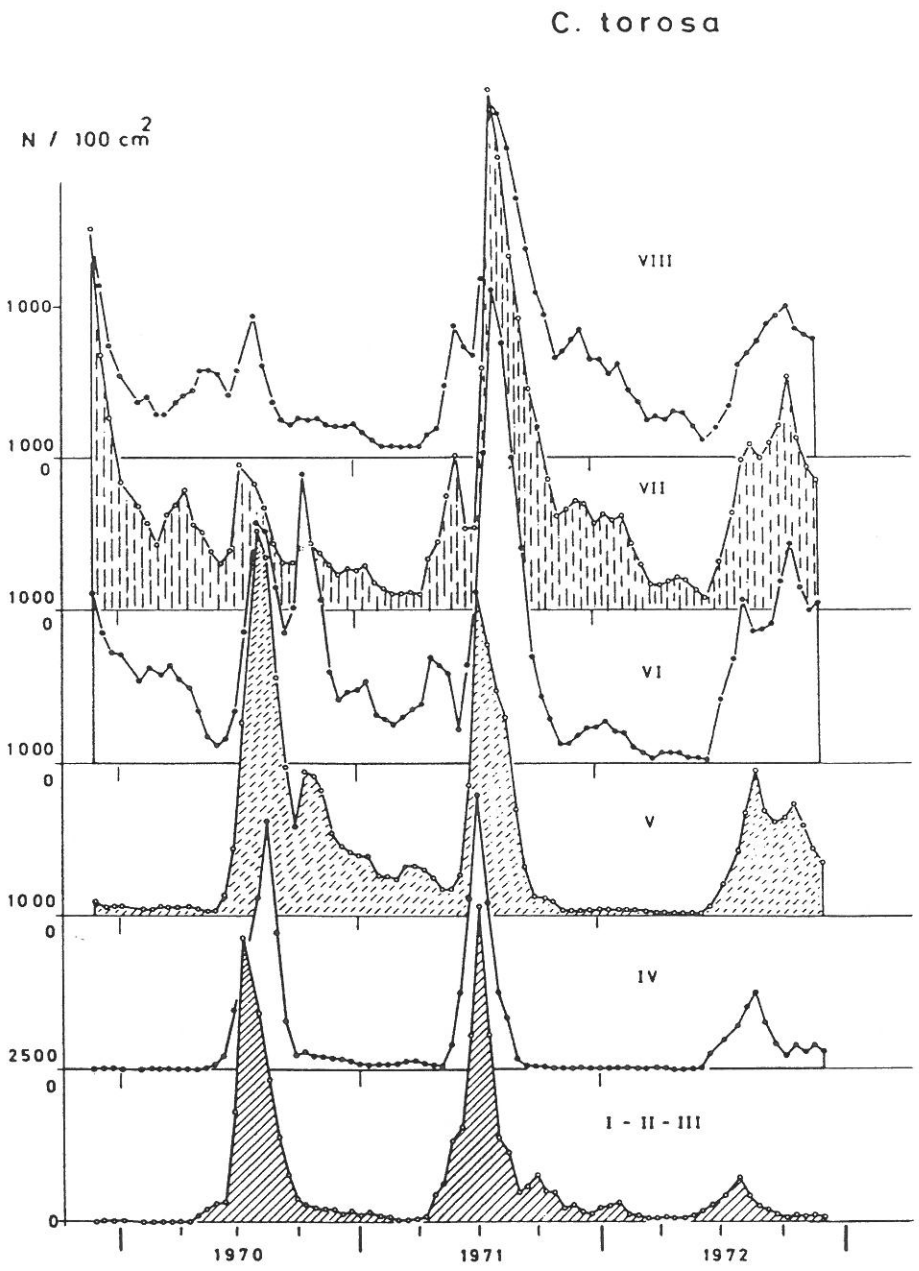


Fig. 3. *Cyprideis torosa*: numbers per 100 cm$^2$ of the eight larval stages, from 1969 to 1972

**Table 5.** Dates of minimum abundance of larval and adult stages of *C. torosa*

| | 1970 | | | 1971 | | | 1972 | | |
|---|---|---|---|---|---|---|---|---|---|
| I-II-III | | 29 Mar | | | 24 Mar | | | 31 Mar | |
| IV | | 16 May | | | 8 May | | | 8 May | |
| V | | 1 Jun | | | 27 May | | | 6 Jun | |
| VI | | 4 Jun | 19 Sep | 28 Feb | 10 Jun | 16 Nov | | 13 Jun | 3 Sep |
| VII | 7 Mar | 19 Jun | 20 Sep | 7 Apr | 30 Jun | 14 Nov | 8 Apr | 17 Jun | 15 Sep |
| VIII | 14 Mar | 2 Jul | 27 Sep | 11 Apr | 7 Jul | 17 Nov | 13 Apr | 15 Jun | |
| Ad. | 13 Apr | | | 5 Apr | | | 15 Apr | | |

**Table 6.** Dates of maximum abundance of larval stages and adults of *C. torosa*

| | 1970 | | | 1971 | | | 1972 | | |
|---|---|---|---|---|---|---|---|---|---|
| I-II-III | | 20 Jul | | | 4 Jul | | | 28 Jul | |
| IV | | 16 Aug | | | 7 Jul | | | 13 Aug | |
| V | | 2 Aug | 10 Oct | | 11 Jul | | | 26 Aug | 13 Oct |
| VI | | 5 Aug | 9 Oct | 4 May | 7 Aug | | 9 Jan | 12 Aug | 26 Oct |
| VII | 19 Apr | 19 Jul | 25 Oct | 7 Jun | 4 Aug | 4 Dec | 12 May | 23 Aug | 25 Oct |
| VIII | 31 May | 3 Aug | 31 Oct | 11 Jun | 6 Aug | 19 Dec | 23 May | 9 Oct | |
| Ad. | | 27 Jul | | | 7 Aug | | | 24 Oct | |

**Table 7.** Duration of larval development of *C. torosa* and mean temperature during that period

| | Duration of development (days) | Mean temperature (°C) |
|---|---|---|
| 1970 | 129 | 15.1 |
| 1971 | 133 | 15.5 |
| 1972 | 152 | 15.4 |

The peak for all stages is attained in July or August, except for the larger ones in 1972 when this occurs much later (Table 6). These larger stages show more than one cycle each year. A second period of increase starts in September (1970, 1972) or November (1971) and gives rise to peaks in October and December which are much smaller than the main one in summer. The third period of increase is in March-April, preceding the increase of the adults in April.

In Table 7 the duration of total development as measured from the dates at which the numbers begin to increase, and the mean temperature during this period, is given. There is a rather large difference in duration of development between 1970 and 1971 on the one hand and 1972 on the other hand although the mean temperature during development is rather similar.

The information from Tables 5 and 6 has been summarized in Figure 4 in which the length of the lines corresponds to the duration of increase.

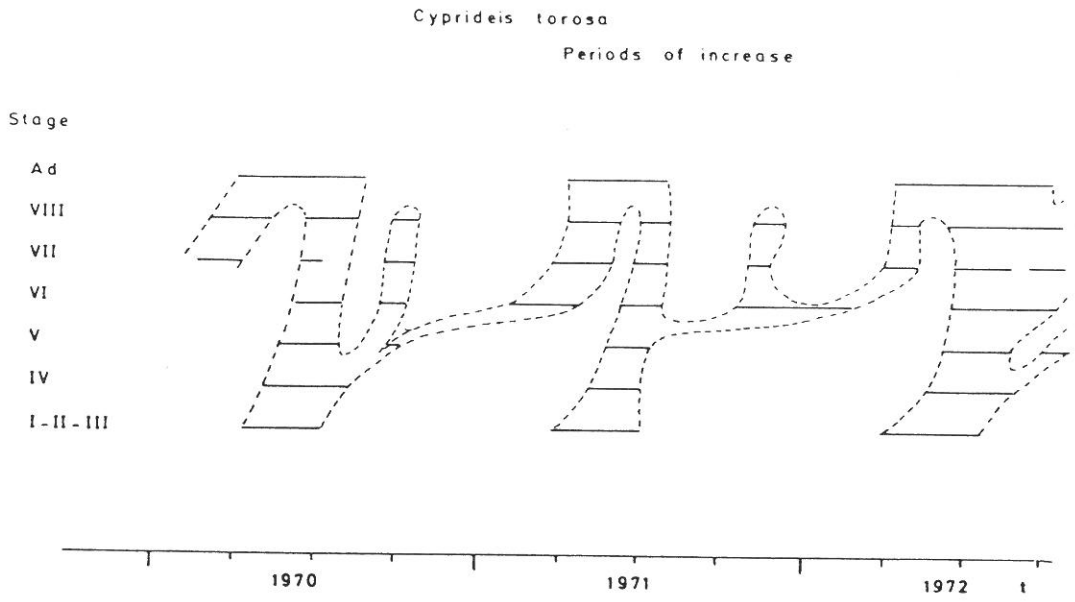


Fig. 4. *Cyprideis torosa*: periods during which the number of the different stages increases

## Discussion

### *Description of the Life-Cycle and Its Causes*

From the information summarized in Figures 1 and 4 and Tables 5 and 6 it is possible to describe the life cycle of *Cyprideis torosa*. There is an overwintering population of large larvae and adults belonging to the same generation. These large larvae start moulting from March onwards, giving rise to adults from April onwards. The percentage of males rises and the percentage of females carrying eggs drops. Both overwintering and new adults produce new larvae from the end of March onwards. This new generation reaches a peak in summer (much later in 1972) which, because of the overlap between larvae produced by the overwintering stock and those produced by the spring generation, consists of different larval stages. Some of the earlier larvae reach adulthood during autumn, when a rise in the percentage of males and the percentage of females carrying eggs occurs. Larvae born later do not succeed in attaining adulthood before winter and spend the winter as larger larval stages, moulting to adults in the next spring. There is thus one generation each year but it is split into two because there is no development during winter.

One of the interesting conclusions of this study is that there occurs only one generation per year in this species. This is unexpected for such a small animal (individuals are about 1 mm long when adult), but it appears that a low number of generations is a general characteristic of meiobenthic populations (Gerlach, 1971), although several groups (e.g. the overwhelmingly dominant nematodes)

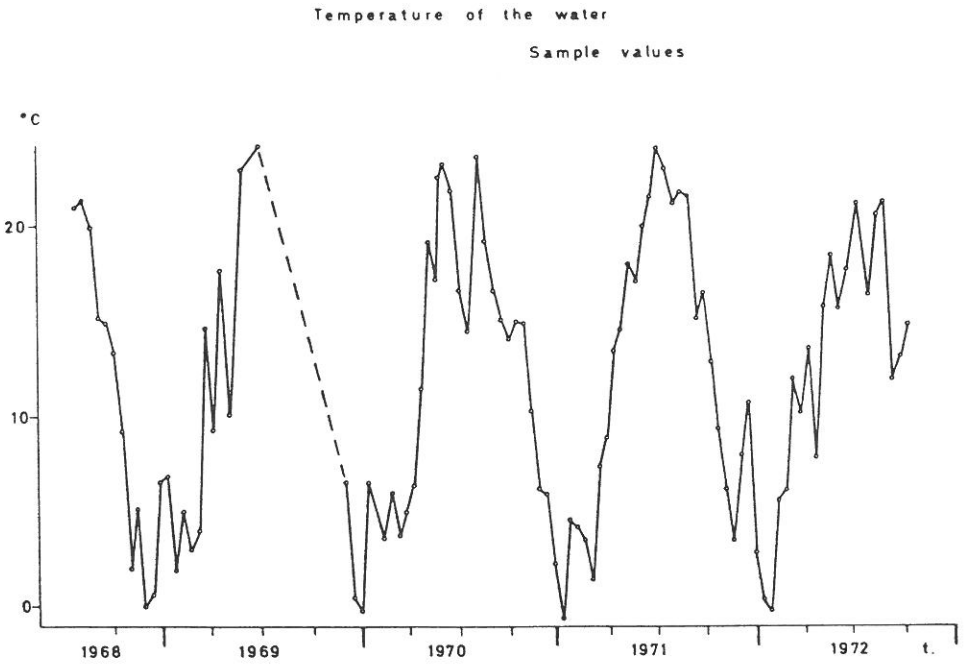


Fig. 5. Temperature of the water when samples were taken

require more study before definite conclusions can be drawn. The phenomenon has been observed in other ostracods studied: Hagerman (1969) described one generation annually for *Hirschmannia viridis* and Elofson (1941) and Theisen (1966) had correctly assumed the existence of one generation annually for *C. torosa*. Theisen (1966) found that one to three generations per year might be the rule for the seven species of ostracods he investigated.

It appears that temperature has the most pronounced influence on the life cycle of this species. Values of temperature as recorded daily were averaged for every fortnight and the regression of temperature against time was calculated using a Fourier analysis. This regression is expressed by $T = 11.2 + 8.3 \sin (t - 117)$ in which $T$ is temperature and $t$ is time, with $t_0 = 31$ December (Heip and Smol, 1976). It allows predicting the mean temperature preceding the sample date or preceding the dates of minimum and maximum abundance as calculated from the exponential regressions.

The daily recordings permitted calculation of the mean temperature of the five days preceding the date of minimum abundance. The means over three years of these 5-day averages are given in Table 8. This mean temperature is lowest for the moulting from larvae VI to larvae VII, which is in agreement with the observation that most larvae belong to stage VII in winter. Stage VI predominated only in winter 1970–1971 and this was also the winter when stage V was numerous. As temperature was much lower in late summer 1970 than in late summer 1971, the reason for this predomination of younger larvae in

Table 8. Mean temperature during 5 days preceding the date when moulting starts in *C. torosa*

| From | To | Temperature (°C) |
|---|---|---|
| Egg | I-II-III | 7.3 |
| I-II-III | IV | 15.6 |
| IV | V | 16.3 |
| V | VI | 10.2 |
| VI | VII | 8.4 |
| VII | VIII | 8.8 |
| VIII | adult | 9.3 |

1970–1971 is obviously the fact that these larvae did not have enough time to moult, because temperature dropped below some critical value too early.

From Table 8 it might appear that the youngest larvae need a much lower water temperature to develop than larvae IV and V. This is not necessarily so because many of these larvae have developed before winter but are held between the valves of the female; the temperature of 7.3° C in Table 8 is the temperature at which they are released in the environment.

The regression between the rate of change $r$ of the number of adults and the mean temperature during development showed that temperature must be above about 15° C before the number of adults increases. The moulting from stage IV to stage V might be the developmental step requiring the highest temperature (Table 8) and therefore determining the minimum temperature needed for complete development.

The existence of a prominent peak in the number of animals seems to indicate predation as a regulating factor. Maximum abundances, with an overall maximum of 1.8 million individuals per $m^2$ on 4 Aug 71, of which 328,000 were adults, are the highest recorded so far. The total biomass of *Cyprideis torosa* at this data is extraordinary and amounts to 48.9 g dry weight per $m^2$ (in preparation). After the summer peak the number of adults declines very constantly during eight months, and this remarkably constant mortality is one of the arguments against predation regulating the peak. The other argument is that we have not been able to find numerical or qualitative changes in the community indicating a species or a combination of species responsible for such predation.

Specific predators for ostracods are not known. The only meiobenthic animal whose importance as a predator of meiobenthos has been stressed (Muus, 1967; Heip, 1971) is the polyp *Protohydra leuckarti*. This species is present but I found ostracods in the atrium only once during 4 years of investigation. The polychaetes *Polydora ciliata*, *Nereis diversicolor* and *Streblospio shrubsoli* are potential predators but their densities do not fluctuate widely during the year; the intensity of predation by these organisms might be rather constant. *Pomatoschistus microps* is another potential predator, but its maximum abundance was attained in the same year (1971) as that of the ostracods; moreover, we did not find ostracods during an examination of stomach content in seven individuals. Hesthagen (1971), who examined their food in winter, reported also the absence of ostracods.

*Cyprideis torosa* is a detritus feeder and the amounts of detritus in the habitat are so large that competion, whether intraspecific or interspecific, does not seem responsible for the decline in numbers after the peak. Moreover, the detritus results from the decay of reed of the previous year and the amount available is therefore not a function of water temperatures during the increase of *C. torosa* in the following year; yet, this increase is directly influenced by water temperature. Bacterial activity is higher at higher temperatures; when we accept that the principal food source in the detritus is bacterial biomass then the higher numbers of ostracods in years with a higher temperature of the water could be explained by the higher production of bacterial biomass.

Another argument against competition as a regulating mechanism is the fact that yearly density fluctuations can be described by only two exponential functions. The sudden change of an exponentially increasing density to an exponentially decreasing density is not consistent with competition, which would lead to a logistic relationship between density and time.

This sudden change from an exponentially increasing to an exponentially decreasing function can be explained by the cessation of one of two exponential processes which were superimposed before. This process appears to be reproduction in the case of *C. torosa*. One generation is raised and the rate at which it develops depends on temperature. The date of maximum abundance is a function of temperature because the rate of increase is a function of temperature. The maximum number, assuming constant mortality, is therefore also a function of temperature besides being a function of the initial number which in turn depends on the maximum number a year before and the period of decrease, both again functions of temperature. There was a considerable difference between the duration of increase in 1970 and 1971 on the one hand and 1972 on the other, but the mean temperature during development was very similar. Although 1972 appears to be the worst year for the species, numbers in October are in fact higher in that year than in others. The net result of reproduction was therefore best in 1972, because more individuals will survive till the next spring. Production on the other hand was lowest in 1972 but this had no direct consequences for the population and is only important on the community level.

The constancy of mean temperature during development might point to the requirement of a constant amount of energy per day development. When development lasts longer, the total amount of energy expended will be larger. As noticed earlier, temperature must be above 15° C before complete development can take place. Taking the mean date of 28 March as the date when development starts (the appearance of young larvae in the environment), the mean temperature of 15° C is attained after 128 days, according to the temperature regression equation. This is nearly exactly the duration of increase as calculated from the dates at which the increase of the different larval stages starts in 1970 and 1971. The temperature regression thus predicts an increase till 3 August on the average.

*Cyprideis torosa* appears to be another example of a meiobenthic species on top of the food chain. The life-cycle of this species can be more or less predicted from the cycle of temperature in the habitat and a knowledge of mortality.

Although it is not possible to say if it is temperature itself or a factor linked with temperature which is the regulating agent, this is of no importance in describing the influence of temperature on the number of individuals of this species. I would like to speculate somewhat on the nature of these regulating factors. When mortality is constant, as in this species, it is predictable. In stable populations natality and mortality have to balance in the long run. This implies that reproductive patterns are linked with mortality. With a constant amount of energy available there is an inverse relationship between the number of offspring and their individual fitness. In predictable environments selection will act by increasing the fitness of the individual offspring (McArthur and Wilson, 1967) and the total number of offspring will be reduced. This is indeed what can be observed in *C. torosa*. Although seasonal, the environment is relatively predictable. The total number of eggs produced by a female of this species is very low, with a mean of 11. Individual fitness of the offspring is increased by holding the larvae between the values until temperature is high enough for development.

Reducing the number of offspring is a bad strategy when catastrophic and inpredictable mortality is a regular phenomenon. Catastrophic mortality might occur when the bottom freezes, which is tolerated only for a little while (Theisen, 1966). I never observed freezing of the bottom but there seems to be an adaptation against this possibility. Laying of the eggs starts in autumn, several months before temperature is at a minimum. Copulation thus occurs when density is still rather high and this may decrease the risk of not finding a partner. Because the eggs can develop between the valves of a dead female and can stand freezing, this behaviour might be an adaptation to the possibility of freezing.

The absence of catastrophic mortality increases the predictability of the environment and the stability of the link between reproductive processes and environmental parameters. If there is a regulation of this link by selective processes it appears reasonable to postulate mortality as the factor on which the process works: mortality in the past is the touchstone on which fertility in the present is based. When fecundity would have been both too high or too low in the past, the population would have gone extinct. It is easy to see how selection can change parameters of fecundity such as the sex-ratio or the number of offspring per female. The age-structure of the population depends on the reproductive cycle and is therefore directly dependent on the environment. Fecundity could therefore be determined by the history of the population in the particular environment in which it lives. In populations which disperse slowly and where there is little gene flow between populations inhabiting different habitats it is possible that important differences in fecundity could exist.

Because the pond which has been studied here is a relatively stable environment, our conclusions may not hold for some of the habitats where *Cyprideis torosa* is normally found (Gerlach, personal communication). It seems clear that the environment will be less stable when we go farther north or in less sheltered habitats because freezing of the bottom or the destruction of the habitat by storms will be a much more common event there. This might have the consequence that the dynamics of populations living farther north or in less sheltered habitats will not be equilibrated to the extent found in this study. Among other things we may predict a larger number of eggs produced by these less stable populations.

## Appendix

### *A Model for the Reproduction of C. torosa*

The change of numbers of a certain stage $X$ during $dt$ may be given by:

$$\frac{dN_x}{dt} = a_{x-1} N_{x-1} - a_x N_x - m_x N_x \tag{1}$$

in which $a_{x-1}$ is the fraction of the previous stage $X-1$ moulting to $X$ during $dt$, $a_x$ is the fraction of stage $X$ moulting to $X+1$ and $m_x$ is the mortality of stage $X$ during $dt$.

$$\int_{N_0}^{N_t} \frac{dN_x}{N_x} = \int_{t_0}^{t} \left( a_{x-1} \frac{N_{x-1}}{N_x} - a_x - m_x \right) dt \tag{2}$$

The best estimate of $\int_{t_0}^{t} \frac{N_{x-1}}{N_x}\, dt$ is obtained by $\frac{\overline{N_{x-1}}}{N_x}(t-t_0)$, in which the ratio of the sum of the numbers of both stages during $t-t_0$ is taken. The solution of (2) is then:

$$N_{x(t)} = N_{x(0)} \exp \left( a_{x-1} \frac{\overline{N_{x-1}}}{N_x} - a_x - m_x \right) (t-t_0)$$

Mortality $m_x$ can be calculated from periods when there is no moulting. To test the model a constant mortality $m = 0.012$ per day was accepted for all stages. The value for $a_x$ is calculated beginning with the adults, for which $a_{ad} = 0$, of course. Because the rate of increase is known, we may write:

$$r_x = a_{x-1} \frac{\overline{N_{x-1}}}{N_x} - a_x - m_x$$

$$a_{x-1} = (r_x + m_x + a_x) \frac{\overline{N_x}}{N_{x-1}}$$

And for the adults:

$$a_{\mathrm{VIII}} = (r_{ad} + m_{ad}) \frac{\overline{N_{ad}}}{N_{\mathrm{VIII}}}$$

The period during which $r_x$ is calculated is the same for all larval stages and corresponds with the period of increase of the adults.

In Table 9 the values of $r_x$, $m_x$, $\sum N_x$ and $a_x$ as calculated in the way described are shown for the three years. Because $a_x$ is the fraction of stage $X$ moulting per unit time, $1/a_x$ is the time required for all individuals to moult. $\sum_{1}^{ad} 1/a_x$ is therefore the development time of the species. In Table 10 these development times are given for the 3 years. The difference between the years is extremely small, being less than one day in 1970 and 1971 and showing a larger value, as was expected, in 1972. This is a success in view of the simplicity of the model. This model is robust against changes in mortality. When taking the values obtained from periods without reproduction ($m_{\mathrm{I-II-III}} = 0.011$; $m_{\mathrm{IV}} = 0.010$; $m_{\mathrm{V}} = 0.011$; $m_{\mathrm{VI}} = 0.014$; $m_{\mathrm{VII}} = 0.016$; $m_{\mathrm{VIII}} = 0.017$ and $m_{ad} = 0.010$), I found for the whole duration of development 59.8 days in 1970, 58.6 days in 1971, and 70.2 days in 1972. The difference between these figures and those of Table 10 is less than 2 days.

The duration of development as calculated with the model is in good agreement with observed values. Theisen (1966) found a development time of 63 days at a somewhat higher temperature of 18–24° C, which agrees very well with our calculated value of 63.1 days for the 3 years averaged. On the other hand, the development of a generation takes about 130 days in 1970 and 1971 and about 150 days in 1972. It thus appears again that development is considerably slower at temperatures below 15° C. This is also obvious from Figure 4 when we compare the times at which the increase starts between subsequent stages. The interval between these times becomes shorter when the stages are older, this is later in the season, when temperatures are higher.

**Table 9.** Observed rate of increase ($r_x$), mortality ($m_x$), sum of numbers ($N_x$) and calculated rate of moulting ($a_x$) during the period in which the number of adult *C. torosa* increased.

| | 1970 (5 May–5 Aug) | | | |
|---|---|---|---|---|
| | $r_x$ | $m_x$ | $N_x$ | $a_x$ |
| Adults | .019 | .012 | 8,066 | 0 |
| VIII | .005 | .012 | 3,996 | .062 |
| VII | .006 | .012 | 3,936 | .081 |
| VI | .021 | .012 | 3,587 | .108 |
| V | .055 | .012 | 4,450 | .114 |
| IV | .069 | .012 | 2,198 | .366 |
| I-II-III | .043 | .012 | 10,936 | .085 |
| | 1971 (15 Apr–4 Aug) | | | |
| Adults | .024 | .012 | 10,856 | 0 |
| VIII | .028 | .012 | 6,654 | .059 |
| VII | .023 | .012 | 8,719 | .075 |
| VI | .015 | .012 | 9,412 | .102 |
| V | .023 | .012 | 7,390 | .165 |
| IV | .038 | .012 | 5,361 | .275 |
| I-II-III | .026 | .012 | 16,760 | .104 |
| | 1972 (21 Jun–16 Aug) | | | |
| Adults | .011 | .012 | 1953 | 0 |
| VIII | .029 | .012 | 1260 | .036 |
| VII | .044 | .012 | 2019 | .048 |
| VI | .061 | .012 | 2188 | .096 |
| V | .044 | .012 | 1335 | .277 |
| IV | .023 | .012 | 1001 | .444 |
| I-II-III | .012 | .012 | 1858 | .263 |

**Table 10.** Duration of development of *C. torosa* as calculated from $1/a_x$

| | 1970 | 1971 | 1972 | Mean |
|---|---|---|---|---|
| I-II-III | 11.8 | 9.6 | 3.8 | 8.4 |
| IV | 2.7 | 3.6 | 2.3 | 2.9 |
| V | 8.8 | 6.1 | 3.6 | 6.2 |
| VI | 9.3 | 9.8 | 10.4 | 9.8 |
| VII | 12.4 | 13.3 | 20.8 | 15.5 |
| VIII | 16.1 | 17.0 | 27.8 | 20.3 |
| Total | 61.1 | 59.4 | 68.7 | 63.1 |

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# THE CALCULATION OF ELIMINATED BIOMASS

3550 ?

by

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ABSTRACT. — The number of individuals which is eliminated from a population whose numbers change exponentially at a rate of r per unit of time and whose mortality is d per unit of time can be calculated from $N_e = (dN_o/r)(e^{rt} - 1)$. This formula permits the use of the concept of eliminated biomass in the calculation of production of populations without restriction to their way of reproduction. The formula was applied to calculate production of adults in the harpacticoid copepod *Tachidius discipes* GIESBRECHT, 1882, where it was shown that the production/biomass ratio P/B = 15.

## INTRODUCTION

Production of a population is defined as the sum of the growth increments of all individuals present in the population during a given period of time (WINBERG *et al.*, 1971). Methods to determine production are fundamentally different for populations where reproduction is limited in time and for populations with continuous reproduction. It is relatively simple to determine production in a species with a long life cycle and a short period of reproduction. The population may then be treated as a cohort of individuals of the same age, decreasing in numbers and increasing in mean weight. In this case production is equal to the difference between the final and the initial biomass to which is added the biomass of the individuals which were eliminated during the period under consideration. The estimation of eliminated biomass is the only difficulty in this case. It may be assessed graphically (ALLEN, 1951), without reference to a particular model for growth and mortality, by measuring production as the area under the curve relating the number of individuals to the mean individual weight at the same time ; or, it may be assessed numerically by multiplying the eliminated numbers $N_e = N_t - N_o$ by the mean weight during the period.

When the interval between sample dates is small enough, this mean weight can be estimated from the arithmetical mean of the initial and the final weight.

For populations with continuous reproduction the concept of eliminated biomass has not been used because it is difficult to assess the recruitment during the time considered. Methods to estimate production in this case are of three basic types (CONOVER, 1974), one of which is based on the finite rate of growth and requires the knowledge of the weight increment of an individual during its life span. In the different variants of this method, daily production is measured either graphically or numerically by dividing the product of daily growth increment and the number of animals belonging to a certain stage or size-group by the duration of development of that particular stage or size-group. To calculate total production one has to know the total duration of the reproductive period. The two other basic methods (radioactive and physiological) have been met with reservations, although the physiological method seems to be preferred when time does not allow for the following up of the population (CONOVER, 1974).

## THE CALCULATION OF ELIMINATED BIOMASS

The purpose of this paper is to show that it is possible to use the concept of eliminated biomass in the estimation of populations with continuous reproduction as well. When the time interval between the samples is small enough, growth of a population during the interval can be treated as exponential following $N_t = N_o e^{rt}$, in which r is the rate of change per unit of time, equal to the difference between instantaneous natality b and mortality d, so that $r = b - d$. When there is no mortality $r = b$, and numbers after a period of time t will be $N_t = N_o e^{bt}$. The difference between the numbers without mortality and with mortality is $N' = N_o e^{bt} - N_o e^{(b-d)t}$. However, this number N' is not the number eliminated during t because it implies that the number dying each moment is proportional to the numbers in the population without mortality and not to the real numbers ; only when the time interval is infinitely small do these numbers coincide. We have therefore to find the value of N' for an infinitely small time interval dt.

We proceed as follows : we divide the time interval into n equal intervals $\Delta t$. We calculate the difference between numbers without and with mortality for each interval $\Delta t$. We sum up these differences and find the limit of this sum for $\Delta t \rightarrow O$. This limit is the real eliminated number of individuals.

$$N' = N_o(e^{b\Delta t} - e^{(b-d)\Delta t}) + N_1(e^{b\Delta t} - e^{(b-d)\Delta t}) + \ldots$$

$$+ N_{n-1}(e^{b\Delta t} - e^{(b-d)\Delta t})$$

$$N' = (e^{b\Delta t} - e^{(b-d)\Delta t}) \Sigma N_i$$

$$\lim_{\Delta t \to 0} N' = \lim_{\Delta t \to 0} \frac{(e^{b\Delta t} - e^{(b-d)\Delta t}}{\Delta t} \lim_{\Delta t \to 0} \Sigma N_i \Delta t$$

$$= \lim_{\Delta t \to 0} e^{b\Delta t} \lim_{\Delta t \to 0} \frac{1 - e^{-d\Delta t}}{\Delta t} \int_0^t N_o e^{rt} dt$$

Noting that $\lim_{\Delta t \to 0} e^{b\Delta t} = 1$ and expanding $e^{-d\Delta t}$, we obtain :

$$N_e = \lim_{\Delta t \to 0} \frac{(1 - 1 - (-d\Delta t) - \frac{(-d\Delta t)^2}{2} - \frac{(-d\Delta t)^3}{3} - \ldots)}{\Delta t} \int_0^t N_o e^{rt} dt$$

$$N_e = \frac{N_o d}{r}(e^{rt} - 1) \qquad (1)$$

We obtain a very simple formula for the calculation of eliminated numbers during the period of time t. To obtain eliminated biomass in order to calculate production one has to multiply these eliminated numbers by an estimate of mean weight during the period. This can be done by taking the arithmetical mean of initial and final weight, as in the classical method for populations without recruitment. In the case of crustaceans, where the main weight increase is during moulting, the difference between individuals belonging to a same larval stage is often far less than the difference between the mean weights of the stages. In this case a very accurate estimate of eliminated biomass can be obtained by multiplying the eliminated numbers of each stage by the mean weight of that stage.

Where there is no recruitment, $r = -d$ and formula (1) reduces to :

$$N_e = N_o(1 - e^{rt}) \qquad (2)$$

Numbers in the population after t will be $N_t = N_o e^{rt}$, hence $N_t - N_o = N_o(e^{rt} - 1) = -N_e$. This shows that equation (1) is a general one which can be applied to populations with or without recruitment and during increase or decrease of the population, on condition that population changes may be described by an exponential function.

Finally, we consider the case $r = 0$, i.e. a stationary population. In this case equation (1) reduces to :

$$N_e = dN_o t = -bN_o t \qquad (3)$$

as can be shown by expanding $e^{rt}$ and putting $r = 0$.

The use of the equations above requires knowledge of the instantaneous mortality rate d and the rate of change r actually observed. This rate of change r is obtained from $r = (1/t) \ln N_t/N_o$ from numbers before and after the period considered. Mortality can be determined in periods when there is no reproduction (e.g. in winter) using the same formula, because then $d = -r$. This value may not be representative for conditions in other seasons. Mortality can also be calculated when natality is known, as $d = b - r$. Natality can be calculated from egg counts or egg ratios and the development time of the species. When D is the development time, p the fraction of females in the population and $N_e$ the number of eggs per female, $b = 1/D \ln (pN_e + 1)$ (eq. 4) (PALOHEIMO, 1974).

It is obvious that the use of equation (1) is subject to the same restrictions which apply to the use of the instantaneous rates r, b and d. It is well known that these rates rarely are what they are required to be, namely constant during the interval, and that one is dealing with average values for each interval. The magnitude of the error introduced by holding these rates constant is a function of the length of the time interval. We will discuss this further when using actual data to calculate production of a harpacticoid copepod.

## PRODUCTION OF ADULTS OF TACHIDIUS DISCIPES GIESBRECHT, 1882

In order to illustrate my point I chose to calculate the production of adults of the harpacticoid copepod *Tachidius discipes*. This is a meiobenthic species and a common inhabitant of brackish water throughout Europe, dominating in most communities where it occurs. The population I studied inhabits a shallow brackish water pond in northern Belgium. In this habitat animals appear late in winter, reach a peak in spring and disappear again in early summer. The decline can be attributed to predation by the polyp *Protohydra leuckarti* GREEFF, 1870 (HEIP and SMOL, 1976a).

Density was measured from samples taken every fortnight, using methods described earlier (HEIP, 1973). Numbers during the peak of 1970 are shown in table 1. Temperature was measured continuously with an automatic recorder. Values were averaged over fourteen days and are also shown in table 1. In order to apply eq. (1) we need to know the instantaneous rates r and d. Values of r are calculated from $r = 1/\Delta t \ln N_t/N_o$ in which $\Delta t$ is the length of the time interval and $N_t$ and $N_o$ are final and initial numbers of that interval. Because instantaneous mortality d is very difficult to estimate I calculated natality instead using eq. (4). Experiments were

carried out in which *T. discipes* was cultured at five different temperatures (HEIP and SMOL, 1976b). It was shown that neither the fraction of females p nor the number of eggs $N_e$ varies significantly with temperature and constant values of $p = 0.67$ and $N_e = 41$ were used. There was a strong influence of temperature on the generation time D which could be described as $D = 527\ T^{-1.13}$. Substitution of these values in eq. (4) yields an equation in which natality is given as a function of temperature only: $b = (0.0064)/(T^{-1.13})$ (eq. 5). Because the generation time D was used in eq. (4), this value of b is "natality" of adults. As b is a non-linear function of temperature, the use of mean temperatures will cause some error in its calculation, but this error will be small when time intervals are not too large.

Tabel I

*Tachidius discipes*: adult numbers N, mean temperature T, instantaneous rate of increase r and natality b, and eliminated numbers $N_e$ during each time interval. T, r, b and $N_e$ are values for the interval following the date on the row.

| Date | N per 100cm² | T °C | r per day | b per day | $N_e$ per 100 cm² |
|---|---|---|---|---|---|
| 16 Jan 70 | 0 | 4.2 | — | 0.032 | 0 |
| 11 Feb 70 | 8* | 4.2 | 0.180 | 0.032 | -75 |
| 25 Feb 70 | 99 | 4.2 | 0.029 | 0.032 | 5 |
| 11 Mar 70 | 148 | 6.4 | -0.029 | 0.051 | 136 |
| 25 Mar 70 | 99 | 6.2 | 0.021 | 0.050 | 47 |
| 8 Apr 70 | 132 | 9.8 | 0.107 | 0.083 | -105 |
| 22 Apr 70 | 594 | 11.3 | 0.026 | 0.098 | 657 |
| 5 May 70 | 833 | 15.5 | -0.028 | 0.139 | 1708 |
| 20 May 70 | 544 | 16.5 | -0.056 | 0.150 | 1085 |
| 3 Jun 70 | 246 | 18.8 | -0.079 | 0.173 | 528 |
| 17 Jun 70 | 82 | 16.6 | -0.117 | 0.151 | 151 |
| 1 Jul 70 | 16 | 18.8 | -0.050 | 0.173 | 36 |
| 15 Jul 70 | 8* | 22.2 | — | 0.209 | 0 |
| 5 Aug 70 | 0 | | | | |
| | | | | Total eliminated: | 4175 |

* Changed zero-value (see text).

Eliminated numbers of adults according to eq. (1) can now be calculated and are given in table 1. In this calculation the last zero value before the peak and the first after the peak were changed because, due to sample size of

6 $cm^2$, densities smaller than 16 per 100 $cm^2$ (one individual per sample) cannot be estimated. Because any density between 0 and 16 is equally possible, I replaced these zero values by 8 per 100 $cm^2$. This procedure is not critical in the calculation, as numbers involved are very small.

The sum of the eliminated numbers during each time interval over the entire period is total production of adults because numbers before and after the peak are zero. This production is then 4175 adults per 100 $cm^2$ in the year 1970. When assuming a wet weight of 5 µg per adult, this amounts to 2.1 g wet weight per $m^2$ per year. This production will represent by far the larger part of total production of this population, because adults have a much longer existence than the larval stages and weight approximately two times more than the largest copepodite stage, four times more than the second largest, and so on.

In principle, the same procedure could be followed for each stage. However, in the case of harpacticoid copepods, where there are six naupliar stages and five copepodite stages which are all passed through in 10-15 days at higher temperatures, it appears impossible to obtain detailed knowledge of the changes of numbers of each stage without complicating sampling to the point of absurdness. In the case of crustaceans with a longer life cycle accurate sampling is entirely feasible and one should be able to obtain very accurate estimates of production following the procedure outlined above, i.e. summation over all stages of eliminated biomass as obtained from the eliminated numbers of each stage multiplied by its mean weight.

Returning to the copepod, I would like to make a suggestion to come out of the difficulties associated with the short life cycle of this organism. The production/biomass ratio P/B can be calculated from numbers because mean weight is the same in both the numerator and the denominator of this ratio. In the case of *Tachidius discipes*, a mean of 179 adults per 100 $cm^2$ is present during the peak in 1970, and the P/B-ratio becomes $P/B = 4175/279 = 15.0$. When this value would be valid for the whole life-cycle, it is possible to calculate production from knowledge of the mean biomass. This could be true because the P/B-ratio seems to be a conservative quantity, and I will demonstrate further that it is not influenced greatly by the length of the time interval used in its calculation.

The problem associated with holding the parameters r and b constant during the time interval under consideration was examined as follows: when assuming that the population increases and decreases exponentially the whole peak can be described by two equations of the type $N_t = N_o e^{rt}$

which are valid over a long time interval. In table 2 the values of $N_o$ and r as obtained from the regression of ln $N_t$ versus t are given for the increase and the subsequent decrease. The intersection of the two regression curves gives the moment when the peak maximum is reached and maximum numbers. Using eq. (5) an estimate of b is obtained from mean temperature and application of eq. (1) yields an estimate of eliminated numbers over the whole increase and decrease which can be compared with the estimate obtained from the summation of values obtained over much shorter time intervals as done in table (1).

Table 2

Calculation of eliminated numbers of adults of *Tachidius discipes*. Increase and decrease are exponential according to $N_t = N_o e^{rt}$. t is the duration of and T is the mean temperature during the period. b is calculated from eq. (5), $N_e$ is calculated from eq. (1). Decrease starts at intersection of the two regression curves.

| | $N_o$ (per 100 cm²) | t (days) | T (°C) | r (per day) | b (per day) | $N_e$ (per 100 cm²) |
|---|---|---|---|---|---|---|
| Increase | 20.5 | 86 | 6.7 | 0.045 | 0.054 | 192 |
| Decrease | 1003.9 | 89 | 18.1 | -0.070 | 0.166 | 3378 |
| | | | | | Total elimination : | 3570 |

A second thing is to calculate eliminated numbers supposing the sampling time interval was not 14 days but 28, 42 and 56 days respectively. When the sampling interval is 28 days we have two series of samples from which elimination can be calculated, when the interval is 42 days we have three series and when it is 56 days we have four series. In table 3 the means of these series for each sampling time interval are given as calculated from both the summation over time intervals and the exponential regressions over the whole increase and decrease. From these calculations it follows that estimates of production have a smaller value when either the sampling time interval or the time interval used in their calculation is longer. The P/B-ratio, as indicated before, is far less affected by the length of the time interval.

Table 3

Production of adults as numbers per 100 $cm^2$ and as gram wet weight per $m^2$ as estimated from density values directly and from the regressions of density values versus time. When the sampling time interval $\Delta t$ is more than 14 days, values are the means of the several possible series.

| | Time interval $\Delta t$ (in days) | 14 | 28 | 42 | 56 |
|---|---|---|---|---|---|
| $N_c$/100 $cm^2$ | Sample values | 4175 | 3966 | 3544 | 2712 |
| | Regression | 3570 | 3026 | 2614 | 2610 |
| P ($g/m^2$) | Sample values | 2.1 | 2.0 | 1.8 | 1.4 |
| | Regression | 1.8 | 1.5 | 1.3 | 1.3 |
| P/B | Sample values | 15.0 | 16.4 | 16.1 | 14.6 |

It appears from these results that the time interval used in sampling is more critical than the interval used in the calculation of eliminated biomass, which suggests that there are no grave errors associated with holding the parameters constant over even relatively long intervals. The proposed equation (1) therefore seems a valid way of calculating production in populations with continuous reproduction, either from field data when mortality can be assessed reliably or from laboratory experiments giving values of natality, provided the time interval between samples is short enough.

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# THE PRODUCTIVITY OF MARINE MEIOBENTHOS

BY

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**Samenvatting**

Het mariene meiobenthos bestaat uit kleine ( < 1 mm) Metazoa, voornamelijk Nematoda en harpacticoide Copepoda. Hoewel het meiobenthos zeer abundant is in alle mariene sedimenten, zijn er nog steeds zeer weinig gegevens bekend over de energiedoorstroming door deze populaties.

De energie die een populatie binnenkomt als consumptie wordt verdeeld over een aantal processen : een deel wordt besteed aan somatische groei en reproduktieve output, samen de produktie van de populatie ; een deel wordt uitgescheiden als faeces en excreta ; het deel dat wordt gebruikt voor onderhoud kan geschat worden door de respiratie te meten.

Er bestaat een aantal verschillende methoden om rechtstreeks de produktie van een populatie te meten. Al deze methoden zijn varianten van twee basisbenaderingen : een sommatie over de tijd van de groei der individuen, of een sommatie van de geëlimineerde biomassa. Zij kunnen verder opgesplitst worden volgens het type van populatie waarop ze van toepassing zijn : cohort-populaties (waarin reproduktie synchroon is en over een korte tijdsspanne plaatsvindt) of populaties met continue reproduktie.

Rechtstreekse produktieschattingen zijn gepubliceerd voor twee harpacticoide Copepoda, maar van Nematoda zijn nog geen produktiestudies uitgevoerd. Wij presenteren hier rechtstreekse produktieschattingen van de harpacticoide *Tachidius discipes*, en van de ostracode *Cyprideis torosa*. De produktie van *C. torosa* werd geschat volgens twee methoden. Een model werd opgesteld waarmee de recrutering, mortaliteit en duur van de stadia kan geschat worden op basis van densiteitsschattingen en tellingen van lege kalkschelpjes in het sediment. De bekomen produktie is in goede overeenstemming met die bekomen met de „size-fréquency"-methode. De produktie van *T. discipes* kon bepaald worden nadat in de densiteitsgegevens de drie gedeeltelijk overlappende generaties werden gescheiden met een statistische methode.

