Oecologia (Berlin) (1983) 58:326–331

Oecologia

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

P.M.J. Herman, C. Heip, and G. Vranken

Marine Biology Section, Zoology Institute, State University of Ghent, Belgium

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.

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$^0/_{00}$, with a mean of 19$^0/_{00}$. 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

---

Offprint requests to: C. Heip

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 $(10\ \text{cm}^2)^{-1}\ (5\ \text{y})^{-1}$.

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)/$(10\ \text{cm}^2 \times 5\ \text{year})$.

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

$$e^{-d_iD_i} = 1 - l_i.$$

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:

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

This can be compared to the actually observed surfaces A_i:

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

from which:

$$N_i = A_id_i/(1 - e^{-d_iD_i}). \tag{5}$$

The surviving fraction $e^{-d_iD_i}$ 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 $e^{-d_9D_9}$: since $N_9 = N_8e^{-d_8D_8}$, and d_9 was set equal to d_8 (ass. 2), we obtain:

$$e^{-d_9D_9} = \frac{A_9(1 - e^{-d_8D_8})}{A_8\, e^{-d_8D_8}} \tag{6}$$

in which the surfaces A_8 and A_9, and the factor $e^{-d_8D_8}$ are known from the observations.

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

$$N_iD_i = A_id_iD_i/(1 - e^{-d_iD_i}). \tag{7}$$

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:

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

ΣD_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:

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

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 $e^{-d_iD_i}$ 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. θ = 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 cm^2)) under the density curves of the different developmental stages (Fig. 1)

Stage	A_i (ind × days/(5 y × 10 cm^2))
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

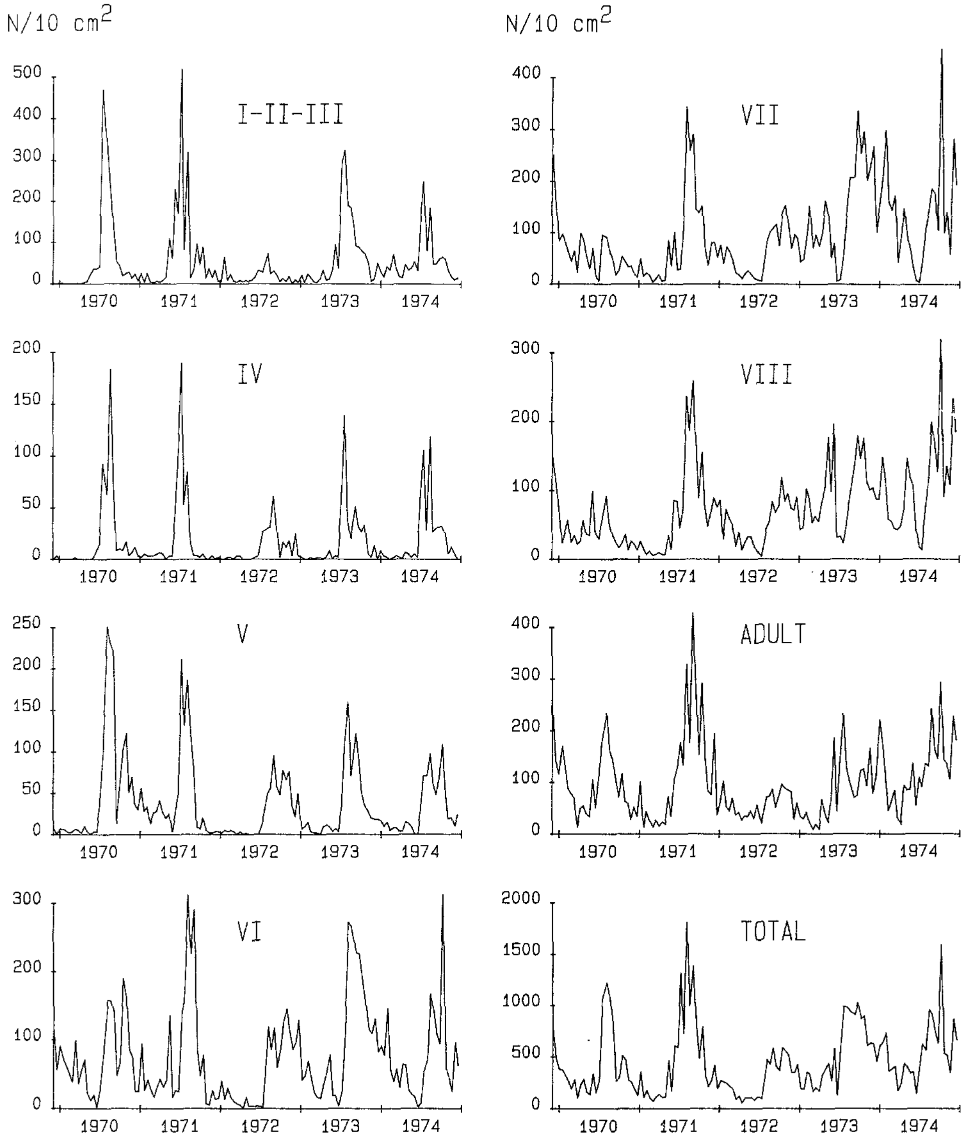

Fig. 1. *Cyprideis torosa*: Densities of the different developmental stages during the 5-year study period ($N/10\ \text{cm}^2$). Stages 1, 2 and 3 are combined, as they cannot be distinguished on the basis of size

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 $10\ \text{cm}^2$)

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 $10\ \text{cm}^2$ 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 $10\ \text{cm}^2$ 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 $\text{m}^{-2}\ \text{y}^{-1}$.

