Influence of Temperature on the Reproductive Potential of Two Brackish-Water Harpacticoids (Crustacea: Copepoda)

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Abstract

The reproductive potential of two harpacticoid copepods, *Tachidius discipes* and *Paronychocamptus nanus*, as measured by the intrinsic rate of natural increase, r_m, has been studied. The influence of temperature on all factors used in the calculation of r_m has been taken into account. Generation time, which has also been determined in a third species, *Nitocra typica*, is the single factor which is most affected by temperature and which has the most pronounced effect on r_m. Values of the reproductive potential differ considerably according to temperature, and thus to the time of the year; during the spring bloom more than half the reproductive potential is realized.

Introduction

It is well known that, after the nematodes, harpacticoid copepods are numerically the most important group of meiobenthic animals in all marine and brackish-water areas (McIntyre, 1969). They are comparatively even more important when taking into account their larger biomass and the fact that copepods may serve as food for larval fishes and contribute to the exploitable yield of the ocean, whereas nematodes are very often on top of the food chain. Knowledge of the production of copepods is important in assessing the suitability of certain habitats for aquaculture and fish farming. Estimation of this production requires the knowledge of such parameters as biomass, generation time and reproductive potential.

The reproductive potential of a species can be measured with the intrinsic rate of natural increase r_m; this is a parameter which measures the speed with which a population will increase in the absence of limiting factors. It is thus a measure of production in an unlimited environment. The estimation of r_m can be performed as follows: when there are no factors limiting, growth of the population will be exponential and can be described by:

$$N_t = N_o e^{r_m t},\qquad(1)$$

in which N_t is the number at time t, and N_o is the initial number. From this we obtain:

$$r_m = \frac{1}{t}\ln\frac{N_t}{N_o}.\qquad(2)$$

For $t = D$, the generation time (2) becomes:

$$r_m = \frac{1}{D}\ln\frac{N_D}{N_o}.\qquad(3)$$

N_D, the number in the population after one generation, is equal to the number of offspring per female multiplied by the percentage of females in the population. This number may contain the number which has died during the interval; however, this factor is of only minor importance. Consider that all N_o individuals present at the beginning of the interval die during it. The number of individuals after D days will be $N_D - N_o$, and r_m will modify to:

$$r_m = \frac{1}{D}\ln(\frac{N_D}{N_o} - 1).\qquad(4)$$

Provided N_D is large enough, this will cause only a minor change in the calculation of r_m.

Taking $N_D = N_e' p'$, with N_e' the number of eggs produced by a female, and $p' = pN_o$ the number of females in the

original population, we obtain from Eq. (3):

$$r_m = \frac{1}{D} \ln pN_e' . \qquad (5)$$

In Harpacticoida and Cyclopoida, eggs are deposited in a single or in two egg-sacs which are carried by the female. As a female may produce several subsequent egg-sacs, we may further modify Eq. (5) to obtain:

$$r_m = \frac{1}{D} \ln pN_e N_s \#, \qquad (6)$$

in which N_e is the number of eggs per egg-sac and N_s is the number of egg-sacs produced by a female.

From Eq. (6) it is clear that the value of r_m will be determined largely by the generation time, D. As this generation time in turn will depend largely on temperature, every calculation concerning the production of these populations must include a study of the influence of temperature on the generation time.

Most work on the development time of copepods has been concentrated on Calanoida and Cyclopoida, with a preponderance of fresh-water studies. Harpacticoid copepods have been nearly neglected; although there are some studies on the duration of development without precise reference to temperature (see Muus, 1967, and Rosenfield and Coull, 1974, for reviews of earlier studies), the only two species which we know to have been studied with respect to the influence of temperature are *Tisbe dilatata* (Muus, 1967) and *Euterpina acutifrons* (Haq, 1972). Moreover, *E. acutifrons* is not a typical harpacticoid copepods, as it is one of the few planktonic representatives of this group.