De P/B (produktie/biomassa) ratio per generatietijd bedraagt voor beide populaties respectievelijk 2,73 en 3,11. Aannemend dat de P/B-waarde per generatie voor meiobenthische populaties ongeveer 3 is, kan de jaarlijkse P/B geschat worden voor die populaties waarvoor uit observatie of uit kweekexperimenten het aantal generaties per jaar bekend is. Een overzicht van de literatuurgegevens toont aan dat het gebruik van één enkele P/B-waarde voor meiofauna moet worden vermeden, en dat een schatting van P/B uitgaande van een log-log verband tussen P/B en lichaamsgewicht betere waarden zou kunnen geven.

De observaties over ecologische efficiëntie P/(P + R) van meiobenthische populaties suggereren dat deze niet verschillend is van andere groepen. Dit verantwoordt het gebruik van schattingen van jaarlijkse populatierespiratie voor de schatting van de jaarlijkse produktie via gepubliceerde log-log verbanden tussen beide.

De produktie van het meiobenthos in Belgische kustwateren werd berekend aan de hand van verschillende benaderingen. De biomassa varieert tussen minder dan 0,1 g $C.m^{-2}$ op de zandbanken tot 0,3 g $C.m^{-2}$ dicht bij de kust. De produktie ligt tussen ongeveer 0,5 en 1,5 g $C.m^{-2}.jaar^{-1}$. Hoewel op de zandbanken de input van energie in het benthisch systeem veel lager is dan dicht bij de kust, ligt de meiobenthische produktie er maar de helft lager : er gaat dus een relatief veel groter deel van de input naar het meiobenthos.

## Introduction

The productivity of aquatic populations has received much attention since the early seventies, especially as a result of the International Biological Programme, when several books appeared that had much influence on later developments in the field (Edmondson & Winberg, 1971 ; Holme & McIntyre, 1971 ; Winberg, 1971 ; Zaika, 1973). One of the important consequences was a uniformization of the concepts and symbols and the acquisition of a large body of data which had its theoretical roots in the paradigm of trophic organisation of ecosystems developed by Lindeman (1942). However, especially in the United States, many ecological theories were developed subsequently in which the role of energy flow as a structuring force in community organisation was completely ignored (Brown, 1981), and a large gap seemed to exist between these developments centering on competitive exclusion and the conceptual frame-work of many aquatic ecologists, both freshwater and marine. As there seems to be growing awareness of this fact, a synthesis, which has already been indicated by Hutchinson (1959), may be reached soon.

The energy entering a population as consumption (C) of food can be allocated to a number of processes : some of the energy is used for individual growth ($G_1$), and for reproduction (gonad output $G_2$) ; some energy is rejected (faeces F) ; and some energy is transformed and lost again as excreta (U). The energy used for maintenance as respiration (R) usually leaves the completely oxidized end product $CO_2$ without any free energy left. When all parameters are measured in the same energy units (e.g. $kJ.m^{-2}.y^{-1}$), and when the time scale considered is long enough, the following equation holds :

$$C = G_1 + G_2 + R + U + F \qquad (1)$$

In using equation (1) one has to consider that whereas the terms in it are equivalent in units of energy, they have completely different meanings as to their roles in the ecosystem. Growth and reproduction yield high-energy particulate

matter, whereas faeces is low-energy particulate matter ; respiration yields $CO_2$, a gaz, and many excretion products are soluble.

Marine benthic communities are among the least studied from the point of view of energetics. This is especially true of the meiofauna, the small metazoans living in or on sediments, other animals and plants, or on hard substrates such as rocks. As meiofauna can be technically defined as all metazoans passing a 1 mm sieve and as all former benthos workers used 1 mm sieves, the importance of meiofauna was not realized until the late sixties when it became widely appreciated that these organisms are very numerous and ubiquitous in all types of environment and that their dominant constituent, the free-living nematodes, are the most numerous multicellular benthic animals in all marine environments, from intertidal beaches to deep-sea trenches. Often second in numerical importance are the harpacticoid copepods but the diversity of meiofauna is such that many phyla are represented and some phyla contain only meiofauna species (e.g. Gastrotricha, Kinorhyncha, Gnathostomulida).

In spite of their numerical importance, nematodes typically numbering several million animals per square meter in shallow subtidal sediments, the ecology of marine meiobenthos has only received little attention. Many of the earlier studies centred on density or species composition and only a few papers dealing with energy flow through these populations have appeared to date. It is still customary to use a highly speculative figure such as the annual production biomass ratio P/B = 9 proposed by Gerlach (1971) on the basis of the life cycle characteristics of two species of nematodes, although it is now known that generation times in nematodes can vary between a few days and a whole year. The first direct estimation of the production of a meiobenthic population was that for the univoltine harpacticoid *Huntemannia jadensis* (Feller, 1977), and there is still not a single value for a marine nematode.

## The measurement of production

The energy entering an animal population (i.e. the consumption C) is partitioned through metabolic processes into several outputs. This is illustrated in fig. 1. The conservation principle requires that, in terms of energy content :

$$c(t) = g_1(t) + g_2(t) + f(t) + u(t) + r(t) \qquad (2)$$

when the time lag, which is inherent in metabolic processes, is neglected. This lag is small compared to the time scales on which production is calculated.

A production flux $p(t)$ can be defined as the sum of the growth fluxes $g_1(t)$ and $g_2(t)$. It can be seen from fig. 1 that

$$p(t) = g_1(t) + g_2(t) = \frac{dB(t)}{dt} + b_e(t) \qquad (3)$$

with $B(t)$ = biomass of the population at time t.

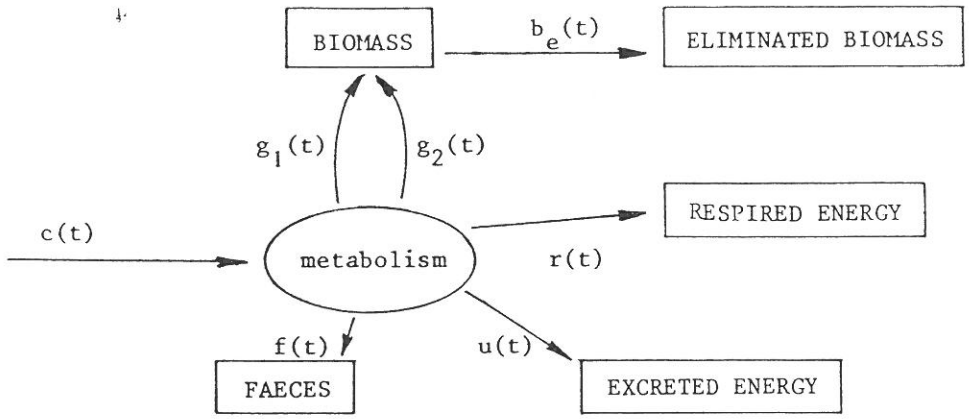


*Fig. 1* Schematic representation of the energy fluxes through a population.

In its conventional meaning production is the integration of this flux p(t) over the time interval $t_2$-$t_1 = \Delta t$ considered, often one year or the generation time :

$$P = \frac{1}{\Delta t}\int_{t_1}^{t_2} p(t)\,dt = \frac{1}{\Delta t}\left[\int_{t_1}^{t_2} g_1(t)\,dt + \int_{t_1}^{t_2} g_2(t)\,dt\right] = \frac{1}{\Delta t}\left[B_{t2} - B_{t1} + \int_{t_1}^{t_2} b_e(t)\,dt\right] \quad (4)$$

Existing methods for the calculation of production have been reviewed by Waters (1977). In essence they are variants of two approaches : integration of the growth fluxes or integration of the biomass elimination flux. They can be further classified according to whether they apply to cohort or non-cohort populations (cohort populations are populations where production is synchronous and limited to a short period compared to the longevity of the species). Table 1 shows the basic methods for the calculation of production.

TABLE 1

An overview of the methods for production calculation.

| | Σ growth increments | Σ elimination |
|---|---|---|
| Cohort populations | – Increment summation<br>– Instantaneous growth rate<br>– Allen curve | – Removal summation |
| Non-cohort populations | – Experimental growth curves<br>– Estimation stage durations | – Size-frequency method<br>– Population dynamical models |

## COHORT POPULATIONS

Cohort populations have two main advantages that greatly simplify the calculations : between the reproduction periods $g_2(t) = 0$ and all changes in density $dN/dt$ are due to mortality (when migration can be accounted for). This implies that

$$b_e(t) = -\frac{dN(t)}{dt}\, w(t) \tag{5}$$

where $N(t)$ = number of animals in the population at time t
$w(t)$ = mean individual weight at time t

Approximating this continuous equation for discrete sampling intervals, the removal summation method calculates production as :

$$P = \frac{1}{\Delta t}\left[(B_{t2}-B_{t1}) + \sum_i (-\Delta N)_i\ \bar{w}_i\right] \tag{6}$$

where i denotes the sampling interval, $\bar{w}_i$ is the mean individual weight averaged over the i-th sampling interval.

In growth increment methods, production of cohort populations between reproductive periods can be expressed as :

$$P = \frac{1}{\Delta t}\int_{t_1}^{t_2} g_1(t)dt \text{ where } g_1(t) = N(t)\ \frac{dw(t)}{dt} \tag{7}$$

Approximation over discrete intervals then gives :

$$P = \frac{\sum_i \bar{N}_i(\Delta w)_i}{\Delta t} \tag{8}$$

When time is eliminated from (7), production equals :

$$P = \int_{w_0}^{w_1} N(w)\, dw \tag{9}$$

when the sampling period is a unit time.

The graphical solution of this equation is known as the Allen-curve method (Allen, 1951). Production is estimated as the surface under the curve relating density and mean weight in successive time intervals.

In equation (7) the flux $g_1(t)$ can be rewritten as :

$$\begin{aligned} g_1(t) &= N(t)w(t).\ \frac{1}{w(t)}\ .\ \frac{dw(t)}{dt} \\ &= B(t).G(t) \end{aligned} \tag{10}$$

where B(t) is the biomass at time t and G(t) the weight-specific growth rate. When the growth between sampling points can be described as an exponential function G(t) is constant in the interval and can be estimated as :

$$G_i = \frac{\ln w_2 - \ln w_1}{t_2 - t_1} \tag{11}$$

Production can then be calculated as

$$P = \sum_i G_i \frac{\int_{t_1}^{t_2} B(t)dt}{t_2 - t_1} = \sum_i G_i \bar{B}_i \tag{12}$$

where i is the sampling interval and $\bar{B}_i$ the mean biomass in the i-th sampling interval. This method of production estimation is known as the instantaneous growth rate method (Ricker, 1946 ; Allen, 1949). It was extended by Allen (1971) to other growth models, although it is reduced to a simple form only in the case of exponential growth.

### Non-cohort populations

In non-cohort populations, as is the case for most meiobenthic populations, production can only be estimated by indirect methods. The size-frequency method was originally designed for the estimation of the 'correct order of magnitude' of production of benthic invertebrate communities (Hynes, 1961). Is was corrected and refined by Hynes & Coleman (1968), Hamilton (1969) and Benke (1979). These refinements restricted the method to the analysis of species groups with similar generation times, size and trophic position. In this method the population is divided into i size classes and the recruitment into each size class is estimated using a simple but robust population model. Recruitment is then used in a removal summation production estimation.

Instead of estimating recruitment (and thus mortality), one can estimate the duration of the life stages in the population. These estimations can be obtained experimentally by culturing the animals in the laboratory or from population models, especially the methods estimating birth and death rates and the stage frequency methods. Once the time spent in a life stage or a size class is known, the methods for cohort populations based on growth increments can be used.

## Direct production estimations

Only two direct production estimations for meiobenthic populations, both for harpacticoid copepods, are known from the literature. Feller (1977) obtained a

yearly P/B = 3.8 for *Huntemannia jadensis* and Fleeger and Palmer (1982) measured a P/B = 18.0 year$^{-1}$ for *Microarthridion littorale*.

We made direct estimations of the production of another harpacticoid copepod, *Tachidius discipes* Giesbrecht, 1882 and of the ostracod *Cyprideis torosa* Jones, 1850. Details of these studies will be published elsewhere, but the results are broadly outlined here. Both populations were studied in a shallow polyhaline brackish water pond in Belgium called „Dievengat". The ostracod *Cyprideis torosa* produces only one generation annually in this habitat (Heip, 1976) but there is considerable overlap between successive generations, due to overwintering of older larvae. Reproduction occurs in late spring and throughout the summer : some of the early larvae become adult before winter, whereas others overwinter in different larval stages. During winter there is no development and maturation is postponed until the next spring.

In the course of their development, the animals pass through eight moults. At each moulting, they shed their calcareous shells and build new ones. The shells are left in the sediment, where they are well preserved in this slightly alkaline environment. Thus an animal dying in stage V will leave shells of the stages I-V on the bottom and the distribution of preserved shells reflects the mortality processes in the population. Combining this information with density estimates of the stages from a five-year sampling period with a fortnightly interval allowed the calculation of recruitment, the duration of the stages and the stage-dependent mortality rate. An increment summation production estimation could be made giving a value of 9.69 g dwt.m$^{-2}$.y$^{-1}$ and – as mean biomass was 3.55 g dwt.m$^{-2}$ – the annual P/B-ratio equalled P/B = 2.73. This result agreed very well with another estimation obtained by means of the size frequency method yielding P = 9.24 g dwt$^{-2}$.y$^{-1}$.

The harpacticoid copepod *Tachidius discipes* is a dominant species in many European and North-American brackish waters. Its size, form and epibenthic life style make it a representative species for an important part of the North Sea harpacticoid fauna. The population was sampled every three days in 1979, and the data showed that three overlapping generations were present. They could be separated in the different stages using a graphical method for the resolution of frequency distributions into Gaussian components (Bhatthacharya, 1968). The means and absolute heights of these Gaussian components correspond with the mean pulse time and the surface under the abundance curve used in the model of Rigler and Cooley (1974). This model estimates the duration of the stages and the recruitment : it provides the necessary parameters for a production estimation. The production of copepodites and adults amounted to 1.1 g dwt.m$^{-2}$ in the spring period when the species was present. The production of nauplii and eggs was based on the number of egg sacs produced and the duration of naupliar development as determined in the laboratory. It is 1.3 g dwt.m$^{-2}$ and thus a very important part of total production. The P/B-ratio for the total population was P/B = 9.34 over the sampling period, this amounts to 3.11 per generation.

**Indirect production estimations**

The direct estimation of production requires a very intensive sampling scheme and makes this approach impracticable for the study of marine populations. It is therefore necessary to consider a number of indirect methods which allow at least an estimation of the order of magnitude of production without requiring the same sampling effort. In remains necessary to obtain reasonably good density and biomass estimates of the population.

An obvious approach is to make use of the generation P/B. As shown by Waters (1969), the P/B per generation falls between 2 and 5 for any biologically sound model of growth and mortality. The modal value is P/B = 3.5. This figure is confirmed in studies of meiobenthic populations, though the tendency is towards a slightly smaller figure of P/B = 3. Waters (1969) showed that an inverse relationship exists between the generation P/B and the fraction of the newborns that reach adulthood. Many meiobenthic populations are characterized by the fact that an important part of the population are adults (Warwick, 1980), hence an inverse relationship is to be expected here. This approach has led to the generally used figure of P/B = 9 on an annual basis for marine nematodes in particular and meiofauna in general (Gerlach, 1971). Obviously, this guess critically depends on the number of generations a year.

Heip *et al.* (1982) review the available information on generation times of marine nematodes. The number of generations a year has been assayed directly only for a few large slowly growing species, which showed to have one to three generations a year. These figures can hardly be considered to be representative for the nematode community as a whole. In the same brackish water pond where *Tachidius discipes* and *Cyprideis torosa* were studied, the large nematode *Oncholaimus oxyuris* is one of the dominant species in spite of the fact that it is a top predator feeding mainly on other nematodes. To sustain a biomass of a predator that is larger on a surface basis than that of its prey obviously requires a high turn-over of the prey. This is exemplified by the following simple calculation. We assume that *O. oxyuris* feeds exclusively on nematodes and that all nematode production other than that of *O. oxyuris* itself is devoted to sustaining *O. oxyuris* ; we further assume that the efficiency P/A of *O. oxyuris* is P/A = 0.3 and that A/C = 0.6 (where A = assimilation = P + R). With 1.5 generations a year (Smol *et al.*, 1981), the P/B of *O. oxyuris* must be around 5. As *O. oxyuris* represents about 40% of total nematode biomass (40 units), its production is 200 units, requiring an assimilation of 667 units and a consumption of 1111 units. The other nematodes thus have a P/B = 1111/60 = 18.52 per year. Overall nematode P/B = 13 per year. As *O. oxyuris* is not the only predatory nematode in this community the annual P/B (and hence the annual number of generations) will still be higher.

Culture experiments that measure development time as a function of temperature can give an indication of the probable number of generations at

temperatures in the field. Published values for nematodes vary from 5 for *Monhystrella parelegantula* in the Sluice Dock of Ostend (Belgium) (Vranken *et al.*, 1981) to 15 for *Chromadorina germanica* in the New York area (Tietjen & Lee, 1972, 1977) and 17 for *Monhystera disjuncta* in Germany (Gerlach & Schrage, 1971). If we derive speculatively a modal value of 10 from these observations for the prey species in the Dievengat, still about 60% of their production is consumed by *O. oxyuris* and the overall nematode P/B would be around 20 per year.

A high diversity in the annual number of generations is also found in harpacticoid copepods. *Asellopsis intermedia* has one generation a year (Lasker *et al.*, 1970), *Huntemannia jadensis* one to two (Feller, 1980) but epibenthic and phytal harpacticoids develop much faster with typical generation times in culture experiments of 2 to 6 weeks (references in Feller, 1980). This fast development is also shown by *Tachidius discipes* in the field.

It is thus cleary spurious to look for an overall P/B-figure for meiobenthos, unless one would be able to show that the distribution of species with regard to both their generation time and their portion of total biomass is constant, a rather unlikely hypothesis.

**P/B-scaling by body weight**

One possible way to circumvent the use of a single P/B-value for meiobenthos is the use of an empirical relationship between annual P/B and body weight at sexual maturity $M_s$ as proposed by Banse & Mosher (1980). These authors demonstrate the existence of a statistically valid log-log relationship between these two parametes for a large number of metazoan and unicellular animals. However, on the basis of the assumed figure P/B = 9 and the size range of the meiofauna, they propose the hypothesis that a separate log P/B – log $M_s$ line exists for meiobenthos, lying considerably lower than the line for other heterothermic metazoans, but with the same slope. This proposal is not substantiated by field data and therefore the proposed definition of meiobenthos as animals with a relatively low specific production is very speculative at the moment indeed. However, when we postulate a generation P/B = 3 it becomes possible to test this hypothesis using published data on development times. Fig. 2 gives an overview of the relevant information. The populations considered and the source of the data are given in table 2. When in the original publication the number of generations in the field was estimated either directly or from culture experiments taking temperature into account this estimation was used. Otherwise the number of generations was calculated on the basis of the temperature regime of the habitat. Weights, if unavailable in the original paper, were estimated using morphological descriptions of the species. For *Tachidius discipes* there are two points on the figure. The uppermost point is the possible P/B calculated from culture

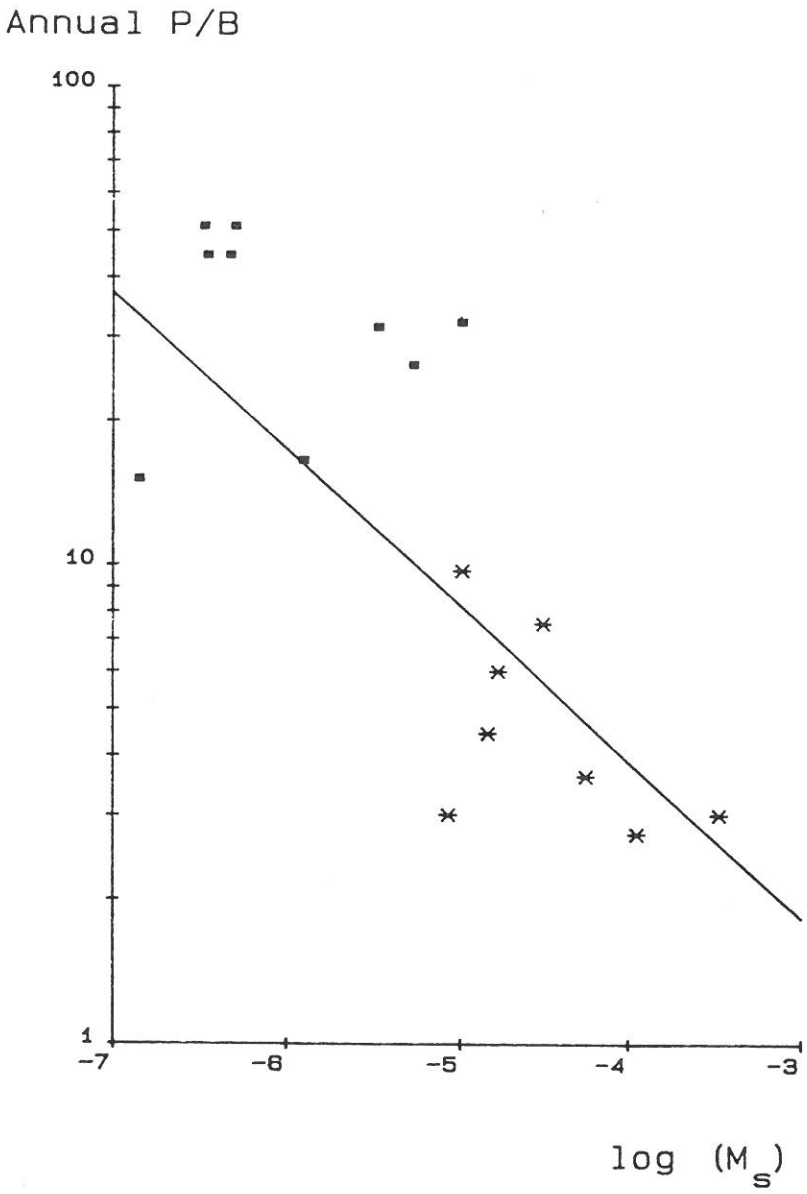


*Fig. 2* Log-log relationship between body mass at sexual maturity $M_s$ (in kcal) and annual P/B, based on the number of generations annually.
■ : data from culture experiments ; * : field observations.
List of species and sources in table 2.
The line represents the relationship proposed by Banse & Mosher (1980).

experiments (Smol & Heip, 1974). The other point is the P/B observed in the field. The discrepancy between the two points is due to the fact that *T. discipes* is only present in spring and thus does not attain its full production potential.

TABLE 2

Species considered and sources of the data represented in fig. 2.

| Species | log (P/B) | log ($M_s$) | Authority |
|---|---|---|---|
| Crustacea | | | |
| Paronychocamptus nanus | 1.42 | − 5.27 | Smol & Heip 1974 |
| Nitocra typica | 1.50 | − 5.47 | id. |
| Tachidius discipes | 1.51 | − 4.99 | id. |
| Tachidius discipes | 0.99 | − 4.99 | this paper |
| Huntemannia jadensis | 0.56 | − 4.25 | Feller 1977 |
| Asellopsis intermedia | 0.48 | − 5.07 | Lasker *et al.* 1970 |
| Cyprideis torosa | 0.44 | − 3.95 | this paper |
| Nematoda | | | |
| Enoplus communis | 0.48 | − 3.47 | Wieser & Kanwisher 1960 |
| Enoploides spiculohamatus | 0.88 | − 4.51 | Skoolmun & Gerlach 1971 |
| Oncholaimus brachycercus | 0.78 | − 4.78 | id. |
| Oncholaimus oxyuris | 0.65 | − 4.84 | Smol *et al.* 1980 |
| Theristus pertenuis | 1.22 | − 5.90 | Gerlach & Schrage 1971 |
| Chromadorina germanica | 1.65 | − 6.45 | Tietjen & Lee 1977 |
| Monhystera denticulata | 1.65 | − 6.32 | Tietjen & Lee 1972 |
| Monhystera disjuncta | 1.71 | − 6.47 | Gerlach & Schrage 1971 |
| Monhystrella parelegantula | 1.18 | − 6.85 | Vranken *et al.* 1981 |
| Diplolaimelloides bruciei | 1.71 | − 6.29 | Warwick 1982 |

It is apparent from fig. 2 that the relationship proposed by Banse & Mosher (1980) agrees with the available approximate data. A large part of the observed variability in the P/B-data of meiobenthos can indeed be explained by the body sizes of the species. However, it must be kept in mind that the log-log representation masks part of the variability and that estimations of the P/B from body size are to be treated with caution. Their use may nevertheless represent a substantial improvement in comparison with a single P/B-ratio for all meiofauna. Moreover, when more data become available it will perhaps be possible to refine the relationship and split up the data according to taxonomical and ecological groups.

In speculating about the possible causes of a lower P/B-$M_s$ line for meiobenthos, it is interesting to consider the ecological efficiencies for meiobenthic animals. The respiration of *Cyprideis torosa* as a function of temperature and body weight was determined by Herman & Heip (in press). The efficiency P/(P + R) for this population was calculated as 0.38. Respiration measures of *Tachidius discipes* from the Dievengat revealed an efficiency of adults and copepodites of 0.30.

Marchant & Nicholas (1975) found an efficiency of 0.38 for the nematode *Pelodera*, but Warwick (1982) found a puzzling value of more than 0.80 for *Diplolaimelloides bruciei*, a figure probably too high as it is higher than the physiological possibilities of bacteria grown on rich diets (Payne, 1970). The other values agree well with the average efficiency of 36.2% for non-insect detritivorous invertebrates (Humphreys, 1979).

These observations suggest that the relatively lower P/B of meiofauna is not the result of lower efficiency. Instead, whereas generation time relative to body weight is longer in meiofauna an efficiency comparable to other animal groups is obtained by a relatively low respiration rate. These characteristics of meiobenthic productivity are in line with the generally observed conservative population strategies of meiobenthos (Warwick, 1980).

**Production and respiration**

Several authors proposed a log-log relationship between production and respiration of populations over a certain interval of time, mostly a year. McNeill & Lawton (1970) found different regression lines for homeotherm, short-lived poikilotherm and long-lived poikilotherm animals. For short-lived poikilotherms the relationship is $\log P = 0.8233 \log R - 0.2367$ when R and P are expressed in $kcal.m^{-2}.y^{-1}$. The slope of the curve differs significantly from 1, which implies that production efficiency $P/(P + R)$ decreases with increasing biomass. Humphreys (1979) analysed 235 data concerning field populations and could distinguish many more groups. For non-insect invertebrates he found $\log P = 1.069 \log R - 0.601$, in $cal.m^{-2}.y^{-1}$. In his results the slopes do not differ significantly from 1, and there is no relationship between production efficiency and weight. In fact, Woodland & Cairns (1980) demonstrated that for reasonable mortality models and a logistic growth model production varies only between about 30 and 37%.

Respiration and meiobenthic organisms is usually measured using Cartesian Diver Respirometry (Holter, 1943). It is traditionally expressed in nl $O_2.ind^{-1}.h^{-1}$ and in terms of body weight using a power equation $R = aW^b$. As in many other poikilotherms the value of $b = 0.75$ for nematodes and copepods. The value of a is a measure of metabolic intensity and gives respiration per unit body weight. There is a fairly large body of data on respiration of nematodes. Warwick & Price (1979) conclude that respiration differs according to feeding type (or trophic position) of the species : non-selective deposit feeders respire less than predators, whereas epigrowth feeders have an intermediate metabolic intensity. Thus the partitioning of feeding types in a nematode community has to be taken into account when respiration has to be calculated from such data. On the other hand, Warwick & Price (1979) suggest an overall figure of 6 l $O_2.m^{-2}.y^{-1}.g\ ww^{-1}$ valid at 20°C for nematode communities, and Heip *et al.* (1982) suggest $\log R = 0.42 + 0.75 \log W$ with R in nl $O_2.h^{-1}$ and W in $\mu$g dwt for the respiration of an individual nematode,

again at 20°C. Such values are certainly preliminary and should be used with caution, but they may be useful when energy budgets have to be calculated and respiration measures are not available.

For harpacticoid copepods fewer observations are available (table 3) but they indicate that active, epibenthic or burrowing species have a higher metabolic intensity (10-12 nl $O_2.h^{-1}.\mu g\ dwt^{-1}$) than truely interstitial species (3-5 nl $O_2.h^{-1}.\mu g\ dwt^{-1}$).

TABLE 3

Respiration per unit body weight for different meiobenthic groups following $\log R = \log a + 0.75 \log W$ at 20°C.
R and a in nl $O_2.\mu g\ dwt^{-1}.h^{-1}$. W in $\mu g$ dwt.

| | log a | a | Source |
|---|---|---|---|
| NEMATODA | | | |
| Non-selective deposit feeders | 0.25 | 1.77 | Warwick & Price (1979) |
| Epigrowth feeders | 0.41 | 2.56 | Warwick & Price (1979) |
| Omnivores-predators | 0.58 | 3.78 | Warwick & Price (1979) |
| OSTRACODA | | | |
| *Cyprideis torosa* | 0.25 | 1.78 | Herman & Heip (in press) |
| COPEPODA | | | |
| *Canuella perplexa* | 0.57 | 3.72 | Herman (unp.) |
| *Mesochra lilljeborgi* | 1.02 | 10.47 | Herman (unp.) |
| *Tachidius discipes* | 1.10 | 12.59 | Herman (unp.) |
| *Paraleptastacus laticaudatus* | 0.62 | 4.20 | Lasserre & Renaud-Mornant (1973) |
| *Hastigerella leptoderma* | 0.53 | 3.42 | Vernberg *et al.* (1977) |

## Production of meiobenthos in the Belgian coastal waters of the North Sea

The Belgian coastal waters are influenced in the east by water leaving the heavily polluted Western Scheldt estuary and turning south for some tens of kilometers during ebb tide until they are again deflected towards the north as a consequence of the flood tide coming in through the Straits of Dover. As a consequence of this turning movement silt and clay with a high content of heavy metals and other pollutants are deposited in an area from the mouth of the river to about 20-30 km to the south-west (fig. 3).

The meiobenthic community in this area has been described by Govaere *et al.* (1980). The coastal zone is characterized by a *Microarthridion littorale-Halectinosoma herdmani* community, named after the dominant copepod species. However, nematodes are overwhelmingly abundant in this area, always accounting for more than 90% of the meiofauna, and the total meiofauna production will therefore be nearly exclusively nematode production. Off-shore, where clean sands predominate, the meiofauna changes drastically and is

characterized by the presence of smaller, truely interstitially (between the sand grains) living copepods. The larger, epibenthic species disappear, probably as the input of organic matter through sedimentation is much lower in this area than in the coastal zone. The Belgian off-shore waters in the west are characterized by the presence of a number of sandbanks, created by the very strong tidal currents, one of which is the Kwintebank also shown on fig. 3.

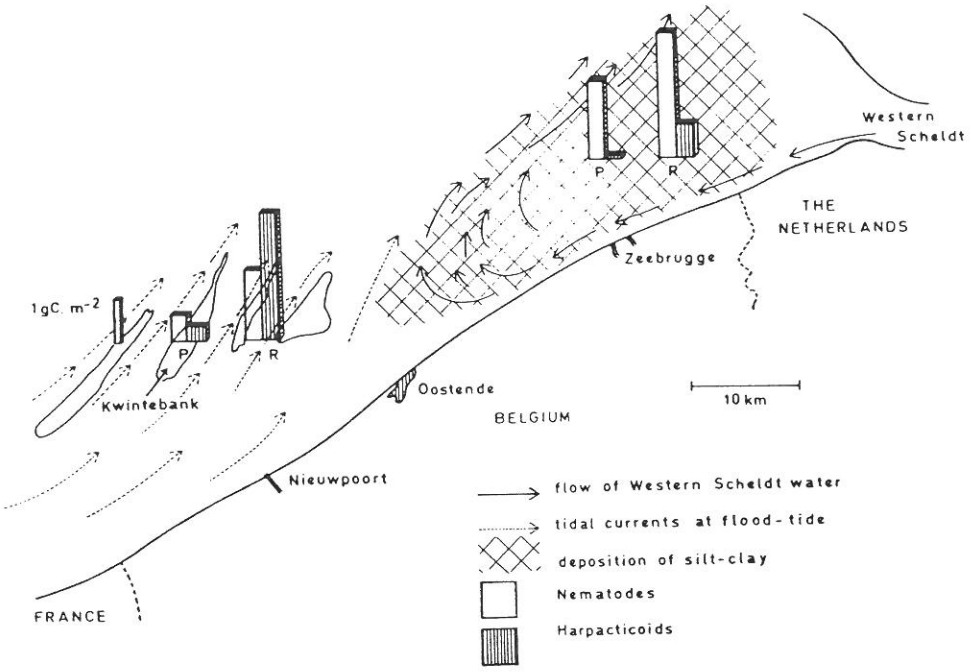


*Fig. 3* Map of the Belgian Coastal Zone showing major currents and sediments characteristics. Indicated are also production (P) and respiration (R) of nematodes and copepods in different area's.

The data used to calculate nematode production in the coastal area and on the sandbank are given in table 4. In the coastal zone the average biomass of the nematodes varies between 0.34 g dwt.$m^{-2}$ in winter and 0.57 g dwt.$m^{-2}$ in summer. With a P/B-ratio equal to 9, production would be 4.1 g dwt.$m^{-2}$ or 1.64 g C.$m^{-2}$. In the eastern part of the coastal area nearly all nematodes are non-selective deposit-feeders with a low metabolic intensity. Taking temperature into account, total annual respiration can be calculated as 5.75 l $O_2$.$m^{-2}$.$y^{-1}$, equivalent to 2.31 g C.$m^{-2}$.$y^{-1}$. From Humphreys' regression we then obtain, taking 1 g C = 12 kcal, P = 1.17 g C.$m^{-2}$.$y^{-1}$, a value corresponding with a P/B-ratio of only 6.4. With a production efficiency of 0.34, P = 0.525 R, P = 1.21 g C.$m^{-2}$.$y^{-1}$.

The same kind of calculations can be performed for the Kwintebank and for harpacticoids and the results are compared in fig. 3. Two interesting conclusions can be drawn from this figure. Nematodes predominate in meiobenthic metabolism in the coastal zone, but on the sandbanks harpacticoids have a higher respiration. Secondly, although the energy input on the sandbanks must be several orders of magnitude lower than in the coastal zone, the total meiobenthic assimilation (P + R) is only about half, indicating that when energy flow is lower a much larger part of it passes through meiobenthos.

TABLE 4

Nematode respiration in summer in the Belgian coastal waters and on the Kwintebank.

| | Coastal Waters | Kwintebank |
|---|---|---|
| Temperature (°C) | 16 | 16 |
| Ind. weight (μg dwt) | 0.26 | 0.26 |
| Density (N. 10 $cm^{-2}$) | 2175 | 628 |
| Biomass (g $dwt.m^{-2}$) | 0.57 | 0.17 |
| Respiration (nl. $ind^{-1}.h^{-1}$) | 0.47 | 0.77 |
| Respiration (l. half $y^{-1}.m^{-2}$) | 4.50 | 2.12 |
| Annual respiration ($l.y^{-1}.m^{-2}$) | 5.75 | 2.64 |
| Annual respiration ($gC.y^{-1}.m^{-2}$) | 2.31 | 1.06 |

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# Growth and Respiration of *Cyprideis torosa* Jones 1850 (Crustacea Ostracoda)

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**Summary.** The ostracod *Cyprideis torosa* Jones 1850 is a dominant species in brackish water habitats. To assess its importance, growth and respiration were measured. The shells form an increasing part of total weight as the animals grow but there is no correlation between shell weight and soft parts weight in the adults, indicating that tissue growth is a continuous process in these ostracods.

Respiration was measured at 20° C. The slope of the log-log regression of respiration on dry weight was 0.746, showing that *Cyprideis torosa* follows the general rule for this relationship. The respiration rate per unit biomass was 0.246 nl $O_2$ $\mu g^{-1}$ $h^{-1}$, which is low but well within the range of observed meiobenthic respiration rates.

The $Q_{10}$, expressing the temperature dependence of respiration, was 2.15. The general validity of Price and Warwick's (1980) hypothesis relating $Q_{10}$ to stability of food supply is questioned.

## Introduction

Information on life-cycles and energetics of meiobenthic species, particularly of ostracods, is still scarce. The importance of the latter as microfossils has directed research mainly to morphological and palaeoecological aspects, to the extent that most studies on ostracod growth do not even mention size or weight of the animal itself but focus entirely on its shells.

In certain habitats ostracods are an ecologically important group and may represent a considerable part of benthic biomass. This is certainly the case for *Cyprideis torosa* Jones 1850, a widespread and extremely common species in shallow, quiet brackish water habitats (Vesper 1972; Heip 1976). The mean annual density of this species in the habitat we studied was around 467,000 individuals $m^{-2}$, and it presumably has an important part in total energy flow.

To assess this importance, we measured respiration of *Cyprideis torosa* as a function of developmental stage and temperature, and its weight. The influence of temperature on respiration was studied because the life-cycle of *Cyprideis torosa* is closely linked to temperature (Heip 1976) and the link may be the general temperature dependence of metabolism. Besides being a measure of metabolic activity, respiration also indicates the magnitude of the energy flow passing through a population (McNeill and Lawton 1970).

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## Materials and Methods

The animals were taken from a very shallow (about 10 cm) brackish water pond, the "Dievengat", situated in a polder in north-western Belgium. Salinity fluctuated between 6 ‰ and 40 ‰ in the period 1968–1980, with a mean of 19 ‰. The sediment is a well-sorted fine sand (median grain size 0.223 mm). It is covered with large amounts of detritus, mostly debris of *Phragmites*. This type of sediment is preferred by *C. torosa* (Vesper 1972).

For the weighings a sediment sample was taken on 9 April 1981. In the laboratory the animals were immediately sorted alive and then fixed in a neutralized isotonic 4% formaldehyde solution, where they remained for no longer than 1 week.

Dry weight was determined on a Mettler ME22 microbalance to a precision of ±1 µg. Before weighing the animals were washed four times in bidistilled water, and dried for 2 h at 110° C.

For the determination of shell weight, the animals were placed in a boiling 1N KOH solution. The shells were then checked under the dissecting microscope, and if soft parts remained, they were carefully removed. The shells were washed, dried and weighed again in the same way as the whole animals. For the adults, total weight and shell weight were determined individually for each animal. This could not be done for the juveniles, where several individuals were weighed together.

Length and height of the left shells were measured. These shells were mounted with the concave side down and drawn with a camera lucida. On these drawings length and height were determined following Vesper (1972).

Respiration was measured with a stoppered diver Cartesian Diver respirometer (Klekowski 1971). The divers had a gas volume of 2 µl for measurements with adults, and 1 µl for the juveniles. Each diver contained one animal. The animals were acclimated to the experimental temperature for at least 3 days in Petri dishes containing natural sediment, which were kept in incubators under constant temperature and a natural light-dark cycle. Salinity was controlled daily and kept constant to 20 ‰. The animals were not kept in the laboratory for longer than 2 weeks.

## Results

The weights of individual adult animals and their shells are presented in Table 1. The weights of the whole animals

**Table 1.** *Cyprideis torosa:* Total weight, shell weight and soft parts weight of adults (µg dwt ind $^{-1}$). Mean and standard deviation of $n$ measurements

| | Total weight (µg) | | | Shell weight (µg) | | | Animal weight (µg) | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | $s$ | $n$ | $\bar{x}$ | $s$ | $n$ | $\bar{x}$ | $s$ | $n$ |
| ♀ | 102.95 | 14.08 | 65 | 88.63 | 15.83 | 16 | 19.81 | 8.23 | 16 |
| ♂ | 81.32 | 9.26 | 47 | 59.19 | 9.77 | 16 | 19.88 | 6.99 | 16 |

**Table 2.** *Cyprideis torosa:* Length and height of adult shell valves (mm). Mean and standard deviation of $n$ measurements

| | Length (mm) | | | Height (mm) | | |
|---|---|---|---|---|---|---|
| | $\bar{x}$ | $s$ | $n$ | $\bar{x}$ | $s$ | $n$ |
| ♀ | 0.9991 | 0.02658 | 20 | 0.57305 | 0.02050 | 20 |
| ♂ | 1.0672 | 0.02322 | 20 | 0.55680 | 0.01444 | 20 |

are normally distributed in both sexes (Kolmogorov-Smirnov test, $P<0.001$), and significantly different for males and females ($P<0.001$). However, the weights of the soft parts (total weight − shell weight) are almost exactly the same in both sexes. The difference in total weight can thus be attributed to the heavier shell of the females.

There is no correlation between total weight and shell weight in males ($r=0.335$; $n=18$; $F=2.02$). Since the form of the shell is different in males and females, and as there is no reason to believe that a difference exists according to sex, only data from males were used. Length and height of these same shells are presented in Table 2. There is a significant correlation between shell length and shell height ($r=0.605$; $n=18$; $P<0.001$). The correlation between shell weight and shell length is almost significant at $P=0.05$, but there is no relationship at all between animal weight and shell length.

Table 3 shows the mean weights of whole animals, shells, and soft parts, respectively, of the last three juvenile instars. Since these weights were not individually determined, no standard deviations can be given. The contribution of the soft parts to total weight declines steadily towards the end of the ontogenetic series, with a sudden drop in adults. Thus growth of the metabolically active tissue is slower than would be inferred from weighings of whole animals. This is reflected in the "growth factors", ratios of values in successive stages, for the measured parameters. (We calculated these growth factors mainly for comparison with other papers on ostracod growth, where they seem to constitute a strong tradition). The growth factors for soft parts are the lowest, but also the most constant, in this set. Measurements of the length of larval stages and adults from the same habitat have been previously published by Heip (1976). In Table 4 we give the growth factors calculated from these figures.

