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JANUARY 1970

**STUDIES ON THE POPULATION
DYNAMICS AND PHYSIOLOGICAL
ECOLOGY OF FOUR SPECIES
OF FRESH-WATER ISOPODS**

BY ARTHUR J. SEIDENBERG

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STUDIES ON THE POPULATION DYNAMICS AND PHYSIOLOGICAL
ECOLOGY OF FOUR SPECIES OF FRESH-WATER ISOPODS

BY ARTHUR J. SEIDENBERG

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ABSTRACT

STUDIES ON THE POPULATION DYNAMICS AND PHYSIOLOGICAL ECOLOGY OF FOUR SPECIES OF FRESH-WATER ISOPODS

The comparative biology of four species of fresh-water isopods has been investigated. Isopods are known to be part of the "pollution fauna" that can inhabit badly polluted areas. The species studied inhabit a temporary pond, a drainage ditch, a small permanent stream, and the subterranean water, all relatively undisturbed areas. Their tolerance to high temperature and survival out of water, growth rates, and duration of embryonic development have been investigated and differences among the species have been suggested to be adaptive for the particular population under study. The general population biology of these species was studied including their life cycles and general ecology. The "basic biology" reported for these organisms will allow investigators to assess more clearly the effects of man-made disturbances on these aquatic organisms.

One of the species studied was found to be an intermediate host of a worm that is a fish parasite. The host-parasite relationships between the worm and the isopod were also investigated. Fish acquire the parasite after eating the isopod. The isopod population was found to be very heavily infected (up to 65%) with these worm larvae. The larvae cause the isopods to lose weight and produce a mortality in heavily infected isopods. This means a drastic reduction in the amount of isopod food available to fish.

KEYWORDS--isopod/parasite/Asellus/Lirceus/Acanthocephalus/ thermal tolerance/
pollution fauna/ population dynamics/host-parasite relationships/fish parasites

TABLE OF CONTENTS

	Page
GENERAL INTRODUCTION.....	1
PART ONE: THE ECOLOGY OF THE ACANTHOCEPHALAN, <u>ACANTHOCEPHALUS DIRUS (VAN CLEAVE,</u> <u>1931), IN THE INTERMEDIATE HOST, ASELLUS</u> <u>INTERMEDIUS FORBES (CRUSTACEA: ISOPODA.....</u>	3
I. INTRODUCTION.....	3
II. MATERIALS AND METHODS.....	5
III. RESULTS.....	9
IV. DISCUSSION.....	23
PART TWO: THE BIOLOGY OF FOUR SPECIES OF FRESH- WATER ISOPODS IN EAST-CENTRAL ILLINOIS.....	32
I. INTRODUCTION.....	32
II. MATERIALS AND METHODS.....	33
III. RESULTS AND DISCUSSION.....	35
SUMMARY.....	60
LITERATURE CITED.....	63

GENERAL INTRODUCTION

In order to understand how aquatic organisms might react to pollution (thermal, industrial, or organic), we must first know and understand how they live and function in the absence of such pollution. In short, some "basic" information must be obtained concerning the biology of aquatic organisms in undisturbed habitats before we can really assess the effects of man-made disturbances. "Before" and "after" studies are difficult to conduct because an investigator can not always anticipate a disturbance of a particular pond, lake, or stream. What is sorely lacking in the scientific literature is some very fundamental information about many groups of aquatic organisms, especially concerning life cycles, tolerances to environmental factors, and relationship to their habitats and the aquatic community in general. The study summarized here was intended to answer many of these general questions with regard to one group of organisms in particular, the fresh-water isopods.

The isopod family Asellidae includes fresh-water members that are worldwide in distribution (Birstein, 1964). Two of the five genera of this family occur in this country; one of these, Lirceus, is endemic to North America. Mackin (1959) indicated that there are about 13 species of Lirceus and 25 species of Asellus that occur in the United States. Since that time numerous subterranean species of Asellus have been described so that our known asellid fauna now totals approximately 50 species. Isopods of the genus Asellus have been shown to be part of an abundant "pollution fauna" which inhabit badly polluted areas (Hynes, 1963). In spite of the relatively large size of these organisms, and, at times, their great abundance (Allee, 1929), little is known about the biology and ecology of the American fauna. Four species were found within a radius of 50 miles of Champaign-Urbana, Illinois. Two of these species are new to science.

One is described in a forthcoming revision of the genus Aseillus by W. D. Williams; the other is being described in a manuscript by the author and Dr. Harrison R. Steeves, III.

During the course of the study, it was discovered that one of the species, A. intermedius, was serving as an intermediate host for a parasitic worm, Acanthocephalus dirus. Part One of this manuscript deals with the life cycle of this worm, a fish parasite, in relation to its intermediate host. Part Two is concerned with the comparative biology of the four isopod species.

PART ONE: THE ECOLOGY OF THE ACANTHOCEPHALAN,
ACANTHOCEPHALUS DIRUS (VAN CLEAVE, 1931), IN THE INTERMEDIATE
HOST, ASELLUS INTERMEDIUS FORBES (CRUSTACEA: ISOPODA)

I. INTRODUCTION

The present study was undertaken to determine the host-parasite relationships between the isopod, Asellus intermedius Forbes, and the acanthocephalan, Acanthocephalus dirus (Van Cleave, 1931). Fresh-water isopods of the genus Asellus have long been known as intermediate hosts of various species of Acanthocephala (Leuckart, 1876).

Acanthocephalus dirus was originally reported by Van Cleave (1931) from the freshwater drum, Aplodinotus grunniens, in the Yazoo River in Mississippi. The freshwater drum was also found to be infected with A. dirus in Reelfoot Lake, Tennessee (Bangham and Venard, 1942). A subsequent report by Van Cleave and Townsend (1936) indicated its presence in the bluegill, Lepomis macrochirus, and the channel catfish, Ictalurus punctatus, in the Ohio River and one of its tributaries in southern Illinois and from fish in the Illinois River and its tributaries near Havana, Illinois. The area of this study is, in fact, a small tributary whose waters enter the Illinois River just south of Havana. Adults of this acanthocephalan were recovered from the bluntnose minnow, Pimephales notatus, and a chub, Hybopsis sp.

There are relatively few comprehensive studies that deal extensively with the relationships of helminth parasites and their crustacean intermediate hosts (Aldrich, 1965; Stark, 1965). The ecology of the Acanthocephala is best known from studies performed in England (Awachie, 1965; Crompton and Harrison, 1965; Walkey, 1967). Aside from studies of development in the invertebrate host and

scattered observations of seasonal variation and incidence of infection, little is known about the general biology and host-parasite relationships of the American acanthocephalan fauna.

II. MATERIALS AND METHODS

Population Sampling

The population of isopods studied was that of a creek, Mud Creek (T22N, R2E, Sect. 31), in McLean County, Illinois. This creek is approximately three miles long. It flows through pasture and cornfields before its confluence with Kickapoo Creek, which eventually flows into the Illinois River.

Sampling stations were set up at Mile 1 and Mile 2, numbered from the source of the stream. The population was qualitatively surveyed from 31 January 1967 to 29 August 1968. The sampling procedure consisted of scooping the rooted aquatic vegetation and the vegetation overhanging the banks with a flour strainer (4.33 mesh per cm). The material thus collected was brought back to the laboratory and isopods were sorted out from the vegetation and debris within 24 hours and preserved in 10% ethyl alcohol.

Isopods less than 4.0 mm long were considered to be juveniles. All isopods over 4.00 mm long were sexed and measured to the nearest tenth of a millimeter with a binocular microscope fitted with an ocular micrometer. The length of the isopod was considered to be the distance from the anterior margin of the cephalothorax to the posterior margin of the telson. Each isopod was then examined for the presence of acanthocephalan larvae in the body cavity. An animal was considered to be parasitized if it contained one or more elongated acanthellae or cystacanths.

Four times during the study a special collection was made. The isopods were sexed and measured, the number of worm larvae were counted, and the isopod and its larvae were dried at 65°C for 48 hours and then weighed on an analytical balance. From these data, least squares regression lines were calculated for the relationship of the number of parasites per host vs. the length of the host,

the incidence of infection vs. the length of the host, and the log weight of the host vs. the log length of the host. These lines were statistically compared by analysis of covariance (Snedecor, 1956, p. 394). Whenever there was no significant difference between slopes, the elevations were compared. The 5% level of significance was used in this and all other statistical tests performed. Unless otherwise specified, Steel and Torrie (1960) was referred to for statistical procedures.

Metabolic Rate Experiments

Oxygen consumption measurements were determined in a Gilson GR-14 differential respirometer (Gilson, 1963) at $15.0 \pm 0.1^\circ\text{C}$ in the light on naturally infected and uninfected control isopods. Prior to oxygen consumption determinations, the test animals were held for a minimum of two weeks at a temperature of $15.0 \pm 1.0^\circ\text{C}$ on a 12-hour photoperiod. During this acclimation period, they were given fresh food (elm leaves) every two days and exposed to gentle constant aeration.

The 15 ml reaction vessel contained 5 ml of dechlorinated water filtered through 3μ Millipore filter. The center well held a piece of filter paper and 0.2 ml of 10% KOH solution. A single isopod was introduced into each flask. Two control flasks containing only filtered water were set up for each run. Corrections were made for differences between control and experimental flasks. Flasks were placed in the temperature bath and allowed to equilibrate for 15 minutes before readings were taken. The flasks were continuously shaken at 110 oscillations per minute. After the equilibration period, readings were taken at 30 minute intervals for two hours. Only the final value of the amount of oxygen consumed at the end of the two hours was used in calculating the metabolic rate.

At the conclusion of the experiment, the animals were sacrificed, examined for the presence of worm larvae, and dried at 65°C for 48 hours. The isopods were then weighed to the nearest 0.01 mg. Metabolic rate was expressed as microliters of O₂ consumed per milligram dry weight per hour. Regression lines of the log oxygen consumption vs. the log body weight were calculated by the least squares method.

Temperature Tolerance Experiments

Temperature tolerance experiments were conducted at 35.0° ± 0.1°C on naturally infected (N=24) and uninfected (N=25) male isopods acclimated to 25.0° ± 1.0°C for at least two weeks. A rectangular plastic test container (17.1 x 12.1 x 6.0 cm) rested in the temperature bath and its contents aerated throughout the test. Isopods (10-16) were introduced into the test container and observations were made at 10-20 minute intervals. The experiment was replicated four times. Inability to respond to tactile stimulation was the criterion of death. Isopods judged to be dead were removed to water at room temperature to see if they would recover. The time of death was calculated as the mid-point between the observation at which death was noted and the observation immediately preceding. These times to death were plotted on logarithmic-probability paper. Lines were fitted by eye to the points. The LT₅₀ values (time to death for 50 per cent of the animals) were calculated according to the method of Reed and Muench (1938) and compared statistically (Woolf, 1968, p. 295).

Survival Out of Water

A test container, similar to the one described by White and Zar (1968), consisted of a plastic pint ice cream container with a tight-fitting lid. A plexiglas ring (8.8 cm in diameter) with nylon cloth (7.1 mesh per cm) cemented to the bottom was used to hold the animals above the test solution.

One hundred milliliters of distilled water was introduced into the container to maintain a relative humidity (R.H.) of 100%. For experiments at 95% R.H., an appropriate glycerol-water solution was prepared, as described by White and Zar (1968).

The container was kept closed for at least 24 hours prior to the introduction of the test animals so that the atmosphere in the container would attain the desired R.H. Animals used in the experiments were kept at the test temperature for approximately 48 hours after collection.

