Breeding Phenology and Reproductive Strategies in Terrestrial Isopod Species (Crustacea Isopoda Oniscidea) from Tunisia

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1. Introduction

Reproduction in terrestrial isopods has been dealt with in numerous studies (summarized in Dangerfield and Telford, 1995). There are remarkable variations in breeding phenology between species (Sutton et al., 1984, Warburg, 1987) and between different populations of the same species (Souty- Grosset et al., 1988). Even within the same population, annual variations have been described (Zimmer and Brauckmann, 1997). A characteristic of many populations, especially those in seasonal environments, is that reproduction is frequently confined to a distinct breeding season or period. These periods are usually located in those months when physical conditions are less severe. It is often an implicit assumption that there is an optimal time of year for release of an individual's offspring, when the physical and biotic environment is most suitable (Willows, 1984).

Theory of life history evolution predicts specific patterns of growth, survivorship and reproduction based on a genotypic strategy (Pianka 1970; Greenslade, 1983). Models based on optimality arguments take into account environmental effects but often predict an optimal strategy or tactic for a given set of environmental conditions (Sibly and Calow, 1986). The breeding phenology of woodlice is influenced by both abiotic and biotic environmental factors, resulting in temporal coincidence of the release of offspring with favourable conditions for growth and survival and thus in discrete annual breeding events in temperate climates (Lawlor 1976; Sutton et al., 1984; Souty-Grosset et al., 1988). However, breeding phenology can vary annually within these constraints (Dangerfield and Hassall, 1992; Zimmer and Brauckmann, 1997). More generally speaking, the optimal time for breeding may be more or less predictable from year to year, but those animals which reproduce at that time may be viewed as the most successful (Willows, 1984).

In arid zones as in temperate ones, there are remarkable variations in breeding phenology. Isopods breed mostly during spring and early summer (Aljetlawi and Nair, 1994; Nair, 1984;

Warburg, 1994; Achouri and Charfi-Cheikhrouha, 2001; 2002), but variations in breeding phenology among both species (Sutton et al., 1984; Warburg, 1987) and different populations of the same species (Souty-Grosset et al., 1988; Achouri and Charfi-Cheikhrouha, 2005) are common. Even within the same population, annual variations have been described (Dangerfield and Hassall, 1992; Zimmer and Brauckmann, 1997). Female fecundity is proportional to female size (Sutton et al., 1984). Thus, population dynamics depend on both the number and size of reproducing females (Rushton and Hassall, 1987; Hassall and Dangerfield, 1990). Due to variable individual growth rates (Hubbell, 1971; "cohort splitting": Sunderland et al., 1976), even a cohort of similarly aged females exhibits a considerable range in size (Zimmer and Kautz, 1997; Achouri and Charfi-Cheikhrouha, 2002; Achouri et al., 2003). Within given species-specific constraints, it is thus advantageous to grow large before reproducing, while, on the other hand, reproductive investment constrains increase in body size (for discussion, see Zimmer and Kautz, 1997). As for intraspecific comparison, we hypothesise that, on an interspecific scale, (1) individuals of larger species are able to invest more of the available energy in reproduction than individuals of small species (cf. Glazier et al., 2003).

In most species of the Porcellionidae, two or more brood waves per year have been observed (Warburg, 1987). Thus, these species have been considered iteroparous. However, it has rarely been demonstrated unambiguously that a single female was capable of breeding more than once in its lifetime (iteroparous) or whether it would not breed again (semelparous) (Cole, 1954); from more than one brood wave per year in a given population, it does not necessarily follow that each individual female breeds more than once (Warburg, 1994). Knowing whether a particular species is semelparous or iteroparious, however, is essential for a comparative interspecific analysis of breeding strategies, since reproductive investment in current reproduction varies inversely with expectation of future offspring. Thus, semelparous females should invest significantly more in their first and only brood than potentially iteroparous females. In iteroparouas species, females may tend to invest less into the first brood and allocate more energy into growth, in order to grow larger for a second brood (cf. Zimmer and Kautz, 1997). We hypothesise that (2) females of semelparous species exhibit high reproductive investment as compared to iteroparous species. Accordingly [see hypothesis (1)], we expect small species to be iteroparous, enabling them to spread their reproductive effort over several breeding events. On the other hand, it may –under certain conditions– be advantageous for large species to be semelparous, concentrating their reproductive effort on a single event, while at the same time reducing the risk of dying prior to a second brood (cf. Zimmer and Kautz, 1997).