**Table 4.** *Cyprideis torosa:* Growth factors for length of successive stages (after Heip, 1976)

| Stage | Growth factor $=L_{n+1}/L_n$ | Stage | Growth factor $=L_{n+1}/L_n$ |
|---|---|---|---|
| VIII | 1.345 | IV | 1.228 |
| VII | 1.335 | III | 1.284 |
| VI | 1.337 | II | 1.246 |
| V | 1.265 | I | 1.265 |

**Table 5.** *Cyprideis torosa:* Mean respiration (nl $O_2$ h$^{-1}$ ind$^{-1}$) of juvenile instars VI–VIII and of adults. Mean and standard deviation of $n$ measurements

| Stage | Mean resp. (nl $O_2$ ind$^{-1}$ hr$^{-1}$) | $s$ | $n$ |
|---|---|---|---|
| AD. Fem. | 19.298 | 4.5836 | 5 |
| AD. Male | 16.0446 | 4.5730 | 5 |
| VIII | 9.8951 | 2.5716 | 13 |
| VII | 6.0053 | 1.2879 | 5 |
| VI | 4.1170 | 0.7301 | 7 |

The results of the respiration measurements at 20° C are presented in Table 5. Figure 1 shows the regression of respiration rate on body weight (i.e. the weight of the soft parts). Individual weighing of the juveniles was technically impossible, and shell measurements were not used because of the absence of any relationship between any shell measurement and tissue weight of the adults. Therefore, we could not determine the body weight of the juveniles used in the experiments, and for this reason we used the mean

**Table 3.** *Cyprideis torosa:* Total weight, shell weight and soft parts weight of instars VI–VIII (µg dwt ind$^{-1}$). GF (growth factor) is the proportion of the weight of successive stages. Mean of $n$ determinations

| Stage | Total (µg) | | | Shell (µg) | | | Soft Parts (µg) | | % SP |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | GF | $n$ | $\bar{x}$ | GF | $n$ | $\bar{x}$ | GF | |
| VIII | 35.75 | 2.574 | 23 | 25.42 | 2.907 | 38 | 10.33 | 1.921 | 28.89 |
| VII | 17.52 | 2.041 | 90 | 12.19 | 2.085 | 38 | 5.33 | 1.938 | 30.44 |
| VI | 8.65 | 2.025 | 69 | 5.78 | 2.109 | 27 | 2.87 | 1.857 | 33.20 |

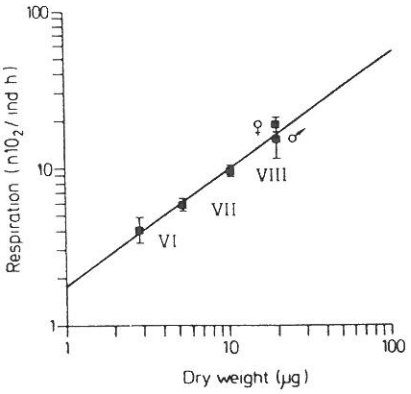


**Fig. 1.** *Cyprideis torosa:* mean respiration (nl $O_2 h^{-1} ind^{-1}$) of instars VI–VIII and adult males and females as a function of body weight (µg dwt $ind^{-1}$). Mean and standard error of 5–13 determinations

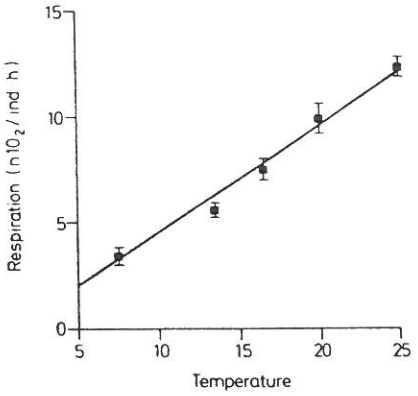


**Fig. 2.** *Cyprideis torosa:* mean respiration (nl $O_2 h^{-1} ind^{-1}$) of instar VIII individuals as a function of temperature. Mean and standard error of 3–13 determinations

**Table 6.** *Cyprideis torosa:* $Q_{10}$ values as calculated from the Arrhenius equation for different temperature intervals

| Temp. °C | 0–5 | 5–10 | 10–15 | 15–20 | 20–25 | 25–30 |
|---|---|---|---|---|---|---|
| $Q_{10}$ | 2.318 | 2.250 | 2.188 | 2.130 | 2.077 | 2.027 |

weight of the stage as the best estimate of their actual weight, both for juveniles and adults.

The dependence of respiration rate on body weight is given by $\log R = 0.246 + 0.746 \log W$ (1) ($n=35$; $r=0.91$; $F=164$), where $R$ is expressed in nl $O_2$ individual$^{-1}$ h$^{-1}$, and $W$ in µg dry weight individual$^{-1}$.

We also calculated the regression of respiration on total weight (including shells). In this case the slope $b=0.618$ (SE 0.046), which is significantly different from 0.75, the generally accepted theoretical value. When the weight of the shell is included, the estimate of the slope is seriously biased.

For the analysis of the relationship between respiration rate and temperature we used only animals of the last juvenile instar, since these were the most abundant in the field population at the time of the experiments. Experimental temperatures were 7.5° C, 13.5° C, 16° C, 20° C and 25° C. Figure 2 shows the results of these experiments. The curve fitted through the points is the function $R = 0.351\ T^{1.100}$ ($r=0.911$; $n=36$; $F=167$), which, of all models tried, gave the best fit.

The $Q_{10}$ values, as calculated from the Arrhenius' curve for different temperature intervals following Ivleva (1980), are given in Table 6. The (constant) $Q_{10}$ calculated directly from the Van 't Hoff equation is 2.15.

## Discussion

One of the purposes of this study was to investigate whether the growth of Ostracoda is continuous or not. In this regard it is interesting to note that there is no correlation between animal (soft tissue) weight and length or weight of the shell. The dimensions of the shell are probably determined by the condition of the animal when it moults, which may be almost independent of its condition several weeks or even months afterwards. This will be true especially when growth of the soft parts is a continuous process, and the absence of a correlation therefore supports this hypothesis. It is further supported by the considerable range in the soft part weights: in fact, several adult animals weighed less than 10 µg, the mean weight of stage VIII animals. When total weight, including shells, is considered, there is no overlap at all.

The growth factors (ratios of successive stages) for length, total weight and soft tissue weight are not constant throughout larval development. This is in agreement with recent studies on ostracod growth (Heitkamp 1979; Gillandt 1977) in which these variations are related to differentiation of organ systems in the animal. An exponential increase in these growth factors, as implicitly assumed by Anderson (1964), was not found in *C. torosa*.

The dependence of respiration on body weight, as described by the slope of the log-log relationship between respiration rate and body weight, is very near to the mean value 0.75, which has been found to apply to a wide range of organisms (Hemmingsen 1960), more especially to Crustacea (Ivleva 1980), and is also well established for meiobenthos (Warwick and Price 1979). However, considerable scatter around this value is observed, and it is not known how much of this represents biological reality. Part of it is undoubtedly due to experimental errors, but other types of error could be important: when the ratio of organic weight to total weight is not constant throughout development, this will result in a biased estimate of $b$. The low $b$ value ($b=0.440$) found for the Ostracod *Conchoecia* sp. (in Ivleva 1980), the only other ostracod species for which a respiration-body weight relationship is known, may result from this error. At present, we may not assume that ostracods are an exception to the 0.75 rule. The value of $a$ in Eq. (1) is a measure of the intensity of respiration, as it represents the corrected respiration per unit biomass. It is difficult to compare $a$-values since they depend on the units of measurement for both respiration and body weight. Recalculated to the units used in Ivleva (1980) (µl $O_2$, mg), we get $a=-0.516$ for *C. torosa*, which is considerably less than her mean value of 0.505 ($s=0.217$) for marine Crustacea at 20° C. For comparison of our $a$-value with other meiofauna, as summarized by Teare and Price (1979; Fig. 5) we assumed a wet weight: dry weight ratio of 4:1 and a specific gravity of 1.1. The respiration-body weight relationship thus recalculated for *C. torosa* is at the lower end, but well within the range of meiobenthic respiration rates.

Possibly respiration intensity of meiobenthos as a whole is lower than average. Compared to the nematode data of Warwick and Price (1979), *C. torosa* would be what these authors call a "moderately slowly" respiring organism.

The $Q_{10}$ value expressing the temperature dependence of respiration rate is around 2.15, which is very near to the value of 2.17 found by Teare and Price (1979) for the meiobenthic harpacticoid *Tachidius discipes* and the value of 2.20, as calculated from Lasker et al. (1970) for *Asellopsis*, another harpacticoid (see Teare and Price, 1979). Ivleva (1980), expressing temperature dependence by the parameter $\mu$ in the Arrhenius equation, finds this parameter to lie within rather narrow limits: $\mu = 55{,}509$ J mol$^{-1}$ ($s = 541$). This $\mu$ value corresponds to a $Q_{10}$ in the 15° C–20° C range of 2.203 ($s = 0.017$). Miller and Mann (1973) find a mean and constant $Q_{10}$ of 2.05 for marine invertebrates from the northern hemisphere. All these data are very consistent.

Price and Warwick (1980), when reviewing $Q_{10}$ values for meiobenthic species, propose that there exist two distinct groups in meiofauna: animals with a "stable food supply" (organic matter, nematodes), with a $Q_{10}$ of 1, and animals with an "unstable food supply" (diatoms, bacteria) with a $Q_{10}$ of 2. However, it is hardly possible to see whether *C. torosa*, which is a selective deposit feeder, actually eats the bacteria or the detritus. In general, the distinction between feeding on bacteria and feeding on other organic material is hard to make. It is tautological to argue that a $Q_{10}$ of 2 evolved because it enables exploitation of temperature-dependent resources. Anyway, there are good reasons to believe that a $Q_{10}$ of 2 is the most primitive state, since it reflects the general temperature dependence of chemical reactions, and one should therefore look for reasons why an animal would evolve towards a lower $Q_{10}$. A stable food supply in itself does not seem to constitute a good reason, as it is not clear why a stable food supply for one species could not be the same for another species, so that only when other limitations are present would competition be prevented. Anyway, it seems better to wait for more data on temperature dependence of meiofauna respiration rates before drawing far-reaching conclusions.

The population dynamics of *C. torosa* in this habitat are in apparent contrast with the hypothesis of Price and Warwick. Heip (1976) suggested that its density is not regulated by food availability. He showed further the profound influence of the yearly temperature-cycle on the dynamics of the species. Since the species survives freezing only in the egg stage, its life-cycle must be adapted to this. This regulation of the life-cycle in agreement with environmental temperature can only be achieved if temperature has a net effect on metabolism, i.e. if the $Q_{10}$ is high enough. Thus there is no adaptive value for the species in evolving towards a lower $Q_{10}$.

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# The production of *Cyprideis torosa* Jones 1850 (Crustacea, Ostracoda)

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**Summary.** The ostracod *Cyprideis torosa* Jones, 1850 is a dominant species in the meiofauna of brackish water habitats. Its production in the field over a five-year period has been calculated using two production models. The first model uses the age-distribution of shells preserved in the sediment to assess the stage-specific mortality rates and the stage durations. The second model is the size-frequency model, modified for use with developmental stages instead of size-classes. Productions calculated with both methods agree very well. Their values are 9.7 and 9.2 g dwt $\cdot m^{-2} \cdot y^{-1}$ respectively. The yearly $P/B$-ratio is 2.7 or 2.6 $y^{-1}$, production efficiency $P/A$ is 0.38 or 0.37.

The production efficiency of *Cyprideis torosa* nearly equals the mean efficiency of non-insect invertebrate detritivores. The species' conservative strategy and long generation time enables it to maintain a relatively high biomass with a fixed amount of food. These characteristics make it a superior competitor.

## Introduction

The energy-flow through marine sediments is related to the metabolism of the biological populations that inhabit them. As metabolism is size-dependent, it is generally accepted that the smaller meiofauna has a larger part in energy flow than an equal biomass of macrofauna. However, apart from such general statements, very little is known on the energetic role of meiofauna. The production of field populations has been estimated for two harpacticoid copepod species only (Feller 1977; Fleeger and Palmer 1982) and estimations of production efficiency (production/assimilation) are known for one harpacticoid copepod and one marine nematode only (Warwick 1981).

McNeill and Lawton (1970) and Humphreys (1979) have shown that respiration data can be used to estimate production. The procedure rests on the assumption that production efficiencies are relatively constant within different ecologically defined groups for which regressions are calculated. If a similar relationship could be shown to exist in meiofauna populations, the steadily accumulating amount of respiration data may be used to obtain a global assessment of the energy-flow passing through this compartment of marine systems.

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*Cyprideis torosa* is a very important meiofauna species in the shallow brackish water habitat we studied. It has a fairly complex life-cycle (Heip 1976). The animals develop through eight larval instars before becoming adult. The eggs are produced during the summer months and are contained between the shells of the mother, as are the instar I animals. In autumn the development of the juveniles slows down and it stops altogether in winter. Due to this prolonged reproduction the population passes the winter in different stages (instar V to adult). Only in the next spring do overwintering juveniles become adult and reproduce. The species thus has one generation annually.

The respiration rate of *Cyprideis torosa* as a function of body weight and temperature has been described by Herman and Heip (1982). In this paper we present production estimates of this population, calculated by two different methods, and estimates of production efficiency.

## Material and methods

### *1. Field samples*

Samples were taken fortnightly from 1970 through 1974, in a very shallow brackish water pond, the "Dievengat", in a polder in north west Belgium. Salinity fluctuated between 6 and 40‰, with a mean of 19‰. The sediment is a well sorted fine sand covered with large amounts of detritus.

The sampling and elutriation procedures are extensively described by Heip (1976). In short, three 6.06 $cm^2$ cores were taken to a depth of 5 cm. They were elutriated following the method of Barnett (1968). The animals were separated from the detritus, grouped in stages according to their size, and counted. Animals of the first three larval stages were counted together.

Population respiration was calculated using the abundance data, and the relationship between respiration rate, body weight and temperature (Herman and Heip 1982). The temperature of the habitat was approximated by a sinusoidal function of time, described by Heip and Smol (1976).

The dry weight of the organisms, used in the production calculations, is the dry weight of the tissues, excluding the weight of the calcareous shells. It was determined for the last four developmental stages by Herman and Heip (1982). For the first stages tissue weight was estimated as 1/3 of the total dry weight.

The model developed to estimate the average duration of the larval stages and the average stage-specific mortality

rates uses the numbers of empty shells found in the uppermost sediment layers. For this purpose a sediment sample was taken on May 8th, 1980, and the 864 shells found were grouped according to stage.

### 2. *The production model*

Because the life-cycle of *Cyprideis torosa* is rather complex, existing production models were not appropriate and a new model was developed. This model is based on the following logic: as an individual passes from one developmental stage to the next, it sheds its shells and builds new ones. An animal dying in stage 7, e.g., thus produces and subsequently sheds shells of stages 1 through 7, which are preserved in the bottom. We thus expect to find more shells of the younger stages. As the sediment is not subject to wave actions or serious water flows, we can assume that these shells reflect the life history of the population in recent years.

Since the empty shells of stages 1, 2, 3 are too small to be distinguished from each other, most of the following analysis is based on the stages 4, 5, 6, 7, 8 and adult.

We first define, for $4 \leqq i \leqq 9$ (in which $i$ denotes stage number): $N_i$ = the number of animals that have entered stage $i$ during the study period of 5 years. $N_i$ has the dimensions individuals $(10\ \mathrm{cm}^2)^{-1}\ (5\ \mathrm{y})^{-1}$.

$L_i$ = the number of animals dying when they are in stage $i$ during the study period. It has the same dimensions as $N_i$.

$k_i = N_i/N_4$ ($N_4$ being the number that have entered stage 4). $k_i$ is dimensionless. It is the fraction of the number of animals that have entered stage 4 and survived until at least the beginning of stage $i$.

$l_i = L_i/N_i$. This dimensionless number is the fraction of the number of animals that have entered stage $i$, and died when they are in this stage.

$S_i$ = number of shells of stage $i$ counted in the sediment sample.

$A_i$ = the surface under the curve of density against time for stage $i$.

$A_i$ is calculated by the trapezoidal rule as $A_i = \Sigma F_j(h_j + h_{j+1})/2$, in which $F_j$ is the observed number of animals at the time $t_j$ and $h_j = t_j - t_{j-1}$ ($t$ in days). $A_i$ has the dimensions (ind. × days)/(10 cm$^2$ × 5 year).

All animals that enter stage 4 leave stage 4 shells in the sediment. When they survive at least until the beginning of stage $i$ ($4 < i \leqq 9$), they also leave stage $i$ shells. Therefore $k_i$ can be estimated from the shell countings (the numbers $S_i$) as:

$$k_i = S_i/S_4 \tag{1}$$

for all stages.

By a similar argument, $l_i$ can be estimated as:

$$l_i = 1 - S_{i+1}/S_i \tag{2}$$

for all stages except the adult stage.

For the ensuing calculations we made two important assumptions:

i) The survival curve within each stage is negative exponential. Representing the instantaneous mortality rate of stage $i$ by $d_i$, and the average duration of the stage by $D_i$, we get

$$e^{-d_i D_i} = 1 - l_i.$$

ii) The maximum time an animal can spend as an adult is fixed to $D_9$. This means that after a time $D_9$ an adult invariably dies. There is, as in juveniles, an exponential mortality with instantaneous mortality rate $d_9$ before the age $D_9$. We cannot estimate $d_9$ from the available data. Therefore we assume $d_9 = d_8$, i.e. the instantaneous mortality rate of adults before the final age is the same as in the last juvenile instar. This is not unreasonable as stage 8 juveniles are long-lived.

With these assumptions, $N_i$ animals entering stage $i$ will give a surface under the density curve of:

$$N_i \int_0^{D_i} e^{-d_i t}\, dt = N_i(1 - e^{-d_i D_i})/d_i. \tag{3}$$

This can be compared to the actually observed surfaces $A_i$:

$$A_i = N_i(1 - e^{-d_i D_i})/d_i \tag{4}$$

from which:

$$N_i = A_i d_i/(1 - e^{-d_i D_i}). \tag{5}$$

The surviving fraction $e^{-d_i D_i}$ equals $1 - l_i$, and is known from the shell countings for stages 4 through 8, but not for the adults, However, Eq. (5) gives the possibility to evaluate $e^{-d_9 D_9}$: since $N_9 = N_8 e^{-d_8 D_8}$, and $d_9$ was set equal to $d_8$ (ass. 2), we obtain:

$$e^{-d_9 D_9} = \frac{A_9(1 - e^{-d_8 D_8})}{A_8\, e^{-d_8 D_8}} \tag{6}$$

in which the surfaces $A_8$ and $A_9$, and the factor $e^{-d_8 D_8}$ are known from the observations.

When $e^{-d_i D_i}$ is known for all stages, Eq. (5) expresses $N_i$ in function of the known surfaces $A_i$, the known survival $e^{-d_i D_i}$ and the unknown mortality rates $d_i$. Multiplication of both sides of Eq. (5) by $D_i$ gives:

$$N_i D_i = A_i d_i D_i/(1 - e^{-d_i D_i}). \tag{7}$$

All terms in the right-hand side of Eq. (7) are known from observation. When, furthermore, both sides are multiplied by the known factor $N_4/N_i = 1/k_i$ and summed over all stages, we obtain:

$$N_4 \sum_i D_i = \sum_i \frac{1}{k_i} A_i \frac{d_i D_i}{1 - e^{-d_i D_i}}. \tag{8}$$

$\Sigma D_i$ is the total time elapsing between the onset of stage 4 and the end of the adult life. When an estimate of this period is available, $N_4$ can be estimated from Eq. (8) as:

$$N_4 = \frac{1}{\sum_i D_i} \sum_i \frac{1}{k_i} A_i \frac{d_i D_i}{1 - e^{-d_i D_i}}. \tag{9}$$

Once $N_4$ is known, all values $N_i = k_i/N_4$ can be calculated. $D_i$ can then be calculated from Eq. (7), and knowing $e^{-d_i D_i}$ and $D_i$, the mortality rates $d_i$ are also obtained.

The above model only treats the stages 4 through adult. A separate estimate of the number of eggs produced (represented as $N_1$) can be made as follows. The mean sex ratio is 0.37. Each female produces 11 eggs on average (Heip 1976). $N_1$ is then given by:

$$N_1 = N_9(1 - 0.37)\ 11. \tag{10}$$

Since $N_4 = N_1 e^{-d_1 D_1}$ (the subscript "1" denotes the combined stages 1, 2 and 3!), $e^{-d_1 D_1}$ can be calculated. Equation (5) then gives $d_1$ and $D_1$.

From weighings of individual adult animals, Herman and Heip (1982) concluded that tissue growth in *C. torosa* is essentially a continuous process. We therefore assume that the mean weight of a stage $i$ animal corresponds to the weight of an animal having half passed this stage. $M_i$, the number of animals alive at the middle of the stage $i$, is given by:

$$M_i = N_i e^{-d_i D_i/2}. \tag{11}$$

Let $M_0$ represent the number of eggs produced, and $M_{10}$ the number of animals dying after having passed a time $D_9$ in the adult stage. Let further $W_i$ be the mean dry weight of a stage $i$ animal, $W_0$ the dry weight of an egg, and $W_{10}$ the dry weight of an adult after having passed a time $D_9$ in the adult stage. $W_{10}$ is estimated as $W_9 + (W_9 - W_8)/2$. Production is then estimated as:

$$P = \sum_i \frac{M_i + M_{i-1}}{2} (W_i - W_{i-1}). \tag{12}$$

*3. Production estimation by the size-frequency method*

This method, in the formulation of Menzie (1980) estimates production as:

$$P = \sum_{j=1}^{i} (N_j - N_{j+1}) (W_j W_{j+1})^{1/2} \tag{13}$$

where:

$$N_j = i \bar{n}_j (P_e/P_a)_j \, 365/\mathrm{CPI} \tag{14}$$

and $i$ = number of size-classes. $P_{ej} = 1/i$ = estimated proportion of the life-cycle spent in size-class $j$. $P_{aj}$ = actual proportion of the life-cycle spent in size-class $j$. CPI = cohort production interval. $\bar{n}_j$ = mean number of animals in size-class $j$.

This method can be applied to species grouped in developmental stages instead of in size-classes, if an appropiate estimation of $P_{aj}$ is available. According to several authors the accuracy of these estimations is not very critical (Hamilton 1969; Benke and Waide 1977).

We made an estimation of $P_{aj}$ by assuming a constant mortality throughout the entire life. In this case we have (Manly 1977):

$$e^{-a_j \theta} = A'_{j+1}/A_j \tag{15}$$

where $a_j$ = duration of stage $j$. $A_j$ = the summed surfaces under the density curves of stage $j$ and all subsequent stages, including adults. $\theta$ = mortality rate.

When the duration of stage 1 is arbitrarily chosen as 1 time unit, the durations of all subsequent larval stages can be calculated in these relative units as:

$$a_j = \frac{-\ln A'_{j+1}/A'_j}{-\ln A'_2/A'_1}. \tag{16}$$

This expression cannot be used for adults. However, it is possible to calculate the mean number of days an animal spends in the adult stage. When mortality is exponential, one can state in general:

$$A_j = \frac{N_j}{\theta} (1 - e^{-a_j \theta}) \tag{17}$$

from which:

$$\lim_{a_j \to \infty} A_j = \frac{N_j}{\theta}. \tag{18}$$

Therefore we have for the adult stage:

$$\frac{A_j}{N_j} = \frac{1}{\theta}. \tag{19}$$

$A_j/N_j$ is the mean number of days spent as an adult. It can easily be evaluated since:

$$\frac{1}{\theta} = -\ln \frac{A'_2}{A'_1}. \tag{20}$$

$P_{aj}$ can then be calculated for all $j$ as

$$P_{aj} = a_j \Big/ \sum_{j=1}^{i} a_j. \tag{21}$$

## Results

The number of animals of the different stages are represented in Fig. 1. Population dynamical characteristics to be drawn from these curves have been fully discussed by Heip (1976). The area's $A_i$ under these curves are given in Table 1.

In total, we counted 864 empty shells. The number of shells in each stage $S_i$ is shown in Table 2. Also represented here are the quantities $l_i$, $k_i$, and $e^{-d_i D_i} = 1 - l_i$.

In order to use Eq. (9), an estimate of $\Sigma D_i = G$ must be available. Since *C. torosa* has most probably one generation a year, the time between hatching of an average egg of one generation and one of the next must, on average, exactly equal 365 days. If this were not the case, there would be a yearly shift in the reproductive period to less favourable seasons. However, we cannot infer from this statement a precise estimate of $G$, as this is not equal to the generation time. As a long post-reproductive life-span is improbable,

**Table 1.** *Cyprideis torosa*: area's $A_i$ ((ind × days)/(5 y × 10 cm²)) under the density curves of the different developmental stages (Fig. 1)

| Stage | $A_i$ (ind × days/(5 y × 10 cm²)) |
|---|---|
| 1–2–3 | 105,920 |
| 4 | 33,542 |
| 5 | 70,768 |
| 6 | 139,133 |
| 7 | 179,676 |
| 8 | 138,583 |
| AD. | 180,253 |

**Table 2.** *Cyprideis torosa*: shell countings in the sediment sample and derived parameters. See text for definitions

| Stage | $S_i$ | $k_i$ | $l_i$ | $e^{-d_i D_i}$ |
|---|---|---|---|---|
| 4 | 226 | 1 | 0.2522 | 0.7478 |
| 5 | 169 | 0.7478 | 0.1479 | 0.8521 |
| 6 | 144 | 0.6372 | 0.1319 | 0.8681 |
| 7 | 125 | 0.5531 | 0.1600 | 0.8400 |
| 8 | 105 | 0.4646 | 0.0952 | 0.9048 |
| AD. | 95 | 0.4204 | – | 0.8641 |

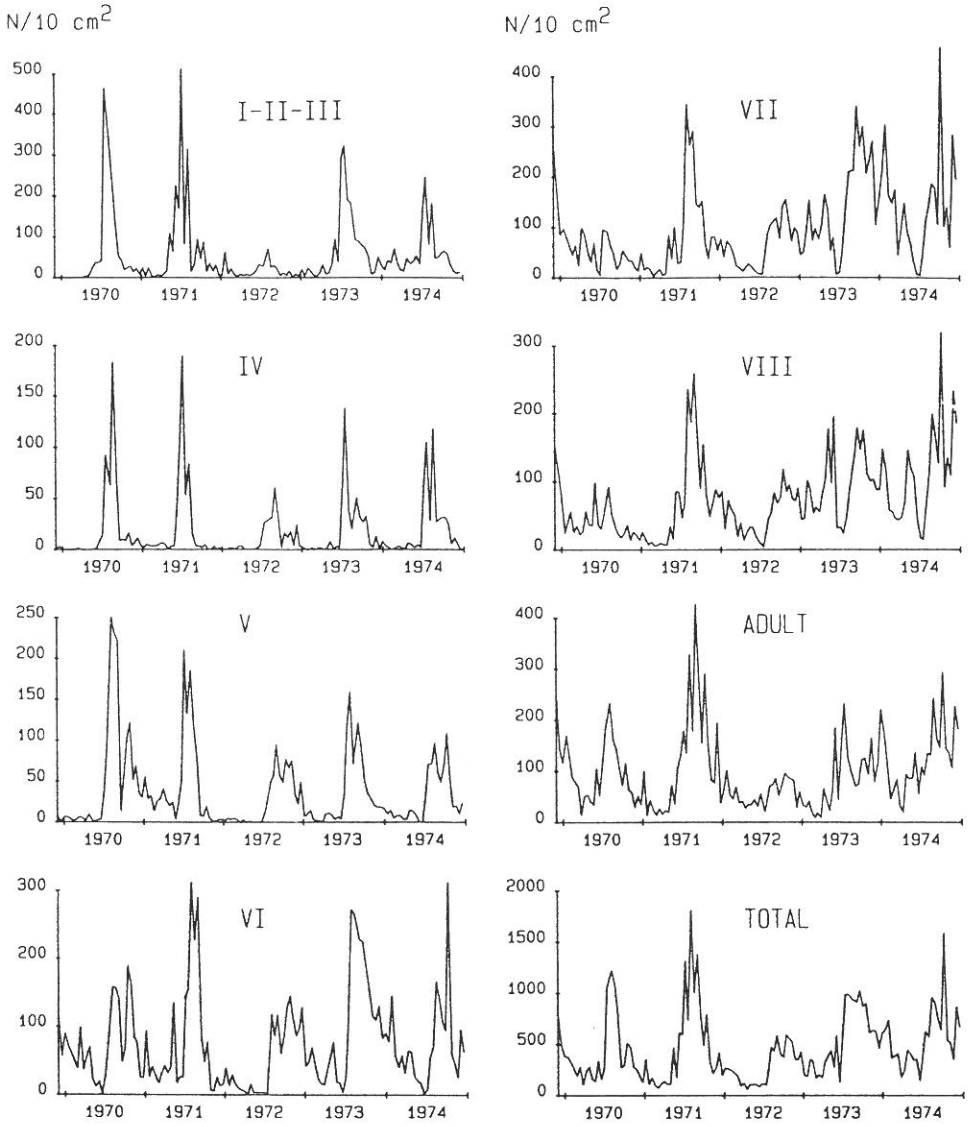


**Fig. 1.** *Cyprideis torosa*: Densities of the different developmental stages during the 5-year study period ($N/10\ cm^2$). Stages 1, 2 and 3 are combined, as they cannot be distinguished on the basis of size

**Table 3.** *Cyprideis torosa*: relative duration of the stages, expressed as $f_i = D_i/\Sigma D_i$ and absolute durations $D_i$ (days) of the stages assuming $\Sigma D_i = 365$

| Stage | $f_i$ | $D_i$ |
|---|---|---|
| 4 | 0.0257 | 9.38 |
| 5 | 0.0681 | 24.86 |
| 6 | 0.1557 | 56.85 |
| 7 | 0.2354 | 85.94 |
| 8 | 0.2085 | 76.10 |
| AD. | 0.3065 | 111.88 |

**Table 4.** *Cyprideis torosa*: Numbers $N_i$ of animals that have entered stage $i$ during the 5 year study period (per 10 $cm^2$)

| Stage | $N_i$ |
|---|---|
| 1–2–3 | 12,003 |
| 4 | 4,119 |
| 5 | 3,080 |
| 6 | 2,625 |
| 7 | 2,278 |
| 8 | 1,914 |
| AD. | 1,732 |

we suggest $G$ not to be much different from one year, though, and put it $G = 365$ days. This is the best estimate we are able to make with the present data. A departure of, e.g., 10% from this value will produce a corresponding bias in the production estimate of 10%. With this estimate of $G$, we get the durations of the stages that are listed in Table 3.

From Eq. (9), $N_4$ is calculated as 4119 individuals per 10 $cm^2$ per 5 years. Table 4 presents the values $N_i$ which can be derived from this Figure. $N_1$ is estimated [Eq. (10)] to be 12,003 individuals per 10 $cm^2$ per 5 years. $D_1$ is then calculated as 14.4 days.

Table 5 lists the values of $M_i$ and $W_i$ that were used in the production calculations.

Production of soft parts amounts to 9.7 g dwt $m^{-2}\ y^{-1}$.

The mean biomass is 3.6 g dwt $m^{-2}$, and the yearly $P/B$ is 2.7 $y^{-1}$. The oxygen consumption is estimated to be 20.38 l $O_2$ $m^{-2}\ y^{-1}$.

Table 5. *Cyprideis torosa*: Values of $M_i$ (ind. per 10 cm$^2$) and $W_i$ (µg dwt) as used in the production calculations

| i | $M_i$ | $W_i$ |
|---|---|---|
| 0 | 12,003 | 0.11 |
| 1–2–3 | 7,031 | 0.28 |
| 4 | 3,562 | 0.93 |
| 5 | 2,843 | 1.50 |
| 6 | 2.446 | 2.87 |
| 7 | 2,088 | 5.33 |
| 8 | 1,821 | 10.33 |
| 9 | 1,610 | 19.85 |
| 10 | 1,497 | 24.61 |

**Table 6.** *Cyprideis torosa*: data for the size-frequency production estimation

| Stage | $A'_j$ | $e^{-\theta a_j}$ | $a_j$ | $N_j$ | $(W_jW_{j+1})^{1/2}$ | $P_j$ |
|---|---|---|---|---|---|---|
| 1–2–3 | 847,875 | 0.875 | 1 | 1108.13 | 0.51 | 46.3 |
| 4 | 741,955 | 0.955 | 0.345 | 1017.14 | 1.18 | 94.2 |
| 5 | 708,413 | 0.900 | 0.790 | 937.18 | 2.08 | 305.8 |
| 6 | 637,645 | 0.782 | 1.843 | 789.80 | 3.91 | 898.3 |
| 7 | 498,512 | 0.639 | 3.356 | 560.12 | 7.42 | 1633.7 |
| 8 | 318,583 | 0.566 | 4.265 | 339.94 | 14.32 | 1264.5 |
| AD. | 180,253 | | 7.494 | 251.64 | 19.85 | 4995.0 |

In Table 6 the data for the production estimation by the size-frequency method are summarized. The first column shows the summed surfaces under the density curves $A_j$; the second column shows the values $e^{-\theta a_j}$, calculated from Eq. (15); the third column gives the relative durations of the stages [Eq. (16)]. The values $N_j$ and $(W_jW_{j+1})^{1/2}$, used in Eq. (13), are shown in the fourth and fifth columns, giving the partial production estimates $P_j$ of the sixth column. The total production is estimated as $P=9.2$ g dwt m$^{-2}$ y$^{-1}$, and $P/B=2.6$ y$^{-1}$.

For the comparison between oxygen consumption and production, we converted these values to energy units. We used the following conversion factors: 1 l $O_2$ consumed is assumed equivalent to 0.4 gC metabolized (Crisp 1971), 1 gC=45.8 kJ (=10.92 kcal) (Salonen et al. 1976), and organic carbon is 52% of ash free dry weight (Salonen et al. ibid.).

Respiration then represents 373 kJ m$^{-2}$ y$^{-1}$ (=89 kcal m$^{-2}$ y$^{-1}$). Production, as calculated by the first model, is 231 kJ m$^{-2}$ y$^{-1}$ (=55 kcal m$^{-2}$ y$^{-1}$). The production efficiency, $P/(P+R)$, is estimated at respectively 0.38 and 0.37.

## Discussion

The use of shells preserved in the sediment to develop our first model has some questionable aspects. It is impossible to know if there is a differential breakdown for shells of different size. Moreover, we don't know if conditions for *C. torosa* in this pond have always been similar. However, we dispose of a long time series of observations, which may well cover a considerable range of possible conditions for the population. Since our conclusions are based on average values, they may give reliable figures of mean annual energy turnover in this population.

Furthermore, the fact that the number of shells decreases with increasing stage number seems to correspond well with the hypothesis that preservation conditions are similar for all shells.

Finally the results of the first model are corroborated by the size-frequency estimate. Although that method basically consists of the fitting of a population dynamical model that is very simple, it is known to give fairly accurate production estimates (Menzie 1980). The adaptation of the method to populations grouped in developmental stages rather than in size classes does not seem to alter this conclusion. Therefore it can be an interesting method for the production estimation of many arthropod populations.

The generation $P/B$, which in this case is the same as the yearly P/B, is not very high. It is in the lower part of the range (2.5–5) indicated by Waters (1969) for aquatic invertebrates. The factor most seriously influencing the specific production is the ratio final: initial population size. This ratio is fairly high in *C. torosa*: 1,732/12,003=0.144.

Heip (1976) stated that *C. torosa* is a meiobenthic species on top of a food chain, living in an environment that is, at least for this species, rather predictable. Both these factors favour a strategy of reducing the number of offspring, thereby increasing the individual offspring's probability to grow adult. It can be seen that, as a by-product, this strategy lowers specific production per generation time.

On the other hand, the "production efficiency", $P/(P+R)$, has almost exactly the value 0.362, the mean of 23 "non-insect invertebrate detritivores", as reviewed by Humphreys (1979). The production we calculated is almost identical to the value predicted from respiration by Humphreys' (1979) regression equation for non-insect invertebrate detritivores. The value predicted by the "Crustacea" regression line is but half the measured production. However, we consider the first line to be the more reliable, since Crustacea comprise, from an ecological point of view, a very heterogeneous group of animals.

A normal proportion of the assimilated energy is thus turned into production, while at the same time a relatively high biomass can be maintained by *C. torosa*. Both this maintenance of high population numbers, and the efficient use of the assimilated energy must increase the competitive ability of the species.

The only comparable values of production efficiency for marine meiofaunal populations are those given by Warwick (1981) for the nematode *Diplolaimelloides bruciei* and the harpacticoid *Tachidius discipes*. The values obtained from culture experiments for *D. bruciei* are exceptionally high: 70 to 80%, with a peak at 86.9%. Even these high values are minimal estimates. Indeed in exponential dynamics the correct measure of specific production is the birth rate, not the intrinsic rate of natural increase (Zaika, 1973). When there is any mortality the birth rate is higher than $r$. For example, assuming a constant mortality rate causing 25% of the juveniles to die before reaching adulthood, the efficiency at 15° C is raised to 88.1%, and the efficiency of the females at this temperature to 91.4%. Even this value is a minimal estimate, not accounting for any excreted organic material (mucus secretion may be important in nematodes) or exuvia. However, as even the efficiencies of bacteria grown on the richest diets do not exceed 85%, we suggest that the efficiencies calculated by Warwick are too high, perhaps due to the long starvation in the respiration experiments.

The production efficiency calculated for the harpacticoid *Tachidius discipes* is about 70%, again a very high value. In this calculation respiration values obtained from animals in the Lynher estuary (Teare and Price 1979) are used together with population dynamical data from the Dievengat (Heip 1977, Heip and Smol 1976). However, it appears from our data that these populations differ in a number of characteristics (Herman and Heip, in preparation). The most important difference in this respect is that the Dievengat population has a much higher respiration rate. The efficiency we calculated with this respiration rate is about 30%. We therefore conclude that there is no strong evidence for the statement that meiofauna efficiencies in general are higher than those of other groups.

The most important factor in determining the yearly $P/B$ is the number of generations per year. A low number of generations per year (1 to 3) was found in seven ostracod species by Theisen (1966). The $P/B$ found in this study, therefore, may be typical for a number of other ostracod species. Banse and Mosher (1980) state that the meiofauna has another relationship between annual P/B and adult weight than the other groups of animals. In fact, they propose to use this lower $P/B$ as the definition criterion of meiofauna. The results of our study fit in well with the $P/B$ – body mass relationship they proposed for meiofauna. However, it can be questioned if *C. torosa* is typical for all meiofaunal groups. Several nematodes, ostracods, Foraminifera, Turbellaria, Harpacticoida are known to have long generation times (Gerlach 1971; Smol et al. 1980; Feller 1980), but other species may have extremely short generation times (e.g. Vranken et al. 1981). In fact the diversity of life histories in meiobenthos may be similar to that found in macrobenthos (Gerlach 1971), although the size range of meiofauna is only about 2 orders of magnitude.

In general, the fact that $P/B$ values can rather well be scaled by adult body mass has no obvious and direct physiological reason. Rather "body mass" is a summary of several characteristics of a species, such as longevity, type of food available, vulnerability to predation etc. It seems that within meiofauna all the different strategies with regard to these factors can occur in species that do not differ very widely in size. *C. torosa* may be somewhere at the end of the meiobenthic size range: species growing bigger than this are indeed likely to become highly vulnerable members of a macrofauna, which is, as a rule, less stable (Warwick 1980). Therefore, if a relationship between body mass and $P/B$ exists at all, we would expect both slope and intercept to be different.

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# THE RESPIRATION OF FIVE BRACKISH-WATER HARPACTICOID COPEPOD SPECIES

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**Abstract:** The dependency of respiration rate on body weight at 20 °C was determined for five meiobenthic copepods from a brackish-water habitat. The respiration rate of the four smaller species was generally high, $\approx 10$–$14$ nl $O_2 \cdot h^{-1} \cdot \mu g$ dry $wt^{-1}$, but was much lower for a larger species, *Canuella perplexa* T. & A. Scott 1893 (2–3 nl $O_2 \cdot h^{-1} \cdot \mu g^{-1}$). This pattern is discussed in terms of the adaptive behaviour of the populations. The significance of respiration rates in the evolution of populations is illustrated by differences between the respiration rates of a Belgian *Tachidius discipes* Giesbrecht 1882 population, and that of *T. discipes* from the Lynher estuary, U.K. It is hypothesized that respiration rates will be lower when species are in competition for relatively stable food sources.

## INTRODUCTION

There exists a considerable literature on the respiration of marine planktonic copepods but very little on benthic species. This can be partially explained because the productivity of meiobenthos is so poorly known that even its potential importance in marine systems is easily overlooked. Moreover, within the meiobenthos, attention has been focused mostly on the respiration of nematodes, as this is the numerically dominant taxon in most habitats (see Warwick & Price, 1979; Heip *et al.*, 1982 for a summary of the respiration data). Copepods may also be very important in biomass, and measurement of their respiration rate is an important step in the assessment of their part in total energy flow through the benthos. This is especially important since it has been shown (McNeill & Lawton, 1970; Humphreys, 1979) that the respiration of a population is a good indication of its secondary production. In the present study we determined the respiration rate of five copepod species from a shallow brackish-water pond. Although very productive, this habitat is poor in species; only nine copepod species have been found, and seldom more than five on any one date.

## MATERIAL AND METHODS

The animals were taken from a poly-mesohaline pond called "Dievengat", situated in a polder in northwestern Belgium (map reference 51°21′30″N : 3°22′15″E). The sediment is a well-sorted fine sand (median grain size 0.223 mm), mixed with large amounts of detritus (mostly debris of *Phragmites*).

For *Tachidius discipes* and *Halicyclops magniceps*, the animals used in respiration measurements were mouth-pipetted directly from sediment samples. They were acclimated to the experimental temperature (20 °C) for a few days in Petri dishes containing natural sediment. These Petri dishes were kept in incubators under constant temperature and a natural light–dark cycle.

*Paronychocamptus nanus*, *Mesochra lilljeborgii* and *Canuella perplexa* were cultured in the laboratory. This was necessary since it is impossible to distinguish living copepodites of the first two species under the dissecting microscope, and we could not extract enough individuals of *C. perplexa* from the samples. These three species were kept in glass vessels of 10 ml with sterilized sand and some boiled detritus from the habitat. The vessels were half filled with water from the Dievengat, which was sieved through a 5 $\mu$m plankton net and adjusted to a salinity of 18‰. To this water one drop of "Vlasblom-medium" (Geraert *et al.*, 1981) and one drop of $Na_2SiO_4$ solution (15 g/l) were added. The vessels were incubated in the light for a few days to obtain sufficient algal development. After the addition of adult animals the cultures were placed in incubators at 20 °C with a natural light–dark cycle.

Respiration was measured with a stoppered diver Cartesian Diver respirometer (Klekowski, 1971). The divers had a gas volume of 1 or 2 $\mu$l. Each diver contained one animal. The number of replicates for each species is given in Table I.

Dry weights were determined on a Mettler ME22 microbalance to a precision of $\pm$ 1 $\mu$g, using batches of $\approx$ 100 individuals belonging to the same developmental stage. Before weighing the animals were washed in twice-distilled water and dried for 2 h at 110 °C. In the respiration–body weight relationship the dry weight of an organism is taken as the mean dry weight of the stage to which it belongs. For *Tachidius discipes* a relationship between measurements of length and width and the body volume was given by Teare & Price (1979). For comparison with their measurements we followed their method. Due to telescopy of the body segments, there is, however, considerable uncertainty about the precision of volume measurements.

