

Life History Traits of Two Chaetonotids (Gastrotricha) Under Different Experimental Conditions

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Summary

A marine and a freshwater species of Chaetonotida (Gastrotricha) were reared under laboratory conditions. Their life tables and principal demographic parameters were determined at 2 different temperatures (20° and 25°C). At 25°C the data relative to the marine species were collected from 5 cohorts kept at 5 different salinity levels (15, 25, 35, 45, 55‰).

A higher temperature increases reproductive activity while shortening its duration in both species, whereas the length of the lifespan remains unaffected. Extreme salinity values (15 and 55‰) reduce the maximum longevity of the marine species and have opposite effects on reproductive activity, which is higher at low salinity and becomes lower at high salinity. The postparthenogenetic phase is remarkably long relative to the life cycle: this was observed in all experimental conditions and may be related to the existence of a second reproductive phase, which is hermaphroditic and follows the parthenogenetic one, as recently postulated from morphological data.

life history, Gastrotricha, reproductive biology, *Aspidiophorus polystictos*, *Chaetonotus maximus*

Introduction

Collecting and handling chaetonotid gastrotrichs is difficult. The microscopic size and cuticle weakness of these organisms, especially freshwater ones, render ineffective the usual extraction methods from the substrate. Laboratory culture also involves many problems since knowledge of food requirements is minimal. Thus the study of the group was generally limited to morphological and ecological aspects and especially to systematics. Some recent advances in laboratory culture techniques have permitted successful research on reproductive biology (Hummon, 1984a,b,c; Levy, 1984a; Balsamo and Todaro, 1987). To date, life history traits and population dynamics have been the object of a few studies, all carried out on the freshwater chaetonotid *Lepidodermella squammata* Dujardin (Faucon and Hummon, 1976; Hummon and Hummon, 1975, 1979; Hummon, M.R., 1986; Hummon, W.D., 1974). Recent success in culturing two chaetonotid species, one marine and the other freshwater, led us to complete a study on the life cycle of the marine species *Aspidiophorus polystictos* (Balsamo and Todaro, 1987) with a particular analysis of its life history traits. Moreover, a parallel study on the freshwater species *Chaetonotus maximus* Ehrenberg has allowed us to compare the 2 life cycles and to look for the possible life strategy of each species.

The observations have been carried out on 2 cohorts of each species, reared at 2 different temperatures (20°C and 25°C) to estimate possible effects of this factor on the biological cycle. *A. polystictos* is a strongly euryhaline species, which is able to tolerate salinities ranging from 5 to 70‰, and to reproduce at salinities between 10 and 60‰ (Balsamo and Todaro, unpublished data). For this reason, the study of this species at 25°C has been carried out at 5 different salinities in order to detect possible modifications by this factor in the course of the life cycle.

Materials and Methods

Mass cultures of *Aspidiophorus polystictos* and *Chaetonotus maximus* were grown from specimens from a sandy beach of the Ionian Sea (Marina di Ginosa, Taranto, 40°25'N, 16°49'E) and from an Apennine pond (Sassomassiccio, Pavullo, Modena, 44°19'N, 11°34'E), respectively. The cultures were reared in 6 cm diameter Petri dishes containing artificial sea water at 35‰ salinity (a solution of marine salt (Prodac Mare, Cittadella di Padova) in spring water (Fonte Levissima, Cepina, Sondriod), and spring water, respectively. Each dish contained 1 or 2 boiled wheat seeds or 0.5–1 cc

of humus infusion (according to Pourriot (1957), with slight modifications). These media allow a bacterial flora to grow, which represents the real food for the animals. Preliminary tests showed no significant difference in culture condition between the 2 media which have therefore been used interchangeably. Temperature was maintained at $20 \pm 0.5^\circ\text{C}$; a 12 hr light/12 hr dark photoperiod was adopted. These physical conditions were within the range of those of the collecting sites at sampling time (September, 1984), and will be referred to hereafter as "physiological". Single eggs from mass cultures, physiologically but not genetically adapted to laboratory conditions, were used to start the various cohorts. The life cycle was studied by placing eggs singly in 0.2 cc of water in the wells of microtest plates (Microtiter System, Greiner P.B.I., Milano). The plates were put in moist chambers; water in the wells was renewed daily and 0.02 cc of humus infusion was added to each pit once a week. Specimens were inspected daily and laid eggs were removed. Life data of each individual were recorded every day until locomotory cilia-ture stopped moving: this event was assumed to coincide with the death of the individual.

