THE PRODUCTION OF TACHIDIUS DISCIPES GIESBRECHT 1881 (COPEPODA : HARPACTICOIDA).

Peter M.J. HERMAN, Carlo HEIP and Bernadette GUILLEMIJN.

Marine Biology Section, Zoology Institute
State University of Gent
Ledeganckstraat 35
B-9000 Gent
BELGIUM

68145

ABSTRACT.

The secondary production of the harpacticoid copepod
Tachidius discipes Giesbrecht 1881 was estimated during the
spring of 1979. The population was sampled every three days.
Three generation peaks were observed. These were clearly dis-
tinct in the first copepodite stages, but gradually showed
more overlap in older stages. Production of copepodites and
adults was estimated in two ways. In the first method
the peaks were separated, and the forward shifting of the
peaks in consecutive stages was used to estimate stage
durations. The second method was the size-frequency method.
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}
resp. The egg production amounts to 0.31 g dwt m^{-2}, and the
naupliar production is roughly estimated at 0.98 g dwt m^{-2}.
The production efficiency, P/(P+R), of copepodites and adults
is 0.36; for the total population it is 0.42. This value
corresponds well to the value estimated from culture experi-
ments with this population.

INTRODUCTION.

Marine benthic communities, and especially the meioben-
thic populations, are among the least studied from the point
of view of energetics. Only very recently have some papers
appeared dealing with direct production estimates of field
populations of meiobenthic crustaceans (Feller, 1982; Fleeger
& Palmer, 1982), but there is still not a single value for
a marine nematode population. The very limited information
available reveals that the productivity (measured by yearly
P/B) of meiobenthic populations can widely differ from the
very speculative and often used figure P/B = 9, proposed by
Gerlach (1971) on the basis of the life cycle characteristics
of two nematode species. However, whereas the use of one
single P/B value for all populations is spurious, the scaling
of P/B by body mass (Banse & Mosher, 1980) may be more useful
(Heip et al., 1982). This scaling reveals a remarkable pattern,
already anticipated by Banse & Mosher (1980), in that the
P/B - body weight line for meiobenthic populations lies con-
siderably lower than would be expected from the extrapolation
from 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 one ostracod (Herman & Heip;

MATERIAL AND METHODS.

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

Samples were taken every three days with a 6.06 cm^2 glass
corer, to a depth of 5 cm, and fixed in a neutralized 4 %
formaldehyde solution, heated to 70 °C. The animals 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 &
Bouwman, 1977).

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

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

In order to suppress the noise in the density data, a
weighted running mean was applied with length three and
weight factors 0.23, 0.54, 0.23 (Velleman, 1977). Inspection
of the density curves of the six developmental stages revealed
the existence of several peaks which can be interpreted as

seperate 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 Gaussians 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 expli-
citly (Bhattacharya, 1967).

The results of this analysis can be used for a production
estimate with the method of Rigler & Cooley (1974): the
means of the Gaussians 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:

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

where i denotes the stage number, D_i the duration (days)
of the stage i and N_i/D_i the number of animals present 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 the stage I the arbitrary duration of 1) by assuming exponential mortality. In the case of <u>T. discipes</u> we also need an estimate of the relative duration of egg + naupliar stages. This is provided by the culture experiments of Smol & Heip (1974) from which it can be concluded that this duration is 3/4 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:

$$N_e = \sum_t \frac{N_t \times c}{T_t} \times E \tag{2}$$

where summation is over all sampling dates t, c is the interval (days) between two samplings, T_t is the embryonic development time at the prevailing temperature at time t, and E is the number of eggs per egg sac. Both T_t and E are available from culture experiments by Smol & Heip (1974) and Heip & 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 exponenial, we have :

$$W_t = W_o \, e^{Gt} \tag{3}$$

$$N_t = N_o \, e^{-Z t} \tag{4}$$

with G and Z the instantaneous growth and mortality rates respectively.

