

Production of the meiobenthic harpacticoid copepod *Canuella perplexa*

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ABSTRACT: Secondary production of the meiobenthic harpacticoid *Canuella perplexa* T. & A. Scott, 1893 was estimated in a brackish water lagoon of the Po River Delta (Italy) from 1978 to 1979. The population was sampled approximately fortnightly with 3 replicate cores at a central, subtidal station. Three generation peaks and a nonproductive overwintering population were observed. Production of copepodites and adults was estimated by direct and indirect methods: (1) Crisp's specific growth rate method, applied both to the pooled C1 to adult stage and to each of the 5 copepodite and the adult stages separately; (2) the size frequency method; (3) the indirect method of the body mass-scaled turnover ratio. The 3 direct estimates of the annual production of copepodites and adults are quite similar: 6.76, 6.09 and 6.78 g dry wt m⁻². Egg production amounted to 0.02 g dry wt m⁻²; nauplii production was roughly estimated at 0.38 g dry wt m⁻². These values show a relatively constant P/B ratio per generation (between 3 and 4), as predicted by theoretical considerations, and agree with empirically-derived production estimates of other species. The indirect method gave an annual P/B value of 6.96, which underestimates production at 4.58 g dry wt m⁻². This is probably due to the weak dependence of the generation number on body mass for meiobenthic copepods.

INTRODUCTION

Secondary production continues to be a major focus of ecological research. Only recently, however, have meiobenthic populations become the subject of production studies that for other species were stimulated in the 1960s and 1970s by the International Biological Programme (Edmondson & Winberg 1971, Holme & McIntyre 1971, 1984, Downing & Rigler 1984). Even at the beginning of the 1980s, Warwick (1980) claimed that 'not a single field estimate of production of a meiofaunal species has been published to date' and, considering only meiobenthic crustaceans, just 4 empirically derived production estimates have been published since then: for 3 harpacticoids (Feller 1982, Fleeger & Palmer 1982, Herman et al. 1984) and one ostracod (Herman et al. 1983). This is surprising because studies on such organisms, in comparison to other groups, are more easily accomplished due to some of the biological characteristics of meiobenthic species such as short generation times and reaching an asymptotic body size after which growth stops and reproduction commences. On the other hand, field production estimates of meiofauna require frequent population samples, painstaking life history reconstructions, and size-specific growth rates estimated from labora-

tory cultures, which could discourage researchers from tackling the task.

Attempts at estimating the production of meiobenthic fauna in general, and of harpacticoids in particular (Heip 1980, Ceccherelli & Cortesi 1985), have also been performed by means of the indirect method of population turnover rates (P/B). Warwick (1980) warns of the problem of using turnover rates improperly although the simplicity of this method makes it appear more attractive. To date this procedure has been performed either using P/B values speculatively derived from the life cycles of only a few species (Gerlach 1971) or by scaling the P/B by body weight through an equation drawn up on the basis of a marginally small data set of production and biomass values of both aquatic and terrestrial invertebrates (Banse & Mosher 1980). The validity of extending general P/B ratios to all meiobenthic populations (or even to all animal populations) remains questionable because estimates of the few species analysed to date present wide disparities.

The present paper reports on production estimates of the meiobenthic copepod *Canuella perplexa* T. & A. Scott, 1893 carried out by means of 2 different direct methods and 1 indirect method in order to compare and discuss their respective reliability. *C. perplexa* is a relatively large (1.0 to 1.1 mm max length) epibenthic

harpacticoid, widely distributed and very common in brackish environments. In the shallow water embayment of the Po Delta studied here, it shows a protracted spring-summer breeding season and is the dominant species of the harpacticoid taxocoenosis (Ceccherelli et al. 1982). Therefore it is an appropriate species for production estimates, with the only drawback that the nauplii, with their planktonic habitus, easily escape core sampling.

MATERIAL AND METHODS

Sampling. *Canuella perplexa* was sampled in a central, 2.0 m deep, subtidal station of the Sacca di Scardovari, a brackish embayment of the Po River Delta, Italy. The site is characterized by a silt and clay sediment, with a median grain size of 0.007 mm. During the period of study, salinity fluctuated between 16 and 32 ‰ and temperature ranged from 26 °C on 3 August 1978 to 1 °C on 18 January 1979; the daily maximum temperature fell below 15 °C at the end of October and rose once more above that value in mid April (Cortesi 1980).

Three replicate 19.6 cm² cores were taken fortnightly from 9 May to 15 November 1978 and from 23 March to 26 April 1979; and monthly from 15 November 1978 to 23 March 1979. The first 5 cm of each core was sieved through a 71 µm mesh net, and all living material fixed in 5 % buffered formaldehyde solution and stained with Bengal rose. All copepodite stages and adults (males, females and ovigerous females) of *Canuella perplexa* from 1/8 or 1/16 of each sample, obtained with an Elmgren (1973) subsampler, were then identified (Vincx & Heip 1979) and counted. Ovisacs were removed from gravid females and the egg number per ovigerous female was assessed.