As reproductive activity and investment may vary with environmental conditions, interspecific comparisons should be restricted to syntopic species that are exposed to similar environments. We performed a long-term study on interspecific differences in breeding phenology and investment in syntopic isopod species, predicting that large isopod species invest high proportions of their energy in reproduction and tend to be semelparous, while the opposite is true for small species. The main aim of this study is to compare the reproductive patterns of seven species of Oniscidea collected in Chambi area, to test whether these syntopic species exhibit interspecific differences in breeding phenology (cf. Zimmer, 2003) and hypothesise that differently sized syntopic species differ in terms of female reproductive investment and to compare their reproductive phenology with others populations from the Mediterranean areas.

2. Material and methods

2.1 Study site and sampling programme

The study area is the Mt. Chambi or Djebel Chambi which includes the highest point of Tunisia (1544m/5066ft). It is accepted as a biosphere reserve by UNESCO in 1977 and declared a National Park in 1981. This mountain is Located in center-oust of Tunisia at 17 km from the city of Kasserine and a few kilometers from the Algerian border.

Several plant species are identified (262). They are distributed in different stages of the mountain. The first stage (up to approximately 900 m) is the area of the alpha, then above, the Aleppo pine which grows in the Phoenician juniper and rosemary. Still above, beyond 1100 m are the oaks.

Populations of *Armadillidium sulcatum* A. Milne-Edwards, 1840, *Leptotrichus panzerii* (Audouin, 1826), *Hemilepistus reaumuri*, *Porcellio djahizi* n. sp. (Medini & Charfi-Cheikhrouha, 2001), *Porcellio laevis*, (Latreille 1804), *Porcellio variablis* Lucas, 1846 and *Porcellionides pruinosus* Brandt, 1833, were hand-collected in the Chambi area. Data were obtained from a field survey of twenty six months (October 2008-December 2010).

2.2 Laboratory procedures

Individuals collected were taken to the laboratory alive, the majority of them are preserved in 70% ethanol and the others are raised for further investigation. Subsequently, we counted and sexed all individuals, and measured their total length (distance between the anterior edge of the head and the end of the pleotelson).

The animals were kept in translucent plastic boxes (20 x 35 x 10cm) containing a loamy soil about 3cm height, under natural conditions, with temperature mostly fluctuating between 20 and 33°C, and the daily photoperiod was 12h. They were fed on disks of carrot, and sporadically, on some fresh linden leaves. To guarantee the detection of all females with brood pouches before manca release, females were examined for the occurrence of brood pouches once a week. Based on the detection of ovigerous females and the young in laboratory populations, we were able to distinguish between seasonal reproduction and continuously breeding populations. Moreover, the appearance of gravid females and juveniles served as a measure for the onset and the duration of the reproductive period and sexual rest.

During the annual reproductive period, 20 ovigerous females of each species were sized using a stereomicroscope (Leica MS5), then they were dissected and marsupial eggs or embryos were counted to estimate fecundity (defined here as the number of eggs for a female for one brood); this should not be confused with fertility, which is the number of young leaving the brood pouch. To find a relation between brood size and body length, studies were conducted on gravid females of varying body dimensions, and simultaneously, it was possible to examine the ovaries after the discharge of the large oocytes. At that point the ovary was largely an empty sleeve-like structure, except for the smaller oocytes (Warburg, 1994). By examining the ovaries, it was possible to check for future generations of oocytes, indicating the potential for iteroparity; their absence was interpreted as indicator of semelparity.

In every reproductive period, 15 to 20 additional gravid females were maintained individually in cylindrical plastic tubes (7x4cm) and fed on disks of carrot until manca release. Using a Mettler AB22204-S balance (±0.1 mg accuracy), each female was weighed weekly during the breeding season, both before (W_0) and immediately after releasing mancae (W_1). The weight loss of the female corresponds to both reproductive allocation and parental investment. Upon hatching, mancae were counted, and they were separated from their mother and kept separately in Petri dishes under the same laboratory conditions (temperature, photoperiod, food) as the adult individuals.

2.3 Data analysis

Since recruitment was discontinuous we estimated field growth rates by tracking recognizable cohorts from size-frequency distribution (0.2mm length classes) on successive sample dates. Size frequency analysis was achieved by using the probability paper method (Harding, 1949), as performed by Cassie (Cassie, 1954; 1963). To test the reliability of the method, we employed the χ^2 and G tests ($P \geq 0.05$) (Fisher, 1950; Sokal and Rohlf, 1981). Computations were performed using ANAMOD software (Nogueira, 1992).

