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Reproductive traits of *Porcellio variabilis* Lucas, 1946 (Isopoda, Oniscidea) from Tunisia

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Abstract: The breeding phenology and reproductive strategies of *Porcellio variabilis* were investigated, both in field and laboratory, in the population of Béja (North of Tunisia). *P. variabilis* Lucas, 1946 is characterized by a seasonal reproduction period followed by a sexual rest phase during November, December and January. Mean fecundity showed a great seasonal variation ranging between 29.612 eggs for females caught in the late summer, and 125.920 eggs for those collected in the spring. *P. variabilis* is an iteroparous species; females were able to produce one (95% of females), two (40% of females) or three broods (20% of females) during their reproduction period. The duration of the gestation period ranged from 34 days in the first brood to 14 days in the third one. Energy allocated to reproduction decreased from the first brood (26.29%) to the last one (4.618%). During the sampling period, eight cohorts were identified, each exhibiting a variable life span estimated around 6 months for cohorts born in early spring, and 12 months for those born in the fall. According to our present results and previous studies in another population of *P. variabilis* in Tunisia, we discuss factors of variability in breeding phenology in this species.

Keywords: Terrestrial Isopods; Breeding phenology; variability; iteroparous species

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1 Introduction

Studies of life-history aim to explain patterns in the evolution of reproductive investment, growth and survival [1]. The fundamental component of life history is largely a trade-off deal. The search for a trade-off between different biological requirements such as age at first reproduction, fertility, survival and mortality should aim to optimize the selective value (fitness). For example, the brood size is positively correlated to the female body size [2-10]. In terrestrial isopods, reproductive traits are often responsive to variation in numerous abiotic and biotic environmental factors [9] resulting in temporal coincidences of the release of offspring with favorable conditions for growth and survival [2]. Thus, terrestrial isopods exhibit different reproductive patterns: discrete (seasonal) or continuous (non-seasonal) [11].

Variations in reproductive traits of woodlice inhabiting arid, temperate and tropical regions have been extensively studied [3,7,8,11-14,16-21]. Variability can be seen between species [2,11] and between different populations of the same species [12]. Seasonal and annual variations can also be observed within the same population [3].

Herein we present the life span, reproductive patterns and reproductive allocation of a number of *Porcellio variabilis* Lucas, 1946 cohorts inhabiting Béja (North Tunisia) to highlight its life history tactic. Another goal of the study is to compare our results with those of a previous study reported by Achouri [9] on the mountain population of Chaambi (Centre West of Tunisia). Finally, we discuss the factors influencing intraspecific variability of reproductive traits.

2 Experimental Procedures

2.1 Study site and sampling

The sampling site was 5 km north of Béja (36°44’ N, 9°10’ E (DMS)) in the bank of Wadi Béja, at an elevation of 223 m. It consists of one half hectare of grassland located outside the urban area of Béja (Figure 1). The climate is warm-temperate characterized by a cool, rainy season and a hot, dry season. In Béja, the mean temperature is 17.5°C and the average annual rainfall is 662 mm. The difference in precipitation between the driest month (July) and the wettest month (December) is 103 mm. Throughout the year, there is a difference of 18°C between the month with the lowest temperatures (January) and the highest temperatures (August).

A sample of *P. variabilis*, an endemic species to North Africa [22], was taken once per month during 18 months using a quadrat of 1 m^2. An average sample size included one hundred specimens. The specimens were collected by hand from under stones. Samples were transported to the laboratory in plastic boxes containing soil from the sampling site.

2.2 Laboratory procedure

In the laboratory, specimens of each sample, fixed in 70% alcohol, were placed in three categories: (1) undifferentiated less than 4 mm, (2) females divided into i) non reproductive females without brood push and ii) reproductive females including breeding females and females with empty marsupium and (3) males. Thereafter, specimens were sized, from the anterior edge of the cephalon to the end of the pleotelson, using a stereomicroscope (+/- 0.01 mm, Leica MS5).

During the reproductive period of February to October [23], 81 breeding females, collected in the field, were sized and dissected under a stereomicroscope and the number of eggs was counted for estimation of fecundity.

