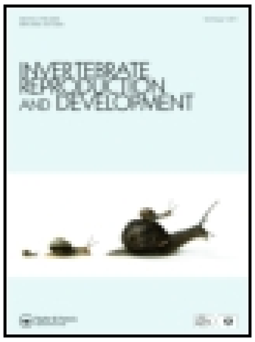

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Breeding patterns in the pre-desert oniscid isopod *Porcellio buddelundi* of Matmata (Gabès, Tunisia)

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ABSTRACT

Porcellio buddelundi inhabits arid areas in Tunisia. The reproductive pattern of a population at Oued El Jir, Matmata (Tunisia) was studied from July 2005 to June 2006. Monthly samples were taken during the study period. The overall sex ratio was biased toward females. Males, females, and newborns all had greater body-mass in autumn than in spring and their lowest mean body-mass was in June and July. Ovigerous females greater than 41.1 mg in body-mass, were collected from March through May and from September through October, suggesting seasonal reproduction with two breeding seasons: the longer one in spring (3 months) and another in the fall (2 months). Fecundity, which was positively correlated with the body-mass of females, varied between breeding seasons with a large number in spring and a small number in autumn. Seasonal variation of fecundity could be explained by the growth rate of ovigerous females affecting the fecundity more in spring than in autumn. The onset of breeding, in *P. buddelundi*, takes place when the day-length exceeds 12 h and the soil moisture decreases.

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Arid environments; xeric species; Crustacea; terrestrial isopod; sex ratio; fecundity

Introduction

Terrestrial isopods are ecologically important, since like other detritivorous invertebrates such as earthworms and most millipedes, they play an important role in decomposition processes through mechanical and chemical breakdown of plant litter and by enhancing microbial activity (Zimmer 2002). Isopod grazing can thus, be considered a key system regulator of ecosystem functions including decomposition and nutrient recycling (Paoletti & Hassall 1999), influencing community composition and functioning of complex woodland soil microbial communities (Crowther et al. 2013). The impact of isopods and decomposition processes is species and litter specific (Abd El-Wakeil 2015).

Besides their important role in litter decomposition, isopods are able to colonize a wide range of environments, even the most hostile such as littoral and desert habitats. Species inhabiting xeric habitats are of particular interest because in habitats too extreme for earthworms and where diplopods are poorly represented (Medini-Bouaziz, personal observation), they may be one of the important agents for desert soil fertility (Crawford 1982; Hornung et al. 2015). Xeric species have also lower permeability to water loss (Greenaway & Warburg 1998) and higher consumption rates and assimilation efficiencies of plant litter (Ghabbour 1983) than temperate species. Hence, the interest to study the population dynamics and reproductive biology of xeric species, such as *Porcellio buddelundi*.

Among the 12 species of *Porcellio* reported from Tunisia, four are well-adapted to arid habitats; only *Porcellio albinus* has a burrowing behavior (Medini-Bouaziz et al. 2017a). Two species *P. buddelundi* and *P. simulator*, are typically found in rocky environments (Reg), but rarely share the same habitat. Since, the population size of *P. simulator* is low and its geographical distribution is very limited (Medini & Charfi-Cheikhrouha 1998), we have focused our investigations on *P. buddelundi*. This species is endemic to Pelagie's island (Italy) (Caruso & Di Maio 1993; Di Maio 1996) and Tunisia. In Tunisia, its distribution covers the southern regions of the Tunisian Dorsal corresponding to the eastern extension of the Saharan Atlas, from Kairouan to Douiret (Tataouine) and Jerba Island (Medini-Bouaziz 2002).

Available information on the reproduction and life history patterns of isopods is based largely on species inhabiting mesic habitats in temperate regions (Warburg 1995). Reproductive phenology of xeric species has been well-studied only for those existing in the desert of the Middle East: *Hemilepistus reaumurii* (Warburg 1994), *Hemilepistus elongates* (Linsenmair 2007), *Hemilepistus klugii* (Kashani et al. 2011), and *Porcellio ficulneus* (Hornung

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Figure 1. Sampling site.

& Warburg 1993). In Tunisia, reproduction has been studied for *H. reaumurii* (Nasri et al. 1996) and recently for the Saharan species *P. albinus* (Medini-Bouaziz et al. 2017b) but nothing is, so far, known about the reproductive traits of the other xeric species of *Porcellio*.

