International Journal of Biology; Vol. 8, No. 4; 2016
ISSN 1916-9671 E-ISSN 1916-968X
Published by Canadian Center of Science and Education

Reproductive Patterns of Terrestrial Isopods (Crustacea, Isopoda, Oniscidea) from Uruguay

Analisa Waller[1] & Ana Verdi[1]

[1] Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay

Correspondence: Analisa Waller, Facultad de Ciencias, Universidad de la República, Montevideo, Igúa 4225, CP 11400, Uruguay. E-mail: anawaller@gmail.com

Received: July 16, 2016 Accepted: August 11, 2016 Online Published: August 23, 2016

doi:10.5539/ijb.v8n4p12 URL: http://dx.doi.org/10.5539/ijb.v8n4p12

Abstract

Armadillidium vulgare (Latreille, 1884) and *Armadillidium nasatum* (Schultz, 1961) are among the most common species of terrestrial isopods in Uruguay. The reproductive pattern of these species was studied, for first time, on a natural population at Department of San Jose (Uruguay) from June 2010 to July 2011. A total of 9136 individuals were sampled, of these 7010 were *A. vulgare* and 2126 were *A.nasatum.* Adults of *A. vulgare* were present throughout the year and juveniles appeared from February to November. Juveniles and adults of *A. nasatum* appeared from January to October, and practically disappeared from November to December. For both species ovigerous females were collected from spring to summer (October to March), this would indicate a seasonal reproduction followed by a sexual rest. In *A. vulgare* reproductive females cephalothorax width that varied between 1.7 to 3 mm, average fecundity was equal to 39 ± 5 eggs and average fertility was equal to 27 ± 4. In *A. nasatum* cephalothorax width of reproductive females oscillated between 1.5 to 2.9 mm and the average fecundity was 44 ± 5 eggs. For both species, fecundity and fertility were positively correlated with the size of the females. The incubation period ($\bar{x}$ = 13 days) and the mancas born ($\bar{x}$ = 21) were similar for both species.

Keywords: Fecundity, Fertility, Incubation, Terrestrial isopods, Reproduction

1. Introduction

Armadillidium vulgare and *Armadillidium nasatum,* are terrestrial isopods crustacean with a worldwide distribution and are ones of the most common and abundant species of terrestrial isopods in fields of the Uruguay. However, nothing is known about terrestrial isopod biology and reproductive pattern in Uruguay. The reproductive patterns of these species have been a subject of detailed studies and exhibit a high intra and interpopulational variability (Madhavan & Shribbs, 1981; Broly & Lawlor, 1984; Mocquard, Juchault & Souty-Grosset, 1989; Souty-Grosset, Nasri, Mocquard & Juchault, 1998; Leistikow & Wägele, 1999; Nasri-Ammar, Souty-Grosset & Mocquard, 2001; Hamaied, Nasri-Ammar & Charfi-Cheikhrouha, 2004). According to Sutton et al. (1984) the successful colonization of all parts of the world is due to its flexible reproductive tactics (onset and duration of the breeding season) and its demographic parameters (longevity, age at sexual maturity, number of broods, etc.) that allow them to overcome the influence of biotic and abiotic environmental factors to which they are subjected. The temperature, precipitation regime and the photoperiod are important factors that regulate isopod reproduction, resulting in temporal coincidences of the release of offspring with favorable conditions for growth and survival (Madhavan & Shribbs, 1981; Quadros, Araujo & Sokolowicz., 2008). Therefore, terrestrial isopods exhibit different reproductive patterns: species in temperate regions have seasonal reproduction while continuous reproduction occurs in tropical and subtropical species (Quadros et al., 2008). Tropical and subtropical isopods exhibit longer breeding periods, higher number of broods per lifetime, and lower reproductive allocation per brood as compared to temperate isopods. Quadros et al. (2008) studied the reproduction of three isopods species (*Atlantoscia floridana, Benthana cairensis,* and *Balloniscus glaber*), from southern region of Brazil, postulated in Neotropical terrestrial isopods, the existence of a continuous reproductive pattern with peaks during spring and summer. Uruguay is in the Neotropical region with a climate defined as humid subtropical, markedly seasonal with hot summers and absence of a dry season (Evia & Gudynas, 2000; Peel, Finlayson & McMahon, 2007). Considering this, is expected that *Armadillidium vulgare* and *Armadillidium nasatum* have this type of reproduction. In order to confirm this, the aim of the present study was to know the reproductive pattern of *Armadillidium vulgare* and *Armadillidium nasatum* in Uruguay.