Materials and Methods

Three species of harpacticoid copepods were cultivated: *Tachidius discipes* Giesbrecht, 1882; *Paronychocamptus nanus* (Sars, 1908) and *Nitocra typica* Boeck, 1864. Specimens were collected regularly from a brackish-water pond in northern Belgium. The methods used to cultivate these species have been discussed by Smol and Heip (1974); they were cultivated on a diet of algae (*Tetraselmis suecica* and *Phaeodactylum tricornutum*) with addition of a small amount of detritus from the habitat. Food was always in excess. Temperature was kept constant with a precision of 0.1C° by using water baths which were adjusted at 0°, 5°, 10°, 15°, 20° and 25°C. Cooling of the baths was performed

with a kryothermat (Haake KT32) and heating with a thermostat (Bühler TH2).

Fecundity of the female *Tachidius discipes* and *Paronychocamptus nanus* was determined by examination of the number of eggs per egg sac of females from field populations and by counting the number of egg sacs produced by females in the laboratory.

Information on the sex ratio of natural populations was obtained from an earlier 4-year study (Heip, 1973b).

Difficulties arose in the calculation of the generation time, and as the value of r_m is very sensitive to variations in the value of D, we will outline the procedure we followed. In agreement with many authors we at first defined generation time as the time elapsed between the appearance of the same stage in two subsequent generations, and we took the mean time elapsed between the appearance of females carrying eggs of two subsequent generations as the generation time. However, we realized that this is only correct when the number of egg sacs is one. Indeed, when simulating life tables for these species it soon became apparent that the mean generation time becomes longer as the number of egg sacs increases. For these simulations we used the result of an experiment which recorded the number of egg sacs produced by 5 females at room temperature (about 20°C). These females produced between 5 and 7 egg sacs, with a 3-day interval between egg sacs; this was true for both *Tachidius discipes* and *Paronychocamptus nanus*. We then performed many simulations in which we calculated life tables with different patterns of mortality and numbers of egg sacs; from these simulations is appeared that, for the type of mortality which is to be expected, i.e., a very low mortality until adulthood (see "Discussion"), the intrinsic rate of natural increase can be estimated best with:

$$r_m = \frac{1}{D_1} \ln pN_e , \qquad (7)$$

in which D_1 is the time elapsed between the appearance of females carrying eggs in two subsequent generations, and N_e is the mean number of eggs per egg sac. Unless very detailed data are available which allow for the construction of life tables based on knowledge of the exact number of egg sacs produced by a female, the error made is less by calculating r_m from Eq. (7) than by calculating it from Eq. (6), in which knowledge of the real generation time is required. The difference between estimates of r_m based on (6) or (7) becomes progressively smaller as generation time increases.

Table 1. Mean time (in days) before appearance of nauplii (N), copepodites (C) and females carrying eggs (A) in 3 species of harpacticoid copepods. x: More than 105 days; -: no data

Culture temperature (°C)	Tachidius discipes N	C	A	Paronychocamptus nanus N	C	A	Nitocra typica N	C	A
25	2.1	5.7	13.9	2.0	7.5	18.6	-	-	-
20	2.3	7.3	17.3	2.4	9.4	22.0	3.3	8.7	16.7
15	2.5	10.4	25.1	3.3	13.8	29.1	4.0	9.3	21.3
10	4.1	18.3	41.5	6.6	21.6	48.4	3.0	17.0	47.0
5	8.6	37.1	83.0	13.8	53.5	x	13.3	46.0	x

Table 2. Application of $D = aT^b$ to describe influence of temperature on development of 3 harpacticoid copepod species. Time (in days) between appearance of females carrying eggs in two successive generations. x: more than 105 days. Exp.: expected, Obs.: observed values; -: no data

