JOURNAL OF CRUSTACEAN BIOLOGY, 21(2): 375–383, 2001

NON-SEASONAL BREEDING IN A PORCELLIONID ISOPOD

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ABSTRACT

Female *Porcellio laevis* (Latreille) raised in the laboratory first reproduced when 7 months old and can breed up to 7 times during their life time irrespective of season. In that, this species differs from most other isopod species studied so far. After a single mating, a female can breed several times without the presence of a male presumably because she stores sperm. Females known to be virgins never became gravid, thus there is no evidence of parthenogenesis. Males are therefore essential for reproduction in *P. laevis.* Sex ratio in the laboratory population was found to be 1 male to 2.5 females. The average time intervals between consecutive broods is 7.7 weeks. Most females reproduce 3 or 4 times in their lifetime (e.g., until the age of about 1 year). The average number of broods is 3.1. Number of mancas in the brood is positively correlated to weight of the mother. The average number of mancas in a brood is 66.6. The average survival of mancas until they are 7 or 8 months old is 44.7%. The ovary of *P. laevis* is typical of an iteroparous isopod in that it contains both large and small oocytes. However, it differs from that known for all other isopod species by having a few large oocytes persisting in the ovaries at all times. Apparently, oocyte cohorts do not mature simultaneously as indicated by the fact that some large oocytes were present at all times but move a few at a time into the brood pouch at a continuous rate.

Different aspects of reproduction in land isopods (or oniscideans) have been previously reviewed (Warburg *et al.*, 1984; Warburg, 1987, 1991, 1994). The main purpose of these studies was to reveal the ecological significance of different reproductive patterns. Many of the earlier studies reviewed were conducted on field populations where the previous breeding history of the female could not have possibly been known (discussed in Warburg, 1987). Consequently, more accurate, detailed analyses of data based on breeding of individual females in the laboratory were needed before any conclusions could be drawn about reproductive patterns and strategies in terrestrial isopods (Warburg, 1991, 1993, 1994). Since then more information has become available on several isopod species (Warburg, 1992a, b, 1993, 1995; Warburg and Cohen, 1991, 1992; Warburg *et al.*, 1993).

Only two of nine isopod species studied until now using this method were proven to be semelparous, meaning that they can breed only once in their lifetime (Warburg, 1992b; Warburg and Cohen, 1991; Warburg *et al.*, 1993). All other species studied so far were shown to be iteroparous species capable of breeding more than once during their lifetime (Warburg, 1992a, b, 1995; Warburg and Cohen, 1992). Among them also several porcellionids were proven to be iteroparous species. These are *Porcellio laevis* (Latreille, 1804), *Porcellio ficulneus* Budde-Lund, 1885, and *Porcellio chuldaensis* Verhoeff, 1923. All three species inhabit the Mediterranean region. Although iteroparous, the latter two species, as well as others, were shown in the laboratory to have a single, discrete, seasonal reproductive season (Hornung and Warburg, 1993; Warburg, 1992a). Some of these aspects have been reviewed in Warburg (1994).

In the present study, we analyse the reproductive pattern in an isopod species kept and bred in the laboratory. This porcellionid, *Porcellio laevis*, is an ideal study animal in that it breeds well under laboratory conditions, and stocks can be maintained for several years.

MATERIALS AND METHODS

All breeding experiments were conducted on laboratory populations that had originated from the Haifa Bay region (elevation 100–150 m), and the Galil Mts. (elevation 500–600 m). These populations flourished at room temperature eating potatoes.

Twenty-seven females were weighed on a Mettler H–311 balance ±0.01 mg accuracy and kept individually in glass jars (2 cm diameter) containing moist, sterilized soil. Their reproductive cycle was followed. The female's weight before and after parturition (i.e., re-

Table 1. Age and weight of first breeding of *P. laevis* females and the number of mancas produced.