In order to study the fertility as determined by the number of mancae (living mancae) hatched per brood and the reproductive allocation, 20 gravid females (females with transparent oostegites before the movement of mature oocytes into the marsupium) collected in the field at the beginning of the reproductive period (February 2010) were sized and weighed using a stereomicroscope (+/- 0.01 mm, Leica MS5) and a Mettler AB22204-S balance (+/- 0.1 mg accuracy) respectively. They were kept individually, under natural laboratory conditions, in translucent plastic boxes (10 × 10 × 10 cm) containing sterilized soil and until mancae release. Every three days, each female was weighed, both before and immediately after mancae release using a Mettler AB22204-S balance (+/- 0.1 mg accuracy). The exact date of parturition and the number of mancae produced by individual females were determined. These females were observed from the day of collection until their death.

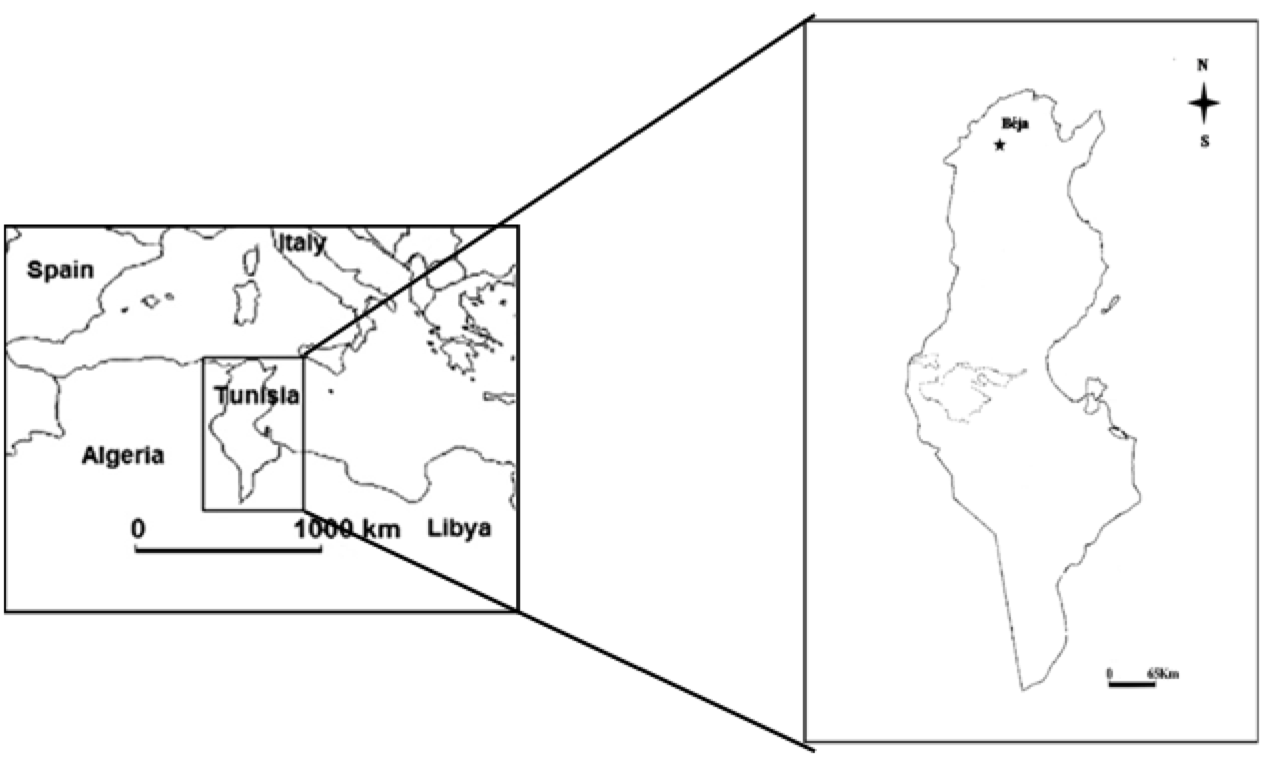

Figure 1. Sample site of *Porcellio variabilis* in Béja area.