Production is given by Allen (1971) as :

$$P = (G/(G - Z)) \, (N_T W_T - N_o W_o) \tag{5}$$

where N_O, W_O, N_T, W_T are numbers present and indiviual weight at time 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 animals 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 relationship (Allen, 1971)

$$P / B^{x} = G \tag{6}$$

which is valid in the case of exponential growth and mortality. Here B^{x} is the biomass - integral :

$$B^{x} = \int_{0}^{T.} N_t W_t \, dt \tag{7}$$

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 & Heip (in press a) with Cartesian Diver microrespirometry. 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.

The respiration of the nauplii 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

$$R_t = a W_o^{0.82} e^{0.82 G t} \tag{8}$$

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

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

$$= a ((N_T W_T^{0.82} - N_o W_o^{0.82}) / (0.82 G - Z)) \tag{9}$$

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 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.).

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

RESULTS.

The mean dry weight of the different stages, and the geometric mean weight of consecutive stages are given in Table I. Fig. 1 (a -f) shows the density curves of the copepodite and adult stages, with the combined fitted Gaussian distributions superimposed. We find three generations during the study period, well distinguished in the first stages, but gradually more overlapping in the older ones.

Table I : Tachidius discipes : dry weights W_i of the copepodite stages. N is the number of animals weighed in a batch. $(W_i W_{i+1})^{1/2}$ is the geometric mean of the weights of two consecutive stages.

STAGE	N	W_i (µg)	$(W_i W_{i+1})^{1/2}$
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 - f): Tachidius discipes : densities (N / 10 cm^2) of the 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.
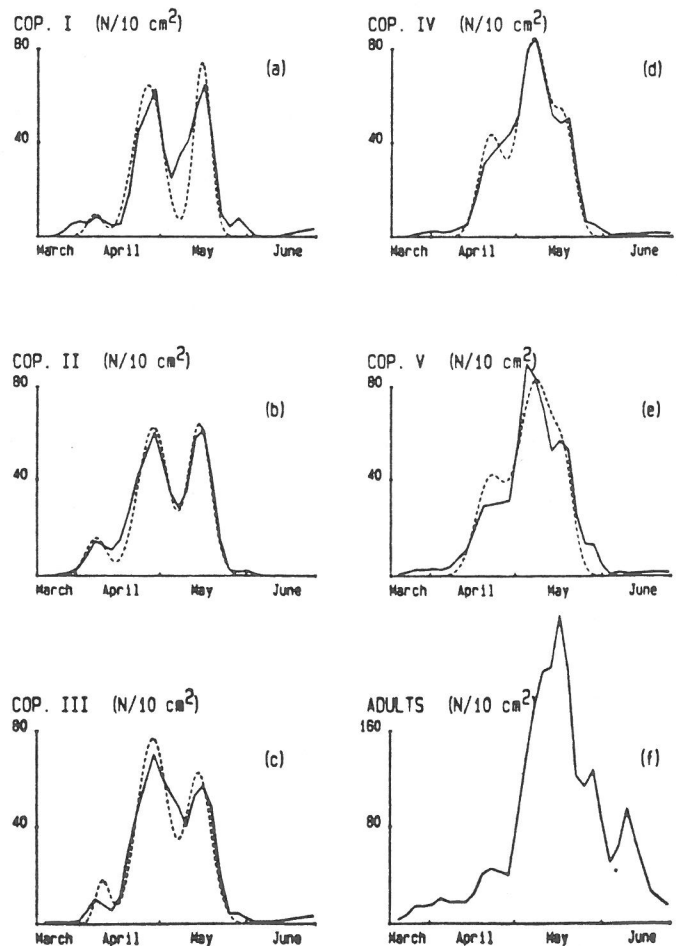
Fig. I