	Weight (mg)	Age at first breeding		No. of mancas
		Month	Week	
	21.8	7	2	13
	20.2	7	2	20
	23.4	7	3	13
	27.1	8	3	16
	22.5	8	3	18
	26.4	9	0	17
	25.4	9	1	21
Av. ± SD	23.8 ± 2.4	8	1.5	16.8 ± 2.9

leasing young), date of manca release, and number of mancas released by a single female were all recorded. Thirty-five cohorts (i.e., born to a single female on the same day) were separated from their mothers, counted, and then placed into larger glass jars (5 cm diameter) containing moist, sterilized soil. Their growth until maturation at about 7 months old (when the males can be distinguished) was followed using a Cahn Gram-Electrobalance ±0.1 μg accuracy. Genders were then separated and placed into individual jars. Three-month-old mancas were separated (before reaching maturity) this way to ensure that the mancas turning into mature females were virgins. These were then kept either in isolation or with a male added.

About 40 females were separated and kept individually in vials together with a male until they produced young. They were then dissected five at a time at intervals of 1, 4, 7, 14, 21, 28, 35, 42, and 49 days following parturition, and their ovaries were excised. The length and width of each ovary were measured as well as the diameter of each oocyte by aid of graticules under a dissecting microscope. The number of oocytes was determined in 74 ovaries. Some of the ovaries were photographed under a M5 Wild dissecting microscope.

Statistical analysis of the data was used to test the significance of the results. Thus, regression analysis was used to establish the significance of the relationship between the number of mancas and the mothers' weights or whether the relationship between the number of mancas and the number of broods in each female was significant.

RESULTS

Age of Female at First Reproduction

The separation technique described above ensured to establish that females were not sexually mature before reaching 7 months. Some of them bred first when 9 months old (Table 1).

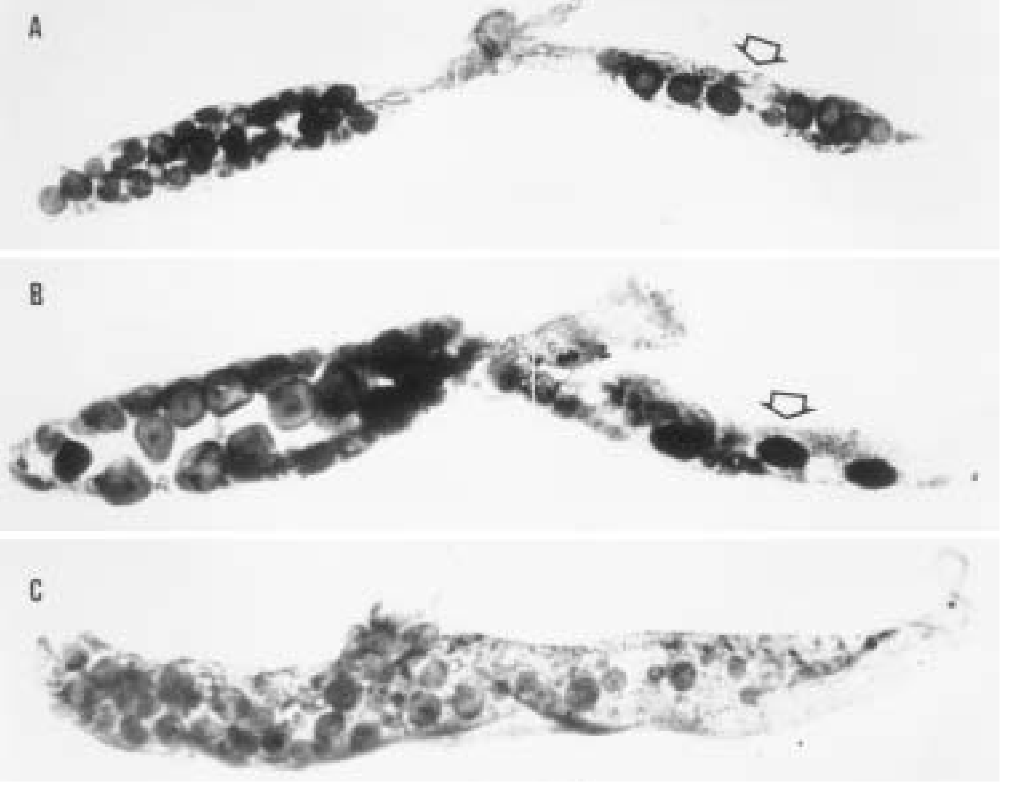

Fig. 1. Ovaries of *Porcellio laevis.* A, four days; B, one week; and C, seven weeks following parturition. Open arrows (in A and B) indicate the presence of a few large oocytes in one ovarian half when most of the large oocytes have moved into the marsupium. In C, only small oocytes are distinguishable. (Light microscopy, A, 25×; B and C, 40×.)

