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Breeding and population biology of *Armadillo officinalis* (Isopoda: Oniscidea) in Benghazi, Libya

AlBashir Ahmed AlJetlawi & G. Achuthan Nair

*Department of Zoology, Faculty of Science, University of Garyounis,
Post Box 9480, Benghazi, Libya (S.P.L.A.J.)*

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The breeding of *Armadillo officinalis* in Libya, coincides with the spring rains, a rise in relative humidity, atmospheric temperature, and day length; and lasts from April to September with a cessation during the hot summer months of June and July. Sexes were distinguished in individuals from 4 mm in length, on the basis of secondary sexual characters. The total number of eggs produced and the total number of young that left the brood pouches are correlated with the body lengths of the gravid females. The average incubation period was 32 days and brood mortality 4.2%. Females carried two to three broods in a year. The newly hatched young had a body length of 1.7 mm and growth was rapid during the early developmental stages. Descriptive accounts were furnished for the period October 1988 to October 1989, on the percentage distribution of size classes based on body length measurements of immature, male, female and ovigerous females, together with details of the standing crop and production of embryos. Sex ratio in the first year age group showed a preponderance of males over females, while in the 1–2-year-old group, females outnumbered males. These findings are discussed in the light of information available on various other species of woodlice.

Key words: *Armadillo*; breeding biology; Oniscidea; population biology; reproduction

Introduction

Armadillo officinalis Duméril is a common pillbug of Benghazi, Libya. Where conditions are favourable, it forms an important member of the soil macro-invertebrate community. Casual collections showed that they occur in large numbers in shady places where soil moisture is moderate; in some, they occurred up to 200–300 m⁻². The genus *Armadillo* constitutes 32.8% of all the isopods near the Mediterranean coasts of Egypt (Kheirallah, 1980) and forms 11.41% of the total isopod population in an oak woodland area in northern Israel (Warburg *et al.*, 1984). In spite of its widespread occurrence along the Mediterranean coasts, not much work has been done on the ecology of this species and the present study investigates its breeding and population biology. These animals offer unique advantages for breeding and population analyses. They are easily available in the field for sampling; the new born young have a body length of 1.7 mm and subsequent growth stages can be observed without much difficulty; the breeding activity is seasonal and growth rates lead to distinct size classes in field populations from which age can be estimated.

Address correspondence to: Dr G. A. Nair, Post Box 9482, Benghazi, Libya (S.P.L.A.J.).

The breeding and population biology of woodlice has been a subject of detailed study by many workers, and a good deal of information is available on the subject from different parts of the world. The chief contributors to this include, among others, Geiser (1934), Miller (1938), Heeley (1941), Paris & Pitelka (1962), Sutton (1968, 1970), Kensley (1974), Sunderland *et al.* (1976), Al-Dabbagh & Block (1981), Shachak & Yair (1984), Nair (1984), Willows (1984, 1987), Williams & Franks (1988), Warburg (1989), Hornung (1989), Paoletti (1989), Mocquard *et al.* (1989), Dangerfield & Telford (1990), and Hassall & Dangerfield (1989).

Materials and methods

Locality and material

Benghazi (32°10'N, 20°06'E) has a Mediterranean climate with moderate wet winters and warm dry summers. In winter (November–February) the temperature drops to 4–5°C during the night and during summer (May–September) the temperature reaches 39°C. Adult *Armadillo officinalis* Duméril (Oniscidea : Armadillidae) have body lengths from 5 to 11 mm. They occur in loamy soils with a rich humus content, and beneath bricks and stones in moist shady places. They are mostly active at night and the early hours of the morning before sunrise, like most other species of woodlouse (Cloudsley-Thompson, 1977).

Sampling site and methods

A site within the campus of Garyounis University, Benghazi, facing the Mediterranean sea to the west, was selected for sampling. The area was covered largely by *Erygynum maritimum* and *Eucalyptus*, *Acacia* and *Casuarina* trees, which provided shade and a rich deposition of litter. During late winter and spring, grass sprouted and formed a carpet over the ground. A dense population of *A. officinalis* occurred at this station throughout the year of study.

An area 15 × 30 m was marked off and subdivided into five rectangles each 15 × 6 m. The population was sampled on a stratified random basis with one replicate taken at random within each rectangle: 20 min was adopted as a constant searching time. Fortnightly collections (second and fourth weeks of every month) were made during the early morning hours over the period October 1988 to October 1989. The animals were collected using the modified Berlese Tullgen funnel method (Wallwork, 1970), after initial hand sorting. In this way, most of the individuals belonging to the initial stages were collected. They were preserved in a mixture of 80% alcohol and 4% glycerol. Body lengths of all specimens were measured and sex was noted in individuals having a body length of 4 mm or more. It was also noted whether the females had brood pouches. When present, the brood pouch was examined to determine the number of eggs and embryos for the estimation of brood size.

It was necessary to culture pillbugs in the laboratory to confirm their breeding habits and periods of moulting, incubation, and release of young, as well as age and growth rates. With slight modifications, the culture method described by Heeley (1941) was found to be most suitable for rearing *A. officinalis* in the laboratory. They thrived for more than 1 year under constant care.

