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LIFE HISTORY OF *TANYMASTIGITES PERRIERI* (ANOSTRACA) IN RELATION TO TEMPERATURE

BY

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ABSTRACT

Growth, longevity, and reproduction of *Tanymastigites perrieri* (Daday, 1910) have been studied under standardized laboratory conditions at six different temperature regimes: 10, 20, 25, 30, 35, and 40°C. The development D of the shrimps as a function of the temperature T is expressed as $K = D(T - C)$. The temperature at which development stopped is $C = 4.32^\circ\text{C}$, while K is a thermal constant, the number of degrees-days above threshold, or the physiological time ($K = 719$ degrees-days). The highest growth rate occurred at 25°C. The greatest body size, however, was attained in animals reared at 10°C (22 mm). Longevity decreased with increasing temperatures (from 41 days to 4 days). Maturation time was inversely related to temperature (from 20 days to 4 days; at 40°C no larvae survived). Offspring per individual varies with temperature (maximum 447 eggs at 20°C); while the innate capacity for increase, r , fluctuates between 0.07 and 0.34.

RÉSUMÉ

La croissance, la longévité et la reproduction de *Tanymastigites perrieri* (Daday, 1910) ont été étudiés sous des conditions standardisées au laboratoire et sous 6 différentes températures: 10, 20, 25, 30, 35, et 40°C. Le développement D de l'espèce en fonction de la température est exprimé par $K = D(T - C)$. La température sous laquelle le développement s'achève est $C = 4,32^\circ\text{C}$, et $K = 719$ degrés-jours, représentant la constante thermique, le degré au-dessus du seuil ou le temps physiologique. Le taux de croissance le plus élevé est observé à 25°C tandis que la plus grande taille est obtenue chez les individus cultivés à 10°C (22 mm). La longévité décroît avec l'accroissement de la température (de 41 jours à 4 jours). Le temps de maturation est inversement proportionnel à la température (de 20 jours à 4 jours; à 40°C aucun nauplius n'a survie). La descendance par individu varie avec la température (maximum 447 cystes à 20°C), alors que le taux d'accroissement momentané, r , fluctue entre 0,07 et 0,34.

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INTRODUCTION

Anostraca or fairy shrimps are typical inhabitants of ephemeral ponds, aquatic environments characterized by strongly variable abiotic conditions. Although some research has focused on population dynamics (Mathias, 1937; Kallinowsky, 1955; Moore, 1957; Prophet, 1963; Bernice, 1972; Sluzhevskaya, 1975, 1982; Anderson & Hsu, 1990; Brendonck et al., 1990; De Walsche et al., 1991; Mitchell, 1991; Ali & Brendonck, 1995; Ali & Dumont, 1995; Mura & Dowgiallo, 1996; Mura, 1997), the complete life cycle of only very few species is known in detail. Lake (1969) described growth, longevity, and egg production in *Chirocephalus diaphanus* (Prévost, 1803) from England. Daborn (1975, 1976, 1977) studied the life history of *Branchinecta gigas* Lynch, 1937, *Eubranchipus bundyi* Forbes, 1876, and *Branchinecta mackini* Dexter, 1956 from Alberta, Canada. Beladjal et al. (2003) compare the life cycle of two sympatric North African species, *Branchipus schaefferi* Fisher, 1834 and *Streptocephalus torvicornis* (Waga, 1942).

The objective of this study is to elucidate survival, growth, and reproduction as a function of temperature of a third North African species, *Tanymastigites perrieri* (Daday, 1910) which has been described as a “thermophilic” species (Thiéry, 1987).