Usually, field growth rates are not constant throughout the year. Thus, results from field growth estimations were fitted to the Von Bertalanffy growth function (VBGF) with seasonal oscillation, according to a model proposed by Gaschütz and co-workers (Gaschütz et al., 1980), and previously applied (Marques et al., 1994; Pardal et al., 2000) with satisfactory results. Length is expressed as:

$$L_t = L_\infty \{1 - e^{-[kD(t-t_0) + C(kD/2\pi)sin2\pi(t-ts)]}\}^{1/D}$$

L_t= length of the organism at a given moment t;
L_∞ = maximum possible length of the organism;
t = time instant;
t_0 = time instant when the organism would have a length = 0;
t_s = time interval between start of growth (when t=0) and the first growth oscillation;
growthis expressed by a sinus curve, with a period of 1year;
k= intrinsic growth rate;
C= constant, ranging from 0 to 1;
D = parameter that expresses metabolic deviations from the Von Bertalanffy 2/3 rule.

Egg loss, brood pouch mortality, number of broods per female, reproductive allocation and the potential of reproduction were quantified:

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

$$R = \frac{(W_0 - W_1)}{W_0} \times 100$$

where W_0 is the initial weight before the mancae release and W_1 is the weight immediately following mancae release (Warburg, 1994).

R estimates a female's reproductive investment, while P quantifies the weight loss of a female in order to produce a single manca: $P = R/N$, where N is the number of mancae per brood (Warburg, 1994).

The estimation of the reproductive potential was based on the number of juveniles released, the proportion of females in the sample, the life span of a female, and the number of broods during a female's lifetime. The reproductive potential (R') was estimated using the Wildish equation $R' = bnp$. (Wildish, 1971, 1979, 1982 *in* El Kaïm et al., 1985), where b represented the mean number of young per brood, n the annual number of broods per female, and p the average number of ovigerous females.

The sex ratio was estimated by the ratio of males to females. The observed and expected values were compared using Chi-square (χ^2) test.

3. Results

3.1 Breeding phenology

Breeding season is defined as the time from the first appearance of gravid females to the time of the last appearance of empty brood pouches in the population. Figure 1 shows that the duration of the reproductive period varied considerably among species, ranging from 3 months in the largest species *Hemilepistus reaumuri* and the two smallest species *Armadillidium sulcatum* and *Leptotrichus panzerii*, to 6 months in *Porcellio variabilis* and *Porcellionides pruinosus*. Marsupial eggs were detected in *Hemilepistus reaumuri*, *Armadillidium sulcatum* and *Leptotrichus panzerii* in May. Mancae emerged during June and July.

Porcellio variabilis carried mature oocytes in February; marsupial eggs were found in March and April. Mancae were released from May to September with a sexual rest during July and August. In *Porcellionides pruinosus*, ovigerous females and juveniles were present throughout the period extended from March to October, however their percentage decreased in June and July (9.43%). For the other species (*Porcellio djahizi* and *Porcellio laevis*), the reproductive period was 5 months with a sexual rest from June to August for the first species, and during July and August for the second one.

These latter species of the genus *Porcellio* and *Porcellionides pruinosus* breed twice a year, in spring and during monsoon in the period extending from the fourth week of August until the second week of October. Females contained mature oocytes during March and April. Egg release into the marsupium began in May, and mancae were released from June to September. In all studied species, the date of the onset of breeding appeared to be correlated to female size. Overall, in species with seasonal reproduction behaviour, larger females started reproducing earlier in the year than smaller ones, except in *Hemilepistus reaumuri* (Fig. 1). Further, on an interspecific scale, larger species started reproducing earlier in the year than smaller ones.

