



Risk reduction strategies in *Branchipus schaefferi* (Crustacea: Anostraca: Branchiopoda) as adaptation to a variable environment

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Received: 2 December 2016 / Revised: 16 February 2017 / Accepted: 4 March 2017 / Published online: 21 March 2017
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Abstract Mud from a temporary pool in Morocco was sequentially inundated and dried at the laboratory to follow the life history of *Branchipus schaefferi*. Once adult, each female was coupled to a male in order to study their life history and reproduction. The average percentage of hatching decreased during the successive inundations, presumably as an adaptation to the unpredictability of the habitat. However, there was no indication that the offspring of the first inundation would preferentially hatch during their first inundation too, neither was there any such preference in the offspring of the delayed hatchings. Each female reduced risk by spreading hatching time of her resting eggs over consecutive inundations. Eggs did not hatch all at the same moment, reducing the chance that a female's entire offspring would die before reaching maturity if the pool would dry out too soon. There was a significant difference between the mean value of the number of resting eggs produced by the females from a large clutch size, and those produced by females from a small clutch size. There

thus appears to be a genetic base for the clutch size of females.

Keywords Anostraca · Morocco · Mediterranean area · Ecological adaptation · Variable biotope

Introduction

Branchipus schaefferi Fischer, 1834, lives in shallow ephemeral pools in the Mediterranean area, the Sahara Desert and central Europe (Dimentman, 1981; Thiéry, 1991; Belk & Brtek, 1995; Eder et al., 1997; Petkovski, 1997; Petrov & Cvetković, 1997; Petrov & Petrov, 1997; Mura, 1999; Cvetkovic-Milicic et al., 2005; Beladjal et al., 1995, 2007a). It produces special resting eggs that undergo diapause in dried pools. The temperature that resting eggs have to endure can be as high as 80°C (McFadden et al., 2005), and they may survive up to 110°C under experimental conditions (Beladjal et al., 2008; Mertens et al., 2008). They survive the water stress and the high temperatures and when the pools are filled with water again, they hatch and initiate a new generation of fairy shrimps. (Fryer, 1996; Jönsson & Järemo, 2003; Gyllström & Hansson, 2004; Beladjal et al., 2007a, b; Atashbar et al., 2012, 2014).

“Living in unpredictable ephemeral pools, each egg of the population has to ‘make a choice’ when to hatch.” If all resting eggs hatch at the same time and the pool dries out before the juveniles reach maturity,

Guest editors: Federico Marrone, D. Christopher Rogers, Paola Zarattini & Luigi Naselli-Flores / New Challenges in Anostracan Research: a Tribute to Graziella Mura

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the whole population will perish. If part of the eggs bank delays hatching, this provides a backup when the hatched larvae do not reach maturity for some reason. Some resting eggs of a female hatch the first time the pool is inundated, yet some others wait and stay in the bottom of the depression until the pool dries up and is inundated again. Resting eggs of a pool never hatch all in a single inundation. There is always a percentage waiting for the second, third or even the eighth or ninth inundation (Mura, 1997, 2001, 2004). In the extreme unpredictable environments where *Branchipus* lives, this has a great evolutionary advantage, allowing the population to survive in time. Two other adaptations are helping survival. One is the rapid hatching of the eggs after inundation, maximizing the lifetime of the offspring (Beladjal et al., 2003). The other is the phenomenon that most nauplii hatch from eggs that are deposited near the edge of the pool. This ensures that the pool is sufficiently filled and will be wet for at least some time allowing the shrimps to mature and reproduce (Hildrew, 1985; Thiéry, 1997, personal observations).

Each resting egg of the population has to ‘decide’ whether to take the risk to quickly hatch, grow and reproduce, or to wait until better environmental conditions occur, depending on its residual survival chances. Hatched individuals, who are not expected to live much longer, are better off when taking their chances immediately, by swift maturation and reproduction. Those that are expected to live long will postpone their hatching and wait for a better environment. Each egg will act in every situation according to its residual fitness, and will thus be consistently prudent or consistently bold, leading to a stable polymorphism in the population, in which both genotypes (risk-taking and risk-avoiding) will be preserved (Wolf et al., 2007).