MATERIAL AND METHODS

Cysts of *Tanymastigites perrieri* were obtained from mud of a temporary pool in the arid region Jbilet in Morocco (31°6'30"N 8°24'00"W). Once in the laboratory, the mud was immersed with distilled water and newly hatched nauplii were collected within 24 hours for the experiments, performed at 10, 20, 25, 30, 35, and 40°C ($\pm 1^\circ\text{C}$). For each temperature, between 60 and 80 nauplii were used. Each nauplius was reared individually in a container filled with 50 ml aerated tap water, and transferred after 3 days to a larger one (150 ml). At sexual maturity they were pair-mated in a 450 ml container. Unicellular algae (*Scenedesmus* sp.) were offered as food at a concentration of 10^5 cells.ml⁻¹. One-third of the medium was renewed daily. The observations (mortality) and measurements (body length, reproduction) occurred during this manipulation. The standard length (from the tip of the head to the posterior margin of the telson) was measured under a stereomicroscope (Wild M5) equipped with a camera lucida, digitized using a Summa Sketch™ III professional digitizing table, and stored on a floppy disk for graphical and statistical use. Clutches of cysts were harvested on a 100 μm sieve, dried at 35°C, and counted under a stereomicroscope.

Cohort life tables, survivorship curves, and fecundity schedules were constructed according to standard demographic techniques (Krebs, 1972; Begon et al., 1996). The maturation time M , and the maturation rate $1/M$ were analysed with one-way ANOVA (STATSOFT, 2000). M_s is the moment at which 50% of the shrimps could be sexed, M_c corresponds to the time at which females produced their first clutch.

The relationship between development D and temperature T can be expressed as $K = D(T - C)$ (Blancquaert et al., 1981). In this relation, the constant C is the temperature at which development stops and K is a thermal constant, the number of "degrees-days above threshold" (Begon et al., 1996), a combination often referred to as the physiological time. In a temperature-time diagram, the developmental time D becomes a hyperbolic function, $D = K/(T - C)$, while the developmental rate $1/D$ is a linear function $y = a + bx$ expressed as $1/D = (T - C)/K = a + bT$. Fitting the experimental data to this linear regression allows calculation of a and b and identification of C and K . The developmental zero C corresponds to $1/D = 0$, or $C = -a/b$, and since the linear regression $1/D = a + bT$ can be written as $1/D = -C/K + (1/K)T$, the slope b of the regression equals $1/K$.

RESULTS

Survivorship and life expectancy

The mean longevity of *Tanymastigites perrieri*, corresponding to the maximal life expectancy e_x (the index x indicates age of an animal, expressed in days), was $e_{19} = 41.17$ days at 10°C ; $e_0 = 27.02$ days at 20°C ; $e_0 = 17.41$ days at 25°C ; $e_0 = 10.24$ days at 30°C ; $e_4 = 3.96$ days at 35°C ; and $e_0 = 0.68$ days at 40°C . Survivorship curves (l_x) and the life expectancies (e_x) are shown in figs. 1 and 2. The life expectancy e_x (fig. 2) followed a linear regression for all temperatures, except during the juvenile period at 10°C . There, e_x increased from 20.5 days at day $x = 4$ to 41.2 days at day 19, corresponding to a doubling of the life expectancy. The high mortality rate in the juvenile period was $d_{10^\circ\text{C}} = 5.1\% \text{ day}^{-1}$ (sd = 5.06, $n = 11$, between $x = 4$ and $x = 15$), while the mortality rate afterwards stabilizes at $d_{10^\circ\text{C}} = 0.40\% \text{ day}^{-1}$ (sd = 0.95, $n = 65$ between $x = 19$ and $x = 83$). The other mortality rates are $d_{20^\circ\text{C}} = 2.17\% \text{ day}^{-1}$ (sd = 2.67, $n = 40$ between $x = 5$ and $x = 45$); $d_{25^\circ\text{C}} = 3.59\% \text{ day}^{-1}$ (sd = 4.01, $n = 23$ between $x = 0$ and $x = 22$); $d_{30^\circ\text{C}} = 5.50\% \text{ day}^{-1}$ (sd = 5.35, $n = 17$ between $x = 1$ and $x = 17$); $d_{35^\circ\text{C}} = 22.5\% \text{ day}^{-1}$ (sd = 17.89, $n = 4$ between $x = 0$ and $x = 3$). At 35°C , 75.0% of the cohort died on the first day. At 40°C no shrimp reached sexual maturity (82.5% died the first day, while the remaining 17.5% followed the next day).