2. Materials and Methods

2.1 Study Area and Sampling

The sampling station is located at Department of San José, Uruguay (34°17′ S 56°54′ W) (Figure 1). This area is characterized by grasslands vegetation and a temperate climate with distinct seasons (Evia & Gudynas, 2000).

Samples were taken monthly, from July 2010 to June 2011. Terrestrial isopods were hand searched by two people for 40 minutes along two parallel transect of 20 meters, summing 80 minutes of sampling effort per transect per month. Samples were transported to the laboratory in plastic boxes containing soil from the sampling site. In each sampling station the soil temperature was taking using a thermometer (Digi-Scense Model N° 8528-30) and the soil moisture was found through the gravimetric method (Forsythe, 1975).

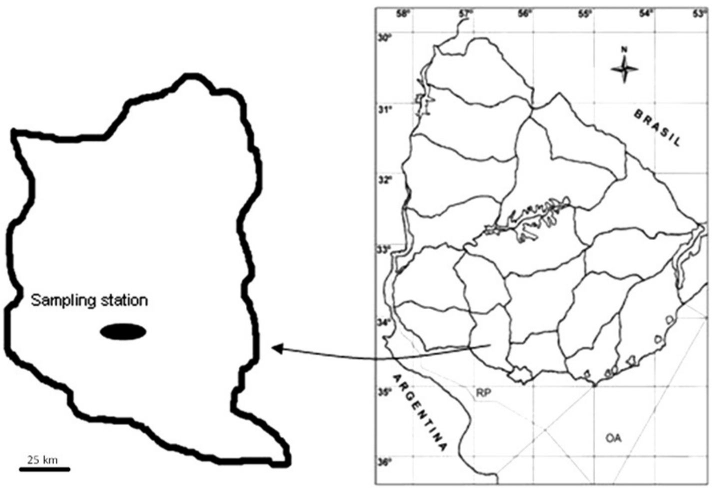

Figure 1. Sampling station. Department of San José, Uruguay

2.2 Laboratory Procedures

Specimens were counted and identified using the keys of Araujo, Buckup & Bond-Buckup (1996), Araujo (1999) and Pérez-Schultheiss (2010). The sex determination was based on the presence or absence of oestegites or a brood pouch in females and of genital apophyses and developed endopodite at the pleopod I in males (Hamaied & Charfi-Cheikhrouha, 2004; Ivanov, 2011). According to their sex-differentiation stages were classified into mancas, juveniles and adults. Three types of females were recognized: (1) Non reproductive females, without brood pouch, (2) Ovigerous females, with eggs, embryos and mancas in the brood pouch and (3) post ovigerous females having empty brood pouch (Araujo & Bond-Buckup, 2005; Ivanov, 2011). Cephalothorax width (CW) of ovigerous females was measured according to Araujo, Quadros, Augusto & Bond-Buckup (2004). Size at the first reproduction was estimated as the size of the smallest ovigerous female. In order to estimate the fecundity (number of eggs produced by brood) and fertility (number of embryos for brood) parameters, the eggs and embryos found in the brood pouches of ovigerous females were removed and counted (Achouri, Charfi-Cheikhrouha & Zimmer, 2008; Montesanto, Musarra Pizzo, Caruso & Lombardo, 2012) . Also the mancas were removed and counted. In the laboratory were reared ten ovigerous females of each species to confirm their incubation period and the number of mancas born. They were individually placed in plastic recipient (9 cm diameter) containing damp piece of filter paper and some cotton to maintain humidity. Litter from sampling area was offered as food (Helden & Hassall, 1998; Brum & Araujo, 2007). Animals were kept at a constant temperature of 20±1°C, with moisture of 50±2% and a day length of 14 hours. Females were daily observed in order to record the time of the mancas release (Montesanto et al., 2012)