Dry weight. For dry weight determination, samples were gathered in September 1983 and in May 1984. Copepods were sorted alive and placed in artificial seawater and carbon-free sand (700 °C for 2 h) for 24 h in order to allow them to clear their guts and scrape their cuticle clear of bacterial epibionts. They were then sacrificed with buffered formalin, immediately identified according to stage and rinsed 2-fold in double distilled water. Replicate batches of 60 to 150 individuals belonging to the same developmental stage were dried for 24 h at 60 °C and weighed using an electrobalance with a precision of 0.1 µg. Eight developmental stages were weighed separately (Table 1). Egg weight was estimated by the difference between the mean weight of egg-carrying females and that of other ovigerous females of the same sample after removal of ovisacs, the eggs of which were separately counted and averaged.

Table 1. *Canuella perplexa*. Mean dry weights of stages. Number of batches weighed per stage and total number of individuals per batch are also given

Stage	$W_j \pm SD$ (µg)	No. of batches	No. per batch
C1	0.354 ± 0.060	3	150
C2	0.570 ± 0.130	3	150
C3	1.135 ± 0.450	3	150
C4	2.075 ± 0.353	3	100
C5	3.860 ± 0.744	3	80
Adult male	5.136 ± 1.056	3	60
Adult female	8.304 ± 1.472	3	60
Ovigerous female	10.059 ± 0.355	3	60

Direct production calculations. In order to achieve a production estimate for *Canuella perplexa*, calculations were performed by different methods. For each of the 3 calculation methodologies, production during the winter (15 November 1978 to 23 March 1979) was assumed to be zero since field data on population dynamics of *C. perplexa* (see 'Results') showed a diapausing, nonproductive biomass during that period.

Copepodite and adult production: Crisp's (1984) instantaneous growth method 3A (production for stocks with recruitment, age classes not separable) was adapted to the pooled developmental stage C1 to Adult. Annual production was estimated as:

$$P = \sum \sum f_i G_i w_i t \quad (1)$$

where f_i = number of individuals of the i^{th} size group (developmental stage) during the time interval t between 2 consecutive sampling dates; w_i = mean weight of that size group; and G_i = weight-specific growth rate. Assuming exponential body growth (G), described by $w_{\text{max}} = w_{\text{min}} e^{\text{DG}}$ (Rigler & Downing 1984), it follows that

$$G = (1/D) \ln(w_{\text{max}}/w_{\text{min}}) \quad (2)$$

where D = temperature-related development time for a particular stage.

Laboratory estimates of D , at different temperatures, were drawn from Vincx (1977) (Table 2) as the developmental time of a *Canuella perplexa* specimen growing from w_{min} to w_{max} of the considered stage. Vincx's D value increased with a temperature rise from 20 to 25 °C whereas a decrease would have been expected. This was probably due to the difficulty of rearing *C. perplexa* (as we, too, unsuccessfully tried) because, very frequently, a film of bacteria is formed around the individuals, which must be removed from older copepodites with a fine needle (Vincx & Heip 1979). The bacterial growth evidently increases with increasing temperature and causes delayed development of affected specimens. In spite of this, Vincx's values are

Table 2. *Canuella perplexa*. Temperature-related developmental times (D) for the various stages reared in laboratory. * Values used for the production calculation: n1 = first nauplius; C1 = first copepodite; Ad. = adult (male/female); Ov. = ovigerous; fem. = female. Values in brackets were estimated by means of the Krogh curve from values at 20 °C (see text). (From Vincx 1977)

Rearing temperature (°C)	D Egg-n1 (d)	D n1-C1 (d)	D C1-Ad. (d)	D Ad.fem.-Ov.fem. (d)
15	10.2	29.3*	(36.7)*	(37.7)*
20	3.9	9.7*	23.4*	24.0*
25	2.9	7.4*	33.3*	25.0*

the only estimates of D for *C. perplexa* at present available.

Production of all copepodite stages, and of adults, was thus calculated by growth rates estimated on the basis of Vincx's mean D values closest to the prevailing field temperature. Unfortunately, Vincx (1977) did not measure developmental time of copepodites at 15 °C, so we extrapolated D by applying a correction according to the 'normal' Krogh curve (Edmondson & Winberg 1971) to the experimental D at 20 °C.

Because of the remarkable difference in weight between adult males and females, production was calculated separately for the 2 sexes. Assuming that the male/female ratio in the copepodite population reflects that of the adults, the mean C1 to C5 biomass at each sampling interval was proportioned to the male/female biomass ratio in the adult population at the subsequent sampling date.

In the growth rate estimation, w_{\min} is always the mean weight of a C1; for the biomass of C1 to C5 specimens which differentiate as males, w_{\max} is the mean weight of males; for the biomass of C1 to C5 specimens which differentiate as females, w_{\max} is the 'basic female weight', i.e. the geometric mean of the weight of females without eggs and the weight of C5 (Rigler & Downing 1984).

An attempt was made to refine the production estimate taking into account density values of each copepodite stage which, in the above calculation, were all pooled across Stage C1 to adult.