The isopods (8.4 - 11.2 mm in length) were blotted dry on paper toweling for about 15 seconds before introduction into the test container, and three to five isopods were placed in each container. Control animals, which had been treated in the same manner as the experimental isopods, were introduced into water in closed containers. The number of isopods utilized in these experiments was: 95% R.H.--42 parasitized, 33 non-parasitized; 100% R.H.--58 parasitized, 51 non-parasitized.

The experiments were performed in the dark at a temperature of $15.0^{\circ} \pm 1.0^{\circ}\text{C}$. The containers were opened at 2-3 hour intervals (95% R.H. experiment) and 12 hour intervals (100% R.H. experiment) for about 15 seconds to observe the progress of mortality. An isopod was considered dead if it failed to respond to tactile stimulation. Isopods judged to be dead were removed and placed in a container of water to see if they would recover. The time of death was determined as in the previous experiment and was plotted on logarithmic-probability paper. Lines were fitted by eye to the points. The LT_{50} values were calculated and compared as described above.

III. RESULTS

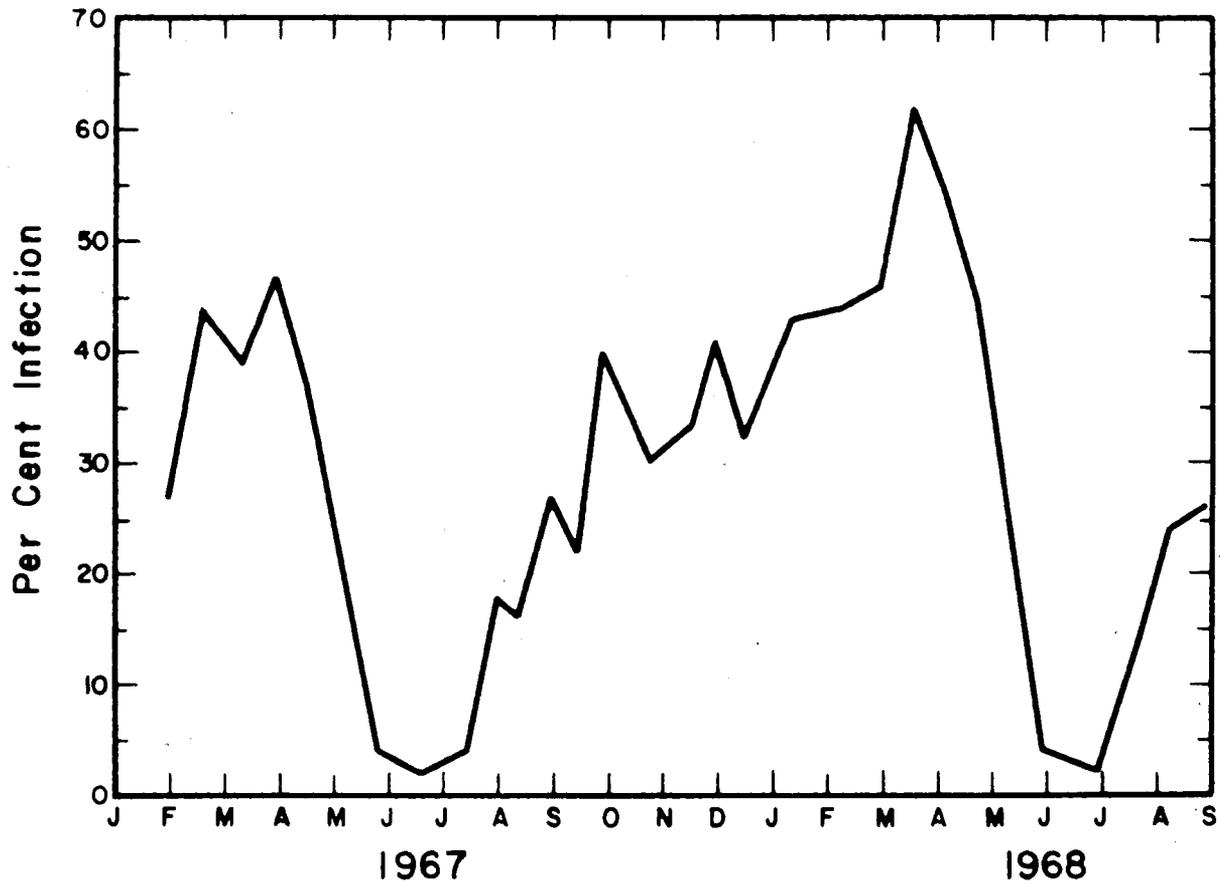
The Life Cycle in the Host and the Incidence of Infection in the Population

The isopod population begins to acquire the worm larvae in the summer (Fig. 1). By the end of July, in both 1967 and 1968, infection of young isopods was apparent both by the increased incidence of infection in the population and by the presence of infected isopods less than 6 mm long. The incidence of infection in the population rapidly increases through the fall and winter months, reaching its highest values in the early spring months of March and April.

Examination of isopods in winter and spring indicates that in October and December, 1967, 21% and 26%, respectively, of the larvae present in the sample were acanthellae. However, by March and April, 1968, only 3% and 5%, respectively, of the larvae were still acanthellae.

The incidence of infection in the population declined abruptly between April and May of both years, although a large percentage of the isopods over 8 mm long were infected. At this time, a new generation of isopods is recruited into the population. When the new generation first became infected in July, the incidence of infection was higher at the downstream collection station (Mile 2) and remained higher there for most of the year.

Fig. 1. Seasonal variation in the incidence of infection of isopods with ancanthocephalan larvae.



Host Susceptibility

Between 23 May 1967 and 1 July 1968, 5340 isopods were examined for the presence of acanthocephalan larvae. Of the 2766 males examined, 26.1% were infected. The total number of females examined were 2574. Of these, 27.0% were carrying larvae. There is no statistical difference between the sexes in susceptibility to parasite infection (2 X 2 chi-square contingency test).

The percentage of infected hosts is nearly the same in male and female isopods up to approximately 8 mm in length (Fig. 2). However, for isopods greater than 8 mm, the relationship between infection and size (age) differs considerably between the two sexes. The data for male isopods are best described by a quadratic regression. Here there is an increased incidence of infection with an increase in host size up to about 10 mm. For any size between 10 and 16 mm in length, approximately 40% of the male isopods are infected. The relationship between incidence of infection and host size is linear for female isopods. The larger a female is, the more likely it is that it will be infected.

Parasite Burden

The mean parasite burden (number of worms per isopod host), for both males and females, is significantly larger (Duncan's Multiple Range Test) in October than in the other three months in which the isopods were sampled (Table 1). On any given date, female isopods carried more worm larvae than male isopods, although none of the differences are statistically significant (Student's t-test).

With an increase in size of the isopod host, there is an increase in the number of acanthocephalan larvae present (Fig.3).

Fig. 2. Relationship between the incidence of infection with acanthocephalan larvae and the size of male and female isopod hosts. The regression equations \pm standard error of estimate are:

Males: $Y = -24.486 + 10.502X - 0.411X^2 \pm 2.655$

Females: $Y = -32.684 + 9.073X \pm 4.053$

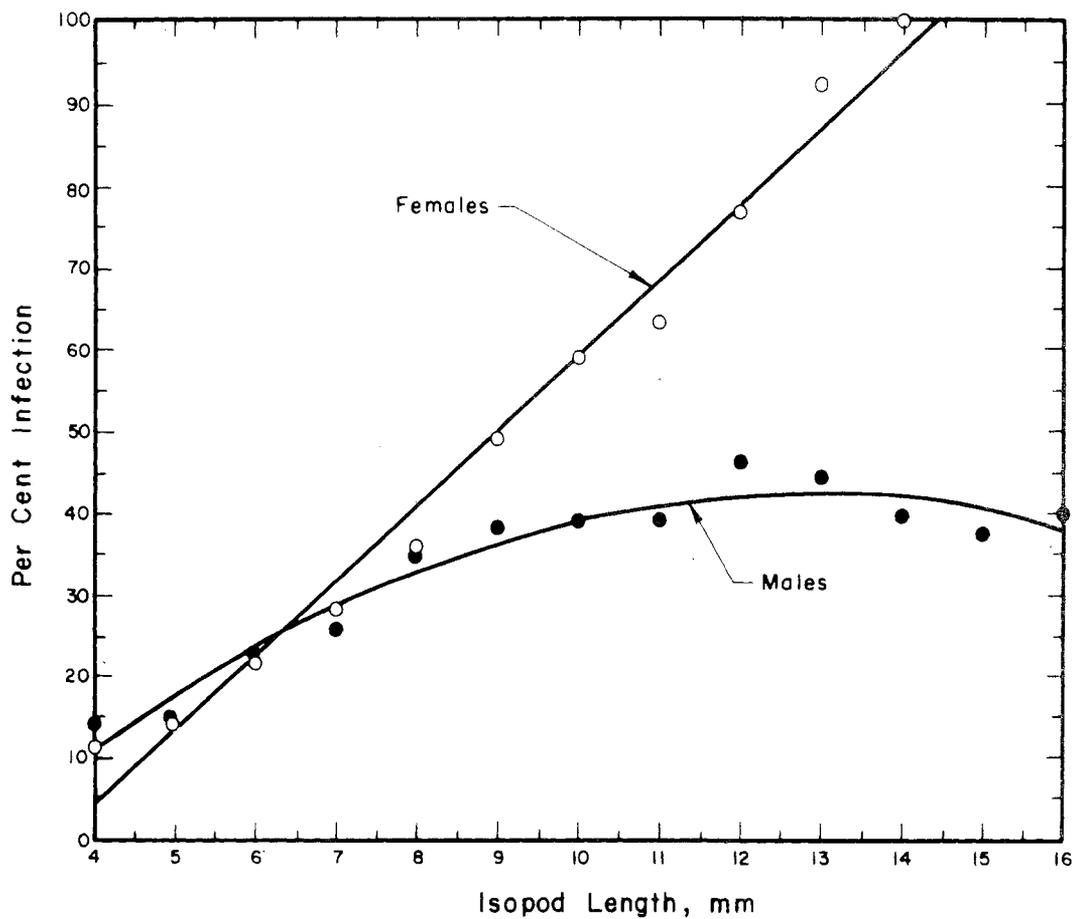


Table 1. Seasonal variation in parasite burden of male and female isopods.