2.3 Data analysis

To determine the population structure, the specimens of each sample were grouped into 19 classes based on their size. The groups ranged from 2 to 20 mm. The cohorts were identified by size frequency distribution analysis using the ANAMOD software application [24].

The relationship between fecundity and female body size was tested by one-way ANCOVA using XLSTAT V 7.5.2. Software. Comparison among mean body size of the breeding females and mean fecundity was done through an ANOVA test using XLSTAT V 7.5.2. Software.

The reproductive allocation (RA) was calculated as the percentage of weight lost by the female during the process of producing a brood of young:

$$RA = \frac{(W0-W1)}{W0} X\ 100$$

Where W_0 is the initial weight before the mancae release and W_1 is the weight immediately following mancae release [4, 25]. An ANOVA test using XLSTAT V 7.5.2. Software was also used to compare mean reproductive allocations.

The weight of individual manca can be calculated by dividing the body mass lost by the female when reproducing, by the total number of mancae the female reproduced [16].

3 Results

3.1 Breeding period

The onset of the breeding season is marked by the first appearance of breeding females, while the end is marked by the disappearance of the last ovigerous females.

In *P. variablis*, the monthly sampling from the Béja region during the sampling period indicated the presence of gravid females from February to October followed by a slight rest during November, December and January (Figure 2). The highest percentage of gravid females was observed in May of the first year and May-June of the second year (100% of the total females were ovigerous, Figure 2). The reproductive females at the onset of reproduction (in the spring) had an average body size of 13.56 ± 1.43 mm (Table 1). However, the mean size of the last gravid females observed in the fall was 9.72 ± 1.3 mm (Table 1). Indeed, the mean size of the breeding females varied significantly between the spring and the summer/fall samples collected (t = 12.092, p < 0.0001, Table 1).

3.2 Fecundity

The number of marsupial eggs per female in *P. variabilis* species ranges from 16 in females 7.5 mm in size, to 195

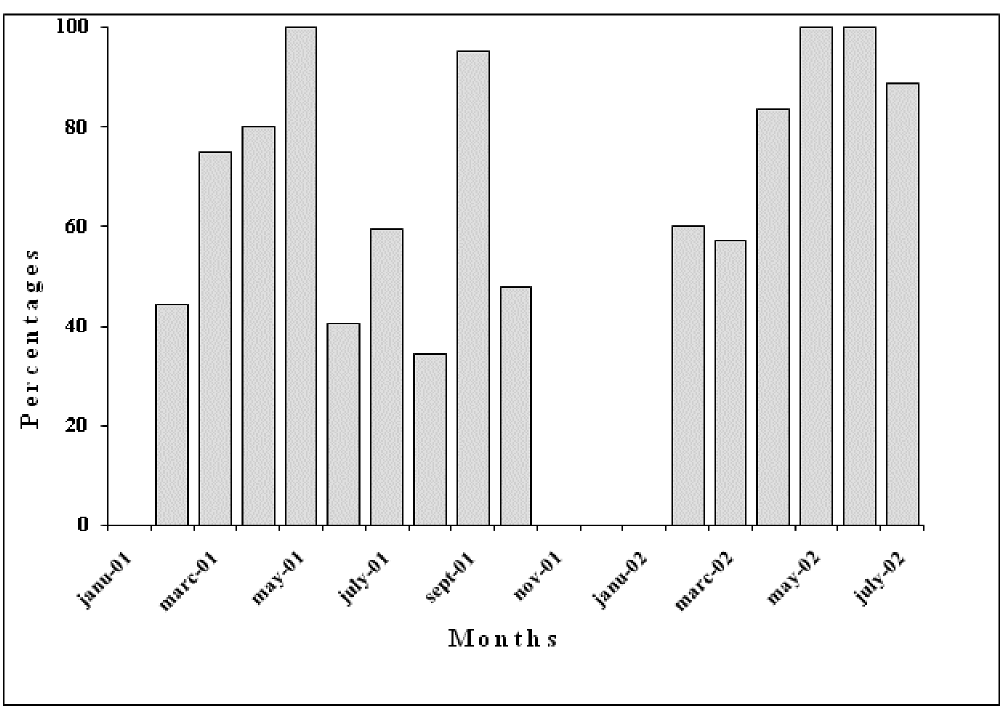

Figure 2. Percentages of breeding females in *Porcellio variabilis* (observed in field samples) during the 18 months of study.