Table 2. Number of broods (= cohorts) per female of *P. laevis.*

	No. of broods	No. of females
	1	6
	2	7
	3	3
	4	6
	5	2
	6	1
	7	1
Total		27
Av. No. of broods	3.1	

Virgin females belonging to cohorts born (to the same female on the same day) and raised in the laboratory that were kept individually isolated since the age of three months, although mature, showed no signs of reproduction. Only following the introduction of a male did they start breeding. This proves without doubt that the species is not parthenogenetic. The first brood (i.e., cohort) of a female averaged 16.8 offsprings or mancas (Table 1).

Number of Times Females Reproduce

A single female is capable of breeding more than once (personal observation). Thereby, it is iteroparous. Moreover, the ovaries contain both large and small oocytes, indicating the putative iteroparity of females (Fig. 1). Most females (n = 27) are capable of reproducing up to four times, a few seven times, averaging 3.1 times during their lifetime (Table 2).

Breeding Period and Size of Breeding Females

Under laboratory conditions, *P. laevis* females, although reproducing continuously

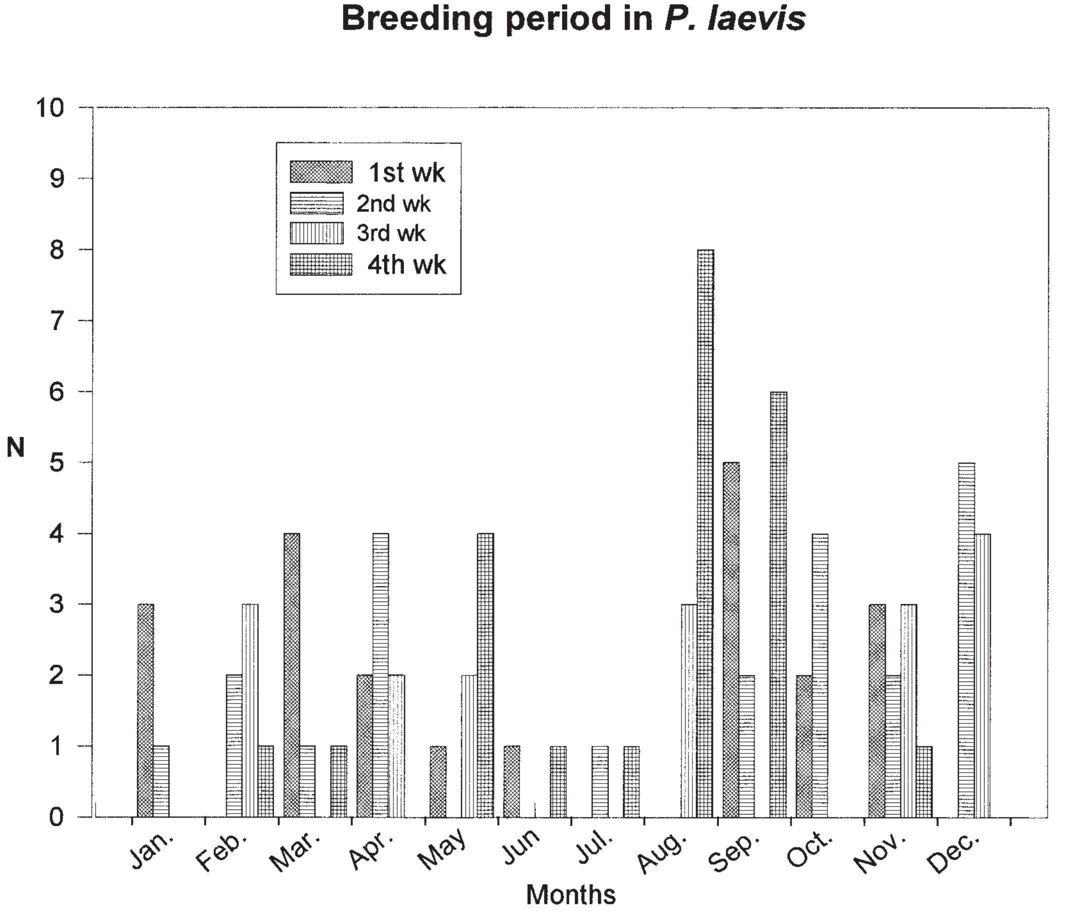

Fig. 2. Number of female *Porcellio laevis* breeding under laboratory conditions throughout the year week by week.