Date of Collection	Number of infected isopods examined	Number of worms found	Worms per Isopod		
			Range	Mode	Mean
<u>Male Isopods</u>					
13 October 1967	61	287	1-23	4	4.70
15 December	44	121	1-8	1	2.75
19 March 1968	34	68	1-5	1	2.00
25 April	25	499	1-6	1	1.96
<u>Female Isopods</u>					
13 October 1967	53	322	1-31	5	6.08
15 December	44	130	1-7*	1	2.95
19 March 1968	33	79	1-7	1	2.39
25 April	21	45	1-6	1	2.14

*with the exception of one individual with 21 larvae

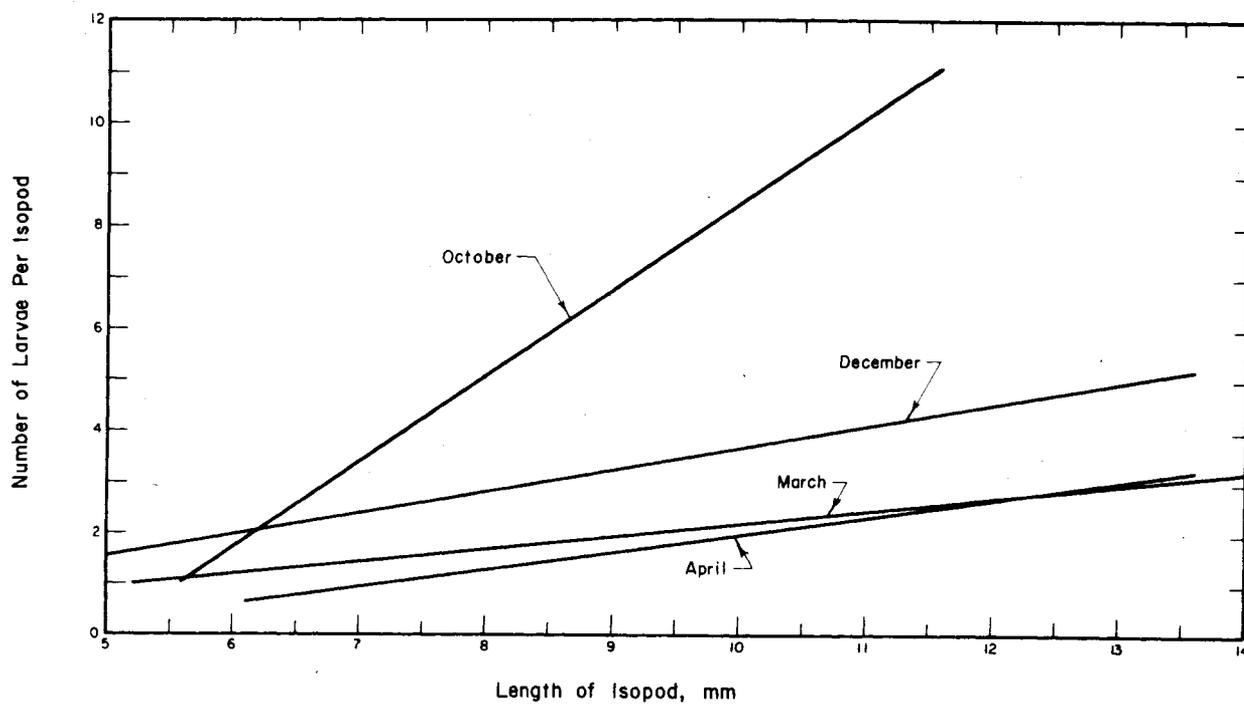
Fig 3. Relationship between size of the isopod host and the intensity of infection with acanthocephalan larvae. The regression equations \pm standard error of estimate and N, the number of points on which the equation is based, are:

October: $Y = -8.441 + 1.694X \pm 4.090$ (N = 114)

December: $Y = -0.557 + 0.426X \pm 2.559$ (N = 88)

March: $Y = -0.228 + 0.246X \pm 1.374$ (N = 67)

April: $Y = -1.499 + 0.349X \pm 1.340$ (N = 46)



The slope of the October regression line is significantly different from the lines for the other three months. The elevation of the December line is significantly different from the March and April lines. There is no significant difference between the March and April regression lines.

The Effect of the Parasite on the Host

In October, parasitized isopods, both male and female, are significantly lighter in weight than non-parasitized isopods (Figs. 4 and 5). In April, parasitized female isopods (but not males) are also significantly lighter than non-parasitized isopods. Parasitized male (but not female) isopods are significantly heavier than non-parasitized isopods in March. The weight of parasitized isopods includes the weight of the worm larvae.

There was no significant difference between the weight-metabolism regression lines of male and female isopods. The data from male and female isopods were therefore pooled to give a single weight-metabolism regression line for parasitized isopods and one for non-parasitized isopods (Fig. 6). There is a significant difference in the oxygen consumption between parasitized and non-parasitized isopods. The oxygen consumption of a 6.0 mg isopod, which was the mean weight of the isopods used in this experiment, was calculated from the weight-metabolism regression lines. A parasitized isopod of this weight has a metabolic rate 31.3% higher than that of a non-parasitized isopod.

Temperature tolerance experiments were conducted at 35.0°C. on 6.0 to 10.1 mm isopods. The LT_{50} of parasitized isopods was 310.4

Fig. 4. Relationship between length and weight of parasitized and non-parasitized male isopods. The regression equations \pm standard error of estimate and N, the number of points on which the equation is based, are:

Non-parasitized: $\log Y = -1.899 + 2.561 \log X \pm 0.064$ (N=42)

March parasitized: $\log Y = -1.823 + 2.532 \log X \pm 0.056$ (N=34)

October parasitized: $\log Y = -2.116 + 2.664 \log X \pm 0.074$ (N=61)

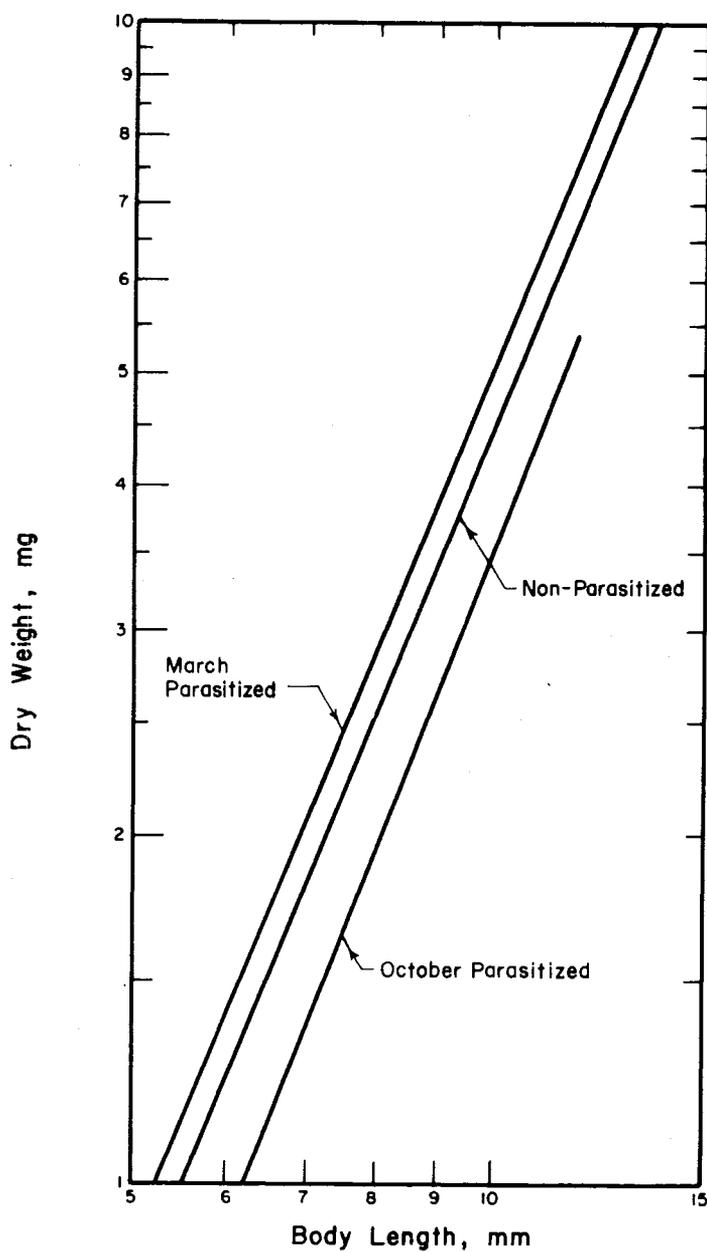


Fig. 5. Relationship between length and weight of parasitized and non-parasitized female isopods. The regression equations \pm standard error of estimate and N, the number of points on which the equation is based, are:

Non-parasitized: $\log Y = -2.223 + 2.979 \log X \pm 0.085$ (N=25)

April parasitized: $\log Y = -1.930 + 2.575 \log X \pm 0.089$ (N=21)

October parasitized: $\log Y = -2.046 + 2.552 \log X \pm 0.102$ (N=53)

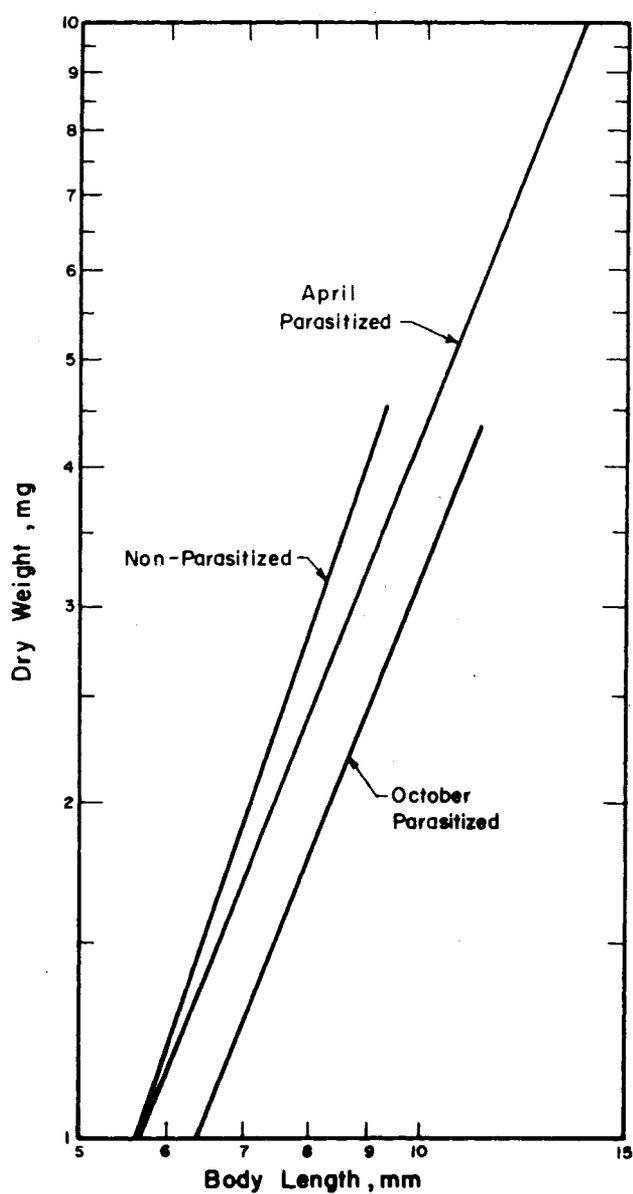
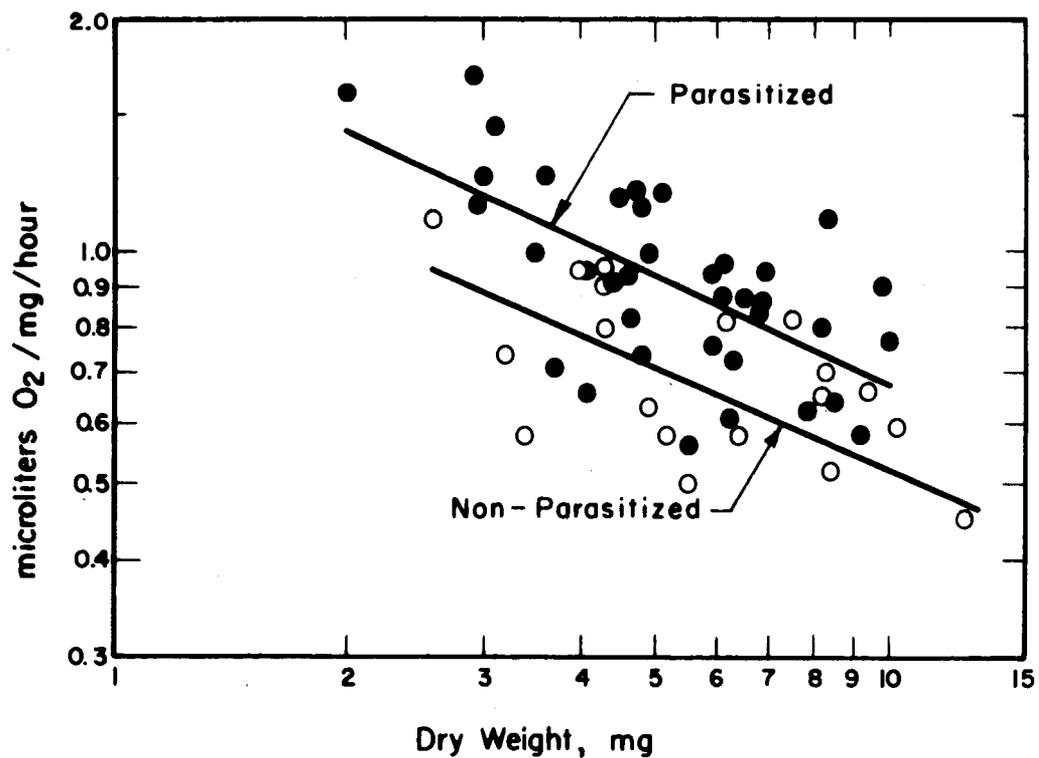


