The Effect of Climate on the Distribution and Abundance of Isopods

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SYNOPSIS

Climate affects both the distribution and abundance of isopods. Humidity and moisture affect their activity and distribution. Survival of juveniles is largely dependent on moisture. The reproductive pattern is affected by temperature and light. Food affects growth and thus, indirectly, also reproduction, as larger females tend to produce larger broods and more frequent broods than smaller ones. Generally in isopods there is little evidence to suggest that food is a very important factor affecting their abundance. Both semelparity and iteroparity are found in isopods and both reproductive strategies are apparently successful. Mortality factors affect the oocytes, the marsupial stages, and most of all the newly released individuals. Apart from climatic factors, predation and, to a lesser extent, parasitism are the main causes of mortality. Longevity of isopods ranges from one to five years. Occasional population explosions of isopods are known to take place, their cause being unknown.

INTRODUCTION

One of the most comprehensive reviews on isopod physiological ecology was undoubtedly Edney's (1954) paper. This presentation (which provided the main stimulus for the senior author to study this group) aimed at pointing out new avenues for promising research on the role of water in the life of isopods.

The isopods as a group are adapted to terrestrial life in ways that differ from those of other arthropods, namely arachnoids, myriapods and insects (Edney, 1968; Warburg, 1968), one main feature being the marsupial pouch that provides protection for the developing young. There can be no doubt as to their success in colonizing most terrestrial habitats in many regions of the world.

A large volume of literature has appeared since Edney's (1954) review and some of it will be discussed here, together with some earlier literature whenever relevant to the points raised. The main aim will be to examine the ways in which isopods select their habitats and form communities, and their population structure and dynamics including their reproductive patterns.

ISOPOD DISTRIBUTION

Seasonal and Diurnal Activity Patterns as Related to Environmental Factors

Isopods cope with environmental conditions in their habitat by adopting various patterns of activity in response to these conditions thus modifying their effects.

In winter, isopods in northern USA (*Trachelipus rathkei*) were found to be active at temperatures down to 1°C, but died at − 2.6°C (Cole, 1946). *Hemilepistus aphganicus* was found to survive a sudden drop to − 4°C after being kept previously at 12°C for weeks (K. E. Linsenmair, unpublished). Before soil temperatures dropped or when the soil dried out, *T. rathkei* migrated down into the soil. In summer they avoided dry soil and preferred microhabitats in which humidities were not lower than 10–15% R. H. Cole (1946) also found a close parallel between low temperatures and the isopods' tendency to aggregate. However, temperature was not the sole factor affecting aggregation and there appeared to be an inherent tendency to aggregate.

In *Hemilepistus reaumuri* activity appears to be greatly influenced by endogenous factors. When animals emerge from their burrows in February their activity to a large extent takes place between 13.00 and 14.00 h, regardless of environmental factors (weather conditions). There is no earlier activity even if conditions seem to be favourable. Later in April activity takes a bimodal pattern after sunrise and later in the afternoon.

A vertical migration in isopods was first described by Brereton (1975) and later also by Den Boer (1961). In woodland a large proportion of the *Porcellio scaber* population ascends the upper parts of deciduous trees in summer and descends to the moss layer at the base of the trunks in late autumn. This phenomenon is not known in tropical and semi-arid regions. A similar vertical migration was described for *Protracheoniscus politus* by Radu & Tomescu (1972). The horizontal activity or the lateral movement on the soil (Den Boer, 1961) takes place during the spring and autumn. The activity increased at higher humidites and in windy conditions and the result was to "regulate" water balance (Den Boer, 1961). Similarly, Paris (1963) observed in *Armadillidium vulgare* increased lateral movements during summer: 13 m in 12 h, as compared with 10 m in six days during winter. He suggested that search for shelter regulated movements in summer. The greatest distance travelled was 25 m during 25 days.

In *Hemilepistus reaumuri*, with breakup of the family in February, individuals disperse in all directions. After 4–5 days marked specimens were located at a distance of 247–458 m away from the burrow. However, out of 1447 marked individuals 38 settled within 27.5 m of the original burrow.

The nocturnal activity of isopods (*Oniscus asellus* and *Porcellio scaber*) was shown to be correlated with wind speed. Thus the number of isopods wandering on the surface decreased with increasing wind speed (Cloudsley-Thompson & Gupta, 1960). Climatic factors also affected the nocturnal emergence of *P. scaber* and *O. asellus* (Cloudsley-Thompson, 1974).

Paris (1963) described the "downward migration" of *Armadillidium vulgare* as seen in soil samples down to 25 cm. He found more isopods during winter inside the soil, and large aggregates of isopods in rodent burrows or at the base of plants (*Brassica* sp.). Similarly, "vertical distribution" of *Ligidium japonicum* down into the soil changed throughout the year, deeper in winter (November–December) and less deep in summer (May–July, see Saito, 1965). *Hemilepistus reaumuri* burrows become deeper as summer progresses (Shachak, 1980). The new burrow is dug mostly by females and reaches about 2–4 cm with pair formation. The depth of the burrow depends to a large extent on soil moisture which is kept preferably above 10 %. In Tunisia most burrows averaged 48 cm ($n = 31$) in depth. In salt pans burrows are dug to a mean depth of 33 cm. In arid habitats under extreme conditions (in Egypt, Libya and Algeria) depths of up to 98 cm and lengths of up to 250 cm are known.

The hours of the day during which *Armadillidium vulgare* was active in summer (in Arizona) indicate that most activity was after dark and before dawn. Thus, isopods were found on the ground during 04.00–10.00 h and 17.00–23.00 h with very few active during midday (Warburg, 1965a). The most extreme temperature and humidity conditions encountered in the field were 40°C and 16% R.H. for *A. vulgare* in a mesic habitat and 45°C and 15% R.H. for *Venezillo arizonicus* in a xeric habitat. In southern Tunisia *Hemilepistus reaumuri* during May–June was mostly active from about 06.30–10.30 and from 16.00–18.30 h; later in summer it became nocturnal. Thus an endogenous rhythm regulates to a large extent the activity rhythm. Tergite temperatures of *H. reaumuri* guards at the burrow opening were $35.8 \pm 1.82°C$ ($n = 8$) when shade temperature above ground was 38°C (sun temperature 45.5°C).

In another study on the vertical separation between three species, *Armadillidium vulgare, Porcellio scaber* and *Philoscia muscorum*, Davis, Hassall & Sutton (1977) have shown that three factors affected the burrowing pattern: temperature, relative humidity and the burrowing ability of the species. The highest correlation was with temperature. No correlation was found between the activity of *A. vulgare* and soil moisture (as affected by monthly rainfall; see Al-Dabbagh & Block, 1981).

There are occasions when soil moisture affects daily activity pattern. Thus in *Porcellio* sp. in the Canary island of Fuerteventura the first week after rain the isopods are active during the day. When it dries, isopods

leave their burrows mainly at night when R.H. is over 90% (K. E. Linsenmair, unpublished).