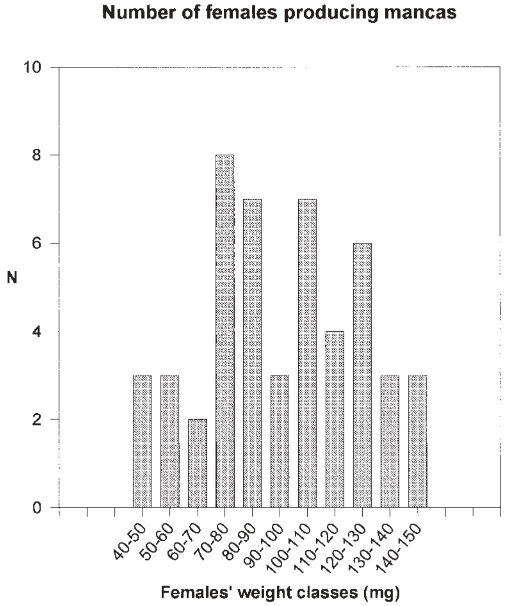

Fig. 3. Number of reproductive females arranged by weight classes of females. Most reproductive females weighed 70–130 mg.

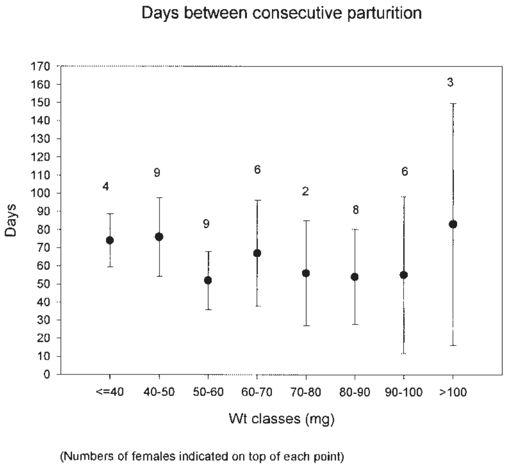

Fig. 4. Days between consecutive parturitions in the different weight classes of females. There is no significant relationship between the female's weight class and the time interval between consecutine breeding (error bars: ± SD). Numbers above bars indicate numbers of females.

throughout most of the year, reached a peak during autumn (Fig. 2). Reproductive females weighed 40–150 mg, with the majority weighing 70–130 mg (Fig. 3).

Time Intervals and Growth of Females Between Reproduction

The average intervals between two consecutive parturitions was 7.7 weeks (Table 3). The interval between two consecutive brood releases (i.e., parturition) ranged 2–20 weeks (Table 3). There was no significant relation-

Table 3. Time intervals between consecutive breedings in *P. laevis* (in weeks).

	Weight (mg)	Number of parturitions						Average
		2nd	3rd	4th	5th	6th	7th	
	29.6	8	12	8	7	–	–	8.8 ± 2
	36.7	6	6	6	5	–	–	5.7 ± 0.4
	40.4	6	7	13	8	4	8	7.7 ± 3
	45.3	8	16	6	–	–	–	10.0 ± 4
	46.7	12	5	6	–	–	–	7.7 ± 4
	54.5	8	–	–	–	–	–	8.0
	54.8	4	6	–	–	–	–	5.0 ± 1
	56.5	12	7	–	–	–	–	9.6 ± 2.5
	56.7	7	6	8	–	–	–	7.0 ± 0.8
	58.5	7	–	–	–	–	–	7.0
	61.3	12	–	–	–	–	–	12.0
	65.6	8	–	–	–	–	–	8.0
	66.6	5	–	–	–	–	–	5.0
	67.0	2	16	8	–	–	–	8.7 ± 6
	70.8	5	–	–	–	–	–	5.0
	72.5	11	–	–	–	–	–	11.0
	85.0	3	5	6	12	7	–	6.6 ± 3
	85.1	5	4	–	–	–	–	4.5 ± 0.5
	89.7	3	9	12	–	–	–	8.0 ± 4
	93.0	4	3	5	6	16	6	6.7 ± 4
	101.1	5	7	20	–	–	–	10.7 ± 7
Av. ± SD								7.7 ± 2.1