Results

Breeding biology

Factors influencing reproduction

Climatic factors including average monthly rainfall, atmospheric temperature, relative humidity and day length were correlated with the breeding cycle in *A. officinalis* (Fig. 1). Breeding began just after the spring rains (March 1989). The high moisture content of the soil, together with plenty of food and an increase in relative humidity (50–75%) and temperature (25–27°C) of the atmosphere probably triggered breeding. Females with

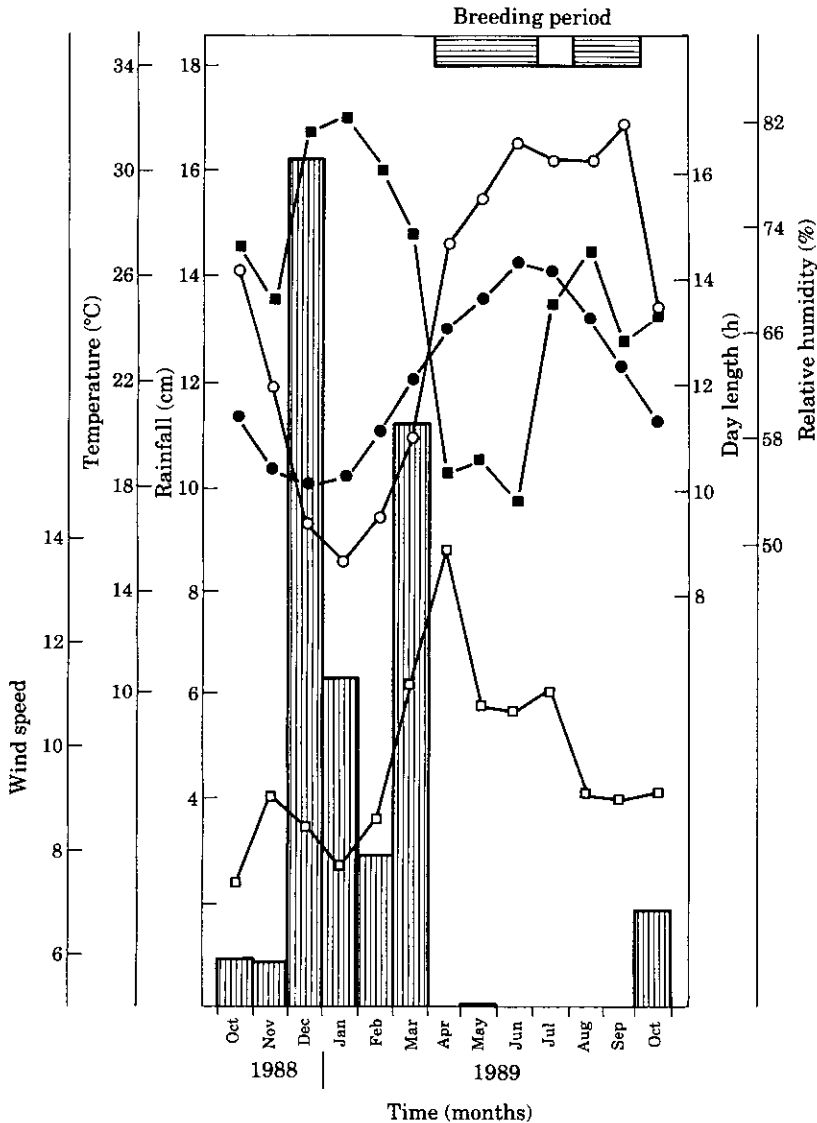


Figure 1. Breeding periodicity of *Armadillo officinalis* correlated with rainfall (▨), temperature (○), relative humidity (■), day length (●) and wind speed (□). Solid horizontal bars at the top indicate the breeding period. The vacant portion in the bar indicates cessation of breeding.

brood pouches carrying freshly deposited eggs began to appear in April. Breeding continued until the first week of June, after which high atmospheric temperature ($+32^{\circ}\text{C}$) coupled with low humidity ($<50\%$) no doubt induced quiescence. Cessation in breeding during the hot summer months from June until the beginning of August was evident in 1989. This was followed by a spurt in breeding activity from the latter half of August until the end of September when the temperature and humidity again became favourable. Day length may also have played a significant role since the major breeding period occurred when it was between 12 to 14 h.

Sex characters and size at sexual maturity

Sexes are separate in *A. officinalis*. The secondary sexual characteristics began to appear when body lengths of 4 mm or more were attained. The males are distinguished by the elongation of the endopodites of the first and second pleopods on the ventral side of the abdomen. The penis can be seen between the first and second pleopods. In the female, all the pleopods are of the same size and the genital opening is seen on the ventral side at the base of the seventh thoracic segment. No colour differentiation was apparent between the sexes. In mature females, before the breeding season, the oostegites were formed as bud-like structures at the bases of the second to sixth thoracic segments which later enlarge into leaf-like pads that accommodate the fertilized eggs.

More than 100 *A. officinalis* of body lengths 4–11 mm were examined to determine the minimum size at which they became sexually mature. The majority of males attained sexual maturity when they were 5–6 mm in length, whereas the females became sexually mature when they reached 6–7 mm. They began to bear broods after reaching 7 mm in body length.