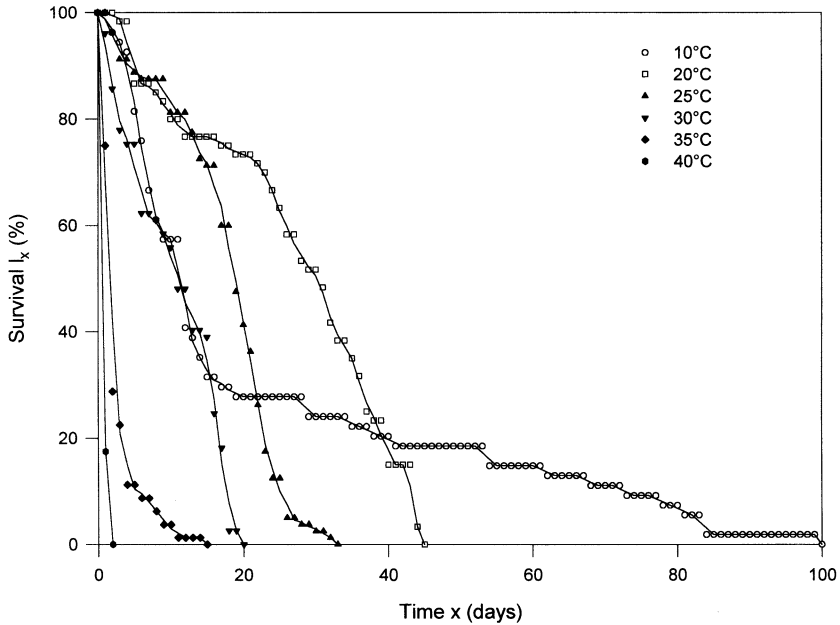


Fig. 1. Survival l_x (expressed in % of the number of nauplii at the start of the experiment) of *Tanymastigites perrieri* (Daday, 1910) as a function of time x (days) at six experimental temperatures (10, 20, 25, 30, 35, and 40°C). The dots represent the daily observed values; the lines connect the running mean values of a period of three days.

The maximum lifetime l_{\max} , being the lifetime of the oldest animal in the cohort, decreased exponentially in function of the increasing temperature. The corresponding rate $1/l_{\max}$ fitted to a regression line $y = a + bx$ (table I, fig. 3). The numerical values of the $1/l_{\max}$ regression were $a = -0.0041$ and $b = 0.0014$ ($r^2 = 0.99$), giving a developmental zero $C = 3^\circ\text{C}$ and $K = 719$ degrees-days. The values $1/e$ of the life expectancy at the start of the reproductive period did not give an acceptable fit ($r^2 = 0.88$).

At the start of the reproductive period of the females M_c (table I), the life expectancies were $e_{10^\circ\text{C}} = 31.04$ days; $e_{20^\circ\text{C}} = 22.97$ days; $e_{25^\circ\text{C}} = 12.49$ days; $e_{30^\circ\text{C}} = 8.54$ days; $e_{35^\circ\text{C}} = 2.27$ days. The mortality rate during the reproductive period at 20°C is $d_{\text{repr.},20^\circ\text{C}} = 0.90\% \text{ day}^{-1}$ (sd = 1.29, $n = 51$ between $x = 8$ and $x = 20$ when reproduction was at its maximum), being less than $d_{s,20^\circ\text{C}} = 2.78\% \text{ day}^{-1}$ (sd = 2.49, $n = 44$ between $x = 20$ and $x = 41$), the value of the senescence period characterized by low reproductivity. At 25°C , $d_{\text{repr.},25^\circ\text{C}} = 1.81\% \text{ day}^{-1}$ (sd = 2.51, $n = 70$ between $x = 7$ and $x = 15$), followed by $d_{s,25^\circ\text{C}} = 1.34\% \text{ day}^{-1}$ (sd = 4.01, $n = 57$ between $x = 15$ and $x = 23$) and $d_{\text{postrepr.},25^\circ\text{C}} = 1.25\% \text{ day}^{-1}$ (sd = 2.28, $n = 10$ between $x = 24$ and $x = 33$), being a short postreproductive period. At higher temperatures, reproduction was