Fig 6. Oxygen consumption of parasitized and non-parasitized isopods at 15.0°C. (● = parasitized; ○ = non-parasitized isopods) The regression equation \pm standard error of estimate and N, the number of points on which the equation is based, are:

Parasitized: $\log Y = 0.298 - 0.468 \log X \pm 0.093$ (N = 37)

Non-parasitized: $\log Y = 0.161 - 0.444 \log X \pm 0.103$ (N = 21)



minutes, while that of uninfected isopods was 343.2 minutes (Fig. 7). There is a significant difference between these two LT_{50} values ($P < 0.05$).

At 95% relative humidity (R.H.), the LT_{50} of parasitized isopods was 18.4 hours (Fig. 8). The LT_{50} of non-parasitized isopods at this same R. H. was 15.3 hours. The difference is statistically significant.

Non-parasitized isopods exhibited a greater level of tolerance to 100% R. H. conditions than parasitized isopods. The LT_{50} of non-parasitized isopods was 162.5 hours; that of parasitized isopods was 124.2 hours. These two LT_{50} values are significantly different.

There is a dichromatism associated with this host-parasite relationship. During the winter there were both "light" and "dark" isopods in the population (Fig. 9). Throughout the year, all light-colored isopods were infected; while most dark individuals were not.

From the fall of 1967 to the spring of 1968, there was an increasing percentage of the light-colored infected isopods. On 10 August 1967, all parasitized isopods were dark. On 31 August 1967, 12% were light; in September, 20% were light; in December, 47% were light; and in April, 1968, 91% of the parasitized isopods were light.

Fig. 7. Mortality of 25 C-acclimated parasitized and non-parasitized male isopods when tested at 35 C. (● = parasitized; o = non-parasitized isopods)

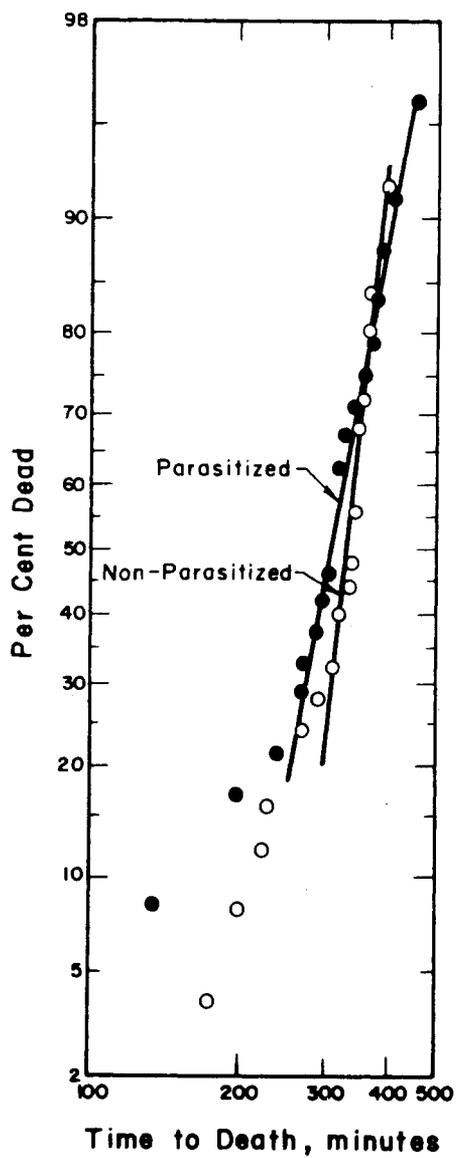


Fig. 8. Mortality of parasitized and non-parasitized isopods out of water in relative humidities of 95% and 100%. Each point represents the time to death of 4-12 individuals for the 95% R. H. experiment and 1-7 individuals for the 100% R.H. experiment. (● = parasitized; o = non-parasitized isopods)

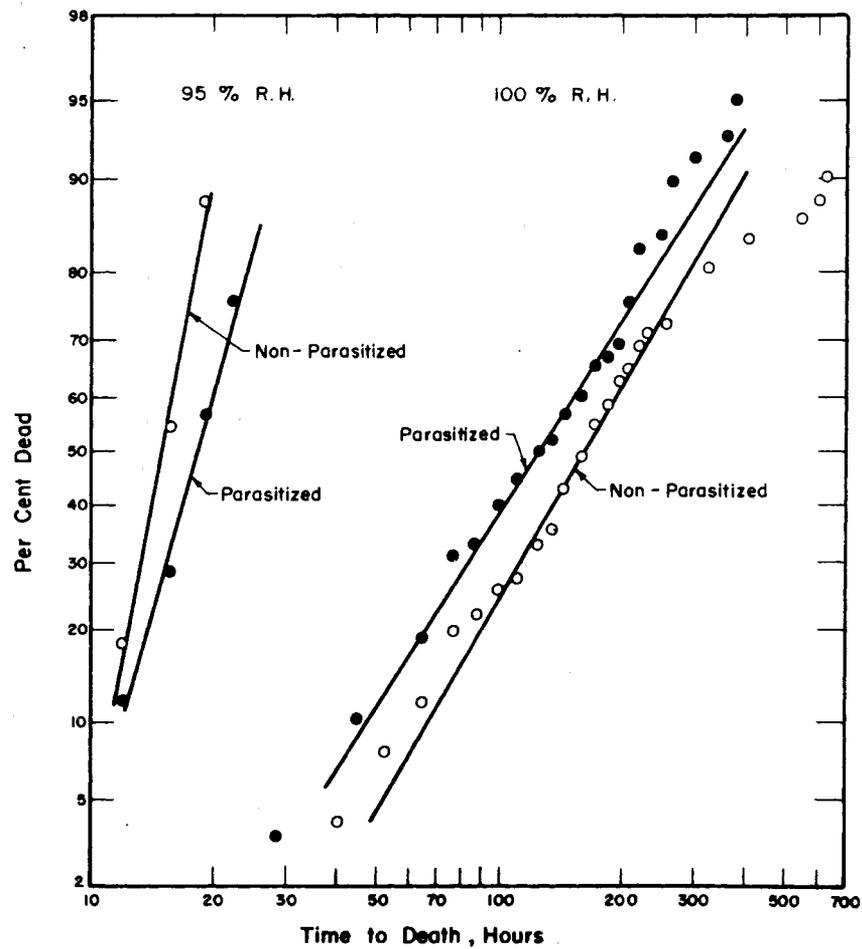
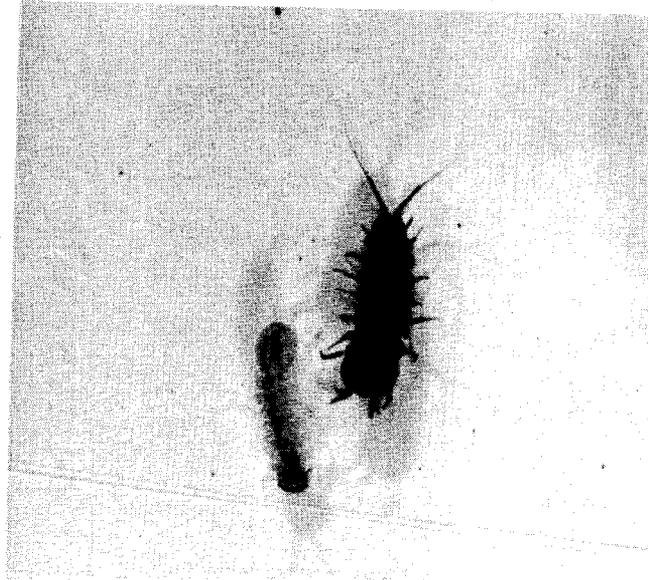


Fig 9. Color dichromatism of parasitized and non-parasitized isopods. A typical light-colored, parasitized isopod on the left, and a dark-colored, non-parasitized isopod on the right.



IV. DISCUSSION

Chubb (1964) has reviewed the seasonal aspects of the life cycles of many acanthocephalan species. The presence of any marked seasonal periodicity is quite variable among the various species of the Acanthocephala.

Relatively little is known about life cycles of the genus Acanthocephalus. Acanthocephalus ranae is parasitic in the anuran, Rana esculenta, in the U.S.S.R. (Dogiel, 1966). Its intermediate host is the isopod Asellus aquaticus. The parasite develops to maturity in the frog during the winter and infects the isopod hosts during the winter and spring. Development in the isopod occurs during the spring and summer.

Acanthocephalus lucii, a parasite of three species of fish in the Dnieper River, deposits acanthors in the summer (Komarova, 1950). Development in the intermediate host takes place during the summer and autumn. Re-infection of the final host occurs at the end of the autumn.

While the final hosts were not investigated during this study, it is reasonable to assume that mature worms are present in the fish hosts at least during the early part of the summer. The initial infection of the new isopod generation is quite apparent by the end of July. Uninfected isopods continue to become infected since the incidence of infected isopods gradually increases for several months. As Nicholas (1967) pointed out, acanthors may remain viable up to 9 months.

The high level of infection reported here for Acanthocephalus dirus in Asellus intermedius may be a reflection of the physical habitat of the isopods: the first two miles of a creek only three miles long.

Moreover, the creek is extremely narrow (2.1-2.5 m wide at Mile 2; 0.6-0.9 m wide at Mile 1). It is apparent that the initial acanthor deposition occurred sometime in the early part of the summer in both 1967 and 1968. During the latter part of both summers, the water level in the creek dropped considerably due to extremely dry conditions. It seems that concentration of the acanthors and isopods would follow, particularly under conditions of lessened stream flow and lowered water level. Downstream "dilution" of the acanthors would not occur as readily under these conditions. Moreover, the initial acanthor deposition during the summer coincides with, and overlaps, a late spring reproductive period, thus exposing a large number of new, uninfected isopods to possible infection.

The abrupt decreased incidence of infected isopods between April and May of both years is only partially due to a loss of infected individuals from the population. Infected isopods larger than 14 mm apparently disappear from the population after the April collection, although a few uninfected isopods in this size range remain. Decreased incidence in the population is due primarily to the addition to the population of many, new uninfected individuals. Stark (1965) noting a similar occurrence in a population of Diplocotyle-infected Gammarus zaddachi, considered the new, uninfected generation to "dilute" the presence of the infected individuals of the old generation.