eggs in females that were16.5 mm in size (Table 1). The fecundity shows a seasonal intra-populational variation: the mean fecundity was 29.612 ± 10.821 eggs for the females caught in late summer and 125.920 ± 33.538 eggs for those collected in spring. After testing the normality of data using Shapiro-Wilk test (W) for both groups (W = 0.978, $p > 0.05$ for the first group and W= 0.953, $p > 0.05$) and using one-way ANCOVA, a positive correlation between body size and fecundity of the two groups of females was reported, but significant differences in body size/ fecundity relationships were recorded between females collected in late summer-fall and those collected in spring (Figure 3). A statistically significant difference in adjacent means of the linear regressions was found between the two groups ($2.144E^{-06}$). However, the probability that the slopes are uniform was quite strong (0.4289).

3.3 Gestation and reproductive investment

During the study period, the rearing females showed only parturial moult. One of them died before mancae release at the first brood. Of the original 20 females, only 8 became gravid a second time and only 4 became gravid a third time. Of the eight females attending the second brood, four died before the post-parturial moult.

These females were able to produce one (95% of females), two (40% of females) or three broods (20% of females) during the same reproduction period without new mating. The duration of the gestation period ranged between 34 days in the first brood and 14 days in the third one (Table 2).

Progeny mass represents 26.29% of the female body mass in the first brood, 13.628% in the second and 4.618%

Table 1. Fecundity and body size in gravid females.

Season	N	Size (mm)				Fecundity		
		Min	Max	Mean ± SE	t	Min	Max	Mean ± SE
summer-fall	31	7.5	13.2	9.729 ± 1.300	12.092	16	50	29.612 ± 10.821
spring	50	10.5	16.5	13.56 0 ± 1.435	p < 0.05	58	195	125.920 ± 33.538
total	81	7.5	16.5	12.093 ± 2.325		16	195	89.061 ± 2.325