The main aim of the present study was to analyze the breeding phenology of *P. buddelundi* making the case that there are certainly important environmental variables in the breeding of terrestrial isopods.

Material and methods

Study site and sampling

The sampling site was Oued El Jir at Matmata, 27 kms from the Gabès region, in the Southeast of Tunisia (33°31′34″ N, 10°7′19″ E (DMS)) (Figure 1). It corresponds to a nearly bare stony 'Reg' which is home to various types of garrigue vegetation, including *Artemisia, Rosmarinus, Stipa,* and *Lygeum*. The climate is a pre-saharan arid climate belonging to the lower arid.

Monthly samples of almost one hundred specimens of *P. buddelundi* were taken during the period from, July 2005 through, June 2006. Specimens were collected by hand from under stones and transported to the laboratory in plastic boxes containing soil from the sampling site.

Soil temperature and soil humidity were measured monthly *in situ* using a thermo hygrometer. Information about precipitation and photoperiod was obtained from CRDA (Regional Commission for Agricultural Development of Gabès).

Laboratory procedures

All sampled individuals were weighed and preserved in 70% ethanol. Then, they were sorted according to sex into three categories: mancae (= newborns = pulli = offspring) whose body-mass did not exceed 30 mg, males, and females that were separated into two groups: (1) non-reproductive females without a brood pouch (= marsupium), and (2) reproductive females (= breeding females) categorized as (a) ovigerous females with eggs, embryos, or mancae in the brood pouch and (b) post-ovigerous females with an empty brood pouch (Achouri et al. 2003; Hamaied & Charfi-Cheikhrouha 2004).

To quantify the fecundity indicated by the number of eggs in the marsupium, 30 ovigerous females early in the development of eggs (dark yellow and rounded eggs) were collected in the field during the breeding period, were weighed, dissected, and their eggs removed from the brood pouch and counted.

Statistical analysis

The relationship between fecundity, female body-mass and season (spring and autumn) was tested by ANCOVA using the GLM procedure of SAS software.

The expected and observed values of the sex ratio were compared, each month, using a χ^2 test. The comparison of mean body-mass of males and females collected for the entire sampling period was carried out using a *T*-test. Correlation between environmental factors and the percentage of ovigerous females were calculated using the Pearson's coefficient.

Results

Sex ratio

In total, 1433 adults (764 females and 669 males) were collected during the sampling period indicating an overall sex ratio biased toward females (1 ♂: 1.2 ♀). Monthly analysis shows that the sex ratio fluctuated throughout the sampling period; the values ranged between 1 ♂: 3 ♀ in April 2006 and 1.8 ♂: 1 ♀ in May 2006 (Figure 2). On most occasions, the sex ratio was significantly different from 1:1; it was skewed toward females in January, March, April, and June 2006 (χ^2 = 5.29, 20.4, 9, and 4.44, respectively; ddl 1; $p < 0.05$) and toward males in November 2005 and May 2006 (χ^2 = 4.38 and 10.84, respectively; ddl 1; $p < 0.05$).

Mean body-mass distribution

Monthly average mean body-mass distribution, for all collected individuals from Oued El Jir Matmata, is distinctly bimodal for both sexes (Figure 3). The first and most important mode was observed in October 2005 for males (mean body-mass of 75.47 ± 3.41 mg), non-reproductive females (body-mass of 61.8 ± 2.81 mg), and ovigerous females (mean body-mass of 90.1 ± 4.39 mg). The second mode of mean body-mass was detected in February 2006 for males

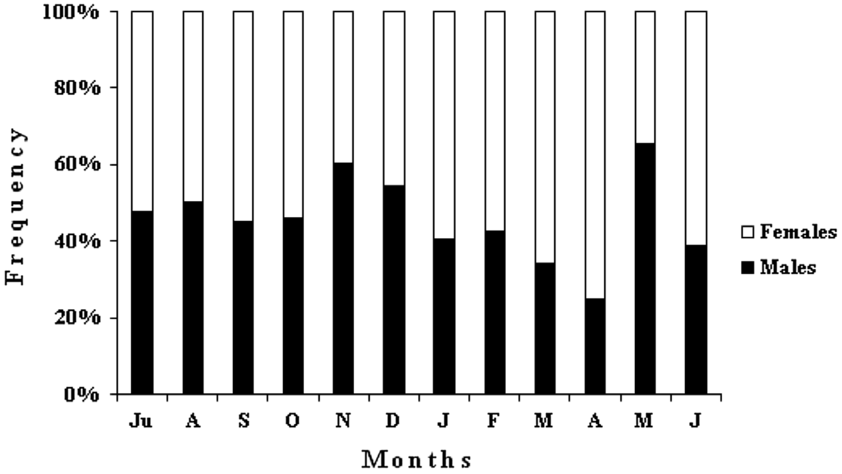

Figure 2. Monthly sex ratio in *Porcellio buddelundi* from Matmata between July 2005 and June 2006.