The marsupial period starts with the parturial moult which is followed a few days later by the movement of mature oocytes into the marsupium. The marsupial eggs then develop into embryos and finally mature to hatch as mancae (Holdich et al., 1984; Warburg, 1994). The marsupial development, defined in this case as the period from the appearance of marsupial eggs to the emergence of mancae, was spread over a period of 22-49 days. It was longest in *Porcellio laevis*, one of the largest species, and *P. variabilis*, and shortest in the smallest species, *Armadillidium sulcatum* (Table 1).
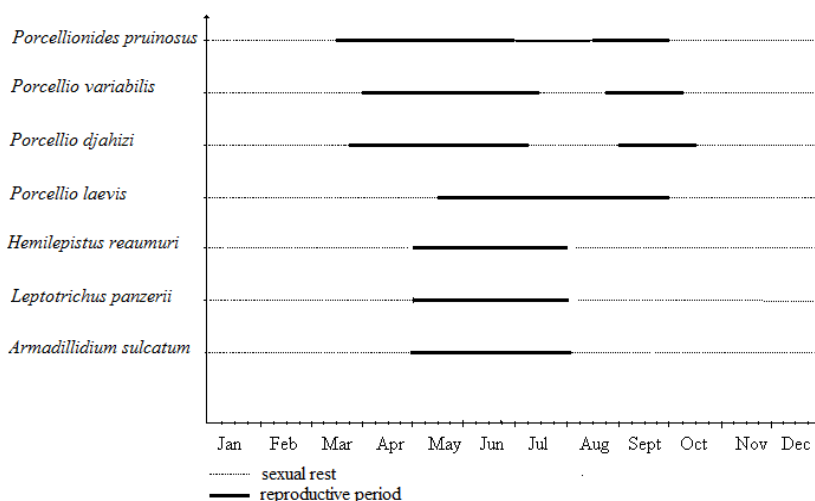
Fig. 1. Onset of reproduction and duration of the reproductive period.

The sexual rest lasted for 9 months in Hemilepistus reaumuri, Armadillidium sulcatum and Leptotrichus panzerii, and about 6 to 7 months in Porcellio variabilis, Porcellionides pruinosus, Porcellio djahizi, and Porcellio laevis (Fig. 1).

Species	Duration of reproductive period	Gravidity (days) [M ± S.D. (N)]	Avg. number Eggs [M ± S.D. (N)]	Avg. number mancae [M ± S.D. (N)]
A. sulcatum	May-June- July	22 ± 2 (31)	14 ± 0.9 (29)	9 ± 2.1 (25)
H. reaumuri	May-June- July	43 ± 4 (45)	68 ± 0.7 (79)	47 ± 1.9 (70)
L. panzerii	May-June- July	23 ± 6 (27)	11 ± 0.5 (25)	9 ± 0.78 (37)
P. djahizi	Mar-May[]Sept-October	39 ± 2 (50)	48 ± 0.6 (57)	38 ± 1.81 (50)
P. laevis	April-June[]Sept-October	49 ± 5 (42)	52 ± 0.8 (48)	41 ± 0.91 (41)
P. variabilis	Feb-May[]Sept-October	46 ± 3 (36)	51 ± 0.5 (54)	43 ± 0.73 (45)
P. pruinosus	Mar- may///August-October	34 ± 5 (38)	26 ± 1.3 (37)	19 ± 1.2 (37)

(N): number of used females, [] sexual rest /// only a few number of ovigerous females was found

Table 1. Marsupial eggs, mancae released numbers and duration of reproductive period in seven terrestrial isopod species from Chambi area.

3.2 Fecundity, fertility and egg losses

Corrected for female size, small species (e.g., *Armadillidium sulcatum* and *Leptotrichus panzerii*) released less mancae than did large species (e.g., *Hemilepistus reaumuri*, *Porcellio laevis* and *Porcellio variabilis*) (Table 1).

In all species, the number of released mancae was lower than the number of eggs released into the marsupium ("Egg loss" in Table 1). This loss in marsupial eggs was low in

Leptotrichus panzerii but relatively high in *Hemilepistus reaumuri*, ranging in total from 2 to 21 (Table 1). Otherwise, both fecundity and fertility was positively correlated with female size and weight (Table 2), but we observed significant interspecific differences in size/fecundity relationships.

Species	Fecundity		Fertility	
	Equation	R^2	Equation	R^2
A. granulatum	Y = 7.1 X -18.7	**0.81**	Y = 5.4 X – 18.9	**0.82**
H. reaumuri	Y = 5.3 X – 13.7	**0.79**	Y = 4.3 X – 12.3	**0.53**
L. panzerii	Y = 13.2 X – 71.1	**0.91**	Y = 8.2 X – 39.2	**0.89**
P. djahizi	Y = 13.6 X – 89.1	**0.88**	Y = 12.1 X – 69.4	**0.91**
P. laevis	Y= 6.9 X – 26.9	**0.89**	Y= 5.1 X – 17.3	**0.73**
P. variabilis	Y = 7. 3 X -35.8	**0.79**	Y = 4.9 X – 15.9	**0.82**
P. pruinosus	Y = 5.8 X - 35.6	**0.92**	Y = 6.5 X – 18.1	**0. 87**

Y is the total number of eggs produced per brood pouch; X is the body length of gravid females

Table 2. Equations and R^2 of relationship between female body length and fecundity and fertility.