Hatching is often highly variable, even within the clutch of a single female, probably as an adaptation to the variable and unpredictable environment (Maffei et al., 2004; Beladjal et al., 2007b). This indicates a potential within-clutch balanced polymorphism in response to environmental cues (Brendonck, 1996). If there are differences in the requirements for hatching between the resting eggs of one species or even within one clutch, that may influence the population dynamics.

In the present work two hypotheses will be tested. The first one states that the moment of hatching is genetically based. The resting eggs produced by

couples that hatched during the x th inundation, will mostly hatch during their x th inundation too. Resting eggs of couples found in the y th inundation will have a hatching maximum when they are inundated for the y th time too.

The second hypothesis states that the number of resting eggs produced by females has a genetic basis. Daughters of mothers that produced many resting eggs will also produce a lot of resting eggs and daughters of mothers that produced only a few resting eggs will also produce a small amount of resting eggs. This would be an adaptation to the variability in volume of the ephemeral pond, by ensuring that the carrying capacity is not surpassed. Some general characteristics of the life history, such as growth rate, sex ratio, and lifespan, are also examined.

Materials and methods

Inundations

Mud used for the experiments was collected in Morocco, at 64 km south of Agadir (61 m a.s.l., 29°57'58"N–09°35'41"W), and taken to the laboratory in dried form. It contained an unknown quantity of resting eggs of several animals, including *B. schaefferi*. Five times 50 g of this mud was immersed with 1 L distilled water in a 5 L mineral water bottle (cut in half and the top half was removed). The fact that there were five plastic containers with mud was purely out of practical reasons, so the five bottles represent one big sample. No distinction was made between the individuals that hatched from different containers. The plastic containers were placed in a water reservoir at a constant temperature of 25°C ($\pm 1^\circ\text{C}$) and with day/night light regime during the whole experiment. This was done to obtain a maximal growth rate (Beladjal et al., 2003; Atashbar et al., 2012, 2014; Gharibi et al., 2016).

Twenty-four hours later, the nauplii were isolated. This day was marked as day one. Every day all containers were checked and the nauplii were taken out, until no more larvae hatched. The excess water was removed and the mud was air dried for 48 h. After that, a waiting period of two weeks at 40°C preceded the next inundation of the mud. This was done fifteen times, after that we were sure no more hatching occurred.

The nauplii were removed from the water, counted and raised in individual plastic containers with 50 mL dechlorinated tap water. Each larva got a unique code and was followed during its whole lifespan. Algae suspensions (*Scenedesmus* sp. 1×10^5 cells mL⁻¹) were added every day as a food source. At sexual maturity (around day seven), random couples of a male and female were formed in a plastic bottle containing 450 mL tap water. Because of the unequal sex ratio (more males than females), the remainder of the males was stored under the same conditions as the couples. Algae were added every day as food supply. When a male died early, its female received a widower or a male from the stock culture (Beladjal et al., 2003, 2007a).

Measuring the body length and filtering the resting eggs

Survival and resting eggs production were checked daily at the same time; one-third of the medium was renewed, and algal food was added at a concentration of 5×10^5 cells mL⁻¹. Resting eggs were harvested using 100- μ m sieves, stored in shallow plastic cups, marked with the date and the code of the mother, air dried and counted under a stereomicroscope (Wild M5) to determine the clutch size. The cups were individually stored in Petri dishes to avoid contamination.

During the egg harvesting, the body length was measured. Each specimen was transferred from its container to a Petri dish, where it was immobilized by sucking away the surrounding water. 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 SummaSketchTM III professional digitizing table, and stored on a computer for graphical and statistical use (see Beladjal et al., 1995, 2003; Atashbar et al., 2012 for details).

Hatching of the offspring

Once all the resting eggs counted, the egg production was calculated for each female. Eggs produced by one female were then inundated in a plastic container filled with 1L distilled water kept at 25°C ($\pm 1^\circ$ C). Twenty-four hours later, the nauplii were counted and transferred to another plastic container with 50-mL tap

water. Every day, the presence of new nauplii was checked until no more larvae had hatched. Then the excess water was removed by filtering the water using 100- μ m sieves. The remaining resting eggs were dried on the sieve inside the plastic container. After two weeks, the resting eggs were inundated again by refilling the container with 1 L distilled water.