Specimens were maintained under physiological photoperiod, at temperatures of either 20 or $25 \pm 0.5^\circ\text{C}$. Additionally, single eggs of *A. polystictos* were reared at a temperature of $25 \pm 0.5^\circ\text{C}$ and salinities of 15, 25, 35, 45 and 55‰.

The lifespan from hatching and the length of each phase of life were estimated for all individuals ($n=164$). Moreover, the "minimum generation time" (T_m) was calculated, being the time between the beginning of embryonic development (0.5–1 hr after deposition for *A. polystictos*, 1 hr for *C. maximus*) and the first deposition by each individual (Parise, 1966). The number of depositions by each individual and by each cohort were also noted.

Analysis of variance (ANOVA) was carried out to study the effect of salinity on lifespan, length of life phases, minimum generation time and number of depositions by *A. polystictos*. The Mann-Whitney or U-test (Siegel, 1956) was applied to compare the effect of a high or a low salinity with that of the "physiological" one. The same test was used to analyze the influence of temperature on life and reproduction traits of both species.

Life tables were compiled (Pielou, 1974) and principal demographic parameters were calculated according to the following bibliographic references:

e_0 : life expectancy at birth (Livi-Bacci, 1986)

r : intrinsic rate of natural increase (Cole, 1954)

R_0 : net reproductive rate (Ricklefs, 1979)

T : mean generation time (Dublin and Lotka, 1925)

DT : population doubling time (Dublin and Lotka, 1925).

The r values were computer calculated by successive approximations up to 0.001. Of the parameters mentioned, Tm , T , DT , and especially r , give data on the time between successive generations and thus characterize population growth; e_0 expresses the mean lifespan of each cohort and R_0 the total number of depositions of an individual over its reproductive period.

Lastly, the “reproductive effort” (r.e.) was determined for each cohort, as the ratio between the net reproductive rate R_0 and the number of reproductive days (Ricci, 1983). It expresses the intensity of the reproductive activity during the reproductive period.

Results

Aspidiophorus polystictos

Life history traits

The life cycle of *A. polystictos* (for details see Balsamo and Todaro, 1987) follows the same pattern as the life cycles of previously studied freshwater species (Hummon, 1986; Levy, 1984a,b). An embryonic phase, which begins 0.5–1 hr after egg deposition and lasts about 2 days, is followed by 3 main phases whose lengths are reported in Table I.

1. Postembryonic or prereproductive phase (pr.ph.) begins at egg hatching and is characterized by rapid growth and development of reproductive maturity.
2. Reproductive or parthenogenetic phase (pa.ph.), during which the animal lays several parthenogenetic eggs successively.
3. Postparthenogenetic phase (pp.ph.), when both male and female gametes are present in the animal body.

Under “physiological” conditions ($T=20^{\circ}\text{C}$, $S=35\text{‰}$) the mean lifespan of *A. polystictos* is 23 days (Table I), although one individual died by day 10 and a few other survived up to 50 days (Fig. 1). Reproductive activity starts on the fourth day on average and leads to the production of 1–10 eggs, most often 4, in the space of about 8 days (Fig. 2). The fecundity curve is characterized by many peaks, the highest of which is located round the 8th day (Fig. 3). Lengths of parthenogenetic and postparthenogenetic phases are quite similar under these conditions (38% and 43% of the entire lifespan respectively) (Fig. 4).

TABLE I.

Means (\pm standard deviations) of lifespan, length of phases of life (in days) and number of depositions and principal demographic parameters of *A. polystictos* and *C. maximus* at 20°C and 25°C