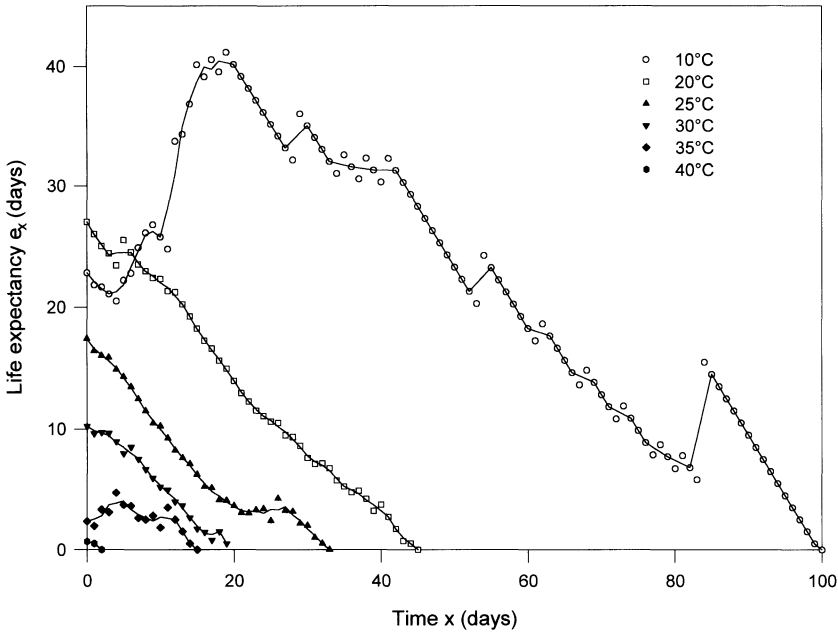


Fig. 2. Live expectancy e_x (expressed in days) of *Tanymastigites perrieri* (Daday, 1910) as a function of time x (days) at the various experimental temperatures (10, 20, 25, 30, 35, and 40°C). The dots represent the daily values; the lines connect the running mean values of a period of three days.

TABLE I

The parameters of the growth curve of *Tanymastigites perrieri* (Daday, 1910) at different temperatures (10, 20, 25, 30°C): the maximum length L_{\max} (mm), the metabolic activity k , and the flexibility parameter m . Parameters of maturation are the maturation time M (days), and the maturation rate $1/M$, defined at the moment of sexual differentiation s and the moment of oviposition c . Survivorship rates are based on the maximum lifetime of the oldest individual in the cohort, and the life expectancy e at the start of the reproductive period

T (°C)	Growth curve			Maturation			Survivorship		
	L_{\max}	k	m	M_s (sd; n)	$1/M_s$	M_c (sd; n)	$1/M_c$	$1/l_{\max}$	$1/e$
10	21.98	0.08	0.70	18.99 (0.36; 7)	0.05	38.14 (4.37; 7)	0.03	0.01	0.032
20	21.82	0.20	0.65	7.22 (0.11; 24)	0.14	10.21 (2.65; 24)	0.01	0.02	0.04
25	19.93	0.28	0.66	5.25 (0.21; 26)	0.19	8.58 (2.08; 26)	0.12	0.03	0.08
30	18.73	0.21	0.47	4.23 (0.55; 15)	0.24	11.36 (2.53; 14)	0.09	0.05	0.12

negligible (30°C, 35°C) or non-existent (40°C). As a consequence, the data of these suboptimal temperatures are not included in the calculations of the development time D and the development rate $1/D$.