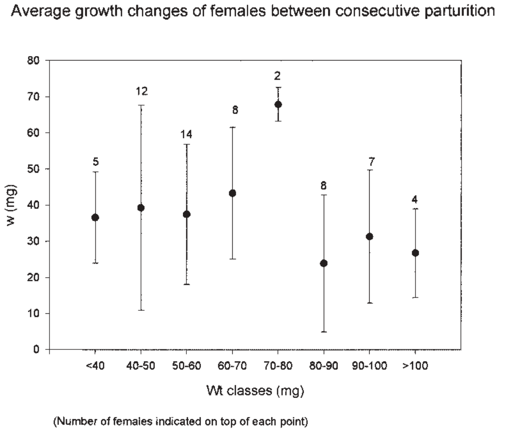

Fig. 5. Growth increments between two consecutive parturitions in the different female weight classes. A marked decline in growth takes place in females over 80 mg. (error bars: ± SD). Numbers above bars indicate numbers of females.

ship between the female's mass and the differences in mass between consecutive breeding (Fig. 7B). Females in the lower weight classes (up to 70 mg) grow slowly (Fig. 4). This is followed by a marked increase in growth until they reach 80 mg (Fig. 5). The larger females (80–100 mg) did not show any significant growth.

Dimensions of Ovaries and Oocytes Measured at Time Intervals Following Parturition

In spite of the fact that ovaries were examined at time intervals not exceeding 14 d, no marked changes in either the average dimensions of ovaries and oocytes or oocyte numbers were noticeable (Fig. 6). The only significant drop in oocyte diameter took place between the third and fifth week following parturition (Fig. 6).

Unlike any other iteroparous ovary studied so far, *P. laevis* ovaries contained large oocytes at all times, even directly after parturition (Fig. 1). This could imply that an oocyte cohort does not mature simultaneously.

Partural Moult

In 14 females we could observe the parturial moult and note the days after the last parturition. This ranged 11–85 days, averaging 33.8 ± 16.6 days (Table 4).

Size of Cohorts

The size of a cohort (or number of mancas released by a single female during a single parturition) was positively related ($P < 0.001$)

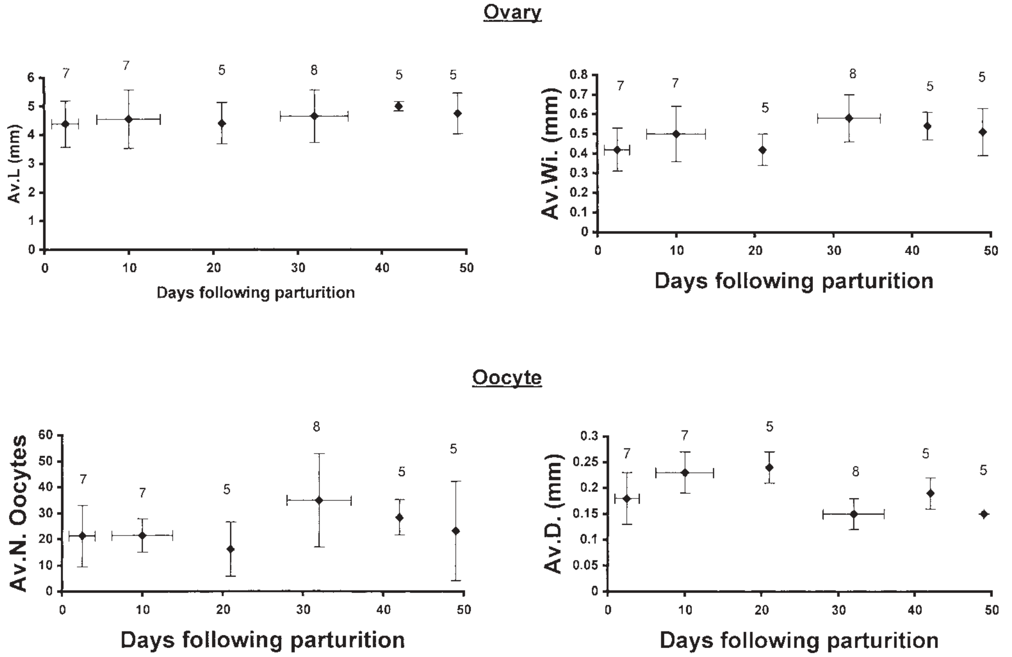

Fig. 6. Ovary and oocyte dimensions measured at time intervals following parturition. Data for days 1 + 4, 7 + 14, and 28 + 35 are united in the graph. Each point indicating an average ± SD. Numbers on top of bars indicate numbers of females dissected.