	<i>Aspidiophorus polystictos</i>		<i>Chaetonotus maximus</i>	
Salinity (‰)	35	35	0	0
Temperature (°C)	20	25	20	25
No. of specimens	22	35	13	28
Lifespan	22.59 \pm 12.72	23.18 \pm 7.94	14.84 \pm 8.33	12.07 \pm 4.97
<i>Phase</i>				
Embryonic	2.00 \pm 0.92	1.65 \pm 0.59	1.23 \pm 0.43	1.10 \pm 1.10
Prereproductive	4.20 \pm 2.37	2.68 \pm 1.73	4.19 \pm 1.99	2.92 \pm 1.53
Parthenogenetic	8.65 \pm 6.40	7.12 \pm 4.42	4.38 \pm 2.36	4.44 \pm 1.49
Postparthenogenetic	9.72 \pm 10.75	13.37 \pm 7.79	6.26 \pm 7.24	4.69 \pm 4.12
No. of depositions	4.77 \pm 2.26	5.54 \pm 2.93	2.69 \pm 1.18	3.53 \pm 0.92
T_m	7.00 \pm 2.19	5.17 \pm 1.85	6.42 \pm 1.93	5.05 \pm 1.66
e_0	23.04	23.71	15.33	12.71
r	0.206	0.315	0.132	0.218
R_0	4.48	5.49	2.38	3.52
T	7.28	5.47	6.56	5.77
DT	3.36	2.20	5.25	3.18
Reproductive effort	0.52	0.79	0.54	0.79

Influence of temperature

The mean lifespan is not significantly influenced by the difference of rearing temperatures, although the age distribution is different (Fig. 1). The lower T and DT indicate a more rapid turnover and doubling time for the 25°C population (Table I). A notable influence of temperature can be seen on the length of the prereproductive phase (U-test, $p < 0.05$): this is reduced from 18% (20°C) to about 11% (25°C) of the total lifespan and is accompanied by an increase of the r value (Fig. 4; Table I). In contrast, with higher temperature the postparthenogenetic period is extended from 43% to 57% of the lifespan and is the longest phase (U-test, $p < 0.05$) (Fig. 4).

The reproductive activity, expressed by the R_0 value, rises slightly with increasing temperature (Table I). The shape of the fecundity curve differs under the 2 thermal conditions: at 20°C it is irregular with several similar peaks, while at 25°C it is nearly triangular with a maximum peak on the fourth life day (Fig. 3). Parthenogenetic activity occurs earlier at 25°C, reaches a higher level and is concentrated in a shorter period (Fig. 3). The reproductive effort is consequently greater (Table I). The mean number of

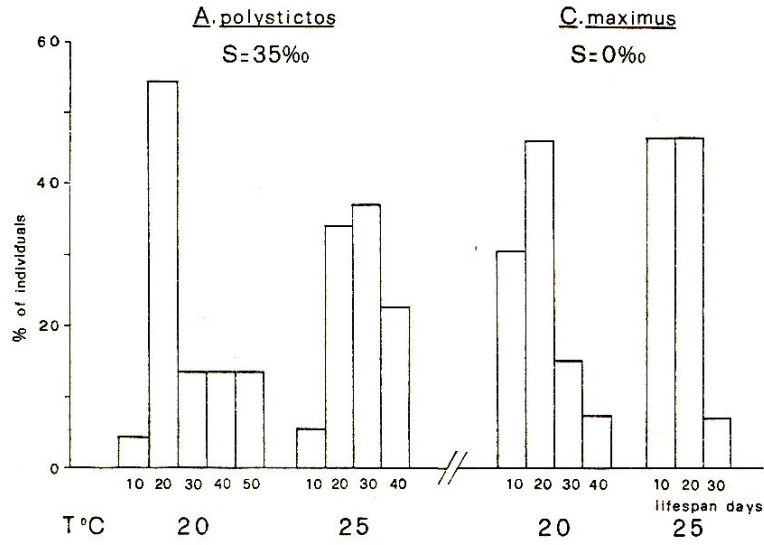


Fig. 1. Distribution of days of lifespan of *A. polystictos* and *C. maximus* at 20°C and 25°C. Individuals are divided into 10 day age classes. Numbers indicate the maximum lifespan for each class.