2.3 Statistical Analysis

The microclimatic variables and the reproductive female's abundance was related using Bubble plot and its degree of correlation was tested using multiple correlation coefficient R and overall ANOVA-type significance test. The sex ratio was estimated by the ratio of females to males. To identify the existence of significant differences between the proportions of each sex, we employed χ^2 test (α = 0,05) (Achouri et al., 2008). The relationship between fecundity and fertility with the cephalothorax width of ovigerous females were described using simple linear regression (Achouri & Charfi-Cheikhrouha, 2002; Achouri et al., 2008; Ivanov, 2011). The comparison of the cephalothorax width of ovigerous females during the reproductive months was made using ANOVA test, and the comparison between species was made using Mann Whitney test. Statistical tests were done using the freely available software PAST 2.14 (Hammer, Harper & Ryan, 2001)

3. Results

A total of 9136 individuals were sampled, among the 7010 were *Armadillidium vulgare* and 2126 were *Armadillidium nasatum* (Table 1). Even though males of *Armadillidium vulgare* outnumbered females in summer, the sex ratio did not differ significantly from a 1:1 ratio for both species (*Armadillidium vulgare*, χ^2: 0,8, p>0,05, df:1; *Armadillidium nasatum*, χ^2: 1,57, p>0,05, df:1) (Table 1.). Juveniles of *Armadillidium vulgare* appeared in the population from February to November, with a peak in March. From end of spring to the beginning of summer juveniles practically disappeared (December to January). Adults were present throughout the year, showing three peaks of abundance in April, May and June (Figure 2a). Ovigerous females were collected from spring to summer (October to March). Juveniles and adults of *Armadillidium nasatum* appeared from February to October, and practically disappeared from November to January. Ovigerous females were found only in October and February (Figure 2b).

Table 1. *Armadillidium vulgare* and *Armadillidium nasatum* recorded throughout the year: N°, number of individuals; %, percentage of individuals; χ^2, Chi² test; p, p value.

	Armadillidium vulgare						*Armadillidium nasatum*					
	Males		Females				Males		Females			
	N°	%	N°	%	X^2	p	N°	%	N°	%	X^2	p
Autumn	1090	49	1150	51	1.6	>0.05	501	52	465	48	1.34	>0.05
Winter	908	49	963	51	1.61	>0.05	114	54	97	46	1.36	>0.05
Spring	333	50	337	50	0.02	>0.05	149	50	152	50	0.02	>0.05
Summer	206	57	154	43	7.51	<0.05	22	50	23	50	0.02	>0.05
Total	2537	49	2604	51	0.87	>0.05	786	52	737	48	1.57	>0.05

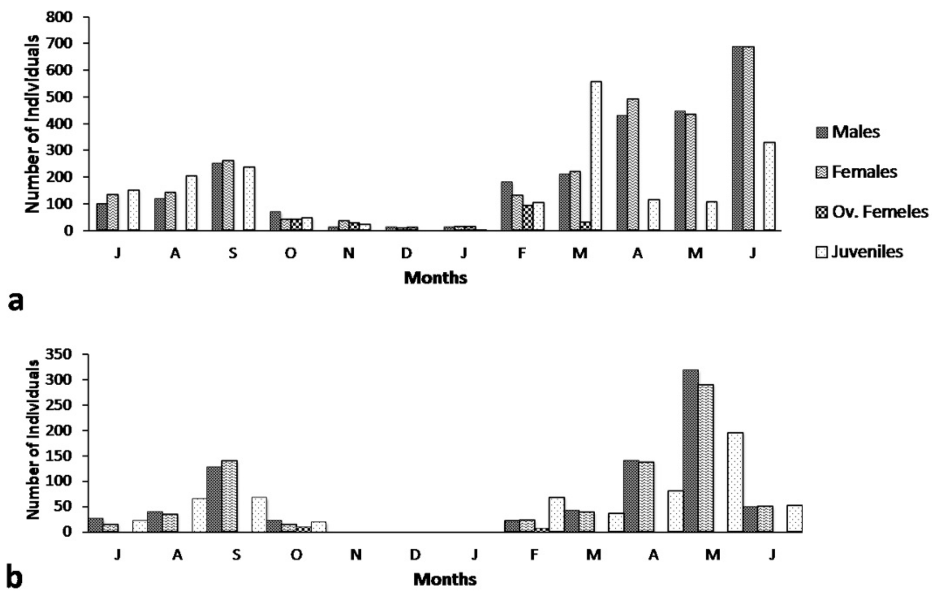

Figure 2. Structure of the population: A - *Armadillidium vulgare*; B – *Armadillidium nasatum*