In order to assign D values for each of the 5 copepodite stages, the assumption was made that time doubles between each subsequent moult (Table 3). To simplify calculations, values used for the period 9 May to 11 October 1978 were calculated from an interpolated developmental time from C1 to Adult of 28.4 d (mean of D at 20 and 25 °C). In calculating G from 11 October to 15 November 1978 and from 23 March to 26 April 1979, the estimated C1 to Adult developmental time of about 36.7 d, derived for 15 °C by means of the Krogh curve, was used. In the calculation of growth rates it was possible to use the actual mean weights of each copepodite stage at each sampling date.

The different numbers of C5 entering the last moult either to male or to female were proportioned according to sex densities in the next sampled adult population and the 'basic female weight' (Rigler & Downing 1984) was once more assumed as w_{\max} of adult female stage.

As an independent test of the whole procedure, copepodite and adult production of *Canuella perplexa* was also estimated by the size frequency method (Menzie 1980) as modified for the analysis of populations grouped in developmental stages by Herman et al. (1983). This method gives an approximation of the duration of each stage by assuming exponential mortality. Moreover the duration of Stage C1 was arbitrarily considered as 1 time unit, so that the duration of all subsequent larval stages is calculated in relative units. The formulation for this method is:

$$P = \sum (N_j - N_{j+1}) (W_j W_{j+1})^{1/2} \quad (3)$$

where N_j is defined as:

$$N_j = i n_j (P_e/P_a)_j 365/CPI \quad (4)$$

and i = number of size-classes (stages); n_j = mean number of individuals in size-class (stage) j ; $P_e = 1/i$ = estimated proportion of the life-cycle spent in size-class (stage) j ; P_a = actual proportion of the life-cycle spent in size-class (stage) j ; CPI = cohort production interval. $(W_j W_{j+1})^{1/2}$ = geometric mean weight between 2 size-classes (stages). (See Menzie 1980 and Herman et al. 1983 for further explanation.)

Table 3. *Canuella perplexa*. Estimated developmental times (D) for each copepodite stage, under the assumption of doubling time intervals between each subsequent moult, used in different months for the calculation of production showed in Table 5

Period	D C1-C2 (d)	D C2-C3 (d)	D C3-C4 (d)	D C4-C5 (d)	D C5-Ad. (d)	D ^a C1-Ad. (d)
9 May-11 Oct	0.9	1.8	3.7	7.3	14.7	28.4
11 Oct-26 Apr	1.2	2.4	4.7	9.5	18.9	36.7

^a See text for explanation

It was not possible to accept a unique value of CPI, the 'cohort production interval', in days from hatching to reaching the adult stage (Benke 1979) because of the different *Canuella perplexa* growth rates during the year. Therefore, as suggested by Menzie (1980), it was necessary to estimate production for 2 periods shorter than a year (cumulative 255 d for the period 9 May to 28 October 1978 plus 23 March to 26 April 1979, and 97 d for the remaining winter months). In the first period we assumed a CPI of 82 d, derived from the time interval between 2 consecutive summer adult peaks (from 6 July to 26 September 1978) in the population density trend (see Fig. 1). In the second period a CPI of 97 d was assumed owing to the absence of reproduction during the winter (see 'Results').

The above-mentioned methods provide estimates for copepodite and adult production only; thus further calculations were needed to assess egg and naupliar production which were then added to each of the 3 above estimates of copepodite and adult production.

Nauplii production: For naupliar production Allen's (1971) method was followed (see also Herman et al. 1984). Assuming that in the naupliar phase both growth and mortality are exponential, we have $w_t = w_o e^{Gt}$ and $N_t = N_o e^{-Zt}$ which make it possible to calculate growth rate G and mortality rate M in the production equation:

$$P = (G/G-M) (N_t w_t - N_o w_o) \quad (5)$$

(considering Gt and Mt as $\ln(w_t/w_o)$ and $-\ln(N_t/N_o)$ respectively, the factor t disappears in the division $G/(G-M)$. N_o = the mean number of eggs counted in each time interval because, assuming zero egg mortality in the ovisac, the number of eggs could be considered equal to the number of first stage nauplii (n_1); N_t = the mean number of C1 in the subsequent time interval; w_o = a rough estimate of n_1 weight obtained by reducing the weight of an egg by 20 % (weight of egg and ovisac membranes) (Rigler & Downing 1984); and w_t = the mean weight of a C1.

Since different methods were applied in calculating production of nauplii and copepodites, the production of C1 was calculated twice. Its value should have been subtracted from the copepodite production: however, this subtraction would actually have been possible only in the second application of Crisp's method; moreover, since the naupliar production estimate was less reliable owing to more uncertain assumptions, we preferred to leave it as it was and to admit a generalized slight overestimation of *Canuella perplexa* production.