Coupling of the offspring

In order to test the second hypothesis (the clutch size of females has a genetic basis), the offspring of the first inundation was paired into couples. This was not done randomly however. All the females of the first inundation were arranged in order of clutch size. From the offspring produced by the most reproductive females, females were isolated for reproduction and coupled with representative males. The same was done for those that had produced the lowest numbers of resting eggs. So there were two sets of couples: one set was composed of couples, consisting of a male from a mother that had produced lots of eggs and a female from another mother that had produced lots of eggs as well. The other set included couples made of a male from a mother that had produced few eggs and a female of another mother that had produced few eggs. In this way, the chance of inbreeding was reduced, and the possible interference of paternal effects on clutch size was taken into account. These couples were treated just like their parents, except for the fact that they were not measured. The resting eggs were also sieved daily.

Statistical analysis

The statistical analysis was done using the SPSS software package (version 22; SPSS Inc.). The Mann–Whitney *U* test was used as non-parametric analysis. $P < 0.05$ was chosen as significance level.

Results

Hatching

The number of nauplii that hatched during the various inundations is presented in Fig. 1. The time interval between two inundations was always the same (2 weeks), except between inundation 3 and 4, where

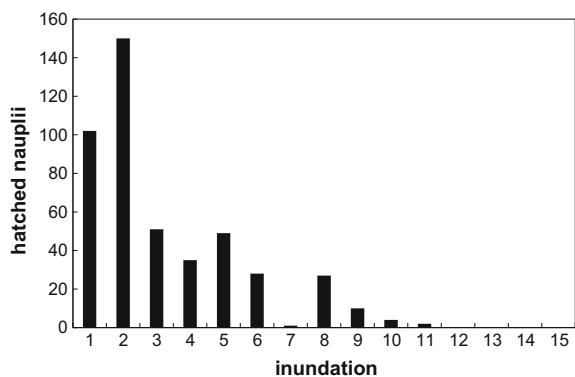


Fig. 1 Number of nauplii hatched during the various inundations of *Branchipus schaefferi* resting eggs

it was 4 weeks. This did not seem to have an influence on the number of resting eggs hatched, since there was not much difference between the number of resting eggs that hatched during the 3rd inundation and those hatched during the 4th one (Fig. 1). A descending trend can be observed in the number of hatched nauplii, but there are some distinct exceptions. Inundation 2 produced the highest number of larvae, not inundation 1; inundation 5 produced more nauplii than 4 and 6, and inundation 8 more than 7, 9, 10, or 11. However, these fluctuations are not very significant (the R^2 value of the trend line is 0.6795).

An unequal sex ratio of approximately 3:2 (1st inundation 1.56; 2nd inundation 1.4, 3rd inundation 1.64) was observed in favor of the males, as expected (Beladjal et al., 2003).

Life span and growth

The life span of males and females of the different inundations are presented in Fig. 2a–c. Only the sexed individuals are included. In the first inundation, the males lived significantly longer than the females (mean 33.41 ± 17.72 days vs 17.00 ± 6.30 ; $P < 0.05$). Males lived up to 85 days, while every female died before day 30. In the 2nd and the 3rd inundation, no significant difference was observed between the life span of the males and the females ($P = 0.8581$ and $P = 0.3134$, respectively). In the 2nd inundation, mean males were 34.00 ± 18.60 days with a maximum of 62 days; mean females were 34.95 ± 18.36 days with a maximum of 57 days. Mean males in the 3rd

inundation were 37.00 ± 14.36 days (maximum 61 days); mean females were 31.36 ± 14.29 days (maximum 51 days).

The individuals grew during their whole lifetime (Fig. 3a–c). No noticeable differences were found in the growth of males and females. However, the specimens from the 3rd inundation grew faster than the ones from the 2nd and the 1st inundation. The general trend of the growth curves is clear as the experimental data were best fitted to the logarithmic trend line. The respective equations and the slopes are given in Fig. 3a–c. The growth parameters are summarized in Table 1.

Resting eggs production of the parents

The number of resting eggs produced by the couples varied a lot in one inundation (Fig. 4). Some females produced no resting eggs at all, some more than 3,000 (maximum 3,522 resting eggs). This polymorphism is found in the three inundations. The total number of resting eggs deposited by a female also depended on her longevity. The females of the 1st inundation produced less eggs than those from the 3rd one because they died earlier.