3.1 Breeding Period

The survey of the percentage of ovigerous females during the research showed that the breeding period to *Armadillidium vulgare* started at the beginning of October and ended in March, while *Armadillidium nasatum* presented two specific periods, one in spring (October) and other in summer (February).

Females of *Armadillidium vulgare* with brood pouches carrying eggs in high number were observed in October and February. Females with marsupial embryos and mancae were found in November to February and with empty marsupial from November to March. The greatest amount of *Armadillidium nasatum* females with marsupial eggs were detected in October. Females with embryos, mancae and empty marsupial were observed in February (Figures 3a-3b).

Reproductive females of *Armadillidium vulgare* had a cephalothorax width of 1.7 to 3 mm, with a median of 2.13 mm. Significant differences in the reproductive females size were observed in December, January and February ($F(96,98)=10,29$, $p = 0.013$, df:1), being larger in December. Reproductive females of *Armadillidium nasatum* had a cephalothorax width of 1.5 to 2.9 mm, with a median of 2.37 mm. Significant differences in the reproductive females size were observed in October and February ($F(104,107)=31,17$, $p = 0.025$, df:1), being larger in October. The difference between the reproductive female size of *Armadillidium vulgare* and *Armadillidium nasatum* was not significant (U: 469, $p > 0.05$, df:1).

During the breeding period, the soil temperature varied from 14.9°C to 26.2°C with a mean value of 20.6°C, the soil moisture varied from 2.4 % to 44.8 % with a mean value of 20.9% and the day length ranged from 12 to 14 hours. The bubble plot showed a correlation between high reproductive females abundance with higher temperature and higher soil moisture (Figure 4). There were multiple correlations between the density of reproductive females and the day length, the soil temperature and the soil moisture (R: 0.80, r^2: 0.64) (F: 4.9, $p < 0.05$).

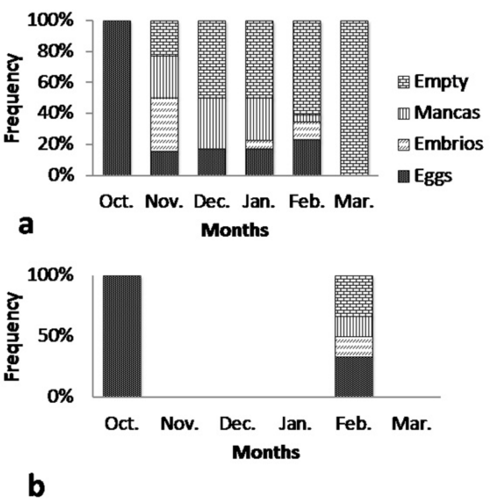

Figure 3. Frequency of ovigerous females with eggs, embryos, mancas and empty marsupial: A - *Armadillidium vulgare*; B – *Armadillidium nasatum*

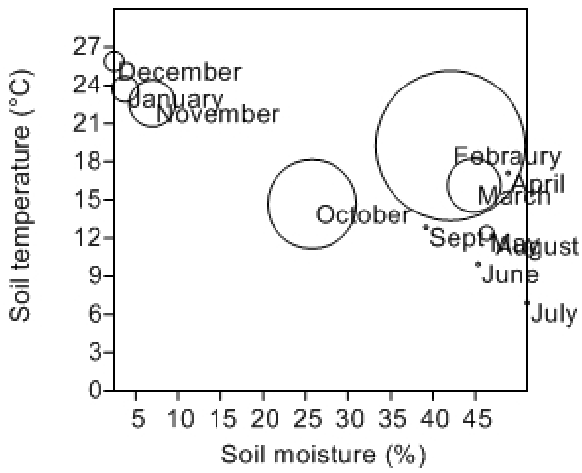

Figure 4. Bubble plot showing the relationship between soil temperature, soil moisture and reproductive females density