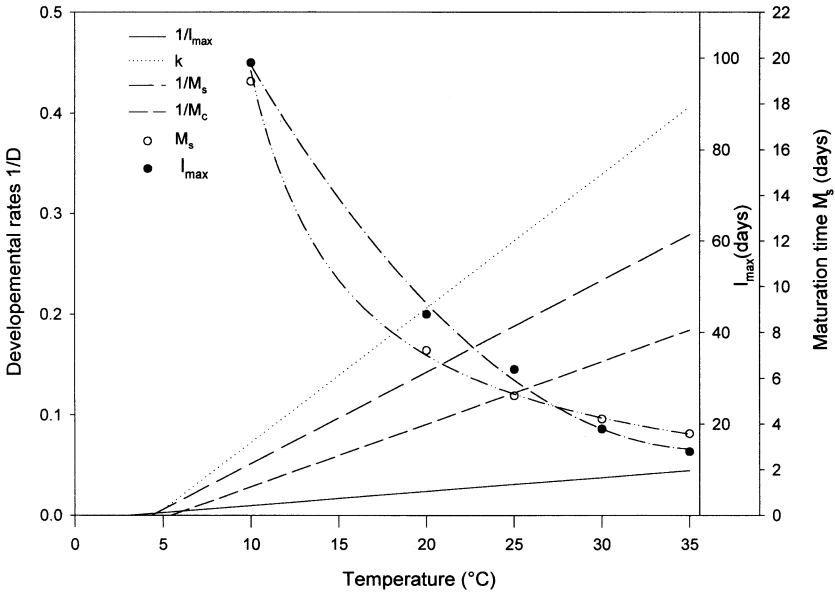


Fig. 3. The maximum lifetime l_{max} and the maturation time M_s corresponding to sexual differentiation (right ordinates) of *Tanymastigites perrieri* (Daday, 1910) plotted against temperature ($^{\circ}C$). The regression lines are development rates $1/D$ (left ordinate) corresponding to $1/l_{max}$; $1/M_c$; $1/M_s$; and k (M_c = maturation time of females corresponding to the production of the first clutch, k = metabolic rate).

Growth and reproduction

The daily mean standard body lengths of all surviving individuals in each cohort are given in fig. 4. There was no difference in growth between the sexes. The curve providing the best fit to all data is $L = L_{max}(1 - Ae^{-kx})^{1/(1-m)}$, giving the body length L in function of time x . L_{max} is the maximum size reached; k is a rate constant which expresses the metabolic activity. Assuming that L_0 is the length of a nauplius at hatching time ($t = 0$), then $A = 1 - L_0/L_{max}$ is the proportion of the maximum length, remaining for growth at time zero. Flexibility is achieved by varying the parameter m .

The numerical values for the growth curves in fig. 4 are summarized in table I. For 10, 20, and 25 $^{\circ}C$ the maximal length was reached at day 56 (10 $^{\circ}C$; $p = 0.05$), at day 22 (20 $^{\circ}C$; $p = 0.05$), at day 16 (25 $^{\circ}C$; $p = 0.05$), in agreement with the increasing metabolic activity (see table I). The suboptimal temperature of 30 $^{\circ}C$ can be recognized by a decrease in metabolic activity ($k_{30^{\circ}C} = 0.206 < k_{25^{\circ}C} = 0.279$) and a reduced maximal length ($L_{max,30^{\circ}C} = 18.7 \text{ mm} < L_{max,25^{\circ}C} = 19.9 \text{ mm}$). At 35 $^{\circ}C$, the mortality rate is too high to detect a K value and to reach the L_{max} .

As for the developmental rate calculated from the survivorship, the metabolic activity (k) for 10, 20, and 25 $^{\circ}C$ was fitted by a linear curve type $y = a + bx$ (fig. 3). In this case, $b = 0.0134$ and $a = -0.0611$ ($r^2 = 0.99$). Metabolic activity