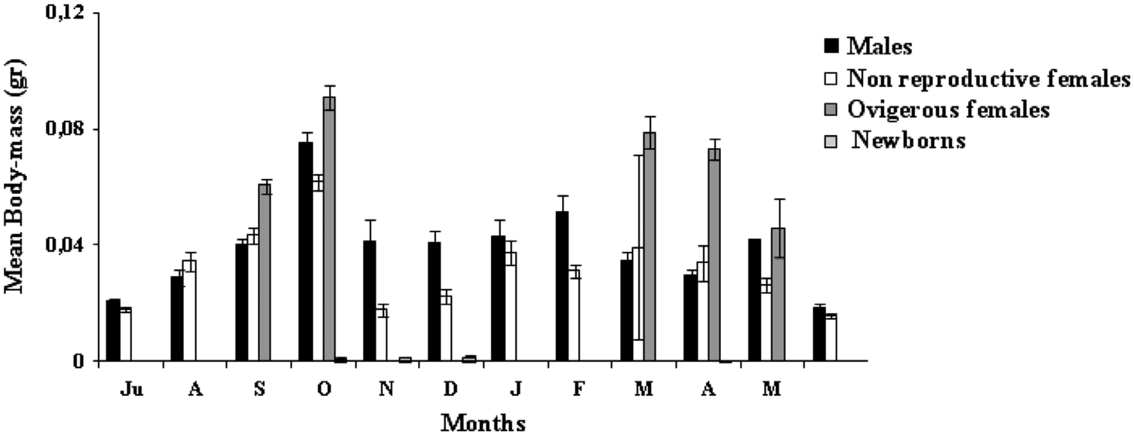

Figure 3. Mean body-mass distributions of *Porcellio buddelundi* males, ovigerous and non-reproductive females, and newborns in Matmata between July 2005 and June 2006.

(51.21 ± 6 mg) and in March 2006 for ovigerous and non-reproductive females (78.86 ± 5.6 mg and 39.25 ± 31.66, respectively). A comparison of the mean body-mass of males and females collected for the entire sampling period showed that males are statistically larger than females (*t*-test; $t = 5.67$, $P < 0.05$). Moreover, the lowest mean body-mass was exhibited for isopods in June and July.

The mean body-mass of newborns ranged between 1.12 ± 0.52 mg in autumn and 0.44 ± 0.21 mg in spring. Significant differences in body-mass of newborns were recorded between autumn and spring (*t*-test; $t = 12.98$, $P < 0.05$).

Monitoring the average body-mass of ovigerous females during breeding periods showed an increase in mean body-mass in autumn from 60.55 ± 2.48 mg in September to 90.1 ± 4.39 mg in October, and a decrease in spring, declining from 78.86 ± 5.6 mg in March to 46.03 ± 10.02 mg in May.

Breeding activity

Females of *P. buddelundi* greater than 41.1 mg body-mass (smallest recorded ovigerous female), were potentially reproductive but the majority of the ovigerous females weighed between 70 and 130 mg. The proportion of ovigerous females to total females (Ov/Tot in %) above the minimum reproductive body-mass (41.1 mg) in each sample is shown in Figure 4 together with average climatic conditions. The Matmata population of *P. buddelundi* exhibited two breeding seasons: one in the fall from September through October 2005 and another one in spring from March through May 2006. During the fall breeding season, the Ov/Tot decreased slightly from September 2005 (52.17%) to October 2005 (41.37%). While in the spring breeding season, this percentage reached the maxima in April (74%) and didn't exceed 18 and 10% in March and May, respectively.