Table 4. Duration of brood pouch (marsupium) in *P. laevis* females.

	Females	No. of days between parturial moult and parturition
	1	33
	2	32
	3	28
	4	32
	5	33
	6	38
	7	11
	8	26
	9	35
	10	30
	11	22
	12	44
	13	25
	14	85
Avg. ± SD		33.8 ± 16.6

to the female's weight and increased proportionately with the size of the female and the differences in the female's weight between consecutive breedings ($P < 0.05$) (Fig. 7A, B). The number of broods (e.g., cohorts) ranged 1–7. There was a positive relationship ($P < 0.001$) between the number of broods and the numbers of mancas in each cohort (Fig. 7C). The average number of mancas (in 26 broods) produced by a female was 66.6, or 21.4 mancas per brood (Table 5).

Sex Ratio Within Cohorts

The sex ratio within members of a brood, which matured at 6 or 7 months, varied greatly. Some cohorts consisted of females only, while others had a high proportion of males. The average sex ratio of 35 cohorts was 1 male to 2.5 females (Table 6). Because the males are essential for breeding in this species, it can be assumed that all cohorts have started with equal numbers of males and females. (The reason for such assumption will be discussed later.) The possibility that some males (in 11 cohorts) might have died before it was possible for us to identify them as males cannot be excluded. However, there is no proof of this possibility.

Growth of Cohorts

The growth of mancas belonging to several cohorts was followed for several months after birth (Fig. 8). Some cohorts grew faster than others during the first 6 months after birth. There was a positive (n.s.) relationship between the age and growth in mancas.

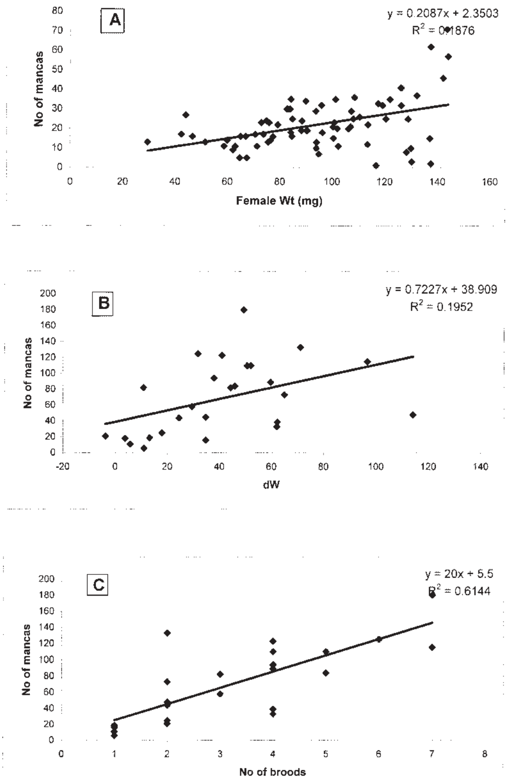

Fig. 7. A, Number of mancas within a cohort as related to their mother's weight; B, Relationship between number of mancas in a cohort and the female's weight differences between consecutive parturitions; C, The relationship between the number of mancas in a brood and the number of broods of a single female (each point represents a different brood).

Survival of Cohorts and Life Expectancy

The average number of mancas belonging to 35 cohorts (averaging 20.8 mancas in a cohort) that survived for 4–8 months ranged between 13.6–30.8 mancas or 3.2–14.8, depending on their age (Table 7).

The calculated average life expectancy of an average female *P. laevis* was found to be about 2 years (Table 8).