Egg production: Production due to eggs was estimated by means of the method of growth increment summation (Rigler & Downing 1984). While eggs are

carried in an ovisac before hatching, we may consider egg mortality = 0. Assuming that all eggs mature at the same constant rate, production can be estimated as:

$$P = N(w_{\max} - w_{\min})/D \quad (6)$$

where $w_{\min} = 0$; w_{\max} = the mean weight of an egg (0.045 μg); and D = Vincx's developmental time for egg (time for a female to produce the egg sac) related to the temperature of each sampling interval (Table 2). Once again we had to estimate developmental time at 15 °C (37.7 d) by means of the Krogh curve.

Indirect production calculation. Secondary production of *Canuella perplexa* was also estimated by means of the indirect method of turnover ratio derived by scaling the annual P/B value on species body mass at sexual maturity, proposed by Banse & Mosher (1980). These authors, on data of 48 species of aquatic and terrestrial (but with aquatic larvae) invertebrates, fitted a set of generalized log-log equations (here after 'B & M equation') of the form:

$$\log P/B = \log a + b \log M_s \quad (7)$$

where P = cumulative production rate ($\text{kcal m}^{-2} \text{yr}^{-1}$); B = mean biomass (kcal m^{-2}); and M_s = body mass at sexual maturity (kcal). Banse & Mosher (1980), having only one field datum, did not estimate equation parameters specifically for meiofauna. However, they hypothetically proposed a temperate meiofauna line lying considerably below that of larger benthic invertebrates but with the same slope. Heip et al. (1982), using published data on developmental times, estimated the number of yearly generations of 6 species of meiobenthic crustaceans and 10 species of nematodes. They argued that, when a generation $P/B = 3$ is postulated, it was possible to derive approximate production data which, in general, were in agreement with the B & M equation. Subsequently, on those same data, Ceccherelli & Cortesi (1985) calculated the parameters of the resulting B & M equation as: $b = -0.39 \pm 0.07$ and $\log a = -0.90 \pm 0.38$ ($r = -0.83$), which are in the range of those posited by Banse & Mosher (1980).

Estimating *Canuella perplexa* production by the latter equation, the mean body mass of male plus female adults was considered as M_s and the actual mean biomass of the population over the entire year was calculated. The mean biomass of copepodites, adults and eggs was obtained by dividing their biomass integral by the days of the investigations (352 d). The mean biomass of nauplii was derived by Allen (1971) relation $P/B^x = G$, where B^x is the biomass integral (see also Herman et al. 1984). Once again, in order to estimate G , naupliar developmental times were derived from Vincx (1977) (Table 2).

As the B & M equation is formulated using kcal, the

energetic conversion 1 g dry wt = 5.3 kcal (Peters 1983) was used in processing data.

From the matrix of 95 % confidence limits of average densities of various stages at each sampling date and from weights of copepodites and adults, the 95 % confidence limits of population mean biomass (except nauplii) were also calculated. Consequently, we were able to approximate 95 % confidence limits of the copepodite and adult production estimates by multiplying the 95 % confidence limits of mean biomass by the P/B ratios, obtained with the 3 above direct calculation procedures.

RESULTS

In Fig. 1 the seasonal trend of the main parameters of the *Canuella perplexa* population are shown.

The mean number of eggs per ovigerous female, when present, ranged from 31 on 3 August 1978 to 89 on 26 April 1979. Another persistent peak of fecundity

was evident during late summer and early autumn, coinciding however with a sharp decrease in the percentage of egg-carrying females during the latter period. No eggs at all were present from 15 November to 23 March, when the overwintering population started reproducing once more. This led us to assume there was no reproduction during the winter.

The proportion of ovigerous females among the total number of adult females was quite high in spring and summer with values constantly over 50 %. Besides the obvious decrease approaching the winter season, another decline in the density of ovigerous females was evident in June, when the overwintering female generation had probably exhausted its spring reproductive effort. Overall, considering the 2 highest spring values (9 May 1978 and 6 April 1979) as analogous, 3 reproduction peaks occurred which most likely mean that the species has 3 generations annually.

The sex ratio in the adult population was close to 1:1 throughout the year except in spring and late summer when the number of females appeared to prevail