When the isopods first became infected in July, the incidence of infection was higher at the downstream station. The incidence remained higher there for most of the year. This is also probably due to the differences in the physical factors of the two collecting stations as they serve as suitable fish habitats. Mile 2 collecting station is

more of a "pool" habitat, being deeper (0.6-0.9 m deep) and wider (2.1-2.5 m wide) than Mile 1, which is very shallow (less than 0.3 m deep) and uniformly narrow (0.6-0.9 m wide). When fish were present in the creek, they were generally observed to congregate in the former "pool" area, while being absent or in substantially reduced numbers in the latter area of the stream. These differences in the distribution of fish in the creek would, ultimately, have an effect on the areas of acantor deposition and the pattern of acanthor dissemination in the stream.

While there is no over-all difference in susceptibility to infection between male and female isopods, there is a distinct difference in the pattern of infectivity (Fig. 2). Female isopods larger than 8 mm in length appear to be more susceptible to infection than male isopods of a corresponding size. On the other hand, female isopods may be more resistant to the parasite's effect on the host. Since male and female isopods are equally susceptible to infection, the pattern illustrated by the male isopods may be a reflection of a lowered resistance to the presence of the parasite among larger males and a consequent mortality down to a level of a 40% incidence of infection.

Female isopods also appear to harbor a larger number of larvae (Table 1). Amante, Fresi, and Laneri (1967) have demonstrated that female Asellus coxallis carry significantly more acanthocephalan larvae than males. These two studies on natural populations of isopods suggest that more experimental work is needed on parasite-resistance among invertebrate hosts to determine if differences between the sexes are widespread. Studies illustrating sex differences in host susceptibility

have been well documented for vertebrate hosts (Dodson, 1961).

The seasonal aspect of the parasite burden (Table 1) and the length-number of larvae relationship (Fig. 3). is very significant. In October, early in the life cycle of the parasite, there is relatively heavy infection of parasites in the isopods. These heavily infected isopods are no longer in the population two months later. The intensity of infection continues to decrease into the spring months.

Kennedy (1965) found a similar occurrence for infections of the cestode, Archigetes limnodrili, in the tubificid, Limnodrilus hoffmeisteri. The number of parasites per host tended to decrease as the parasite became more mature, i.e., larger. In his study, heavy infection did not kill the host, but resulted in the death of some of the parasites. However, Archigetes iowensis in L. hoffmeisteri causes the death of its host under heavy infections. (Calentine, 1964).

Spaeth (1951) found a heavy mortality of the amphipod, Hyalella azteca, experimentally infected with Leptorhynchoides thecatus. High mortality coincided with the period of time of rapid growth in body length of the acanthellae. At this time, the parasite occupied most of the hemocoel of the host.

Hynes (1955) suggested that small infected amphipods died off rapidly. He later found heavy infections to weaken and kill their amphipod hosts (Hynes and Nicholas, 1963). Fischer (1968) found that experimentally infected copepods with heavy infections died within a week. The results of these laboratory studies and the field data presented in this study suggest that the disappearance of the heavily

infected isopods may have been due to mortality caused by the growth of the numerous larvae present in the early part of the life cycle of the parasite. This might serve as an important mechanism for the regulation of density of the isopod population.

A parasite's effect on its definitive or intermediate host can manifest itself in a number of ways. One of the most common effects, particularly with heavy infections, is that of decreased host growth. Hunter and Hunter (1938) experimentally demonstrated a significant reduction in weight of smallmouth bass parasitized by metacercariae of a strigeid trematode. Fox (1962) has reviewed the literature dealing with growth retardation by parasites of various fish hosts. Some studies have demonstrated an effect on the host's growth rate, while others have found no such effect. Kannevorff (1965) found that the growth of amphipods, Ampelisca macrocephala, was retarded when they were infected with the turbellarian Kronborgia amphipodicola.

The data presented here on the length-weight relationships of parasitized and non-parasitized isopods illustrate one of the physiological effects of these acanthocephalan larvae on their isopod hosts (Figs. 4 and 5). The only date on which both parasitized male and parasitized female isopods were significantly lighter in weight than non-parasitized isopods occurred early in the life cycle, in October. This date coincides with the heaviest infection recorded for the four sampling dates (Table 1). Thus, with a heavy infection of acanthocephalan larvae, there is an actual loss in weight.

Von Brand (1966) has summarized the literature dealing with the effect of parasites on the respiratory rates of their host. In the only report involving a parasitized crustacean host, Klekowski and Guttowa

(1968) demonstrated that the copepod, Eudiaptomus gracilis, infected with Diphyllobothrium latum larvae showed a lower mean oxygen consumption than noninfected copepods.

Hurts (1927) found the oxygen consumption of parasitized Physa occidentalis was 7% greater than non-parasitized snails at room temperature. Von Brand and Files (1947) found no difference between Schistosoma-infected snails and normal snails at 30° C. Parasitized Stagnicola palustris exhibited a lower metabolic rate at 25° C than non-infected snails (Becker, 1964).

Vernberg and Bernberg (1965) studied the thermal acclimation patterns of a snail and two species of larval trematodes. All three exhibited different acclimation patterns, although the thermal environment to which they were all exposed was the same. Duerr (1967) found a lowered and more variable metabolic rate in parasitized snails than in laboratory-bred snails when tested at 25°C.

Recently, Vernberg and Vernberg (1967) tested warm and cold-acclimated snails at a series of test temperatures. They only found differences at the extremes, i.e., warm-acclimated snails at the coldest test temperature and cold-acclimated snails at the warmest test temperature. In each case, the metabolic rate of the parasitized snails was higher, 48% and 22%, respectively.

The reported effects of parasitism on the metabolic rate of the host snails vary widely and no generalizations can yet be made. While some differences may be attributed to the investigator and the particular techniques utilized, it may also be true that the metabolic rate of trematode-infected snails differs from species to species and under varying degrees of parasitism.

The data presented here represent moderate infection levels of parasitism; an average of 2.1 larvae per isopod host (range of 1-6 worms). The animals were collected at a time when approximately 42% of the isopod population was infected with larval acanthocephalans. Furthermore, the acclimation and test temperature approximate the water temperature for the time of the year in which the animals were collected. In terms of numbers, the isopods were the predominant macro-invertebrate in the creek. The ecological significance of the increased metabolic rate of parasitized isopods concerns the energy flow through the stream community. Saito (1965) found the RQ of a terrestrial isopod to be 0.9, which has a caloric equivalent of 4.9 cal/ml O₂. Assuming this RQ is approximately the same for aquatic isopods, the energy expended by a 6.0 mg parasitized isopod in 23 hours is 6.0 g-cals. The amount expended by a non-parasitized isopod of the same weight in this time would be 4.6 g-cals. With nearly half the isopods infected with acanthocephalans, there would be a considerable amount of daily respiratory energy lost over and above that which would be lost if the population consisted only of non-parasitized isopods.

The parasitized isopods utilized in the temperature tolerance experiments were only lightly infected with larvae (1-2 larvae present) and most of the larvae were acanthellae. Vernberg and Vernberg (1963) investigated the effect of trematode larvae on the thermal resistance of parasitized and non-parasitized Nassarius obsoleta. They found that uninfected snails were more resistant, but this depended on the test temperature and the exposure period. The greater sensitivity to high temperature shown by parasitized isopods may be a consequence of their

greater metabolic rate. That is, a parasitized isopod at a near-lethal temperature, expending considerably more energy to stay alive, would die sooner than a non-parasitized isopod.

The discussion of the previous experiments indicate that the presence of worm larvae may affect the isopod's physiology in various ways, depending on the nature of the response being investigated. The different responses of infected and uninfected isopods to survival in 95% and 100% relative humidity conditions points up the complexity of the problem. A satisfactory explanation of the cause of the differences presented here (uninfected isopods being more tolerant at 100% R.H. but less tolerant at 95% R.H.) cannot be offered at this time. It is clear that more experimental work needs to be done to determine the precise nature of the causes of these different physiological effects of the parasite on its intermediate host.

The occurrence of a relationship between an acanthocephalan parasite and a possible effect on the pigmentation of its intermediate host was first noted by Munro (1953). In a collection of parasitized isopods, Asellus aquaticus, he found over 90% to be darker than normal. Balesdent (1965) also found infected A. aquaticus to be darker than non-parasitized individuals. This differs from the response noted in this study, where, in the spring, over 90% of the parasitized isopods were decidedly lighter than uninfected isopods.

That the appearance of light-colored isopods coincides with the later stages of the development of the parasite is clearly adaptive from the standpoint of the parasite. Early in the fall, most of the isopods are dark and most of the parasites are acanthellae. However,

in the spring, the reverse is true. Most of the isopods are light and most of the larvae are cystacanths. For example, on 25 April, 91% of the parasitized isopods are light; while 98% of these are carrying cystacanths. The isopod habitat consists of the muddied roots of grasses and overhanging masses of vegetation along the banks of this creek, a habitat that is dark in color. Presumably, the chances of a light-colored infected isopod on a dark background being eaten by a potential definitive host is greater than that of a dark isopod being eaten on the same background. This modification of the host's pigmentation by the parasite and its coincidence with the infective stage of its development would considerably increase the possibility that the parasite would be able to complete its life cycle successfully.

PART TWO: THE BIOLOGY OF FOUR SPECIES OF FRESH-
WATER ISOPODS IN EAST-CENTRAL ILLINOIS

I. INTRODUCTION

Although the American fresh-water isopod fauna consists of 50 or more species, their biology is not very well known. For many years, Allee (1912, 1913, 1914, 1929) studied the problems of rheotaxis and aggregations in Asellus communis. Ellis (1961) determined the life cycle and studied the ecology of A. intermedius, and Engemann (1963) studied a pond population of A. communis, both in Michigan. The life cycle and physiological ecology of Lirceus fontinalis was studied by Clifford (1966) in a temporary stream in Indiana. Styron and Burbanck (1967) and Styron (1968) studied the physiological tolerances of L. fontinalis.

Of the 25 or more species of subterranean isopods in this country, descriptive information is available for only a few. Hoffmann (1933) gave some rather detailed, though limited, ecological information on A. tridentatus in Kansas. Banta (1910a, b) compared the physiological reactions of A. stygius with A. communis. There is more information available concerning fresh-water asellids, but it is in the form of scattered notes and observations. Although a number of species occur in Illinois, the life cycle of only one has been studied (Markus, 1930; Dexter, 1954).

11. MATERIALS AND METHODS

Asellus sp. (pond) was studied in a vernal pond in "Busey Woods", a small wooded area within the city limits of Urbana, Illinois. This pond is a typical midwestern temporary pond in that it is dry for a varying number of months each year.

Asellus intermedius was found in a small, permanent creek. This habitat has already been discussed in Part One.

Asellus sp. (cave) is a typical subterranean isopod, i.e., albinistic and without eyes. It was collected from the subsurface water discharge emanating from drain tiles. Perforated plastic pails were placed below the drain tile opening so that the water would flow through the pail, leaving the animals inside the container. The tiles discharge into a drainage ditch in Champaign County, Illinois (T20N, R10E, Sects. 29, 35), although they cease flowing during the summer dry months.

Lirceus garmani was studied in the first mile of a drainage ditch in Champaign County, Illinois (T20N, R10E, Sect. 29). During the summer, the ditch dries up, except for a small pool at the head of the ditch. The ditch is fed by water from numerous drain tiles.