Hatching of the offspring

Tables 2, 3, and 4 show the hatching pattern of the offspring of the couples from the 1st, the 2nd, and the 3rd inundation. There seems to be no correlation between the total number of resting eggs and the percentage that hatched. In almost every case, the percentage of nauplii that hatched during the second inundation was lower than during the first. The amount of resting eggs deposited by a female is no indication for the hatching percentage.

Coupling of the first offspring

The number of resting eggs produced by the couples from parents with many resting eggs and from parents with less eggs are presented in Fig. 5. A significant difference was observed between the mean value of the number of eggs produced by the couples that originated from mothers with a large clutch size, and those produced by the couples originating from mothers with a small clutch size ($P < 0.05$).

Fig. 2 Lifespan (expressed in days) of *Branchipus schaefferi* from three different inundations as a function of time (days). **a** 1st inundation, **b** 2nd inundation, **c** 3rd inundation

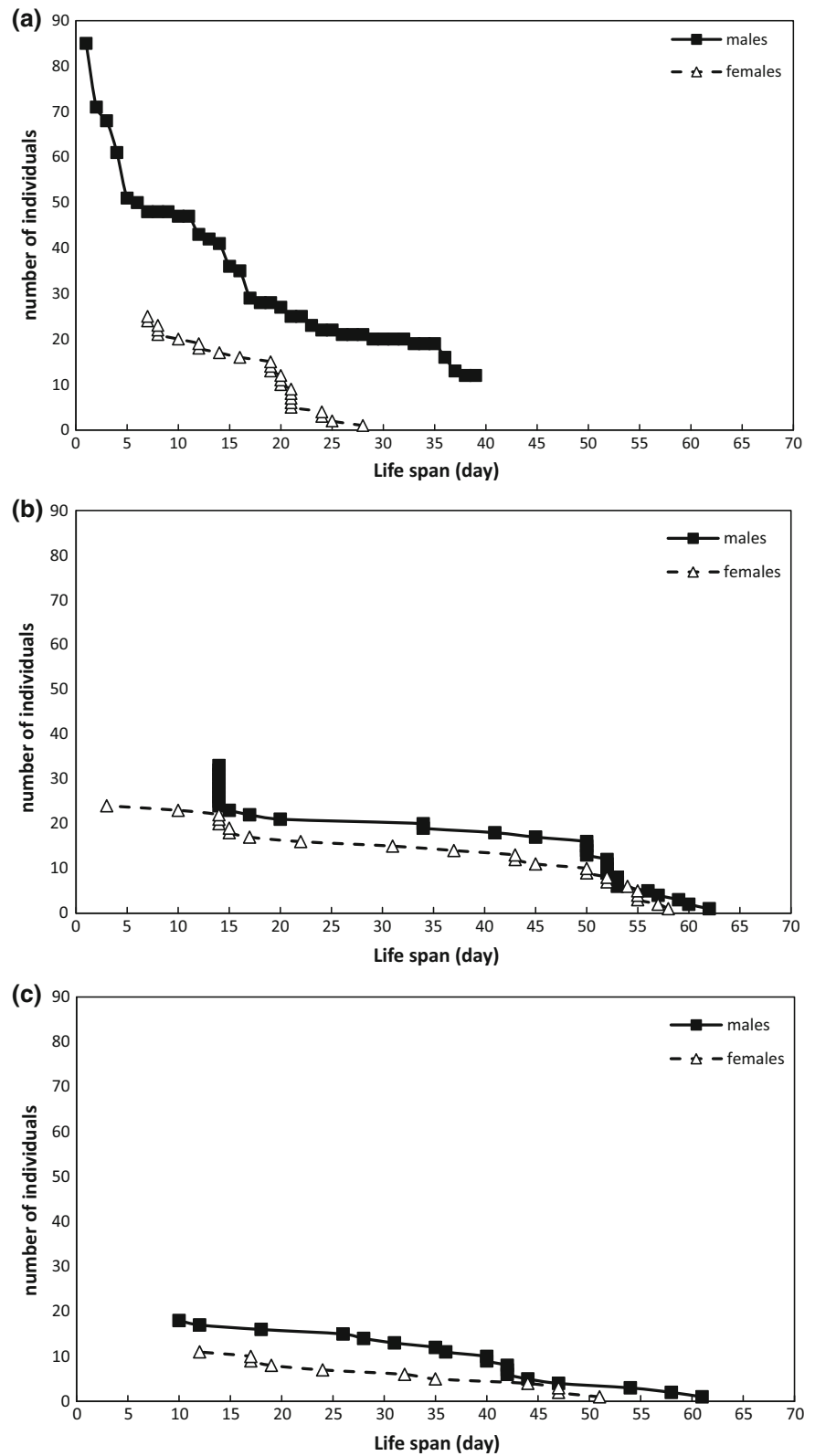


Fig. 3 Growth curves of *Branchipus schaefferi* males and females from Morocco. The *dots* are the mean experimental values; the *lines* are the best fitting curves, expressed as body length (mm) as a function of time (days). **a** 1st inundation, **b** 2nd inundation, **c** 3rd inundation

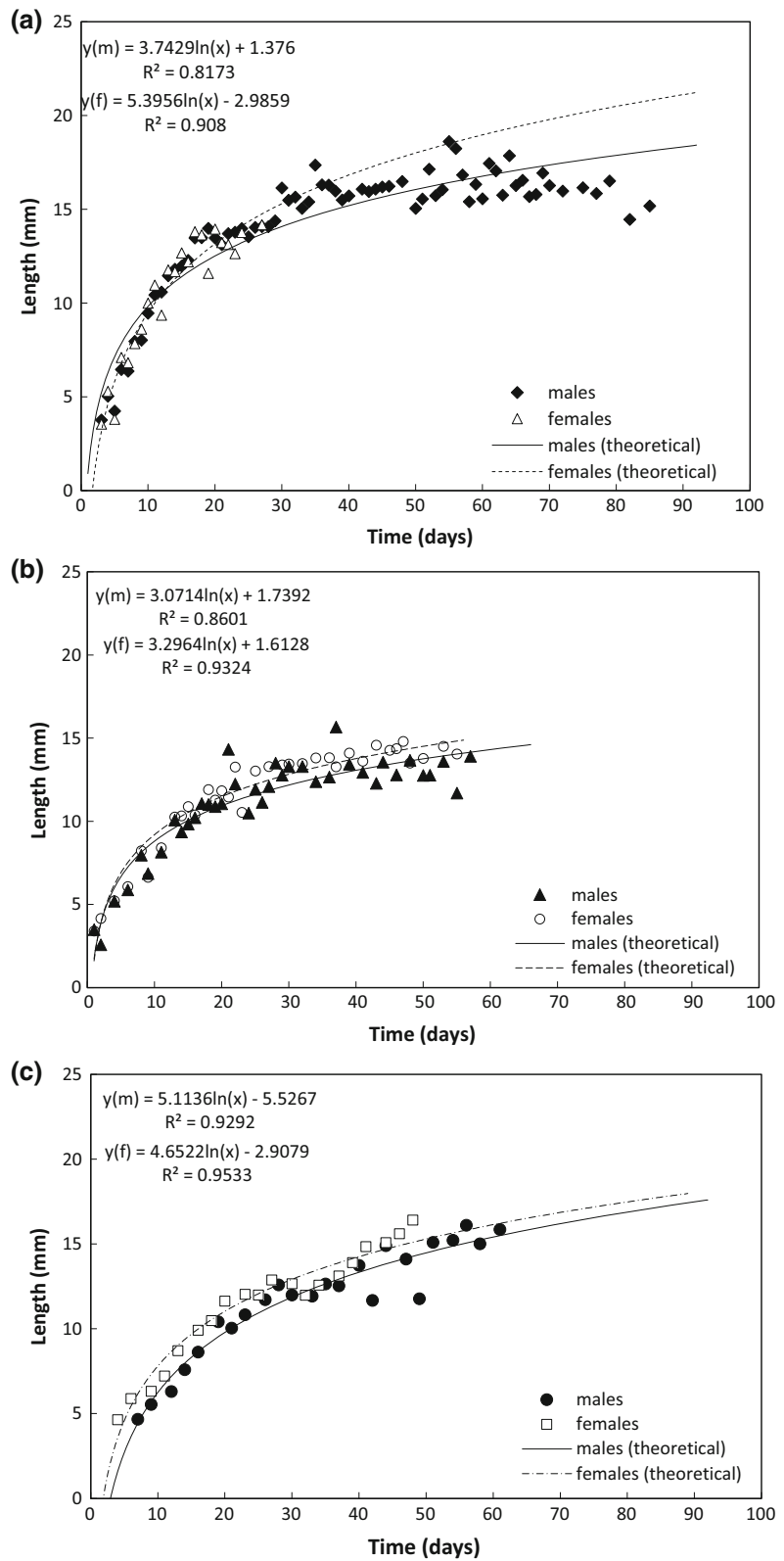
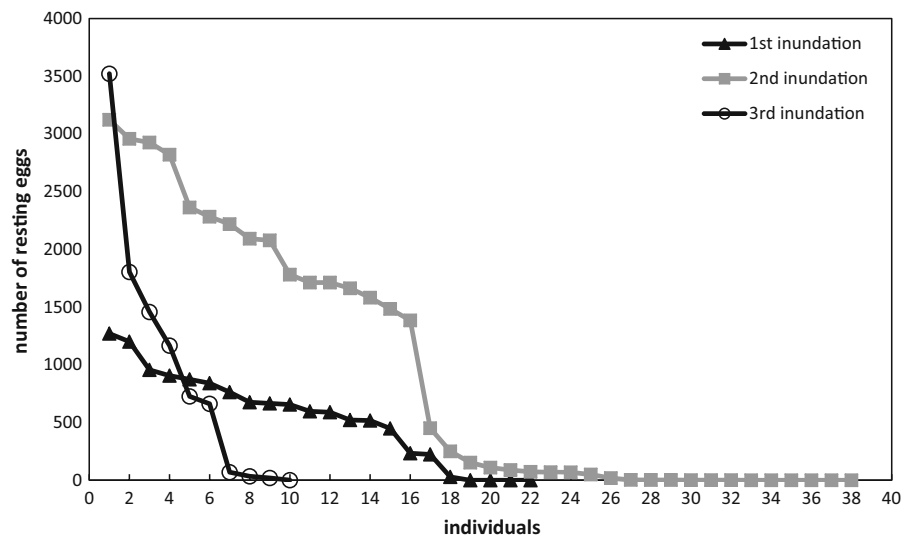