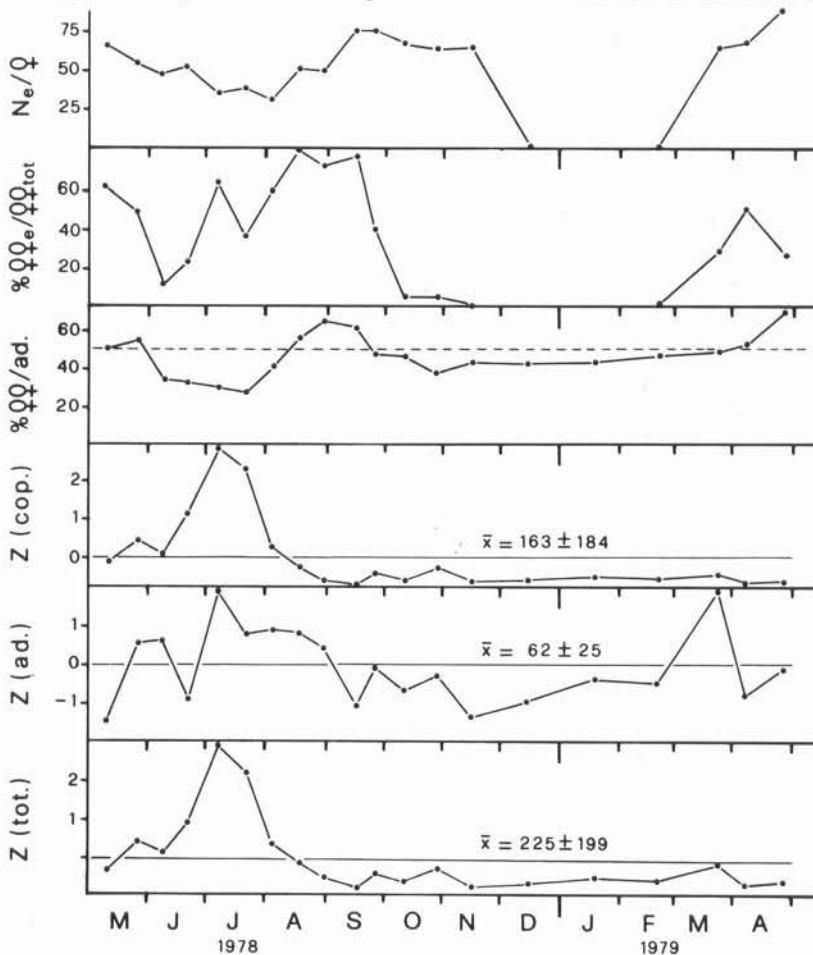


Fig. 1. *Canuella perplexa*. Mean parameters of population in the period under investigation. Mean number of eggs per ovigerous female, percentage of gravid females over the total number of females, percentage of females over the total of adults, standard normal deviate (Z) values of copepodites, adults and total harpacticoid population. Annual mean densities (ind. 10 cm⁻²) ± standard deviations are also indicated

slightly over males. A lower percentage of females was evident in June and July, when the female/male ratio decreased to about 1:3. This was probably due to the time lag in the life cycle of the 2 sexes (Heip 1980).

The standard normal deviate ($Z = [X - \mu] / \sigma$; Snedecor & Cochran 1967) values of copepodite densities were close to 0 (mean value) practically throughout the year. A massive increase in the copepodite population was evident from May to July (Z over +2), while another slight peak of copepodite density, although not as evident as the first, was recorded in late summer-early autumn. It is worth noting that the overwintering copepodites were only C4 and C5 and that their densities were fairly constant. Very likely they were in diapause during cold season and this fact, together with the absence of reproduction, makes it possible to assume no population productivity during winter.

Z values for adults showed larger fluctuations and peaked especially in July, when the yearly maximum of total population occurred, and in March, when the overwintering C4 and C5 moulted into adults to restart reproduction. Other adult density increases were recorded in May–June, after the 9 May 1978 peak of ovigerous females, and again in summer–early autumn. Since copepodites were the dominant life history stage, the yearly trend of total population Z values was strongly affected by them.

Average total biomass was obtained by summing the biomass integral of nauplii ($1.99 \text{ g m}^{-2} \text{ d}^{-1}$) and that of copepodites and adults (males, nongravid females and ovigerous females) ($229 \text{ g m}^{-2} \text{ d}^{-1}$) and dividing by

352 d of investigations. C5 and adults accounted for most of the biomass present throughout the year. Annual mean biomass of the *Canuella perplexa* population amounted to 0.658 g m^{-2} (0.006 and 0.652 g m^{-2} for nauplii and copepodites plus adults respectively). The 95 % CL of population mean biomass (except nauplii) are 0.312 and 0.989 g m^{-2} .

Production estimates of copepodites and adults depended on the calculation method adopted.

In Table 4 data for a secondary production estimate of *Canuella perplexa* calculated by the age (stage) specific growth rates method are reported. Total production for the period under investigation amounted to $6.763 \text{ g m}^{-2} \text{ yr}^{-1}$: $3.0 \text{ g m}^{-2} \text{ yr}^{-1}$ for males and $3.7 \text{ g m}^{-2} \text{ yr}^{-1}$ for females. The corresponding annual P/B (for a mean B of 0.652 g m^{-2}) is 10.37 which allows us to indirectly estimate the range of 95 % CL from 3.2 to $10.3 \text{ g m}^{-2} \text{ yr}^{-1}$.

The amount of copepodite and adult production obtained by applying the specific growth rate method to each copepodite stage (Table 5) is $6.085 \text{ g m}^{-2} \text{ yr}^{-1}$ ($P/B = 9.33 \text{ yr}^{-1}$), with 95 % CL from 2.9 to $9.2 \text{ g m}^{-2} \text{ yr}^{-1}$.