The mean biomass is 3.6 g dwt m^{-2}, and the yearly P/B is $2.7\ \text{y}^{-1}$. The oxygen consumption is estimated to be $20.38\ \text{l}\ \text{O}_2\ \text{m}^{-2}\ \text{y}^{-1}$.

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	$(W_j W_{j+1})^{1/2}$	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 $(W_j W_{j+1})^{1/2}$, 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.

The first two authors acknowledge a grant from the Belgian Fund for Scientific Research (NFWO). The third author acknowledges a grant from the Institute for the Encouragement of Scientific Research in Industry and Agriculture (IWONL). Part of this research was carried out within the program FKFO 2.0010.78. of the Fund for Collective Fundamental Research 'Productivity of Marine Ecosystems'.

References

Banse K, Mosher S (1980) Adult body mass and annual production/biomass relationships of field populations. Ecol Monogr 50:355–379

Barnett PRO (1968) Distribution and ecology of harpacticoid copepods of an intertidal mudflat. Int Rev ges Hydrobiol Hydrogr 53:177–209

Benke AC, Waide JB (1977) In defense of average cohorts. Freshwater Biol 7:61–63

Crisp DJ (1970) Energy flow measurements. In: Holme NA, McIntyre AD (eds) Methods for the study of marine benthos. Blackwell, Oxford, pp 197–279

Feller RJ (1977) Life history and production of meiobenthic harpacticoid copepods in Puget Sound. Dissertation Univ of Washington, Seattle, pp 249

Feller RJ (1980) Quantitative cohort analysis of a sand-dwelling meiobenthic harpacticoid copepod. Est Coast Mar Science 11:459–476

Fleeger JW, Palmer MA (1982) Secondary production of the estuarine meiobenthic copepod *Microarthridion littorale*. Mar Ecol Prog Ser 7:157–162

Gerlach SA (1971) On the importance of marine meiofauna for benthos communities. Oecologia (Berlin) 6:176–190

Hamilton AL (1969) On estimating annual production. Limnol Oeanogr 14:771–782

Heip C (1976) The life cycle of *Cyprideis torosa* (Crustacea, Ostracoda) Oecologia (Berlin) 24:229–245

Heip C (1977) On the evolution of reproductive potentials in a brackish water meiobenthic community. Mikrofauna Meeresboden 61:105–112

Heip C, Smol N (1976) Influence of temperature on the reproductive potential of two brackish-water Harpacticoids (Crustacea, Copepoda) Mar Biol 35:327–334

Herman PMJ, Heip C (1982) Growth and respiration of *Cyprideis torosa* Jones 1850 (Crustacea, Ostracoda). Oecologia (Berlin) 54:300–303

Humphreys WF (1979) Production and respiration in animal populations. J Anim Ecol 48:427–453

Manly BFJ (1977) A further note on Kiritani and Nakasuji's model for stage-frequency data including comments on the use of Tukey's jackknife technique for estimation of variances. Res Pop Ecol 18:177–186

McNeill S, Lawton JH (1970) Annual production and respiration in animal populations. Nature 225:472–474

Menzie CA (1980) A note on the Hynes method of estimating secondary production. Limnol Oceanogr 25:770–773

Salonen K, Sarvala J, Hakala I, Viljanen H (1976) The relation of energy and organic carbon in aquatic invertebrates. Limnol Oceanogr 21:724–730

Smol N, Heip C Govaert M (1980) The life cycle of *Oncholaimus oxyuris* (Nematoda) in its habitat. Annales Socr Zool Belg 110:87–103

Teare M, Price R (1979) Respiration of the meiobenthic harpacticoid copepod, *Tachidius discipes* from an estuarine mudflat. J exp mar Biol Ecol 41:1–8

Theisen BF (1966) The life history of seven species of Ostracods from a Danish brackish water locality. Meddelelser fra Danmarks Fiskeri og Havundersøgelser 4:215–270

Vranken G, Thielemans LK, Heip C, Vandycke M (1981) Aspects of the life cycle of *Monhystera parelegantula* (Nematoda, Monhysteridae). Mar Ecol Progr Ser 6:67–72

Warwick RM (1980) Population dynamics and secondary production of benthos. In: Tenore KR Coull BC (eds) Marine benthic dynamics. The Belle W Baruch library in marine sciences 11. Univ of South Carolina Press, pp 1–24

Warwick RM (1981) The influence of temperature and salinity on energy partitioning in the marine nematode *Diplolaimelloides bruciei*. Oecologia (Berlin) 51:318–325

Waters TF (1969) The turnover ratio in production ecology of freshwater invertebrates. Am Nat 103:173–185

Zaika VE (1973) Specific production of aquatic invertebrates. Halsted press. John Wiley, New York Toronto, pp 154

Received January 25, 1983