The procedure of sampling these populations and measuring the isopods is the same as described in Part One. The methods used to determine the length-weight relationship, survival out of water, and thermal tolerance have also been discussed. During the study, ovigerous females were collected, sacrificed, and the contents of the brood pouch enumerated. Three developmental stages were recognized. "Eggs" were considered to be any developmental stage that was spherical in shape. "Embryos" were comma-shaped; somewhat elongated, but curved. Individuals with fully formed appendages and ready to leave

the brood pouch were "young". The data on the size of the female and the number of individuals in the brood pouch were utilized in calculating least squares regression lines for the relationship of the log size of the female vs. the log fecundity. The slopes of all regression lines are significantly different from zero, unless otherwise specified. All statistical hypotheses were tested at the 5% level.

Growth rate experiments were conducted at a temperature of $15.0^{\circ} \pm 1.0^{\circ}\text{C}$ and a 12-hour photoperiod. Isopods that had recently been released from the brood pouch were placed in a plastic container (11.9 x 8.1 x 6.0 cm). For the first ten days, three isopods were kept in each container; after ten days each was reared in an individual container. They were maintained on elm leaves, and the water was changed weekly. Lengths of the animals were determined at 10-day intervals in the early part of the study and at 15-day intervals later on. Only the lengths of those that survived for the duration of the study were used in the determination of growth curves. The number of individuals used to calculate the growth curves for each species was: Asellus sp. (cave), 16; Asellus sp. (pond), 20; A. intermedius, 43; L. garmani, 38. Growth rates were determined and compared according to the method of Ricklefs (1967).

Developmental time was considered to be the duration of time from the deposition of eggs in the brood pouch until the release of all the young. The sequence of events leading up to the deposition of eggs in the brood pouch is: pairs in precopula, female molts the posterior half of her exoskeleton, copulation, female molts anterior half of her exoskeleton, eggs are deposited in the brood pouch. The time at which these events occurred was taken as the midpoint between consecutive observations. Developmental times were compared to each other by Duncan's Multiple Range Test. The 5% level of significance was used.

III. RESULTS AND DISCUSSION

Breeding biology and general life history

Lirceus garmani

After the dry period of the summer of 1967, water began accumulating in the ditch in October and November. The first Lirceus reappeared in November, at which time the water temperature was approximately 5°C. Ovigerous females carrying eggs were first found in early March, 1968. By the end of March, 15% of the ovigerous females were carrying late embryos. By 20 April, almost all the ovigerous females were carrying either late embryos or young. The new generation began entering the population in late April and early May, at which time adults of the previous generation began to die. A few ovigerous females were still present on 4 July, but, by late July, the ditch started to dry up. In August only a small pool remained at the head of the ditch. Very few Lirceus were collected from this pool during the summer, presumably the new generation follows the disappearing water down into the substrate.

Observations of the population in early 1967 indicate that the life cycle was basically the same, i.e., a single reproductive period, but the timing of the events was slightly altered. In 1967, the first female isopods became ovigerous in early January, and by the end of March, some individuals were carrying young. On 23 April, the ovigerous females were carrying either late embryos or young. Although individuals of the new generation were not collected in the sampling procedure, they must have begun entering the population in early April. The first females with empty brood pouches were collected on 23 April.

The percentage of ovigerous isopods slowly increased through the winter and spring and appeared to stabilize at slightly over 60%. Ovigerous females were found only in the 10-14 mm classes. However, laboratory rearing experiments conducted at a temperature of $15.0^{\circ} \pm 1.0^{\circ}\text{C}$ indicated that it took L. garmani females approximately 97 days to become ovigerous, at which time they had attained a length of about 9 mm (range = 8.8 to 9.8 mm).

Males predominate in the larger size classes. The largest male collected was 22.4 mm long; the largest female examined was 18.0 mm long. By 23 March, it was apparent that some of the adult males had begun to die off.

Asellus sp. (pond)

In 1967, pairs were in precopula in early March, but the first ovigerous females did not appear until late March. Although juveniles were not collected on 9 April, the new generation of isopods were presumably entering the population since some females had empty brood pouches. Most females were still carrying eggs and young in May. Adult individuals of the previous generation gradually disappeared. The pond began to dry up in early July and was nearly completely so by early August. Standing water did not reappear until December. Soon after, ice cover formed over the pond. The timing of the life cycle events in 1968 was nearly the same as in 1967. The first ovigerous females were observed in late March, and individuals of the new generation began to enter the population by the end of April. Some females were still ovigerous in May. In 1968, the pond dried up completely in August.

Asellus sp. (cave)

The only ovigerous females observed were collected in June, 1967, and July, 1968. These females ranged from 6.2 to 8.8 mm in length.

Asellus intermedius

Although ovigerous females were not present in the population during every month of the year, breeding was continuous enough for there to be at least some juvenile isopods always present. The statistic "per cent ovigerous females of total females" is misleading in that on 29 August 1968, at Mile 1 Station, no ovigerous females were collected, but many ovigerous females were observed at Mile 0, in the area of the drain tile at the head of the creek. These ovigerous females and many pairs in precopula were congregating at the mouth of the tile and actually entered the tile itself. Thus, reproduction was occurring in the population, although it was not evident in the regular sampling program.

Individuals that entered the population in April or May reproduced twice; once in early summer and once in early winter. Those that entered the population in early summer reproduced in late summer and late winter. However, those females that bred in March and April entered the population in autumn (September-November) and reproduced only once. Large adults that survived the winter gradually disappeared from the population in the spring.

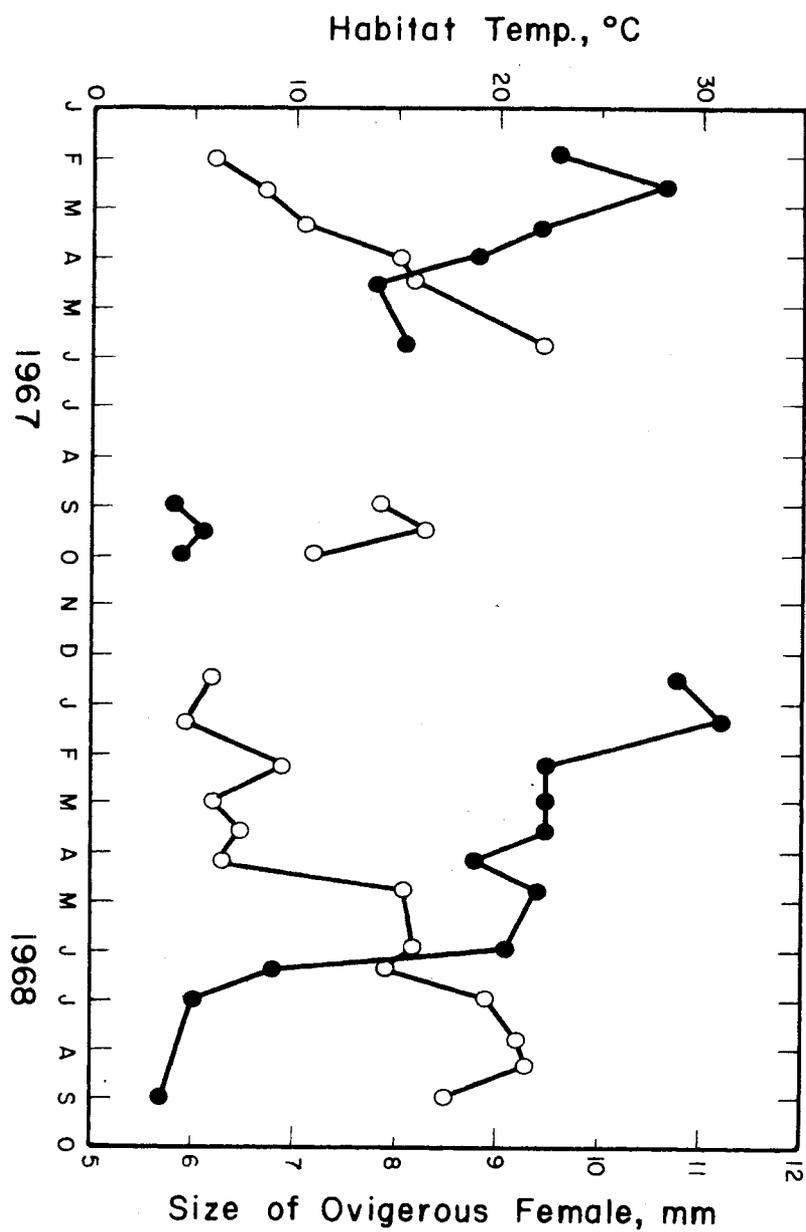
There is an apparent inverse correlation between the size of the ovigerous females and the season of the year, i.e., the water temperature (Fig. 10 and 12). Ellis (1961) found a similar inverse correlation between the water temperature (Ellis and Gowing, 1957) and the size of ovigerous A. intermedius in a Michigan trout stream, and this correlation has also been noted for A. aquaticus and A. meridianus in England (Steel, 1961). A series of laboratory experiments were designed to analyze this relationship and especially to determine the time to sexual maturity at different constant temperatures. At $15.0^{\circ} \pm 1.0^{\circ}\text{C}$, it took a mean of 97 days for a

female (N = 5) to become ovigerous. At this time, the mean length of these females was 9.1 mm (range = 8.5 to 9.5 mm). On the other hand, at $25.0^{\circ} \pm 1.0^{\circ}\text{C}$, females (N = 8) became ovigerous in 38 days and had a mean length of 6.4 mm (range = 5.5 to 7.8 mm). Maercks (1930) found that A. aquaticus took 13 months to attain sexual maturity at $5\text{-}10^{\circ}\text{C}$, while at room temperature it took only 3 months. Thus it appears to be not the attainment of a particular size (age) that is important in reaching sexual maturity, but the duration of the exposure to a particular temperature.

There is a considerable intra- and interspecific variation of life cycle patterns. The life cycle of A. intermedius in a Michigan trout stream (Ellis, 1961) is basically similar to that of A. intermedius in Illinois. A. intermedius in a montane lake in Colorado (Buscemi, 1961) shows a single, short reproductive period, quite unlike the Illinois creek or Michigan trout stream populations. Moreover, the largest isopods encountered in the Colorado population were only 10 mm in length. The largest male in the Michigan population was 16 mm, and the largest female was 13 mm. The largest male collected in the present study was 20.0 mm, and the largest female was 16.4 mm.

Clifford's (1966) study of L. fontinalis with a single reproductive period found the percentage of ovigerous females to vary from only 3 to 7%. Markus (1930) and the present author, working on the same population of L. garmani, but in two distinctly different ecological situations, found the percentage of ovigerous females to increase slowly in the spring to high values of 51% and 65% respectively. The percentage of ovigerous females in a temporary pond population of L. communis ranged from 50% to 100% during their single breeding period (Engemann, 1963). Presumably, it is more adaptive for a population with a single reproductive period to have as many of the available females as possible become ovigerous before the relatively short reproductive season is over.

Fig. 10. Relationship between water temperature, size of ovigerous females, and season of the year of Asellus intermedius. (o = water temperature; ● = size of ovigerous female)



The life cycle of the A. intermedius population is remarkably similar to that of A. aquaticus and A. meridianus in England (Steel, 1961). That is, those born in the spring breed the following spring and die soon after. He found the life span of the autumn young to be about 9 months, while for those that bred twice it was 12 months. However, the life span of the Illinois A. intermedius that bred once was about the same as those which breed twice, i.e., 8 to 10 months.

The loss of adult male crustaceans after reproductive activities has been well documented for a variety of amphipods and isopods (Steel, 1961; Kannevorff, 1965; Mills, 1967). For this reason, the life span of female isopods, at least those with only one generation a year, may be considerably longer than that of males.