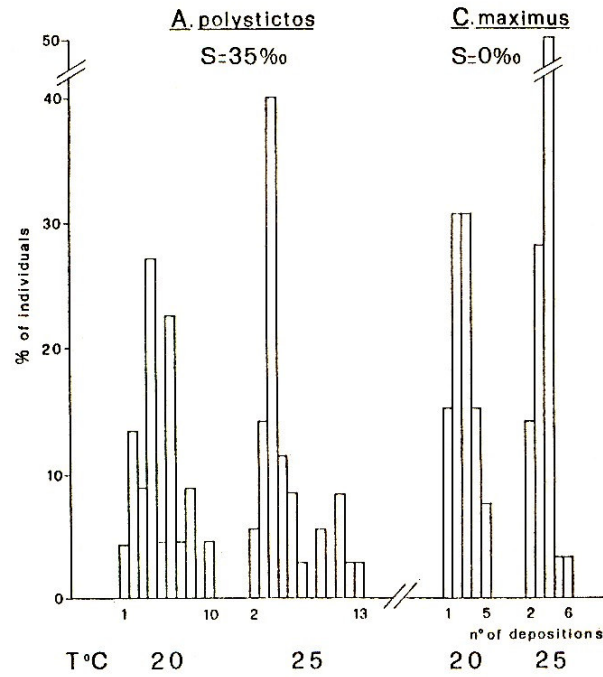


Fig. 2. Distribution of number of depositions by *A. polystictos* and *C. maximus* at 20°C and 25°C.

depositions for animals kept at 25°C is not significantly different from that of animals reared at 20°C (Table I), although the range is broader. The percentage of individuals producing only 4 eggs is the highest under this condition too (Fig. 2).

Influence of salinity

The significance of the effect of salinity on the lifespan of *A. polystictos* is related only to the especially short lifespan of animals kept at 55‰ (Table II). With this one exception, the salinity seems to have little influence on the mean lifespan of *A. polystictos*, which always ranges from 22 to 24 days. The age distribution differs in various situations, showing a gradual percentage increase of lower age classes parallel to the salinity increase (Fig. 5).

At 55‰ salinity, more than 50% of the individuals die within 10 days. The survivorship curve reflects this situation, showing an earlier and sharp fall at 55‰, while the pattern is more regular at lower salinities (Fig. 6).

The prereproductive phase lengthens with the salinity value, moving from about 8% up to 40% (Fig. 7). This lengthening is consistent with the variations of T , DT and r (Table II). The parthenogenetic period is longer at "physiological" salinity, while the postparthenogenetic phase shortens when salinity increases (Table II). This last period is however the longest one of the life cycle in all conditions except the extreme case of 55‰ salinity (Fig. 7).

Parthenogenetic activity is strongly influenced by the increase in salinity, reduction in deposition being especially severe at the 2 higher salinities (Table II). The value of R_0 and the maximum level of the fecundity curve also show a parallel decrease (Fig. 6). Parthenogenetic activity is concentrated in a short period of life (Fig. 7). At a salinity of 15‰, this activity is greatest and occurs for the shortest period: the reproductive effort is thus maximal (Table II). Four is the relatively most frequent deposition number in all rearing conditions. The sole exception is the 55‰ salinity where the most represented number of eggs laid is 1 (Fig. 8) and the total absence of egg deposition has been observed in the 15% of the individuals. This phenomenon never occurred at lower salinities.

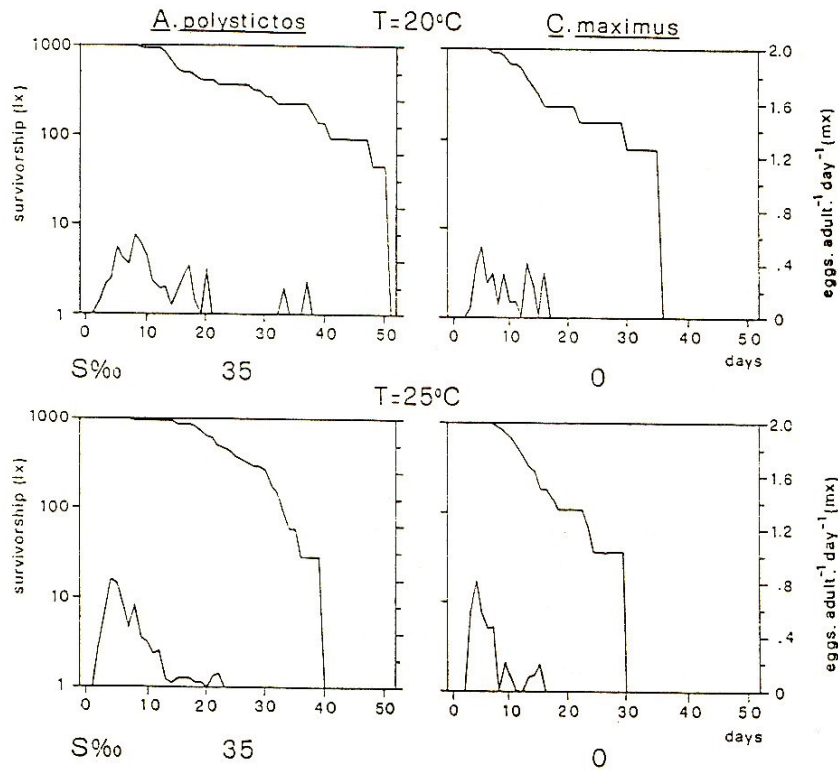


Fig. 3. Survivorship (\log_{10}) and fecundity in *A. polystictos* (left) and *C. maximus* (right) at 20° (upper) and 25°C (lower). l_x = age-specific survivorship; m_x = age-specific fecundity.