3.3 Growth and life span

We analysed size frequency distributions for recognisable cohorts. Based on data from the first sampling results, one cohort could be identified for these species, *Armadillidium sulcatum*, *Hemilepistus reaumuri*, and *Leptotrichus panzerii*, and three to four cohorts in *Porcellio variabilis*, *Porcellio djahizi*, *Porcellio laevis* and *Porcellionides pruinosus*. Additionally, new cohorts appeared, respectively, in June and july for *A. sulcatum*, *H. reaumuri*, and *L. panzerii*, (one cohort), in May and October for the other species (two cohorts). The minimum average length of newly recognized cohorts ranged from 3.5 ± 0.136mm to 4.87 ± 0.163mm.

Growth was approximately continuous throughout life, but field growth rates were clearly higher in early life phases. Growth rates were also higher during spring (Fig. 2), but showed, on the other hand, a decline during autumn and winter (Fig. 2). We could follow new cohorts (appeared in our sampling) from detection up to their extinction, which allowed estimating the average life span at 14 to 25 months. In *Porcellio variabilis*, *Porcellio djahizi*, *Porcellio laevis* and *Porcellionides pruinosus* cohorts born by the end of the reproductive period had longer life span (19 to 25 months) than those (born in spring; 14 to 18 months). Data on field growth rates from these cohorts (followed in sampling period) were fitted to the Von Bertalanffy growth function. Parameters were estimated from each cohort data set, and the resulting model was used to simulate the expected growth in each case (Fig. 2). The degree of fit was assessed from correlation (r^2) between predicted values and observations.

3.4 Life cycle

Size frequency analysis allowed identifying the cohorts to which males and ovigerous females belonged, and thus we could evaluate the possible contribution of each cohort to

recruitment. These results suggest that cohorts born in early spring for *P. djahizi*, *P. laevis*, *P. variabilis*, and *P. pruinosus*, will in principle be able to reproduce in the same reproductive period, and most probably also in the beginning of the next. Cohorts born late in the reproductive period will grow slower during winter and not reproduce until the next spring, (the next reproductive period). However, in *A. sulcatum*, *H. reaumuri*, and *L. panzerii*, from July to October, this was a period of rapid growth in all size classes, and the bimodality in size class distribution observed during this period disappeared from November to next July.
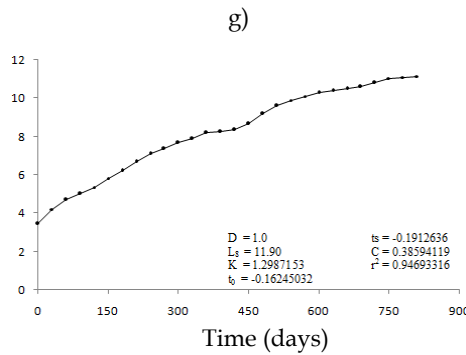
g)