In *Hemilepistus reaumuri* the reason for the change in activity pattern during the year cannot be explained by climatic factors alone. When the offspring are very young and need to be fed by the parents the latter are largely diurnal (in May–June). In returning to its burrow from foraging excursions *Hemilepistus* is not dependent on external cues but such cues as the sun's position and the polarized light pattern facilitate its orientation considerably allowing more runs per time and greater foraging distances. (K. E. Linsenmair, unpublished; Hoffman, 1983a,b). Later in the year (September–October) they are nocturnal to a great extent.

Habitat Selection and Community Structure

The way in which isopods select their habitat shows a pattern which indicates their adaptation to terrestrial life (Edney, 1968). Early on Herold (1925) and Verhoeff (1931) noticed that some isopod species are more abundant in wetter habitats whereas others are more abundant in drier ones. They tried to "analyse" the isopods in a meaningful, ecological way. Verhoeff found that *Porcellio laevis* was more typical of warm cellars, *Porcellio dilatatus* of cooler ones, whereas *Porcellio pictus* was found in caves. Other species were more typical of calcium-rich habitats: *Armadillidium vulgare* was more abundant in a stony region, *Armadillidium zenckeri* in meadows and *Armadillidium pulchellum* in detritus. He also found that some species were more typical of hilly regions (*Trachelipus ratzeburgi*), others of flatland (*Oniscus asellus, Trachelipus rathkei*).

Miller (1938) studied eight species of isopods in the upper littoral zone in California. Thus *Actoniscus lindahli, Actoniscus tuberculatus, Alloniscus perconvexus* and *Porcellio littorina* were all found under rocks along sandy beaches, although sometimes *A. perconvexus* burrows into the sand. Both *Ligia occidentalis* and *Ligia pallasii* were found in rocky beaches or sea cliffs. Finally, *Philoscia richardsoni* and *P. littorina* were found higher up in the more grassy regions. Further away from the sea in the higher terrestrial zone the following isopods were found: *Porcellio scaber, Porcellio spinicornis* and *Porcellio laevis* as well as *Metoponorthus pruinosus** and *Armadillidium vulgare*.

Eight species of isopods were found to share garden refuse at Oxford: *Oniscus asellus, Trichoniscus pusillus, Androniscus dentiger, Philoscia muscorum, Metoponorthus pruinosus, Porcellio laevis, Porcellio scaber* and *Armadillidium vulgare* (Brereton, 1957). These showed some degree of microhabitat

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* *Metoponorthus pruinosus* is considered to be synonymous with *Porcellionides pruinosus*, the latter taking precedence. As the Israel Isopod Fauna is under review we have decided to leave the name on this and other pages as the author submitted it. — Eds.

separation. Thus, *Oniscus asellus* and *Porcellio scaber* seem to differ to some extent in refuge and/or food preferences. Whereas *P. scaber* was found in large numbers at the base of trees in winter, *O. asellus* was common only under stones during this time of the year. *T. pusillus* was common in dead wood, whereas *P. muscorum* avoided dead wood and was found in litter.

Beyer (1957/58) classified some species according to their habitats. In the forest he found *Ligidium hypnorum, Trichoniscus pusillus, Hyloniscus riparius* and *Oniscus asellus*. Also found there, but in wetter parts of the forest, were *Armadillidium pulchellum, Armadillidium vulgare* and *Porcellio conspersum*. In the dry pine forest he found no isopods, whereas *Protracheoniscus saxonicus* resided in oak woods. Finally, he classified as ruderal species *Porcellio laevis, Oniscus asellus, Porcellio scaber* and *Armadillidium vulgare;* the last two species also inhabited fields and meadows.

Later, Beyer (1964) found that isopods preferred microhabitats according to moisture condition. Thus, *Ligidium hypnorum* was found mostly in wet habitats, *Armadillidium opacum* and *Porcellio conspersum* in moist habitats, and dry habitats were inhabited by *Porcellio nasatum*.

Radu & Tomescu (1976) studied isopods that occurred in an elder wood. These species, *Ligidium hypnorum, Hyloniscus transylvanicus, Trichoniscus pusillus* and *Porcellio conspersum*, have apparently similar ecological requirements (high R.H.). Two additional species were found in the same habitat but differed in their microhabitats. Thus *Trachelipus affinis* was found under the bark of trees and *Protracheoniscus politus* around damp litter.

Davis & Sutton (1977a) found that spatial separation was associated with litter cover and the amount of loose sand. Thus *Philoscia muscorum* preferred stable dunes, whereas *Porcellio scaber* and *Armadillidium vulgare* preferred more mobile conditions of the dune crest. There was a slight difference (about 1.5 cm) in the mean depth to which they burrowed. These differences probably reflect differing burrowing ability. There was also a clear non-random distribution of individuals of the three species all of which tend to aggregate. This may indicate that the separation of the microhabitat could be associated mostly with habitat factors, possibly also food. Other evidence comes from a study by Tsukamoto (1977) on two *Ligidium* species which colonized a slope of broad-leaved deciduous forest in Japan. One species, *Ligidium paulum*, colonized only the bottom of the slope which was moist. There appears also to be some advantage in that area as individuals grew more quickly there than elsewhere.

Not only moisture conditions affect the distribution of these isopods, but also firmness of the soil and its constituents such as calcium carbonate and other salts. We know that *Hemilepistus reaumuri* can be found mostly on firm soil, *Porcellio albinus* on sandy soil. The reason for this is due to the difference in their burrowing capabilities.

TABLE I

Number of specimens of the four most abundant species found in the Mediterranean region of northern Israel

Species	Gilboa Mts.	Lower Galilee	Mt. Carmel	Upper Galilee	Total
Metoponorthus pruinosus	63	550	378	62	1053
Philoscia muscorum	83	655	68	24	830
Armadillo officinalis	1	75	31	23	130
Schizidium festai	22	53	33	—	108
Total	169	1333	510	109	2121

For details see Warburg et al. (1978).

TABLE II

The number of isopod species in the Mediterranean region of northern Israel and the diversity indices (H')

Area	Precipitation (mm)	No. of species	H'
Gilboa Mts.	500	14	1.48
Lower Galilee	650	13	1.40
Mt. Carmel	800	9	1.37
Upper Galilee	1000	5	1.29

H' (species diversity) = $- \Sigma p_i \log_e P_i$ (P_i = proportion of species in sample).
More details in Warburg et al. (1978).

In a study on mesic and xeric habitats within the Mediterranean region of northern Israel (Lower Galil) 15 species of isopods were found; of these four species were most abundant (Warburg, Rankevich & Chasanmus, 1978; see also Table I). The largest number of isopod species (14) was found in xeric grassland (Table II). The species diversity (H') (as calculated from the formula = $H' = - \Sigma p_i \log_e P_i$) was highest there and also in the oak-woodland (Table II). It is of interest to note that higher biomass values were found for isopods inhabiting grassland (Davis & Sutton, 1977b) due to Armadillidium vulgare and Philoscia muscorum being more abundant in grassland. In the study by Warburg et al. (1978) Metoponorthus sp. and Philoscia sp. were the most abundant species. Armadillo officinalis was more characteristic of the oak woodland. Philoscia sp. was a typical "winter" isopod abundant mostly during the rainy season, whereas Metoponorthus sp. was more abundant later in the season and A. officinalis during March–April.