Table 1 Parameters of the growth curves of *Branchipus schaefferi* for the 3 inundations: growth rate, r ; maximum length, L_{max} (mm); mean length, L (mean) (mm); standard deviation, SD

	1st inundation		2nd inundation		3rd inundation	
	Males	Females	Males	Females	Males	Females
r	3.74	5.40	3.07	3.30	5.11	4.65
L_{max}	17.86	14.17	14.32	14.50	16.10	16.42
L (mean)	14.24	10.50	11.09	11.52	11.71	12.71
SD	3.32	3.34	2.98	3.18	3.25	4.20

Fig. 4 Resting eggs production in *Branchipus schaefferi* from the 3 inundations



Discussion

As expected, there was a general decreasing trend in the amount of resting eggs that hatched during the successive inundations. This is expected, since there was no new input of eggs, and the resting eggs bank present in the mud became smaller with every inundation.

However, one has to be prudent with the conclusions that can be drawn from these numbers. Not all of the resting eggs in the samples taken from the pool were produced by the same females, nor were they deposited at the same time. It is not known how many inundations occurred before the sample was taken. The first inundation in the laboratory was not necessarily the first one that resting eggs experienced. Still, it is remarkable that even after eleven inundations, there were still resting eggs hatching. This seems to be a stabilized adaptation to the unpredictability of

ephemeral pools. Even after a series of unsuccessful hatchings, the population would still be able to recover.