Chaetonotus maximus
Life history traits

The life cycle of *C. maximus* is also triphasic. Embryonic development begins 1 hr after the deposition and is completed within about 1 day. At 20°C the mean lifespan is 15 days (Table I). Reproduction begins on the fourth day of life on average and leads to the laying of 1–5 eggs (Fig. 2). The fecundity curve shows an irregular shape (Fig. 3). The difference in length of the 2 last life phases is considerable: the parthenogenetic period is 29% of the entire lifespan and the postparthenogenetic one amounts to the 42% (Fig. 4).

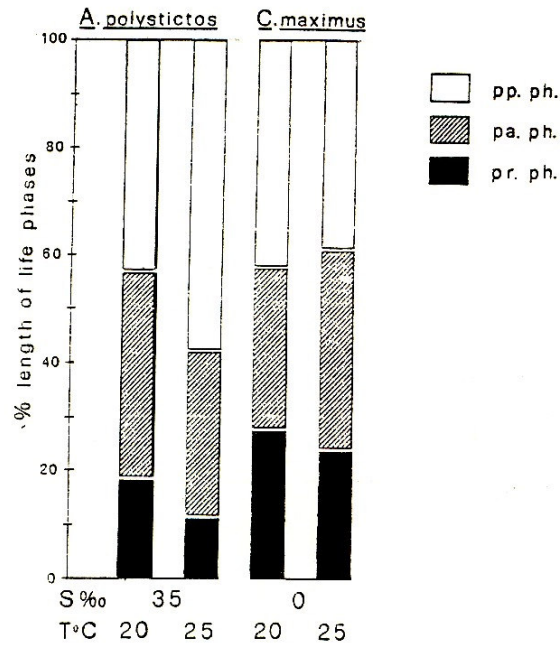


Fig. 4. Mean percent of lifespan occupied by the prereproductive phase (pr.ph.), parthenogenetic phase (pa.ph.) and postparthenogenetic phase (pp.ph.) of *A. polystictos* and *C. maximus* at 20°C and 25°C.

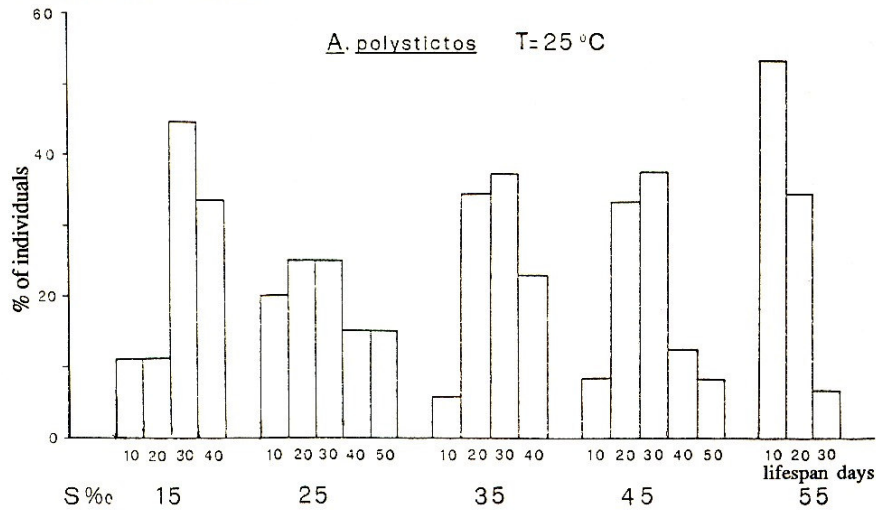


Fig. 5. Distribution of days of lifespan of *A. polystictos* under different conditions of salinity at 25°C. Individuals are divided into 10 days age classes. Numbers indicate the maximum lifespan for each class.