Time (days)
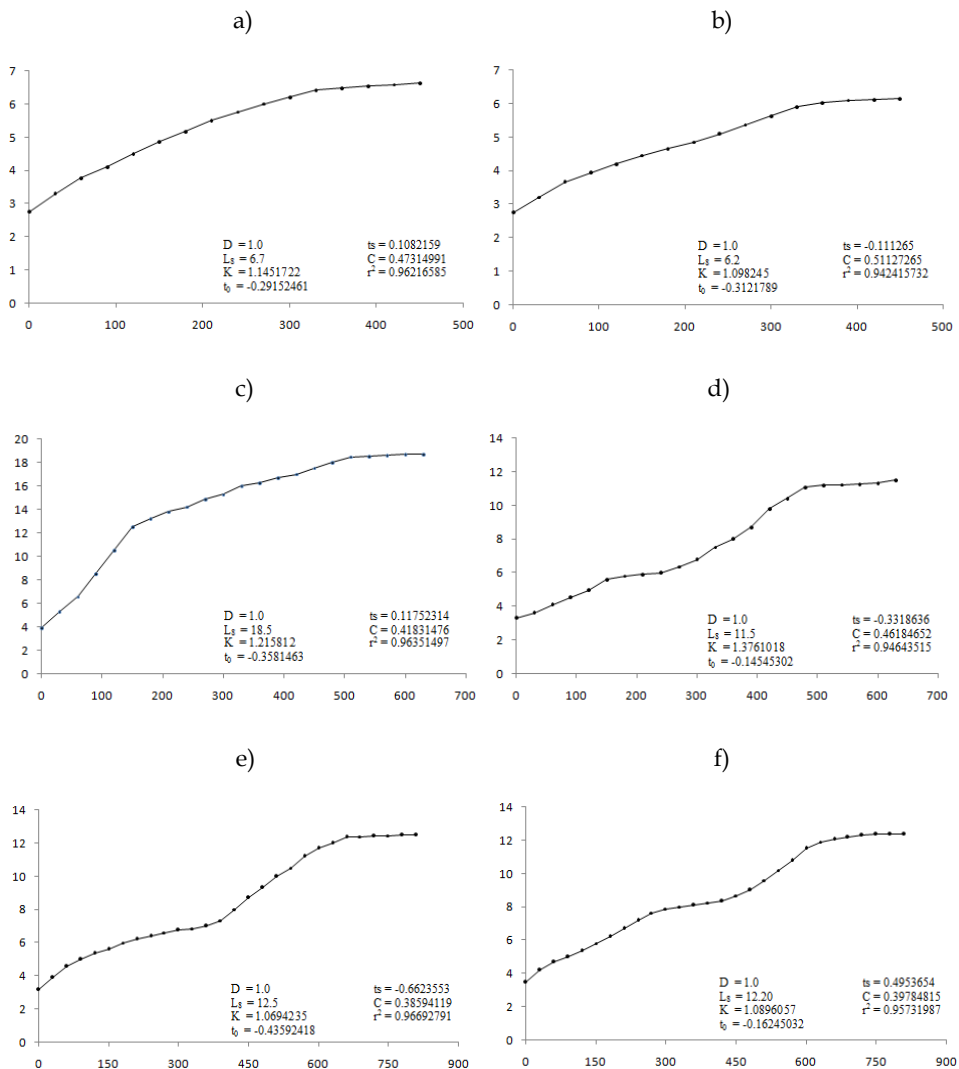
Fig. 2. Growth model of studies species at Chambi area. Graphic adjustment of the growth curves of cohorts: a. *A. sulcatum*, b. *L. panzerii*, c. *H. reaumuri*, d. *P. pruinosus*, e. *P. variabilis*, f. *P. laevis* and g. *P. djahizi* is given. Values of mean length estimated for each given instant are also plotted; r², correlation between adjusted curves and plotted values.

3.5 Reproductive strategies

Four out of seven species were iteroparous, with single females reproducing repeatedly. On the other hand, twenty females, each, of *Armadillidium sulcatum*, *Leptotrichus panzerii* and *Hemilepistus reaumuri*, were undoubtedly semelparous. In all other species, we found immature oocytes inside the ovary after mature eggs had been released into the marsupium upon mating, indicating the potential for a subsequent brood. Contrary to our hypothesis (2), the semelparous species are among the two smallest *Armadillidium sulcatum*, *Leptotrichus panzerii*, and the largest *Hemilepistus reaumuri*, in the Chambi area.
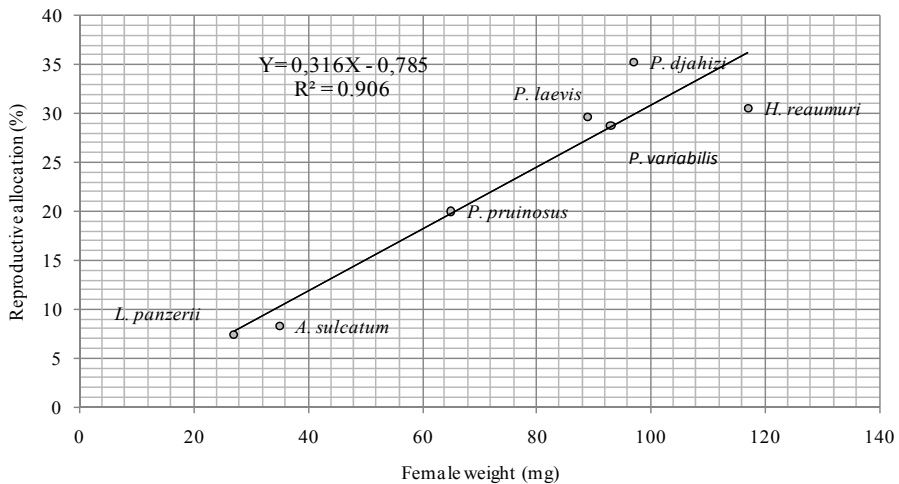

Fig. 3. Relationship between mean female weight and mean reproductive allocation of seven isopod species.