For isopods inhabiting a temporary environment and having one breeding period, the timing of events undoubtedly varies according to specific habitat conditions, i.e., how early or late in the fall or winter water reappears and how early or late in the summer the water disappears. Thus, in a 13 month study, Clifford (1966) first found ovigerous L. fontinalis in April of the first year, but as early as February of the second year. Lirceus garmani began breeding in January in 1967, but did not commence reproducing until March in 1968.

Kenk (1949) presented evidence to suggest that A. militaris remained active and grew during the summer dry period. Observations on individuals of Asellus sp. (pond) that were found soon after standing water returned to Busey Woods Pond did not indicate any growth during the dry season. This is similar to the results reported for a temporary pond population of A. communis (Engemann, 1963).

The presence of aggregations of A. intermedius noted at the head of the creek on 29 August 1968 resembles the increased tendency of A. communis to collect in groups at the beginning of the breeding season (Allee, 1912). Allee also found that stream isopods are normally positively rheotactic. Such behavioral responses should increase the probability of isopods of the opposite sex coming into contact with each other, and thus ensuring successful reproduction.

In isopod populations, it appears to be a general tendency for males to grow larger than females (Naylor, 1955b; Clifford, 1966; Narver, 1968). Steele and Steele (1969) found this to be true for the amphipod Gammarus duebeni and suggested that the males were larger than females because of their faster growth rate and better survival. Steel (1961) also found a slightly faster growth rate for male A. aquaticus and A. meridianus. In my laboratory growth rate studies on A. intermedius and L. garmani conducted at 15°C, there was never more than 0.7 mm difference between male and female isopods of a comparable age. This does not mean that there may not be sexual differences in growth rates under natural conditions. However, the size differences may also be related to the females discontinuing growth with the onset of reproductive activities while the males continue to grow.

Reproductive cycles of cavernicolous animals have been summarized by Poulson (1964) and Vandel (1965). Some species have seasonal breeding, although others apparently are noncyclic. This appears to be true of American troglobitic isopods (Table 3). Banta (1907) found ovigerous A. stygius in all seasons in a cave in Indiana. There is a suggestion of a spring-summer breeding cycle for A. tridentatus, as Hoffman (1933) made collections in every month for at least 18 months and found ovigerous females only in June.

These ovigerous females ranged from 6.5 to 12.7 mm.

Asellus sp. (cave) in Illinois subterranean waters, appears to show a spring-summer breeding period. The range in size of ovigerous Asellus sp. (cave) females, 6.2 to 8.8 mm, is considerably less than that found for A. tridentatus.

Fecundity

A relationship exists between the number of eggs and body length (Fig. 11). The slope of the Asellus sp. (cave) regression line is not significantly different from zero. Of the other 3 regression lines, only the slopes of Asellus sp. (pond) and L. garmani are statistically indistinguishable from one another; the elevations of these two lines are significantly different from each other. The A. intermedius regression line was computed by pooling all the available data for ovigerous females collected in January, April, May, July, August, and September.

The most striking difference among the species studied is the low fecundity exhibited by Asellus sp. (cave). Moreover, it is the only species in which fecundity is not significantly dependent on size. Troglotic organisms typically show a reduction in the number of eggs produced (Vandel, 1965, p. 356.) Poulson (1964) pointed out that most of the available data have not been on a length-fecundity or weight-fecundity basis, and comparative evaluation has been difficult. A. cavaticus, a European subterranean isopod, reproduces from 3.4 to 5.5 mm and carries a maximum of 31 eggs (Henry, 1965). Hoffman (1933) found a maximum of 70 eggs in a 13.4 mm A. tridentatus female. A least squares regression line which was computed for Hoffman's length-fecundity data also did not show a significant dependence of fecundity on size. There is not enough information available in the literature about

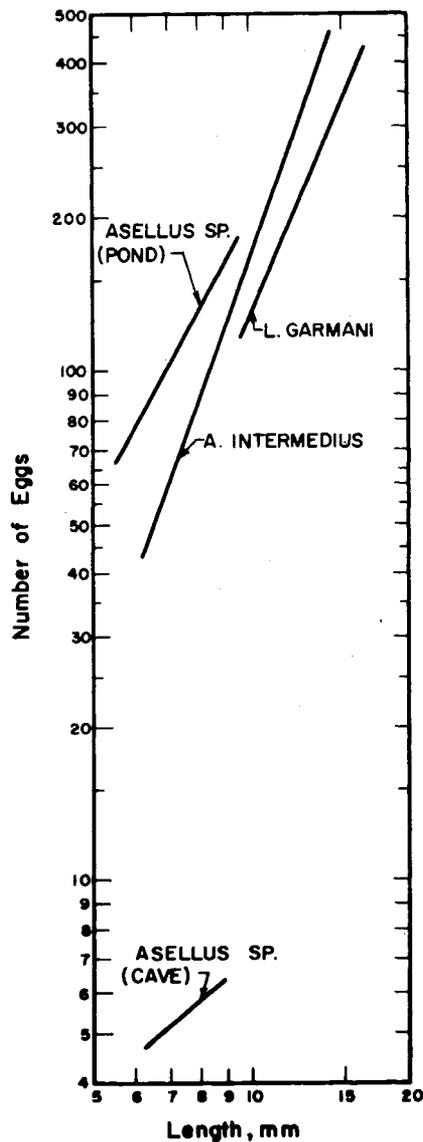
Fig. 11. Relationship between number of eggs in the brood pouch and the size of the female. The regression equations \pm standard error of estimate and N, the number of points on which the equation is based, are:

Asellus sp. (pond): $\log Y = 0.402 + 1.907 \log X \pm 0.084$ (N=45)

Asellus sp. (cave): $\log Y = -0.146 + 1.015 \log X \pm 0.213$ (N=48)

A. intermedius: $\log Y = -0.629 + 2.852 \log X \pm 0.066$ (N=123)

L. garmani: $\log Y = -0.293 + 2.400 \log X \pm 0.054$ (N=57)



fecundity in troglobitic isopods to suggest that this is a general occurrence among these organisms.

It would appear that the smaller size of ovigerous females of Asellus sp. (pond), compared to L. garmani, for example, would be more adaptive in a temporary environment. Obviously, if growth rates were similar it would take less time for a female to attain sexual maturity if the size at which she became sexually mature were relatively smaller. For an organism inhabiting a temporary environment, time is of the utmost importance. The organism must complete all its necessary life cycle stages before the environment becomes inimical by drying up.

Ellis (1961) calculated a length-fecundity regression line for A. intermedius in a Michigan trout stream. However, since his data included females with eggs, embryos, and young, a comparison with the data presented here for females with eggs cannot be made. The slope for his regression line, 2.68, however, was similar to the 2.85 for the Illinois A. intermedius population.

There are some data available on fecundity in other species of Lirceus. Clifford (1966) found 225 to be the mean number of eggs in a 12.5 mm ovigerous L. fontinalis female. On the other hand, the mean numbers of eggs of L. fontinalis, which breeds at a considerably smaller size in two Georgia populations, was 23 and 28 for 5.0 mm females. The values for these two widely separated L. fontinalis populations come very close to falling on the extrapolated L. garmani regression line. It would be interesting to have a more complete set of fecundity data for L. fontinalis populations to see how much intra- and interspecific variation really exists within the genus Lirceus.

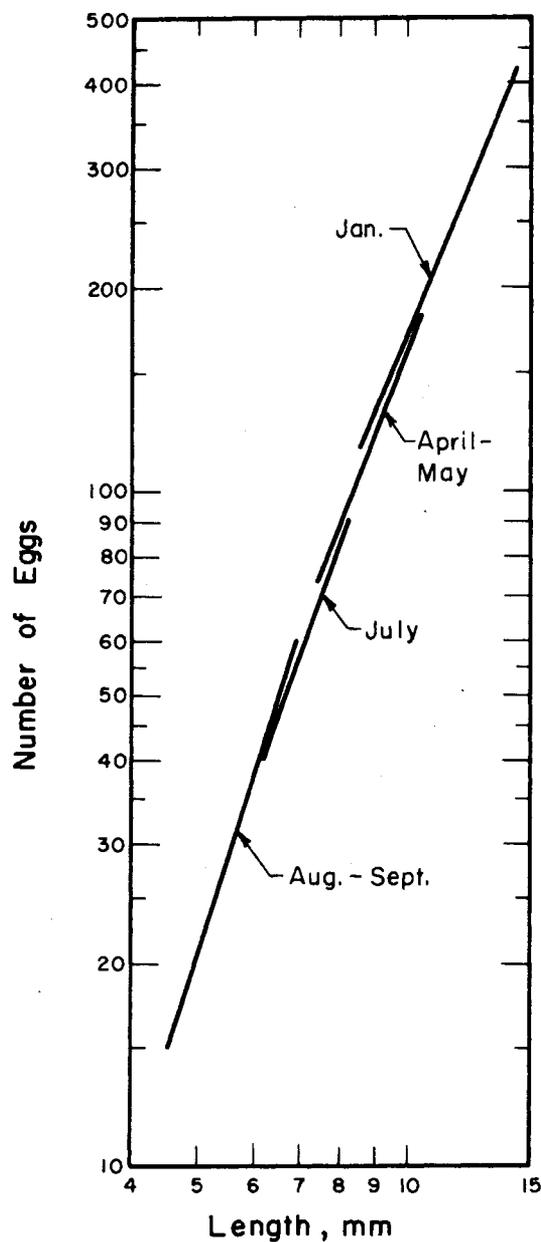
Fig. 12. Seasonal variation in the length-fecundity relationship of Asellus intermedius. The regression equations \pm standard error of estimate, and N, the number of points on which the equation is based, are:

January: $\log Y = -0.267 + 2.505 \log X \pm 0.052$ (N = 67)

April-May: $\log Y = -0.574 + 2.794 \log X \pm 0.079$ (N = 35)

July: $\log Y = -0.763 + 2.991 \log X \pm 0.079$ (N = 21)

Aug-Sept: $\log Y = -1.042 + 3.362 \log X \pm 0.095$ (N = 24)



Accompanying the seasonal variation in the size of reproductive A. intermedius females is a seasonal variation in the length-fecundity relationship (Fig. 12). The slopes of the January and the August-September lines, and the elevations of the January and the July lines are significantly different from each other. Thus, although the size range of ovigerous females does not overlap in winter (January) and summer (July), the winter females are carrying significantly more eggs than summer females. The following pairs of lines are statistically indistinguishable: January and April, April and July, April and August, and July and August.

Seasonal variation in fecundity has also been demonstrated for amphipods. Steele and Steele (1969) found winter Gammarus duebeni generally to contain more oögonia than summer females. Kinne (1961) showed that laboratory-reared G. zaddachi had a larger egg number at 14-16°C than at 18-20°C. On the other hand, Cheng (1942) found that females of the same weight produce more eggs in spring than in the winter in a few species of gammarid amphipods. He attributed this to better environmental conditions, i.e., temperature and food, in the spring.