TABLE III

Monthly rainfall (in mm) as measured in the oak-woodland in the Lower Galil

Month	1973–1974	1974–1975
September	2.2	0.0
October	15.2	0.0
November	137.0	65.1
December	40.2	243.5
January	274.3	96.5
February	52.7	138.4
March	42.8	55.8
April	53.7	9.9
May	0.2	0.0
Total	618.3	609.2

Data from the Government Meteorological Service, Bet Dagan for Allonim, (Lower Galil).

TABLE IV

Isopod community structure in the oak-woodland (Lower Galil)

Species	Total no. of specimens	Percentage of specimens in community
Philoscia muscorum[a]	1082	55.37
Metoponorthus pruinosus[a]	516	26.40
Armadillo officinalis	223	11.41
Nagurus carinatus[a]	44	2.25
Schizidium festai	41	2.09
Armadillo tuberculatus	26	1.33
Leptotrichus naupliensis[a]	10	0.51
Porcellio sp.[a]	7	0.35
Armadillo sp.[a]	3	0.15
Bathytropa wahrmani	2	0.10
Total	1954	100.00

[a]Currently under review by the Fauna Palestina Project of the Israel Academy of Sciences.

In a study of zonation of isopods near the coast of Somalia, Chelazzi & Ferrara (1978) classified 12 species of isopods according to their distribution and ecological requirements. Thus *Ligia exotica* and *Tylos africanus* inhabit the sea cliffs, whereas *Littophiloscia compar, Armadilloniscus mirabilis, Buchnerillo oceanicus* and *Alloniscus robustus* were all found in the same littoral zone. Finally, *Rhyscotus somaliensis, Tura candida* and *Periscyphis similis* were all found in the dune zone, the latter at a distance of 500 m inland, whereas *Periscyphis rubroantennatus* was found 1 km inland and

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Periscyphis ruficauda further away together with *Somaloniscus ecolinii* and *Somalonicus simoetti*.

Recently, Watanabe (1980) studied three species of isopods inhabiting the evergreen broad-leaved forest in Japan. He found 77% of *Armadillo dorsalis*, 7% of *Porcellio* sp. and 16% of *Trichoniscus* sp. Similarly, Kheirallah (1980) analysed the isopods near the Mediterranean coast of Egypt and found 32.8% *Armadillo* sp., 26.3% *Porcellio albinus*, 14.6% *Hemilepistus reaumuri*, 8% *Philoscia* sp., 9.8% *Porcellionides pruinosus* and 8.9% *Leptotrichus panzeri*.

Finally, the community structure of isopods was studied during a 16-month period in an oak-woodland area (of 1 ha or 100 × 100 m) in the Lower Galil in northern Israel. The climate there was typically Mediterranean with hot and dry summers lasting up to eight months and a short rainy winter of 600–650 mm rainfall (Table III). In this area 10 isopod species were found (Table IV). Three species were most abundant:* (1) *Philoscia* sp. (probably *muscorum*), (2) *Metoponorthus* sp. (probably *pruinosus*), and (3) *Armadillo officinalis*, arranged in order of their frequency of appearance. Thus, *Philoscia* sp. comprised 55.37% of the total population, *Metoponorthus* sp. 26.40% and *A. officinalis* 11.41%. The remaining species were less frequent. The active population of the three species was studied throughout this period (Figs 1–4).

The most abundant woodlouse (*Philoscia* sp.) was found in large numbers and comprised more than half of the total active isopod population (Table IV). It was especially abundant during winter (January–March) (Fig. 2). The next species (*Metoponorthus* sp.) had already appeared by autumn and was found during winter at somewhat lower numbers than the first species (Fig. 3). The pillbug *Armadillo officinalis* was more abundant during spring (March–April) although it was already to be found during winter (Fig. 4).

The next group of isopods, which were found less frequently, included three species, each of them comprising over 1% of the total isopod population. In this group were *Nagurus** sp. (probably *carinatus*?), *Schizidium festai* and *Armadillo tuberculatus*, the latter being a rare species appearing during a limited period of the year and usually associated with ant nests. It was, however, found here on several occasions although only for a very limited period during spring (Fig. 4).

Finally, the last group of isopod species included four species, each of them comprising less than 0.5% of the total isopod population. Three out of these four species (*Armadillo* sp., *Porcellio* sp., *Leptotrichus naupliensis**), although found here only rarely, cannot be considered rare

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*The Israel Isopod Fauna is currently under review by the Israel Academy of Sciences, Fauna Palestina project.
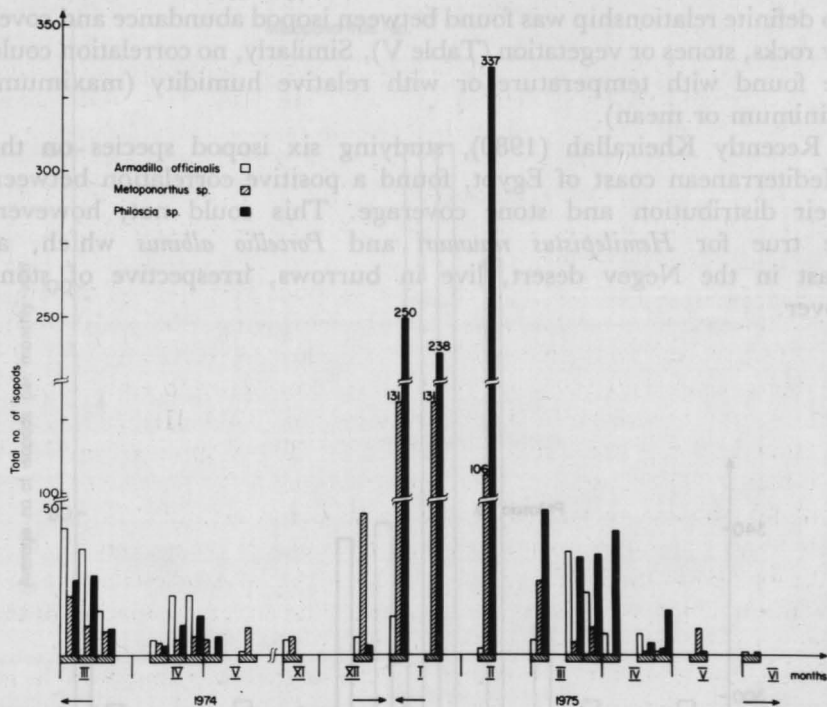
FIG. 1. Phenology of the three isopod species most abundant in the oak-woodland of northern Israel. Hatched bars under the abscissa are dates of sampling.

species in the Mediterranean oak-woodland generally. On the other hand, the last species, *Bathytropa wahrmani*, is very rare and was recorded only once.