Culture temperature (°C)	Tachidius discipes $(D = 527\ T^{-1.13})$ Exp.	Obs.	Paronychocamptus nanus $(D = 528\ T^{-1.05})$ Exp.	Obs.	Nitocra typica $(D = 1489\ T^{-1.52})$ Exp.	Obs.
25	13.9	13.9	18.0	18.6	11.2	-
20	17.9	17.3	22.7	22.0	15.7	16.7
15	24.7	25.1	30.7	29.1	24.3	21.3
10	39.1	41.5	47.1	48.4	45.0	47.0
5	85.5	83.0	97.4	x	129.0	x

Results

Table 1 shows D_1, the mean time elapsed between the appearance of females carrying eggs in two successive generations, for the three species. It is clear that D_1 is strongly dependent on temperature. Description of the relationship between temperature and generation time has, in the case of marine calanoids, been traditionally performed by the use of the equation of Belehradek: $D_1 = a\ (T - \alpha)^b$, in which a, b and α are constants. The use of this equation originates from McLaren (1963), to whom the reader is referred for further interpretation of the parameters. However, the equation has been criticized (Winberg, 1971; Heip, 1974; Bottrell, 1975). Heip (1974) compared different equations and concluded that the simple power equation $D_1 = aT^b$ gives a good fit to the data. In this equation, a and b are constants.

The results of the application of the power equation are given in Table 2. The equation for the three species are: Tachidius discipes, $D_1 = 527\ T^{-1.13}$ ($r = 0.998$). Paronychocamptus nanus, $D_1 = 528\ T^{-1.05}$ ($r = 0.99$); Nitocra typica, $D_1 = 1489\ T^{-1.52}$ ($r = 0.98$). From Table 2 it is clear that the agreement between the observed values and the values calculated accord-

ing to the power equations is very good. The numbers of eggs per female were determined for Tachidius discipes and Paronychocamptus nanus from field populations. For both species, the values were not significantly different between months. The material for Nitocra typica was not sufficient to permit statistically meaningful estimates of the number of eggs; however, it is certain that this species lays less eggs than the other two. The mean number of eggs per egg sac was 19 for P. nanus (mean from 88 females) and 41 for T. discipes (mean from 73 females).

For both species where the mean number of eggs per egg sac could be determined, Eq. (7) can be written more explicitly as:

Tachidius discipes:
$$r_m = \frac{\ln(p \times 41)}{527\ T^{-1.13}}\ ; \qquad (8)$$

Paronychocamptus nanus:
$$r_m = \frac{\ln(p \times 19)}{528\ T^{-1.05}}\ ; \qquad (8')$$

The percentage of females in the adult population, p, was determined from an ongoing study of field populations. The percentage of females is far from being constant throughout the year in

Table 3. Percentage of females of 2 harpacticoid copepod species. Mean values of samples from wild populations grouped in classes corresponding to mean temperature of fortnight preceding sample date. -: Population absent from samples

Temperature ($^{\circ}$C)	Tachidius discipes	Paronychocamptus nanus
0.0- 3.9	47.1	87.0
4.0- 7.9	69.4	84.0
8.0-11.9	62.9	74.6
12.0-15.9	67.0	65.2
16.0-19.9	68.9	72.4
20.0-23.9	-	65.5

Table 4. Reproductive potential, measured as r_m/day, and doubling time, t_2 (in days), at different temperatures for 2 harpacticoid copepod species

Temperature ($^{\circ}$C)	Tachidius discipes		Paronychocamptus nanus	
	r_m	t_2	r_m	t_2
5	0.039	17.8	0.028	24.8
10	0.085	8.2	0.057	12.2
15	0.134	5.2	0.083	8.4
20	0.186	3.7	0.113	6.1
25	0.239	1.8	0.142	4.9

either species. Mortality is higher in males than in females, resulting in a large excess of females at the end of the winter (up to 90% in March) in *Paronychocamptus nanus*. During the spring bloom, the percentage of males increases very rapidly, and approaches a maximum of about 40% in May. The percentage remains around 40% until the end of October and then decreases, in some years almost linearly, until March (Heip, in preparation).