Copulation and formation of the brood pouch

Copulation in *A. officinalis* occurred during spring and followed the usual woodlouse pattern (Nair, 1984). After pairing, the female sought a secluded hiding place and awaited completion of ecdysis and formation of the brood pouch. After moulting the oostegites, until then represented by small club-like processes, became fully developed and formed the brood pouch. The overlapping oostegites allowed the pouch to expand as the developing brood required more room.

Egg production, incubation and brood mortality

The number of eggs was found to be related to the body lengths of incubating females: 26 gravid females (with body lengths ranging from 7 to 11 mm) were examined and the number of eggs in the marsupia recorded. A positive correlation was observed between the body length and number of eggs ($r = 0.835$, $F = 55.33$, $p < 0.01$). The overall mean of eggs per brood pouch was found to be 25. The period of incubation ranged from 27 to 37 days. In 37 gravid females with body length ranging from 7 to 11 mm, whose total incubation period was determined, the average was 32 days. The total incubation period was related to the body lengths of gravid females. As body size increased, the incubation period increased correspondingly ($r = 0.620$, $F = 15.00$, $p < 0.05$). To determine brood mortality, 22 gravid females, 7–11 mm long, with well-developed embryos in their brood pouches, were examined. Of the 333 embryos in early and late embryonic stages of development, 14 were dead, indicating 4.2% mortality.

Breeding frequency and the number of young released

Samples collected during the period of investigation showed that egg production began in April and continued until September, with a cessation during June and July. Most of the females in the 1–2-year age groups (>7.5 mm in body length) bore their broods during the early part of the breeding period. After liberating the young, they did not breed during June and July, but a majority of them bore second broods during August and September. A small percentage of females which had reached 1 year of age (7 mm) also bore their first broods during this period. Thus females produced two to three broods in a year; one during April and May and the other one or two broods during August and September.

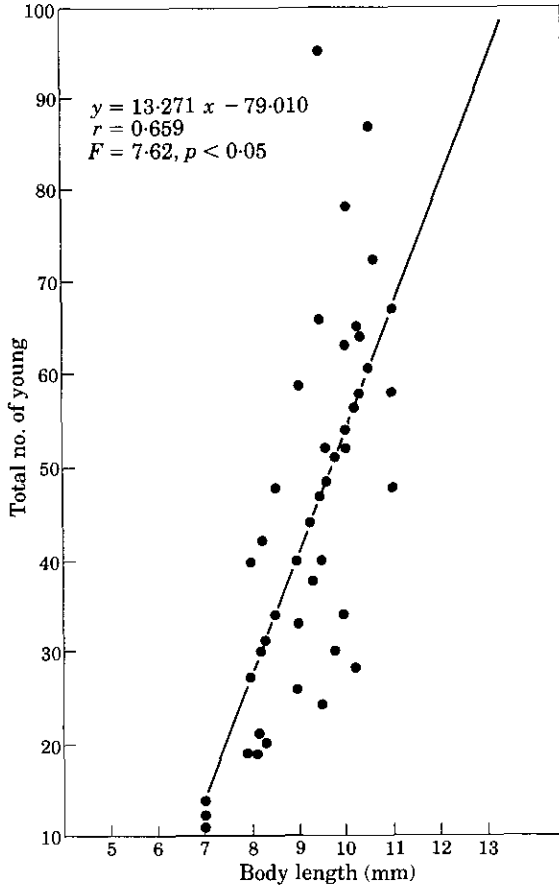


Figure 2. Total number of young liberated by the female in a year in relation to female body length.

A linear regression estimate of the number of young liberated (y) by females of different body lengths (x) showed a positive relationship (Fig. 2) ($r = 0.659$, $F = 7.62$, $p < 0.05$). The largest number of young produced by a single female in 1 year was 95 from three broods, while the lowest number was 15, produced by a female from a single brood.

Growth rates and salient features of the young

The growth rates of the young of *A. officinalis* hatched from the maternal brood pouch over a period of 49 weeks and the growth curve are presented in Fig. 3. The mean body length of the newly hatched young was 1.7 mm. Growth occurred after moulting and was rapid during the early developmental stages. These reached 4 mm in body length after 14 weeks when the secondary sexual characteristics began to appear. It took almost 40 weeks to attain a body length of 6 mm when the animals were sexually mature. The growth rate of the young was $0.049 \text{ mm day}^{-1}$ for the first 5 weeks. From 5 to 12 weeks, growth proceeded at a rate of $0.010 \text{ mm day}^{-1}$. This was followed by rapid growth ($0.023 \text{ mm day}^{-1}$) until an age of 20 weeks. This slowed down to $0.014 \text{ mm day}^{-1}$ from 20 to 49 weeks. The overall growth rate was $0.015 \text{ mm in body length day}^{-1}$.

The newly hatched young were whitish in colour having only six thoracic segments and six pairs of pereopods. After 1 week, the dorsal surface became pale brown in colour and the seventh segment and seventh pair of legs began to appear as rudimentary structures. After 4 weeks, the seventh thoracic segment was fully formed, with the seventh pair of legs folded. The body colour became greyish brown after 5 weeks and the seventh pair of legs were fully stretched. The animals continued to grow even after becoming sexually mature and reached a maximum length of 11 mm. Longevity was about 2–2.5 years.