Three additional porcellionid species were found in the surrounding area (but are not listed here). Two of these species cannot be considered rare although they were rare in the study area. One of them (*Porcellio ficulneus**) is typical of shrubland, the other, *Porcellio myrmecophilus*, is found in ant nests.

An attempt was made to analyse quantitatively the micro-climatic conditions and microhabitat components in the area in order to explain the distribution pattern of the isopod community. These results indicate a possible relationship between the precipitation patterns and isopod phenology (Table III). This correlation was noticeable as isopod numbers increased one month after the onset of precipitation. On the other hand,

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no definite relationship was found between isopod abundance and cover by rocks, stones or vegetation (Table V). Similarly, no correlation could be found with temperature or with relative humidity (maximum, minimum or mean).

Recently Kheirallah (1980), studying six isopod species on the Mediterranean coast of Egypt, found a positive correlation between their distribution and stone coverage. This could not, however, be true for *Hemilepistus reaumuri* and *Porcellio albinus* which, at least in the Negev desert, live in burrows, irrespective of stone cover.
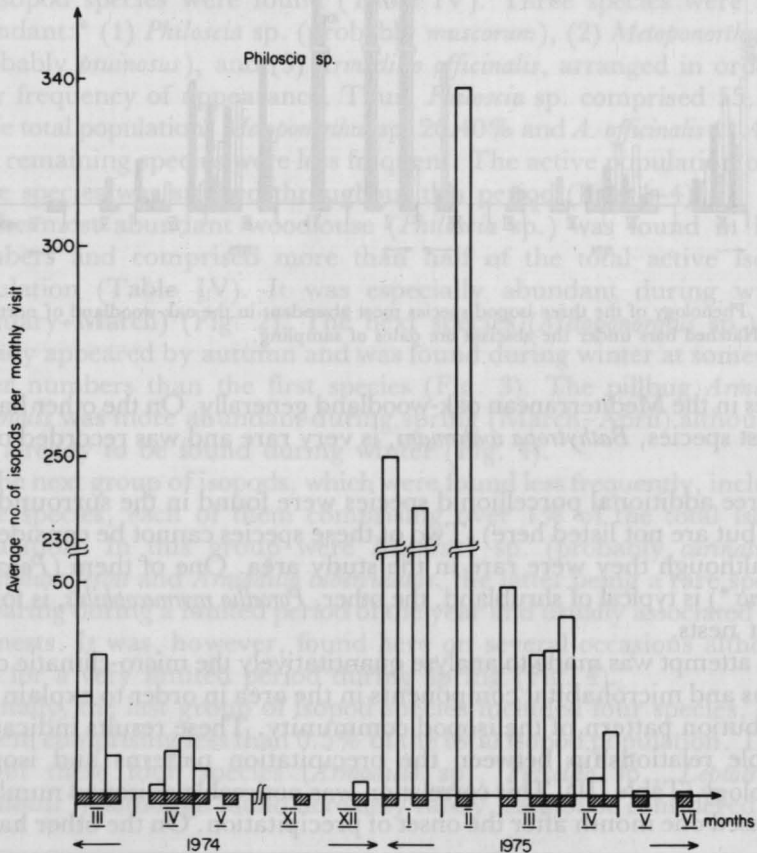

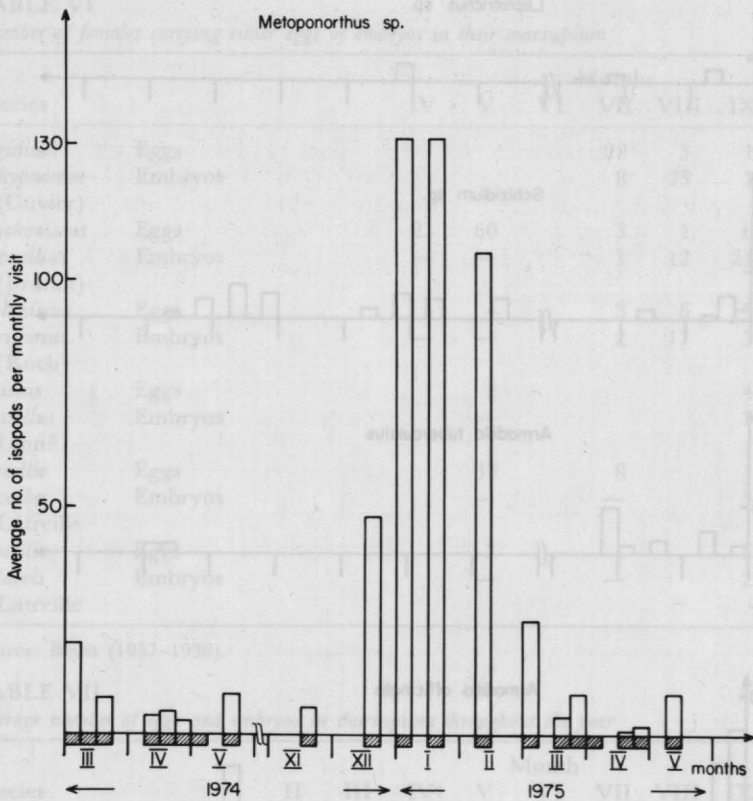FIG. 2. Phenology of *Philoscia* sp. in the oak woodland (as in Fig. 1).

FIG. 3. Phenology of *Metoponorthus* sp. in the oak woodland (as in Fig. 1).

TABLE V

Estimate of stone and plant coverage in the study area of 1 Ha

Cover by rocks (m^2)	112
No. of large stones	4
No. of medium stones	18
No. of small stones	103
Av. % cover by trees and shrubs	21%
Av. % cover by herbs	72%