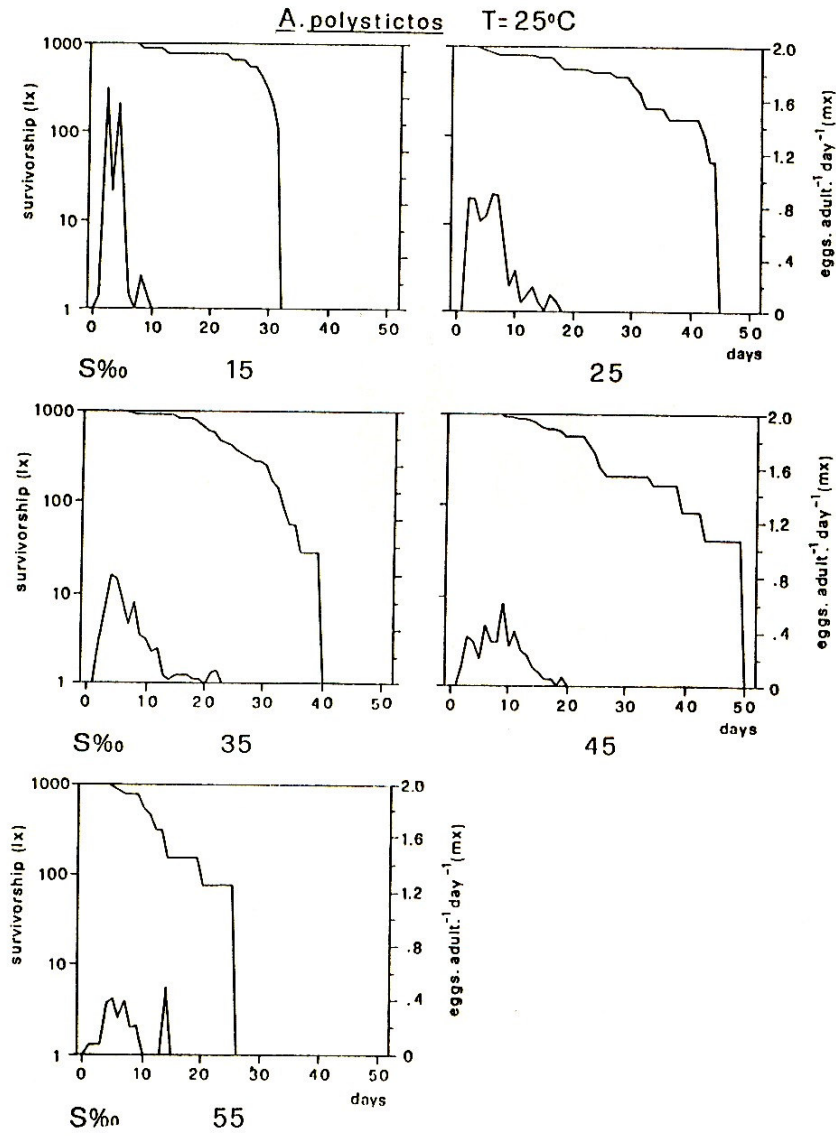


Fig. 6. Survivorship (\log_{10}) and fecundity in *A. polystictos* under different conditions of salinity at 25°C. l_x = age-specific survivorship; m_x = age-specific fecundity.

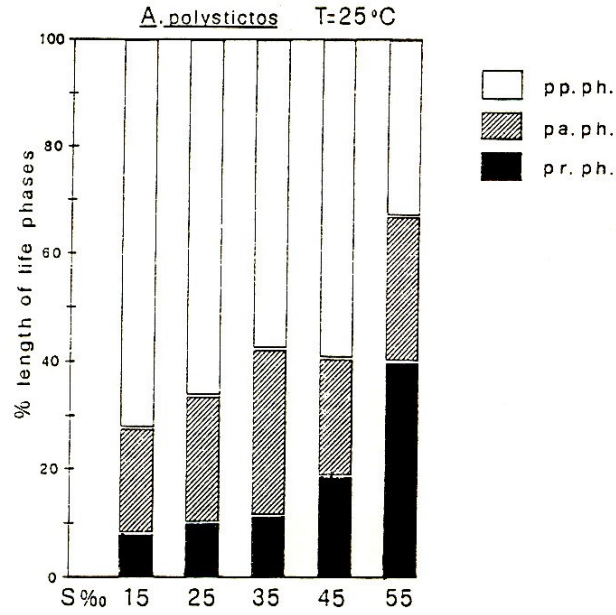


Fig. 7. Mean percent of lifespan occupied by the prereproductive phase (pr.p.h.), parthenogenetic phase (pa.p.h.) and postparthenogenetic phase (pp.p.h.) of *A. polystictos* under different conditions of salinity at 25°C.