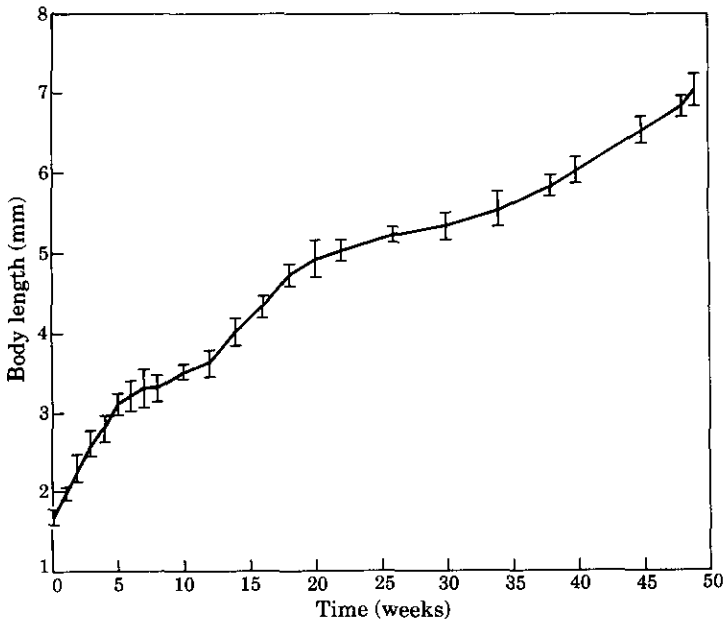


Figure 3. Growth rate of young hatched from the maternal brood pouch over a period of 49 weeks. The vertical bars show the S.E.M.

Population characteristics

*Size structure in *Armadillo officinalis**

Size influences both natality and mortality. The various size groups in a population indicate its reproductive status. Changes in the abundance of *A. officinalis* are related to changes in age structure. The monthly changes in size are presented in Figs 4–7. These show the frequency distribution of size, based on body length measurements. The number in each size class is shown as a percentage of the total number sampled. A major assumption was that the upward progression of size classes represent growth as in the findings of Sutton (1968) and Nair (1984) in various species of woodlice in England and India respectively. A brief description of the size structure of *A. officinalis* is given below.

A collection made in October 1988, consisted mainly of individuals of 1–2-year age groups (body length >7.5 mm): immature specimens formed 13.33% of the total population sampled. The bimodal size distribution observed during October 1988, persisted until December 1988. From November 1988 to February 1989, the animals were mostly inactive but there was slow growth in the different size classes. By January–February 1989, the oldest age groups had virtually disappeared from the population. During March most of the young ones recruited during the preceding year attained body lengths of 4 mm or more, and their sexes could be distinguished, while the bimodal size distribution began to change to a unimodal one. An increase in the number of males over females was noted during March–April, before the commencement of the breeding season.

By April, gravid females belonging to 1–2-year age groups began to appear in the population and fresh recruitment of young took place during April–May. This changed the unimodality in size distribution to a bimodal one. The newly recruited young formed 41.9% of the total population sampled during May, and a drastic reduction in the percentages of adult males took place. This was probably due to high mortality following breeding. During June, the upward progression of all size classes was evident. A slow termination of breeding was observed in the latter half of June when the onset of summer

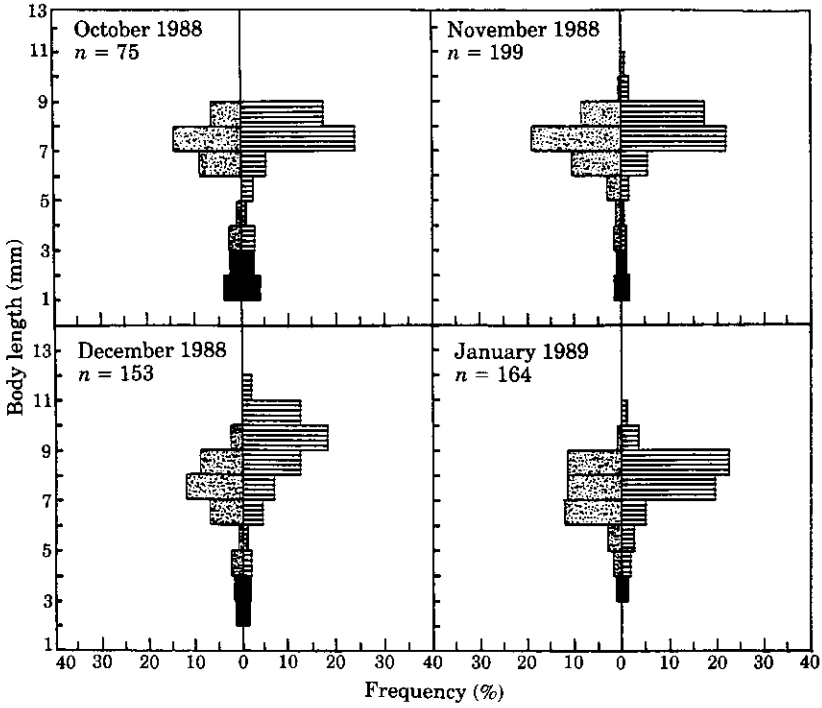


Figure 4. Percentage composition of *Armadillo officinalis* population samples taken from October 1988 to January 1989 showing size class and sex distribution. *n*, Size of sample; [stippled], male; [horizontal lines], female; [solid black], immature individuals.