## Results and Discussion

Fig. 1a–e shows the dependency of respiration ($R$) on body weight ($W$) for the five species studied. This dependency is described by the log-log relationship

$$\log R = a + b \log W \tag{1}$$

with $R$ in nl $O_2 \cdot h^{-1}$ and $W$ in $\mu$g dry wt. In this relationship, the parameter $a$ is a weight-independent measure of the metabolic intensity. In most species the parameter $b$ has a value $\approx 0.75$ (Hemmingsen, 1960). The values for $a$ and $b$ in our experiments are given in Table I. For *T. discipes*, the relationship between respiration and body volume ($V$) is given by:

$$\log R = 0.34 + 0.92 \log V \quad (V \text{ in nl}; r = 0.90, n = 42) \tag{2}$$

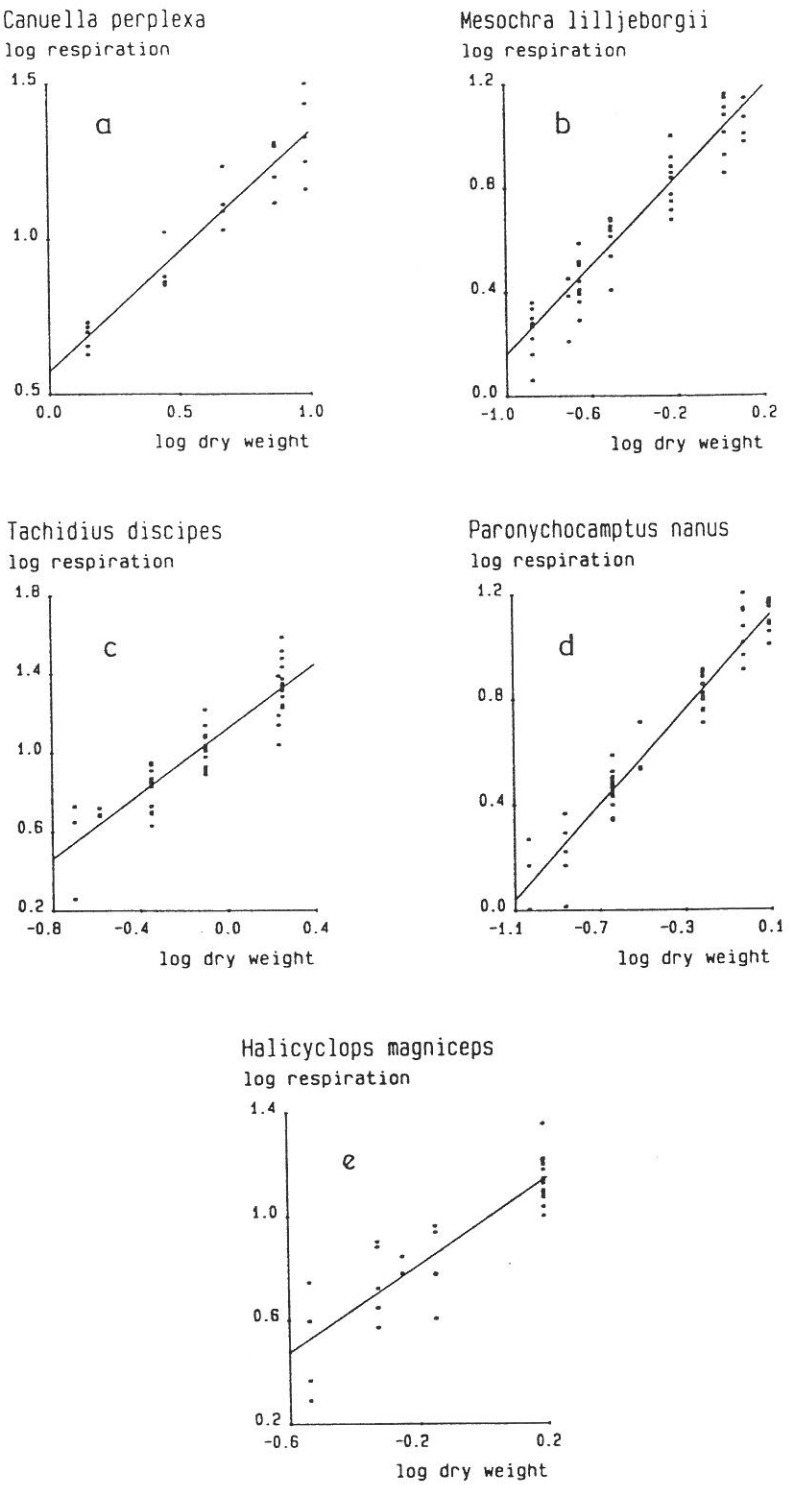


Fig. 1. Relationship between respiration and body weight for five species of meiobenthic copepods: parameters of the regressions are given in Table I; respiration in nl $O_2 \cdot h^{-1}$; body weight in $\mu$g dry wt.

This relationship is based on the same respiration measurements as the one shown in Fig. 1c, except that for seven animals no length and width measurements could be made.

In most papers dealing with the respiration of benthic copepods, the respiratory rate is expressed as respiration per unit body weight, obtained by dividing the respiration of one or more individuals by their weight. When the individual weight is not given, as is often the case, it is difficult to use this measure for comparisons, since it depends on the weights of the experimental animals used. From Equation (1) one sees that $R/W = a\ W^{b-1}$, where in general $b$ differs from 1. For comparison with published data, we calculated from our regressions two values for the weight specific respiration, giving $R/W$ corresponding to the mean weight of the youngest stage studied and of the adults. These values are given in Table II, in which the available data on respiration per unit body weight of meiobenthic copepods are summarized.

TABLE I

Parameters $a$ and $b$, correlation coefficient and number of determinations in the regressions of respiration on body weight for five species of meiobenthic copepods.

| Species | $a$ | $b$ | $r$ | $n$ |
|---|---|---|---|---|
| *Canuella perplexa* T. & A. Scott, 1893 | 0.57 | 0.77 | 0.95 | 22 |
| *Mesochra lilljeborgii* Boeck, 1864 | 1.02 | 0.86 | 0.94 | 51 |
| *Tachidius discipes* Giesbrecht, 1882 | 1.12 | 0.86 | 0.94 | 49 |
| *Paronychocamptus nanus* (Sars, 1908) | 1.03 | 0.90 | 0.97 | 54 |
| *Halicyclops magniceps* (Lilljeborg, 1853) | 0.98 | 0.84 | 0.89 | 39 |

TABLE II

Summary of the available information on the respiration of meiobenthic copepods: the values given are weight-specific respiration rates ($R/W$), except for the relationships between respiration ($R$) and body volume ($V$ in nl) given by Teare & Price (1979).

| Species | $R/W$ (nl $O_2 \cdot h^{-1} \cdot \mu g$ dry $wt^{-1}$) | Reference |
|---|---|---|
| *Asellopsis intermedia* | 3.8 | Lasker *et al.*, 1970 |
| *Hastigerella leptoderma* | 3.42 | Vernberg *et al.*, 1977 |
| *Nannopus palustris* | 4.99 | Vernberg *et al.*, 1977 |
| *Thompsonula hyaenae* | 10 | Sellner, 1976 |
| *Paraleptastacus spinicauda* | 4.2 | Lasserre & Renaud-Mornant, 1973 |
| *Enhydrosoma propinquum* | 2.0 | Coull & Vernberg, 1970 |
| *Longipedia helgolandica* | 6.6 | Coull & Vernberg, 1970 |
| Harpacticoids brackish water | | |
| "Class I" (9.0 $\mu$g dry wt) | 4.0 | Lasserre *et al.*, 1975 |
| "Class II" (1.5 $\mu$g dry wt) | 10.0 | Lasserre *et al.*, 1975 |
| *Tachidius discipes* field animals | $\log R = -0.10 + 0.82 \log V$ | Teare & Price, 1979 |
| lab. reared | $\log R = -0.07 + 1.10 \log V$ | Teare & Price, 1979 |
| *Canuella perplexa* | 3.46–2.21 | This paper |
| *Mesochra lilljeborgii* | 13.80–10.05 | This paper |
| *Tachidius discipes* | 17.44–11.75 | This paper |
| *Paronychocamptus nanus* | 13.71–10.50 | This paper |
| *Halicyclops magniceps* | 11.71– 8.97 | This paper |

It is difficult to convert the data in Teare & Price (1979) to weight units. When comparing with literature data, these authors converted dry weights to body volumes assuming a body volume to dry weight ratio of 4 : 1. Our data on *T. discipes* suggest that at least for our population the body volume to dry weight ratio exceeds 7 : 1. Even using this higher ratio, the respiration per unit dry weight of Teare & Price's adult animals from the field is only 4 nl $O_2 \cdot \mu g^{-1} \cdot h^{-1}$ and for adults from the laboratory it is $\approx 7.5$ nl $O_2 \cdot \mu g^{-1} \cdot h^{-1}$. This is considerably lower than our value of $\approx 12$ nl $O_2 \cdot \mu g^{-1} \cdot h^{-1}$ for adults.

This is not the only difference between these two populations of *T. discipes*. In the Lynher estuary (Teare & Price, 1979) the species occurs and reproduces throughout the year whereas in the Dievengat it is only present from early spring until early summer. The size of the adult animals is also different. The modal body volume of a wild adult (sex not specified but there is little sexual dimorphism in size in this species) is $\approx 8$ nl (value read from the figures). In the Dievengat population, the modal body volume of an adult is 12.5 nl.

There are several reasons to suggest that these differences are at least in part genetically determined and that they may arise from different selection pressures in the respective habitats of the two populations. First, respiration of the Dievengat animals follows a strikingly different pattern. Teare & Price (1979) find for the respiration–body volume relationship of their laboratory population a slope of 1.10, which is significantly higher than the slope of 0.82 for their wild animals. Although our animals are bigger than their laboratory animals, the slope of our regression is intermediate, 0.92. The intercept of the relationship is, on the contrary, not significantly different for Teare & Price's wild and laboratory populations. Thus, whereas the respiration of the smallest nauplii is about the same for laboratory and wild animals of the Lynher estuary, the growing animals in the laboratory gradually respire more and grow bigger than the wild animals. The intercept for the Dievengat population is 0.34, much higher than the values of $-0.1$ and $-0.07$ found by Teare & Price, and implies a 2.5-fold increase in the weight-specific respiration. The Dievengat population with both a slope smaller than 1 (although the animals are larger than their laboratory animals) and a much higher intercept thus clearly falls outside the pattern of phenotypic variability exhibited by the Lynher population.

Secondly, that physiological responses can be under selective control has already been demonstrated by Vernberg & Moreira (1974) for the planktonic harpacticoid *Euterpina acutifrons*. They demonstrated differences in acclimation patterns between two geographically isolated populations of this species.

If differences in respiration rate between populations of the same species can be induced by natural selection, a fortiori the same mechanism should be at work between different species. There are some good indications that this is indeed the case. Lasserre *et al.* (1975) measured the respiration rates of harpacticoids from a poly-mesohaline brackish-water area near Arcachon (France), which is similar to the Dievengat in several respects. Both their "small" and "large" copepods have weight-specific respira-

tion rates similar to those found by us (*Canuella perplexa* is the only large species in our study), and these values are all higher than the respiration rates found for truely marine harpacticoids (Table II). (Sellner, 1976, studied *Thompsonula hyaenae* in very artificial circumstances.) Furthermore, all meiobenthic copepods have lower weight-specific respiration rates than planktonic copepods. Marshall (1973) calculated an interspecific respiration-body weight relationship for planktonic copepods which gives a weight-specific respiration of 11.5 nl $O_2 \cdot \mu g^{-1} \cdot h^{-1}$ for 1-$\mu$g dry wt animals. In this regression she did not correct for differences in experimental temperature and most experiments were performed at $\approx 10\,^{\circ}C$. Ivleva (1980) also gives an interspecific respiration–dry weight relationship for marine calanoid copepods but only takes into account experiments made at 20 °C. From this regression a weight-specific respiration of 30 nl $O_2 \cdot \mu g^{-1} \cdot h^{-1}$ is calculated for 1-$\mu$g dry wt animals. The effect of temperature accounts for much of the difference between the two values.

We have compared the respiration rates of two populations of the same species *Tachidius discipes*, of large and small benthic copepods from two similar brackish-water areas, of brackish-water and marine benthic copepods, and of benthic and planktonic copepods. From these comparisons we derive the following general scheme. When we compare "small" and "large" copepods, it is striking that there is a lower respiration per unit body weight for the larger species. This lower respiration of (in our case) *Canuella perplexa* cannot solely be explained by the allometry of the respiration–body weight relationship, as the intercept (the metabolic intensity) of this species is only about half the intercept for the other species. Likewise, the explanation of the lower values found by Lasserre *et al.* (1975) by allometry alone would imply a very low value ($b$ = 0.49) for the exponent in Equation (1). A low intercept (0.25) was also found for the ostracod *Cyprideis torosa* (adult dry wt without shells $\approx 20\ \mu g$) in the Dievengat (Herman & Heip, 1982). Both *C. torosa* and *Canuella perplexa* have long generation times in the Dievengat (1 yr, and 6 months, respectively). Since the ratio of body mass to generation time is much lower in these species than in the faster breeding smaller copepods, their growth rate is also lower. A relatively lower respiration rate has a direct and important effect on production efficiency. With a relatively low growth rate the absolute amount of assimilated food turned into production per unit time is relatively low. At least in *Cyprideis torosa*, where it has been explicitly measured (Herman *et al.*, in press), the production efficiency remains relatively high (0.37), and this is due to the low respiration rate. This results, therefore, in the same amount of food being able to sustain a higher biomass while the population production efficiency remains comparable with that of populations with a higher respiration rate. This conservation of energy may be essential for the dominant position that *Cyprideis torosa* occupies in the habitat. The same argument may be valid for *Canuella perplexa*, which is a key species in competitive situations, and whose dynamics are relatively unaffected by the presence of other species (Herman & Heip, in press).

Populations such as *Cyprideis torosa* and *Canuella perplexa* with their long generation times are unable to track short-term fluctuations in the environment. Thus, only when

resources are relatively stable, will the long generation time and low respiration rate of these populations be an advantage in competitive situations. The comparison of the two *Tachidius discipes* populations reinforces this point. The Dievengat population lives in an ecological vacuum, develops very quickly in early spring and disappears in early summer, not because the habitat becomes unsuitable, as the number of eggs produced per female remains high, but because of intense predation (Heip, 1980). In such a situation a relatively high respiration rate is advantageous, as competition from other species is almost absent. The Lynher estuary population is present and dominant during the whole year and is, therefore, subjected to a totally different set of environmental factors.

In general, in brackish-water areas where the species number is low and productivity is high, we find higher respiration rates than in marine habitats. Respiration rates are lower in benthic systems where the characteristic time scales of environmental changes are longer than in planktonic systems, and where stability and the intensity of competitive interactions are greater.

All these observations indicate that the respiration rate of a population in a particular habitat is subjected to selective pressure and forms part of a population's adaptation to that particular habitat.

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# Long-term dynamics of meiobenthic populations



Meiofauna
Population dynamics
Spectral analysis

Méiofaune
Dynamique de population
Analyse spectrale

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ABSTRACT

Seven years (1970-1976) of density data on three harpacticoid copepods were analysed by Maximum Entropy Spectral Analysis. The spectra are very different, indicating population regulation is also different. *Tachidius discipes* is regulated by external seasonal factors, mainly the annual light cycle, and has a very simple spectrum. *Canuella perplexa* has much longer cycles in its spectrum and can be treated as a single species problem with logistic dynamics. *Paronychocamptus nanus* has also a complex spectrum that can partly be explained by competitive interactions.

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RÉSUMÉ

Dynamique à long terme de populations méiobenthiques

Sept années (1970-1976) de données sur les densités de trois copédodes harpacticoides ont été analysées par la « Maximum Entropy Spectral Analysis ». Les spectres sont très différents, montrant que la régulation des populations est aussi différente. *Tachidius discipes* est régulé par des facteurs externes et saisonniers, surtout par le cycle annuel de la lumière ; cette espèce a un spectre très simple. *Canuella perplexa* a des cycles beaucoup plus longs dans son spectre, et peut être traitée comme une espèce isolée avec une dynamique logistique. *Paronychocamptus nanus* a aussi un spectre compliqué qui peut être partiellement expliqué par des interactions compétitives.

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## INTRODUCTION

The study of long-term ecological time series is a topic of great practical and theoretical interest. In the field of population biology, theoretical models have shown that populations can exhibit very different types of behaviour in time, ranging from extreme stability to apparently random behaviour (May, Oster, 1976). In the field of systems theory, the thermodynamics of non-linear open systems far from equilibrium suggest that ecosystems, that can be considered as typical dissipative structures, should be characterised by periodic behaviour in time and space (Platt, Denman, 1975). From a practical point of view, in the absence of knowledge on the dynamics of a system prediction is only possible when it is based on long enough time series (Poole, 1978).

The link between theoretical ecology and the actual situation in the field is not very clear. What is clear, however, is that cyclicity is an important component of the behaviour of real populations and communities and that ecological variables should be analysed for it. An obvious tool in this study is spectral analysis. This method determines how much of the observed variability of a time series can be explained by cyclical components of varying frequency. Ideally, the important cyclicities thus resolved should be related to hypotheses generated in theoretical models or to observed external oscillators.

In the present study a relatively simple community of meiobenthic copepods was monitored at fortnighly intervals over a seven year period (1970-1976). The study area is a brackish water pond in northern Belgium, called " Dievengat ". It is a shallow (10-20 cm depth) habitat with pronounced seasonal fluctuations. Superimposed on these, several physico-chemical parameters such as oxygen concentration, pH and nutrient concentrations show important long-term fluctuations (Herman, Heip, in prep.).

Three copepod populations are discussed here. *Tachidius discipes* Giesbrecht 1882 is a medium size harpacticoid living epibenthically, and feeding on diatoms and other algae. *Canuella perplexa* Scott 1893 is a relatively large animal, the adults measuring well over 1 mm in length. It lives buried in the sediment, which is a mixture of fine sand and detritus, on which this species feeds. *Paronychocamptus nanus* (Sars, 1980) is the smallest species. It is also a detritus feeder.

## MATERIAL AND METHODS

Samples were taken with a 6.06 $cm^2$ glass core to a depth of 5 cm. Elutriation techniques are described by Heip *et al.* (1974). The spectral analysis was performed on detrended ln-transformed data with the recently developed " Maximum Entropy Spectral Analysis " (MESA) method (Kirk *et al.*, 1979; Rust, Kirk, 1977 and references therein). This method has the advantage that components with a period about equal to the length of the time series can be resolved. The greater accuracy in the low frequency range is mainly due to the fact that MESA minimizes the assumptions about the unavailable data (*i.e.* the data of the stationary time series before and after the period that observations were made). Mathematically the method is derived by imposing the condition that the most random spectrum (*i.e.* with highest entropy in the information theoretical sense) must be found which is consistent with the autocorrelation data of the time series studied.

The time series consist of 184 data points spaced 14 days apart. Fitting of cycles to the data was performed with a multiple linear regression program according to Bulmer (1974).

## RESULTS

The three time series are shown in Figure 1. In *T. discipes* there is only one peak in spring in each year, except in the very dry summer of 1976 when a second peak is present. The analysis of 3-day interval samples of the 1979 peak showed that it is composed of three overlapping generations, contrary to the opinion of Heip (1980) who thought only one generation present each year.

In contrast, *C. perplexa* is constantly present in the habitat, but it is difficult to reveal a pattern in its abundance. The percentage of ovigerous females in the adult population shows that in most years two reproduction peaks occur. Culture experiments confirmed that this species most probably has two generations annually.

*P. nanus* as well is present throughout the year. Reproduction occurs from early spring till October-November. The analysis of five-day interval samples, combined with laboratory experiments (Smol, Heip, 1974) showed the existence of about eight generations each year, again much more than had been estimated earlier (Heip, 1980).

Figure 2 shows the spectra of the three time series. It is clear that, even in closely related species, a wide variety of time dependent behaviour can be observed. In the spectrum of *T. discipes* (Fig. 2 *a*) there is only one pro-

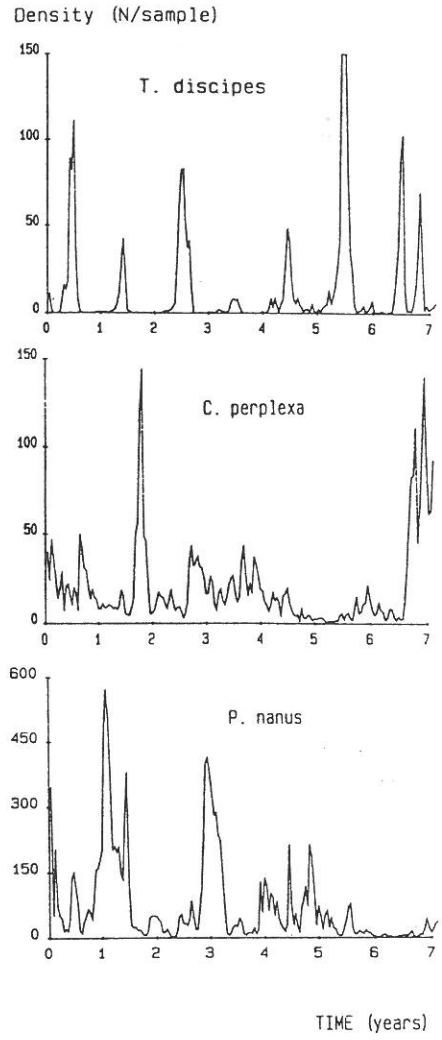


Figure 1

*Densities (number per 6.06 $cm^2$ sample) of the three copepod species in the seven-year period 1970-1976.*

minent peak corresponding to a period of one year. The minor peaks occuring besides the one year peak are harmonics of this one, showing that although the important cyclicity is yearly the process is not a pure sine wave.

The spectrum of *C. perplexa* (Fig. 2 *b*) is dominated by a peak corresponding to a period of 3.5 years. Next in importance are peaks of 1 year, 1.3 year and 0.5 year. The spectrum of *P. nanus* (Fig. 2 *c*) is dominated by a peak on 1.5-2.0 years. This is followed by peaks on 4.6 years, 1 year, 0.5 year and 0.3 year, the latter two being harmonics of the 1 year period.

The autocorrelation functions of these time series show that in *T. discipes* there is only a short serial correlation (1 to 2 months) whereas in *C. perplexa* and *P. nanus* consecutive densities remain positively correlated over a period of about half a year.

## DISCUSSION

The appearance of *Tachidius discipes* in the community in early spring is most probably determined by the availability of food algae and thus ultimately by light.

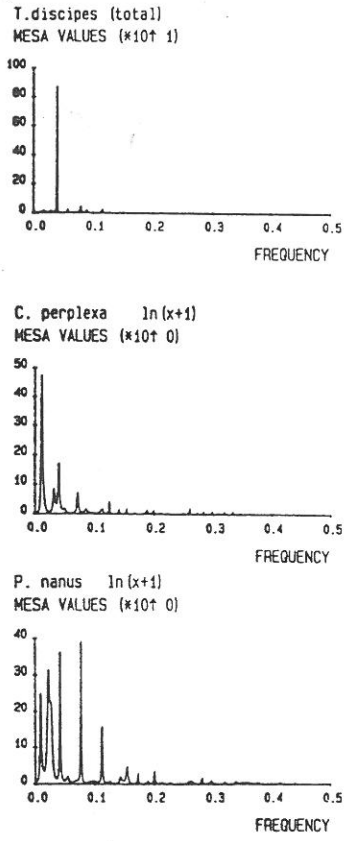


Figure 2

*MESA spectra of the ln-transformed und detrended series of the densities of three copepod species. The relative importance of the peaks is proportional to the surface under the peak. The ordinate is dimensionless, the abscissa has units 14 days$^{-1}$.*

Its disappearance in July is caused by an increasing predation, mainly from the polyp *Protohydra leuckarti* (Heip, Smol, 1975). Culture experiments showed that its intrinsic rate of increase remains high at the temperatures experienced by the population at that time (Smol, Heip, 1974). Furthermore, the animals are well fed and have high reproduction until they disappear. This population is thus regulated by external factors which are seasonal. In the very dry summer of 1976 part of the sediment in the pond dried, and the density of *T. discipes* rapidly increased again in the recovering community. It was followed by a peak in *Protohydra* density, as is normally observed in spring.

In view of this, the short serial correlation and the dominance of the yearly period in the spectrum can be understood as the result of a short generation time and seasonal regulating factors. The important long-term fluctuations in physico-chemical parameters of the environment are not tracked by this species. Its strategy of fast reproduction until it is barred by predation apparently makes it relatively insensitive to the overall state of the environment. Although considerable variation in the height of the peaks exists from year to year, these differences are non-cyclical and probably depend on the density of the population reached before serious predation starts.

For *Canuella perplexa* we first note that its generation time is about half a year. This implies by itself a longer serial correlation, since the population has a longer memory of previous states. The dominance of longer periodicities in the spectrum can be related to density-dependent regulation. There are indications that this indeed exists. The percentage of ovigerous females in the adult population decreases with increasing population density. Figure 3 shows the plot of the logarithmic rate of increase against the log of density. This plot was calculated from the density curve after application of 0.5 year moving average (0.5 year being the estimated generation time of this species). The log rate of increase is given by $R = \log(N_{t+0.5}/N_t)$. The lines in this plot are the time trajectory of the system.

In models of logistic single species systems the slope of the regression line between R and N can be related to the intensity of density dependent regulation mechanisms, whereas the intercept with the y-axis ($y = 0$) relates to the carrying capacity (Royama, 1977; Hassell *et al.*, 1976). It can be seen from Figure 3 that whereas the intercepts differ, the slopes of the R-N lines are rather constant. Using values of the parameters estimated from this figure, one can calculate that after perturbation the population of *Canuella perplexa* will return to equilibrium in a series of slowly damped oscillations. Such a population is likely to track cyclical environmental fluctuations and to start oscillating in resonance to them (Nisbet, Gurney, 1982).

A remarkable correlation in this respect exists between the long-term behaviour of the *Canuella perplexa* population and the concentration of ammonium in the habitat. The spectrum of this parameter is also dominated by a 3.5 year periodicity. When fitted to the data, the 3.5 year cycles of *C. perplexa* and ammonium are almost exactly in phase. As the concentration of ammonium can be an indicator of the decomposition rate it may be an indicator of the carrying capacity of the environment for *C. perplexa.*

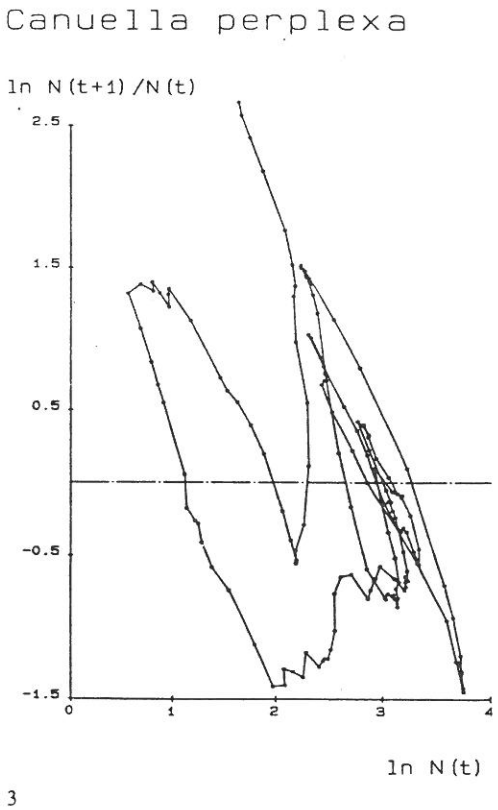


Figure 3

Canuella perplexa : *logarithmic rate of increase plotted against density (see text for details). Lines connect consecutive points in time.*

A more complex problem is posed by the spectrum of *Paronychocamptus nanus*. The long serial correlation in this time series cannot be explained by a long generation time, and neither could we demonstrate density dependence in this population. It has been shown in model systems that long serial correlations can be produced by coupling of several species in competitive interactions (Royama, 1977). There is evidence that such interactions do indeed exist. The time series of the total number of species has a spectrum that is, most remarkably, dominated by peaks of 3.5 and 4.6 years. Not only do these periods correspond to those found in *C. perplexa* and *P. nanus* but the phases fit as well (Fig. 4). This means that when conditions are bad for *C. perplexa* and *P. nanus* they are even worse for other species and may cause their disappearance from the habitat. We think that *C. perplexa* can nevertheless be treated as a single species problem because of its greater size, which makes it a superior competitor (a key-species).

For *Paronychocamptus nanus* both the long serial correlation and the 1.5 and 2.0 years oscillations can be interpreted as resulting from competitive coupling. However, we do not believe this to be true for the 4.6 years periodicity, which may be the result of tracking of a varying parameter in the system which we have not been able to identify.

The results of this study show that long-term cycles or quasi-cycles are important in these short-living species and that spectral analysis may be a useful tool in unraveling temporal patterns. Explanation of these patterns remains difficult : both the characteristic dynamics and interaction patterns of each species determine its apparently variable degree of direct dependence on the physical environment.

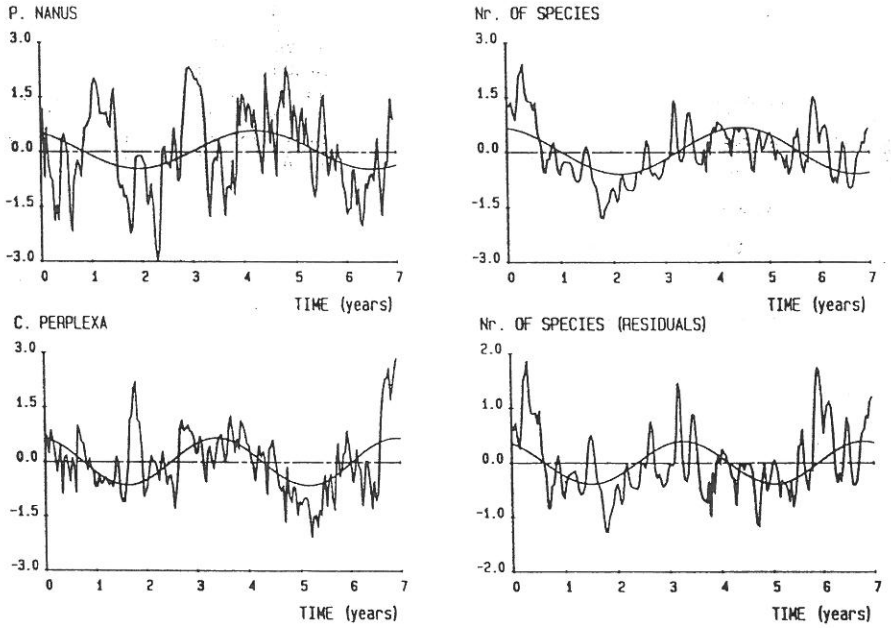


Figure 4

*Time series with long period cycles fitted :* a) P. nanus *with cycle 4.6 yr. ;* b) C. perplexa *with cycle 3.5 yr. ;* c) *number of species with cycle 4.6 yr. ;* d) *number of species. (residuals after extraction of the 4.6 yr. cycle) wath cycle 3.5 yr.*

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

BY

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The life-cycle of *Rhabditis marina* Bastian 1865 was studied at 25°C and 20‰ 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 (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:

$$dN/dt = r_m N \tag{2}$$

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):

$$r_c = (\ln R_0)/T_c \tag{3}$$

where $R_0$ is the net reproductivity,

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

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

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

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

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*:

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

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

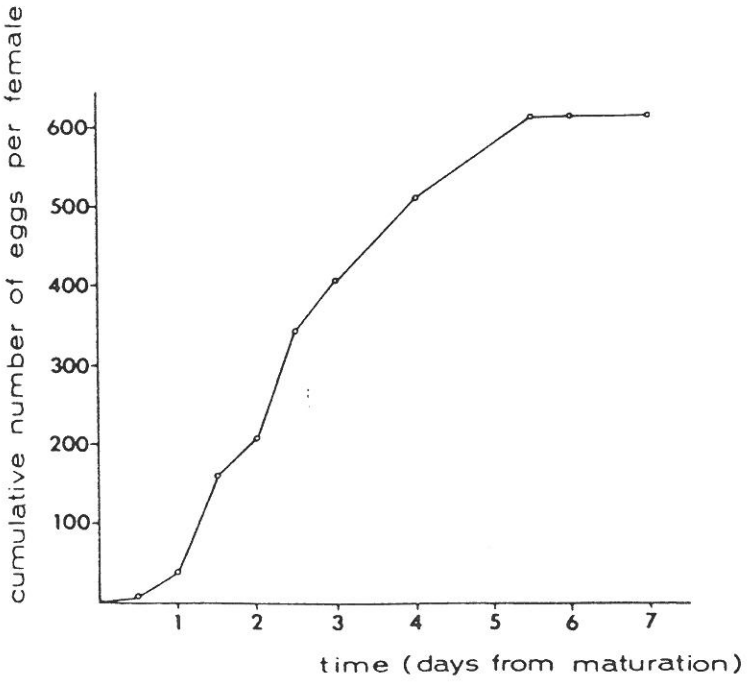


Fig. 1. *R marina*: Cumulative egg-production per female at 25°C and $20^0/_{00}$ salinity (mean of 10 females).

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‰ 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 $R_0$ 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. theritieri* | 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:

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

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: $r_m \approx 1/20 \ln (0.5 \times 1.5) = -0.014$ day$^{-1}$ ln day$^{-1}$, whereas life table calculations give an $r_m = 0.0932$ day$^{-1}$, a birth rate $b = 0.0976$ day$^{-1}$ and a death rate $d = 0.0044$ 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 $r_m \approx 1/126 \ln (0.5 \times 1.08) = -0.005$ day$^{-1}$ ln 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.

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*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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# Production of *Tachidius discipes* (Copepoda: Harpacticoida)



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ABSTRACT: The secondary production of the harpacticoid copepod *Tachidius discipes* Giesbrecht 1881 was estimated during spring 1979. The population was sampled every 3 d. Three generation peaks were observed. These were clearly distinct in the first copepodite stages, but gradually showed more overlap in older stages. Production of copepodites and adults was estimated in 2 ways: (1) Peaks were separated and the forward shifting of peaks in consecutive stages was used to estimate stage durations; (2) the size-frequency method was applied. Both estimates of the production of copepodites and adults are in good agreement: 1.10 g dwt $m^{-2}$ and 1.02 g dwt $m^{-2}$. Egg production amounts to 0.31 g dwt $m^{-2}$; naupliar production is roughly estimated at 1.11 g dwt $m^{-2}$. The production efficiency, P/(P+R), of copepodites and adults is 0.36; for the total population it is 0.43. This value corresponds well to the value estimated from culture experiments with this population.

## INTRODUCTION

Meiobenthic populations are among the least studied from the point of view of energetics. Only recently have papers appeared dealing with direct production estimates of field populations of meiobenthic crustaceans (Feller, 1982; Fleeger and Palmer, 1982). The limited information available reveals that the productivity (measured by yearly production/biomass rates, P/B) of meiobenthic populations can differ widely from the speculative and often used value P/B = 9. This value was proposed by Gerlach (1971), based on the life cycle characteristics of 2 nematode species. Whereas the use of a single P/B value for all populations is not advisable, the scaling of P/B by body mass (Banse and Mosher, 1980) may be more useful (Heip et al., 1982). This scaling reveals a remarkable pattern, already anticipated by Banse and Mosher (1980), in that the P/B-body weight line for meiobenthic populations lies considerably lower than would be expected from the extrapolation of values for larger organisms. The scaling of the intrinsic rate of natural increase $r_m$ by body weight (Banse, 1982) corroborates this observation, since both $r_m$ and P/B are highly correlated with the generation time, and thus with each other.

Not only are P/B and $r_m$ relatively lower in meiobenthic populations, the review of Banse (1982) also shows that the respiration rate of meiofauna is lower than would be expected from extrapolation from the respiration of larger organisms. We could confirm this trend for 1 ostracod (Herman and Heip, 1982) and 5 copepod species (Herman and Heip, 1983) from a brackish water habitat. The low respiration rate of the ostracod *Cyprideis torosa* explains why the production efficiency (P/[P+R]) of this slow-growing species is almost equal to the mean value for non-insect detritivores given by Humphreys (1979) (Herman et al., 1983). The question of production efficiencies in meiobenthic populations is not at all settled. Several studies on nematodes (Schiemer et al., 1980; Warwick, 1981; Schiemer, 1982a, b) yielded extremely high values for the production efficiency, one value even exceeding 90 %.

For the harpacticoid copepod *Tachidius discipes*, Warwick (1981) calculated a production efficiency of ca. 70 %. His calculation was based on field data from the 'Dievengat', a brackish water pond in northern Belgium (Heip and Smol, 1976; Heip, 1977), and from respiration measurements of copepods from the Lynher estuary (S.W. England) (Teare and Price, 1979). Elsewhere we show that there is a considerable difference



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in respiration rates between the 2 populations of this species examined (Herman and Heip, 1983). In this paper we treat in more detail the production of the Dievengat population so that a more accurate calculation of the production efficiency is possible.

*Tachidius discipes* is a widely distributed member of estuarine meiofauna (Muus, 1967). In the community we studied, it typically occurs in large numbers during spring (Heip, 1979; Herman and Heip, in press). Maximum densities are ca. 100,000 individuals $m^{-2}$, one peak value exceeding 300,000 ind. $m^{-2}$. The species lives epibenthically and feeds on benthic microalgae.

## MATERIAL AND METHODS

During spring 1979 (March–June), a population of *Tachidius discipes* was studied in a 10 cm deep brackish water pond, the 'Dievengat', northern Belgium. Salinity fluctuated between 11 and 16 ‰ (mean: 14.6 ‰) during the period of investigation. The sediment is a well-sorted fine sand (median grain size 0.223 mm), covered with large amounts of detritus.

Samples were taken every 3 d with a 6.06 $cm^2$ glass corer, to a depth of 5 cm, and fixed in a neutral 4 % formaldehyde solution, heated to 70 °C. The copepods were extracted from the sediment as described by Heip et al. (1974), except that centrifugation of the finer fractions was done with LUDOX, a silica-gel, instead of sucrose (De Jonge and Bouwman, 1977).

It was impossible to sample the nauplii quantitatively in this detritus-rich sediment. Copepodites and adults were extracted with high efficiency. On each date the number of copepods in each developmental stage (from Cop I to adult) was recorded. The descriptions of the copepodites of *Tachidius discipes* by Teare (1978) were used.

Dry weights were determined on a Mettler ME22 microbalance to a precision of ± 1 µg. Batches of 50 to 100 individuals belonging to the same developmental stage were dried for 2 h at 110 °C before weighing.

In order to suppress the random variation ('noise') in the density data, a weighted running mean was applied with length 3 and weight factors 0.23, 0.54, 0.23 (Velleman, 1977). Inspection of the density curves of the 6 developmental stages revealed the existence of several peaks which can be interpreted as representing separate generations. These peaks are well separated in the first stages, but become gradually less distinct and more overlapping in the older ones. In order to separate them we used a method devised for splitting statistical frequency distributions into Gaussian components (Bhattacharya, 1967). In this method the mean and variance of the constituting Gaussians are determined graphically on a plot of $\ln(Y_{i+1}/Y_i)$ against $X_i$ (where $X_i$ is the class midpoint of the i-th class, and $Y_i$ the corresponding frequency). The absolute numbers $N_j$ in each of the Gaussian components are determined by solving a system of k equations (k being the number of Gaussians). This gives a good fit, although it does not consider error terms explicitly (Bhattacharya, 1967).

The results of this analysis can be used for a production estimate with the method of Rigler and Cooley (1974): the means of the Gaussian components correspond to their 'mean pulse time' of the peaks, and the numbers $N_j$ to the surfaces under a peak's curve. For each generation the production is estimated as:

$$P = \sum_{i=1}^{5} \left( \frac{N_{i+1}}{D_{i+1}} - \frac{N_i}{D_i} \right) \times (W_{i+1}\, W_i)^{1/2} \quad (1)$$

where i = stage number; $D_i$ = duration (days) of the stage i; $N_i/D_i$ = number of copepods in the stage.

As an independent test of the whole procedure we also estimated the production with the size-frequency method, as modified for the analysis of populations grouped in developmental stages by Herman et al. (1983). This method gives an approximation of the relative duration of each stage (giving Stage I the arbitrary duration of 1) by assuming exponential mortality. In the case of *Tachidius discipes* we also need an estimate of the relative duration of egg + naupliar stages. This is provided by culture experiments of Smol and Heip (1974) from which it can be concluded that this duration is ¾ of the copepodite stages combined. The method further requires only an estimate of the number of generations occurring during the study period, which in this case is 3.

The number of eggs produced was calculated from the observed density of females carrying eggs by the formula:

$$N_e = \sum_t \frac{N_t \times c}{T_t} \times E \quad (2)$$

where summation is over all sampling dates t; c = interval (days) between 2 samplings; $T_t$ = embryonic development time at the prevailing temperature at time t; E = number of eggs per egg sac. Both $T_t$ and E are available from culture experiments by Smol and Heip (1974) and Heip and Smol (1976).

This estimate of the number of eggs produced allows a rough calculation of the naupliar production. Assuming that within the naupliar phase both growth and mortality are exponential, we have:

$$W_t = W_o\, e^{Gt} \quad (3)$$

$$N_t = N_o\, e^{-Zt} \quad (4)$$

where G and Z = instantaneous growth and mortality rates, respectively.

Production is given by Allen (1971) as:

$$P = (G/[G-Z])\ (N_T W_T - N_o W_o) \quad (5)$$

where $N_o$, $W_o$, $N_T$, $W_T$ = numbers present and individual weight at times o and T, respectively. We estimated $W_o$ as the weight of an egg, and $W_T$ as the weight of a Copepodite I. $N_T$ is the number entering the Copepodite I stage, and $N_o$ is the number of eggs produced. G and Z can be calculated from Eq. (3) and (4), provided an estimate of T is available. An estimate of G, and thus of T is necessary for the biomass integral (see below), but for the production estimation by Eq. (5) it is sufficient to estimate GT and ZT, since the factor T disappears in the division G/(G–Z). GT and ZT are estimated as ln $(W_T/W_o)$ and –ln $(N_T/N_o)$, respectively.

One complication arises because this estimate of naupliar production is based on the growth increment principle, whereas the production of copepodites is based on the principle of summation of elimination (see Heip et al., 1982 for a discussion). As a consequence of this difference, it can be seen that the production of Copepodite I is calculated twice. As this production belongs most logically to the naupliar stage, it is subtracted from the copepodite production for the calculation of production efficiency.

In order to estimate the mean biomass of the nauplii we use the relation (Allen, 1971)

$$P / B^x = G \quad (6)$$

which is valid in the case of exponential growth and mortality. Here $B^x$ = biomass – integral:

$$B^x = \int_o^T N_t W_t \, dt \quad (7)$$

Once $B^x$ is known for the nauplii, the calculation of the mean biomass of the total population is straightforward.

The mean respiration of the different stages of copepodites and adults at 20 °C was determined by Herman and Heip (1983) with Cartesian Diver microrespirometry. The respiration-body weight relation was given by $R = 13.18\ W^{0.82}$, with R in nl $O_2$ ind.$^{-1}$ h$^{-1}$, and W in µg dwt. Total population respiration was calculated from these values after adjustment for temperature in the field with Krogh's normal curve (Winberg, 1971). The production efficiency was calculated directly for copepodites and adults.

Respiration of nauplli was estimated in the following way. Assuming exponential growth and mortality (cf. above) we have at any time t : $W_t = W_o\ e^{Gt}$ and from $R_t = a\ W_t^{0.82}$ we get

$$R_t = a\ W_o^{0.82}\ e^{0.82\,G\,t} \quad (8)$$

The respiration integral, by analogy to the biomass integral, is given by:

$$R^x = a\ N_o W_o^{0.82} \int_o^T e^{(0.82\,G\,-\,Z)\,t}\, dt$$

$$R^x = a\ ([N_T W_T^{0.82} - N_o W_o^{0.82}] / [0.82\,G - Z]) \quad (9)$$

This respiration is compensated for temperature effects by the same factor as was obtained for females carrying eggs.

For the conversion of dry weights to energy units we used the following conversion factors: 1 l $O_2$ consumed is assumed equivalent to 0.4 g C metabolized (Crisp, 1971); 1 g C = 45.8 kJ (= 10.92 kcal) (Salonen et al., 1976), and organic carbon is 52 % of ash free dry weight (Salonen et al., 1976).

All production estimates given in the text are production over the study period of 99 d.

## RESULTS

The raw data (i.e. counts 6.06 cm$^{-2}$ of the different stages) are given in Table 1. Mean dry weight of the stages, and geometric mean weight of consecutive stages are given in Table 2. Fig. 1(a–f) shows the density curves of copepodite and adult stages (running means), with the combined fitted Gaussian distributions superimposed. We found 3 generations during the study period, well distinguished in the first stages, but gradually more overlapping in the older ones.