Data for the production estimate obtained with the size-frequency method are given in Table 6. Production due to the 5 copepodite stages and to adults is $6.778 \text{ g m}^{-2} \text{ yr}^{-1}$ ($P/B = 10.40 \text{ yr}^{-1}$), with 95 % CL from 3.2 to $10.3 \text{ g m}^{-2} \text{ yr}^{-1}$. Naupliar production estimated by Allen's method was $0.382 \text{ g m}^{-2} \text{ yr}^{-1}$. Mean number of eggs produced during the period under investigation was $626\,250 \text{ m}^{-2} \text{ yr}^{-1}$, corresponding to an egg production of $0.02 \text{ g m}^{-2} \text{ yr}^{-1}$.

Table 4. *Canuella perplexa*. Production (P) of the stage C1 to Adult for 1978–79 by the specific growth rate (G) method. Separate calculations for production estimates of males (B_m , G_m) and females (B_f , G_f) are reported. Dashes indicate winter zero production (see text)

Dates	t (d)	B_m (g m^{-2})	G_m (d^{-1})	B_f (g m^{-2})	G_f (d^{-1})	P ($\text{g m}^{-2} \text{ yr}^{-1}$)
9 May–25 May	16	0.106	0.108	0.210	0.118	0.579
25 May–7 Jun	13	0.200	0.108	0.207	0.118	0.599
7 Jun–20 Jun	13	0.229	0.108	0.174	0.118	0.589
20 Jun–6 Jul	16	0.388	0.108	0.246	0.118	1.134
6 Jul–20 Jul	14	0.491	0.076	0.323	0.083	0.897
20 Jul–3 Aug	14	0.306	0.076	0.225	0.083	0.587
3 Aug–17 Aug	14	0.086	0.076	0.186	0.083	0.308
17 Aug–30 Aug	13	0.038	0.076	0.130	0.083	0.178
30 Aug–16 Sep	17	0.017	0.108	0.067	0.118	0.165
16 Sep–26 Sep	10	0.046	0.108	0.097	0.118	0.164
26 Sep–11 Oct	15	0.071	0.108	0.135	0.118	0.354
11 Oct–28 Oct	17	0.114	0.108	0.130	0.118	0.470
28 Oct–15 Nov	18	0.084	0.069	0.146	0.076	0.304
–	–	–	–	–	–	–
23 Mar–6 Apr	14	0.075	0.069	0.147	0.076	0.228
6 Apr–26 Apr	20	0.013	0.108	0.076	0.118	0.207
Total annual production ($\text{g m}^{-2} \text{ yr}^{-1}$)		6.763				

Table 5. *Canuella perplexa*. Production by developmental stage for 1978–79 by specific growth rate method. Each column is like the P ($\text{g m}^{-2} \text{yr}^{-1}$) column of Table 4 calculated for each stage. Dashes indicate winter zero production (see text)

Dates	Developmental stage					
	C1–C2	C2–C3	C3–C4	C4–C5	C5–Male	C5–Fem.
9 May–25 May	0.074	0.092	0.127	0.111	0.026	0.082
25 May–7 Jun	0.078	0.093	0.079	0.111	0.030	0.049
7 Jun–20 Jun	0.022	0.150	0.154	0.134	0.035	0.037
20 Jun–6 Jul	0.196	0.389	0.320	0.193	0.031	0.074
6 Jul–20 Jul	0.211	0.407	0.241	0.181	0.091	0.120
20 Jul–3 Aug	0.063	0.093	0.182	0.192	0.045	0.100
3 Aug–17 Aug		0.014	0.068	0.136	0.009	0.043
17 Aug–30 Aug	0.004	0.007	0.106	0.069	0.004	0.033
30 Aug–16 Sep	0.009	0.021	0.037	0.033	0.006	0.021
16 Sep–26 Sep		0.007	0.036	0.023	0.012	0.024
26 Sep–11 Oct		0.037	0.047	0.047	0.022	0.041
11 Oct–28 Oct		0.025	0.038	0.099	0.045	0.061
28 Oct–15 Nov		0.009	0.029	0.061	0.017	0.033
–	–	–	–	–	–	–
23 Mar–6 Apr				0.028	0.014	0.049
6 Apr–26 Apr			–0.002	0.012	0.008	0.030
Total by stage	0.657	1.344	1.462	1.430	0.395	0.797
Total production for entire time period	6.085 $\text{g m}^{-2} \text{yr}^{-1}$					

Table 6. *Canuella perplexa*. Data for the production estimate by the size-frequency method. A_j = summed surfaces under the density curves of the j^{th} and all subsequent size categories (developmental stages); $e^{-\theta a_j} = A_{j+1}/A_j$ ratio; θ = mortality rate; a_j = relative duration of the j^{th} stage, where a_1 is arbitrarily chosen equal to 1; N_j = number of individuals growing to the j^{th} stage ($N \times 10 \text{ cm}^{-2}$); $(W_j W_{j+1})^{1/2}$ = geometric mean weight between 2 subsequent stages, except for Ad., where the mean adult population weight is reported (μg); P_j = production of the j^{th} stage ($\text{g m}^{-2} \text{yr}^{-1}$) (see Herman et al. 1983 for further explanation)