For the calculations of the stage duration with Rigler & Cooley's (1974) method it is necessary to draw a smooth curve on a plot of mean pulse times against stage numbers. Fig. 2 shows the effect of this smoothing. The only important modification is that the smoothed mean pulse time μ_s of copepodite IV in the first peak is shifted forward. The resulting stage durations and the number of animals in each stage are shown in Table II. A problem is posed by the adult stage. The method of Rigler & 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
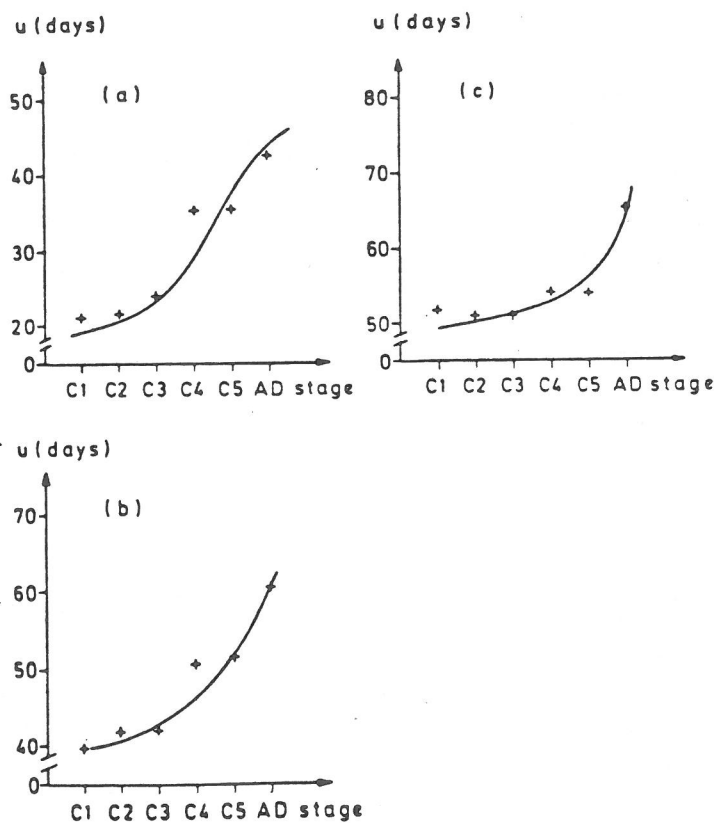

Fig. II (a -c): _Tachidius_ _discipes_ : mean pulse times of the
different developmental stages plotted against stage
numbers for the three peaks in the spring of 1979. The
smooth lines are used for the application of Rigler &
cooley's (1974) method.

Table II : Tachidius discipes : duration D of the copepodite
stages and number of animals recruited to the stage N
for the three peaks in the spring of 1979, determined
by the method of Rigler & Cooley (1974).

	STAGE	DURATION (days)	N = A/D (per 10 cm^2)
	COP I	0.85	79
	COP II	2.15	69
1° 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
2° 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
3° peak	COP III	1.30	536
	COP IV	1.30	302
	COP V	1.70	175

last longer and there is considerable mortality (as in the
adult stage, where all animals 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 the copepodite V animals
and the adult stage. The assumption that all copepodite V
animals become adult therefore introduces only a very light
bias, and circumvents the tricky problem of estimating
the adult stage duration. The production of copepodites
and adults thus calculated is 1.57 g dwt m^{-2}. This figure
includes the production of the biomass entering the copepo-
dite stage as copepodite I (see Material & 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 III 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 III : Tachidius discipes : production estimation by the size-frequency method. a_j is the relative duration of stage j (where a_1 is arbitrarily chosen as 1), $\overline{n}_j$ is the mean number of animals in stage j, N_j is an estimate of the recruitment into stage j, and "P_j" of the production of stage j.

STAGE	a_j	$\overline{n}_j$	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

The egg production, estimated by eq. (2) is: P_e = 0.31 g dwt m^{-2}. The number of eggs produced is 22048 per 10 cm^2.

The naupliar production, estimated by eq. (5) is: P_n = 0.98 g dwt m^{-2}.

The total production amounts to 2.39 g dwt m^{-2} and 2.31 g dwt m^{-2}, depending on whether the first or second estimate of P_c is used.