3.2 Fecundity and Fertility

In *Armadillidium vulgare*, the number of eggs for a brood varied from 20 to 96, with an average of 39 ± 5. The number of embryos found varied from 20 to 36, with an average of 27 ± 4; and the mancas varied from 12 to 30 with an average of 24 ± 3. Fecundity (r = 0.71) and fertility (r = 0.69), showed a positive correlation with the female size (Figures 5a-5b). A positive correlation was also observed between the number of mancas released and the cephalothorax width of the females (r = 0.72) (Figure 5c). In *Armadillidium nasatum*, the number of eggs for a brood varied from 20 to 60, with an average of 44 ± 5. Fecundity (r = 0.89) showed a positive correlation with the female size (Figure 5 d). Fertility could not be calculated because only one female (CW: 1.7 mm) with 20 embryos in the brood pouch was captured in the studied area. Also only one female (CW: 2.4 mm) with 22 mancas was captured.

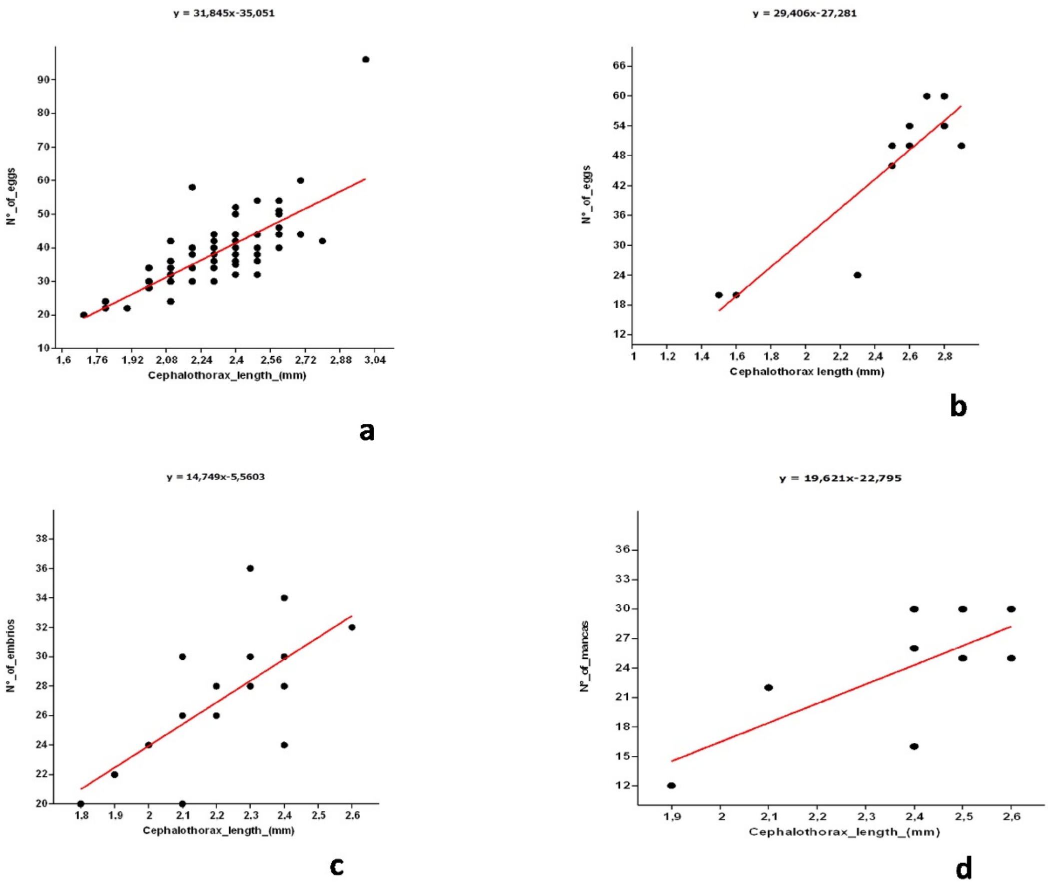

Figure 5. Fecundity, relationship between number of eggs in brooding females and the size of the female: a, *Armadillidium vulgare*; b, *Armadillidium nasatum.* c, Fertility, relationship between number of embryos per brood and the size of *Armadillidium vulgare* females; d, Relationship between number of mancas per brood and the size of *Armadillidium vulgare* females