Only in the 1st inundation, a significant difference in lifetime between the males and females was observed. The 2nd and the 3rd inundations showed no significant differences, although the last surviving individual of all three inundations was a male. The difference in inundation one may be biased, since all females died relatively fast (after 17 days, while living for more than 30 days in inundation two and three) and one male lived very long. Beladjal et al. (2003) studied the life history of *B. schaefferi*, and did not find any differences in lifetime between males and females, in contrast with *Streptocephalus torvicornis* (Waga, 1842) in which males live 2.8 times longer than females (325 days vs 114).

Previous studies on the sex ratio of *B. schaefferi* have reported that in populations coming from

Table 2 Number of nauplii hatched from the resting eggs produced by the couples of the 1st inundation

Females	Number of resting eggs Inundated	1st inundation		2nd inundation	
		Nauplii	%	Nauplii	%
1	1,571	161	10.25	40	2.55
2	1,270	301	23.70	0	0.00
3	1,201	198	16.49	8	0.67
4	1,133	48	4.24	0	0.00
5	906	174	19.21	100	11.04
6	874	247	28.26	153	17.51
7	841	218	25.92	101	12.01
8	763	171	22.41	46	6.03
9	656	8	1.22	4	0.61
10	620	34	5.48	119	19.19
11	597	28	4.69	0	0.00
12	589	102	17.32	47	7.98
13	521	52	9.98	88	16.89
14	517	25	4.84	63	12.19
15	448	267	59.60	0	0.00
16	233	2	0.86	1	0.43
17	224	9	4.02	0	0.00
18	28	0	0.00	0	0.00
Mean			14.36		5.95
SD			14.62		7.05

Morocco and Algeria (Beladjal et al., 2002) and from Poland (Korinkova & Goldyn, 2011), there is a shift in sex ratio towards males (2:1). In most other populations, the sex ratio is 1:1 or there is even a shift towards females (Hildrew, 1985; Korinkova & Goldyn, 2011).

Beladjal et al. (2002) showed that this distortion is most likely caused by a supernumerary ('B') chromosome, possibly with an accumulation mechanism in males. They state that only a few males are responsible for this shift, not the whole population. Also, this characteristic is passed down from father to son, but not to daughter. In this study, a sex ratio shifted towards the males was observed, as expected.

We observed a polymorphism in the number of resting eggs produced by the females. Some produced very little resting eggs, some produced a lot. This is partly caused by the variable life span of the females. Some died sooner than others, and had less time to produce eggs. This can reflect a polymorphism in risk strategies in their ephemeral and unpredictable habitat. If part of the females quickly produce eggs and die soon, they have an advantage if the pond dries out fast, but they will not be able to make as many eggs as the

females that first grow bigger and then produce at a steady rate larger clutch sizes. In unpredictable pools with fluctuating inundation volumes, neither of these strategies will be advantaged, and a stable polymorphism of risk-prone and risk-averse should arise (Wolf et al., 2007).

Most of the resting eggs hatched during the first inundation. The second inundation always yielded much less nauplii. There is no difference in this pattern between the resting eggs produced by the couples from the different inundations. While most of the females followed this pattern, there were some that did not. Therefore, no evidence for the first hypothesis was found. So there is no correlation between hatching time of parents and offspring, expressed as dry-wet cycles of the pool. The offspring of couples from the second inundation also had its maximal hatching at the first inundation. The same goes for the resting eggs of the couples from the third inundation. Apparently, it is a characteristic of every female that her resting eggs do not all hatch at the same moment, reducing the chance that her entire offspring dies before it reaches maturity when the pool dries out too soon. However,

Table 3 Number of nauplii hatched from the resting eggs produced by the couples of the 2nd inundation

Females	Number of resting eggs Inundated	1st inundation		2nd inundation	
		Nauplii	%	Nauplii	%
1	3,123	381	12.20	259	8.29
2	2,958	597	20.18	75	2.54
3	2,926	303	10.36	39	1.33
4	2,821	214	7.59	13	0.46
5	2,363	490	20.74	25	1.06
6	2,283	334	14.63	111	4.86
7	2,158	557	25.81	332	15.38
8	2,093	459	21.93	63	3.01
9	2,078	131	6.30	386	18.58
10	1,781	228	12.80	184	10.33
11	1,712	289	16.88	50	2.92
12	1,712	139	8.12	55	3.21
13	1,663	217	13.05	135	8.12
14	1,582	303	19.15	14	0.88
15	1,484	431	29.04	78	5.26
16	1,385	347	25.05	12	0.87
17	451	39	8.65	15	3.33
18	250	16	6.40	11	4.40
19	153	47	30.72	0	0.00
20	109	64	58.72	1	0.92
21	88	19	21.59	8	9.09
22	73	8	10.96	0	0.00
Mean			18.22		4.77
SD			11.68		5.01