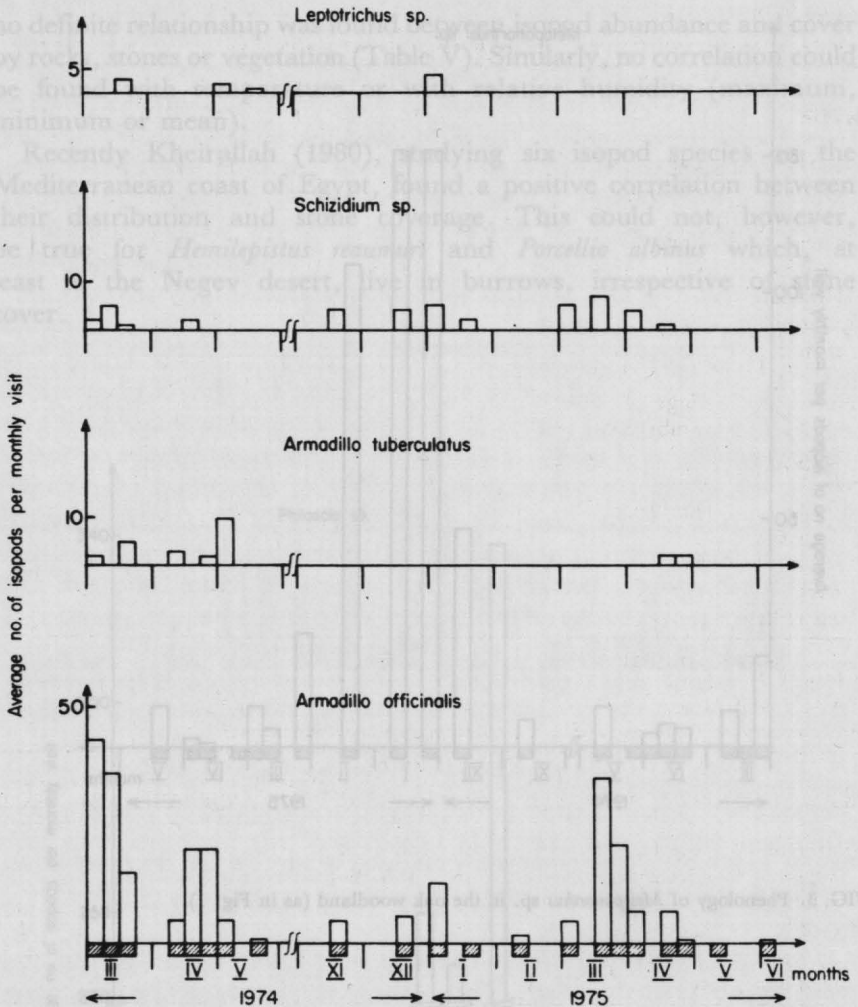More details in Warburg *et al.* (1978).

FIG. 4. Phenology of *Armadillo officinalis* and some other isopods in oak woodland (as in Fig. 1).

ISOPOD ABUNDANCE

Natality and Breeding Patterns

Number of progeny

A linear relationship between the number of eggs or embryos per brood pouch and the weight or size of the female has been established in some species (in *Oniscus asellus*, see Phillipson & Watson, 1965, and in *Trachelipus rathkei*, see Snider & Shaddy, 1980). However, the pattern

TABLE VI

Number of females carrying either eggs or embryos in their marsupium

Species		IV	V	VI	Months VII	VIII	IX	X
Ligidium	Eggs				20	3	1	
hypnorum	Embryos				8	23	1	
(Cuvier)								
Trichoniscus	Eggs	21	60		3	1	6	—
pusillus	Embryos	—	—		1	12	21	4
(Brandt)								
Hyloniscus	Eggs	4	4		3	6	3	
riparius	Embryos	—	—		2	17	3	
(Koch)								
Oniscus	Eggs		2				4	
asellus	Embryos		—				3	
Linné								
Porcellio	Eggs		63		8		1	
scaber	Embryos		—		—		5	
Latreille								
Porcellio	Eggs		3		1		6	
laevis	Embryos		—		—		2	
Latreille								

Source: Beyer (1957–1958).

TABLE VII

Average number of eggs and embryos in marsupium throughout the year

Species		II	III	IV	V	Month VI	VII	VIII	IX	X
Schizidium	Eggs	107	140	133	51					
festai	Embryos	—	—	92	—					
(Dollfus)										
Armadillo	Eggs			33	49				124	1
officinalis	Embryos				25				44	84
(Dumeril)										

Source: Present study.

of breeding throughout the year and the number of eggs per brood pouch varies considerably among the various species studied (see Tables VI, VII, VIII). Some have relatively few eggs per brood (*Ligidium hypnorum, Trichoniscus pusillus, Armadillo dorsalis, Venezillo arizonicus* and *Venezillo evergladensis*), whereas others have a relatively large number of eggs. There is a considerable difference in the number of eggs in the various populations of *Hemilepistus reaumuri* in the Negev or Tunisia. Thus the average number of eggs per 28 early-breeding females in the Negev was 103 whereas in Tunisia it was 77 ($n = 31$). There appears to be a good correlation between dry weight of female and brood size.

TABLE VIII
Breeding patterns of representative isopod species

Species	Author/ year	Family	Breeding months	No. of broods (per year)	Duration of gravidity (days)	Number of eggs in marsupium	embryos	No. of marsupial mancas	Source
Tylos punctatus	Holmes & Gay 1909	Tylidae	Summer	1	73	~100	av.13.6		Hamner, Smyth & Mulford (1969)
Ligia oceanica	(Linné 1767)	Ligiidae	I–X peak VII			17–35 (av. 27)			Vandel (1960)
Ligidium hypnorum	(Cuvier 1792)	Ligiidae	VI–IX		42	7–19			Beyer (1957–8)
L. japonicum		Ligiidae	V–X			13–61			Kato (1976)
Trichoniscus pusillus	Brandt 1833	Trichoniscidae	II–IV	2	37.5	4–7 (av. 5.5)			Heeley (1941)
Hyloniscus riparius	(C. L. Koch 1838)	Trichoniscidae	IV–V, VI, VIII–IX	3		9–32			Beyer (1957–8)
Platyarthrus hoffmanseggii	Brandt 1833	Platyarthidae	IV–VI			2–9			Vandel (1962)
Philoscia muscorum	(Scopoli 1763)	Oniscidae	IV–IX peak VII			6–54 (av. 24)			Vandel (1962)
Oniscus asellus	Linné 1758	Oniscidae	V–IX		41–45	45			Beyer (1957–8)
Cylisticus convexus	(De Geer 1778)	Cylisticidae		2–3	44–62 (av. 52)	10–70 (av. 33)	24		Hatchett (1947)
Trachelipus rathkei	(Brandt 1833)	Porcellionidae		1–3	35–42 (av. 39)		17	6–29 (av. 17)	Hatchett (1947)

Species		Family						Source
T. ratzeburgi	(Brandt 1833)	Porcellionidae			17–55 (av. 34)			Herold (1960)
Porcellio conspersum	C. L. Koch 1844	Porcellionidae	VII			9–32 (av. 19)		Herold (1960) Vandel (1962)
Metoponorthus pruinosus	(Brandt 1833)	Porcellionidae	III–X	3–6		3–35		Menon, Tandon & Jolly (1969) Menon, Tandon & Rait (1970)
Lepotrichus naupliensis	(Verhoeff 1901)	Porcellionidae		4–6	18	79		Shereef (1970)
Porcellio scaber	Latreille 1804	Porcellionidae	II–III	3	49–72 (av. 35) max. 102			Verhoeff (1917)
P. dilatatus	Brandt 1833	Porcellionidae	II–VIII		46.5	17.5		Heeley (1941)
P. laevis	Latreille 1804	Porcellionidae	III–IV	4–6	15	91	81	Mahmoud (1954) Shereef (1970)
P. monticola	Lereboullet 1853	Porcellionidae				29–81 (av. 49)		Herold (1960)
P. olivieri	Aud. et Sav. 1825–6	Porcellionidae	III–IV	1	(av. 50)	35–106	24–38	Kheirallah & Awadallah (1981) Present study
P. spinicornis	Say 1818	Porcellionidae	III–IV	1–2		18–65		McQueen & Carnio (1974)
Hemilepistus reaumuri	Aud. et Sav. 1826	Porcellionidae	IV–V	1		30–150 (av. 92)		Shachak (1980) Present study
Periscyphis granai	Arcangeli 1929	Eubelidae	I–III		22			Kheirallah (1979a)