N, number of gravid females; t, student test

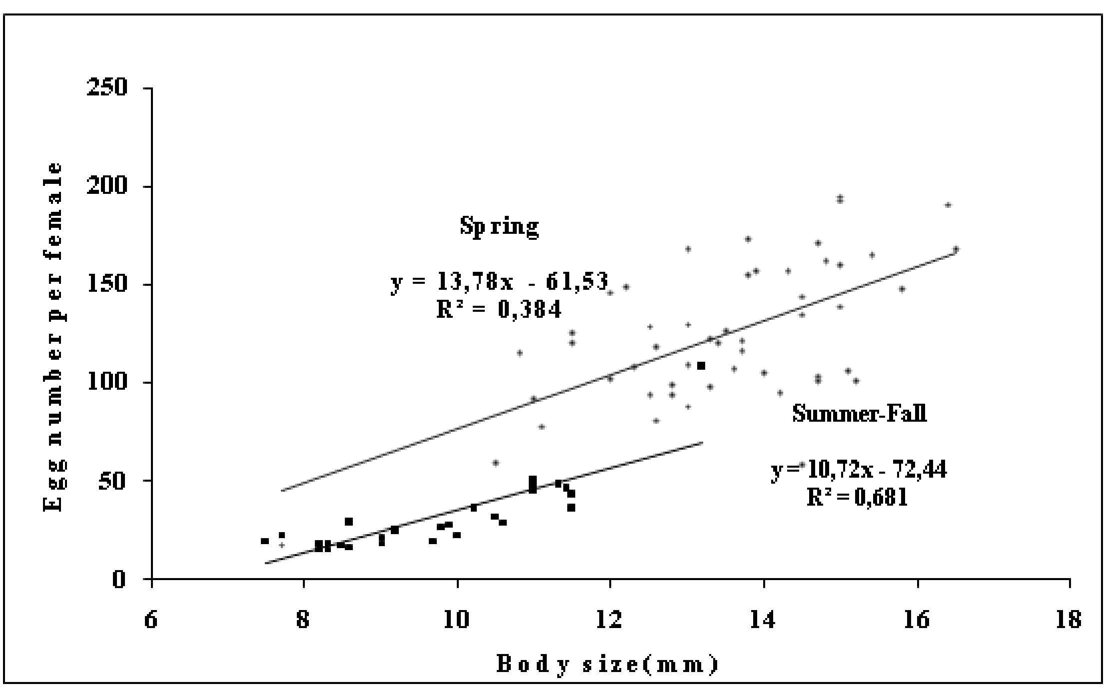

Figure 3. Relationship between body size (mm) and egg number in gravid females of *Porcellio variabilis*.

in the third (Table 2). The reproductive allocation (RA) decreases from the first brood to the last one. There was a significant difference in the mean values between broods ($F = 3.869$, $p = 0.030$).

There was a positive correlation between the female body size and fertility in all three broods. However, female fertility varied within each brood with 93 ± 33 mancae in the first brood, 58 ± 18 mancae in the second and 26 ± 8 mancae in the third (Figure 4). Furthermore, the number of mancae released, as well as their individual mass, decreased from the first brood to the third one (Table 2).

3.4 Identification, life span and recruitment of cohorts

Size frequency distribution was analyzed to recognize the different cohorts (Figures 5- 6). The Anamod software application [24] allowed the identification of eight cohorts (C_1-C_8) during the sampling period (Figure 5). During the first year, two cohorts - C_1 and C_2 - were detected in January, and three cohorts - C_3, C_4 and C_5- were born in April, July and September, respectively. C_6 and C_7 appeared in April-May of the second year and C_8 in July. The three cohorts (C_3-C_5), were followed from their detection up to their mortality, allowing for the estimation of the life span at six to eleven months. Cohorts C_1 and C_2 generated cohort C_3 in the spring, forming the first generation in the reproductive period. While cohort C_1 disappeared in early spring of the first year, cohorts C_2 with C_3 gave birth to cohort C_4 in summer and then disappeared respectively in July and September of the first year. This latter cohort, together with cohort C_3, contributed to the recruitment of cohort C_5 in the late summer of the first year, constituting the second breeding activity. C_4 and C_5 were able to survive until the spring of the second year and give birth to C_6

Table 2. Duration of gestation and reproductive investment per brood.

	N	Duration of gestation (j) (M ± SE)	Δ W (mg)	RA (%)	Number of mancae (M ± SE)	Individual mass of mancae (mg) (M ± SE)
First brood	19	34.384 ± 1.909	59.916 ± 17.212	26.29 ± 5.54	93 ± 33	0.68 ± 0.203
Second brood	8	21.428 ± 2.318	20.75 ± 8.084	13.628 ± 4.69	58 ± 18	0.373 ± 0.159
Third Brood	4	14.25 ± 1.108	7 ± 1.414	4.618 ± 0.681	26 ± 8	0.268 ± 0.039

N, number of gravid females; Δ W, female weight loss; RA, reproductive allocation