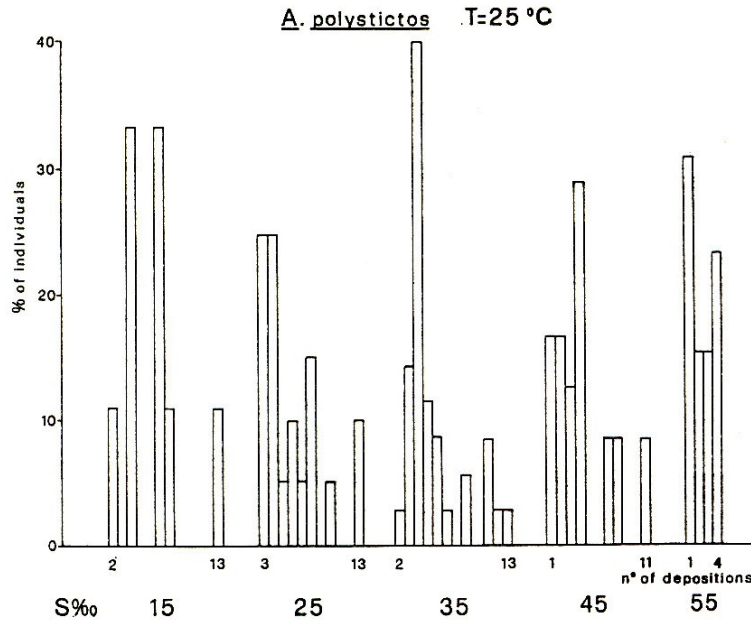


Fig. 8. Distribution of number of depositions by *A. polystictos* under different salinity conditions at 25°C.

TABLE II.
Means (\pm standard deviations) of lifespan, length of phases of life (in days), number of depositions and principal demographic parameters of *Aspidiophorus polystictos* under different conditions of salinity, at 25°C

	<i>Aspidiophorus polystictos</i>						ANOVA	
	15	25	35	45	55		F	p<
Salinity (‰)	15	25	35	45	55			
No. of specimens	9	20	35	24	13			101
Lifespan	24.88 \pm 9.29	22.82 \pm 12.96	23.18 \pm 7.94	23.06 \pm 10.48	11.04 \pm 4.39		4.603	0.002
<i>Phase</i>								
Embryonic	1.44 \pm 0.53	1.27 \pm 0.44	1.65 \pm 0.59	1.77 \pm 0.92	1.80 \pm 1.10		1.703	n.s.
Preproductive	2.05 \pm 0.39	2.35 \pm 1.54	2.68 \pm 1.73	4.37 \pm 2.27	4.46 \pm 3.57		5.231	0.001
Parthenogenetic	4.83 \pm 2.00	5.35 \pm 3.66	7.12 \pm 4.42	5.00 \pm 3.22	3.00 \pm 2.31		3.523	0.010
Postparthenogenetic	18.00 \pm 8.94	15.12 \pm 12.33	13.37 \pm 7.79	13.68 \pm 10.30	3.69 \pm 4.95		4.215	0.003
No. of depositions	6.22 \pm 3.23	5.95 \pm 3.18	5.54 \pm 2.93	4.20 \pm 2.96	2.00 \pm 1.47		5.210	0.001
Tm	4.11 \pm 0.78	4.30 \pm 1.65	5.17 \pm 1.85	7.02 \pm 2.99	6.77 \pm 3.84		5.787	0.001
e_0	25.37	23.35	23.71	23.58	11.57			
r	0.577	0.399	0.315	0.210	0.120			
R_0	6.23	5.79	5.49	4.23	1.95			
T	3.17	4.40	5.47	6.86	5.56			
DT	1.20	1.73	2.20	3.30	5.77			
Reproductive effort	1.31	1.11	0.79	0.73	0.65			

Influence of temperature

Many of the observations made for *A. polystictos* are also valid for *C. maximus*. Mean lifespan is not significantly influenced by temperature. The higher temperature brings both a shortening of the prereproductive phase (U-test, $p < 0.05$) and a lowering of T and DT , with an increase of r value (Table I).