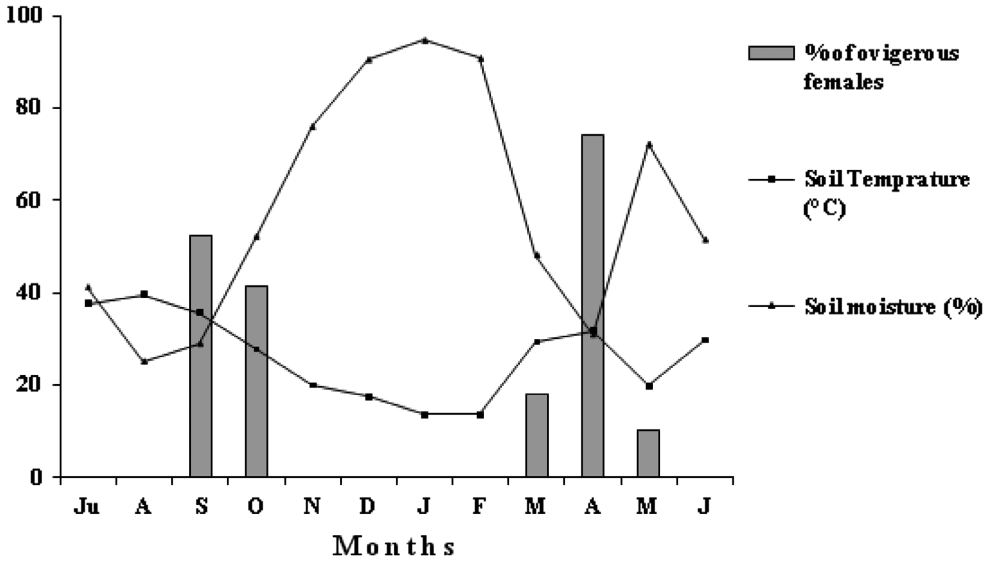

Figure 4. Monthly changes in climatic conditions together with the percentage of ovigerous females in the natural population of *Porcellio buddelundi* (Matmata, Gabès) during the study period.

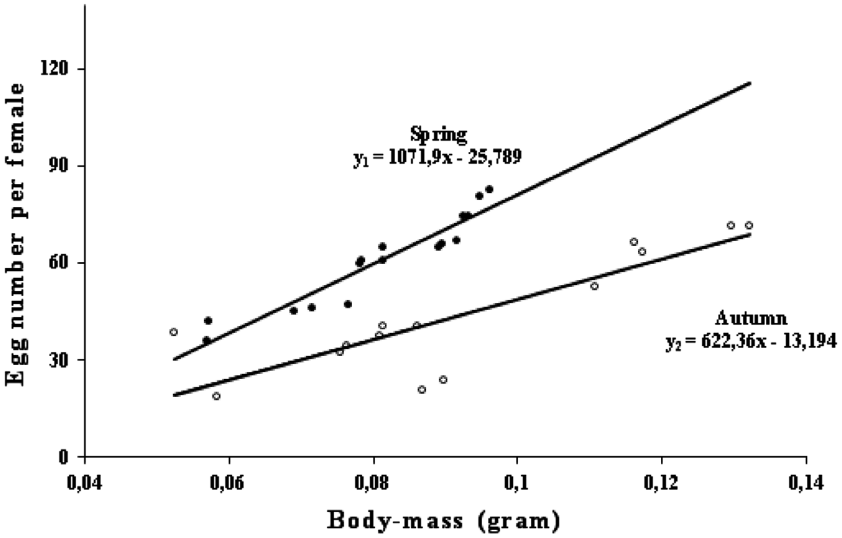

Figure 5. Correlation between egg number and body-mass in ovigerous females of *Porcellio buddelundi*.

Fecundity

The number of marsupial eggs per ovigerous female ranged from 19 eggs (female body-mass 58 mg) to 83 eggs (female body-mass 96 mg) with an average of 53.13 ± 3.2 eggs. Fecundity showed a seasonal intra-populational variation (Figure 5): the mean fecundity was higher in spring (60.93 ± 3.48 eggs for females of 80.90 ± 3.07 mg) than in autumn (44.21 ± 5 eggs for those of 92.24 ± 6.53 mg). Using the ANCOVA test, a positive correlation between fecundity and body-mass was revealed in the two seasons without any significant and direct effect of the breeding season on fecundity (Table 1). However, the interaction between body-mass of the ovigerous females and the breeding season is statistically significant. This suggests that the effect of body-mass on fecundity is higher in spring (R^2 = 89.56%) than in autumn (R^2 = 71.14%):

Table 1. Summary statistics of the fecundity of *Porcellio buddelundi* related to ovigerous females body-mass and the breeding season.

	ddl	Mean square	*F*	*P*
Breeding seasons	1	40.13	0.66	0.4252
Body-mass	1	5253.84	85.93	<0.0001
Body-mass*Breeding season	1	369.926	6.05	0.0209

Note: Mass*Breeding season: Interaction between breeding females body-mass and autumn/spring breeding season.