3.3 Incubation Period

The incubation period observed for *Armadillidium vulgare,* was between 12 and 14 days, with a mean of 13 days, whereas for *Armadillidium nasatum* was between 14 and 15 days, with a mean of 13 days. An average of 21 mancas were born for the two species

4. Discussion

Even though *Armadillidium vulgare* and *Armadillidium nasatum* are species characteristic in fields of the Uruguay, up to the present had not been studied the reproductive patterns of these species. Both species showed a seasonal reproduction (spring/summer) followed by a sexual rest, resembles the majority of terrestrial isopods species, which usually reproduce only during the warmer months (Sutton et al., 1984). Quadros et al. (2008) studied the reproduction of Neotropical isopod, *Atlantoscia floridana, Benthana cairensis,* and *Balloniscus glaber,* in southern Brazil showed that the two first species share continuous breeding throughout the year and similar fecundity ranges, similar to tropical species. On the other hand, *Balloniscus glaber* shows the temperate mode of reproduction restricted to spring and summer. They do not know if the reproductive pattern of *Balloniscus glaber* is to be the rule or the exception and argue that this difference may be explained by the habitat specialization (very restricted distribution and burrowing abilities) of this species. In based on they studied the authors postulated for Neotropical terrestrial isopods, the existence of a continuous reproductive pattern with peaks during spring and summer. This pattern is not reflected in this study, where populations of *Armadillidum vulgare* and *Armadillidium nasatum,* in the same biogeographically region and with good colonization ability, show the temperate mode of reproduction likely observed in *Balloniscus glaber*. This could be the result of microevolutionary responses to differences in selection pressures caused by differences in the environment (Hassall, Helden, Goldson & Grant, 2005).

Armadillidium vulgare has been widely studied in different regions and its reproductive pattern might change according to world region of occurrence, in temperate regions occur seasonal reproduction and in tropical and subtropical occur continuous reproduction. (Lawlor, 1976; Sorensen & Burkett, 1977; Hassall & Dangerfield, 1997; Souty-Grosset at al., 1998; Nishi & Numata, 1999). These differences were a response to environmental variables rather than being a species-specific trait, other species living at temperate regions such as *Armadillidium pelagicum* (Hamaied et al., 2004; Hamaied & Charfi-Cheikhrouha, 2004) *Armadillidium album* (Vader & De Wolf, 1988) and *Porcelio scaber* (Zimmer & Kautz, 1997), also show a seasonal reproduction. According with Willows (1984), this kind of reproduction is actually a response to favorable conditions for rapid development and offspring release, as was observed in this study. In *Armadillidium vulgare* and *Armadillidium nasatum* reproductive patterns associated especially with higher soil moisture and high temperatures. Similar results were reported in an Argentinean population of *Armadillidium vulgare* by Cuartas and Petriella (2001); for *Armadillo albomarginatus* by Warburg (1994); for *Atlantoscia floridana* by Araujo and Bond Buckup (2005) and for *Balloniscus glaber* by Quadros and Araujo (2007).

According to Schultz (1961), *Armadillidium nasatum* populations are more active in the winter which could explain the disappearance of the population throughout the hot months maybe due to vertical migration. Vertical migrations were also observed in populations of *Armadillidium vulgare* (Paris & Pitelka, 1961; Paris 1963), and *Trichuniscus pussilus* (Sutton et al., 1984) which during the summer are buried under 10 cm deep, returning to the surface when the soil becomes moist, as a way of better withstanding climatic conditions in the absence of physiological adaptations. The sex ratio in the population of *Armadillidium nasatum* was 1:1 throughout the year, while for that of *Armadillidium vulgare*, it recorded a low number of females, coinciding with the breeding season in summer. This disagrees with registered in other populations, both the same (Geiser, 1934; Paris, 1963) or other species (Achouri & Charfi-Cheikhrouha, 2002; Araujo & Bond Buckup, 2005; Achouri et al., 2008) in which the sex ratio seems biased towards females. According to Paris (1963), the sex ratio is equal at birth, but the female mortality at the time of reproductive ecdyses resulted in greater male survival. Moreover, the trend toward a higher number of males could be associated with the absence of infection by *Wolbachia* a feminizing bacteria (Chevalier et al., 2012) and as well as with the absence of parthenogenesis (Neiman, 2004; Araujo & Bond Buckup, 2005).