TABLE VIII—*(cont.)*

Species	Author/year	Family	Breeding months	No. of broods (per year)	Duration of gravidity (days)	Number of eggs	embryos in marsupium	No. of marsupial mancas	Source
Eluma purpurescens	B.-L. (1879, 1885)	Armadillidiidae	VI–VII	1					Juchault, Mocquard et al. (1980)
Schizidium festai	(Dollfus 1894)	Armadillidiidae	II–V	1			60–228 (av. 124)	76–128 (av. 92)	Present study
Armadillidium vulgare	Latreille 1804	Armadillidiidae	V–VII		33	113		39–175 (av. 113)	Heeley (1941)
Armadillidium vulgare	Latreille 1804	Armadillidiidae		2–3		30–40			Warburg (1965b)
A. opacum	C. L. Koch 1844	Armadillidiidae		1					Verhoeff (1917)
Armadillo officinalis	Dumeril 1816	Armadillidae	VI–VIII	1	26	50	45		Shereef (1970)
Armadillo officinalis	Dumeril 1816	Armadillidae	IV–V, IX–X	2–3		(av. 35)	(av. 33)		Present study
Venezillo arizonicus	Mulaik & Mulaik 1945	Armadillidae	VII–VIII	1		2–4			Warburg (1965b)
V. evergladensis	Schultz 1963	Armadillidae				4–13			Johnson (1982)
Cubaris robusta	Collinge 1914	Armadillidae		1–2		9–38			Menon, Tandon & Rait (1970)

Brood pouch mortality

Some eggs fail to develop (Table IX), but this loss, or brood pouch mortality, is usually rather small, varying between 0.8% in *Philoscia muscorum* (Sutton, 1968) and 8% in *Armadillidium vulgare* (Paris & Pitelka, 1962). Correct calculation of this percentage involves both accurate and sufficient counts of both eggs and embryos in the marsupium as well as finding the exact number of young released from the brood pouch. This last figure is rather difficult to obtain as it must be taken as soon after release as possible and under normal conditions. Some of the data are given in Table IX. In spite of the variability, the figure is rather low.

TABLE IX
Brood pouch mortality

Species	Percentage mortality		Source
Tylos punctatus	1		Hamner *et al.* (1969)
Ligidium hypnorum	6–10		Krumpál (1976)
Trachelipus rathkei	5.7–6.7		Krumpál (1976)
Hyloniscus riparius	2.6–3.7		Krumpál (1976)
Porcellio laevis	3.9		Nair (1978a)
Philoscia muscorum	0.8		Sutton (1968)
Philoscia muscorum	(1st brood)	3.6	Sunderland *et al.* (1976)
Philoscia muscorum	(2nd brood)	4.6	Sunderland *et al.* (1976)

Number of broods

The number of broods per female varies in the different species studied so far (Table VIII). Likewise, the duration of the gravidity period varies among species (Meinertz, 1950). Furthermore, there are several species where only a single brood per year is known (*Tylos punctatus, Ligia dilatata, Philoscia muscorum, Hemilepistus reaumuri, Eluma purpurescens, Armadillidium opacum, Armadillo officinalis* and *Venezillo arizonicus*). In some of these species, at least, it is possible that more than one brood is produced during the female's lifetime. On the other hand, there can be no doubt that in others (like *H. reaumuri*), we are dealing with true semelparous species which are capable of reproducing only once in their lifetime. Many of the remaining species listed in Table VIII (33 altogether) are iteroparous and are capable of reproducing several times, even during the same year. These species, as well as the semelparous ones, do not show any particular pattern which can enable us to arrive at any conclusion or make any predictions as to the possible advantage of one reproductive strategy over the other.

Factors affecting breeding

Breeding patterns vary among different geographical and physiological races in *Armadillidium vulgare* (Juchault, Pavese & Mocquard, 1980). Thus, populations from lower latitudes respond more quickly to factors affecting and stimulating reproduction than those from higher latitudes and thus breed earlier. This is not surprising as we know that both the onset and duration of breeding, as well as the number of broods, at least to some extent both depend on temperature and respond to the length of the day.

Effects of temperature

In Canada, *Porcellio spinicornis* starts breeding at temperatures above 13°C (McQueen, 1976a) and can breed at between 17.5 and 27.5°C with a peak at 22.5°C. In *Porcellio dilatatus* the onset of breeding takes place when temperatures rise (McQueen, 1976a). Moreover, the duration of gravidity is temperature-dependent (in *Trachelipus rathkei*, see Snider & Shaddy, 1980). Thus at 15°C it lasts 51.4 days, at 21°C, 37.5 days and at 26.7°C only 17.6 days. Similarly, also in *Porcellio dilatatus*, duration of breeding is temperature-dependent and lasts 60 days at 15°C, but only 25 days at 25°C (McQueen, 1976b). Higher temperature shortens the period between two successive reproduction periods in *Oniscus asellus* (McQueen & Steel, 1980).

In *Hemilepistus reaumuri* at normal spring temperature (18–22°C) breeding takes place when both partner and burrow are available. Mating is not a prerequisite for egg maturation or marsupial moult, for when temperatures reach 26–28°C the parturial moult is initiated even without a partner (or burrow) and the eggs are thus unfertilized (Linsenmair, 1979, 1984). On the other hand, higher temperature had little accelerating effect on *Armadillidium vulgare* (Mocquard, Pavese & Juchault, 1980).

Effect of day length

Wieser (1963) has already shown that a long day (16 h light (L):8 h dark (D)) can stimulate breeding in *Porcellio scaber*. Similarly, in *Porcellio dilatatus* breeding depends on increased length of day. Thus, long day length (18 h L:6 h D) doubles the reproductive period in *Armadillidium vulgare* (Mocquard *et al.*, 1980). Long day length affected earlier onset of reproduction in *Oniscus asellus* (McQueen & Steel, 1980). It apparently accelerated ovarian maturation and caused a longer breeding season as well as two broods in *Eluma purpurescens* (Juchault, Mocquard, Bougrier & Besse, 1980). However, even in almost total darkness, initiation of reproduction can take place in *A. vulgare* as this isopod is apparently capable of integrating very low light intensities (Jassem,

Mocquard & Juchault, 1981). More research is needed to clarify this point which is of special interest as a mechanism important to cryptozoic animals such as isopods.

Age structure

Population structure and fluctuations during short periods of up to two to three years have been studied in only a few species (Table X). In all studies age structure was based on size distribution. The population structure of these species changes from a bimodal pattern when the young recruits are released, to a unimodal pattern when they have grown. This has already been described by Hatchett (1947) in *Cylisticus convexus* and for various other species such as *Armadillidium vulgare* (Paris & Pitelka, 1962 and Al-Dabbagh & Block, 1981), *Ligidium japonicum* (Saito, 1965), *Trichoniscus pusillus* (Sutton, 1968) and *Trachelipus rathkei* (Breymeyer & Brzozowska, 1967).