The postparthenogenetic phase is not significantly different in individuals kept at 20°C and 25°C (Fig. 4; Table I). Reproductive activity is higher at 25°C, as is reflected by the larger number of depositions (U-test, $p < 0.05$) and the higher R_0 (Table I). The fecundity curve has a different pattern at the 2 temperatures (Fig. 3). At 25°C the reproductive effort and the r value are greater, indicative of an earlier and more intense reproductive activity (Table I). Unlike at 20°C, at 25°C producers of 4 eggs form the largest fraction (50%) (Fig. 2).

Discussion

Culture of the 2 species under nearly natural ("physiological") conditions show that the life cycles follow a similar pattern, characterized by parthenogenetic activity which starts early, lasts a relatively short time (maximum duration is 38% of the complete lifespan, in *A. polystictos* at 20°C) and leads to the production of several, in most cases 4, eggs.

The postparthenogenetic phase is typically longer than the other phases, under all conditions (except at 55‰ salinity, as already noted) and may represent up to 70% of the life cycle (*A. polystictos* at 15‰ salinity) (Figs. 4, 7).

The differences between the life cycles of the 2 species under "physiological" conditions are basically a shorter lifespan and a lower net reproductive rate (R_0) in *C. maximus*.

The longer prereproductive period and the shorter parthenogenetic one of *C. maximus* agree with the lower Tm , T and r and higher DT values of this species (Fig. 4; Table I). However, the length of the postparthenogenetic period does not differ significantly in the 2 species. In both cases it exceeds 40% of the lifespan and represents the longest phase (Fig. 4). At 20°C *C. maximus* lays an average of about half as many eggs as *A. polystictos* (2.6 vs. 4.7), but a shortened parthenogenetic period leads to an equivalent intensity of reproductive effort in the 2 species (Table I). The difference in total number of depositions between the 2 species at 20°C was observed also at the higher temperature (Fig. 3). The rise in temperature causes a parallel rise in the reproductive activity of both species and the shape of the fecundity curve

charges from irregular to triangular (Fig. 3). The net reproductive rate R_0 , the intrinsic rate of natural increase r and the reproductive effort increase at the same time (Table I).

Temperature thus seems to influence the duration and intensity of reproductive activity rather than lifespan. A similar modification of reproductive activity with rising temperature was found by Hummon (1986) for *Lepidodermella squammata*.

A. polystictos is an euryhaline species. Our observations not only confirm the great adaptability of this species, but also point out the basic uniformity of its life cycle under different rearing conditions. Only the fecundity level changes, becoming lower as salinity rises. The total absence of depositions observed in some individuals kept at 55‰ salinity is most likely related to closeness of this salinity level to the reproductive lethal limit for the species, i.e. 60‰. It is evident that *A. polystictos* more readily tolerates decreased rather than increased levels of salinity, the latter actually being highly improbable in nature (Fig. 6). The euryhalinity of *A. polystictos* is probably related to its habitat, the shoreline, where thermal and saline conditions can fluctuate rapidly.

The substantial parallelism between the life histories of the 2 species, confirmed also by that of *L. squammata* (Hummon, 1986), is indicative of the uniformity of the life cycle of chaetonotid gastrotrichs. It appears to be independent of type of habitat, whether marine or freshwater. The life strategy seems to favour a short life cycle and early parthenogenetic reproductive activity limited to the first part of the life, for which a considerable reproductive effort is required. This life strategy generally occurs in organisms living in environments that have abundant resources but are susceptible to abrupt changes of chemical and physical conditions leading to high mortality (Margalef, 1963; Gadgil and Bossert, 1970).

The significance of the long duration of the postparthenogenetic phase, also reported for the life cycle of other chaetonotids (Hummon, 1984c, 1986; Levy, 1984a,b), is still uncertain. In chaetonotids this period is not apparently characterized by the morphological and physiological modifications of "senescence", known, for example, in bdelloids rotifers (Meadow and Barrows, 1971). It probably coincides with a second reproductive phase, whose completion is yet to be confirmed, but which would justify a selective mechanism favouring this long survival period. The significance of this postparthenogenetic phase otherwise remains obscure.

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