Stage	A_j	$e^{-\theta a_j}$	a_j	N_j	$(W_j W_{j+1})^{1/2}$	P_j
C1	72169	0.941	1.0	2106.2	0.449	0.092
C2	67932	0.875	2.199	1900.9	0.804	0.206
C3	59469	0.844	2.794	1645.0	1.535	0.723
C4	50221	0.733	5.142	1172.9	2.830	1.197
C5	15133	0.589	8.758	749.9	4.995	0.985
Ad.	21663		16.530	552.7	6.468	3.575
Total C1–Ad. production ($\text{g m}^{-2} \text{yr}^{-1}$)	6.778					

Summing up the above different values for stage production gives 3 total estimates which appear quite consistent.

Total annual production estimated by applying Crisp's method to the broader Stage C1 to Adult is $7.165 \text{ g m}^{-2} \text{yr}^{-1}$. Annual P/B is 10.89 yr^{-1} (for a mean B of 0.658 g m^{-2}). Refining the estimation by applying Crisp's method to each of the 5 copepodite developmental stages, a value of $6.487 \text{ g m}^{-2} \text{yr}^{-1}$ is obtained, yielding a P/B ratio value of 9.86 yr^{-1} . Calculating copepodite and adult production by means of the size-frequency method gives a total annual production of $7.180 \text{ g m}^{-2} \text{yr}^{-1}$, with a P/B of 10.91.

The calculation method by means of the B & M equation (Table 7) yielded the lowest estimate. A derived P/B ratio of 6.96 yr^{-1} was obtained corresponding to a production value of $4.58 \text{ g m}^{-2} \text{yr}^{-1}$.

Table 7. *Canuella perplexa*. Production calculated by the indirect method of the P/B ratio, estimated by means of the Banse & Mosher log-log equation:

$$\log P/B = -90 - 0.39 \log M_s$$

Adult body mass M_s (kcal)	Turnover ratio P/B (yr^{-1})	Annual mean biomass B (g m^{-2})	Production P ($\text{g m}^{-2} \text{yr}^{-1}$)
3.4×10^{-5}	6.96	0.658	4.58

DISCUSSION

Depending on season, *Canuella perplexa* represents from 32 to 99 % of the harpacticoid fauna of the Sacca di Scardovari (Ceccherelli et al. 1982). It is present

throughout the year in the muddy bottom of that embayment, but the curve of the percentage of females carrying eggs indicates that it has roughly 3 generations per year: a spring generation starting in April–May, a summer generation corresponding with the highest population density peak in July and the late summer-early autumn generation from August to mid-September. This last generation shows a decrease in the first copepodite stages and a recruitment of the C4 and C5 and adult stages which make up the bulk of the overwintering population. These survive the cold season, suspending reproduction, until the next spring when reproductive activity begins. Using long-term records in a brackish water pond in northern Belgium, Herman & Heip (1983) studied a *C. perplexa* population which showed, in most years, 2 generations annually. The slight discrepancy between their population life cycle and the present one could easily be explained by latitudinal differences in climate.

To estimate the production of *Canuella perplexa*, direct and indirect methods were used here because of the biases possibly introduced by the simplifying assumptions that characterize each method. With Crisp's (1984) method 3A individual growth rates are measured on the basis of developmental times as functions of size (stage) and season (temperature).

Production values obtained by both the simplest specific growth rate method applied to the global C1 to Adult stage and the refined, but time-consuming, method applied stage by stage are quite similar: 7.165 and 6.487 g m⁻² yr⁻¹ respectively (with corresponding P/B ratios of 10.89 and 9.86). This suggests that, in the second case, assuming geometric progression of developmental times of copepodite stages is reasonable. Overall, assessing annual production by splitting the whole copepodite population according to developmental stage and calculating different growth rates for each stage at each date, may not have been worth the effort in the present case.

The weakness of Crisp's method is the underlying assumption that laboratory growth occurs at similar rates as for field populations. Therefore, another independent estimate was obtained using a procedure which did not consider developmental times. The size-frequency method estimates production by determin-

ing the numbers of individuals removed between successive size categories (stages). This has a different kind of bias, assuming a constant mortality rate in all copepodite stages. Once again, however, a value was obtained which is quite close, 7.180 g m⁻² yr⁻¹ (P/B: 10.91), to that obtained with the Crisp method. On the one hand, this adds some confidence to our estimates and, on the other, it seems to provide good evidence that, although obtained under difficult laboratory conditions, Vincx's developmental times for *Canuella perplexa* are probably not so dissimilar from those in the field.