The two smallest species exhibited the lowest reproductive allocation, corroborating our hypothesis (1) (Table 3). The largest species, *Hemilepistus reaumuri*, *Porcellio djahizi* and *Porcellio laevis* were among the three species, with the highest reproductive allocation, and the numbers of both marsupial eggs and mancae released were highest in these species. Although *Porcellio variabilis* females on average were heavier than those of the other species, they produced much smaller numbers of both marsupial eggs and mancae than the other species; despite their large mancae, reproductive allocation was intermediate. Overall, however, reproductive allocation was positively correlated with female weight (Fig. 3; R^2 = 0.906).

Parental investment in producing a single manca varied between 0.61 (*L. panzerii*) and 0.89 (*P. djahizi*) mg per manca. Parental investment was not significantly correlated with female weight (R^2 = 0.1313).

The reproductive potential differed greatly between the small and large species. *H. reaumuri* (2386 juveniles released) *P. variabilis* (2456) *P. laevis* (2284) and *P. dalensis* (2284) exhibited the highest reproductive potential. These species produced six times more offspring than did *L. panzerii* (154) (176) and *A. sulcatum* (Table 4).

4. Conclusion

Various parameters used to define reproductive strategies herein covaried with species-specific female size. Overall, small isopod species from the Chambi area tend to be semelparous [contrary to hypothesis (2)], to allocate less energy in reproduction [corroborating hypothesis (1)], to produce less mancae (corrected for female size), to start breeding later in the year, and to exhibit a shorter reproductive period and a shorter marsupial development than large species.

Overall, the isopod species studied herein confirmed several aspects of breeding phenology that had been described in other syntopic woodlice species in the Mediterranean area (Warburg 1994; Medini et al., 2000; Hamaied et al., 2004; Achouri and Charfi-Cheikhrouha, 2006; Achouri et al., 2008). However, no clear relationship emerges between the reproductive pattern, on the one hand, and either the taxonomic status or the environment, on the other hand; rather the period from April (spring) to October (autumn) can generally be considered favourable for reproduction in the Mediterranean, irrespective of species identity. Thus, the reproductive pattern of terrestrial isopods appear to be independent, to a certain extent, of the habitat condition (cf. Warburg, 1994). Based on our present results, we hold that it is rather the species-specific body size of females that determines reproductive strategies. It remains, however, unclear why – in contrast to our hypothesis (2) – the smallest species rather than the larger ones are semelparous in Chambi area.

The loss in marsupial eggs did not covary with female size in the present study, and was in the same range of magnitude as values found by Warburg (1994) in species inhabiting the Negev desert and xeric and mesic habitats in the Mediterranean region (ca 26 %). Reproductive allocation to produce one brood pouch ranged between 6 and 35%, depending on female size. Warburg (1994) reported reproductive allocation of 7-52 % in seven species from Palestine, but in all but one species it was less than 22 %. The maternal investment in producing offspring ranged between 0.6 and 1.6 mg per manca, covering the range of 0.6-1.4 Warburg (1994) reported for different species in the Negev desert and the Mediterranean. Females of the small species, *Armadillidium sulcatum*, and *Leptotrochus panzerii* invested less than did females of large

species [hypothesis (1)], and overall, semelparous species exhibited a lower reproductive potential than iteroparous species, although the latter showed high interspecific variation in this respect. Reproductive investment and output of the species in this study were positively correlated with female size and weight, both within and among species. Intraspecific variation in size-adjusted reproductive output frequently occurs (e.g., Dangerfield and Telford, 1990; Nair, 1984) that may be explained by individual differences in the ability to accrue resources, the timing of allocation of resources to reproduction, genetic determinants of reproductive characteristics, or seasonal variation in environmental conditions during individual development and reproduction. This may also hold true for interspecific comparison, but further studies are needed to unambiguously decide upon this issue.

According to the present results, iteroparous species *P. variabilis*, *P. djahizi*, *P. laevis*, and *Porcellionides pruinosus* were reproductively active from February/March to August/October with a cessation during June and July, when semelparous species *H. reaumuri*, *A. sulcatum* and *L.panzerii* engaged in reproduction. Although we did not test for competitive exclusion or character displacement in the presence of a superior competitor, it is interesting to speculate that small species in the Chambi area may avoid competition for their young by the larger offspring of larger species through a shift in time of reproduction (cf. Zimmer, 2003, Achouri et al., 2008).