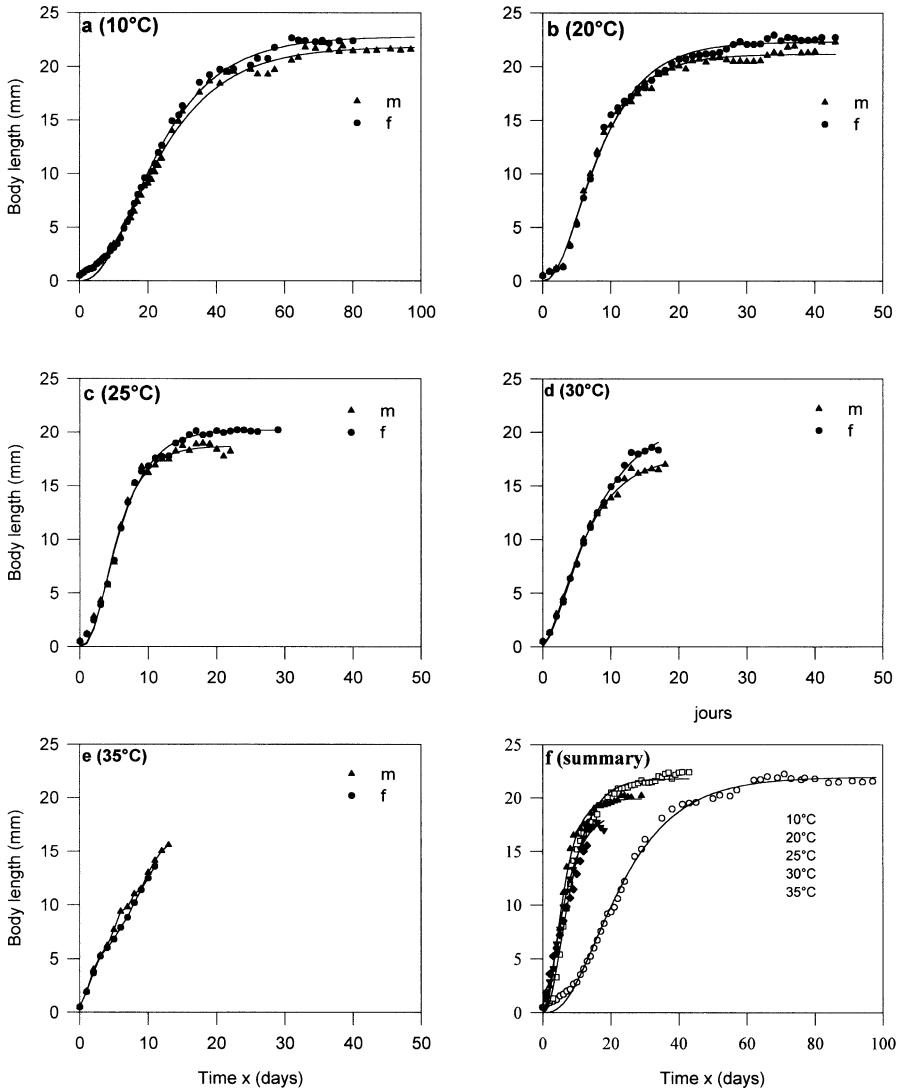


Fig. 4. a-e, Growth curves of *Tanymastigites perrieri* (Daday, 1910) reared at the different experimental temperatures ($^{\circ}\text{C}$): a = 10, b = 20, c = 25, d = 30, e = 35. The dots are the mean experimental values, the lines are the best fitting curves, expressed as body length (mm) in function of time (days), for males and females. A summary of all growth curves is given in f, males and females taken together.

stopped at temperature $C = 4.58^{\circ}\text{C}$ (threshold temperature or developmental zero). Comparable results are found for the maturation time M (days), which increased exponentially as a function of the temperature (fig. 4). The maturation rates $1/M_s$ and $1/M_c$ were not significantly different from $y = a + bx$ for all temperatures. Here, $a = -0.0395$ and -0.0339 and $b = 0.0091$ and 0.0063 (variation 99.68%

TABLE II

Reproduction characteristics of *Tanymastigites perrieri* (Daday, 1910): fertility (the total number of cysts produced per female); reproductive period (expressed in days); cyst production per day per female, with the mean of all values (n), and the standard deviation (sd), maximum (max.), and minimum (min.); also the net reproductive rate R_0 (number of offspring produced by an individual), generation time G (in days), and intrinsic rate (r) of natural increase at the experimental temperatures T ($^{\circ}\text{C}$)

	Temperature ($^{\circ}\text{C}$)				
	10	20	25	30	35
Fertility					
Mean (n; sd)	296.0 (7; 133)	447.4 (24; 232)	262.2 (26; 156)	67.1 (15; 65)	25.0 (1; -)
max.	514	938	682	235	-
min.	153	118	47	1	-
Reproductive period					
Mean (n; sd)	32 (7; 16)	26 (24; 7)	12 (26; 4)	11 (15; 3)	2 (1; -)
max.	48	34	17	13	-
min.	5	9	3	4	-
Cyst production					
Mean (n; sd)	9 (7; 14)	18 (24; 20)	21 (26; 21)	6 (15; 21)	13 (1; 2)
max.	98	97	87	44	15
R_0	38	191	85	12	0
G	52	21	13	14	9
r	0.07	0.25	0.34	0.18	-0.12

and 99.21%, $r = 0.998$ and 0.991). The maturation rates decreased linearly to $C = 4.34^{\circ}\text{C}$ and 5.39°C and the K values are 109.89 and 158.98 day.degrees.