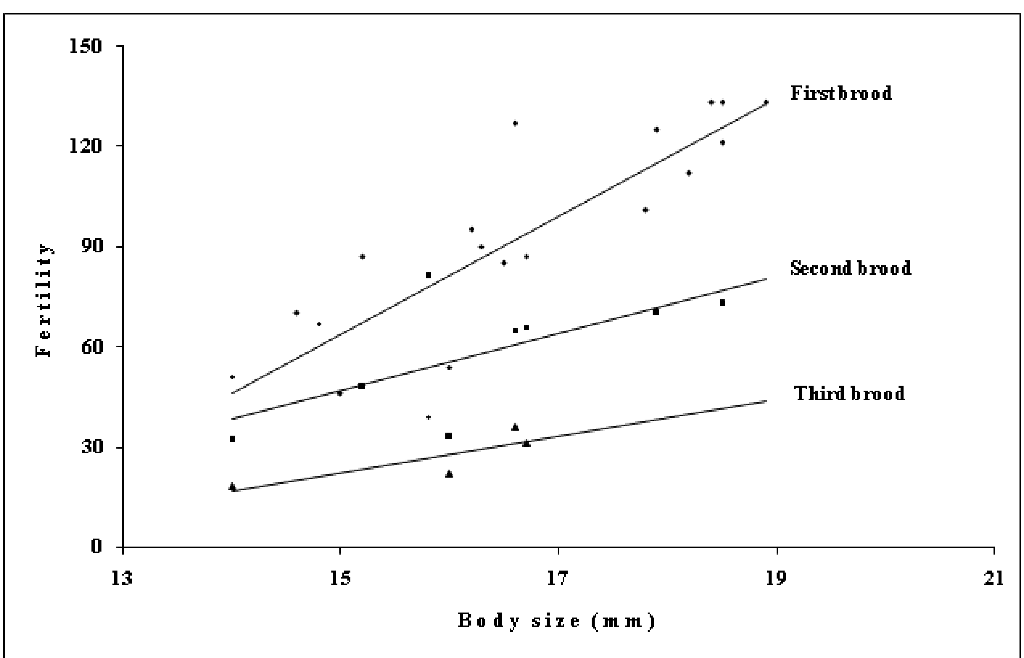

Figure 4. Relationship between body size (mm) and fertility in gravid females of *Porcellio variabilis*.

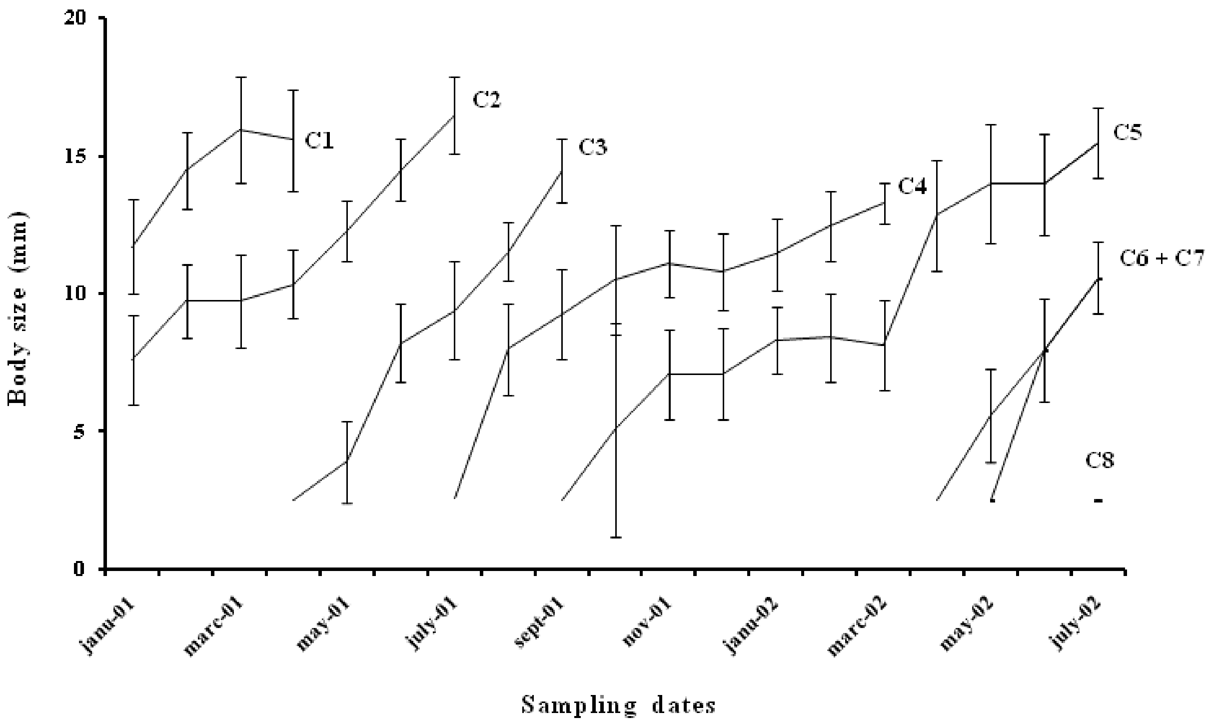

Figure 5. Graphic adjustment of the growth curves of cohorts (mean body size in mm, standard deviation).