For calculations of the stage duration with Rigler and Cooley's (1974) method it is necessary to draw a smooth curve on a plot of mean pulse times against stage numbers. Rigler and Cooley (1974) advise performing the smoothing in such a way that each stage is longer than the preceding one, and that negative mortality is minimal. Fig. 2 shows the effect of this smoothing. The only important modification is that the smoothed mean pulse time $\mu_s$ of Copepodite IV in the first peak is shifted forward. There is no negative mortality. The resulting stage durations and the number of copepods in each stage are shown in Table 3. A problem is posed by the adult stage. The method of Rigler and Cooley (1974) implies that all mortality occurs at the transition of one stage to the next. This assumption does not lead to serious bias as long as the stages are of short duration, but when they last longer and there is considerable mortality (as in the adult stage, where all individuals eventually die) it results in a relative forward shift of the mean pulse time. Therefore the mean pulse time of the adults is not reliable as a basis for the estimation of its duration. Fortunately there is almost no somatic growth between Copepodite V and adults. The assumption that all Copepodite V become adult therefore introduces only

Table 1. *Tachidius discipes*. Original counts (No. 6.06 $cm^{-2}$) on which the production estimates were based. CI, ..., CV: Copepodites 1 to 5; AD: total number of adults; FCE: number of females carrying eggs

| Date | CI | CII | CIII | CIV | CV | AD | FCE |
|---|---|---|---|---|---|---|---|
| 21. 3. 79 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
| 24. 3. 79 | 0 | 0 | 1 | 0 | 1 | 2 | 1 |
| 27. 3. 79 | 1 | 1 | 0 | 1 | 2 | 12 | 3 |
| 30. 3. 79 | 3 | 0 | 1 | 1 | 1 | 10 | 2 |
| 2. 4. 79 | 6 | 3 | 0 | 2 | 2 | 7 | 1 |
| 5. 4. 79 | 0 | 2 | 2 | 1 | 2 | 17 | 6 |
| 8. 4. 79 | 9 | 14 | 10 | 1 | 0 | 8 | 3 |
| 14. 4. 79 | 1 | 3 | 2 | 3 | 8 | 11 | 0 |
| 17. 4. 79 | 1 | 7 | 0 | 6 | 10 | 13 | 1 |
| 20. 4. 79 | 11 | 20 | 29 | 27 | 21 | 24 | 3 |
| 23. 4. 79 | 22 | 15 | 13 | 13 | 17 | 39 | 8 |
| 29. 4. 79 | 55 | 52 | 62 | 37 | 17 | 4 | 1 |
| 2. 5. 79 | 14 | 21 | 27 | 17 | 25 | 57 | 8 |
| 5. 5. 79 | 11 | 23 | 35 | 60 | 73 | 85 | 12 |
| 8. 5. 79 | 25 | 15 | 34 | 52 | 40 | 101 | 19 |
| 11. 5. 79 | 22 | 16 | 13 | 41 | 54 | 152 | 32 |
| 14. 5. 79 | 31 | 41 | 41 | 31 | 19 | 92 | 34 |
| 17. 5. 79 | 50 | 40 | 30 | 23 | 39 | 191 | 96 |
| 20. 5. 79 | 22 | 26 | 39 | 43 | 39 | 131 | 68 |
| 23. 5. 79 | 1 | 5 | 5 | 10 | 9 | 56 | 13 |
| 26. 5. 79 | 1 | 0 | 1 | 1 | 6 | 62 | 26 |
| 29. 5. 79 | 8 | 1 | 4 | 5 | 12 | 98 | 30 |
| 1. 6. 79 | 1 | 2 | 1 | 1 | 0 | 44 | 15 |
| 4. 6. 79 | 0 | 0 | 0 | 0 | 0 | 26 | 5 |
| 7. 6. 79 | 0 | 0 | 1 | 1 | 2 | 28 | 9 |
| 10. 6. 79 | 0 | 0 | 0 | 1 | 0 | 76 | 21 |
| 13. 6. 79 | 0 | 0 | 1 | 0 | 1 | 42 | 7 |
| 19. 6. 79 | 1 | 0 | 1 | 2 | 1 | 7 | 4 |
| 25. 6. 79 | 3 | 0 | 3 | 0 | 1 | 11 | 5 |

Table 2. *Tachidius discipes*. Dry weights $W_i$ of copepodite stages. N = number of copepods weighted in a batch. $(W_iW_{i+1})^{1/2}$ = geometric mean of the weights of 2 consecutive stages

| Stage | N | $W_i$ (µg) | $(W_iW_{i+1})^{1/2}$ |
|---|---|---|---|
| COP I | 50 | 0.20 | 0.23 |
| COP II | 54 | 0.26 | 0.34 |
| COP III | 108 | 0.45 | 0.60 |
| COP IV | 70 | 0.80 | 1.18 |
| COP V | 68 | 1.73 | 1.76 |
| AD | 325 | 1.80 | |
| Egg sac | 60 | 0.43 | |

a very light bias, and circumvents the tricky problem of estimating adult-stage duration. The production of copepodites and adults thus calculated is 1.57 g dwt $m^{-2}$. This value includes the production of the biomass entering the copepodite stage as Copepodite I (see 'Material and Methods'): this amount of 0.47 g dwt $m^{-2}$ is better included in the naupliar production. $P_c$, the production of copepodites and adults, is then estimated as $P_c$ = 1.10 g dwt $m^{-2}$.

Table 3. *Tachidius discipes*. Duration (D) of copepodite stages and number of copepods recruited to the stage for the 3 peaks in spring 1979, determined by the method of Rigler and Cooley (1974)

| | Stage | Duration (d) | Recruitment (per 10 $cm^2$) |
|---|---|---|---|
| | COP I | 0.85 | 79 |
| | COP II | 2.15 | 69 |
| 1st peak | COP III | 1.85 | 62 |
| | COP IV | 8.15 | 55 |
| | COP V | 9.85 | 49 |
| | COP I | 0.50 | 1615 |
| | COP II | 1.50 | 563 |
| 2nd peak | COP III | 2.50 | 434 |
| | COP IV | 4.00 | 277 |
| | COP V | 6.00 | 211 |
| | COP I | 0.90 | 635 |
| | COP II | 1.10 | 600 |
| 3rd peak | COP III | 1.30 | 536 |
| | COP IV | 1.30 | 302 |
| | COP V | 1.70 | 175 |

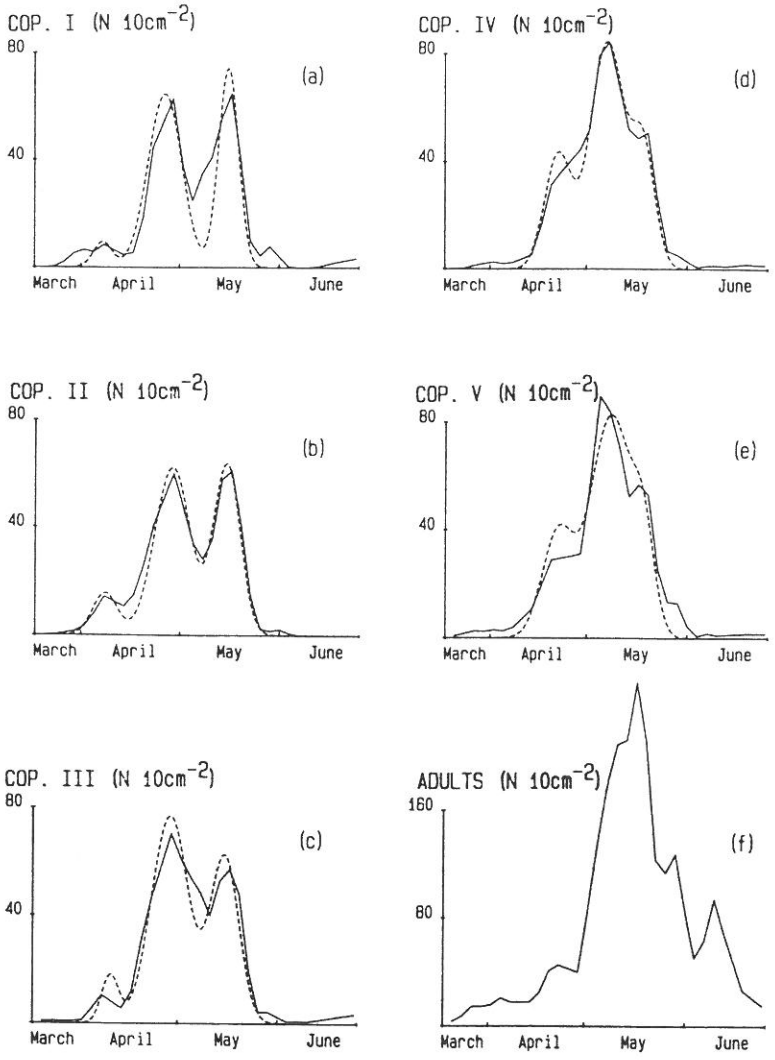


Fig. 1. (a–f): *Tachidius discipes*. Densities (N 10 cm$^{-2}$) of copepodite stages I (a), II (b), III (c), IV (d), V (e) and of the adults (f) in a brackish water pond during the spring of 1979. Full lines: trendline (see text) through observations. Broken lines: combined Gaussians fitted to the data

Table 4 gives the production estimation with the size-frequency method. The $P_c$, corrected for Copepodite I production by the value 0.47 g dwt m$^{-2}$ (of the previous estimate) is: $P_c$ = 1.02 g dwt m$^{-2}$.

Table 4. *Tachidius discipes*. Production estimation by the size-frequency method. $a_j$ = relative duration of Stage j (where $a_1$ = arbitrarily chosen as 1); $\bar{n}_j$ = mean number of copepods in Stage j; $N_j$ = an estimate of the recruitment into Stage j, '$P_j$' of the production of Stage j

| Stage | $a_j$ | $\bar{n}_j$ | $N_j$ | '$P_j$' |
|---|---|---|---|---|
| COP I | 1 | 17.13 | 1199.36 | 28.50 |
| COP II | 1.14 | 17.49 | 1074.36 | 50.26 |
| COP III | 1.53 | 20.26 | 927.38 | 90.53 |
| COP IV | 1.86 | 20.63 | 776.50 | 182.11 |
| COP V | 2.24 | 21.49 | 621.65 | 137.01 |
| AD | 9.43 | 73.27 | 544.03 | 995.56 |
| | 17.38 | | | 1483.98 |

Egg production, estimated by Eq. (2) is: $P_e$ = 0.31 g dwt m$^{-2}$. Number of eggs produced is 29,161 10 cm$^{-2}$.

Naupliar production, estimated by Eq. (5) is: $P_n$ = 1.11 g dwt m$^{-2}$.

Total production amounts to 2.52 g dwt m$^{-2}$ and 2.44 g dwt m$^{-2}$, depending on whether the first or second estimate of $P_c$ is used.

Duration of the copepodite stages is 23, 14.5 and 7.5 d for the 3 peaks. Duration of the naupliar stage is about half that of the copepodite stage (Smol and Heip, 1974). Using this experimentally obtained ratio, the duration of the naupliar phase is estimated to be 8 d. The biomass integral $B^x$ for the nauplii then becomes: $B^x$ = 2.96 g dwt × days × m$^{-2}$. The biomass integral for copepodites, adults and eggs is 22.77 g dwt × days × m$^{-2}$. Mean biomass $\bar{B}$ = 25.73/99 = 0.26 g dwt m$^{-2}$. $P/\bar{B}$ is 9.7 over the study period, or 3.2 generation$^{-1}$.

Respiration of copepodites and adults is estimated as $R_c$ = 3.3 l $O_2$ m$^{-2}$ over the sampling period. Their production efficiency is 0.30.

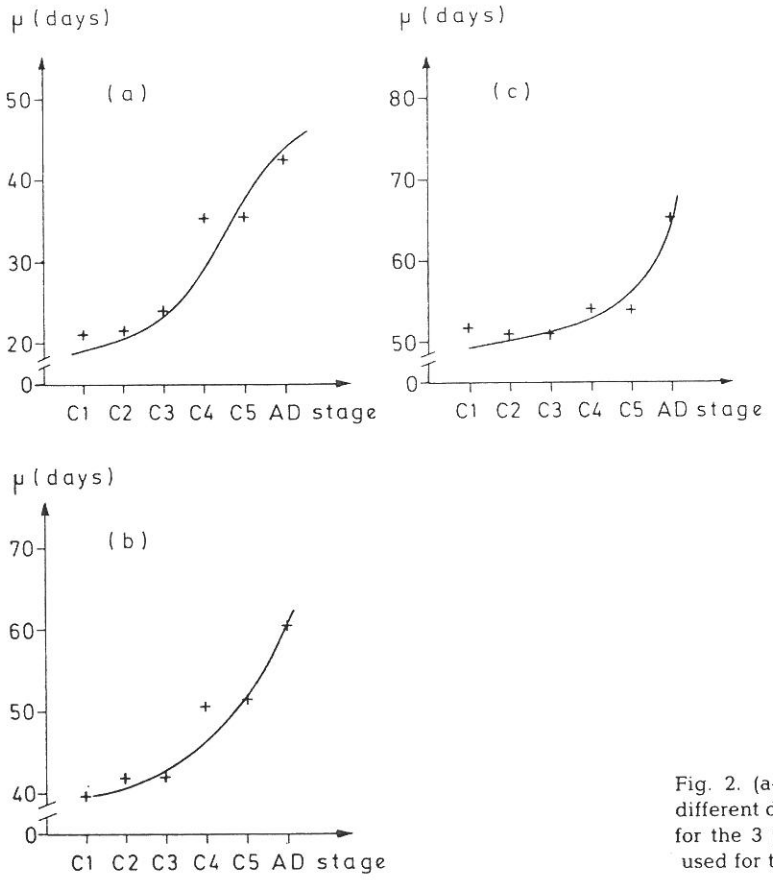


Fig. 2. (a–c): *Tachidius discipes*. Mean pulse times of the different developmental stages plotted against stage numbers for the 3 peaks in the spring of 1979. The smooth lines are used for the application of Rigler & Cooley's (1974) method

When egg production is attributed to the adult population, production efficiency becomes 0.36. With an estimated naupliar respiration of 1.12 l $O_2$ $m^{-2}$ (Eq. [9]), the production efficiency of the total population is calculated as 0.43.

## DISCUSSION

*Tachidius discipes* produced 3 generations in spring 1979. In a 5 d interval sampling in 1980 (essentially aimed at another population) we could distinguish the same pattern. It was, as a whole, shifted to 10 to 12 d later.

Therefore we suppose this pattern occurs consistently each year. Previously, it was not revealed by Heip (1980) in fortnightly samples with all copepodite stages pooled. One single peak was described, and it was concluded that growth is slower under natural conditions than in laboratory cultures. It is shown here that sampling intervals should be very short, and that the copepods should be subdivided into short-living stages in order to reveal the dynamics of a rapidly developing population such as *Tachidius discipes*.

We estimated the production in 2 different ways, each characterized by a number of simplifying assumptions. In the first method, the smoothing of the mean pulse times may well be the most critical step, especially in Copepodites IV and V. Because of the bias, possibly introduced by this extensive data handling, we made a second, independent estimate. This has a weakness in the assumption of a constant mortality rate in all copepodite stages. Both estimates are relatively close to one another, though. This adds some confidence to our estimates.

Due to the rapid development, the production of *Tachidius discipes* is relatively high. The species is

Table 5. P/B of meiobenthic crustaceans determined from field observations

| Species | P/B ($yr^{-1}$) | Source |
|---|---|---|
| *Huntemannia jadensis* | 3.6 | Feller (1982) |
| *Microarthridion littoralis* | 18.0 | Fleeger & Palmer (1982) |
| *Cyprideis torosa* | 2.7 | Herman et al. (1983) |
| *Tachidius discipes* | 34.3 | This study |

only found during spring in this habitat. Expressing the $P/\bar{B}$ on a yearly base by changing the time dimension, it becomes $P/\bar{B} = 35\ yr^{-1}$. Compared to other meiobenthic populations for which direct production estimates have been made, this is very high (Table 5). It should be kept in mind here that *T. discipes* does not realize this high productivity. As it is restricted in appearance to the most favourable season, many 'maintenance costs' experienced by other species in adverse seasons, are probably less important to this species. Therefore the value $P/\bar{B} = 35\ yr^{-1}$ is of limited significance. Only when the mean biomass would be estimated from samples, regularly spaced over a full year, this biomass would have to be multiplied by 35 to find the yearly production.

The production efficiency of *Tachidius discipes* is much higher than 21 %, the mean value given by Humphreys (1979) for non-insect invertebrate herbivores. It is nearly equal to 39 %, the mean value for non-social insect herbivores, and it also approaches the mean for non-insect invertebrate detritivores (36 %). The formation of the 2 groups 'non-social insects' and 'non-insect invertebrates' was the best possible statistical inference Humphreys (1979) could make on the basis of the existing data. In these data certain taxonomical (and probably also ecological) groups are overemphasized, whereas others are almost unstudied. It is highly improbable that the grouping in non-social insects and non-insect invertebrates will remain unchanged when more data are accumulated. Anyway, *T. discipes* has a production efficiency very near to that of the non-social insects, to which it is both taxonomically and ecologically more akin than to the molluscs, which constitute the bulk of Humphreys' non-insect invertebrates.

It must be noted here that Banse (1979) did not find differences in production efficiency according to the species' weight at maturity, longevity or feeding type. He used a limited, but more critically selected data base. When sample size is small, it is, of course, difficult to prove the existence of significant differences. Nevertheless, Banse's (1979) study indicates that the differences between groups in Humphreys (1979) could, at least in part, also be due to different methodologies used in the study of different groups. This is an important ecological question which requires further study.

The production efficiency calculated here is considerably lower than the value calculated by Warwick (1981) for the same species. This discrepancy is entirely due to the combination of field data and respiration data from 2 different populations. Table 6 lists the efficiencies for different temperatures using Warwick's calculation method, with the appropriate respiration data. That calculation is performed for an exponentially increasing population, with stable age distribution, where the production per unit biomass is estimated as $r_m$, the intrinsic rate of natural increase. (A more consistent measure of it is the birth rate b, which, however, is not known for *Tachidius discipes*, and will not be much higher than $r_m$ in an exponentially increasing population with little mortality and a short generation time.) The population structure in the field is clearly different from a stable age distribution, and obviously the mortality is quite important. Nevertheless, the production efficiency found in this study is exactly equal to the predicted value of 43 % at 15 °C. This corroborates the findings of Woodland and Cairns (1980) that, given certain parameters (respiration rate, longevity, ratio final : initial weight), the production efficiency is almost independent of the precise population age structure within the rather wide limits of 'biologically reasonable' mortality patterns.

Table 6. *Tachidius discipes*. Production efficiency calculated from culturing data of Heip and Smol (1976)

| Temp. (°C) | P ($J.J^{-1}\ d^{-1}$) | R ($J.J^{-1}\ d^{-1}$) | P/(P + R) |
|---|---|---|---|
| 5 | 0.036 | 0.086 | 0.30 |
| 10 | 0.086 | 0.122 | 0.41 |
| 15 | 0.136 | 0.180 | 0.43 |
| 20 | 0.186 | 0.259 | 0.42 |
| 25 | 0.236 | 0.374 | 0.39 |

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# Problems in meiofauna energy-flow studies

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Keywords: meiofauna, marine meiobenthos, energy-flow, production, respiration, biomass

**Abstract**

The direct estimation of energy flow through marine meiobenthic populations poses several difficulties, mainly relating to sampling problems. The usefulness of some indirect estimation methods is discussed.

Direct production estimates and respiration measurements for three brackish water crustacean populations are given, indicating a relative constant proportion between population production and respiration. The production: assimilation ratio for these populations fluctuates between 0.3 and 0.4. This is contrasted to literature data revealing much higher production: assimilation ratios as determined in the laboratory for nematode populations. Using data on laboratory cultures of the nematode *Monhystera disjuncta* some factors that can possibly generate this discrepancy are discussed. An analysis of P:B in different life stages of this population justifies the use of a life-cycle turnover of about 3 for meiobenthic populations, provided some conditions are met. Among these is that no drastic change in productivity occurs between juveniles and adults, and that the biomass of hatchlings, not of freshly laid eggs, is considered as generative production.

## Introduction

Since the start of the International Biological Programme, considerable scientific effort has been devoted to the study of the productivity of marine populations. These studies focus in the first place on a good description of average standing stocks and transfer rates between compartments in black box models. The final aim of the study of ecosystems from the energetic point of view is an understanding and quantification of the time-dependent dynamics of the system.

In this framework, relatively little attention has been paid to the meiofauna. Although a great number of data have been gathered on density, diversity and species composition of meiofauna, it is still very problematic to derive from these an estimation of the rate of energy flow through these populations. As a consequence, the detailed study of the interactions in which meiobenthic populations are involved is impaired. The quantification and indeed the proof of the existence of competition in meiofauna remains a far and elusive goal. The same is true for several predator–prey type relationships: grazing by meiofauna on microflora, predation by epibenthos on the meiofauna, and predation within the meiofauna. Energy flow measurements are required to evaluate both the grazing pressure on lower trophic levels, and the amount of energy and material made available to higher trophic levels.

Methods for the estimation of production in aquatic populations are extensively reviewed by Waters (1977). They can be reduced to two types: summation of eliminated biomass, or summation of growth increments (including reproductive output). According to the method used, one needs good data either about growth, reproduction and recruitment, or about mortality and changes in biomass. In populations with overlapping genera-

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tions and continuous reproduction, this procedure requires fitting of a demographic model to the available data, or alternatively the extrapolation of culture data to field situations. Especially in marine populations, both frequent sampling with sampling intervals in the order of days, and culturing in the laboratory are often impossible.

In the instances where direct estimates are impossible, production may be estimated indirectly by assuming a proportionality between respiration and production energy flows in the population. In a study comprising ecologically very different populations, Hymphreys (1979) could define several groups, all of which showed a significant log-log relationship between production and respiration with a slope not significantly different from 1. This implies that within these groups the production efficiency, approximated by $P/(P + R)$, is independent of the population's size (where P is production and R respiration, both expressed in the same units, e.g. Joules). Banse (1979) also showed that the production efficiency ('Net growth efficiency') in a number of invertebrates from temperate regions is independent of the animals' size at first maturity. The assumption of proportionality between respiration and production may therefore be a reasonable base for indirect production estimation.

The empirical relationship between yearly P:B (where B is mean biomass) and adult size, established by Banse & Mosher (1980) is another possibility to estimate production indirectly. Although it is difficult to establish the assumptions by which this relationship can be expected, the empirical data suggest that it may be useful. Furthermore, it is of particular interest to meiobenthologists because these authors propose another, lower line for meiobenthos than for similarly sized species from other ecological groups.

In this paper we shall discuss some field and laboratory data on production and respiration of meiobenthic populations. Our discussion will focus on the applicability of the above-mentioned shortcut methods for production estimation.

## Production and respiration

In our work on a shallow brackish water pond, the Dievengat in north-western Belgium, we measured both the production and the respiration of some meiobenthic crustaceans. Respiration as a function of body weight at 20 °C was determined by Cartesian Diver microrespirometry for most developmental stages of one ostracod (Herman & Heip, 1982) and five copepod species (Herman & Heip, 1983). The metabolic intensity, measured by the intercept $a$ in the allometric relation $\log R = a + b \log W$ (where $R$ is respiration, $W$ body weight and $a$ and $b$ constants) is similar in four of these species. In the two larger and longer-lived species, the copepod *Canuella perplexa* and the ostracod *Cyprideis torosa*, it is much lower.

The production in the field was estimated directly for three of these populations. The results of these studies are summarized in Table 1.

The ostracod *Cyprideis torosa* has only one generation annually in this habitat, but there is considerable overlap between successive generations, due to overwintering of the older larvae. Its production was estimated in two ways (Herman *et al.*, 1983). In the first method the distribution over the developmental stages of the empty shells in the bottom was used to estimate stage-specific mortality rates, and the duration of the stages. The second method is a modification of the size-frequency ('Hynes') method. Both results are in good agreement.

The population of the harpacticoid copepod *Tachidius discipes* was sampled every three days in the spring of 1979. The production of the copepodites and adults was estimated by two estimation procedures (Herman *et al.*, 1984). These are based on Rigler & Cooley's (1974) method, and on the size-frequency method. The production efficiency of 36% is calculated with neglection of the nauplii, for which neither good production nor respiration measurements are available. Inclusion of (rather rough) estimates of naupliar production and respiration raises the efficiency slightly, to 42%. For this naupliar production estimate, an exponential model for mortality and body growth was assumed. Thus estimated, the naupliar production accounts for 41% of the total production.

The harpacticoid copepod *Paronychocamptus nanus* was sampled every five days in 1980. The production estimation of copepodites and adults (Herman & Heip, in prep.) was based on the size-frequency method. Again the production efficiency (37%) had to be estimated with neglection of the nauplii. However, with the same method as for *T.*

*discipes*, a crude estimate of the naupliar contribution to overall production was made: 25%. Our estimates can be compared to the 35% contribution found by Fleeger & Palmer (1982) for *Microarthridion littorale*, and the 39% estimated for *H. jadensis* (Feller, 1982). They confirm the important role of the nauplii in the population production, stressed by Hicks & Coull (1983). However, as our calculations for *T. discipes* indicate, they probably have no profound influence on the estimation of the population's production efficiency.

As shown in Table 1, the production efficiencies of these three populations are nearly equal to one another. This neat proportionality between respiration and production is remarkable because the populations differ considerably in a number of characteristics (Table 2). The values for the production efficiency are in good agreement with the values expected from Humphreys' (1979) regression between log P and log R for non-insect detritivores. Also in good agreement is the value (38%) found by Marchant & Nicholas (1974) for the nematode *Pelodera*. These production efficiencies, however, are much lower than those obtained for nematodes in culture by Warwick (1981b), Schiemer *et al.* (1980), Schiemer (1982a, b) and Tietjen (1980). These authors all find very high production efficiencies, in the order of 70% to 90%. It is an important question if, and how the major discrepancy between these two groups of values could be explained. We think that several factors should be considered.

*Table 1.* Summary of energy-flow studies in three meiobenthic crustacean populations from a brackish-water habitat (The 'Dievengat' in northern Belgium).

| | |
|---|---|
| *Cyprideis torosa* (Ostracoda) (data in Herman *et al.*, 1983) | |
| Production: | |
| - 'empty shells model': | $P = 9.69$ g dwt $m^{-2}$ $a^{-1}$ |
| - 'size-frequency' method: | $P = 9.24$ g dwt $m^{-2}$ $a^{-1}$ |
| Mean biomass: | $B = 3.55$ g dwt $m^{-2}$ |
| Respiration: | $R = 20.38$ l $O_2$ $m^{-2}$ $a^{-1}$ |
| Production efficiency: | $P/(P + R) = 0.38$ |
| P:B | P:B = 2.73 $a^{-1}$ = 2.73 generation $^{-1}$ |
| *Tachidius discipes* (Copepoda) (Herman *et al.*, 1984) | |
| Production of copepodites and adults (during the spring peak) | |
| - Separation of generation peaks | $P_c = 1.1$ g dwt $m^{-2}$ |
| - size-frequency | $P_c = 1.0$ g dwt $m^{-2}$ |
| Egg production | $P_e = 0.31$ g dwt $m^{-2}$ |
| Mean biomass | $B = 0.26$ g dwt $m^{-2}$ |
| Respiration | $R = 3.304$ l $O_2$ $m^{-2}$ |
| Production efficiency | $(P_c + P_e)/(P_c + P_e + R) = 0.36$ |
| P:B | P:B = 9.34 (spring) = 3.11:gen. |
| *Paronychocamptus nanus* (Copepoda) (Herman & Heip, in prep.) | |
| Production of copepodites and adults (size-frequency) | $P_c = 1.9$ g dwt $m^{-2}$ $a^{-1}$ |
| Egg production | $P_e = 1.2$ g dwt $m^{-2}$ $a^{-1}$ |
| Mean biomass | $B = 0.17$ g dwt $m^{-2}$ |
| Respiration | $R = 6.67$ l $O_2$ $m^{-2}$ $a^{-1}$ |
| Production efficiency | $(P_c + P_e)/(P_c + P_e + R) = 0.37$ |
| P:B | P:B = 24.5 $a^{-1}$ = 3.2 generation$^{-1}$ |

## *1. Field versus laboratory conditions*

The nematode data are obtained from lab cultures. The conditions in these cultures are obviously different from the conditions in the field. In his study on *Caenorhabditis briggsae*, Schiemer (1982a, b) showed, for instance, that feeding conditions have a profound influence on the production efficiency. Other environmental factors will undoubtedly have a similar effect. The measured differences in efficiency could therefore imply that meiofauna in nature lives in fairly unfavorable conditions. However, this difference between lab and field con-

*Table 2.* Characteristics of the three meiobenthic populations for which energy budgets were constructed.

| | *C. torosa* | *T. discipes* | *P. nanus* |
|---|---|---|---|
| Adult size (µg dwt ind. $^{-1}$) | 19.8[a] | 1.8 | 0.6 (♂)-1.0 (♀) |
| Metabolic intensity[b] | 0.25 | 1.1 | 1.0 |
| Number of generations: year | 1 | 3[c] | 8 |
| Food source | detritus | algae | detritus |

[a] without the weight of the shells, see Herman & Heip (1982)

[b] expressed as the parameter $a$ in Log R = $a$ + $b$ log W, with R in ln $O_2$ ind.$^{-1}$ at 20 °C, and W in µg dwt ind.$^{-1}$

[c] only present during a 2-3 months spring period.

ditions alone is insufficient as an explanation. Both *Tachidius discipes* and *Paronychocamptus nanus* have been cultured in the laboratory (Smol & Heip, 1974; Heip & Smol, 1976; Heip, 1977). Applying our respiration data to the stable age distribution derived from the culture data yields an efficiency of about 40% for both species at 15 °C. Furthermore, the efficiency of *Pelodera* (Marchant & Nicholas, 1974) has also been estimated in the laboratory.

*2. Differences in metabolic pathways*

Respiration in function of the body weight has been measured for the two congeneric nematodes *Caenorhabditis briggsae* (Schiemer, 1982a) and *C. elegans* (De Cuyper & Vanfleteren, 1982). In both studies the respiration rate of the juvenile stage I is relatively low: the observations lie under the allometric relation determined for the other stages. De Cuyper & Vanfleteren (1982) could explain this phenomenon by the prevalence of a different metabolic pathway, the glyoxylate cycle, by which the fat stores are consumed in eggs and early juveniles of nematodes. In this pathway less oxygen is consumed for the same amount of energy metabolized. Obviously this is of importance in the estimation of assimilation as $A = P + R$, since no simple conversion factor of R to metabolized energy is available.

In the case of *Caenorhabditis*, this factor may only have a minor importance for the population's energy budget. For partially anaerobic species, however, it may be much more important.

*3. Neonate weight versus egg weight*

A third factor, which may well be the most important one, creates considerable difficulties for the concept of production. In nematodes, the weight of a neonate is consistently lower than the weight of a freshly deposited egg. The weight loss during egg development is sometimes 3/4 of the fresh egg weight. Presumably the adults put organic matter into the eggs in a relatively unorganized state, and the weight loss in the eggs is the energetic cost of both maintenance and of the organization of this material into living tissue.

Due to this energy loss in the egg stage it is unclear what should be considered as 'production': the weight of the eggs produced or the weight of the neonates. If the organic matter of the egg mass is called production, the population's energy budget should comprise a term for the 'negative production' in the egg development. In this stage an amount of organic matter disappears from the population: the energy lost during the development is dissipated as heat. The inclusion of the eggs' 'negative production' may considerably lower the total population's production efficiency, and bring it back to more realistic values. For the reproducing females, however, it remains very high (Warwick (1981) and Tietjen (1980) record values over 90%). This high efficiency is artificial if the energy cost of storing organic material in the eggs is lower than the energy cost of storing an equivalent quantity of material in the individual's own body growth.

An alternative definition of generative production could resolve some of the conceptual difficulties discussed. When the biomass of the neonates is defined as production, the total population's production efficiency is the same as the value obtained by incorporating the eggs' 'negative production'. The reproducing females' efficiency is lowered, and the two allocations of organic matter - own tissue growth and neonates' tissue - are more comparable as far as energetic cost is considered. In this definition of production the females become 'conceptually viviparous'. However, this definition suffers from inconsistency with classical production theory: once the eggs are formed, they do represent an amount of energy which is available to higher trophic levels.

Although there remain conceptual problems, whatever definition of generative production is chosen, the fact that a lot of energy stored is lost from the population during egg development should be taken into account for the calculation of energy budgets. In most nematode populations for which very high efficiencies have been described, the bulk of the production is egg production. When the developmental energy loss is subtracted from these production figures, the efficiency will be considerably lower. For example, adjusting Schiemer's (1982a, b) data for *Caenorhabditis briggsae* (at a food density of $10^{10}$ bacterial cells $ml^{-1}$), yields a cumulative efficiency over a nematode's life span of about 40% instead of 62%, although a peak value of over 60% is still observed in early reproductive females.

In conclusion we think that the high production efficiencies in laboratory cultures are overestimations, and that with the present data there is no clear

evidence that meiobenthic efficiency is higher than the efficiency in other groups. On the other hand, we need more data to be able to estimate the range of production efficiencies in meiobenthic populations. The estimation of production from respiration by assuming an efficiency of e.g. 40% is still very tentative.

**Production: Biomass (P:B) and body weight**

Some of the points made above are also of importance for a discussion of the scaling of P:B by body weight in meiofauna. The few field production estimates of meiobenthic populations show a P:B per generation time of about 3. This figure was used by Heip *et al.* (1982) to estimate P:B of nematodes from culture data on generation times. It was first generalized for the meiobenthos by Gerlach (1971), who derived it from a partially hypothetical nematode life history. Both papers cite, as a justification for the generalization, the model study of Waters (1969). In this paper it was shown that for a wide variety of growth and mortality models, the lifetime P:B does not vary greatly around a modal value of about 3.5.

However, on closer inspection it appears that nematodes are very different from the type of populations Waters (1969) modelled. He derived the lifetime, not the generation time turnover and showed that for stationary cohort populations this equals the P:B per period between two reproductive peaks. Nematodes on the contrary have continuous reproduction and their reproductive output is an important contribution to overall production: it cannot be neglected as Waters (1969) does. The main questions to ask, if one wishes to generalize about nematode P:B, are therefore: can the term 'generation time be exactly defined, and is there a justification to use the figure P:B = 3 "per generation time"?' (In contrast to the demographic literature, where several exactly defined measures of generation time are used, the term has a loose meaning in production studies.)

To clarify these points, we shall use data on *Monhystera disjuncta*, cultured in agar dishes at 12 °C and 30‰ salinity (Vranken *et al.*, in prep.). Bacterial food in these cultures was abundant, but its composition was not controlled. For this nematode, complete life tables and fecundity tables were determined. From these tables many demographic parameters were computed: the intrinsic rate of natural increase $r_m$, the stable age distribution at exponential growth, the birth rate b, the minimum generation time $T_{min}$, the cohort generation time $T_c$, etc. . .

It was proven by Zaika (1973) that in stable age distribution populations, the P:B equals the birth rate b. Thus the overall population turnover rate for this population was calculated as P:B = 0.18 $day^{-1}$, corresponding to 65 $year^{-1}$. This P:B can be partitioned among the different life history stages as follows.

The juvenile body growth was studied at 17 °C (Fig. 1). It can be described very well by the exponential function $W_t = W_0 e^{Gt}$ where $W_t$ is the wet weight at time t, and $W_0$ and G are constants. The parameters of this equation are $W_0$ =0.014 $\mu$g wwt, G = 0.37 $day^{-1}$ ($r^2 = 0.995$; F = 1135). Taking into account the development times at 12 °C and 17 °C, the growth rate G at 12 °C becomes 0.21 $day^{-1}$. Because of the exponential fit, this figure also equals the juvenile P:B.

Egg deposition occurs at a nearly constant rate of 5.1 eggs per female alive per day, until after about 40 days senescence starts rather abruptly, and almost no eggs are deposited any more.

Neglecting adult somatic growth, which is not important in stable age distributions as most adults

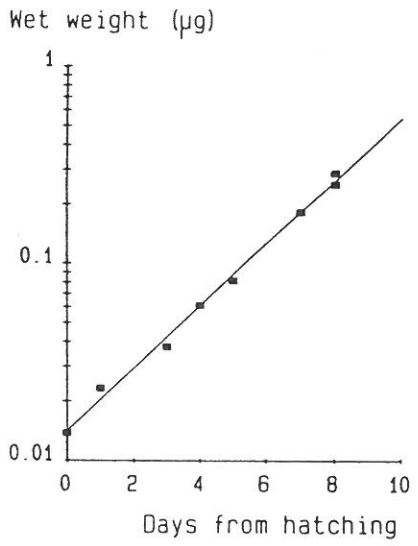


*Fig. 1. M. disjuncta*: juvenile body growth between hatching and adulthood in agar cultures at 17 °C.

are very young, the adults' P:B is given by the formula:

$$P:B = (1/\text{adult weight}) \times \text{no. eggs produced/female day} \times \text{egg weight} \times \text{fraction females}$$

The P:B equals 0.33 day $^{-1}$. As was mentioned before, if we calculate the adults' P:B with the egg's weight, we must incorporate a negative production in the egg stage. In this case, this egg P:B amounts to $-0.13$ day$^{-1}$. Alternatively, we can calculate the adults' P:B by taking into account only the weight of the neonates. The adult P:B then becomes 0.20 day$^{-1}$, almost exactly equal to the juvenile P:B.

Because of this equality, the population's age structure can only affect its P:B through adult body growth, which however we think is not very important in this case. Thus the population P:B equals the juvenile P:B which, due to the exponential growth is given by:

$$P:B = \ln(W_T/W_0) = G\,T$$

per developmental period, where $W_T$ and $W_0$ are the body weights at the end and the start of the juvenile period respectively, and T is the developmental period.

This figure gives a reliable estimate of the population P:B because the following conditions are met:

1. The neonates' weight is called 'production', or a term for 'negative production' in the egg stage is incorporated in the budget.
2. The juvenile body growth is exponential.
3. The adult body growth is not too important.
4. The productivity of the (young) adults is not much different from the juvenile productivity.

It is not clear whether the last three conditions can be generalized to nematodes as a group, and thereby provide a justification for the use of an overall figure for P:B per developmental period. The available information suggests that juvenile growth in nematodes does not depart too widely from an exponential model. Table 3 gives some approximate values for $\ln(W_T/W_0)$, showing that this value does not vary too widely either.

The most important condition then becomes 4. This condition is rather difficult to check in published studies. Intuitively one would expect that the weight-specific production of adults defined in terms of neonates' weight cannot be higher than the weight-specific production of the juveniles. In general, the intensity of metabolism decreases with age. Although the data on *M. disjuncta* suggest a fairly constant rate, it may in fact decrease after the first days of adulthood, if the adults have some somatic growth.

An unresolved problem in these data is the allocation of the adults' production between the sexes. As the weight-specific production of the adults, as a whole, is almost equal to the juveniles', females have a higher productivity than juveniles, and males a much lower one. Whatever the mechanism is that allows females to have a higher productivity than juveniles, it is difficult to understand why this has not evolved in the juvenile stage. Possibly the hypothesis that male sperm contributes to the energy stored in the eggs (Warwick, 1981a; Jennings & Deutsch, 1975) could explain these data. On the other hand, observations by Jensen (1982) have made this hypothesis less probable.

The conditions (1–4) stated above clarify the as-

*Table 3.* Natural logarithms of the ratio of final ($W_T$) to initial ($W_0$) weight of nematode juveniles. See text for details. Number in brackets for *C. briggsae* and *P. palustris* refer to bacterial densities.

| Species | $\ln(W_T/W_0)$ | | |
|---|---|---|---|
| *Monhystera disjuncta* | 2.9 | (17 °C) | This paper |
| *Chromadora nudicapitata* | 2.8 | (12 °C) | Vranken, unpubl. |
| *Monhystrella parelegantula* | 2.3 | (25 °C) | *id.* |
| *Caenorhabditis briggsae* | 3.5 | ($5 \times 10^8$) | Schiemer, 1982a |
| | 3.7 | ($10^9$) | |
| | 4.0 | ($10^{10}$) | |
| *Plectus palustris* | 3.4 | (1 K) | Schiemer *et al.* 1980 |
| | 3.6 | (10 K) | |
| *Eudiplogaster pararmatus* | 4.1 | (12 °C) | Romeyn *et al.*, 1983 |
| | 2.3 | (21 °C) | |
| *Diplolaimelloides bruciei* | 3.6 | (20 °C) | Warwick, 1981a |

sumptions by which a P:B = 3 per 'generation time' may be expected in nematodes. At the same time, it is demonstrated that the juvenile developmental period should be used as the (previously ill-defined) 'generation time'.

## Conclusions

From our discussions we can make a few generalizations about meiofaunal productivity. We have argued that there is no evidence for a difference in production efficiency between meiofauna and other ecological groups. The conditions for the use of a P:B = 3 per juvenile development period have been stated. They seem to apply well to nematode populations. This adds confidence to the graph given by Heip *et al.* (1982), which shows that the P:B body weight line for meiobenthos in Banse & Mosher (1980) fits the data rather well. Thus the statement of these authors that a relatively low productivity is a definition criterion for meiofauna, is corroborated, although not proven.

Apart from these general considerations, however, considerable problems remain if one wishes to estimate the production of a population for which only biomass estimates are available. In particular, the estimations based on a constant production efficiency, and those based on a P:B body weight relationship may be inconsistent. Warwick & Price (1979) noted that, after correction for temperature, the *community* respiration of nematodes nearly equalled 6 l $O_2$ g $wwt^{-1}$ $a^{-1}$ in several different habitats: the Lynher mudflat (UK), two salt marshes in Massachusetts (USA) (Wieser & Kanwisher, 1961), a salt marsh in Georgia (USA) (Teal & Wieser, 1966). For the coastal area and a sandbank in the Southern North Sea (data in Heip *et al.*, 1984) these values are 5.53 and 5.87 l $O_2$ g $wwt^{-1}$ $a^{-1}$ respectively. This constantcy is remarkable (and problematic) as the mean individual weight of a nematode in these habitats differs by more than an order of magnitude (range 0.33–8.64 $\mu$g wwt ind.$^{-1}$). Assuming a constant efficiency for all species would result in a constant P:B, whereas a weight dependence in P:B would give P:B-differences by about a factor 8. Presumably it is the constant efficiency assumption which is violated in this instance. The large predatory: omnivorous nematodes (mainly Oncholaimida) have a high respiratory intensity (Warwick & Price, 1979) while it is known at least for a few species that they have only one to two generations a year in the field (Smol *et al.*, 1980; Wieser & Kanwisher, 1961; Skoolmun & Gerlach, 1971).

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# Secondary production of the harpacticoid copepod *Paronychocamptus nanus* in a brackish-water habitat

3206

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*Abstract*

The secondary production of the harpacticoid copepod *Paronychocamptus nanus* (Sars, 1908) in a shallow, brackish-water pond was estimated during spring and summer 1980. The population was sampled every 5 d. Production of copepodites and adults, calculated by the size-frequency method, amounts to 1.91 g $m^{-2}$ dry wt over the sampling period (March–November). Egg production is 1.23 g $m^{-2}$; naupliar production is roughly 1.09 g $m^{-2}$. The production efficiency (ratio of production to production plus respiration) of copepodites and adults is 0.37; for the total population it is 0.42. $P:B$ of the population is 24.45 over the sampling period, or 3.2 per generation.

Warwick (1984) advocated a biological definition of the group of small benthic metazoans called meiobenthos. Conventionally, the meiobenthos is defined in methodological terms and roughly covers metazoans that pass through a 1-mm sieve. Warwick (1984) showed that there are two separate peaks in body size distributions of species in benthic communities, corresponding to the traditional meio- and macrofauna and argued that each category represents a separate evolutionary unit, with an "internally coherent set of biological characteristics." These characteristics include lifespan, feeding strategy, reproductive pattern, and growth type, all of which affect the productivity of a population. It is possible, therefore, that the meiofauna differs from the macrofauna in productivity, whereas within both groups production rates are more consistent.

There are indications of meiofauna–macrofauna discontinuities in the relationship between production : biomass ratio ($P:B$) and body size (Banse and Mosher 1980; Heip et al. 1982) or in the relationships between respiration, intrinsic rate of natural increase, and body size (Banse 1982). To corroborate these generalizations, we need more data on the productivity of meiobenthic populations.

This paper is part of a series of studies of the energy flow through the dominant meiobenthic crustaceans in a shallow, brackish-water pond. This community was monitored at 2-week intervals for 7 years (1969–1976) (Herman and Heip 1983*b*) and later production and respiration were measured to investigate the resource utilization of the dominant populations. We have reported on the respiration and production of the ostracod *Cyprideis torosa* (Herman and Heip 1982; Herman et al. 1983), the respiration of five meiobenthic copepods (Herman and Heip 1983*a*), and the production of the harpacticoid *Tachidius discipes* (Herman et al. 1984).