TABLE X
Isopod species in which population structure was analysed

Species	Source
Ligia dilatata	Koop & Field (1980)
Ligidium hypnorum	Stachurski (1972)
L. japonicum	Saito (1965)
	Kato (1976)
Trichoniscus pusillus	Sutton (1968, 1970a)
	Standen (1970, 1973)
Philoscia muscorum	Sutton (1968, 1970a)
	Sunderland et al. (1976)
	Davis & Sutton (1977b)
Cylisticus convexus	Hatchett (1947)
Protracheoniscus politus	Radu & Tomescu (1972)
Trachelipus rathkei	Breymeyer & Brzozowska (1967)
Porcellio laevis	Nair (1978a,b,c)
P. scaber	Davis & Sutton (1977b)
P. olivieri	Kheirallah & El Sharkawy (1981)
P. spinicornis	McQueen & Carnio (1974)
	McQueen (1976a,b)
Hemilepistus reaumuri	Shachak (1980)
Periscyphis granai	Kheirallah (1979b)
Armadillidium vulgare	Paris & Pitelka (1962)
Armadillidium vulgare	Al-Dabbagh & Block (1981)
Armadillidium vulgare	Davis & Sutton (1977b)

The main peak in size is reached when the young recruits that make up the cohort of that same year are released. Juveniles of the year dominate and form the bulk of the population. The older generation generally comprises only up to 10% of the total population. Thus, in *Periscyphis granai* only about 4% survived beyond the first year, but not a second year. In *Armadillidium vulgare* very few survived the third year. The difference is largely due to the difference in maturation pattern. Thus, *Philoscia muscorum* breeds in its first year and *A. vulgare* only in its second year (Davis & Sutton, 1977b). The population of the latter is apparently replaced every four to five years (Paris & Pitelka, 1962). Differences in longevity are found between the sexes especially when their growth pattern differs. Thus in *Porcellio spinicornis* males live only one year, whereas females may survive two years (McQueen, 1976a). Similarly in *Philoscia muscorum* different patterns were observed in the population of males and females (Sunderland, Hassall & Sutton, 1976).

Density

The absolute density of isopods is difficult to establish, owing to their vertical movements into the soil, as many are soil-dwelling species. Thus, in Arizona a total of 954 specimens of *Armadillidium vulgare* was counted under cover of 75 stones and logs in an area of 20 m^2 or 47.7 isopods per m^2 (Warburg, 1960). An average of 538 isopods per m^2 were counted in California for the same species by Paris & Pitelka (1962).

However, Al-Dabbagh & Block (1981) counted 200–1000 isopods of the same species per m^2 in England. These are highly variable figures obtained for the same species which was the most abundant species of isopod in all three localities.

In another isopod, *Trachelipus rathkei*, between five and 50 specimens were counted per m^2 over a period of three years (Breymeyer & Brzozowska, 1967). Rather high densities were recorded by Sutton (1968) in *Trichoniscus pusillus* with 1500–2150 isopods per m^2, while *Philoscia muscorum* densities were much lower, 115–265 isopods per m^2. Finally, Shachak (1980) reported for *Hemilepistus reaumuri* only 0.14–1.2 isopods per m^2. This figure is much too low if it takes into consideration areas favoured by the isopods. In such places 6–12 burrows per m^2 are not uncommon, and if we assume each burrow contains about 50 individuals per family on average, then 300–600 individuals per m^2 is a good estimate. In highly populated areas the figure can easily be two to three times more.

Longevity and Mortality

The life span of only relatively few isopod species (about a dozen) is known (see Table XI). This ranges between one and five years. Among the causes of mortality we can list difficulties in moulting (in *Porcellio scaber*, see Bakker, 1956), cannibalism of different ontogenetic stages (Heeley, 1941; Brereton, 1957; Menon, Tandon & Jolly, 1969; Linsenmair, 1972), predation (see reviews by Sutton, 1970b and Sunderland & Sutton, 1980) and, probably most important of all, climatic factors. These include relative humidity (McQueen & Carnio, 1974), drought, which affects mostly the juveniles (Al-Dabbagh & Block, 1981), and floods (Kheirallah, 1979a).

In certain regions in southern Tunisia which for two years had no rain, a dense population of *Hemilepistus reaumuri* mostly disappeared. Soil moisture content did not reach 10% (K. E. Linsenmair, unpublished). When heavy rains fell late in the season (in May–June) many of the juveniles died in their burrows, being covered in mud and unable to free themselves. Adults can survive even 36 h under water in flooded burrows.

Food and parasites and other diseases appear to be of somewhat less significance as regulating factors.

The main mortality occurs within the first month following the release of young from the brood pouch. Only 10% of *Porcellio scaber* survived over one month (Brereton, 1957). In *Porcellio spinicornis* about 60% survived the first 50 days and 50% survived three months (McQueen & Carnio, 1974). Similarly, in *Trichoniscus pusillus* and in *Philoscia muscorum*

TABLE XI
Longevity of oniscid isopods

Species	Life-span (years)	Source
Ligia pallasii	1.5–2	Carefoot (1973b)
L. dilatata	2	Koop & Field (1980)
Trichoniscus pusillus	2	Sutton (1968)
Platyarthrus hoffmanseggii	5	Collinge (1945)
Philoscia muscorum	2	Sutton (1968, 1970a)
Oniscus asellus	4.25	Collinge (1945)
Cylisticus convexus	3	Hatchett (1947)
Protracheoniscus politus	2.5	Radu & Tomescu (1972)
Porcellio laevis	1–1.5	Nair (1976)
P. spinicornis	1.5	McQueen & Carnio (1974)
Hemilepistus reaumuri	1.3	Shachak (1980)
Armadillidium vulgare	3–4	Paris & Pitelka (1962)
A. vulgare	3.5	Al-Dabbagh & Block (1981)

20% and 35% respectively survived the first three months (Sutton, 1968, 1970a).

Predation

Many animals feed on isopods, mostly on non-conglobating forms, the main predators being arthropods (centipedes, spiders and scorpions and beetles), but also lower vertebrates (amphibians and reptiles) and insectivorous mammals (shrews). The subject has been reviewed by Sutton (1970a) and Sunderland & Sutton (1980).

Myriapod predators

Cole (1946) could not find evidence that in the field centipedes prey upon isopods. However, Saito (1965), Sutton (1970a) and later Sunderland & Sutton (1980) established that *Lithobius* can account for 42% of total isopods killed. Recently we found direct evidence that a scolopendrid centipede preyed upon *Hemilepistus reaumuri* in the Negev.

