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

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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<sup>-2</sup> dry wt over the sampling period (March–November). Egg production is 1.23 g m<sup>-2</sup>; naupliar production is roughly 1.09 g m<sup>-2</sup>. 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<sup>2</sup>). 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 ( $\pm 0.1 \mu\text{g}$ ). 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  $\mu\text{g ind}^{-1}$ ; for females carrying eggs, three weighings yielded 1.26, 1.28, and 1.23  $\mu\text{g ind}^{-1}$ . 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

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

and  $i$  is the number of size classes,  $W_j$  the mean weight of an individual in size class  $j$  ( $\mu\text{g dry wt ind}^{-1}$ ),  $f_j$  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<sup>-1</sup>), and CPI the cohort

production interval (time needed to grow into the largest size class, days). If we multiply  $1/\text{CPI}$  (days<sup>-1</sup>) by the constant 365 d yr<sup>-1</sup>,  $365/\text{CPI}$  has dimensions yr<sup>-1</sup>.  $N_j$  therefore has dimensions number of individuals surface<sup>-1</sup> yr<sup>-1</sup>. 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 Dievangat 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  $365/\text{CPI}$  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

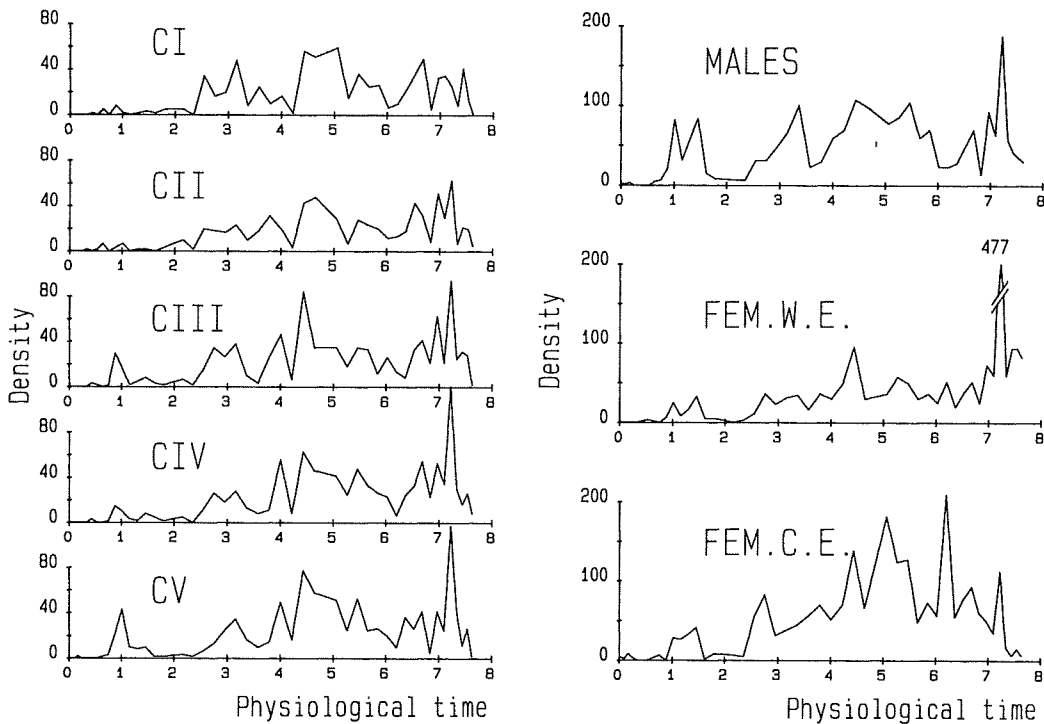


Fig. 1. *Paronychocamptus nanus*. Density (No. per 10 cm<sup>2</sup>) of the developmental stages on a physiological time scale (in units of developmental periods, see text). Females without eggs—FEM.W.E.; females carrying eggs—FEM.C.E.

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

$$f_j = \frac{f_{tj}}{\sum_j f_{tj}} \quad (6)$$

where  $f_{tj}$  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 1983a). 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	$N$	$W_j$ ( $\mu\text{g ind}^{-1}$ )
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  $j$ ;  $f_j$ —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  $j$ ; Prod $_j$ —estimate of the production of stage  $j$ .

Stage	$A_j$	$f_j$	$f_j$	$\bar{n}_j$ (ind 10 cm <sup>-2</sup> )	$N_j$ (ind 10 cm <sup>-2</sup> )	Prod $_j$ ( $\mu$ g 10 cm <sup>-2</sup> )
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<sub>2</sub> 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  $f_j$  of the copepodite stages (taking the duration of CI as 1) is 6.78 units, and the duration of egg + nauplius is estimated as  $6.78 \times 0.8 = 5.42$  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 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<sup>2</sup> dry wt.

The number of egg sacs produced is estimated as 3,961 per 10 cm<sup>2</sup>. 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<sup>2</sup> 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:  $P_t = 1,228 + 1,086 + 2,237 - (3,622 \times 0.09) = 4,225 \mu$ g per 10 cm<sup>2</sup> dry wt.

The mean biomass of the nauplii is estimated as 24  $\mu$ g per 10 cm<sup>2</sup>. For copepodites, adults, and eggs, it is 149  $\mu$ g per 10 cm<sup>2</sup>. The mean biomass of the total population is  $\bar{B}_t = 173 \mu$ g per 10 cm<sup>2</sup>. 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<sub>2</sub> per 10 cm<sup>2</sup> during the sampling period. Naupliar respiration is estimated as 0.86 ml O<sub>2</sub> per 10 cm<sup>2</sup>.

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<sup>-1</sup>. 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.

	<i>T. discipes</i>	<i>P. nanus</i>
Adult weight ( $\mu\text{g}$ dry wt)	1.8*	0.83
Egg weight ( $\mu\text{g}$ 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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