In *Tachidius discipes*, which is present from February to May, June or July, the percentage of females is more constant, varying between 50 and 80%; this value decreases towards the end of the period during which the species is present.

In order to determine the relationship between the percentage of females in natural populations and temperature, the values of p were grouped in temperature classes corresponding to the mean temperature of the fortnight preceding the sample date. It is clear from Table 3, in which these values are given, that, except for low temperatures where the species does not reproduce at all, the percentage of females is nearly constant for *Tachidius discipes*; a value of $p = 0.67$ has therefore been used in subsequent calculations. The percentage of female *Paronychocamptus nanus* changes as a function of temperature, but appears to approach a minimum value at higher temperatures which is nearly the same as the average value for *T. discipes* (mean of three lowest values of $p = 0.68$). At lower temperatures the increase in p is nearly linear, and can be described by $p = 0.92 - 0.0168\ T$ from 2° to 14°C.

Selected value of r_m at different temperatures [calculated from Eqs. (8) and (8')] are given in Table 4. From this table it is clear that temperature has a profound influence on the reproductive potential of these species. This is perhaps more easily visualized when comparing the doubling time. This time can be calculated as $t_2 = (\ln 2)/r_m$ (see Table 4).

It has been shown (Heip, 1973b) that water temperature in this habitat can be described as a simple sinusoidal function of time. Regression of water temperatures measured daily and averaged over every fortnight for 3 years gave:

$$T = 11.2 + 8.3 \sin (t-117). \qquad (9)$$

This relationship predicts a maximum average temperature of 19.5°C on July 26 and a minimum temperature of 2.9°C on January 26. When the yearly temperature cycle as described by Eq. (9) is known, it is possible to calculate reproductive potentials (or corresponding doubling times) during a yearly cycle. This can be done by introducing Eq. (9) into Eqs. (8) and (8'). Because p is known, these equations now become:

Tachidius discipes: $r_m =$

$$\frac{1}{159.07\ (11.2 + 8.3 \sin (t-117))^{-1.13}} \qquad (10)$$

Paronychocamptus nanus: (a) $r_m =$

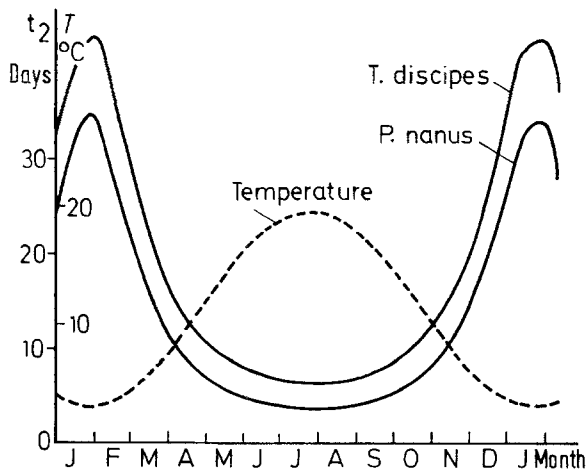$$\frac{\ln\ (0.92-0.0168(11.2 + 8.3\sin(t-117))\times19)}{528(11.2 + 8.3 \sin (t-117))^{-1.05}} \qquad (10')$$

Fig. 1. *Tachidius discipes* and *Paronychocamptus nanus*. Reproductive potential measured as doubling time, t_2, during a yearly cycle.

$$\text{(b)} \quad r_m = \frac{1}{206.35 \ (11.2 + 8.3 \sin \ (t-117))^{-1.05}}$$

$$(T<14°C)$$
$$(T>14°C).$$
$$(10'')$$

The annual cycle of the reproductive potential of the two species calculated in this way is shown in Fig. 1 as doubling times. It is clear that there are very large differences according to season: in winter the capacity for reproduction is low, and it takes nearly 6 weeks for *P. nanus* and nearly 5 weeks for *T. discipes* to double the size of their population, even in an unlimited environment. In summer, the corresponding times are only between 3 and 8 days.