Armadillidium vulgare and *Armadillidium nasatum* exhibited a great interpopulation variability in the size of the reproductive females. This may be explained by the existence of different growth rate in terrestrial isopod populations from habitats with different ecological conditions (Ivanov, 2011). Kight (2008) argued that two genetically identical females reared in different growth condition could have different adult body size.

According to that reported for most terrestrial isopods from different world regions (Cuartas & Petriella, 2001; Glazier, Wolf & Kelly, 2003; Hamaied & Charfi-Cheikhrouha, 2004; Quadros, Caubet & Araujo, 2009; Achouri et al., 2008; Kight, 2008; Ivanov, 2011; Achouri, 2012; Montesanto et al., 2012; Medini-Bouaziz, El-Gtari & Charfi-Cheikhrouha, 2015), *Armadillidium vulgare* showed a positive correlation between fecundity and fertility and the body length of ovigerous females. Fecundity in *Armadillidium nasatum* also showed this positive correlation, this result is in agreement with the observer by Glazier et al. (2003) for a population of the same species in central Pennsylvania. The variation of terrestrial isopods fecundity might be explained by a combination of factors influencing individual growth and ecophysiology: the genetic determinant of the growth rate, the ability of individuals to utilize resources, the given environmental conditions, the birth date in seasonal environments, the timing of allocation of resources to reproduction, and the timing within the temporal sequence of reproductive (Hamaied & Charfi-Cheikhrouha, 2004; Ivanov, 2011). *Armadillidium vulgare* females with similar cephalothorax width, showed higher fecundity values than fertility values, indicating that not all of the eggs developed into embryos. Intramarsupial mortality has been found in others population of *Armadillidium vulgare* (Al-Dabbagh & Block, 1981; Cuartas & Petriella, 2001) and in other species such as *Atlantoscia floridana* (Araujo & Bond Buckup, 2005) and *Porcellio siculoccidentalis* (Montesanto et al., 2012). The number of released mancas found in the marsupial pouch of *Armadillidium vulgare* were lower than those that have been reported for the same species (Faberi, López, Clemente & Manetti, 2011) from Argentina but larger than some Neotropical species of Oniscidea as *Atlantoscia floridana*, *Benthana cairensis* (Araujo & Bond Buckup, 2005; Socolowicz & Araujo, 2008; Socolowicz & Araujo, 2013) and *Balaniscus glaber* (Quadros et al., 2009). According with Faberi et al., (2011) the published data about the number of released mancas produced per brood by *Armadillidium vulgare* females, is quite variable and much of this variation is related to differences in the size of the female and the different N content diets. The number of released mancas was lower than the number of eggs into the marsupian. This could be the result of their expulsion from the brood pouch when females impacted the conservation liquid (Araujo & Bond Buckup, 2005; Ivanov, 2011).

The incubation period in *Armadillidium vulgare* and *Armadillidium nasatum* were similar ($\bar{x}$ = 13 days). This differ with the observed in Argentina in the same biogeographically region by Fabery et al., (2011) for *Armadillidium vulgare*, who registered incubation periods of 27 and 31. According to Sokolowicz and Araujo (2008) the incubation period varies regionally and according to the climatic conditions and indirectly according to the diet.

5. Conclusion

This study represents our first attempt to understand reproductive patterns in *Armadillidium vulgare* and *Armadillidium nasatum* from Uruguay. We found that both species show the temperate mode of reproduction with a seasonal reproduction followed by a sexual rest. This could be the response to environmental conditions will determine the potential of a species to adapt to different climatic condition. Better understanding of reproduction and population dynamics in terrestrial isopods from Uruguay is needed. This will be a future task and a natural continuation of the present work

Acknowledges

The authors wish to thank to PEDECIBA (Programa de Ciencias Básicas) for grant to Analisa Waller.

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