The duration of the copepodite stages is 23, 14.5 and 7.5 days for the three peaks. The duration of the naupliar stage is about half that of the copepodite stage (Smol & Heip, 1974). Using this experimentally obtained ratio, the duration of the naupliar phase is estimated to be 8 days. The biomass integral B^x for the nauplii then becomes: B^x = 2.62 g dwt x days x m^{-2}. The biomass integral for copepodites, adults and eggs is 22.77 g dwt x days x m^{-2}.

The mean biomass $\bar{B}$ = 25.39 / 99 = 0.26 g dwt m^{-2}. The P/$\bar{B}$ is 9.3 over the study period, or 3.1 per generation.

The respiration of copepodites and adults is estimated as R_c = 3.3 1 0$_2$ m^{-2} over the sampling period. Their production efficiency is 0.30.

When egg production is attributed to the adult population, the production efficiency becomes 0.36. With an estimated naupliar respiration of 0.97 1 0$_2$ m^{-2} (eq. (9)), the total population's production efficiency is calculated as 0.42.

DISCUSSION.

Tachidius discipes produced three generations in the spring of 1979. In a five-day interval sampling in 1980 (essential-ly aimed at another population) we could distinguish the same pattern. It was, as a whole, shifted to 10-12 days 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 animals should be subdivided into short-living stages in order to reveal the dynamics of a rapidly developing population such as _T. discipes_.

Due to this rapid development, the production of T. _discipes_ is relatively high. Expressed on a yearly base, it is about 9 g dwt m^{-2} y^{-1}. This is of the same order as the production of the larger (20 µg dwt adult weight)

ostracod <u>Cyprideis</u> <u>torosa</u> in the same habitat (Herman et
al., 1983). The P/$\overline{\text{B}}$ on a yearly base is 34. Compared to
other meiobenthic populations for which direct production
estimates have been made, <u>T. discipes</u> is a very productive
species. (Table IV).

The production efficiency of <u>Tachidius</u> <u>discipes</u> 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

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

Species	P/B (per year)	Authority
<u>Huntemannia jadensis</u>	3.6	Feller. (1982)
<u>Microarthridion littoralis</u>	18.0	Fleeger & Palmer (1982)
<u>Cyprideis torosa</u>	2.7	Herman et al. (1983)
<u>Tachidius discipes</u>	34.3	this study

detritivores (36 %). The formation of the two 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 over-
emphasized, 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, <u>T. discipes</u> 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.

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 two different populations. Table V gives 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 T. 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

Table V : Tachidius discipes : production efficiency calculated from culturing data of Heip & Smol (1976). See text for explanation.

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

quite important. Nevertheless, the production efficiency of about 42 % is very near to the predicted value of 43 % at 15 °C. This correspondence, corroborates the findings of Woodland & 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.

References.

Allen, K.R. (1971). Relation between production and biomass. J. Fish.Res.Bd.Canada 28 : 1573-1581.

Banse, K. (1982). Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. Mar.Ecol.Progr.Ser. 9 : 281-297.

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

Bhattacharya, C.G. (1967). A simple method of resolution of a distribution into Gaussian components. Biometrics 23: 115-135.

Crisp, D.J. (1971). Energy flow measurements. In: Methods for the study of marine benthos. IBP Handbook no.16. Blackwell Scientific publications, Oxford, pp. 197-279.

De Jonge, V.N. and L.A. Bouwman. (1977). A simple density separation technique for quantitative isolation of meio-benthos using the colloidal silica Ludox-TM. Mar.Biol. 42: 143-148.

Feller, R.J. (1982). Empirical estimates of carbon production for a meiobenthic harpacticoid copepod. Can. J. Fish. Aquat.Sci. 39 : 1435 - 1443.

Fleeger, J.W. and M.A.Palmer (1982). Secondary production of the estuarine meiobenthic copepod Microarthridion littorale. Mar.Ecol. Prog.Ser. 7 : 157 - 162.

Gerlach, S.A. (1971). On the importance of marine meiofauna for benthos communities. Oecologia (Berl.) 6 : 176-190.