Table 4 Number of nauplii hatched from the resting eggs produced by the couples of the 3rd inundation

Females	Number of resting eggs Inundated	1st inundation		2nd inundation	
		Nauplii	%	Nauplii	%
1	3,522	1,388	39.41	105	2.98
2	1,804	309	17.13	182	10.09
3	1,458	345	23.66	58	3.98
4	1,166	386	33.10	69	5.92
5	727	8	1.10	2	0.28
6	662	216	32.63	14	2.11
7	69	0	0.00	3	4.35
8	34	0	0.00	8	23.53
9	20	0	0.00	0	0.00
Mean			16.34		5.91
SD			16.45		7.28

as said before, there is no evidence that the nauplii that hatched from the sample taken in the field did not experience inundations before they were taken to the

laboratory. There is also no reason to assume that the female and the male of a couple hatched during the same inundation in their life.

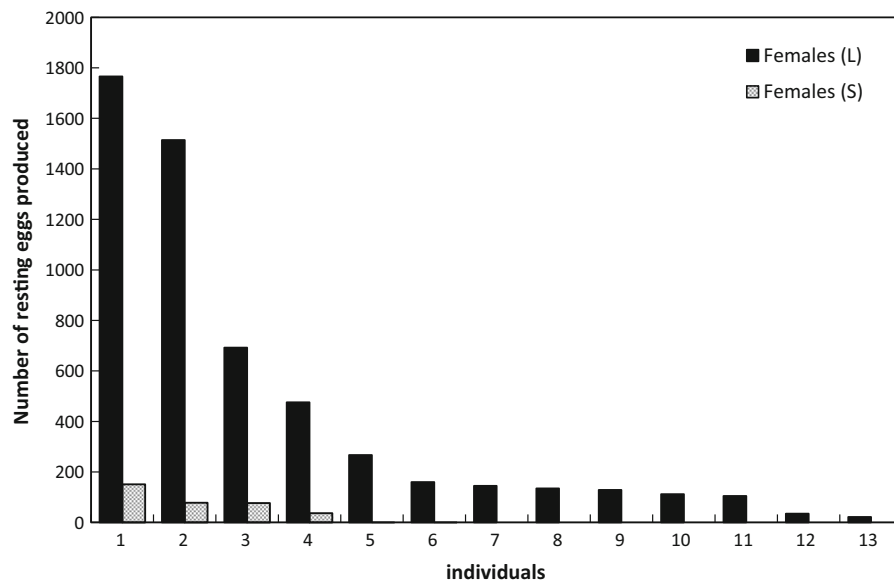


Fig. 5 Total number of resting eggs produced by the offspring of *Branchipus schaefferi* with large clutch size (L) and small clutch size (S)

There was a significant difference in the mean cyst production of the couples from females that deposited many resting eggs, and the value of the couples from those that had laid few resting eggs. Only one couple of that last group managed to produce more than 100 eggs, while several of the couples of the first group laid more than 500 eggs. There seems to be a genetic basis for the number of clutches, confirming the second hypothesis: daughters of mothers that produced many resting eggs will also produce a lot of resting eggs and offspring of females producing only a few eggs will also have a small amount of eggs.

Conclusion

The hatching of *B. schaefferi* resting eggs is divided over several inundations, as risk spreading of offspring survival in ephemeral habitats. This adaptation prevents that all offspring would die when the pond dries out too soon. However, most resting eggs hatch during the first inundation.

The amount of resting eggs produced by a female is genetically based and together with the life span of the females this may reflect a polymorphism in risk strategies to cope with the ephemeral character of the habitat.

Acknowledgments Paola Zarattini (Università degli Studi di Trieste, Italy) and one anonymous referee are acknowledged for providing constructive comments on the manuscript. We thank Prof Gilbert Van Stappen (Ghent University, Belgium) for having the kindness to improve the English language.

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