The numerical data of the reproduction characteristics are summarized in the fecundity schedules of table II and shown in fig. 5. At 20°C , the highest number of cysts per female is produced (mean 447; max. 938; sd 232) and at 10°C the fertility is a little bit higher than at 25°C (296 vs. 262), which results in a reproductive rate $R_0 = 190.97$ at 20°C . This later becomes smaller at 10°C than at 25°C ($R_0 = 38.44$ vs. $R_0 = 85.20$), due to the higher mortality rate at 10°C than at 25°C . There is no correlation between body length of the female and clutch size ($r^2 = 0.0738$).

Time-temperature combinations

The developmental rates $1/D$ mentioned above ($1/l_{\text{max}}$, $1/e$, $1/M_c$, $1/M_s$, and k) are derived from the temperature range over which no deviations from linearity were observed (10 , 20 , 25°C). Since for $1/e$ the response is not effective by linear ($r^2 = 0.88$), these values have not been taken into account. All these rates were plotted against temperature in fig. 3. The mean value at which the development stops is the threshold temperature expressed as the mean developmental zero $C =$

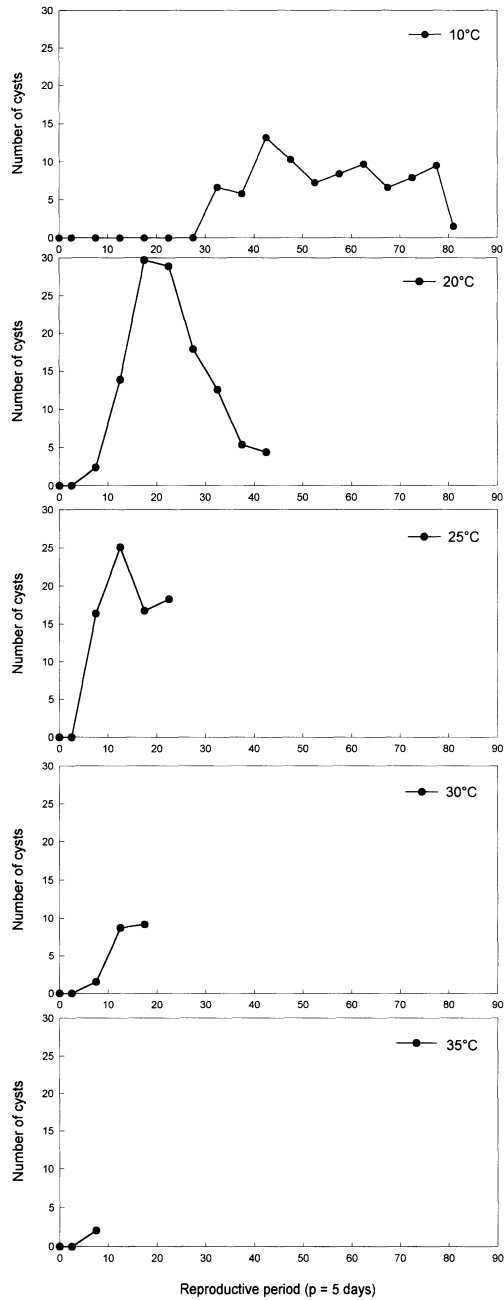


Fig. 5. Cyst production of *Tanymastigites perrieri* (Daday, 1910) during the reproductive periods (5 days time interval) at the various experimental temperatures (°C).