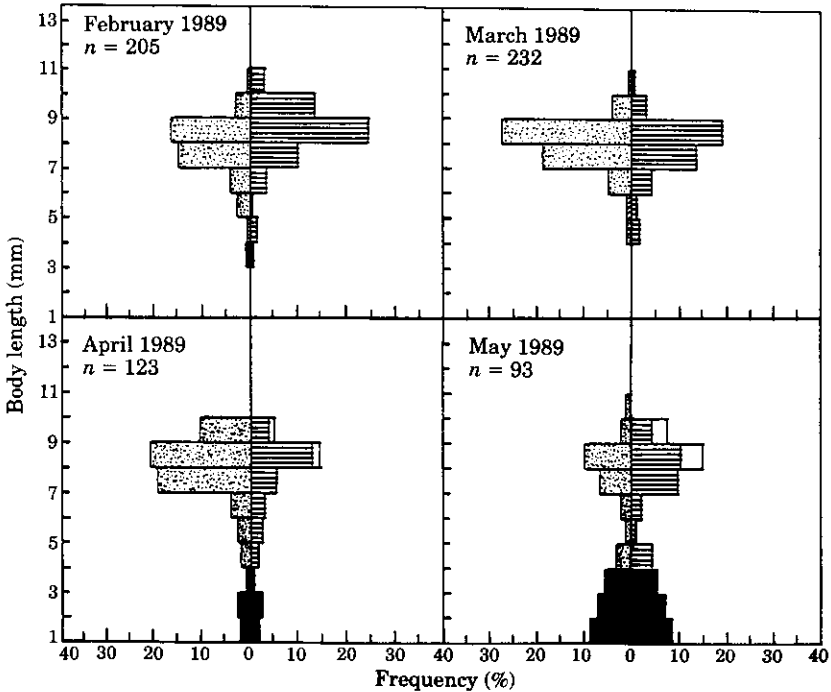


Figure 5. Percentage composition of *Armadillo officinalis* population samples taken from February to May 1989 showing size class and sex distribution. *n*, Size of sample; [stippled], male; [horizontal lines], female; [white], gravid female; [solid black], immature individuals.

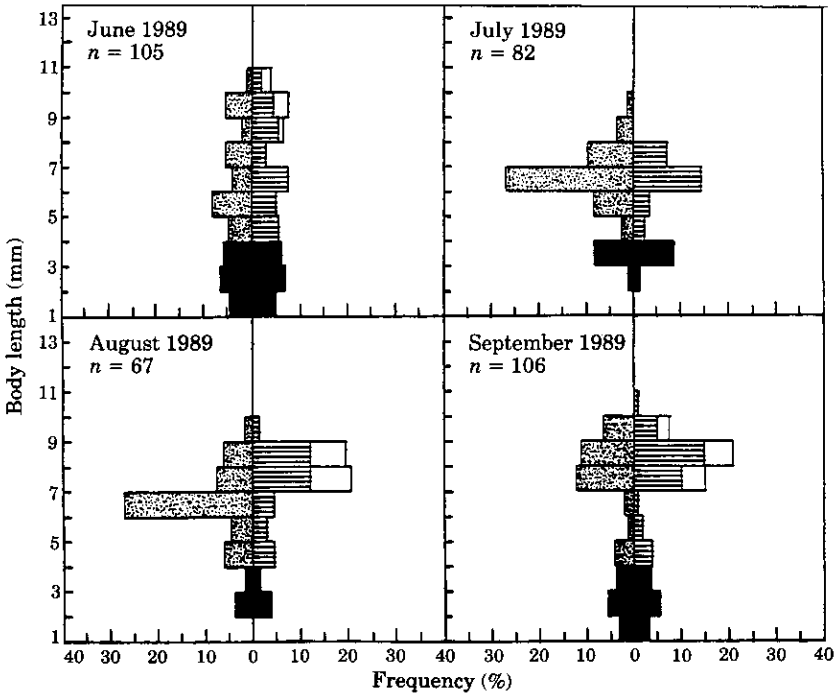


Figure 6. Percentage composition of *Armadillo officinalis* population samples taken from June to September 1989 showing size class and sex distribution. *n*, Size of sample; ▨, male; ▩, female; □, gravid female; ■, immature individuals.

compelled many individuals to take shelter in deep burrows. July was a period of inactivity but the bimodal size distribution was retained even though the upper and lower modes had disappeared.

During July–August 1989, most of the animals recruited during 1988 attained body lengths of 6–7 mm with males outnumbering the females. By August, gravid females

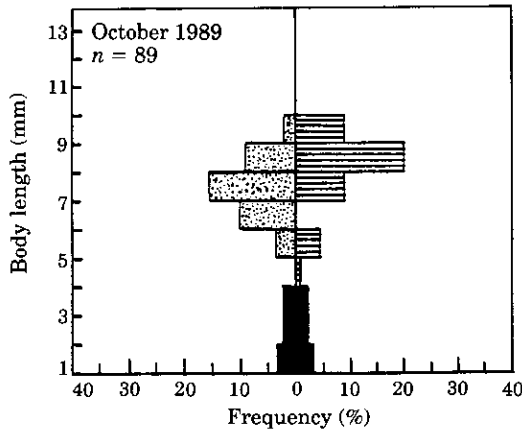


Figure 7. Percentage composition of *Armadillo officinalis* population samples taken for the month of October 1989 showing size class and sex distribution. *n*, Size of sample; ▨, male; ▩, female; ■, immature individuals.

belonging to both age groups reappeared and formed 44.1% of the total females sampled ($n = 37$). Breeding continued until the end of September 1989, and freshly recruited young began to appear in large numbers. This was a period of rapid growth in all size classes, and the bimodality in size class distribution observed during April 1989 continued until October.