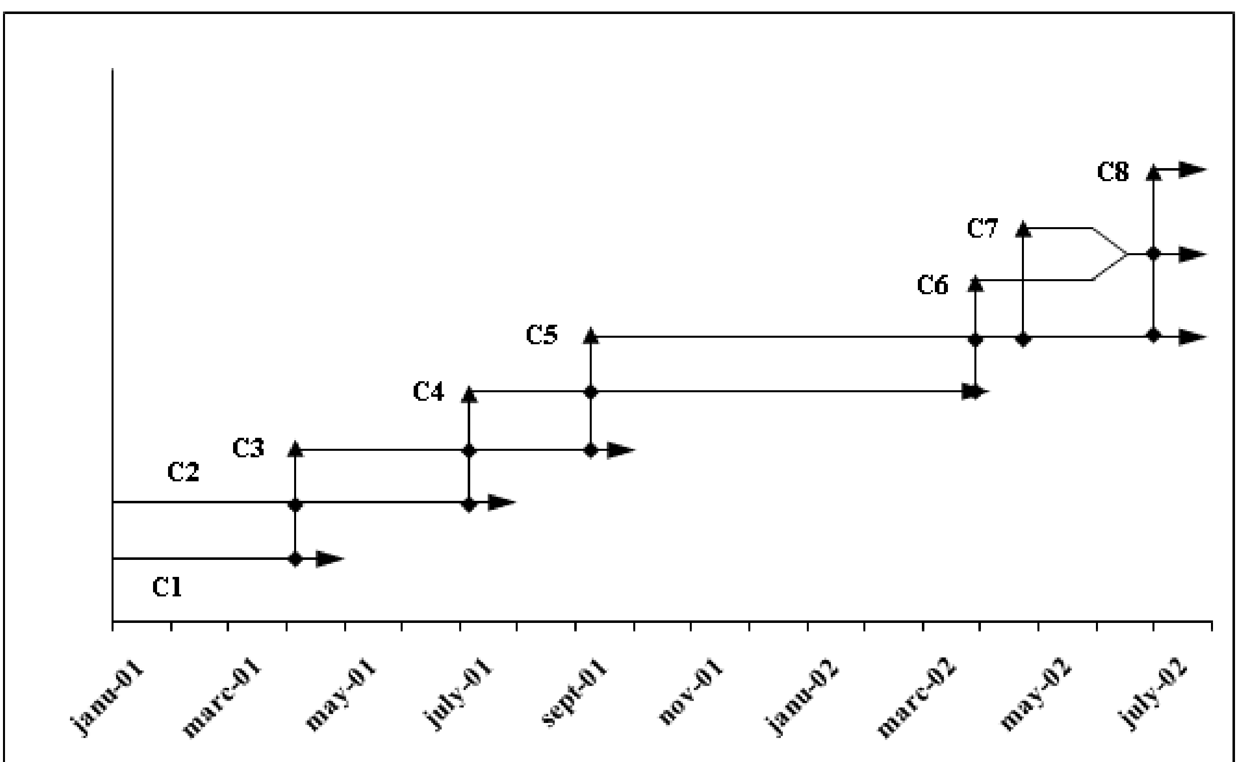

Figure 6. Analysis of the recruitment pattern of the population of *Porcellio variabilis* during the study period.

in April. C_5 was the progenitor of C_7 whereas C_8 was the newborn of mating in C_5 and merged cohorts C_6 and C_7.

3.5 Reproductive pattern

The analysis of the different demographic parameters of *P. variabilis* shows three categories of females (Figure 5).

The first cohort (C_3) of the breeding period, born in April, had a short life span (6 months) and an average size fluctuating between 2.5 mm at birth and 14.5 ± 1.16 mm at the end of life. This cohort started its reproductive activity in the same year of birth during late summer into autumn, and produced one or two broods.

Those born in June and July (C_4) could survive up to 9 months and their average size ranged from a minimum of 2.55 mm to a maximum of 13.294 ± 0.751mm. These females were able to produce two broods: the first at the end of the breeding season of the same year of birth, and the second at the beginning of the following year's reproduction period.