Arachnid predators

Both lycosid and dysderid spiders are important predators (Sutton, 1970a). Isopods (*Porcellio scaber*) comprise 84% of the diet of the spider *Steatoda* (Barmeyer, 1975). Similarly, opilionids (Sunderland & Sutton, 1980) and scorpions (Kheirallah, 1979a; Shachak, 1980) feed on isopods. There seems to be a close association between *Scorpio maurus palmatus* and *Hemilepistus reaumuri* in the Negev, where the former is the major predator of the latter. However, in Tunisia *Scorpio maurus tunetanus* does not feed to the same extent on *Hemilepistus reaumuri*. In the oak-woodland of northern Israel *Scorpio maurus fuscus* preys upon *Armadillo officinalis*.

Insect predators

Carabid beetles (Cole, 1946) and staphylinids (Sutton, 1970a; Sunderland & Sutton, 1980) feed upon isopods in the field. Thus in the Canary island of Fuerteventura, the carabid *Scarites sp.* digs out the burrows of a *Porcellio* sp. to feed upon them (K. E. Linsenmair, unpublished). Ants (Cole, 1946; Saito, 1965) and the cricket *Stenopalmatus* (Paris & Sikora, 1967) also feed on isopods.

Vertebrate predators

These include mostly urodele amphibians (Miller, 1938; Paris, 1963) and frogs (Stachurski & Zimka, 1968) as well as lizards (Paris, 1963; Kheirallah, 1979a). Finally shrews have been shown to prey on isopods (Brereton, 1957; Sutton, 1970b).

Climatic Factors Affecting Isopod Populations

Terrestrial isopods in general are cryptozoic animals and thus inhabit cool and humid microhabitats. Attempts have been made to measure the microclimate within these habitats (Warburg, 1965b). Many species burrow inside the soil (vertical movements) thereby escaping the summer heat especially in the desert (*Hemilepistus* spp. Schneider, 1971; Linsenmair, 1975; Shachak, 1980). Although *Hemilepistus* is diurnal in spring, it rarely suffers from dehydration during that season. Drought can affect it during summer and autumn. Animals may drown when the floods rush down from the hills in winter. This was observed in the Negev desert as well as in the northern Sahara.

A similar phenomenon was described in *Armadillidium vulgare* (Paris, 1963) and *Periscyphis granai* (Kheirallah, 1979a). Drought, on the other hand, affected *A. vulgare* during autumn (Paris, 1963) and both *Philoscia muscorum* and *Trichoniscus pusillus* in summer (Sutton, 1968).

Population Fluctuations

The fluctuations in numbers within the year are largely due to the young recruits. A major increase in numbers due to their release from the marsupium is followed by a drop in numbers resulting from their high mortality. From the time this drop occurs until the new recruits appear, the first and second year generations are more stable. As the life span of isopods is generally short, varying between one and five years (Table XI), the first and second year generations comprise the bulk of the population. In some species, the fluctuations in population numbers between years are rather small (in *Philoscia muscorum*, see Sunderland et al., 1976; in *Porcellio scaber*, see Davis & Sutton, 1977b; and in *Periscyphis granai*, see Kheirallah, 1979b). In other species the numbers fluctuate greatly. This was observed in *Armadillidium vulgare* (Davis & Sutton, 1977b; Al-Dabbagh & Block, 1981) and in *Armadillo officinalis, Metoponorthus* sp. and *Philoscia* sp. (Fig. 1). In the latter these fluctuations could be related to seasonal rainfall patterns. A similar correlation was described for the oscillations in *Trachelipus rathkei* (Breymeyer & Brzozowska, 1967).

Population Explosion, Dispersal and Migration

On rare occasions a large number of isopods have been observed moving from one area to another. This phenomenon, although observed by some authors, has never really been studied and thus cannot be related to the population density factors nor to the climatic ones. On one occasion in March 1969, very large numbers of *Hemilepistus reaumuri* were seen by

FIG. 5. Swarms of *Porcellio* sp. on Mt. Canaan (Galilee, Israel) in September, 1982.

the senior author, on the main highway from Beer Sheva to Eilat in the Negev. They crossed the road from east to west on a front of about 1 km, in a rather directional movement not far from Avdat, and were later seen in large numbers on some chalk cliffs 2–3 km away. An earlier observation was made by Dr John Munro (personal communication by letter to the senior author) in Warren, NSW, Australia, in the morning of April 21, 1963, when he described a "large procession of isopods in the order of 10^4–10^5 which was not seen to move in any preferred direction". These were later identified as *Buddelundia* sp. The climate on both occasions was seasonal and no outstanding environmental factor could be attributed to that phenomenon. In recent years the present authors observed a similar phenomenon in the Galil when large numbers of *Porcellio* sp. (possibly *Porcellio obsoletus*) were observed flooding large areas near the town of Safed on Mt. Canaan (Fig. 5) and also swarming into the nearby Kibbutz (Amiad) from the west towards the east. Study of the phenomenon has started this year, and although it is still only in the initial stages, the following remarks can be made: the isopods studied during the swarming appear to be mostly juveniles, with males comprising only a fifth of the population. The behaviour of these isopods was abnormal in the sense that they were active during all hours of day and night, whereas normally they were largely nocturnal and not active in light. This behaviour is consistent with one of the criteria of migration, namely movement as a priority activity (see Southwood, 1962) which must have some adaptive value.

We do not as yet know whether it is suicidal in the sense that it will eventually result in a substantial decline in population numbers, nor do we know the causes either of the initiation of the outburst and releasing of this migratory behaviour, or of their cessation.

DISCUSSION AND CONCLUSIONS

In their activity patterns isopods show a strong relationship to climatic factors. Thus, they respond to temperature and humidity of the air and moisture conditions in the soil. Most behavioural studies were carried out under laboratory conditions (Warburg, 1968) and thus need to be supplemented by field studies. Micro-habitats are selected as refuges by isopods according to the animals' moisture preferences and, to some extent, also the concentration of salts (sodium chloride and calcium carbonate) in the soil.

There is no good explanation for the abundance of isopods in certain habitats. Food is also apparently of only limited importance as a factor in selecting a suitable habitat. Moreover, the large variability and abundance of food that is palatable and suitable to isopods, and the wide spectrum of preference shown by them for particular food does not indicate that under normal conditions food could be the factor limiting their abundance. Apparently feeding on different food items is not reflected in their energy balance (Carefoot, 1973a, in *Ligia*). The isopods on the whole, although generally short-lived (one to five years), show a clear tendency for iteroparity. True semelparous species are rare, in our opinion, but this point needs further research. Furthermore, the total number of broods and the size of batches produced by iteroparous species need to be known and compared with the batch size of the single brood of the semelparous species. Brood pouch mortality data are not satisfactorily known as the true number of young released in nature is mostly unknown. Mortality due to predation is probably of less significance than mortality due to climatic factors, but there are no accurate figures on either. The oscillations in population numbers are probably related mostly to climatic conditions air humidity and rain, as well as soil moisture conditions (in xeric species), and temperature (in the mesic species). However, no satisfactory explanation is known for the periodic outburst of isopods.

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