*Paronychocamptus nanus* (Sars, 1908) is the smallest and most abundant copepod in this habitat. It is a detritus feeder that lives in the upper few centimeters of the sediment. The species is found throughout the year. It reproduces from February through November. Most animals found in other months are adults.

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## *Field samples*

*Paronychocamptus nanus* was sampled in a very shallow, brackish-water habitat, the Dievengat, in a polder in northwest Belgium (map reference 51°21′30″N, 3°22′15″E). Water at the sampling site is 10 cm deep. The sediment is a well sorted, fine sand covered with large amounts of detritus. Salinity

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fluctuated between 7 and 25‰ during the sampling period.

A sediment sample was taken every 5 days, to a depth of 5 cm, from 19 March to 14 November 1980 with a glass corer (6.06 $cm^2$). Two samples were lost (7 June and 16 August). The material was fixed in neutral 4% formaldehyde (final concn) heated to 70°C. Elutriation was according to Heip et al. (1974) except that a silica gel (LUDOX) was used for centrifugation of the finer fractions instead of sucrose (de Jonge and Bouwman 1977).

Nauplii could not be sampled quantitatively in this detritus-rich sediment. On each date the number of animals in other developmental stages (copepodites and adults) was recorded. Copepodite stages could easily be recognized by the number of body segments.

Dry weights were determined on a Mettler ME22 microbalance (±0.1 μg). Batches of 50–100 animals belonging to the same developmental stage were rinsed two times in double-distilled water, dried for 2 h at 110°C, cooled in a desiccator, and weighed. Replicate weighings show high reproducibility: for males, two weighings yielded 0.59 and 0.63 μg $ind^{-1}$; for females carrying eggs, three weighings yielded 1.26, 1.28, and 1.23 μg $ind^{-1}$. No duplicates were determined for the other stages.

*Production*

Production of the copepodites and adults was calculated by the size-frequency method. Simplifying the formulation of Menzie (1980), we calculate production as

$$P = \sum_{j=1}^{i} (N_j - N_{j+1})(W_j W_{j+1})^{1/2} \quad (1)$$

where

$$N_j = \bar{n}_j \frac{1}{f_j} \frac{365}{\mathrm{CPI}}, \quad (2)$$

and $i$ is the number of size classes, $W_j$ the mean weight of an individual in size class $j$ (μg dry wt $ind^{-1}$), $f_j$ the proportion of the life cycle spent in size class $j$, $\bar{n}_j$ the mean number of individuals observed in size class $j$ (No. ind $surface^{-1}$), and CPI the cohort production interval (time needed to grow into the largest size class, days). If we multiply 1/CPI ($days^{-1}$) by the constant 365 d $yr^{-1}$, 365/CPI has dimensions $yr^{-1}$. $N_j$ therefore has dimensions number of individuals $surface^{-1}$ $yr^{-1}$. It is an estimate of the number of individuals per unit surface that grow into the size class $j$ during a year.

As shown by culture experiments (Smol and Heip 1974; Heip and Smol 1976), temperature has a profound influence on the development time of *P. nanus*. Our samples cover a considerable part of the year, with variations in water temperature of about 15°C, so that the parameters relating to stage durations cannot be assumed constant throughout the sampling period. We therefore converted the time axis to a physiological time scale. Heip and Smol (1976), from culture experiments with excess food, described the development time $D$ from egg to female carrying eggs as a function of temperature $T$:

$$D = 528T^{-1.05}. \quad (3)$$

These workers also described the yearly temperature cycle in the Dievengat by the sinusoidal function

$$T = 11.2 + 8.3 \sin(t - 117) \quad (4)$$

where $T$ is the water temperature in °C and $t$ the time in days from 31 December. From Eq. 3 and 4, the calendar time $t$ (expressed in days since 31 December) is transformed to the physiological time $t'$ (expressed in units of developmental periods) by

$$t' = \sum_{i=1}^{t} (1/528)[11.2 + 8.3 \sin(i - 117)]^{1.05}. \quad (5)$$

On this scale, the sampling period (19 March–14 November) covers 7.63 developmental periods. We used 7.63 for the term 365/CPI in Eq. 2.

The relative proportions of the life cycle spent in the copepodite and adult stages (giving CI the arbitrary duration of 1) can be estimated by assuming an exponential mortality model for copepodites and adults with a constant mortality rate (Herman et

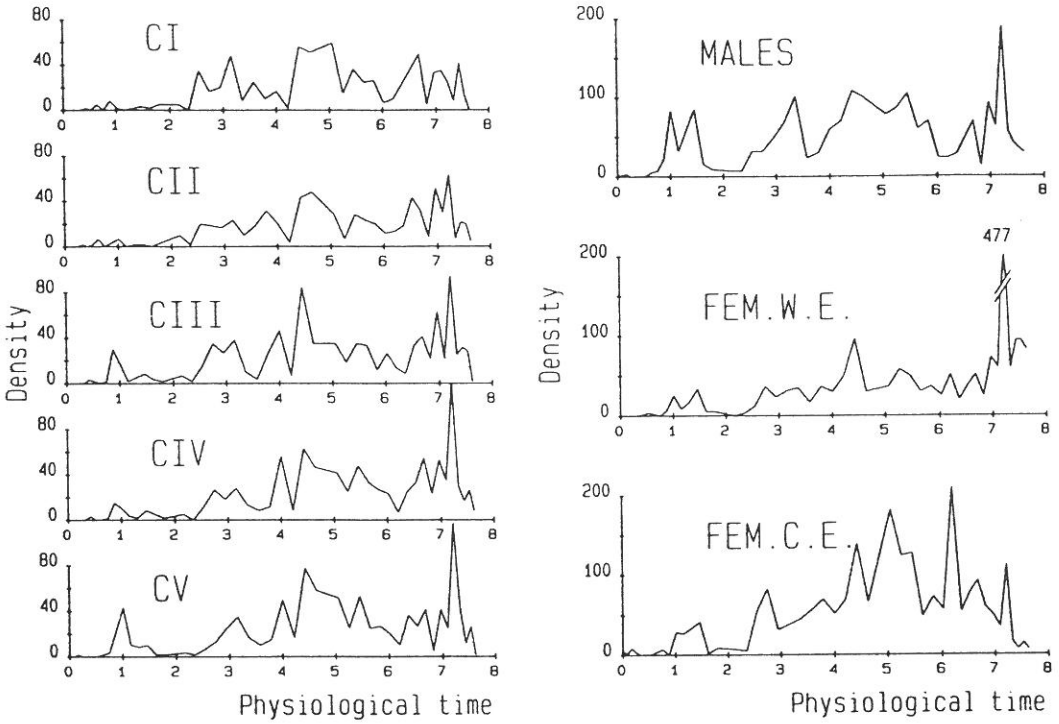


Fig. 1. *Paronychocamptus nanus*. Density (No. per 10 cm²) of the developmental stages on a physiological time scale (in units of developmental periods, *see text*). Females without eggs—FEM.W.E.; females carrying eggs—FEM.C.E.

al. 1983). In culture experiments (Smol and Heip 1974) it was observed that the ratio of embryonic and naupliar phase to the copepodite stage was 0.8. The absolute proportions of the life cycle $f_j$ spent in each stage $j$ are then calculated as

$$f_j = \frac{f_{rj}}{\sum_j f_{rj}} \qquad (6)$$

where $f_{rj}$ are the relative proportions (in units of CI durations).

The mean respiration of the different stages of copepodites and adults at 20°C was determined by Cartesian Diver microrespirometry (Herman and Heip 1983*a*). Total population respiration was calculated from these values after adjustment for temperature in the field with Krogh's normal curve (Winberg 1971).

Methods for the estimation of egg production and of naupliar production, biomass, and respiration are the same as those used for *T. discipes* (Herman et al. 1984). Egg production is obtained from the number of females carrying eggs and the development time of the eggs at the prevailing temperature. Development times are given by Smol and Heip (1974). Nauplii could not be counted in the field samples; a rough estimate of their production and mean biomass is made by assuming exponential mortality and growth. With these simplifying assumptions, production and mean bio-

Table 1. *Paronychocamptus nanus*. Dry weights ($W_j$) of copepodite stages and adults. Number of copepods weighed in a batch—$N$.

| Stage | $N$ | $W_j$ (µg ind$^{-1}$) |
|---|---|---|
| CI | 119 | 0.09 |
| CII | 80 | 0.14 |
| CIII | 109 | 0.22 |
| CIV | 107 | 0.31 |
| CV | 132 | 0.48 |
| Male | 203 | 0.61 |
| Female (−eggs) | 121 | 0.95 |
| Female (+eggs) | 196 | 1.26 |

Table 2. *Paronychocamptus nanus*. Production estimates by the size-frequency method. $A_j$—Surface under the curve of density against physiological time of stage $j$; $f_{rj}$—duration of the stage in units of CI duration; $f_j$—proportion of the total life cycle spent in stage $j$; $\bar{n}_j$—mean number of copepods in stage $j$; $N_j$—estimate of the recruitment into stage $j$; $\text{Prod}_j$—estimate of the production of stage $j$.

| Stage | $A_j$ | $f_{rj}$ | $f_j$ | $\bar{n}_j$ (ind 10 cm$^{-2}$) | $N_j$ (ind 10 cm$^{-2}$) | $\text{Prod}_j$ ($\mu$g 10 cm$^{-2}$) |
|---|---|---|---|---|---|---|
| CI | 148 | 1 | 0.041 | 19 | 3,622 | 31 |
| CII | 131 | 0.96 | 0.039 | 17 | 3,348 | 54 |
| CIII | 167 | 1.35 | 0.055 | 22 | 3,038 | 84 |
| CIV | 173 | 1.56 | 0.064 | 23 | 2,712 | 138 |
| CV | 184 | 1.91 | 0.078 | 24 | 2,356 | 115 |
| Adult | 1,092 | 12.32 | 0.502 | 143 | 2,174 | 1,814 |

mass are calculated from their initial and final weight, initial and final numbers, and the proportion of the life cycle spent in the naupliar phase. An estimate of naupliar respiration is made from the same parameters, plus the respiration–body weight relationship.

For the conversion of dry weights to energy units we used the following conversion factors: 1 liter of $O_2$ consumed is assumed equivalent to 0.4 g of C metabolized (Crisp 1971); 1 g of C = 45.8 kJ (Salonen et al. 1976), and organic carbon = 52% of ash free dry wt (Salonen et al. 1976).

All production estimates given are for the entire study period of 245 days.

## *Results*

The densities of the copepodite and adult stages in the consecutive samples are shown in Fig. 1 on a physiological time scale (original data available on request). The mean dry weight of the developmental stages is given in Table 1. This species shows a pronounced sexual dimorphism; males are considerably smaller than females. Taking into account the sex ratio in the field, we find the mean weight of an adult is 0.83 $\mu$g (without egg sacs).

In Table 2 the data for the production calculation are given. The sum of the relative durations $f_{rj}$ of the copepodite stages (taking the duration of CI as 1) is 6.78 units, and the duration of egg + nauplius is estimated as 6.78 × 0.8 = 5.42 units. The sum of all durations is 24.52, which is used to calculate $f_j$, the proportion of the life cycle spent in each stage. Under $\text{Prod}_j$ the values $(N_j - N_{j+1})(W_j W_{j+1})^{1/2}$ are given. The summation of these values gives the production of copepodites and adults, 2,237 $\mu$g per 10 cm$^2$ dry wt.

The number of egg sacs produced is estimated as 3,961 per 10 cm$^2$. The mean number of eggs per egg sac is 19, and the mean number of hatching nauplii is 17 per egg sac (Smol and Heip 1974). The estimated initial number of nauplii is 67,334; of these, 3,622 develop into CI. With 0.016 and 0.09 $\mu$g as initial and final weight of the nauplii, the naupliar production is estimated as $P_n$ = 1,086 $\mu$g per 10 cm$^2$ dry wt. For calculation of total production, we must take into account that the size-frequency method is a removal-summation method, whereas the calculation method for the naupliar production is based on the increment-summation method (*see* Herman et al. 1984). As a consequence, the production of the 3,622 CI animals is incorporated in both the naupliar and the copepodite production figures. The correct estimate of total production is thus: $P_t$ = 1,228 + 1,086 + 2,237 − (3,622 × 0.09) = 4,225 $\mu$g per 10 cm$^2$ dry wt.

The mean biomass of the nauplii is estimated as 24 $\mu$g per 10 cm$^2$. For copepodites, adults, and eggs, it is 149 $\mu$g per 10 cm$^2$. The mean biomass of the total population is $\bar{B}_t$ = 173 $\mu$g per 10 cm$^2$. The $P:B$ is 24.45 over the sampling period, or 3.2 per generation. The respiration of copepodites and adults is estimated as 6.67 ml $O_2$ per 10 cm$^2$ during the sampling period. Naupliar respiration is estimated as 0.86 ml $O_2$ per 10 cm$^2$.

With egg production attributed to the adult population, the production efficiency $P/(P + R)$ of copepodites and adults is 0.37. The production efficiency of the total population is estimated as 0.42.

## *Discussion*

The size-frequency method used in this estimate of production was also used for the copepod *T. discipes* (Herman et al. 1984) and the ostracod *C. torosa* (Herman et al. 1983) from the same habitat. In both studies the results were in good agreement with that of an independent estimate. For *C. torosa*

the independent estimate was based on the age distribution of empty ostracod shells in the sediment. For *T. discipes,* a modified version of the method of Rigler and Cooley (1974) was used.

Feller (1982) strongly recommended calculating confidence intervals for estimating production. However, many elements enter into calculating production, which often involves nonlinear functions. The confidence intervals calculated by Feller (1982) for the copepod *Huntemannia jadensis* incorporate most (but not all) structural elements of the procedure for estimating production. As a consequence, they almost span two orders of magnitude: 0.1–14.7 around a production value of 1.75 g C $yr^{-1}$. Such values greatly increase the probability of type II errors in comparisons of production estimates. Moreover, there are many possibilities of introducing bias in calculating production, so that even when a confidence interval can be calculated it is not certain at all that it really encompasses the true production value with a given probability.

The most important factors that influence the accuracy of our production estimate are sampling error and the extrapolation of laboratory data to field situations. In scheduling our sampling program we have chosen to take samples at brief intervals, rather than to devote our sampling effort to more replicates at longer intervals. This is the most appropriate schedule for computing the areas under the abundance curves of the stages—the basic quantities from which the calculations start.

Of the laboratory data extrapolated to the field, the most critical is the time needed to mature, used in calculating the physiological time scale. Smol and Heip (1974) tried several diets and cultivation techniques and determined generation times in what they found to be optimal conditions. These cultures contained sediment; detritus from the habitat and a mixture of algal species were added. This seems sufficiently close to natural conditions to yield reliable extrapolations.

Naupliar and egg production make up a considerable fraction of total production of *P. nanus*: 26% of the total for nauplii and 29% for eggs. Production of copepodites and adults accounts for 45% of the total. This high proportion of egg and naupliar production seems to occur consistently in meiobenthic copepods. For *T. discipes* in the same habitat the ratio of egg : naupliar : copepodite production was 13 : 41 : 46 (in % of the total). Feller (1982) found 20 : 35 :45 for *H. jadensis* and Fleeger and Palmer (1982) estimated that naupliar production was 39% of the total for *Microarthridion littorale* (egg production was not estimated).

The proportion of eggs that eventually develop to the adult stage is twice as high in *P. nanus* as in *T. discipes* (Table 3). Thus, although the intrinsic rate of natural increase is higher in *T. discipes,* due to the higher number of eggs and the shorter development time, the realized rate of increase is about equal in the two species (Heip 1977). In both populations about 5% of the animals survive the naupliar stage, but the mortality of the copepodites is markedly higher in *T. discipes.*

*Tachidius discipes* is also very fast-growing. Although its adult weight is more than twice that of *P. nanus* it matures in only 80% of the time needed by the latter. This fast growth allows explosive exponential development of the species in spring when benthic diatoms bloom. However, the disappearance of *T. discipes* in summer is not caused by a decline in food availability; it is correlated with increasing predation, mainly by the polyp *Protohydra leuckarti* and the fish *Pomatoschistus microps.* These predators restrict their activities to the water or the surface of the sediments and are unimportant to the deeper-living *P. nanus.*

Banse and Mosher (1980) have argued that low production rates have evolved in meiofauna because predation pressure is relatively low and a low food intake per unit time is advantageous. This is a rephrasing of the classical *r-K* selection theory, except that competition is not considered explicitly. Our data for the copepods *P. nanus* and *T. discipes* and for the ostracod *C. torosa* fit this hypothesis: *T. discipes* is probably predator-controlled; *P. nanus* suffers considerable predation on the nauplii but less on copepodites and adults; *C. torosa* is least subject to predation. An estimated 14% of hatched juveniles of *C. torosa* reach adult-

Table 3. Comparison between some life history parameters of *Tachidius discipes* and *Paronychocamptus nanus* of the Dievengat, Belgium.

| | *T. discipes* | *P. nanus* |
|---|---|---|
| Adult weight (μg dry wt) | 1.8* | 0.83 |
| Egg weight (μg dry wt) | 0.010* | 0.016 |
| Eggs per egg sac† | 41 | 19 |
| Adults/copepodites | 0.76* | 1.36 |
| Adults recruited/eggs produced | 0.019–0.015* | 0.032 |
| Egg sacs produced/adult d | 0.098* | 0.132 |
| Development time (egg–egg, d)† | | |
| 20°C | 17.9 | 22.7 |
| 15°C | 24.7 | 30.7 |
| 10°C | 39.1 | 47.1 |
| $P/(P + R)$ | 0.43 | 0.42 |

* From Herman et al. 1984.
† From Heip and Smol 1976.

hood, even though the population overwinters mainly as juveniles (Herman et al. 1983). This ostracod lives in the sediments and its calcareous shells protect it from meiofaunal predation. In the few months that it is present, *T. discipes* is the most productive of the three species; *P. nanus* is next and *C. torosa* is the least productive (annual $P:B$ is 2.7).

Differences in the productivity of these populations are not due to differences in the production efficiency. In fact, we obtained very similar values for efficiency: 0.36 for *C. torosa*, 0.43 for *T. discipes*, and 0.42 for *P. nanus*. Apparently the food intake is directly related to the productivity.

Annual $P:B$ values for meiofaunal populations are still scarce. The values available vary widely between populations. No single annual $P:B$ for meiofauna as a group can be used. However, the $P:B$ per developmental period (egg-to-egg development time) always has a value around 3. This figure was proposed by Gerlach (1971) and no conflicting results have since been published. Banse and Mosher (1980) scaled annual $P:B$ values by body weight of the adults and proposed a separate $P:B$–body weight line for the meiobenthos, with the same slope but a lower intercept than the line for the other invertebrates, including the macrobenthos. The $P:B$ of *P. nanus* is higher than the value predicted by Banse and Mosher's meiobenthos line (predicted value, annual $P:B = 12$). However, it is much lower than the annual $P:B$ of 60 predicted from extrapolation of the general line for invertebrates. Other data confirm that, although considerable scatter is left, the Banse and Mosher line for meiobenthos represents meiofaunal productivity reasonably well (Heip et al. 1982).

The evidence that meiofauna is relatively less productive than macrofauna is in accord with Warwick's (1984) hypothesis of a different evolutionary history for the two groups, but why the particular traits responsible for this lower productivity should have evolved remains unclear.

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# THE STABILITY OF A BENTHIC COPEPOD COMMUNITY



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(Figs. 1–6)

A benthic copepod community has been monitored over seven years (1970–6). The density of the different species and total density, diversity, species richness, biomass and respiration of the copepod community were analysed using Maximum Entropy Spectral Analysis. The spectrum of density shows the existence of long-term cyclicity in most species, although the annual cycle is always important. This long-term cyclicity can be explained partially by salinity changes in the habitat and partially by the intensity of decomposition processes. Diversity and species richness have long-term components as well, and these are also related to salinity changes to which the community appears to adjust with a lag of one year. The functional characteristics of the community, especially respiration, do not show significant cyclicities of longer than two years and the annual cycle is predominant.

## INTRODUCTION

The stability of ecosystems is a matter of obvious concern to man and has been the subject of much speculation and debate over the last 15 years since the first attempt towards conceptualization was made by Lewontin (1969). In this approach the stability of the system is defined as its ability to return to equilibrium after perturbation. The system is closed and described by the abundances of selected species which are affected by interspecific interactions modelled after first-order Lotka–Volterra equations and presented in a matrix. The stability properties of this matrix can then be investigated.

Views on the usefulness of such an approach have changed since the initial enthusiasm, as shown by two statements made by one of the leaders in the field, R. M. May. In 1973, May wrote: 'Within the formal framework of neighborhood stability analysis, the community matrix is held up as an entity which both epitomizes the biology of the community and also sets its stability character' but in 1984, May's opinion is different: 'It is lunacy to imagine that the dynamic behavior of real communities bears anything but the vaguest metaphorical relation to the linearized stability properties of the conventional community matrix.'

A different view on the stability of ecosystems has been phrased by Nicolis & Prigogine (1977). They show that when open systems are brought far from equilibrium they become unstable but may then evolve towards new structures with non-linear but coherent behaviour characterized by large fluctuations that can only be maintained by a large energy-flow through the system. The stability regime for such non-linear systems is a dynamic regime consisting of periodicities and cycles. The basic element of temporal organisation is the cycle: all real

thermodynamical machines capable of maintained behaviour, including all ecosystems, exhibit a dynamic stability characterized by non-linear, but cyclical, processes. Although a formal application of these ideas to ecosystems is still largely lacking, they are intuitively appealing; when ecosystems are, in fact, open systems far from equilibrium, their stability, their persistence, must be linked to cyclical processes and the identification and interpretation of the characteristic frequencies in the system becomes an essential part of their study.

The cyclicities in time series are resolved by spectral analysis (Platt & Denman, 1975). Spectral analysis is a kind of analysis of variance in which the variance is divided into contributions to frequencies that are harmonics of the length of the time series. It amounts to the fitting of sinusoidal curves with amplitudes that, when ordered, explain less and less of the total variance in the time series. A finite number of such sine and cosine functions are fitted together to the time series.

The system investigated here is a shallow brackish-water pond in northern Belgium; the community studied consists of all benthic copepods in this particular pond. These include *Canuella perplexa* T. & A. Scott, *Tachidius discipes* (Giesbrecht), *Amphiascoides debilis* (Giesbrecht), *Nitocra typica* Boeck, *Mesochra lilljeborgi* Boeck, *Paronychocamptus nanus* (Sars), and *Halicyclops magniceps* (Lilljeborg). Data on the density of all species have been collected since 1968, but only the period 1970–6 will be treated here. Furthermore, respiration and production of the dominant species were determined. Traditionally, the density of the species selected to represent the community is used in most models of stability. These models have always had a much greater impact in terrestrial ecology than in marine ecology, where much attention has been devoted to energy flow as a structuring force instead. Energy flow, respiration and even biomass are considered to be better parameters than density.

## MATERIALS AND METHODS

Samples were taken fortnightly between 1970 and 1976 with a 6·06 cm² glass corer to a depth of 5 cm from the Dievengat, a meso-polyhaline brackish water pond in northern Belgium. Elutriation follows the technique of Heip, Smol & Hautekiet, (1974). All copepods were counted according to sex and age; copepodites were grouped together, nauplii disregarded.

From the density of the individual species, diversity was calculated according to Brillouin's formula $H = (1/N) \log_2 (N!/(N_1!N_2!\ldots N_n!))$. Evenness was calculated according to Heip (1974) as $E = (e^H - 1)/(S - 1)$, in which $S$ is the number of species and $H$ has been converted to ln. This formula was used because of the low species number and is essentially a corrected version of Sheldon's (1969) index $e^H/S$, falling into the general notation proposed by Hill (1973).

The respiration of the individual species was measured by Cartesian Diver Respirometry as described by Herman & Heip (1983*a*). Production was calculated from field data for *Tachidius discipes* (Herman, Heip & Guillemijn, 1984) and *Paronychocamptus nanus* (Herman & Heip, in the Press).

In total, 184 data points of specific and total density, biomass, diversity, evenness, species richness and total respiration were analysed. The periodicities in these time series were extracted using Maximum Entropy Spectral Analysis (MESA) (Kirk, Rust & Van Winkle, 1979). In this method components with a period about equal to the length of the time series can be resolved. The method is derived by imposing the condition that the most random spectrum (with the highest entropy) must be found that is consistent with the autocorrelation of the time series.

## RESULTS

### *Population parameters*

Fig. 1 shows the densities of the six most important copepod species over the seven years studied. The corresponding (integrated) spectra are shown in Fig. 2. The densities and spectra of the three dominant species *Tachidius discipes*,

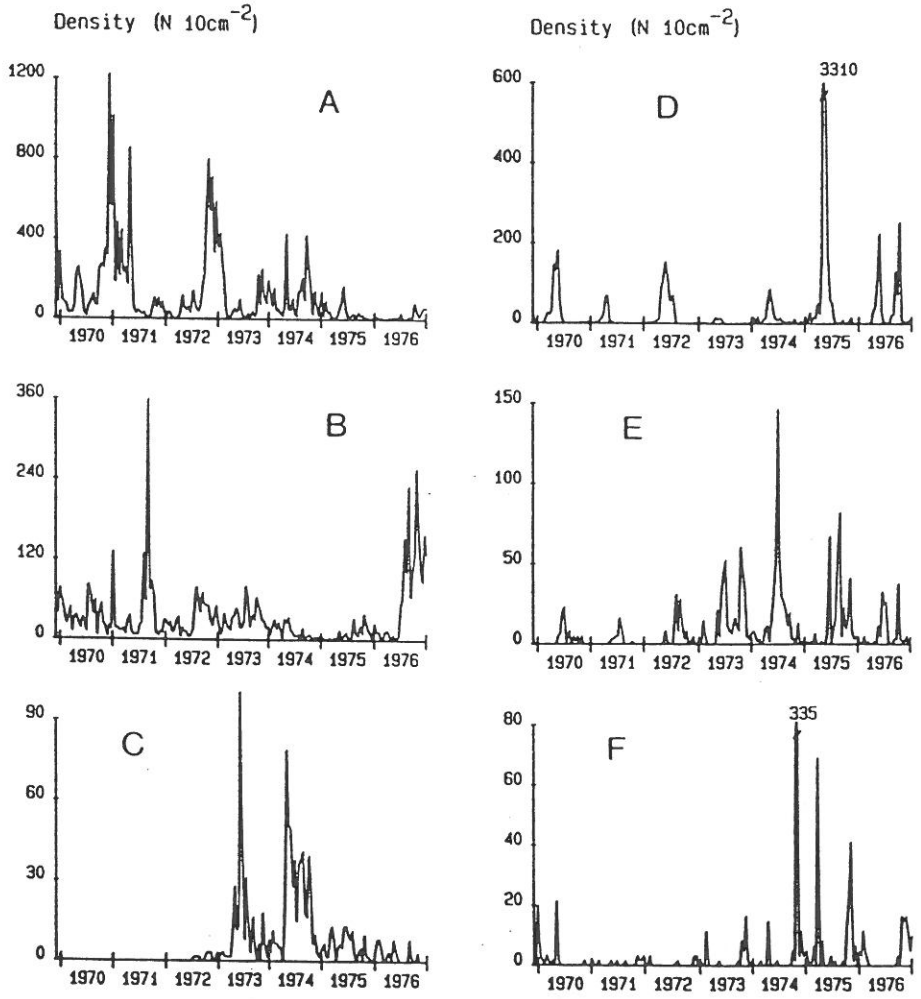


Fig. 1. Density (numbers 10 cm$^{-2}$) of six benthic copepod populations over the period 1970–6. (A) *Paronychocamptus nanus*. (B) *Canuella perplexa*. (C) *Amphiascoides debilis*. (D) *Tachidius discipes*. (E) *Halicyclops magniceps*. (F) *Nitocra typica*.

*Canuella perplexa* and *Paronychocamptus nanus* were discussed in a previous paper (Herman & Heip, 1983*b*). In that paper we pointed out that the abundance of the herbivore *Tachidius discipes* is determined by seasonal (yearly) factors. As shown in Fig. 3, for temperature, important yearly driving forces exist in this shallow habitat. The spectrum of temperature (Fig. 4) is entirely dominated

by a peak at a frequency of 1 cycle per year. Chlorinity (Fig. 3, spectrum Fig. 4) also varies seasonally, due to changes in the evaporation-precipitation balance. In winter, chlorinity is generally lower than in summer. However, longer periodicities are also important in the spectrum.

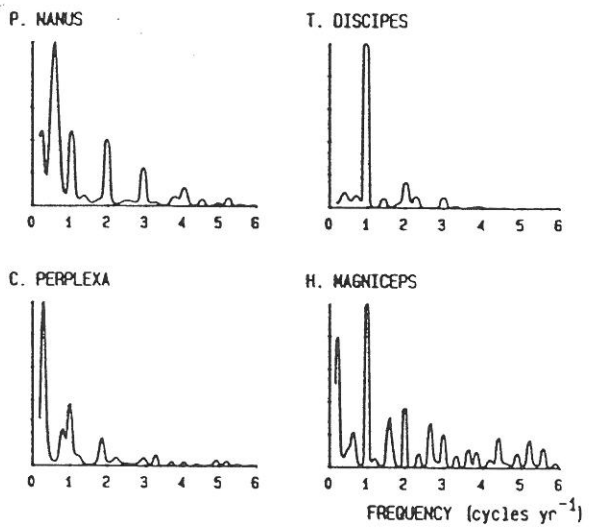


Fig. 2. MESA-integrated spectra of the ln-transformed, detrended density data of the four dominant benthic copepods: *Paronychocamptus nanus*, *Canuella perplexa*, *Tachidius discipes* and *Halicyclops magniceps*. The abscissa is frequency in cycles year$^{-1}$, the ordinate is dimensionless.

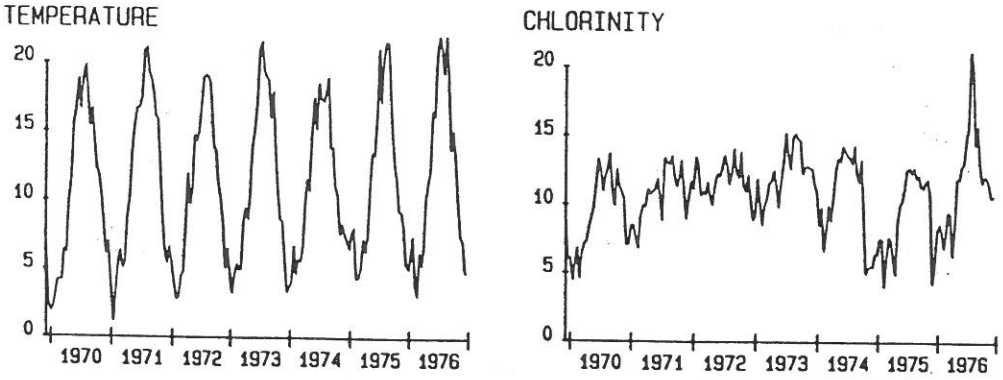


Fig. 3. Temperature (°C) and chlorinity (‰) of the brackish water habitat.

With regard to the large detritivore *Canuella perplexa*, we argued that this species can be treated as a single species problem, and that its density follows a fluctuating environmental parameter. The highest peak in this spectrum is found for a period of 3·8 years; when fitted to the data, this cycle is perfectly in phase with a cycle of the same period in $NH_4^+$-concentration, a possible indicator of decomposition processes in the environment. Our argument that this population shows density-dependent rates of increase is based on incorrect evidence; as pointed out to us by R. H. Green (personal communication) a correlation

between ln $(N_{t+1}/N_t)$ and ln $N_t$ is to be expected even when $N_{t+1}$ and $N_t$ are uncorrelated.

*Paronychocamptus nanus* is the numerically-dominant species. Its spectrum (Fig. 2) is relatively complex with three peaks in the range 1–2 years and a peak at period 4·6 years. We interpreted the periodicities of 1·4 and 2 years as the result

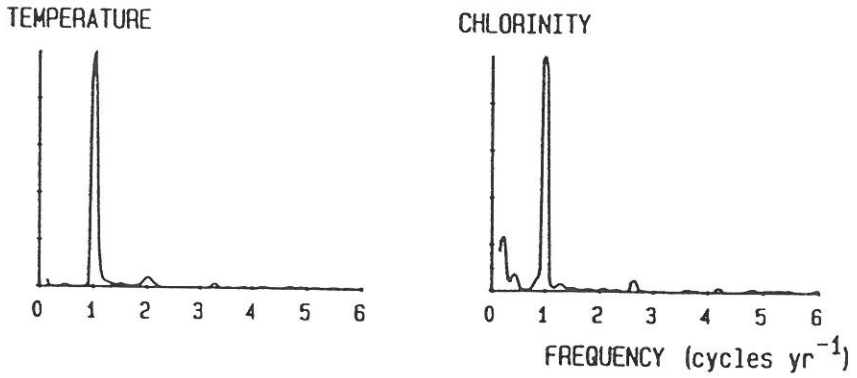


Fig. 4. MESA-integrated spectra of the temperature and chlorinity time series.

of 'competitive coupling' between this short-lived and other species. The 4·6-year period was vaguely interpreted as the tracking of an external oscillating parameter.

This same 4·6-year peak is found in the spectrum of *Halicyclops magniceps* (Fig. 2), where it is the most important peak after the yearly cycle. *H. magniceps* is a herbivore with a regular pattern of appearance in the community, always lagging behind *Tachidius discipes* to which it is similar in general habitus, feeding and microdistribution. The 4·6-year peak in *H. magniceps* is perfectly in phase with the same cycle in *P. nanus*, indicating a common cause for these fluctuations in both species.

There are three other, more erratic, species in the community. Due to the large number of zero densities in their time series, they could not be analysed successfully by spectral analysis. *Mesochra lilljeborgi* (densities not shown here) is never very abundant and occurs at irregular intervals. Only in early 1970 and late 1975 were more than two individuals per sample found. *Amphiascoides debilis* is a detritivore which is ecologically similar to *Paronychocamptus nanus*. It has a more coherent abundance pattern than *M. lilljeborgi* (Fig. 1 C). The species had already been found in 1968–9 but was completely absent from the community in 1970 and 1971. In 1972 a few individuals apparently immigrated and the population increased through 1973 to attain a maximum density in 1974. But subsequently the population gradually died out again. The same pattern, though less clear, is found for *Nitocra typica* (Fig. 1 F), an opportunistic species that dominates cultures, or left-over samples, after a few weeks in the laboratory.

*Community parameters*

The diversity $H$ of this community shows an increasing linear trend during the seven years of study (Fig. 5A). Its spectrum (Fig. 6) has peaks at periods of 1 year, the seasonal component, of 2 years and again of 4·6 years. The number

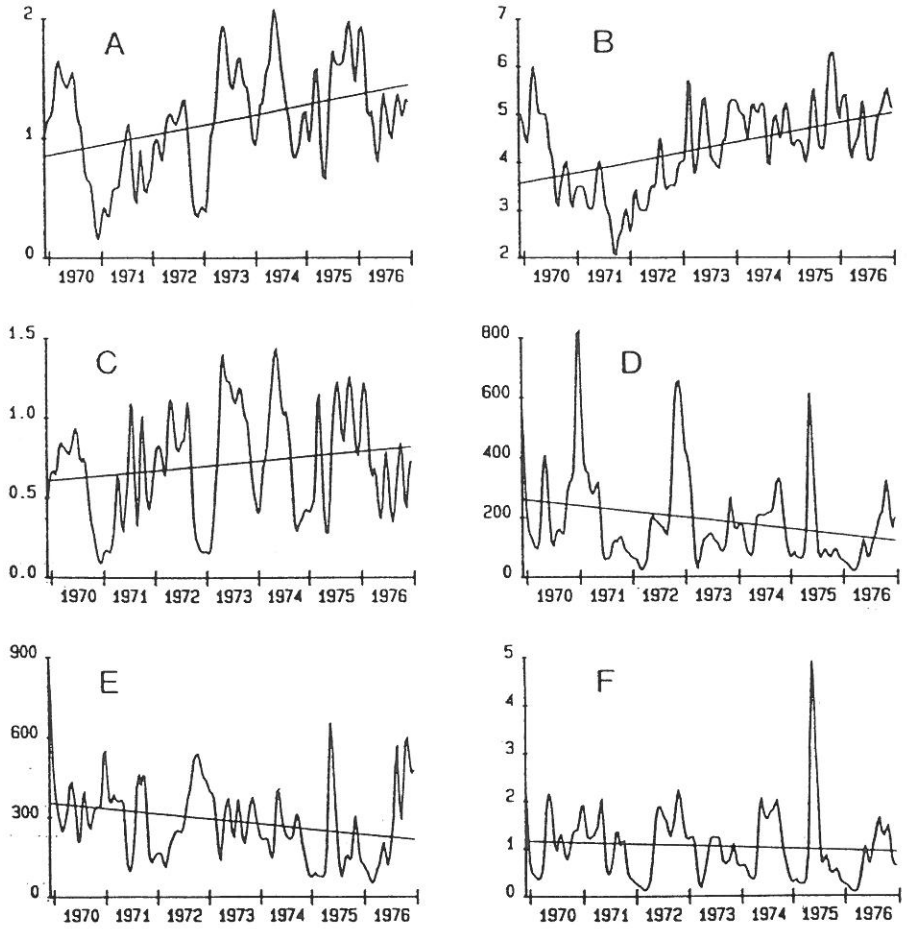


Fig. 5. 'Community parameters' of a benthic copepod taxocene: The curves are weighted running means with length 3 and weights 0·23, 0·54, 0·23. (A) Brillouin diversity. (B) Number of species. (C) Evenness. (D) Density (numbers 10 $cm^{-2}$). (E) Biomass ($\mu$g dwt 10 $cm^{-2}$). (F) Respiration ($\mu l$ $O_2$ 10 $cm^{-2}$ $h^{-1}$).

of species accounts for most of the linear trend in diversity (Fig. 5B); its spectrum also shows the 4·6-year period (Fig. 6), which is in phase with the same cycle in *P. nanus* and *H. magniceps*. Evenness has an only marginally-significant linear positive trend (Fig. 5C) and its spectrum is dominated by peaks at 1 and 2 years (Fig. 6). A very long period fluctuation (5·7 years) is also present in its spectrum.

The total density of the copepods over the seven years is shown in Fig. 5D. It has a slightly negative trend which is marginally significant ($0{\cdot}05 > P > 0{\cdot}025$).

Its spectrum has peaks on periods of 1–2 years (Fig. 6) but not in the longer period range. Total density thus shows less variation in the longer time scales than the densities of the single species.

Total copepod biomass also shows a negative trend (Fig. 5E). In its spectrum (Fig. 6) we find the same 3·8 year periodicity that dominated the spectrum of the largest species *C. perplexa* (not surprisingly, as this species is 5–10 times heavier than the others).

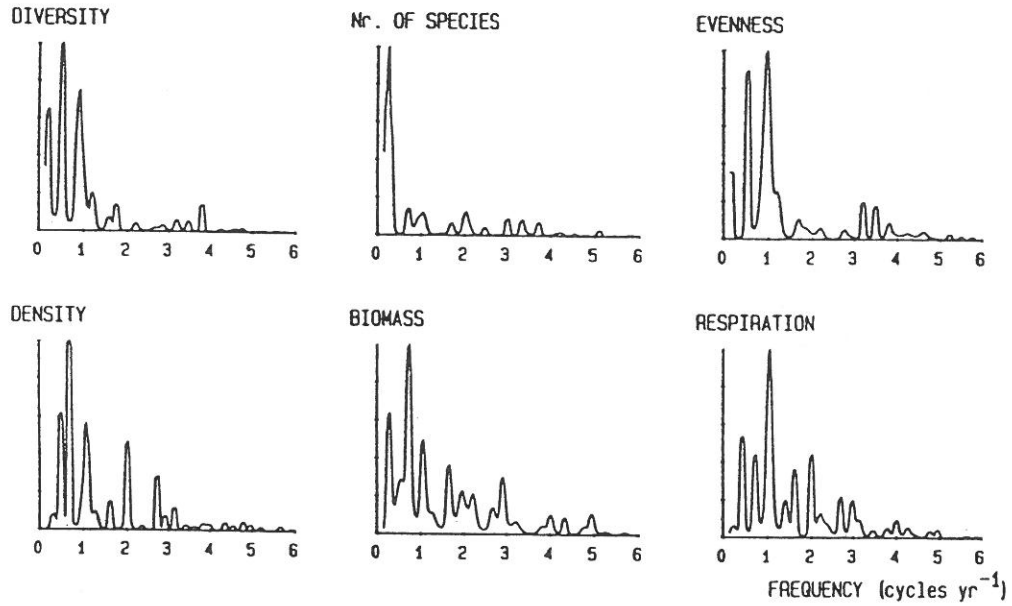


Fig. 6. MESA-integrated spectra of the (detrended) community parameters shown in Fig. 5.

Total community respiration, as calculated from the density data, is shown in Fig. 5F. There is no linear trend in respiration, despite the trends found in density, biomass and diversity. A positive trend is found in respiration per unit biomass, probably due to a shift in species composition from species with lower metabolic rates to species with higher, since no trend in mean weight was found. The spectrum of respiration (Fig. 6) has no peaks at periods longer than two years; as is the case for density, respiration appears to be relatively invariant on longer time scales.

## DISCUSSION

Cycles in population densities or community parameters may be driven by external, abiotic oscillators, or by biotic interactions, or by both. An obvious, important external oscillator in this habitat is the yearly cycle of light. The large amplitude of temperature fluctuations (Fig. 3) clearly exemplifies this point. It is not surprising therefore to find peaks at a one-year period in most of the spectra constructed from our time series data.

It is more difficult to find longer period cycles in these short-lived species

Generation times range from a few weeks for the smaller species, to half a year for the large *Canuella perplexa*, much shorter than the observed long-term periodicities in their spectra. For *C. perplexa*, the coupling of the 3·8-year period to the period in $NH_4^+$ seems relatively straightforward. Why a 3·8-year periodicity in the intensity of decomposition processes should exist is unclear, but the error on these estimates is unknown and 3·8 is close to 4.

Another intriguing question is posed by the 4·6-year periods observed in the spectra of *P. nanus* and *H. magniceps* and in diversity and the number of species. All these cycles are in phase, with a maximum occurring in early 1974. The same periodicity is found in chlorinity, but this cycle runs almost exactly one year before the cycles in the biological data.

The importance of salinity in determining species richness in brackish water has been known for many decades (Remane, 1934); at the meso-polyhaline boundary especially a slight increase of salinity may permit the existence of more species. Our data show that the coupling may be intense and that it operates with a lag. This lag can be understood by examining the appearance of *Amphiascoides debilis* in the community. It takes about one year between the appearance of the first specimen in our samples and the first population peak of the species. Maximum density is not achieved until one year later. It seems reasonable to postulate that immigration and establishment of a population are responsible for the time lag between abiotic and biotic time series.

Many spectra show important peaks at about 1·5–2 years. This is also the time scale of most of the variation in evenness. Evenness reflects the partitioning of resources among species, whereas number of species reflects the viability of the environment for all potentially present species. In an environment which constantly changes the partitioning of resources is not an immediate process, since there is a constant imbalance in the community structure as species try to adjust to the changing environment. This introduces instability at a time scale of one to two years, and an equilibrium does not exist; in the sense of returning to an equilibrium point, this community is never stable.

Although the community structure is changing over long time scales, the functional aspects of the community remain stable. The density and biomass of the copepods still show long-term linear trends and there is a long-term cycle in biomass, but these long-term fluctuations are less pronounced than those found in diversity for example. The most striking, however, is the relative constancy of community respiration. In this series there is neither a trend nor a longer period cycle. Apparently, a relatively constant set of resources is used by the copepods in this habitat year after year, independent of the composition of this community. Elmgren (1984) concluded that, within a scale factor, general energy flow models in different marine systems are very comparable as long as no entire trophic group is absent. These observations may provide a justification for the use of black-box models in energy-flow studies as well.