Embryo standing crop and embryo production

A positive correlation between the body lengths of the gravid females and the total number of eggs produced per brood was observed in *A. officinalis*. The regression of the relation of brood size to body lengths of females was estimated as $y = 6.0179x - 30.527$ (Fig. 8) where y is the total number of eggs produced per brood pouch and x is the body length of gravid females.

An estimate was made of the total number of developing young in the brood pouches of *A. officinalis* in each sample, based on the body lengths of gravid females and computing the total eggs produced from the regression equation. This was taken as the embryo standing crop, from which embryo production for each month for the period October 1988 to October 1989 could be calculated using the formula:

$$\text{Embryo production} = \frac{\text{Embryo standing crop} \times \text{Sampling interval}}{\text{Development time}}$$

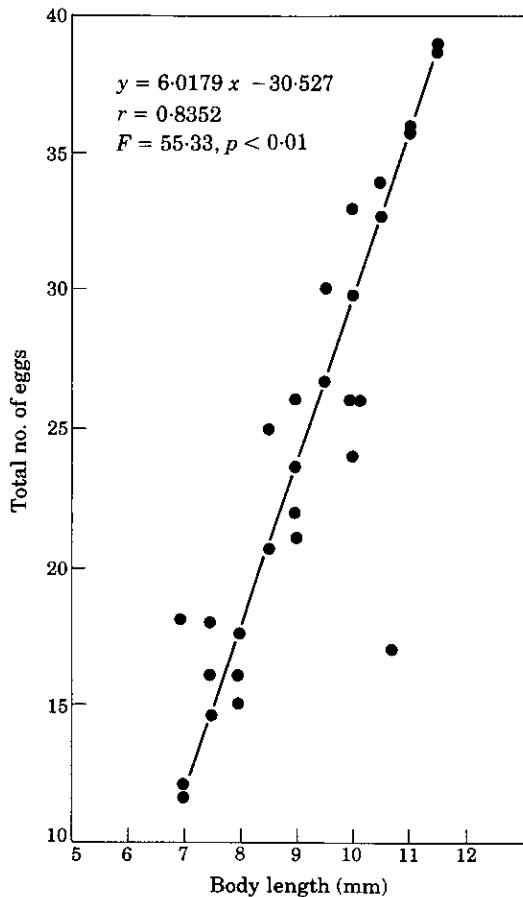


Figure 8. Total number of eggs deposited in the brood pouch in relation to the body length of the gravid female.

The above formula was also used by Sutton (1968) and Nair (1984) for various species of woodlice in England and India respectively. For calculating embryo standing crop and production, the last weekly sample taken in each month was used (Table 1). When computing total embryo production from embryo standing crop data, due allowance was made for the 4.2% brood mortality observed in the population. The development time was taken as 32 days which was the average incubation period of *A. officinalis*.

There was no standing crop during the period from October 1988 to March 1989. The standing crop in April 1989 was 66, which increased to 150 during May and June 1989. By July, there was a lull in the increase of embryo standing crop, followed by a spurt during August and September 1989, when the values stood at 171 and 240 respectively (Table 1). An index of embryo production was provided by the presence of very young animals (body length > 1.7 mm) in the population samples. There was a limited production of young during April 1989, which increased further during May and June; the second phase had started by August and continued till the end of September. Maximum embryo production was observed during September and the minimum during April 1989.

Sex ratio

The sexes are approximately equal in the population of very young woodlice of various species, even though later in life one of the sexes may become predominant (Geiser, 1934). Observations were therefore made on sex ratio in *A. officinalis*. Samples were taken over the period October 1988 to October 1989 and used for the study. The samples were pooled and the results are presented on monthly basis along with χ^2 and *p* values in Table 2. The animals were categorized into three groups: (1) immature, (2) male, and (3) female. Males and females were distinguished on the basis of secondary sexual characters when they had attained 4 mm or more in body length. Males and females sampled in each month were divided into two sub-groups; (a) 0-1-year age group (4-7 mm body length) and (b) 1-2-year age group (7-11 mm).