Discussion

The influence of temperature on the reproductive potential of the harpacticoid copepods *Tachidius discipes* and *Paronychocamptus nanus* is profound. Values of the intrinsic rate of natural increase, r_m, vary between 0.039/day at 5°C and 0.239/ day at 25°C for *T. discipes*, and between 0.028/day at 5°C and 0.142/day at 25°C for *P. nanus*. The corresponding times needed to double the population numbers are between 17.8 days (5°C) and 2.9 days (25°C) for *T. discipes* and between 24.8 days (5°C) and 4.9 days (25°C) for *P. nanus*. From these results it is clear that every attempt to extrapolate values of the reproductive potential obtained from laboratory experiments to natural situations has to take the effect of temperature into account.

Another factor which might influence reproductive potential is food (Weglenska, 1971). This has not been studied here, but the composition of the food has been tested (Smol and Heip, 1974) and food was always given in excess of requirements; in this way this factor will be largely eliminated as a source of variation in the calculations of r_m.

One factor which has not been considered in the calculation of r_m is mortality during the postembryonic period. Survival from eggs to adults has been calculated by several authors. Volkmann-Rocco and Fava (1969) and Volkmann-Rocco and Battaglia (1972) took survival from the egg until the adult stage into consideration when calculating the reproductive potential of *Tisbe* species. However, mortalities have to be extrapolated from laboratory experiments, and it can be argued that values obtained in this way will be maximum values. There is no advantage in a process which allows for a high percentage of mortality due to genetically inbuilt mechanisms; of course, due to the very nature of evolutionary processes, there will always be a certain number of offspring not fit to survive. However, this number will be smaller than that inferable from mortality observed in laboratory experiments. Survival from egg until adulthood was more than 80% in most cases in both species (Smol and Heip, 1974), and the same high survival has been observed by Muus (1967) in several species, including *Tachidius discipes*. These low mortalities, when taken into account, would not modify the r_m value very much. We tested this in many simulations based on the assumption that the number of eggs per egg sac does not change with age (this being true except for the last egg sacs produced by a female). Moreover, the use of Eq. (7) yields values which are even closer to life-table values using moderate values for mortality (30% or less from egg until adulthood). One can demonstrate the low impact of mortality by using Eq. (4), taking $N_D = 0.80 \times pN_e$. For *Tachidius discipes* at 5°C, $r_m = 0.036$ per day, instead of $r_m = 0.039$ per day using Eq. (7).

Mortality during embryonic development is also very low. To test this we counted the number of nauplii in the cultures and compared this with the number of eggs per egg sac in field populations. For *Paronychocamptus nanus*, $n_e = 19$ and the number of nauplii = 17 ± 0.8; for *Tachidius discipes* $n_e = 41$ and the number of nauplii = 38 ± 1.0.

In the power equation, the parameter *b* measures the degree to which temperature influences development time, since

Table 5. Value of b, from the power equation $D = aT^b$ relating development time and temperature, for different copepod species and for various developmental stages