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# 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 $\mu$g wet weight):$\log T_{min} = 2.202 - 0.0461\ t + 0.627 \log W$. When multiplied by the constant biomass turnover per generation $(P/B)_{gen} = 3$, 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 *Pellioditis 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 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 |
|---|---|
| *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 |

$$\log T_{min} = 2.202 - 0.0461\ t + 0.627 \log W \quad (1)$$
$$(R^2 = 0.88;\ F(2,46) = 173;\ n = 49)$$

As an example eq. (1) was used to determine the annual production of a subtidal community from a muddy sediment (median grain size 45 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, 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 by experimental nematologists. Nematode-communities in the field, especially of subtital 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 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.

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# THE PRODUCTIVITY OF MARINE NEMATODES

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## 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 *Monhystera 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 $C \cdot m^{-2}$. Coastal sedimentary systems receive a carbon input in the order of 50-150 g $C \cdot m^{-2} \cdot an^{-1}$, 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 $P/B = 9 \cdot an^{-1}$, 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.

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## 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 *Paracanthonchus 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 reproductivity $R_0$ (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 *Paracanthonchus 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: Dievengat population.

| Species | Salinity ‰S | Temp. °C | $T_{min} \pm SD$ | n |
|---|---|---|---|---|
| *Diplolaimella dievengatensis* | 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 |
| *Monhystrella parelegantula* | 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 |
| *Monhystera parva* | 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 |
| *Monhystera disjuncta* | 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 |
| *Chromadora nudicapitata* (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 |
| *Chromadora nudicapitata* (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 |
| *Paracanthonchus caecus* | 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 (°C). $r^2$ is the coefficient of determination. $T_m$ and $T_0$ are the optimum and basal temperature (°C). $D(t)$ is the number of juvenile periods realized in the field. SD: Sluice Dock population; D: Dievengat population.

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

$$T(t) = 11.2 + 8.3\sin(t - 117)$$ Dievengat (Heip & Smol 1976a)
$$T(t) = 11.5 + 8{,}5\sin(t - 120)$$ 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 (SD = 1.2; n = 956). The females become gravid 17.2 days (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 (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 μg 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%

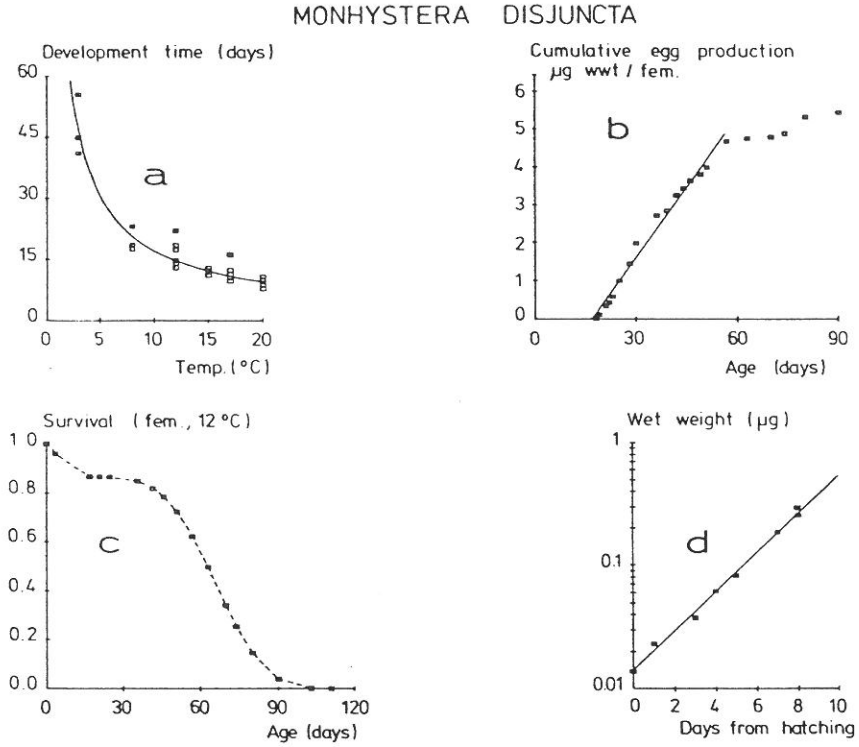


*Fig. 1. Monhystera disjuncta*: life cycle at 30‰S; a: relationship between female development time ($T_{min}$) and temperature (°C); b: cumulative egg production (µg wet weight) per female at 12°C; c: survival of females at 12°C, time zero: moment of egg deposition; d: juvenile somatic growth at 17°C.

(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 reproductivity 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 reproductivity; $r_m$: 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 |
|---|---|---|---|---|---|---|---|---|
| *Diplolaimella dievengatensis* | 20 | 20 | 65 | 0.238 | 0.257 | 2.6 | 12 | this study |
| *Monhystrella parelegantula* | 30 | 30 | 37 | 0.307 | 0.347 | 2.2 | 5 | this study |
| *Monhystera disjuncta* | 30 | 12 | 123 | 0.171 | 0.181 | 3.1 | 14 | this study |
| *Monhystera parva* | 30 | 12 | 76 | 0.156 | 0.156 | 3.1 | 1.5 | this study |
| *Chromadora nudicapitata* | 30 | 12 | 246 | 0.135 | 0.135 | 3.3 | 1 | this study |
| *Pellioditis marina* | 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 joule·joule$^{-1}$·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 reproductivity $R_0$ and birth rate of five other nematode species. These values are given in Table 3. Net reproductivity 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 ($J \cdot J^{-1} \cdot day^{-1}$) | Annual P/B |
|---|---|---|---|---|
| *Diplolaimella dievengatensis* | 16.0 | 196 | 0.135 | 26 |
| *Monhystrella parelegantula* | 16.0 | 200 | 0.108 | 22 |
| *Monhystera disjuncta* | 11.5 | 365 | 0.173 | 63 |
| *Chromadora nudicapitata* | 11.5 | 365 | 0.129 | 47 |
| *Monhystera parva* | 14.0 | 270 | 0.194 | 52 |
| *Oncholaimus oxyuris** | 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*. *Pellioditis 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 *Pellioditis 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 *Paracanthonchus 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 $2 \times 10^8$ cells $\cdot$ ml$^{-1}$ the development time of this species is ten days, at $5 \times 10^{10}$ 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 $8 \times 10^9$ 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 Dieven-gat (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 *Anticoma limalis*, observed in Kiel by Schütz (1966), assuming its life cycle is similar to that of *Anticoma 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.

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PAPER

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# The Production of Meiofauna.



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## Introduction.

The productivity of aquatic populations has received much attention since the International Biological Programme during which several books appeared that much influenced later developments. Among the standard works in the field one needs to mention Edmondson & Winberg (1971), Holme & McIntyre (1971, 1984), Winberg (1971), Zaika (1973). One of the important consequences was the standardization of concepts and symbols and the acquisition of a large body of data which had its theoretical roots in the paradigm of trophic organisation of ecosystems developed by Lindeman (1942).

In steady state conditions the energy budget of an organism may be described by the well known equation:

$$C = P + R + F + U$$

where C is food intake or consumption, P is production of biomass, R is respiration, F is egested faeces and U is excretion. Production is the sum of somatic growth and reproductive output $P = P_g + P_r$. Absoption (Ab) is the portion of the consumption not egested as faeces $Ab = C - F = P + R + U$. Assimilation (A) is the portion of consumed energy used for production and respiration $A = P + R$.

In this equation all variables have to be expressed in the same units, e.g. $kJ.m^{-2}.an^{-1}$. One has to be aware that even then the ecological meaning of each term is quite different: growth and reproduction yield high energy particulate organic matter, respiration has as its end product $CO_2$, a gaz, faeces is low-energy particulate matter and many excretion products are soluble and may be organic or inorganic. In order to evaluate their pathways in the ecosystem the redox-potential of these end-products may be a useful parameter.

## 2. Production

Production measures the part of the energy consumed by a population that is transformed into organic matter (body tissues and reproductive products) potentially available for consumption by populations from a higher trophic level. Gross and net growth efficiencies of animals ($K_1$ and $K_2$) and production efficiency P/A = P/(P+R) of populations may be relatively predictable, and are therefore worth studying.

## 2.1. Somatic growth.

Production by somatic growth is the sum of the growth increments of all individuals in the population during a certain time, including the growth of the individuals that died during the interval. The methods used to measure production depend on the life history of the population. These methods can be reduced to two types: summation of eliminated biomass or summation of growth increments. According to the method used one needs good data either about growth, reproduction and recruitment or about mortality and changes in biomass.

The equivalence between both approaches has been demonstrated by Crisp (1971). In the first case growth processes can be ignored if the biomass eliminated during the time period $\Delta t$ considered can be accounted for:

$$P = B_1 - B_0 + M$$

where M is the eliminated biomass during $\Delta t$.

When the finite mortality rate $\Delta N/\Delta t$ of individuals from weight class i (mean weight $\bar{w}_i$) is $Z_i$ then the expected mortality during $\Delta t$ is $Z_i \Delta t$ and the expected loss of biomass is $Z_i w_i \Delta t$. Thus :

$$M = \Sigma_i Z_i \bar{w}_i \Delta t$$

and

$$P = \Delta B + \Sigma_i Z_i \bar{w}_i \Delta t \qquad (1)$$

In the second case production is measured as the sum of the growth increments of all individuals in the population during $\Delta t$:

$$P = \Sigma_i N_i G_i w_i \Delta t \qquad (2)$$

where $G_i$ is the instantaneous weight specific growth rate

$$G_i = \frac{1}{w_i} \frac{dw_i}{dt}$$

and $N_i$ is the mean number of individuals alive in weight class i during the interval.

In both equations (1) and (2) growth and mortality have to be known as a function of individual weight. Using (1) one needs to know weight-specific mortality, using (2) one needs to know weight-specific growth.

## Cohort populations.

If cohorts (same-aged individuals) are recognizable as a result of semi-simultaneous reproduction, production measurement is relatively easy if emigration an immigration can be accounted for. The methods require accurate estimates of abundance and weight over time. Four basic and equivalent methods exist (Waters & Crawford, 1973 ; Heip et al., 1982a) :

- increment-summation : production during a time interval is the product of the average abundance on two successive dates and the change in average weight of an individual :

$$P = \Sigma_i \ \overline{N}_i \ (\Delta w)_i$$

- removal-summation : production during a time interval is calculated as the change in abundance multiplied by the average individual weigth during the interval :

$$P = B_2 - B_1 + \Sigma_i \ (-\Delta N)_i \ \overline{w}_i$$

- instantaneous growth : the average biomass in a sampling interval is multiplied by the instantaneous weight-specific growth rate (assumed constant during the interval) :

$$P = \Sigma_i \ G_i \ \overline{B}_i$$

- Allen curve : mean weight is plotted against abundance (survivorship) and production is the surface under the curve.

## Non-cohort populations.

When cohorts are not identifiable, as is the case for most meiofauna populations, due to overlapping generations or continuous reproduction, methods to calculate production require data on incremental increases in weight of individuals from the time they are born until they die. Most methods are based on knowledge of the finite growth rate of an individual over its life. Growth increment methods use experimental growth curves or estimations of stage durations, elimination methods include the size-frequency method and population dynamical models.

The size frequency method was originally designed for estimation of the correct order of magnitude of production by Hynes (1961) and subsequently

refined (Hynes & Coleman, 1968; Benke, 1979). Thereby the method was restricted to the analysis of species groups with similar generation times, size and trophic position. The population is divided into size classes of similar duration. It was adapted to, and used for, populations divided in developmental stages by Herman et al. (1983, 1984a) and Herman & Heip (1985).

Estimations of the duration of life stages in the population can be obtained from laboratory experiments or from population models fitted to the field data. Laboratory experiments offer the possibility to establish complete life and fertility tables (e.g. Vranken & Heip, 1983). However, they pose the problem of extrapolating the results to the field.

Fitting models to field data (e.g. the methods of estimating birth and death rates or stage-frequency methods) requires additional data or assumptions on the population. Stage-frequency methods are extensively reviewed by Southwood (1978). Threlkeld (1979) gives an example of estimating birth and death rates by using extra information on the age distribution of Daphnia embryos. Herman et al. (1983) estimate the duration of developmental stages in the ostracod Cyprideis torosa by counting empty shells in the sediment : the distribution of the empty shells over the stages gives information about the mortality in the different stages.

## 2.2 Reproductive output.

Reproductive output may make up a considerable part of the total production of a population. In three populations of meiobenthic copepods it was estimated as between 13 and 29 % of the total production (Feller, 1982, Herman & Heip, 1985).

Values for nematodes in lab cultures range from 10 % (Warwick, 1981) to over 90 % (Schiemer, 1983). These values strongly depend on the culturing conditions (Vranken & Heip 1983, 1986; Vranken et al. in press).

Apart from the experimental conditions, the age structure of the population is important in determining the relative importance of reproductive output. If the population is in stable age distribution at exponential growth, it will mainly be composed of fast-growing juveniles. However, if juvenile mortality is important the population age structure will be different and the relative importance of egg production may well increase. This is most probably the case in the above-mentioned copepod populations, where naupliar mortality rates are much larger than copepodite and adult mortality rates (this does not prevent that naupliar production was quite important : naupliar and egg production together accounted for 54-55 % of the total production in all three studies mentioned).

**Meiofauna production.**

In practice it is often impossible to use any of the described methods for meiofaunal populations. Direct production estimates of field populations only exist for a few species : four harpacticoid species (Feller, 1982; Fleeger & Palmer, 1982; Herman et al. 1984a; Herman & Heip, 1985), and an ostracod species (Herman et al., 1983).

Laboratory experiments pose their own problems. Many species of nematodes and copepods have now been cultured (see reviews by Heip et al., 1985 and Hicks & Coull, 1982). Two trends seem clear. In setting up experiments, one almost automatically selects the more "weedy" species. It is no wonder that so many data are available on the genera Monhystera (for nematodes) or Tisbe (copepods). Second, the more one knows about a species, the clearer become the effects of the culture conditions. As an example, Vranken et al. (in press) show that for Monhystera disjuncta, cultured with different bacterial strains as food and with different densities of one strain, the minimum generation time can differ with a factor 1.4, whereas the egg production rate differs with a factor 3.5.

In view of the gross uncertainties introduced using laboratory experiments, indirect approaches have been advocated. The following are to be mentioned :

- **Measurement of respiration.** When a proportionality between production and respiration of a population is assumed, respiration measurements may be used to estimate production, though respiration measurements also are technically difficult for meiofauna. Humphreys (1979) showed a significant log-log relationship between population production and population respiration whith a slope equal to one, which implies that $P/(P+R)$ is independent of size. This study covered populations from widely different ecological and taxonomical groups, but no meiofauna. Herman et al. (1984b) were able to compare respiration and field production of three meiofaunal populations (one ostracod and two harpacticoid copepods) and found indeed a constant value $P/(P+R) \approx 0.4$.

For nematodes, Schiemer et al. (1980), Tietjen (1980), Warwick (1981) and Schiemer (1982a,b) found much higher values, in the order of 60-90 %. Herman et al. (1984b) discuss some of the factors possibly responsible for such a large difference. However, Herman & Vranken (submitted) also found very high production efficiencies (> 60 %) for a cultured population of Monhystera disjuncta, even when factors such as the "negative production" (due to weight loss) in the egg stage is taken into account. High production efficiencies seem to be a consistent feature of nematode populations.

Are nematodes so much more efficient than e.g. copepods, converting up to 90 % of their energy intake into production ? At the moment, this cannot be excluded, although it seems improbable. An interesting alternative hypothesis is that respiration measurements underestimate the energy losses. Microelectrode measurements show that in many sediments no free oxygen is present from a depth of a few mm onwards (see e.g. Revsbech et al., 1980). In these sediments one can easily find nematodes down to a depth of...10 cm. This is also true in sediments without animal burrows, which have been advocated to be a major source of oxygen to the meiofauna (Reise & Ax, 1979). It is almost inevitable to conclude that most nematodes live (at least partially) anaerobically. It is possible that

even in the presence of oxygen, where they do have a measurable respiration, they do not use fully aerobic metabolic pathways. This is a field of research which surely provides the scope for interesting studies. In the meantime, the estimation of production based on respiration becomes quite questionable. At least it seems safest to assume a very high "apparent production efficiency" for nematodes.

When the problem of production efficiencies could be solved, the estimation of production from respiration has some practical advantages. Warwick & Price (1979) showed that, after correction for temperature, the community respiration of nematodes nearly equalled 6 l $O_2$ $g^{-1}$ wwt $an^{-1}$ in several habitats, where individual nematode weight differed by an order of magnitude.

- **P/B ratios and body weight:** Gerlach (1971) provided the first estimate of annual P/B = 9 for meiofauna in general. The figure has two components, a life cycle turnover of three and three generations annually. The justification for the first assumption lies in a model study by Waters (1969) who showed that for a wide variety of growth and mortality models, the lifetime P/B does not vary greatly around a modal value of 3.5. Herman et al. (1984b) showed that for nematodes under certain conditions (neonate weight is production, juvenile growth is exponential, adult growth is not too important and the generation time is defined as the development time of juveniles) a P/B = 3 per generation (juvenile period) may be expected.

Scaling of annual P/B to body size has been proposed by Banse & Mosher (1980), who showed a log-log relationship between the two variables. It was applied to meiofauna by Heip et al. (1982a) and to nematodes by Vranken & Heip (1986). Both compilations of meiofauna data show that the weight dependence coefficient in meiofauna is similar to the general value found by Banse & Mosher (1980). However, the intercept values are much lower, in the order of 1/10 the intercept values of the macrofauna. This feature was anticipated by Banse & Mosher (1980), and discussed by Heip et al. (1982a) and Vranken & Heip (1986). However, no conclusive arguments have been found to explain it.

- **The number of generations** : since the P/B per generation (juvenile developmental period) is around three a fairly accurate indirect estimation of production may be obtained by multiplying the number of generations produced annually by this figure. The reviews of Heip et al. (1982b, 1985) and Hicks & Coull (1982) give data on the annual number of generations in nematodes and copepods respectively. For both these groups it is clear that a uniform value for the number of generations produced annually does not exist and that each population has to be studied in its own right.

For nematodes the existing data from lab cultures have been reviewed by Vranken et al. (1986) who proposed the following equation relating the egg to egg development time $T_{min}$ to temperature and adult female weight W :

$$\log T_{min} = 2.202 - 0.0461\ t + 0.627 \log W$$

When multiplied by the constant biomass turnover per generation $(P/B)_g$ = 3, development rate $1/T_{min}$ can be used as a predictor of daily P/B.
This estimate is as representative for the nematode community as the cultured species are. The danger thus exists that the estimate, based on

"weed" species, gives an overestimate of the real production. However, some comforting evidence regarding its usefulness was presented by Vranken et al. (1986).

**Production and Biomass of meiofauna in the North Sea.**

Energy flow models for the North Sea use meiobenthic biomass to evaluate the trophic role of the meiofauna. Usually, the biomass (around 1-2 g dwt $m^{-2}$ for subtidal sediments) is multiplied by a constant factor (often 8-10) to obtain a production of 8-20 g dwt $m^{-2}$ $an^{-1}$ and energy consumption, which is perhaps around five times this value, i.e. 40-100 g dwt $m^{-2}$ $an^{-1}$, or 16-60 g C $m^{-2}$ $an^{-1}$. Gross uncertainties are present in such extrapolations and the use of a single P/B ratio has been strongly discouraged by Vranken & Heip (1986).

The reasonably constant production efficiency P/A $\approx$ 0.4 found in "aerobic" meiofauna poplations may be used to obtain estimates of production from respiration measurements. In order to evaluate the energy consumption of a population one may try to obtain similar constants for P/C. Very few data exist on which such extrapolations might be based. Heip et al. (1985) summarize the data for nematodes. Consumption of bacteria and algae by three species of nematodes varied between 14 and $60.10^{-2}$ µg C $d^{-1}$. Admiraal et al. (1983) estimated that a nematode eats about double its own carbon content each day. A community with a standing stock of 0.3 g C $m^{-2}$ would then consume about 220 g C $m^{-2}$ $an^{-1}$. However, it is unreasonable to extrapolate the (spring) rates from a highly productive intertidal community to subtidal communities without <u>in situ</u> primary production.

The evaluation of nematode production given by Heip et al. (1982a) and Heip et al. (1984) for areas in the Southern Bight have been revised by Heip et al. (1985). Two constrasting situations were compared. On a linear sandbank with little organic input nematode biomass was 0.07 g C $m^{-2}$. Nematode respiration was calculated as 1.06 g C $m^{-2}$ $an^{-1}$. If production efficiency is 40 %, nematode production then would be 0.71 g C $m^{-2}$ $an^{-1}$ and with an assimilation efficiency of 20 %, consumption would amount to 8.8 g C $m^{-2}$ $an^{-1}$. However, with a production efficiency of 70 %, total consumption would be 17.7 g C $m^{-2}$ $an^{-1}$. In the first case P/B per year would be 10.1, in the second case it would be 35.3.

Use of the P/B - body weight relation necessitates the knowledge of the distribution of adult sizes of the species in the community. A gross estimate, taking an average female size of 0.4 µg dwt (average individual size is 0.26 µg dwt), results in a yearly P/B of 16.6, using the equation given by Vranken & Heip (1986). This is in between the two previous estimates. It is near to the annual P/B of 20 estimated by Vranken et al. (1986) for an impoverished sublittoral nematode community in the North Sea.

It is at least as difficult to estimate the production of the harpacticoid copepods in the North Sea. A very rough guess could proceed as follows. We assume an average biomass of 20 µg dwt / 10 $cm^2$: this is based on the observation that when density is high, individual weight is

low, thus compensating for the higher numbers. We further assume an average respiration rate of 3 nl $O_2$ $h^{-1}$ ($\mu$g dwt)$^{-1}$. This is in the lower end of the range described by Herman & Heip (1983), and in the same order as found by Gee & Warwick (1984) for interstitial species. Respiration would then amount to 0.21 gC $m^{-2}$ $an^{-1}$. With a production efficiency of 0.4, production is 0.14 gC $m^{-2}$ $an^{-1}$. With an assimilation efficiency of 20 %, total consumption would thus amount to 1.75 gC $m^{-2}$ $an^{-1}$. Annual P/B would equal around 14.

It should be stressed that these estimates are not much more than guesses. They show that consumption by meiofauna is in the order of 10 gC $m^{-2}$ $an^{-1}$. Nematodes are almost an order of magnitude more important than harpacticoids.

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# Studies of the life-history and energetics of marine and brackish-water nematodes

## I. Demography of *Monhystera disjuncta* at different temperature and feeding conditions

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**Summary.** Aspects of the demography of *Monhystera disjuncta* were investigated at different temperatures (in agnotobiotic cultures) and in different feeding conditions (monoxenic cultures with different bacterial strains, and different densities in the feeding suspension with one strain). Embryonic development time, minimum generation time, egg deposition rate and adult longevity depend on temperature, quality and quantity of food offered. Body mass at maturity is an allometric function of food density. It is shown that a previously inferred selectivity in food uptake is an artifact of culture conditions. pH buffering and addition of sterols permit culture of the species on a wide variety of bacterial strains. *M. disjuncta* is less well adapted to take advantage of high food density than are nematodes from polysaprobic environments. The animals channel surplus energy intake into a larger body mass, without being able to increase their rate of population growth accordingly.

**Key words:** Nematodes – Demography – Feeding – Meiobenthos – Culture

Nematodes constitute an important fraction of the meiofauna in marine sediments. Yet, they have not always received the attention they deserve. In particular, their role in energy transfer in the sediment ecosystem and their importance as food for higher trophic levels remains unestablished (Heip et al. 1985).

Experimental studies point to an important contribution of nematodes in stimulating the breakdown of detritus (Abrams and Mitchell 1980; Findlay and Tenore 1982; Tietjen 1980). However, more recent observations seem to question this aspect too, at least for conditions of high detritus stocks (Alongi 1985a, b).

For the study of nematode productivity, we are entirely dependent on laboratory experiments. Production of field populations is extremely difficult to measure, as almost all populations have continuous reproduction. In previous publications (Heip et al. 1985; Herman et al. 1984; Vranken et al. 1986; Vranken and Heip 1986) we approached the problem of nematode productivity in several indirect ways. These approaches were based on data obtained from agnotobiotic nematode cultures (i.e. cultures in which the composition of the food is not controlled). Although food was believed to be offered in excess, no explicit study was made about the importance of its quality or quantity.

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In this paper we shall discuss the demography of *Monhystera disjuncta*, cultured at different temperatures and in different feeding conditions. Demographic data from agnotobiotic cultures at 12° C were already given by Vranken and Heip (1986). They will be completed by data obtained at 3° C and 17° C. For the purpose of bio-assay studies a monoxenic culture method of this species was developed using *Alteromonas haloplanktis* (strain "ISC2") as a food source. This change in culture conditions was reflected in the demographic parameters (Vranken et al. 1984).

Density of the bacterial food is known to be a major determinant for the life cycle of bacterivorous nematodes. Schiemer (1982a, b, 1983), Schiemer et al. (1980) and Klekowski et al. (1979) studied the demography and energetics of *Plectus palustris* and *Caenorhabditis briggsae* at different food concentrations. They showed that the life history of both species is quite flexible. This flexibility itself is an adaptive trait, which differs between the two species. *C. briggsae*, which is limited (in nature) to very high bacterial densities, only grows optimally at the highest bacterial densities that were experimentally feasible. Its growth ceases at around $10^8$ bacteria $ml^{-1}$, which is still a relatively high density.

*P. palustris*, on the other hand, survives at a bacterial density one order of magnitude lower. Its optimal food density is also lower. This corresponds to its occurrence, in nature, in less saprobic (although still quite enriched) environments.

Food quality is important, as nematodes appear to be selective in the food species they take up (e.g. Trotter and Webster 1984). *Monhystera disjuncta* did not grow on many potential food species occurring in its natural environment (Vranken et al. 1984). The reasons for this apparent selectivity were not clear. It is possible that some bacteria are indigestible by the limited array of enzymes synthesized by nematodes (Deutsch 1978). Alternatively, these bacteria may condition the agar medium adversely, or, finally, they may miss an essential growth factor for the nematodes. These last possibilities were tested by buffering the pH of the agar, and adding a sterol mixture to the medium (Vanfleteren 1980).

## Material and methods

### *Culture techniques*

*Monhystera disjuncta* was sampled in the Sluice Dock of Ostend, a marine lagoon near the Belgian coast. A few ml of sediment were inoculated in 4 spots, made in 14 cm diameter petri dishes with (DIFCO) bacto-agar (1% in

water from the natural habitat, see Vranken et al. 1981). After 1–2 weeks incubation, the nematodes (and other organisms) invade the agar surrounding the detritus spots. They were picked out of the agar individually to start the pure cultures.

Agnobiotic cultures were set up in small petri dishes (diameter 3.5 cm) filled with 4 ml of 0.4% bacto-agar. This agar was made up with Sluice Dock water and enriched with 1% Vlasblom medium (0.278 g $FeSO_4 \cdot 7\,H_2O$, 3.0 g $NaHPO_4 \cdot 2\,H_2O$, 30.0 g $NaNO_3$, 0.47 g $MnCl_2 \cdot 4\,H_2O$, 50.0 g glycine in 1 l aq. dest.: Vlasblom 1963) and 0.5% of a 15 g/l solution of $Na_2SiO_3 \cdot 9\,H_2O$. Salinity was controlled with a refractometer and kept between 29‰ and 31‰ by the addition of distilled water when necessary. The agar was inoculated with a few drops of paper-filtered water from the Sluice Dock. Bacteria grew rapidly on the medium.

After a few days the petri dishes were inspected. Dishes showing development of fungi were discarded. The rest was inoculated with adult *M. disjuncta* from the extraction plates.

At regular intervals these stock cultures were renewed by transferring at least 20 females and 10 males (preferably not all coming from the same old stock culture dish) to a new petri dish: 4–5 stock culture dishes were simultaneously kept. The Sluice Dock was routinely sampled and extraction dishes set up, so that wild animals could regularly be added to the laboratory stock.

The methods for the life table experiments in monoxenic cultures were extensively described by Vranken et al. (1985) and will only be summarized below. A bacterial strain belonging to the *Alteromonas haloplanktis* rRNA group, coded ISC2, was isolated from the Sluice Dock. It is deposited in the collection of the Laboratory for Microbiology, State University of Gent (Dir. Prof. De Ley), where it was identified. Bacterial suspensions were injected in a central ring in the sterile bacto-agar. The agar was only enriched with 5% sterol mixture, containing 10 µg $ml^{-1}$ of cholesterol, stigmasterol, ergosterol, 7-dehydrocholesterol and sitosterol each; the cultures were buffered to pH 7.5–8.0 by the addition of 0.005 M TRIS buffer.

Nematodes were isolated from field samples as described above, axenised during 24 h in agar containing 10000 IU penicillin and 10 mg $ml^{-1}$ streptomycine, and transferred to the monoxenic cultures.

Experiments with different bacterial strains were conducted in the same way. Bacterial strains were obtained from the Scottish collection of marine bacteria, Torry Research Station, Aberdeen, Scotland. The bacteria were incubated overnight in nutrient broth, separated by centrifugation, washed in artificial sea water, concentrated again by centrifugation and injected in the nematode culture dish.

For the life table experiments in excess-food monoxenic cultures, bacterial density in the suspension was $\geq 10^{11}$ cells $ml^{-1}$.

Concentrations gradients of ISC2 were prepared by dilution of a stock suspension with a density of $10^{11}$ cells $ml^{-1}$. Density was controlled with a Petroff-Hauser counting chamber. 20 µl of a suspension of known density was added in the ring. In the monoxenic experiments, including those with varying food density, the nematodes were inoculated in the experimental dish when 3.5 d old. This allowed for a standardized density per dish. In the agnotobiotic cultures this factor was not standardized due to the cohort raising technique used: 20 to 50 adult females and 10 males were placed on a fresh culture dish. They deposited eggs until the next day when they were removed. The developing eggs constituted the experimental cohort.

*Estimation of the life history parameters*

Egg development time (E), minimum generation time ($T_{min}$) of males and females, % hatching success, % juvenile (post-embryonic) mortality, and sex ratio were determined simultaneously in 3–8 replicate experiments with a total of at least 100 individuals. $t_0$ is taken as halfway between the moments of introduction and removal of the adults that deposited the eggs constituting the cohort. Thus adults were removed at $t = 0.5$ d.

The culture dishes were controlled daily, and the number of juveniles, mature (=egg-bearing) females and males recorded. All mature adults were removed from the culture dish to avoid confusion with the next generation.

Egg deposition rate was determined in several replicate cultures, each containing 1–3 females and 1–3 males. At least every 3 days the number of eggs was counted. Daily egg production was calculated as the mean number of eggs produced per female per day in the observation interval. Approximately every $T_{min}/2$ the adults were transferred to fresh cultures. The deposited eggs were followed until maturation, thus allowing a direct observation of the number of female offspring produced per female alive aged $x$. This observed value does not equal $m_x$, as it is lowered by embryonic and juvenile mortality.

However, by calculating the adult survival values relative to a value 1.0 at the onset of maturity, the $m_x l_x$ values are correct.

Age-specific survival values were determined in 3–4 replicate cultures, started with individuals aged $T_{min}$.

Both sexes were kept together in the cultures, so as to keep the animals sexually active. They were transferred to new culture dishes every $T_{min}/2$ or sooner.

Following Gehan and Siddiqui (1973) a risk analysis was performed which compared several functional descriptions of the survival data: exponential, linear, Gompertz and Weibull functions. The Weibull distribution most often provided the best fit, although the Gompertz curve was in some instances slightly better. For uniformity, the Weibull distribution was fitted to all observed survival curves. The fitting method of Pinder et al. (1978), using double logarithmic transformation, was applied. The Weibull distribution is given by:

$$N_t = N_o \exp\left(-(t/b)^c\right)$$

where

$N_t$ = number of surviving organisms at time $t$

$N_o$ = number of organisms at the start of the experiment (age $T_{min}$).

$c$, $b$ = constants to be fitted

$t$ = time from onset of the experiment

Survival values at each age $x$ were calculated from the fitted distribution, which provided an excellent fit in all cases. Mean adult longevity (MAL) was calculated as:

$$MAL = b\,\Gamma(1 + 1/c)$$

with $\Gamma$ the gamma function.

Given the products $m_x l_x$ at age $x$, the demographic variables $R_0$, $T_c$ and $r_m$ were calculated according to standard methods (see also Vranken and Heip 1983).

**Table 1.** *M. disjuncta* in agnotobiotic culture: Mean development times, 95% confidence intervals, and number of animals observed for embryonic development (embr.), development to adult male and to adult female at 6 different experimental temperatures

| Temperature | Embr. | | | Female | | | Male | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | CI | $n$ | $\bar{x}$ | CI | $n$ | $\bar{x}$ | CI | $n$ |
| 3° C | 9.8 | 0.2 | 490 | 52.3 | 1.0 | 287 | 47.6 | 1.2 | 158 |
| 8° C | 5.1 | 0.2 | 115 | 18.6 | 1.0 | 56 | 16.9 | 1.1 | 33 |
| 12° C | 3.5 | 0.1 | 956 | 17.2 | 0.3 | 662 | 15.8 | 0.5 | 245 |
| 15° C | 2.9 | 0.1 | 375 | 11.8 | 0.3 | 241 | 11.7 | 0.4 | 71 |
| 17° C | 2.9 | 0.1 | 1275 | 10.9 | 0.3 | 226 | 11.0 | 0.6 | 90 |
| 20° C | 2.3 | 0.1 | 458 | 9.3 | 0.3 | 291 | 9.6 | 0.4 | 111 |

**Table 2.** *Monhystera disjuncta* in agnotobiotic culture: parameters of the allometric relationships (development time $= a$ temp$^{-b}$) describing the dependence of embryonic development time (d), and of development time (d) to the adult female and adult male stages on temperature (°C)

| Stage | $a$ | $b$ | SE ($b$) | $r^2$ |
|---|---|---|---|---|
| Embryonic | 23.75 | −0.76 | 0.051 | 0.88 |
| Female | 118.13 | −0.84 | 0.051 | 0.90 |
| Male | 108.19 | −0.82 | 0.053 | 0.89 |

**Table 3.** Mean $T_{min}$ (days) and 95% confidence interval of *M. disjuncta* fed eight different bacterial strains (monoxenic cultures at 17° C). Each mean is based on four replicate cultures, each with 30 nematodes

| Bacterial strain | Females | | Males | |
|---|---|---|---|---|
| | Mean | 95%CI | Mean | 95%CI |
| ISC2 | 7.35 | 0.15 | 7.13 | 0.16 |
| E. coli | 8.41 | 0.24 | 7.98 | 0.20 |
| Micrococcus sp. | 8.13 | 0.19 | 8.17 | 0.24 |
| Ps. fluorescens | 7.81 | 0.23 | 7.73 | 0.17 |
| Ps. marina | 7.82 | 0.19 | 7.40 | 0.18 |
| KB1a1 | 7.62 | 0.19 | 7.43 | 0.18 |
| KB1a3 | 8.68 | 0.21 | 7.85 | 0.17 |
| KB1a5 | 7.61 | 0.22 | 7.65 | 0.20 |

## Results

The dependence of $T_{min}$ on temperature in agnotobiotic culture was already discussed by Vranken and Heip (1986). It can be described by the allometric function:

$$T_{min} = aT^{-b}$$

where $T$ is temperature in °C. This function can also be applied to describe the dependence of embryonic development time on temperature. Table 1 gives the mean values of embryonic development time and of $T_{min}$ at different temperatures in the agnotobiotic cultures. The parameters of the allometric functions are given in Table 2. The basal temperature (biological zero) is implicitly assumed to be 0° C when this function is fitted. This is realistic for *M. disjuncta*. The lowest temperature we tried was 3° C, but Gerlach and Schrage (1971) report a culture of *M. disjuncta* at between −1° C and +1° C.

Apart from temperature, feeding conditions also influence $T_{min}$. Table 3 gives the mean $T_{min}$ at 17° C with different bacterial strains as food. Analysis of variance (Table 4) demonstrates a significant effect of food type on $T_{min}$. The sexes differ significantly in their development time. In general, males have a shorter development time, although this too seems to depend on food type (cf. significant interaction between food type and sex in Table 4).

**Table 4.** *Monhystera disjuncta* in monoxenic cultures at 17° C: ANOVA of mean development times with different bacterial strains as food sources. Mean development time of a sex in a replicate culture was used as the basic variable. Analysis is according to the completely randomized split-plot design, in which bacterial strains are the main plots, and sexes the subunits

| Source of variation | df | SS | MS | F | |
|---|---|---|---|---|---|
| Bacteria | 7 | 7.08 | 1.01 | 18.43 | $P<0.005$ |
| error | 24 | 1.32 | 0.05 | | |
| Sex | 1 | 1.14 | 1.14 | 23.92 | $P<0.005$ |
| Interaction | 7 | 1.29 | 0.18 | 3.85 | $P<0.01$ |
| error | 24 | 1.15 | 0.05 | | |
| Total | 63 | 11.98 | | | |

**Table 5.** Mean $T_{min}$ (days) and 95% confidence intervals of *M. disjuncta* fed 7 different densities of bacterial strain ISC2 in monoxenic cultures at 17° C. Each mean is based on 4 replicate cultures, each with 30 nematodes. Also indicated is the % of the inoculated nematodes that eventually matured. Up to 7.5 days of age, no mortality was observed in the cultures

| | Bacterial Density | | | | | | |
|---|---|---|---|---|---|---|---|
| | $10^{11}$ | $10^{10}$ | $5\cdot10^{9}$ | $10^{9}$ | $5\cdot10^{8}$ | $10^{8}$ | $10^{7}$ |
| Females | | | | | | | |
| $\bar{x}$ | 7.61 | 7.70 | 7.76 | 8.01 | 8.17 | 8.62 | 10.55 |
| CI | 0.10 | 0.14 | 0.15 | 0.26 | 0.28 | 0.41 | 0.62 |
| Males | | | | | | | |
| $\bar{x}$ | 7.61 | 7.65 | 7.75 | 8.58 | 8.82 | 9.52 | 10.21 |
| CI | 0.07 | 0.10 | 0.14 | 0.36 | 0.36 | 0.44 | 0.60 |
| % Matured | 100.0 | 97.5 | 100.0 | 93.3 | 94.2 | 86.7 | 41.7 |

Table 5 shows the influence of bacterial density (strain ISC2) on $T_{min}$ at 17° C. Analysis of variance (Table 6) shows a signficant effect of food density and sex, but no significant interaction between them. Down to a bacterial density of $5\cdot10^{8}$ ml$^{-1}$ virtually all nematodes matured, with a $T_{min}$ only slightly influenced by food density. The few losses are animals which crawl out of the agar, stay in the water film at the border of the dish, and die there. They can be considered technically inevitable losses. However, at $10^{8}$ and (much more) at $10^{7}$ bacteria ml$^{-1}$ part of the nematodes never mature. They live for a long time as juveniles, and eventually die before reaching adulthood. Consequently, they cannot be incorporated in the calculation of $T_{min}$. The effect of food density on $T_{min}$ seems relatively small, but this impression is, at least at $10^{7}$ bacteria ml$^{-1}$, partially an artifact. The effect is similar in both sexes, resulting in a quite constant sex ratio in those animals that do mature.

Egg deposition rates were studied at 3° C, 12° C and 17° C in agnotobiotic culture, and at 17° C in monoxenic (high food density) culture on ISC2 (Fig. 1). Daily egg deposition is nearly constant in the first period following maturity. The length of this period depends on temperature and

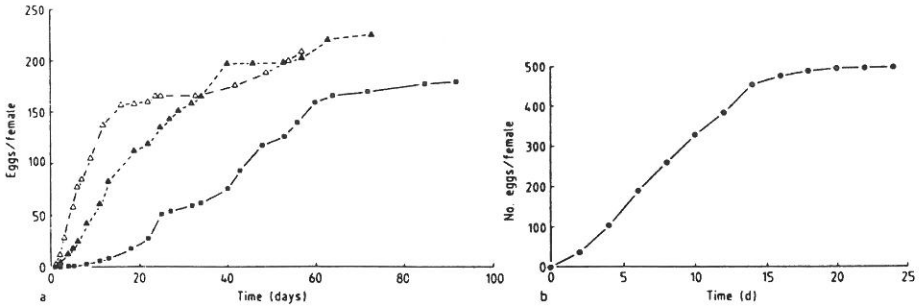


**Fig. 1.** *Monhystera disjuncta*: cumulative curves of egg deposition (number of eggs per female) vs. time in (**a**) agnotobiotic cultures at 3° C (closed squares), 12° C (closed triangles) and 17° C (open triangles), and (**b**) in high food density monoxenic cultures on ISC2 at 17° C. Note differences of scale in the Y-axis between the two graphs

**Table 6.** *Monhystera disjuncta*: ANOVA of mean development times with different bacterial densities of the strain ISC2 in monoxenic cultures at 17° C. Same design as in Table 2

| Source of variation | df | SS | MS | F | |
|---|---|---|---|---|---|
| Density | 6 | 56.09 | 9.35 | 21.74 | $P<0.005$ |
| error | 21 | 9.04 | 0.43 | | |
| Sex | 1 | 2.12 | 2.12 | 10.12 | $P<0.005$ |
| Interaction | 6 | 1.88 | 0.31 | 3.85 | ns |
| error | 21 | 4.40 | 0.21 | | |
| Total | 55 | 73.54 | | | |

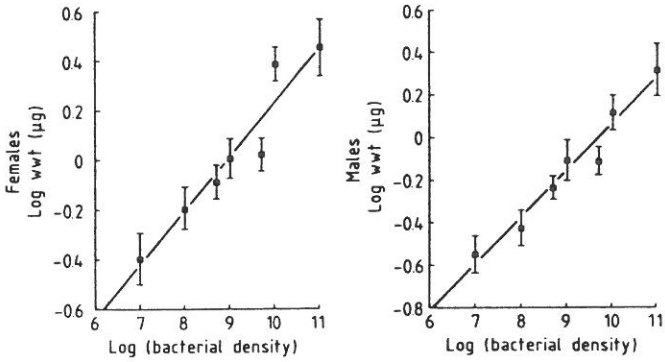


**Fig. 2.** *Monhystera disjuncta*: relation between body weight (µg wet weight per individual) and bacterial density in the food suspension (strain ISC2 at 17° C)

**Table 7.** Egg production of *M. disjuncta* (eggs/female day) 7 days after adulthood in monoxenic cultures at 17° C, with different bacterial strains as food. Each mean is based on 4 replicate cultures with 30 nematodes each. The number of females in each culture is variable

| Bacterial strain | Mean | St. err. |
|---|---|---|
| ISC2 | 35.10 | 3.50 |
| E. coli | 39.50 | 3.60 |
| Micorococcus sp. | 35.00 | 3.90 |
| Ps. marina | 41.75 | 2.78 |
| Ps. fluorescens | 38.00 | 5.55 |
| KB1a5 | 20.00 | 0.91 |

**Table 8.** *Monhystera disjuncta*. Demographic parameters in agnotobiotic culture at 3° C, 12° C and 17° C, and in monoxenic culture on strain ISC2 at 17° C: $R_0$ (dimensionless), $r_m$ (intrinsic rate of natural increase, $d^{-1}$), $T_0$ (generation time, d), egg production (number of eggs per female per day), pre-adult mortality (%), and MAL (Mean Adult Longevity, d)

| Parameter | Agnotobiotic | | | ISC2 |
|---|---|---|---|---|
| | 3° C | 12° C | 17° C | 17° C |
| $R_0$ | 111 | 123 | 102 | 302 |
| $r_m$ | 0.058 | 0.171 | 0.285 | 0.422 |
| $T_0$ | 80.8 | 28.1 | 16.2 | 13.5 |
| egg prod. | 2.7 | 5.1 | 9.2 | 32.3 |
| $T_{min}$ female | 52.3 | 17.2 | 10.9 | 8.1 |
| male | 47.6 | 15.8 | 11.0 | 8.0 |
| pre-ad. mort. | 23 | 14 | 8 | 8 |
| MAL female | 123 | 49 | 38 | 23 |
| male | 201 | 90 | 54 | – |

food. Although egg production can continue afterwards for quite a long period, this is only a minor contribution to the total reproductive output. We estimated daily egg production as the slope of the linear regression of cumulative egg production on time, during the period that this function was linear.