Females outnumbered males in most months. The χ^2 and *p* values showed no significant differences between male and female populations during October and November 1988, and January 1989, even though the females were more numerous. By March 1989, the trend changed and the proportion of males increased. In May and June the ratios were almost equal but during July and August males predominated. During September and

Table 1. Sampling details of embryo production for the period October 1988 to October 1989

| Sample date | No. of gravid females | Per cent of gravid females | No. of embryo standing crop | Sample interval (days) | Embryo production |
|-----------------|-----------------------|----------------------------|-----------------------------|------------------------|-------------------|
| 30 October 88 | 0 | 0.0 | — | — | N.R.* |
| 30 November 88 | 0 | 0.0 | — | 30 | N.R. |
| 31 December 88 | 0 | 0.0 | — | 31 | N.R. |
| 26 January 89 | 0 | 0.0 | — | 26 | N.R. |
| 27 February 89 | 0 | 0.0 | — | 32 | N.R. |
| 30 March 89 | 0 | 0.0 | — | 31 | N.R. |
| 24 April 89 | 3 | 37.5 | 66 | 25 | 49 |
| 14 May 89 | 7 | 24.1 | 150 | 20 | 90 |
| 10 June 89 | 6 | 40.0 | 150 | 27 | 122 |
| 30 July 89 | 0 | 0.0 | — | 50 | N.R. |
| 26 August 89 | 11 | 47.8 | 171 | 27 | 138 |
| 30 September 89 | 14 | 35.0 | 240 | 35 | 230 |
| 28 October 89 | 0 | 0.0 | — | 28 | N.R. |

* N.R., No recruitment.

October, an increase in the proportion of females was observed. The ratio of males to females in the first age group was 1:0.69 ($n = 333$), while, in the 1–2-year age group, the ratio was 1:1.17 ($n = 1170$). The overall ratio of males to females over the entire period was 1:1.04 but this was found not to be statistically significant.

Discussion

Armadillo officinalis is found throughout the year in coastal areas around Benghazi. It plays an important role in trophic dynamics by hastening the decomposition of vegetation. The breeding activity of the species coincides with the spring rains, a rise in relative humidity and temperature, and day length. Breeding occurs from April to the beginning of June and from the latter half of August to the end of September, when all the above mentioned factors are favourable. Warburg *et al.* (1984) also observed the breeding period of *A. officinalis* in Israel from April to May and during September and October. However, Shereef (1970) reported that the breeding of this species in Egypt only occurs between June and September. The effects of temperature and day length on the onset of breeding in woodlice have been reported by various workers (McQueen, 1976; McQueen & Steel, 1980; Linsenmair, 1984; Nair, 1984).

A relationship between the number of eggs or embryos in the brood pouch and the body length of gravid females has been established. This is a common phenomenon among woodlice (Snider & Shaddi, 1980; Phillipson, 1983; Nair, 1984). The mean number of eggs per brood pouch in *A. officinalis* in Benghazi was 25. This is lower than that reported by Shereef (1970) for the same species from Egypt (45–50 eggs per brood pouch) and by Warburg *et al.* (1984) from Israel (33 to 35 eggs per brood pouch). The average number of eggs per brood pouch in various woodlice depends upon the species and locality (Hatchett, 1947). This is also true of the incubation period which varied from 27 to 37 days with a mean of 32 days in the present study. This is in contrast with a mean of 26 days reported for the same species by Shereef (1970).

Some embryos fail to develop within the brood pouch, and brood mortality of this species was found to be 4.2%. Brood pouch mortality in various species of terrestrial isopods ranges from 0.8 to 10% (Warburg *et al.*, 1984).

Armadillo officinalis produces two to three broods in 1 year in the coastal belts of Benghazi. The initial broods are carried by 1-year-old animals, and subsequent broods by the 1–2-year age groups. The present observation is confirmatory with that of Warburg *et al.* (1984) who also reported two to three broods per year in the same species in Israel, whereas Shereef (1970) observed only one brood per year in Egypt. There was a positive correlation between the body lengths of the gravid females of *A. officinalis* and the total number of young that left her marsupia, as in other woodlice (Hatchett, 1947; Nair, 1984).

Moulting showed the usual terrestrial isopod pattern. The animals moulted the posterior half of the body 1–2 days before the anterior half. Eating of exuviae was not observed and the first moult took place within 24 h after the emergence from the maternal brood pouch. The second and third moults occurred 10–15 days later. The subsequent moults occurred at longer intervals. The rate of growth was faster in the initial stadia. This is important from the point of view of survival since it reduces the period of vulnerability to desiccation. The overall growth pattern observed was similar to that of *Porcellio laevis* (Nair, 1984) and of *Trichoniscus pusillus* (Standen, 1970).

Variations in population size are based on four factors: (1) addition of new recruits, (2) growth rates, (3) inactivity during the unfavourable months, and (4) death of reproductive adults after breeding.

A bimodal size distribution was observed during the post-reproductive months (October–December 1988). In spite of the severe winter, slow progress in the growth of the different size classes was evident and, by January 1989, disappearance of older age groups from the population was evident. During the early part of 1989, a unimodal size