Table 2. Summary statistics of the analysis of the variation in interactions between ovigerous females body-mass and breeding season.

	Breeding season	R^2 (%)	Slope α	SE	F	P
Body-mass	Autumn	71.14	622.355	114.409	29.59	0.0002
	Spring	89.56	1071.934	97.796	120.14	<0.0001

fecundity increases more with the increase in body-mass in the spring (Figure 5; Table 2; $F = 120.14$, $p < 0.0001$, $n = 16$) than in autumn (Figure 5; Table 2; $F = 29.59$, $p = 0.0002$, $n = 14$).

Climatic factors associated with breeding

A Pearson correlation test showed that soil moisture and temperature, as well as the photoperiod and the dew point, are correlated (Table 3). Therefore, these variables are redundant.

In *P. buddelundi*, a close parallel between low soil moisture and breeding was found (Figure 4). A Pearson correlation test showed that ovigerous females and soil moisture are negatively correlated ($r = -0.638$); ovigerous females appear in the population when the soil moisture is about 48.1% in spring and 28.9% in autumn. Excess soil moisture was accompanied by a decrease in the proportion of ovigerous females; in winter, soil moisture was not lower than 75%, females of *P. buddelundi* stopped reproducing.

Discussion

Porcellio buddelundi can be found in large numbers in Matmata especially during autumn and winter when this species is more active. The low number or the absence of individuals throughout the hot months may be owing to vertical migration in the absence of physiological adaptation (Waller & Verdi 2016). This is not the case in other woodlice inhabiting burrows such as *P. albinus* (Medini-Bouaziz et al. 2017b) and *H. reaumurii* (Linsenmair 2007). The latter species also has a physiological adaptation corresponding to a thicker and more calcified cuticle reducing water evaporation in arid environments (Ayari et al. 2016).

The overall sex ratio of *P. buddelundi* was skewed toward females in the population. This agrees with results recorded in some species (Achouri & Charfi-Cheikhrouha 2002; Hamaied & Charfi-Cheikhrouha 2004; Khemaissia & Nasri-Ammar 2008; Medini-Bouaziz et al. 2015), but not in species where the sex ratio was 1:1 (Kashani et al. 2011; Waller & Verdi 2016). The fact that males of *P. buddelundi* outnumbered females just after the breeding seasons (November 2005; May 2006), may be explained by higher reproductive investment of females during the breeding season resulting in the higher mortality of females compared to the males, and by the high mortality of females at the time of reproductive ecdyses after each breeding season. Nevertheless, the values were close to the expected ratio of 1:1 just before the breeding seasons, as found in a population of *P. albinus* (Medini-Bouaziz et al. 2017b).

Porcellio buddelundi from Matmata, weighing up to 90 mg, could be considered a small woodlouse, as is the case for *Porcellio chuldaensis* and *Armadillo albomarginatus* in the Negev (Warburg 2007), and *Armadillidium sp.* from Ichkeul, Tunisia (Hamaied & Charfi-Cheikhrouha 2016). Males were larger than females reaching a maximum body-mass in October 2005 (up to 125 mg) similar to the desert species *P. albinus* of Zarat (Medini-Bouaziz et al. 2017b). By contrast, females were larger than males in *Porcellio variabilis* from Béja (Medini & Charfi-Cheikhrouha 1998).

Oniscids from arid and semi-arid regions of Tunisia have two reproductive patterns: one with two breeding seasons, the most important one in spring and the second in autumn (Achouri 2012; Medini-Bouaziz et al. 2017b), while the second is a single breeding period (late spring to early summer) (Nasri et al. 1996). *Porcellio buddelundi* from Matmata like other *Porcellio* species *P. laevis*, *P. djahizi*, and *P. variabilis* studied in the Chaambi area by Achouri (2012), and *P. albinus* of the sandy coastal area of Zarat (Medini-Bouaziz et al. 2017b), has the first type of reproductive pattern. However, the oniscids, *Armadillidium sulcatum,* and *Leptotrichus panzerii,* studied previously in the Chaambi area (Achouri 2012) and *Hemilepistus reaumurii* of Kairouan (Nasri et al. 1996), have the second type of breeding pattern that is exhibited by the majority of terrestrial isopods from xeric habitats of the Middle East (Warburg 1995, 2007; Kashani et al. 2011).