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

Heip, C. (1979). Density and diversity of meiobenthic copepods: the oscillatory behaviour of population and community parameters. In: E. Naylor and R.G. Hartnoll, eds.: Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford,New York, pp. 43 - 47.

Heip, C. (1980). The influence of competition and predation on
    production of meiobenthic copepods. In: K.R. Tenore and
    B.C. Coull, eds.: Marine benthic dynamics. The Belle
    W. Baruch Library in Marine Science, No. 11. University
    of South Carolina Press, Columbia, pp. 167-177.

Heip, C., P.M.J. Herman and A. Coomans (1982). The productivity
    of marine meiobenthos. Academiae Analecta, 44: 1-20.

Heip, C. and N. Smol (1976). Influence of temperature on the
    reproductive potential of two brackish-water Harpacticoids
    (Crustacea, Copepoda). Mar. Biol. 45 : 255 - 260.

Heip, C., N. Smol and W. Hautekiet (1974). A rapid method for
    extracting meiobenthic nematodes and copepods from mud
    and detritus. Mar. Biol. 28 : 79-81.

Herman, P.M.J. and C. Heip. (1982). Growth and respiration of
    Cyprideis torosa Jones 1850 (Crustacea, Ostracoda).
    Oecologia (Berlin) 54: 300-303.

Herman, P.M.J. and C. Heip (in press a). The respiration of five
    brackish-water harpacticoid species. J. Exp. Mar. Biol.
    Ecol. 71.:

Herman, P.M.J. and C. Heip (in press b). Long-term dynamics of
    meiobenthic populations. Oceanologica Acta.

Herman, P.M.J., C. Heip and G. Vranken. The production of Cyprideis
    torosa Jones 1850 (Crustacea, Ostracoda). Oecologia
    (Berlin) 58: 326 - 331.

Humphreys, W.F. (1979). Production and respiration in animal
    populations. J. Anim. Ecol. 48: 427-453.

Muus, B.J. (1967). The fauna of Danish estuaries and lagoons.
    Distribution and ecology of dominating species in the
    shallow reaches of the mesohaline zone. Medd. Danm.
    Fisk. Havund. 5 : 1-316.

Rigler, F.H. and J.M. Cooley (1974). The use of field data
    to derive population statistics of multivoltine copepods.
    Limnol. Oceanogr. 19 : 636-655.

Salonen, K., J. Sarvala, I. Hakala and M. Viljanen (1976). The
    relation of energy and organic carbon in aquatic inver-
    tebrates. Limnol. Oceanogr. 21 : 724-730.

Schiemer, F. (1982a).Food dependence and energetics of freeliving nematodes I. Respiration, growth and reproduction of Caenorhabditis briggsae (Nematoda) at different levels of food supply. Oecologia (Berlin) 54 : 108-121.

Schiemer, F. (1982 b). Food dependence and energetics of freeliving nematodes. II. Life history parameters of Caenorhabditis briggsae (Nematoda) at different levels of food supply. Oecologia (Berlin) 54 : 122-128.

Schiemer, F., A. Duncan and R.Z. Klekowski (1980). A bio-energetic study of a benthic nematode, Plectus palustris de Man 1880, throughout its life cycle. Oecologia (Berlin) 44 : 205-212.

Smol, N. and C. Heip (1974). The culturing of some harpacticoid copepods from brackish water. Biol. Jb. Dodonaea 42 : 159-169.

Teare, M. (1979). Post-embryonic development of Tachidius discipes Giesbrecht 1881 (Copepoda, Harpacticoida). Cah.Biol.Mar. 19 : 343-353.

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

Velleman, P.F. (1977). Robust nonlinear data smoothers: definitions and recommandations. Proc. Natl. Acad. Sci. USA 74 : 434-436.

Winberg, G. (1971). Methods for the estimation of production of aquatic animals. Academic Press, London, New York. 175 pp.

Woodland, D.J. and S.C. Cairns (1980). Sensitivity of population energy efficiency indices to differences in mortality rates. Oecologia (Berlin) 46 : 214-216.