Both temperature and food have highly significant effects on egg deposition ($P<0.001$). In the cultures with different bacterial strains as food the egg deposition was checked 7 days after $T_{min}$. The results are summarized in Table 7. Food quality had a significant effect ($0.005<P<0.01$). This effect is due to the low egg production with the KB1A5 strain (which is significantly lower than all the other strains: "T" a posteriori test at the 5% level). The other strains were not significantly different from one another.

Adult survival was studied at 3° C, 12° C and 17° C in agnotobiotic culture and at 17° C in high density culture with ISC2. Temperature and food influence survival. In general, Mean Adult Longevity (MAL) (Table 8) is inversely correlated with egg production. Males live longer than females.

The above consequences of temperature and food are summarized in the demographic parameters (Table 8).

The influence of food density (strain ISC2) on adult body mass (measured the second day after maturation using Andrassy's (1956) formula) is shown in Fig. 2. Log (body mass) is a linear function of log (bacterial density), given by the equations:

$$\log(W) = -1.955 + 0.219 \log(D) \text{ (females)}$$

$$\log(W) = -2.143 + 0.221 \log(D) \text{ (males)}$$

**Table 9.** *Monhystera disjuncta*: literature data on culture of the species. Indicated are the salinity (‰), temperature (°C) at which the cultures were held, and the minimum generation time (d) obtained (mean and range of the observations)

| Salinity | Temp. | $T_{min}$ (d) | Authority |
|---|---|---|---|
| Seawater | 20–24 | 30 | Chitwood and Murphy (1964) |
| 5 | 20–22 | 23 (18–28) | von Thun (1968) |
| 32 | 26 | no growth | Gerlach and Schrage (1971) |
| 32 | 17–22 | 12 (8–15) | idem |
| 32 | 13–15 | 15 (9–20) | idem |
| 32 | 9–12 | 17 (13–24) | idem |
| 32 | 7 | 22 (14–32) | idem |
| 32 | 0–2 | 78 (77–81) | idem |
| 32 | −1–+1 | 131 (128–134) | idem |

where W is adult wet weight in µg and D bacterial density (bacteria $ml^{-1}$).

The regressions are highly significant ($F = 55.0$ and 50.7 resp., with 6 and 133 df; $P < 0.001$). Slight but significant deviations from linearity are observed ($P < 0.001$ for females, $0.025 < P < 0.05$ for males). These are due to the low values observed at $5 \cdot 10^9$ bacteria $ml^{-1}$.

## Discussion

*M. disjuncta* has previously been cultured by von Thun (1968), Chitwood and Murphy (1964), Gerlach and Schrage (1971). $T_{min}$ values in these studies are summarized in Table 9. Whereas the values for $T_{min}$ obtained in earlier studies are considerably higher than our values, those of Gerlach and Schrage (1971) correspond extremely well with our equation which predicts $T_{min}$ values of 9.73 d, 12.86 d, 16.37 d, 23.01 d and 65.92 d at 19.5° C, 14° C, 10.5° C, 7° C and 2° C resp. In contrast to this good correspondence for $T_{min}$, Gerlach and Schrage (1971) find an egg production during her entire lifetime of only 37 eggs $female^{-1}$ at 17–22° C. This observation is puzzling. The development times indicate similar conditions for both (agnotobiotic) experiments. One would expect to find a similar egg production too, as development time and egg production are negatively correlated in our data set.

It was concluded by Vranken et al. (1984) that *M. disjuncta* is highly selective in its feeding habits, not being able to grow or reproduce on most bacterial strains offered. This conclusion became questionable after we observed that the addition of a sterol mixture and of TRIS buffer greatly improved the culture on ISC2, the only bacterial strain that allowed monoxenic culturing even without these additions.

The present experiments confirm that these factors, rather than the presumed selectivity, are responsible.

Addition of TRIS buffer, without sterols, allows 25–50% of the individuals (depending on the bacterial strain given as food) to mature, albeit only after approximately 15 days. With sterols but without buffer, only ISC2 allows growth of the nematodes. In the *E. coli* agar dish, the pH was as low as 3.7 after two days. *M. disjuncta* does not survive when pH is lower than approximately 6.5.

Incidently, we discovered that the silicate solution added to the Vlasblom medium in the agnotobiotic cultures was only useful as a pH buffer.

Although there is a significant reduction in $T_{min}$ at high food concentrations, *M. disjuncta* is not as flexible in the regulation of its generation time as *Caenorhabditis briggsae* (Schiemer 1982a, b). With a (low) food density of $2 \cdot 10^8$ bacteria $ml^{-1}$ the $T_{min}$ of the latter species is more than three times as long as with a high food density ($10^{11}$ bacteria $ml^{-1}$). This factor is only 1.4 in our experiments. Probably we did not include the very limiting food density in the experimental series, although *M. disjuncta* did not survive at $5 \cdot 10^6$ bacteria $ml^{-1}$, and at $10^7$ bacteria $ml^{-1}$ only half the individuals reached adulthood.

On the other hand, we observe an enormous flexibility in the adult body mass of *M. disjuncta*. Adults reared at $10^{11}$ bacteria $ml^{-1}$ are about 7 times as heavy as adults reared near the limiting food density. This is a much larger variability than in *C. briggsae* (Schiemer 1982a), where wet weight at $5 \cdot 10^{10}$ bacteria $ml^{-1}$ is 1.4 times the wet weight at $5.10^8$ bacteria $ml^{-1}$ (using our regression equations to interpolate, we arrive at a factor 2.74 for exactly the same range in *M. disjuncta*). In the agnotobiotic cultures both $T_{min}$ and adult body weight were similar to those obtained at $10^7$ ISC2 $ml^{-1}$.

Daily egg production rate in agnotobiotic cultures is 3.5 times lower than in optimal monoxenic cultures. The period of egg production is somewhat longer, resulting in a 3-fold difference in $R_0$. However, as $T_{min}$ does not change very drastically, $r_m$ differs only by a factor 1.5. The total production of a female during her lifetime (somatic and egg production) differs by a factor 3.75.

Apparently, *M. disjuncta* is not as good in taking advantage of abundant food, as *Caenorhabditis briggsae* or even *Plectus palustris*. At high food density, a larger proportion of a female's production during her lifetime is chanelled into somatic production (around 30% at $10^{11}$ bacteria $ml^{-1}$, compared with around 11% at $10^7$ bacteria $ml^{-1}$, neglecting the somatic production from 2 days after maturation onwards in both cases). The larger body size does not result in higher survival probabilities (on the contrary, MAL is shorter) nor in a better viability of the eggs. It seems to be only a by-product of the fact that development into an adult takes a certain, relatively unflexible, minimum time. Extra energy becoming available during this period is chanelled into extra body mass, but without any apparent adaptive reason.

This could indicate that *M. disjuncta* is adapted to lower food levels in nature than the species studies by Schiemer (1983). The minimal concentration of bacterial carbon at which it can survive is 0.006 mg dwt $ml^{-1}$. This is 1/4th of the value for *P. palustris* and 1/16th of that for *C. briggsae*. Nonetheless, *M. disjuncta* can maintain a relatively high $r_m$ at low food concentrations. $r_m$ in the agnotobiotic cultures is about equal to the $r_m$ of *P. palustris* in optimal culture conditions (the $r_m$ of *C. briggsae* in optimal conditions is 4 times higher).

Egg production rate too, does not seem to depend as strongly on food density as it does in *C. briggsae*. Adult body growth (i.e. body growth after maturation) is much more important in high food density cultures than in low density cultures (G. Vranken, personal observation). This may also be a by-product of a relatively fixed egg production rate: whereas somatic growth in the juvenile phase increases by a factor 7 over the density range studied, egg production rate increases only by a factor 3.5.

In *M. disjuncta*, which seems to be adapted to a (rela-

tively) lower food density regime, the proportion of egg production in the total (egg + somatic) production during a female's lifetime decreases with increasing food density.

The reverse is true for *C. briggsae*, where the proportion devoted to egg production raises from 76% to 84% over a food density range from $10^8$ to $10^{10}$. In *P. palustris* the proportion remains constant at about 70%.

Although some species are more variable than others in their life history parameters, it is now clear that nematode populations are capable of considerable flexibility. Whether this flexibility is in itself adaptive, probably depends on the particular species. In species living in temporary environments, such as the polysaprobic *C. briggsae*, flexibility is very much needed. The species is only competitively superior at high bacterial densities (Schiemer 1983). It must be able to profit as much as possible of these circumstances. Probably for species normally living in less enriched environments, this extreme flexibility is less called for.

Flexibility is important if we want to draw general conclusions about energy transfer through nematode populations from our culture data. Of course, this conclusion may be biased, since lab culturing methods tend to select for the most versatile ("weed") species. Anyway, we should keep this versatility in mind. In previous compilations (Heip et al. 1985; Vranken et al. 1986) we have used the agnotobiotic cultures as the best approximations of field conditions. How can we be sure about their validity? Comparison of bacterial densities in sediments with those in agar cultures is not useful as a basis for justification: individual size, nutritional value and availability to grazing of the bacteria may be very different. Thus we still remain in a situation where the characteristics of field populations are, at best, approximated by our cultures, but remain largely unknown.

In the meantime, generalizations such as given by Vranken et al. (1986), remain useful but also dangerous tools.

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# Studies of the life-history and energetics of marine and brackish-water nematodes

## II. Production, respiration and food uptake by *Monhystera disjuncta*

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**Summary.** An energy budget was constructed for the marine nematode *Monhystera disjuncta*. Respiration was measured with a modified Cartesian diver technique, in which the nematodes were kept in agar inside the diver 'head'. The relationship between respiration and body weight was: $R = 1.53\ W^{0.75}$. Body growth was exponential during the juvenile phase, with a growth rate equal to 0.61 $d^{-1}$. After maturation the growth rate fell to 0.17 $d^{-1}$. Food uptake was measured in experiments with radiolabeled bacteria. In one series of experiments the accumulation of radiolabel in the nematodes was followed. In a second series the decrease in labeling was followed when pre-labeled nematodes fed on unlabeled bacteria. A model for label uptake permitted the calculation of assimilation efficiency and consumption rates. Consumption rates thus measured, correspond well to those calculated from the growth, reproduction and respiration rates. Assimilation efficiency was low, around 25%. Production efficiency ($P/(P+R)$) was high: 60% for the population at stable age distribution, and up to 75% for reproducing females. This seems to be a general feature in nematodes.

**Key words:** Nematodes – Meiobenthos – Energy-flow – Respiration – Feeding

Although they are small and inconspicuous animals, the often very high densities (in the order of $10^6\ m^{-2}$) of marine nematodes make them a potentially important constituent of the benthic food chain. It is still difficult to quantify this importance. A number of species have been cultured; on the basis of these data we have proposed an approximate relationship to estimate yearly production figures (Vranken et al. 1986). However we possess a very limited data base to estimate the assimilation rate or assimilation efficiency of marine nematodes.

Tietjen (1980) presents energy budgets of three marine species. The experimental data on which these budgets were based were, to our knowledge, never detailed. Admiraal et al. (1983) give a grazing rate for the herbivorous species *Eudiplogaster pararmatus*. Carbon intake was estimated as 1.7 times the nematodes' own body weight per day. This very high intake had no significant influence on the diatom standing stock in nature.

Warwick (1981) constructed an energy budget for a marine nematode, *Diplolaimelloides bruciei*. As in other (non-marine) nematodes, he found a very high production efficiency (Production/(Production + Respiration)) in this species. Egg-laying females especially, had an efficiency of around 90%.

More data are available on freshwater species, especially from highly saprobic environments. Energy budgets were detailed for *Pelodera sp.* (Marchant and Nicholas 1974), *Plectus palustris* (Duncan et al. 1974), *Paroigolaimella bernensis*, *Diplogasteritus nudicapitatus* and *Rhabditis curvicaudata* (Woombs and Laybourn-Parry 1985).

A budget for *Caenorhabditis briggsae* (Nicholas et al. 1973) did not correspond to later observations on this species (Schiemer 1983).

These studies all indicate that nematodes in general have high to very high production efficiencies, and low assimilation efficiencies. Their overall ecological efficiency (production/total food uptake) would therefore not be very large, despite the high production efficiencies.

Based on field estimates of production and respiration of meiobenthic crustacean populations, we formerly (Herman et al. 1984) put forward the hypothesis that a production efficiency of about 0.4 would be a reasonable figure for meiobenthic populations. We implicitly questioned the very high figures (0.6–0.9) found in laboratory studies (at optimal culture conditions) of (mainly semi-aquatic or freshwater) free-living nematodes. These studies, however, are very consistent in their (extreme) conclusions. We decided to put our prejudices to the test with *M. disjuncta*, a species which we extensively studied with regard to demography (Herman et al. 1984; Vranken and Heip 1986; Vranken et al. 1988). The study of its energetics was completed by measuring respiration and food uptake.

Nematode grazing rates in the field are hardly known at all. Montagna (1984) made direct measurements, indicating that nematode grazing may be quantitatively unimportant for the sediment bacteria. Indirect assessments of the influence of nematodes on the sediment microbiota on the other hand, indicate that they may have a considerable impact. The measurement of assimilation efficiency permits an evaluation of the impact of nematode grazing on the bacteria. This would make it possible to evaluate if grazing per se, rather than bioturbation or nutrient excretion, could provoke the experimentally measured influences.

### Material and methods

*M. disjuncta* was cultured monoxenically with the *Alteromonas haloplanktis* strain 'ISC2' (bacterial density about $10^{11}$ cells $ml^{-1}$) as food. Culture methods are described in Vranken et al. (1988).

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Respiration rates were measured at 17° C with Cartesian Diver respirometry (Klekowski 1971). Stoppered divers (gas volume 1 µl) were filled with sterile bacto-agar in artifical sea water in the following way. The diver 'heads' were prefilled with hot sea water. Boiling agar was poured in a petri dish, and by use of a mouth pipette the sea water in the diver was replaced by fluid agar. The diver was then transferred into cold sea water; the agar became quickly solid. Most agar stricking to the outer surface and inside the diver 'neck' was removed with the pipette. The diver was then transferred into hot sea water again, and the rest of the agar, except inside the diver head, carefully removed. Finally it was put in cold sea water, and the nematodes were introduced into the agar with a fine needle. The nematodes were precleaned by letting them crawl around in sterile agar. Animals in one diver were taken out of the same cohort. In all experiments relatively young animals (juveniles up to 2nd day adults) were used. 8–10 nematodes per diver were used together.

The nematodes moved around in the agar in quite the same way as in the culture dishes. At the end of an experiment the diver was put in hot sea water again. The heat melted the agar and killed the nematodes. They were pipetted out of the diver and brought onto an object slide. Body length and maximal width were measured to give an estimate of body mass by Andrassy's (1956) formula.

Within a species, respiration rate is usually an allometric function of body mass, with an exponent $b$ of about 0.75. Consequently, when several individuals' are used in one measurement, it is no good practice to take their mean or total biomass as measurement of their weight.

Warwick and Price (1979) solved this problem by taking $\Sigma_i V_i^{0.75}$ (where $V_i$ was the volume of individual $i$) as a measure of the biomass in one diver. We determined the exponent $b$ iteratively by calculating the regression of $\log(R)$ (where $R$ is the respiration measured in a diver) on $\log(\Sigma_i W_i^b)$ (where $W_i$ is the wet weight of the $i$-th individual in that diver) and varying $b$ until the slope of the regression equalled 1. The procedure is justified by the following reasoning: if the respiration rate $R_i$ of an individual nematode is given by $R_i = aW_i^b$ then the total respiration in a diver is $R = a\Sigma_i W_i^b$, and $\log R = \log a + \log(\Sigma_i W_i^b)$ where the slope can be seen to equal 1.

For the feeding experiments bacteria were grown in heart infusion broth (DIFCO: 1.25 g in 50 ml artificial seewater) for 24 h. They were harvested by centrifugation and resuspended in 40 ml artificial seawater, to which a small amount of heart infusion broth and 50 µCi $^{14}$C-glucose (Amersham, 270 mCi/mmol) were added. After incubation for another 24 h the bacteria were harvested, washed and resuspended in approximately 1 ml artificial seawater.

This procedure resulted in a better labeling than adding the label directly to the heart infusion broth, presumably due to substrate competition. Bacterial density in the feeding suspension was measured either in a Petroff-Hauser counting chamber or by plate-counting. Both methods yielded approximately the same results. The labeled bacteria were added to sterile agar dishes in the same way as in the other experiments.

Experiments were performed with nematodes aged 7.5 and 11.5 d (measured from the moment of egg-laying). The experiments consisted of two series. In the first, 100 (or 50 in case of adult females) animals were transferred from 'cold' cultures to cultures with labeled bacteria, incubated for a variable time, and then transferred to sterile bacto-agar. In the second series, nematodes were incubated with labeled food for at least 6 h, transferred to sterile agar, and then to agar containing unlabeled bacteria. After incubation for a variable time, they were transferred back into sterile agar.

In both series the nematodes were transferred immediately from the sterile agar into a drop of sterile distilled water in a scintillation vial. For Oh time experiments in the second series, the animals were not incubated with unlabeled bacteria, but transferred directly from the sterile agar into a scintillation vial. It took approximately 10 min to transfer 100 nematodes twice.

To the scintillation vial with the nematodes 1 ml of Lumasolve (Lumac, 3M) was added upon completion of the transfer. Ater digestion 10 ml of Lipoluma (Lumac, 3M) was added as scintillation liquid. Scintillation was counted in a Beckman liquid scintillation counter for 3 × 5 min.

For each experiment 10 µl of the bacterial suspension was digested and its scintillation counted. The bacterial density in the suspension was determined. This yielded the number of counts per bacterial cell, which was subsequently used to express the labeling of the nematodes in numbers of bacteria per nematode.

The dry weight of the bacteria was determined on a Mettler ME22 microbalance (precision 0.1 µg). 10 aluminium microtrays were dried at 110° C for 2 h, placed in a desiccator, and preweighed. Five of them were filled with 10 µl bacterial suspension, and five with artificial seawater. Dry weight was determined after drying (2h at 110° C) and cooling in a desiccator. The weight of 10 µl bacterial suspension was calculated as the difference between the mean weights of the two series. Bacterial density was determined and the mean weight of a bacterial cell calculated.

A growth curve for the nematodes was constructed by sampling animals of different ages from different cohorts.

One cohort was sampled only once, assuring independence of the errors at different ages. A logarithmic growth curve

$$W = W_0 e^{mt}$$

was fitted to the data.

The following conversion factors were used for the calculations (after Schiemer, 1982a, b, and references therein): dry weight = 15% of fresh weight; 1 g dry weight represents 25 kJ; an oxycaloric coefficient of 20.2 J per ml $0_2$ is assumed.

### *A model for label uptake*

A model was constructed to describe the radiolabel uptake and excretion by the nematodes. It was assumed that the contents of the gut are homogenised continuously. This assumption is justified by the constant vivid motion of the gut contents which can be observed in living nematodes. We further assumed that per time unit a constant proportion of the gut content is incorporated into the body and a constant proportion is excreted as faeces. Ingestion rate is also assumed to be constant.

The amount of label in the gut is then described by:

$$\frac{dG}{dt} = -iG - fG + U \qquad (1)$$

where $G$ = amount of label in the gut content (bacteria/nematode).

$i$ = rate of incorporation into the body, expressed as a fraction of the gut content ($h^{-1}$).

$f$ = defaecation rate, expressed as a fraction of the gut content ($h^{-1}$)

$U$ = uptake rate (bacteria nematode$^{-1}$ $h^{-1}$).

Solving this equation yields:

$$G = \frac{U}{(i+f)}(1-e^{-(i+f)t}) \tag{2}$$

when $t$ is relatively large, $G$ becomes constant:

$$G_\infty = \frac{U}{i+f}. \tag{3}$$

The amount of label incorporated into the body increases due to incorporation, and decreases due to respiration:

$$\frac{dL}{dt} = iG - rL \tag{4}$$

where

$L$ = amount of label in the tissues (bact./nematode)

$r$ = respiration rate, expressed as a fraction of the body label ($h^{-1}$).

The solution of eq. 4:

$$L = \frac{iU}{i+f}\left(\frac{1-e^{-rt}}{r}\right) + \frac{iU}{i+f}\left(\frac{e^{-(i+f)t}-e^{-rt}}{i+f-r}\right) \tag{5}$$

can be simplified by observing that $r$ is two orders of magnitude lower than $(i+f)$ (see results): $r \approx 0.008$ whereas $i+f \approx 0.5$. Neglecting $r$, eq. 4 reduces to:

$$\frac{dL}{dt} = iD \tag{6}$$

and eq. 4 becomes:

$$L = \frac{i}{i+f}(Ut - G). \tag{7}$$

The total amount of label found in a nematode at time $t$ will be:

$$L+G = \frac{iUt}{i+f} + G\frac{f}{i+f} \tag{8}$$

which is a linear function of time as soon as $G(t)$ approaches its equilibrium value $G_\infty$. The intercept $a$ and the slope $b$ of this linear function will be:

$$a = G_\infty \frac{f}{i+f}$$

$$b = \frac{iU}{i+f} = iG_\infty. \tag{9}$$

The second series of experiments (radiolabel excretion) is started with nematodes having an amount $G_0$ and $L_0$ of radiolabel in their gut and tissues, respectively. During the course of the experiment the gut content is described by:

$$\frac{dG}{dt} = -(i+f)G$$

$$G = G_0 e^{-(i+f)t}. \tag{10}$$

For the label incorporated into the tissues we have:

$$\frac{dL}{dt} = iG = iG_0 e^{-(i+f)t}$$

$$L = L_0 - \frac{iG_0}{i+f}(e^{-(i+f)t} - 1). \tag{11}$$

The total amount of radiolabel per nematode is:

$$L+G = L_0 + \frac{iG_0}{i+f} + \frac{f}{i+f} G_0 e^{-(i+f)t}. \tag{12}$$

Fitting this function of the form $Y = u + ve^{-wt}$ with non-linear fitting methods (Snedecor and Cochran, 1967) gives an estimate of $i+f$. The other parameters relate to the particularities of the experiment ($L_0$ and $G_0$) and the estimates of their values are not relevant. The estimate of $i+f$, together with the estimates of $a$ and $b$ from the first experiment, permit the calculation of $i$, $f$, $G$, $U$, and of the assimilation efficiency, $i/(i+f)$.

## Results

### *Respiration*

Figure 1 shows the results of the respiration measurements. $\log(R)$, where $R$ is the total respiration in one diver, is plotted against $\log(\Sigma_i W_i^b)$, where $W_i$ is the weight of animal $i$ in the diver. $b$ was iteratively determined. Ironically, $b$ turned out to equal exactly 0.75. Thus Warwick and Price's (1978) method, which assumed $b = 0.75$, would have given identical results! $a$, the coefficient of metabolic intensity in the equation $R = aW^b$, equalled 1.53 (where $R$ is expressed in nl $O_2$ $h^{-1}$ and $W$ in µg wwt). Respiration was 0.7% of the body weight $h^{-1}$ for 15 µg wwt animals, and 1.3% $h^{-1}$ for 0.1 µg wwt animals.

These small values justify the neglection of the respiration rate in the model for radiolabel uptake.

### *Growth*

The growth data are shown in Fig. 2. It can readily be seen that the juveniles had exponential body growth. As soon as the animals matured, however, growth slowed down.

The fact that males were smaller than females, but had the same growth rate between ages 10 and 12 days, can be explained by their earlier maturation (see Vranken et al. 1988). The instantaneous growth rate of the juveniles equalled 0.61 $d^{-1}$. For males and females alike, it equalled 0.17 $d^{-1}$ between days 10 and 12.

### *Feeding*

The results of the feeding experiments are shown in Fig. 3 (first series: uptake experiments) and in Fig. 4 (second series: excretion experiments). In these figures the fitted curves are also shown. The estimates of the model parameters, calculated from these fitted curves, are given in Table 1.

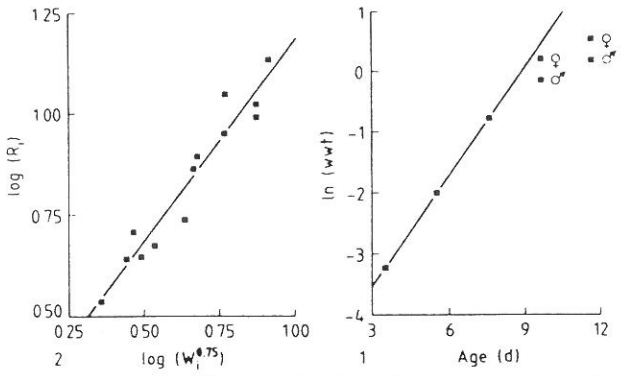


**Fig. 1.** *Monhystera disjuncta*: log-log relation between respiration in a diver ($\Sigma_i R_i$ where $i$ denotes the individuals in the diver) and the sum of the transformed individual weights ($\Sigma_i W_i^{0.75}$). $R$ in nl $O_2$ $h^{-1}$, $W$ in µg wwt. Experiments were conducted at 17° C. See text for details on the transformation used

**Fig. 2.** *Monhystera disjuncta*: growth curve at 17° C, for animals grown on high density cultures of ISC 2. The line is fitted through the first three points (juveniles). Wwt in µg $ind^{-1}$

Table 2 shows the correspondance between the measured food assimilation rates, and the calculated energy needs for (somatic and generative) production and respiration (mean rates for the 12 h following the time indicated as "age").

Growth production of the 11.5 d adults was calculated with an instantaneous growth rate of 0.17 $d^{-1}$. The generative production of females of this age corresponds to an egg production of 33.5 eggs $fem^{-1}$ $d^{-1}$. We found an excellent correspondance between the measured energy uptake and the calculated energy needs for 7.5 d juveniles and for 11.5 d adult females. For males a scope for sperm production of 31 $10^{-6}$ J $h^{-1}$ per individual was found. This is about 25% of a female's generative production.

**Table 1.** *Monhystera disjuncta*: estimation of the model parameters from the uptake and defaecation experiments. $a$: intercept of the uptake curve (bact. $nem.^{-1}$); $b$: slope of the uptake curve (bact. $nem.^{-1}$ $h^{-1}$); $i$: fraction of the gut content assimilated per h ($h^{-1}$); $f$: fraction of the gut content defaecated per h ($h^{-1}$); $E$: assimilation efficiency $= i/(i+f)$; $U$: uptake rate (bact. $nem.^{-1}$ $h^{-1}$)

| | 7.5 d | 11.5 d ♂ | 11.5 d ♀ |
|---|---|---|---|
| $i+f$ | 0.83 | 0.41 | 0.74 |
| $a$ | 24587 | 42940 | 52930 |
| $b$ | 4387 | 6554 | 14054 |
| $i$ | 0.15 | 0.11 | 0.20 |
| $f$ | 0.69 | 0.30 | 0.55 |
| $E$ | 0.18 | 0.27 | 0.26 |
| $U$ | 24868 | 24298 | 53269 |

**Table 2.** *Monhystera disjuncta*: comparison between the energy needs for somatic production (Som. $P$), generative production (Gen. $P$), respiration ($R$) and the measured energy uptake (Meas.). Tot. is the sum of Som. $P$, Gen. $P$ and $R$. All energy values in 10 J $h^{-1}$ $nem^{-1}$

| Age (d) | Som. $P$ | Gen. $P$ | $R$ | Tot | Meas. |
|---|---|---|---|---|---|
| 7.5 | 45 | – | 17 | 62 | 66 |
| 11.5 ♀ | 46 | 120 | 46 | 213 | 212 |
| 11.5 ♂ | 32 | ? | 36 | 68 | 99 |

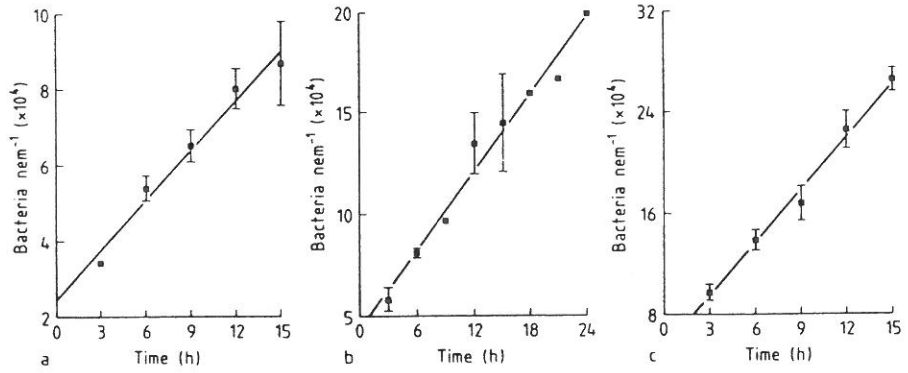


**Fig. 3.** *Monhystera disjuncta*: results of the experiments on uptake of labeled bacteria for juveniles (**a**), males (**b**) and females (**c**). Curves fitted according to the model. See text for details

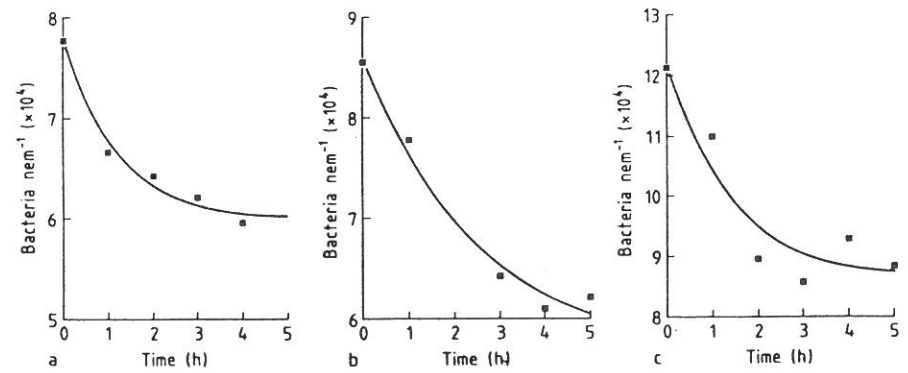


**Fig. 4.** *Monhystera disjuncta*: results of the second series of experiments (defaecation of labeled bacteria) for juveniles (**a**), males (**b**) and females (**c**). Curves fitted according to the model. See text for details

**Table 3.** *Monhystera disjuncta*: calculation of the Respiration/Biomass ratio ($d^{-1}$) for the entire population at stable age distribution. $F$ is the fraction of the population biomass in the age class, $R/B$ is the respiration/biomass ratio for that age class. The population ratio is the sum of $F \times R/B$ over all age classes

| Age class | $F$ | $R/B$ | $F \times R/B$ |
|---|---|---|---|
| 0 2.5 | 0.151 | 0.541 | 0.0817 |
| 2.5–3.5 | 0.035 | 0.504 | 0.0177 |
| 3.5 5.5 | 0.119 | 0.380 | 0.0450 |
| 5.5 7.5 | 0.172 | 0.280 | 0.0481 |
| 7.5 9.5 | 0.148 | 0.212 | 0.0314 |
| | 0.062 | 0.222 | 0.0137 |
| 9.5 11.5 | 0.123 | 0.180 | 0.0221 |
| | 0.043 | 0.196 | 0.0085 |
| >11.5 | 0.109 | 0.173 | 0.0188 |
| | 0.038 | 0.188 | 0.0072 |
| Total | | | 0.2942 |

**Table 4.** *M. disjuncta*: energy budget of a cohort of 1000 animals. Production and respiration are given in J per 1000 animals during the age span indicated. $P$ male and $P$ fem are the production realized by males and females respectively; $R$ male and $R$ fem the respiration by males and females. $P/(P+R)$ is the production efficiency of the total population, $P/(P+R)$ fem the production efficiency of the female part. In the cohort of 1000 animals we assumed there were 332 males and 668 females

| Age | $P$ male | $R$ male | $P$ fem | $R$ fem | $P/(P+R)$ | $P/(P+R)$ fem |
|---|---|---|---|---|---|---|
| 0 3.5 | 0.02 | 0.02 | 0.04 | 0.05 | 0.44 | 0.44 |
| 3.5 5.5 | 0.11 | 0.06 | 0.22 | 0.13 | 0.63 | 0.63 |
| 5.5 7.5 | 0.37 | 0.16 | 0.75 | 0.32 | 0.70 | 0.70 |
| 7.5 9.5 | 0.46 | 0.32 | 1.73 | 0.74 | 0.67 | 0.70 |
| 9.5–11.5 | 0.40 | 0.46 | 3.90 | 1.21 | 0.72 | 0.76 |
| 11.5–13.5 | 0.51 | 0.53 | 4.11 | 1.37 | 0.71 | 0.75 |
| 13.5–15.5 | 0.53 | 0.53 | 4.24 | 1.37 | 0.72 | 0.76 |
| 15.5–17.5 | 0.47 | 0.53 | 3.76 | 1.37 | 0.69 | 0.73 |
| 17.5–19.5 | 0.46 | 0.53 | 3.72 | 1.37 | 0.69 | 0.73 |
| 19.5–21.5 | 0.37 | 0.53 | 2.96 | 1.37 | 0.64 | 0.69 |
| 21.5–23.5 | 0.31 | 0.50 | 2.48 | 1.30 | 0.61 | 0.66 |
| 23.5–25.5 | 0.11 | 0.46 | 0.85 | 1.19 | 0.37 | 0.42 |
| 25.5–27.5 | 0.05 | 0.42 | 0.40 | 1.09 | 0.23 | 0.27 |
| 27.5–29.5 | 0.02 | 0.34 | 0.14 | 0.89 | 0.11 | 0.13 |
| 29.5–31.5 | 0.00 | 0.27 | 0.00 | 0.70 | 0.00 | 0.00 |
| 31.5–33.5 | 0.00 | 0.21 | 0.00 | 0.54 | 0.00 | 0.00 |
| 33.5–35.5 | 0.00 | 0.15 | 0.00 | 0.40 | 0.00 | 0.00 |
| 35.5–37.5 | 0.00 | 0.10 | 0.00 | 0.27 | 0.00 | 0.00 |
| 37.5–39.5 | 0.00 | 0.03 | 0.00 | 0.09 | 0.00 | 0.00 |
| Total | 4.19 | 6.14 | 29.32 | 15.78 | | |
| Global | | 0.41 | | 0.65 | | |
| $P/(P+R)$ | | | 0.60 | | | |

Calculations of the energy budget of the population in exponential growth are shown in Table 3. The stable age distribution and the birth rate were calculated from the demographic data discussed in Vranken et al. (1988).

The birth rate equalled $b = 0.440\ d^{-1}$. It is an estimate of the daily $P/B$. The relative contribution of the different age classes to the total biomass was calculated for the stable age distribution. Multiplying these factors with the weight specific respiration and summing yielded the average $R/B$ for the population. From $P/B$ and $R/B$ a production efficiency $P/(P+R)$ of 0.60 was calculated for the total population at stable age distribution.

In a second approach the production and respiration of a cohort (starting with 1000 eggs) during their lifetime is shown in Table 4. The cumulative budgets showed an efficiency of approximately 0.60 by the end of life.

Productivity was highest in adult egg-laying females (around 0.75 production efficiency). It was considerably lower for males (we assumed that males had a generative production 25% of the females', as was deduced from our experiments with 11.5 d animals).

## Discussion

With respect to the number of animals used and the time duration of the incubations, our feeding experiments are intermediary between the approaches of Duncan et al. (1974) and Marchant and Nicholas (1974). Duncan et al. (1974) measured uptake of bacteria by individual nematodes during short time intervals (30 min maximum). Their results rely heavily on the assumption that the gut is emptied completely with each defaecation, so that its contents are renewed every few minutes. This is definitely not the case in *M. disjuncta* (own observations). However, the (functional) anatomy of the digestive tract in Rhabditids and Monhysterids is sufficiently different to allow for different mechanisms here.

Woombs and Laybourn-Parry (1984, 1985) also calculate low assimilation efficiencies in three Rhabditid species. Ingestion is estimated from pumping frequencies by assuming that the volume of the dilated pharyngeal metacorpus is the ingested volume per pumping cycle, and that the density of the bacteria in the ingested fluid is the same as in the feeding suspension. This assumption seems justified by morphological observations on *Caenorhabditis elegans* (Albertson and Thompson 1975): during the pumping cycle fluid containing bacteria is sucked in and subsequently filtered. Superfluous fluid is excreted via the rami of the pharyngeal lumen, and only the packages of bacteria are ingested. In *M. disjuncta*, the mechanism is different. The structure of the pharynx suggests that suction can only be exerted on a short distance range, and that the bacteria are taken individually or in small packages (L.J. Jacobs, personal communication). This difference could very well explain why Rhabditids in general require very high bacterial densities for growth (see Vranken et al. 1988): at low densities random pumping is very energy-inefficient.

Marchant and Nicholas (1974), on the other hand, also worked with a Rhabditid nematode (*Pelodera* sp.), but found much lower rates of ingestion and production than we did: ingestion 0.370 $J\ h^{-1}\ mg^{-1}$ dwt of nematodes, production 0.083 $J\ h^{-1}\ mg^{-1}$ dwt of nematodes. In the same units our estimates of ingestion are 2.62 for 11.5 d females, 1.69 for 11.5 d males, and 4.56 for 7.5 d juveniles. The production of 0.083 $J\ h^{-1}\ mg^{-1}$ dwt corresponds to a daily population birth rate ($P/B$) of about 0.08, to be compared with the value 0.44 for *M. disjuncta*.

The assimilation efficiency, defined as $(P+R)/I$, is much higher in *Pelodera* (0.598 compared with about 0.25).

Note, however, that implicitly different assumptions have been made regarding the source of the respired energy.

In their experimental set-up and interpretation, Marchant and Nicholas (1974) assume that the assimilated carbon is the immediate source of energy for the respiration. Our model on the other hand assumes that all the body carbon forms a pool from which a fraction is continually being respired.

Neither of the two will be exactly true. Nicholas et al. (1973) found that after a 24 h period, no less than 30% of the ingested carbon was present in the form of low molecular weight metabolites. This fraction probably represents the pool of organic mater forming the basis for anabolic metabolism.

Our model can be changed to accomodate other metabolic pathways. It is relatively easy to adjust it for the assumption that all assimilated energy is instantaneously divided in a part to be respired immediately, and a part to be built into stable compounds. Eq. 3 becomes:

$$\frac{dL}{dt} = i(1-r)G \qquad (13)$$

where $(1-r)$ is the fraction to be built in stable compounds. Working out this model, the estimate of $(i+f)$ remains unchanged. The estimate of $i$ is increased by a factor $1/(1-r)$, and $f$ changes accordingly to adjust the sum $i+f$.

Taking $r=0.30$, a crude estimate derived from the energy budget, we have for 11.5 d females, $i=0.28\ h^{-1}$ and $f=0.46\ h^{-1}$. The assimilation efficiency is 0.38. The value $212\ 10^{-6}$ J $h^{-1}$ $nem^{-1}$, the estimate of total assimilation in Table 2, now becomes the estimate of the production. Total assimilation is increased with an estimated $91\ 10^{-6}$ J $h^{-1}$ $nem^{-1}$ respiration. This model clearly fits less well with the energy budget observations.

In principle, it is also possible to model what is probably nearest to the true situation: besides the gut content and the stably incorporated organic matter a pool of labile organic compounds is defined from which material is drawn for either incorporation or respiration. Due to the extra parameters, this model can no longer be fitted to the experiments. However, qualitative investigations show that for parameter values which are compatible with the observations in the experiments, the results are in between those obtained with the other two model versions. In conclusion, we have good evidence that our estimates of assimilation rate and assimilation efficiency are probably somewhat low, but not too far from reality.

Intuitively, one would expect an inverse relationship between gut retention time (proportional to $1/(i+f)$) and assimilation efficiency. This is observed when 7.5 d juveniles are compared with adults. However, within the adults the males do not achieve higher efficiency than the females, despite their longer gut retention time. We suppose that a physiological limit may be approached near an efficiency of 0.30. This relatively low assimilation efficiency is in contrast with the very high net production efficiency.

High production efficiencies now seem to be a well-established feature in nematodes (Schiemer 1983; Warwick 1981; Woombs and Laybourn-Parry 1985). For *M. disjuncta*, as for other nematodes, this mainly results from the enormous egg production rate. During the embryonic development there is considerable respiration (weight loss from 0.023 µg to 0.014 µg). This "negative production" was explicitly incorporated in our budget calculations. We formerly suggested (Herman et al. 1984) that non-incorporation of this aspect could probably account for the very high efficiencies. This argument remains valid, but its quantitative importance seems limited.

Schiemer (1983) showed a linear relationship between the metabolic intensity paremeter $a$ in $R=aW^b$ ($R$ in nl $O_2$ $h^{-1}$, $W$ in µg wwt) and $r_{max}$ (the intrinsic rate of increase at the optimal temperature). *M. disjuncta* perfectly fits this relationship, which is a reflection of a similar production efficiency in the different species (This is only true because the species are of similar size; otherwise the exponent $b$ would trouble the picture, as $a$ would then be largely different from the weight-specific respiration for very large or very small organisms).

Apparently, the metabolic intensity of a species is a good indicator for its potential productivity. It is questionable, of course, if species also realise these potentials in the field. However, even if they do, their quantitative impact on the bacterial community in the sediments must be extremely limited. The mean consumption of bacteria by the nematodes in our experiment is 3 $d^{-1}$ (g dwt of bacteria/g dwt of nematodes). The standing stock of bacteria in a typical marine sediment is of the order of $10^{10}$ cells $ml^{-1}$ wet sediment. Many cells are very small: Montagna (1984) gives a mean weight of $2.48\ 10^{-14}$ gC per cell, or about $5\ 10^{-14}$ g dwt. Assuming the (unrealistic) high consumption rates from our experiments, a typical nematode community with a biomass of 0.3 g dwt $m^{-2}$, occurring in the upper 5 cm of the sediment, would consume 0.9 g $d^{-1}$ (dwt of bacteria), i.e. 3.6% of the bacterial biomass. These crude but maximal estimates suggest that nematodes may not be capable of regulating bacterial numbers: the turnover rate of nematode biomass would be 0.44 $d^{-1}$, more than 10 times higher than the turnover (due to nematode grazing) of the bacterial biomass.

The conclusions of these calculations are in apparent contrast with some experimental results. In organically enriched 'sediments', nematodes have been found to exert a stimulating influence on the bacterial metabolism (Abrams and Mitchell 1980; Findlay and Tenore 1982). It seems probable that the indirect effects, mainly bioturbation, are more important than direct grazing. With grazing rates in the order of a few percent per day, nematodes are not able to remove senescent cells quickly enough to stimulate bacterial growth in that way.

Abrams and Mitchell (1980) observe that the influence of nematodes is most pronounced in organically enriched sediments. They conclude from that observation that bioturbation effects may be more important than direct grazing. On the other hand, Alongi (1985) did not find any effect on bacteria by the nematodes in his experiments, although here too, the sediments were organically enriched.

Probably the difference in $N$-content between sewage sludge (Abrams and Mitchell 1980) and mixed cereal (Alongi 1985) may explain these different experimental outcomes, because bioturbation may be more important in nutrient-poor situations. Anyhow, this conclusion would also indicate that it is not nematode grazing per se which influences the bacteria.

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