Discussion

The porcellionid *P. laevis* has been previously studied in Egypt (Shereef, 1970) and India (Nair, 1978, 1984). Nair found a sex ratio of 1 male to 1.6 females in the natural population as compared to the present findings on the laboratory populations that showed a 1 male to 3.6 female ratio. Shereef found that *P. laevis* produced 4–6 broods dur-

Table 5. Number of broods (cohorts) of mancas produced by 27 single female *P. laevis.*

	W_1 (mg)	W_2 (mg)	$(W_1–W_2)$ (mg)	No. of broods	Total no. of mancas	Av. no. of mancas per brood
	29.6	75.6	46.0	5	84	16.8 ± 5.3
	36.7	88.8	52.1	5	110	22.0 ± 4.8
	40.4	137.2	96.8	7	115	16.4 ± 9.4
	42.7	77.5	34.8	1	16	16.0
	45.3	83.2	37.9	4	94	23.5 ± 9.2
	46.7	106.3	59.6	4	89	22.3 ± 4.1
	54.5	168.7	114.5	2	48	24.0 ± 1.0
	54.8	84.3	29.5	3	58	19.3 ± 2.6
	55.5	66.6	11.1	1	6	6.0
	56.5	100.9	44.4	3	82	17.3 ± 12.2
	56.7	107.4	50.7	4	110	27.5 ± 4
	57.3	63.1	5.8	1	11	11.0
	58.5	76.5	18.0	2	25	12.5 ± 1.5
	61.3	126.3	65.0	2	73	36.5 ± 4.5
	64.6	–	–	1	16	16.0
	65.6	90.2	24.6	2	44	22.0 ± 3.0
	66.6	101.4	34.8	2	45	22.5 ± 10.5
	67.0	129.1	62.1	4	33	8.3 ± 2.6
	70.8	67.1	–3.7	2	21	10.5 ± 5.5
	72.5	143.7	71.2	2	133	66.5 ± 4.5
	85.0	116.8	31.8	6	125	20.8 ± 12.3
	85.1	96.0	10.9	3	82	27.3 ± 5.3
	86.8	90.7	3.9	1	18	18.0
	89.7	152.0	62.3	4	39	9.8 ± 7.3
	93.0	142.3	49.3	7	180	25.7 ± 18.6
	96.4	109.7	13.3	1	19	19.0
	101.1	142.1	41.0	4	123	30.8 ± 5.8
Av ± SD	65.4 ± 19.1	105.5 ± 29.4	41.1 ± 28.1	3.1 ± 1.8	66.6	21.4 ± 11.5

W_1 = Female's weight at 1st brood. W_2 = Female's weight at last brood.

ing the six months following maturity. Likewise, Vandel (1962: 687) found that *P. laevis* breeds seven times between April–October. In that, he probably meant that they have seven breeding periods and not that a single female breeds seven times. All these studies were conducted on field populations of females or on females brought back from the field but not kept separately under laboratory conditions. Conclusions were therefore not based on single females with a known previous breeding history. The number of mancas emerging from the brood pouch was found to range between 14 and 26 as compared the average number of 66.6 mancae found here.

In this study, the sex ratio of the cohorts varied. Some cohorts included only females, whereas others had a variable proportion of males. Most other isopod species that were studied by us until now start with a 1:1 sex ratio (Warburg, 1993). This may later change to a low proportion of males in the adult population. We have observed this phenomenon in the semelparous armadillidiid, *Schizidium tiberianum* Verhoeff, 1923, where young males are cannibalized after having mated with the females. Consequently, the sex ratio changes from 1M : 1F in the maturing cohorts to 1M : 9F in field populations (Warburg and Cohen, 1991; Warburg *et al.*, 1993). This subject is more fully discussed by Juchault and Legrand (1989) and Warburg (1993, 1994).

One main point emerging from the present study is the fact that in the laboratory, *P. laevis* breeds continuously irrespective of season. In this it resembles two other porcellionids *Porcellio olivieri* (Audouin, 1825) and *Agabiformius obtusus* Budde-Lund, 1909, both of which are rare, fossorial, desert species. Aspects of their reproductive pattern have been described elsewhere (Warburg, 1995). The intervals between parturitions in *P. laevis* were rather short, although not as short as in *A. obtusus* where they were about three-week intervals (Warburg, 1995).

The cosmopolitan isopod species *Porcellionides pruinosus* Brandt, 1833, was found to be capable of reproducing several times during different seasons (Dangerfield and

Table 6. Sex ratio and percentage in cohorts of *P. laevis*.