4.32°C ($n = 4$; $sd = 1.00^\circ\text{C}$). Each straight line in fig. 3 shows a developmental rate in function of the temperature or that fraction of the total development ($= 1$) that is passed in one day. The slopes b are $b_{L_{\max}} = 0.00139$; $b_{M_c} = 0.00629$; $b_{M_s} = 0.009100$; $b_k = 0.0134$.

DISCUSSION

Our results prove that the life strategy of *Tanymastigites perrieri* is adapted to warm water, ranging between 20 and 25°C, of temporary ponds that stay inundated for 10 to 20 days at least. Although growth and sexual maturity were rapidly reached at 30-35°C, shrimps did not survive for long nor did they reproduce significantly. At the lower temperature of 10°C, the slow growth rate delayed sexual maturity and the fitness was negligible compared to 20°C.

In *T. perrieri*, total length decreases with increasing temperature. The same observations have been made by Lake (1969) in *Chirocephalus diaphanus* (21.20 mm at 10°C and 14.99 mm at 25°C) and by Anderson & Hsu (1990) in *Streptocephalus seali* Ryder, 1879. Except at 35°C, *T. perrieri* females were longer than males at the end. As for other species (Moore, 1957; Daborn, 1976, 1977; De Walshe et al., 1991; Mura, 1991; Thiéry, 1991), *T. perrieri* females continue their growth at the beginning of the reproductive period.

Our experimental results on fertility of *T. perrieri* agree with the observations in the field by Thiéry & Brtek (1984) who found for this species (as *Tanymastigites jbiletica*, cf. Belk & Brtek, 1997) that the ovisac of mature females (length 21.3 mm) can contain 80-90 eggs. No correlation between body length of the female and clutch size was found ($r^2 = 0.0738$). Slushevskaya (1975) as well as Alonso (1980), observed a positive correlation between body length and clutch size in *Streptocephalus*, while Beladjal et al. (2003) found no correlation for *Streptocephalus torvicornis* and only a slight one for *Branchipus schaefferi* ($r^2 = 0.52$). According to Daborn (1976) no significant relationship could be found between female length and egg number in *Eubbranchipus bundyi*. However, Daborn (1977) mentioned that for *Branchinecta mackini*, such a correlation is only apparent among younger females, and vanishes with age, when egg-laying becomes more irregular.

At 25°C, females produce more cysts per day. In consequence, the innate capacity for increase expressed by the intrinsic rate r was maximal at this temperature ($r = 0.34$). Because of the high longevity of females at 20°C, the net reproductive rate R_0 was better than at 25°C (191 and 85, respectively).

In the arid region of Jbilet, *T. perrieri* co-occurs with *B. schaefferi*, in the same temporary pools (Thiéry & Brtek, 1984). Bernice (1972) noted in the case of

the sympatric species *Branchinella kugenumaensis* (Ishikawa, 1895) and *Streptocephalus dichotomus* Baird, 1860 that one of the two species is characterized by a rapid growth, small maximal length, and early reproduction in a short period, a low number of cysts, and a short life cycle. Mura (1991) and Beladjal et al. (2003) mentioned these characteristics for *C. diaphanus* and *Tanymastix stagnalis* (Linnaeus, 1758), and for *S. torvicornis* and *B. schaefferi*, respectively. These phenomena were observed in our laboratory under the same culture conditions: *B. schaefferi* lives longer and produces more cysts than *T. perrieri*; however, the adult size of *T. perrieri* is larger than that of *B. schaefferi*.

The geographical distribution of *Tanymastigites* is limited to North Africa. Except for *T. brteki* Thiéry, 1986, all other *Tanymastigites* species are typical for the arid areas, sometimes with Saharan influence (Daday, 1910; Thiéry & Brtek, 1984; Thiéry, 1987).

The dayas' (Arabic word for temporary pond) hydrological cycle from where *T. perrieri* originated, lasts one to two months, once or twice a year (Boutin et al., 1982). This explains the short life cycle of *T. perrieri* as an adaptation to such a habitat. The large K value confirms the thermophilic and stenothermic characteristics of the species. Because of its sensitivity to temperature, its distribution is limited to such regions in northern Africa. The species might be unable to colonize other regions nearby. Indeed, the genus is absent in the countries of the northern Mediterranean.

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