Very few papers have dealt with empirically derived production estimates from field populations of meiobenthic harpacticoids. For the large (ca 1.1 mm), abundant, sand-dwelling *Huntemannia jadensis*, Feller (1982) calculated production values ranging from 1.88 to 4.38 g m⁻² yr⁻¹ on 3 intertidal sand beaches in Puget Sound, Washington, USA. Fleeger & Palmer (1982) calculated about 0.14 g m⁻² yr⁻¹ for the small (ca 0.54 mm), less abundant, mud-dwelling *Microarthridion littorale* in a South Carolina (USA) salt marsh (North Inlet estuary). Finally, for the similar sized (ca 0.60 mm) but denser, epibenthic *Tachidius discipes* in a brackish water pond of northern Belgium, Herman et al. (1984) assessed a production of 2.44 to 2.52 g m⁻² during 99 spring days (the period of mass occurrence of this species).

Although production estimates of all these species, including the present one on *Canuella perplexa*, appear very different, it is interesting to note the corresponding values of the cohort's turnover ratios (P/B) shown in Table 8. With the exception of *Microarthridion littorale*, they are very similar and constant. Moreover they are also very close to the value of 3.5 which, according to Waters (1969), represents the mode (range about 2.5 to 5) of the turnover ratios per generation for any biologically sound model of growth and mortality.

The anomalous value of *Microarthridion littorale* could be disputed. Fleeger & Palmer (1982) measured, during another year, a production for *M. littorale* much lower than that reported in Table 8. That particular year may prove to be an unusual one, with abundances and production much higher than the average year.

Table 8. Number of generations (No.), P/B and cohort turnover ratio (TR) for meiobenthic harpacticoids determined from field observations

Species	No.	P/B	TR	Source
<i>Huntemannia jadensis</i> (yr ⁻¹)	1	3.7	3.7	Feller (1982)
<i>Microarthridion littorale</i> (yr ⁻¹)	12	18.0	1.5	Fleeger & Palmer (1982)
<i>Tachidius discipes</i> (99 d ⁻¹)	3	9.7	3.2	Herman et al. (1984)
<i>Canuella perplexa</i> (yr ⁻¹)	3	10.6	3.5	This study

Moreover, the way Fleeger (1979) estimated the number of 12 overlapping generations (Table 8) could be questioned. It was inferred by assuming a general value of copepod developmental time of 3 wk, which was derived, in turn, by laboratory estimates of 2 different species made by Heip & Smol (1976). Subsequently, Palmer & Coull (1980) calculated generation times (egg to egg) for *M. littorale* collected in the same salt marsh and reared in the laboratory. They reported a generation time of 21.6 d but only at 33 °C; at 25 °C, this increased to 29.6 d and, at 15 °C, it was estimated to ca 70 d. Furthermore, the intertidal salt marsh where *M. littorale* production was studied by Fleeger & Palmer (1982) was a highly unpredictable environment affected by wide short-term temperature fluctuations and exposure to both desiccation and rain (Palmer 1980). It is thus conceivable that the actual number of generations of that species in the field was lower than expected from laboratory cultures. For example, if the putative 12 cohorts of *M. littorale* were reduced to 8, we would obtain the value 2.25 for the P/B ratio per generation, which is closer to the other values shown in Table 8 and to the range of theoretical values suggested by Waters (1969). Hence, it seems that harpacticoid populations, too, conform to that rule, although more studies on harpacticoid production would be required to confirm this.

The method of scaling the P/B ratio by species body-mass at sexual maturity (Banse & Mosher 1980) is attractive for its simplicity, and has also been used by other investigators (Heip 1980, Tremblay & Roff 1983, Ceccherelli & Cortesi 1985, Asmus 1987). However, the principal assumption of the B & M model, that organisms of similar size will have similar turnover rates, has been harshly criticized (Feller 1982, McLaren & Corkett 1984) and the present estimates of *Canuella perplexa* production by this method must be interpreted judiciously.

The P/B value for *Canuella perplexa* (Table 7) has here been estimated (see 'Material and methods') by means of a B & M equation. Parameters were calculated (Ceccherelli & Cortesi 1985) on the basis of an array of annual turnover ratios of meiobenthic crustaceans (*Huntemannia jadensis* and *Tachidius discipes* included) and nematodes derived from published data on species-specific developmental times and postulating a P/B per generation of 3. In light of the above discussion on Table 8 data, the latter assumption can now be judged reasonable. Thus the above B & M equation is most likely the best for meiofauna at present. Nevertheless it gives a yearly P/B ratio of 6.96 for *C. perplexa* which appears to be an underestimate in comparison to the mean value obtained by the direct methods (Table 8). This strong discrepancy is the consequence of the fact that the equation would predict

about 2 generations per year for a relatively large-sized harpacticoid such as *C. perplexa*, whereas it actually shows 3 annual generations in the present environment.

It seems that, among copepods, developmental rates, number of yearly cohorts and by implication P/B ratios are not related to body mass, particularly when development is continuous and food abundant (McLaren & Corkett 1984) as in brackish environments. That a general relationship exists overall between body size and life history traits is indubitable (Banse & Mosher 1980, Peters 1983) but that such a relationship may not apply within a given taxon of small organisms, like meiobenthic copepods, also appears to be the case as confirmed by the present investigation.

The least one can say is that a great deal of more data are needed before it becomes possible to refine the relationship and to establish unique equations according to taxonomic and ecological groups.

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