The last category was females born in the fall, at the end of the breeding season (C_5). Their average size was between 2.5 mm at birth and 15.5 ± 2.02 mm at the end of their life. They lived longer (11 months to one year) and could provide up to three broods during the breeding season of the following year.

Discussion

P. variabilis is an iteroparous species [23]. As most temperate species like *Armadillidum pelagicum* Arcangeli, 1955 [3,19], *Tylos ponticus* Grebnitsky, 1874, *Halophiloscia couchii* (Kinahan, 1858) and *Armadillium album* Dollfus, 1887 [20], *Porcellio dalensi* Caruso and Di Maio, 1990, *Porcellio laevis* Latreille, 1804, *Soteriscus gaditanus* Vandel, 1956, *Armadillidium granulatum* Brandt, 1833, *Porcellionides pruinosus* (Brandt, 1833) and *Agabiformius lentus* (Budde-Lund, 1885) [7], *Porcellio lamellatus* Budde-Lund, 1885 [20,26], *P. variabilis* in Béja exhibited large seasonal reproductive activity extending over nine months.

A different reproductive phenology pattern was reported in the population of the Chaambi area, which showed mature oocytes in February, marsupial eggs in March and April, and mancae release from May to September. They exhibited more sexual rest in July and August [9]. This variation in reproductive phenology of the two populations of *P. variabilis* in Béja and Chaambi would be due to local environmental conditions such as bioclimatic stage (humid in Béja and semi-arid in Chaambi), rainfall (662 mm and 335 mm), and altitude (223 m and 1544 m).

Size at breeding is an important life history parameter for *P. variabilis* as it influences female fecundity. Both in the Béja and Chaambi populations, large females produce larger broods. The positive relationship between female size and fecundity is noted in several terrestrial isopod species [6,7,10,13,19,21,27]. However, the mean fecundity of *P. variabilis* showed seasonal intra and inter-population variability and was much lower in the population of Chaambi (51 ± 0.5 eggs) than in that of Béja (89.061 ± 2.325 eggs). Variation in fecundity could be attributed to differences in microclimate parameters (temperature, rainfall), and could also be associated with other factors, such as diet [28]. For example, *Armadillidium vulgare* reared on dicotyledonous food sources exhibit higher growth rates and fecundity in comparison to those reared on monocoty-ledonous food [29]. In addition, feminizing *Wolbachia* infections detected in *P. variabilis* [30] also appeared to diminish fecundity (e.g. *Oniscus asellus*) [31].

Another parameter used to define reproductive strategies in *P.variabilis* is reproductive allocation, which shows variability in broods. Females invested more in their first brood because 58% of them would die out after releasing mancae. Reproductive effort decreases, resulting in fewer and smaller offspring. Many questions could be raised regarding this: could this variability be an outcome of multi-parenthood? Alternatively, could it stem from a differential embryo growth? [11]. Another possibility to consider is if it is a response to abiotic-environmental stresses such as temperature or drought? Overall levels of reproductive effort for the two populations of the Béja and Chaambi areas were approximate to those recorded for temperate species [2,7]. However, they were higher than the levels of reproductive effort of three North African species reaching their extreme (11.3%) in *Porcellio simulator*-females somatic dry weight [32].

In both populations of *P. variabilis*, cohorts showed different seasonal life span. The cohorts born by the end of the reproductive period had a longer life span (19 months for Chaambi and 12 months for Béja) than those born in spring (14 months for Chaambi and 6 months for Béja).

Overall, considering its life span and its reproductive traits, *P. variabilis* seems to be r-strategists. In its reproductive pattern, the species showed intra-specific differences among the studied population of Béja and that of Chaambi, as reported by Achouri [9]. These differences were a response to environmental variables rather than being a species-specific trait [33]. In order to better understand the importance of these factors in affecting breeding patterns, it would be interesting to study other populations of *P. variabilis*, especially the Ain Drahem population which seemed to be the most morphologically and genetically distinct [34].

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Conflict of interest: Authors declare nothing to disclose.

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