According to Achouri (2012) and Medini-Bouaziz et al. (2015), the breeding pattern of *P. buddelundi* is a response to favorable conditions for offspring release and rapid development, as was observed by Waller and Verdi (2016). It seems that abiotic environmental factors,

Table 3. Coefficient of regression (*R*) below the diagonal and *p* values above the diagonal for analyzed population of *Porcellio buddelundi*.

Variables	Soil temprature (°C)	Soil moisture (%)	Dew point (%)	Rainfall (mm)	Photoperiod (mn)
Soil temprature (°C)		**0.000**	**0.006**	0.119	**0.014**
Soil moisture (%)	**−0.967**		**0.049**	0.071	**0.016**
Dew point (%)	**0.740**	**−0.578**		0.463	0.093
Rainfall (mm)	−0.475	0.538	−0.234		0.067
Photoperiod (mn)	**0.685**	**−0.674**	0.507	−0.544	

Note: Bold values correspond to the factor for which the square cosine is the largest.

such as soil moisture and photoperiod, are associated with breeding in female *P. buddelundi*. Low soil moisture associated with long days stimulates reproduction in *P. buddelundi.* Similar results of the effect of day-length on reproduction were noted for terrestrial isopod populations in seasonal environments (*P. ficulneus*, Hornung & Warburg 1993; *H. reaumurii*, Nasri et al. 1996; Souty-Grosset et al. 1988). The opposite effect of soil moisture was observed in *Armadillidium vulgare* and *Armadillidium nasatum* from Uruguay (Waller & Verdi 2016).

As in the reports of most terrestrial isopods from different world regions (Quadros et al. 2008; Kashani et al. 2011; Hamaied & Charfi-Cheikhrouha 2016; Khemaissia et al. 2016; Waller & Verdi 2016), a positive correlation between fecundity and female body-mass has been established in *P. buddelundi*. However, the fecundity varied between breeding seasons with a large number in spring and a small number in autumn confirming the results of Medini-Bouaziz et al. (2015) in two groups of *P. variabilis*. This seasonal variation of *P. buddelundi* fecundity could be explained by a combination of factors influencing the female's growth and ecophysiology as reported by Waller and Verdi (2016): the given environmental conditions and the ability of individuals to utilize resources, the birth date in spring or in autumn, and the growth rate of ovigerous females affect the fecundity more in spring than in autumn.

Highest fecundity and lowest mass of mancae reported in the spring would be an adaptation of the population to increase the survival of its offspring which are confronted with two major problems: the summer desiccating conditions in a pre-saharian environment and predation mainly by scorpions and reptiles (Medini-Bouaziz, personal field observation). Selection for this strategy of small offspring size is supported by (1) the fact that the strategy of large body size and low permeability to water which seemingly offer greater security in dry habitats has not been universally selected for in desert isopods, as a very large range of body size exists (Greenaway & Warburg 1998), and by (2) behavioral mechanisms in small desert isopods (Warburg 1965), expressed by vertical migration of *P. buddelundi* during the harsh desiccating conditions in summer in search of moist microhabitat, which may be more important for water balance than large body size and extreme reduction in permeability (Greenaway & Warburg 1998).

By contrast, for autumnal ovigerous females, the fecundity is less and the mass of mancae is higher. The offspring will be faced with temperate climatic conditions with low moisture (28.9%) having effects on aggregation, growth, and survivorship (Dixie et al. 2015) and in the absence of predators entering into hibernation during winter.

In conclusion, this study on the reproduction of *P. buddelundi* in Tunisia has shown that the reproductive pattern of this species is seasonal: there are two breeding seasons, one in spring and another in autumn, followed by sexual rest; and fecundity is high in spring and low in autumn. Since, its reproduction was associated with soil moisture, more investigation is needed to better understand how this microclimatic variable influences the reproductive ecology of this terrestrial isopod belonging to arid habitats of Tunisia. The soil moisture must be studied in various natural microhabitats to determine unfavorable extremes. The behavioral and physiological mechanisms of *P. buddelundi* must be studied and described, and in addition, the influence of soil moisture on reproductive parameters must be tested and confirmed experimentally.

Disclosure statement

No potential conflict of interest was reported by the authors.

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