	No. of males	No. of females	Sex ratio M/F
	0	5	0
	1	10	0.10
	0	10	0
	3	10	0.30
	7	2	3.50
	0	10	0
	4	17	0.24
	0	1	0
	1	0	–
	3	2	1.50
	0	2	0
	0	5	0
	0	7	0
	3	6	0.50
	3	5	0.60
	1	9	0.11
	5	18	0.28
	2	10	0.20
	1	6	0.17
	0	2	0
	4	4	1.00
	4	11	0.36
	0	27	0
	3	9	0.33
	6	27	0.22
	0	4	0
	3	18	0.17
	3	4	0.75
	2	8	0.25
	6	4	1.50
	1	0	–
	0	17	0
	2	4	0.50
	6	19	0.32
	8	7	1.14
Av. ± SD	2.4 ± 2.3	8.6 ± 6.9	0.42
Av. Ratio = 1 M : 2.5 F			
Total M/F = 82/300 = 0.27			

Telford, 1990). However, again, it is not clear whether this study was based on observation of individual females whose breeding pattern was followed throughout their reproductive cycles, or, more likely, it was based on the presence of gravid females (i.e., with fully developed marsupium) within either a laboratory or a natural population.

Table 7. Survival of *P. laevis* cohorts.

Age (months)	*n*	Av. no. of mancas born in cohort	Av. no. of mancas surviving in cohort	Percentage survival
4–5	14	30.8 ± 12.6	14.8 ± 9.2	48
5–6	11	21.5 ± 8.6	10.4 ±5.0	48.4
6–7	5	13.6 ± 5.4	3.2 ± 2.4	23.5
7–8	5	17.8 ± 7.4	8.8 ± 3.2	50.6
Total	35			
Average		20.8 ± 5.7	9.3 ± 4.1	44.7

n = number of cohorts.

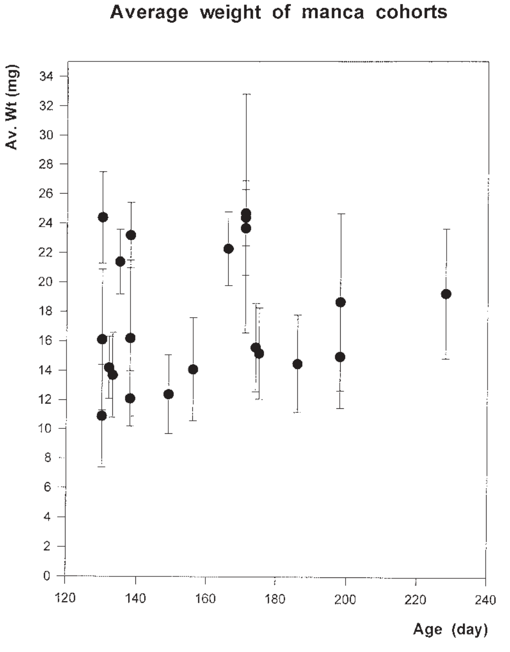

Fig. 8. Changes in average weight of different manca cohorts during their first half year of life. Each point indicates a cohort. Growth was followed in 21 cohorts some of them growing faster than others. Due to the difficulties in weighing so many small animals on the Cahn Gram Electrobalance, cohorts were weighed at different times. There appears to be a tendency of growth between 10–20 or even 25 mg within the first six months of life. (error bars: ±SD).

The fact that a *P. laevis* female is capable of reproducing so soon after it has released her young, and that her ovaries contain large oocytes at all times, indicates three theoretically interesting possibilities: 1. Unlike in most isopods, when oogenesis is time limited, in *P. laevis* oogenesis is almost continuous. 2. Mature ova undergo embryogenesis followed by organogenesis very rapidly; thus, embryos remain inside the marsupium for only a very short period before they are released as mancas. 3. The marsupium must be ready immediately after parturition, in order to contain the new batch of ova. These possibilities need further investigation.

Table 8. Calculated life expectancy of weight classes in *P. laevis* (in months).

Weight class (mg)	Life expectancy (months)
20–40	8
40–120	10
120–150	5
Total	23

ACKNOWLEDGEMENTS

We thank Ms. Yelena Tichomirova for her technical assistance.

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RECEIVED: 9 December 1999.
ACCEPTED: 17 August 2000.