Interspecific variation in the onset and the duration of reproduction prevailed in the studied species despite the imposed equal conditions of temperature, photoperiod and nutrition. Since interspecific interactions were absent in our experimental design, we hold that individual genotypes dictate individual phenology. Direct genetic control (De Jong, 1991), or a genetically determined norm reaction (Stearns and Koella, 1986), exist for reproduction traits such as the timing of reproduction (Dangerfield and Telford, 1995). However, flexibility in female reproductive tactics is apparent in many isopod species. Lifetime brood production, phenology of brood production, fecundity and offspring size all differ to some degree between individuals. The theoretical concepts of bet-hedging (Slatkin, 1974) and phenotypic plasticity (Bradshaw, 1965; Caswell, 1989) consider such variation in reproductive traits as strategies capable for maximising female reproductive success under changeable environmental conditions (Houston and McNamara, 1992). In the long run, flexibility in phenology in response to environmental conditions (cf. Dangerfield and Hassall, 1992; Zimmer and Brauckmann, 1997) will determine the potential of a species to adapt to changing climatic conditions.

The outputs from our calibrated growth model showed that growth rates are always higher in the initial life cycle stages, slowing down when individuals become mature, viz., during the reproductive phase. This is consistent with observations carried out on *Porcellionides sexfasciatus*, as well as other Oniscidea species (Matsakis, 1955). Cohorts born in late summer and autumn may in principle live 19 to 25 months, while cohorts born in spring will live only 14 to 18 months. Since cohorts born in spring will be able to produce offspring in the same reproductive period, differences observed might be explained by the fact that females from these cohorts invest in reproduction in an early phase of their lives, and face the harsh winter conditions immediately after. On the contrary, cohorts born later in the season will live through the winter and reproduce only in the next year, at a later stage in their life. These will face more favourable conditions after their reproductive effort and consequently will tend to survive longer.

Next to effects on fecundity, variable growth rates appear to be important as determinants of the maturation of young individuals. In combination with discrete breeding events, growth rates also control lifetime brood production. For instance, in a population of *Armadillidium vulgare* relaxation of intraspecific competition and favourable growth conditions allowed young born in July to grow rapidly and reproduce the following summer, thus breaking the normal sequence of two years maturation and semelparity (Dangerfield and Hassall, 1992).

Combining biological observations with the growth model output makes it possible characterize the life cycle of the populations studied of *Porcellio djahizi*, *P. laevis*, *P. variabilis*, and *Porcellionides pruinosus*, as that of a semi-annual species, with iteroparous females and bivoltine life cycle. However, *H. reaumuri*, *A. sulcatum* and *L. panzerii* could be a semi-annual species, with semelparous females and univoltine life cycle.

Reproductive allocation to produce one brood pouch ranged between 7.46 and 35.21% and thus showed marked interspecific differences. Overall, reproductive allocation was positively correlated with female weight. For seven isopod species in England, the reproductive allocation ranged from 24 to 47 % (Sutton et al., 1984), and Warburg (1994) reported reproductive allocation of 7-52 % in seven species from Palestine, but in all but one species it was less than 22 %. The maternal investment in producing offspring ranged between 0.61 and 0.89 mg per manca, covering the range of 0.6-1.4 Warburg (1994) reported for different species in the Negev desert and the Mediterranean. Females of the small species, *Armadillidium sulcatum*, and *Leptotrichus panzerii* invested less than did females of large species, and overall, semelparous species exhibited a lower reproductive potential than iteroparous species, although the latter showed high interspecific variation in this respect.

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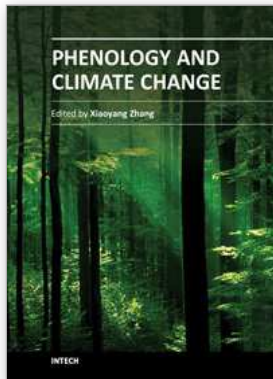
Phenology and Climate Change

Edited by Dr. Xiaoyang Zhang

Phenology, a study of animal and plant life cycle, is one of the most obvious and direct phenomena on our planet. The timing of phenological events provides vital information for climate change investigation, natural resource management, carbon sequence analysis, and crop and forest growth monitoring. This book summarizes recent progresses in the understanding of seasonal variation in animals and plants and its correlations to climate variables. With the contributions of phenological scientists worldwide, this book is subdivided into sixteen chapters and sorted in four parts: animal life cycle, plant seasonality, phenology in fruit plants, and remote sensing phenology. The chapters of this book offer a broad overview of phenology observations and climate impacts. Hopefully this book will stimulate further developments in relation to phenology monitoring, modeling and predicting.

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