Species	b	Source
Cyclopoida		
Cyclops abyssorum	-1.06	Smyly (1973)
C. abyssorum	-0.71	Lewis *et al.* (1971)
C. vicinus	-0.74	Munro (1974)
C. vicinus	-0.76	Munro (1974)
C. vicinus	-1.58	Spindler (1971)
Thermocyclops hyalinus consimilis	-1.65	Burgis (1970)
Calanoida		
Calanus finmarchicus	-0.79	Marshall and Orr (1953)
C. helgolandicus	-0.52	Corkett (1972)
C. hyperboreus	-0.51	McLaren *et al.* (1969)
C. glacialis	-0.44	McLaren *et al.* (1969)
Eurytemora hirundoides	-0.80	Corkett and McLaren (1970)
E. affinis	-0.79	Katona (1970)
E. affinis	-0.92	Verreth (1974)
E. herdmani	-0.58	Katona (1970)
Pseudocalanus minutus	-0.60	Corkett and McLaren (1970)
Acartia clausi	-0.96	McLaren *et al.* (1969)
A. tonsa	-2.38	McLaren *et al.* (1969)
Metridia longa	-0.58	McLaren *et al.* (1969)
Centropages furcata	-2.53	McLaren *et al.* (1969)
Tortanus discaudatus	-0.91	McLaren *et al.* (1969)
Temora longicornis	-1.21	Corkett and McLaren (1970)
Diaptomus pallidus	-1.59	Geiling and Campbell (1972)
Eudiaptomus gracilis	-1.02	Munro (1974)
E. gracilis	-1.17	Munro (1974)
E. gracilis	-1.15	Eckstein (1964)
Acanthodiaptomus denticornis	-1.43	Eichhorn (1957)
Mixodiaptomus lacinatus	-1.02	Eichhorn (1957)
Harpacticoida		
Euterpina acutifrons	-1.98	Haq (1972)
Tisbe dilatata	-1.45	Muus (1967)
Tachidius discipes	-1.13	Present paper
Nitocra typica	-1.52	Present paper
Paronychocamptus nanus	-1.05	Present paper

it is the slope of the plot of log T versus log D. In Table 5, values of b have been calculated from different literature sources. It is interesting that the mean value for the three orders of copepods is nearly equal: close to -1. The calculation of a mean slope has been rightly criticized by Bottrell (1975) but, as even this author admits, its use may be justifiable for general surveys of entire ecosystems or when detailed experiments are lacking. The mean values of b are: Cyclopoida -1.08 ± 0.18 (n = 6); Calanoida -1.04 ± 0.13 (n = 21); Harpacticoida -1.42 ± 0.16 (n = 5). The larger value for the Harpacticoida largely results from the high value for *Euterpina acutifrons*, which is not a benthic but a planktonic species. When this species is not taken into account, the value of b reduces to -1.29. Furthermore, the value of b for the two harpacticoid species in which this parameter has been most adequately determined is still lower; it appears therefore unjustified to postulate a higher impact of temperature on the development of harpacticoids than of other copepods until more data are available.

Taking $b = -1$, the power equation reduces to $DT = a$, which is the equation of a hyperbola. This formula can be modified to include the possibility of a temperature asymptote other than $T = 0$ by writing $D = a/(T -a)$. In this equation, a represents a biological zero, a value below which no development takes place. Calculation of a from this equa-

tion yields: *Tachidius discipes:* 1.65°C; *Paronychocamptus nanus:* 0.24°C; *Nitocra typica:* 4.33°C. There is a close agreement between these values of α and the temporal succession of the three species as observed by Heip (1973a): *P. nanus* has a much longer reproductive period than the other species and in spring *N. typica* appears later than both other species.

Values of the reproductive potential of other harpacticoid copepods are scarce. We can, however, compare our values with those of Volkmann-Rocco and Fava (1969) and Volkmann-Rocco and Battaglia (1972). These authors reported r_m values as follows: *Tisbe reluctans:* 0.102/day at 18°C; *T. persimilis:* 0.088/day at 18°C; *T. clodiensis:* 0.187/day at 18°C; *T. dobzhanskii:* 0.291/day at 18°C. These values are of the same magnitude as those found by us, which would be at 18°C: *Tachidius discipes:* 0.165/day and *Paronychocamptus nanus:* 0.101/day.

It has been shown (Heip, 1972) that the rate of natural increase realized by these populations during the exponential growth phase of the spring bloom is not very different between species, values of 0.040 to 0.060/day being found. Taking the mean temperature during the bloom into account, the intrinsic rate of increase would be 0.065/day for *Tachidius discipes* and 0.051/day for *Paronychocamptus nanus*. This demonstrates that more than half the reproductive potential of these species is realized during the spring bloom, over a period of several weeks.

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