Table 2. Distribution of sex ratio in various age groups of the population with χ^2 and p values for the period October 1988 to October 1989

| Month of sampling | Total animals | 0-1-year age group | | | | 1-2-year age group | | | | Sex ratio |
|-------------------|---------------|--------------------|--------|--------------|----------------|--------------------|--------|--------------|----------------|-----------|
| | | Male | Female | Percent male | Percent female | Male | Female | Percent male | Percent female | |
| October 88 | 65 | 3 | 5 | 12.0 | 12.5 | 22 | 35 | 88.0 | 87.5 | 1:1.59 |
| November 88 | 188 | 11 | 6 | 12.5 | 6.0 | 77 | 94 | 87.5 | 94.0 | 1:1.22 |
| December 88 | 144 | 16 | 12 | 30.8 | 13.0 | 36 | 80 | 69.2 | 87.0 | 1:2.22 |
| January 89 | 160 | 28 | 15 | 41.2 | 16.3 | 40 | 77 | 58.8 | 83.7 | 1:1.93 |
| February 89 | 202 | 14 | 11 | 16.3 | 9.5 | 72 | 105 | 83.7 | 90.5 | 1:1.46 |
| March 89 | 232 | 16 | 15 | 11.9 | 15.3 | 118 | 83 | 88.1 | 84.7 | 1:0.70 |
| April 89 | 110 | 10 | 9 | 13.7 | 24.3 | 63 | 28 | 86.3 | 75.7 | 1:0.44 |
| May 89 | 54 | 6 | 7 | 25.0 | 23.3 | 18 | 23 | 75.0 | 76.7 | 1:1.28 |
| June 89 | 68 | 18 | 19 | 54.5 | 54.3 | 15 | 16 | 45.5 | 45.7 | 1:1.07 |
| July 89 | 66 | 31 | 17 | 72.1 | 73.9 | 12 | 6 | 27.9 | 26.1 | 1:0.50 |
| August 89 | 60 | 25 | 8 | 71.4 | 32.0 | 10 | 17 | 28.6 | 68.0 | 1:1.70 |
| September 89 | 79 | 7 | 7 | 17.9 | 17.5 | 32 | 33 | 82.1 | 82.5 | 1:1.03 |
| October 89 | 75 | 12 | 5 | 33.3 | 12.8 | 24 | 34 | 66.7 | 87.2 | 1:1.42 |
| Total | 1503 | 197 | 136 | | | 539 | 631 | | | 1:1.17 |

| Month of sampling | Total animals | Total males | Total females | Per cent male | Per cent female | Sex ratio | χ^2 | <i>p</i> |
|-------------------|---------------|-------------|---------------|---------------|-----------------|-----------|----------|----------|
| October 88 | 65 | 25 | 40 | 38.5 | 61.5 | 1:1.60 | 3.46 | >0.05 |
| November 88 | 188 | 88 | 100 | 46.8 | 53.2 | 1:1.14 | 0.77 | >0.05 |
| December 88 | 144 | 52 | 92 | 36.1 | 63.9 | 1:1.77 | 11.11 | <0.01 |
| January 89 | 160 | 68 | 92 | 42.5 | 57.5 | 1:1.35 | 3.60 | >0.05 |
| February 89 | 202 | 86 | 116 | 42.6 | 57.4 | 1:1.35 | 4.46 | <0.10 |
| March 89 | 232 | 134 | 98 | 57.8 | 42.2 | 1:0.73 | 5.59 | <0.05 |
| April 89 | 110 | 73 | 37 | 66.4 | 33.6 | 1:0.51 | 11.78 | <0.10 |
| May 89 | 54 | 24 | 30 | 44.4 | 55.6 | 1:1.25 | 0.67 | >0.05 |
| June 89 | 68 | 33 | 35 | 48.5 | 51.5 | 1:1.06 | 0.06 | >0.05 |
| July 89 | 66 | 43 | 23 | 65.2 | 34.8 | 1:0.53 | 6.06 | <0.05 |
| August 89 | 60 | 35 | 25 | 58.3 | 41.7 | 1:0.71 | 1.67 | >0.05 |
| September 89 | 79 | 39 | 40 | 49.4 | 50.6 | 1:1.03 | 0.01 | >0.05 |
| October 89 | 75 | 36 | 39 | 48.0 | 52.0 | 1:1.08 | 0.12 | >0.05 |
| Total | 1503 | 736 | 767 | | | 1:1.04 | 0.64 | >0.05 |

distribution emerged. Most of the recruits of the previous year became sexually mature during the spring of 1989 with a predominance of males over females. With the onset of breeding in April, a mixed population consisting of both older and younger groups led to bimodality in size structure, with new recruits forming a major share. The bimodality in population structure during the breeding season is a common phenomenon in woodlice (Paris & Pitelka, 1962; Sunderland *et al.*, 1976; Sorensen & Burkett, 1977; Kheirallah, 1979; Nair, 1984; Williams & Franks, 1988). The spring and early summer months are periods of especially rapid growth.

Studies on the standing crop and production of embryos showed a large increase during the second phase in breeding (August–September 1989) compared with the first (April–June 1989). This was mainly due to the addition of gravid females. If breeding is disrupted by unfavourable climatic conditions, these losses are compensated by increased production of embryos in the succeeding periods (Paris & Pitelka, 1962; Nair, 1984). Males were more numerous than females in the first year age group, while there was a preponderance of females in the 1–2 year age group. With few exceptions, females usually outnumbered males in terrestrial isopods (Geiser, 1934; Howard, 1940; Hatchett, 1947; Menon *et al.*, 1969; Nair, 1978; Kheirallah, 1979; Frankel *et al.*, 1981; Williams & Franks, 1988). The increased proportion of males during the breeding months may be due to high mortality among gravid females. Except for short periods during June–July and December–January, climatic conditions in the habitat of these animals are well within their tolerance limits (Nair *et al.*, 1989).

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