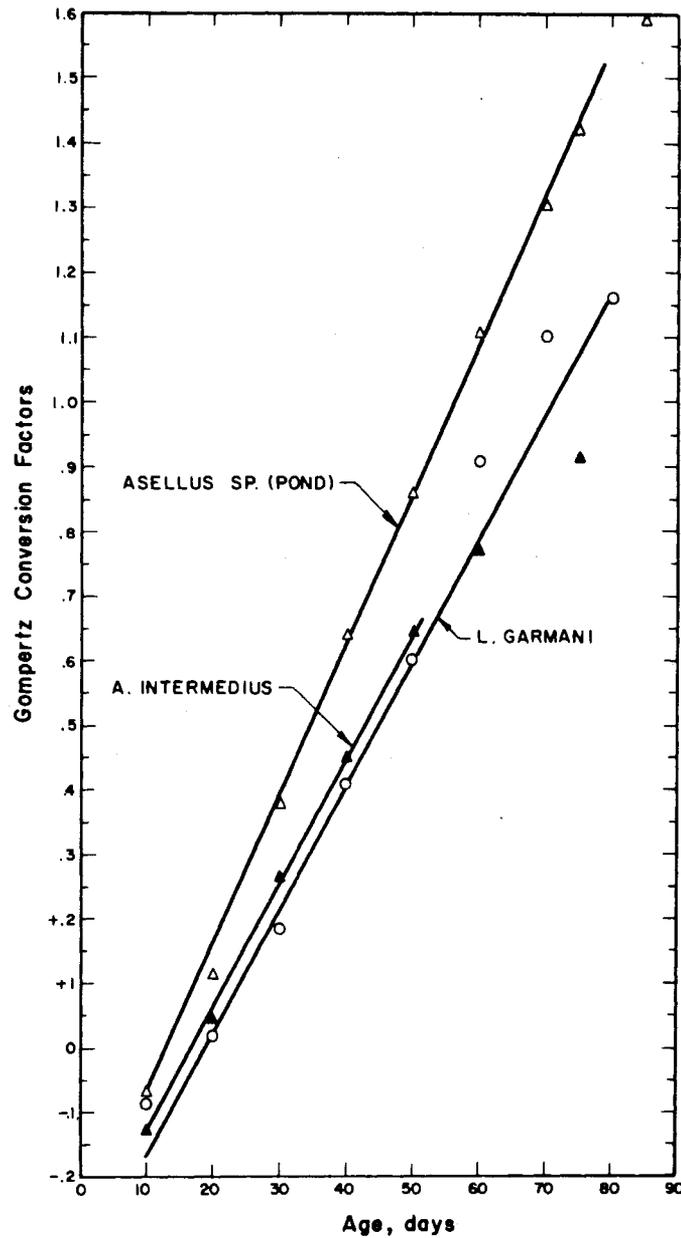
Hutchinson (1951) has reviewed the literature regarding seasonal variation in brood size in planktonic crustaceans. For many species, individuals reproducing in the spring carry more eggs than during other times of the year. He suggested that this might be a result of an increased food supply during the spring and that those producing more eggs in the spring would leave more offspring in an environment rich in food supply. Burgis (1967) has shown that food supply, up to a certain level, does increase egg production in two species of cladocerans. For a benthic detritus feeder such as Asellus (Williams, 1962) associated with dead and

decaying plant material, the period of maximum environmental food supply would be in the autumn-early winter after leaf fall and when previously growing plant material has died and begun to decompose. Minshall (1967) found that the amounts of attached particulate organic matter and allochthonous leaf material were highest in a spring-fed stream in Kentucky in mid-winter and late autumn-early winter, respectively. Although the A. intermedius population inhabited a stream that was not surrounded by trees, increased food material is evidenced when the water level rises in the autumn and submerges the vegetation that was previously overhanging the bank of the stream. Thus, an increased food supply would be available for the long period of colder water temperature. The larger size of the more slowly maturing females in the winter permits them to carry a larger brood. If, during this period prior to the attainment of sexual maturity, sufficient food were not available, the necessary development of the reproductive tissues would not be accomplished. It is suggested that as food supply abundance in the spring underlies brood size differences in planktonic crustaceans, the increased food supply in the autumn allows the female A. intermedius of winter to realize the greater reproductive potential that is afforded them by their larger size.

Growth Rate

Asellus sp. (cave) was reared for only 60 days after release from the brood pouch. Growth rates were determined for the other three species of isopods for as long as 140 days. Since the size difference between the sexes at any particular age was never more than 0.7 mm, and was generally less, the data for males and females were pooled and a single growth curve was calculated. The possibility of growth rate differences between the

Fig. 13. Converted growth curves of isopods. The values of K , the rate constant of the growth equation ($K = e \frac{dW_i}{dt}$), are: Asellus sp. (pond), $K = 0.0625$; A. intermedius, $K = 0.0516$; Lirceus garmani, $K = 0.0516$.



sexes under natural conditions has already been discussed. Moreover, it should be noted that laboratory-reared organisms did not get to be as large as animals collected in the field. This is similar to the findings of Markus (1930) and Levanidov (1949), working with L. garmani and A. aquaticus, respectively.

The data (except for Asellus sp. (cave)) were analyzed according to the method of Ricklefs (1967) and are presented in Fig. 13. Based on the calculated rate constant (K) values, the growth rates of A. intermedius and L. garmani are identical. The growth rate of Asellus sp. (pond) is 1.21 times as fast as that of either A. intermedius or L. garmani. This increased growth rate of Asellus sp. (pond) in a temporary environment may be an adaptation in permitting the population to reach sexual maturity as quickly as possible so that reproduction can successfully occur before the habitat dried up.

Markus (1930) performed field growth experiments with L. garmani in wire cages. He found a growth rate of approximately 2 mm per month, which is similar to the values presented here for 90-day old L. garmani in the laboratory at 15°C. However, his experiments were performed at a time of the year when the water temperature averaged less than 10°C. It appears that some factors inherent in laboratory experiments may serve to inhibit growth rates under artificial conditions.

Ellis (1961) presented growth rate data for A. intermedius at various temperatures, but his isopods never got to be as large as the A. intermedius discussed here. This is probably due to differences in experimental procedure; he did not follow the growth of isolated individuals, but reared them in broods and probably got a crowding effect.

Developmental Time

The length of time required for embryonic development from the time of the deposition of the eggs in the brood pouch until the release of young was determined at a number of temperatures (Table 2 and Fig. 14). Except for the 5°C data, statistical comparisons were made between pairs of species using Duncan's Multiple Range Test for the 15° and 20°C data and using Student's t-test for the 8° and 25°C data. The developmental time of Asellus sp. (pond) was significantly different from that of A. intermedius or L. garmani at all temperatures. At each temperature, the developmental times of A. intermedius and L. garmani are statistically indistinguishable. Although the developmental time varies somewhat from species to species, the Q_{10} values (Table 3) for a number of temperature intervals are remarkably similar between species.

One ovigerous female of Asellus sp. (cave) was collected and the eggs allowed to develop. The young were released in 25 days at 15°C. Since it is not known how long she had been carrying the eggs, this can be considered the minimal amount of time necessary for embryonic development. This time is greater than any observed for the other three species at the same temperature. It is well known that troglobitic species have longer developmental times compared to epigeal species (Poulson, 1964; Vandel, 1965, p. 370) which is considered to be a consequence of their generally lower metabolic rate.

Estimates of the developmental time under natural conditions were made by utilizing data of various life history events for three of the four isopod species. The first L. garmani females became ovigerous about

Table 2. Developmental time (D) in days and rate of development (1/D) of isopod eggs as a function of temperature. Values are expressed as the mean number of days + S.E. N = the number of isopods tested.

Species	TEMPERATURE														
	5°C			8°C			15°C			20°C			25°C		
	N	D	1/D	N	D	1/D	N	D	1/D	N	D	1/D	N	D	1/D
<u>Asellus sp.</u> (pond)	4	49.9± 1.7	0.020	13	18.6± 0.2	0.054	12	11.8± 0.2	0.085	18	9.1± 0.1	0.110			
<u>Asellus sp.</u> (cave)				1	25										
<u>A. Intermedius</u>	4	101.3± 3.4	0.0099	6	59.6± 0.9	0.017	14	21.9± 0.4	0.046	10	15.2± 0.3	0.066	13	11.1± 0.1	0.090
<u>Lirceus garmani</u>	1	100.9	0.0099	15	22.1± 0.18	0.045	5	15.1± 0.22	0.066						

Asellus intermedius eggs would not develop at 20°C; L. garmani eggs would not develop at 25°C.

Fig 14. Developmental time (D), in days, and rate of development ($1/D$) of isopod eggs as a function of temperature.

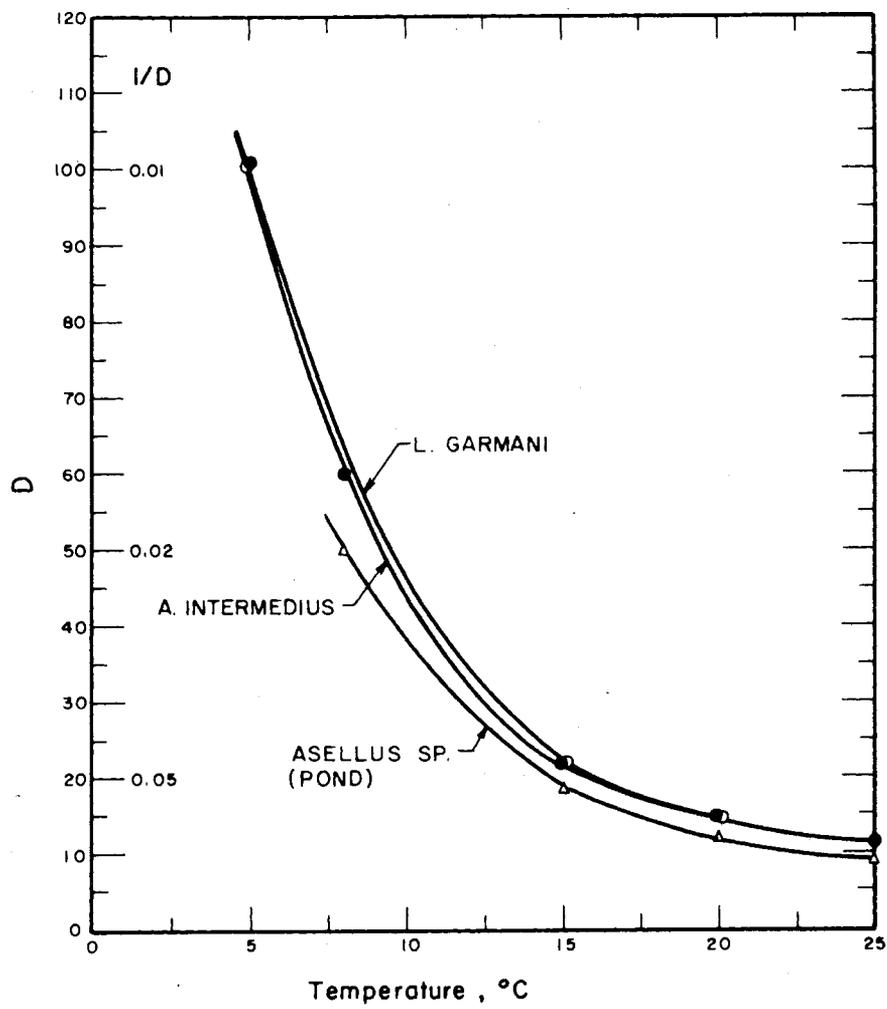


Table 3. Q_{10} values for developmental time of isopod eggs.

Temperature Range °C	Species		
	<u>Asellus</u> sp. (pond)	<u>A. intermedius</u>	<u>L. garmani</u>
5-15		4.62	4.56
8-15	4.10	4.18	
15-20	2.48	2.08	2.14
15-25	2.04	1.97	
20-25	1.68	1.88	

9 January 1967, the mid-point between the collections of 26 December 1966 and 22 January 1967. Females with empty brood pouches were collected on 23 April, so that 8 April was assumed to be the approximate time of release of the young of the first females to become ovigerous. This gives a time interval of about 90 days for the development of early winter L. garmani embryos. During this interval, water temperature ranged from 4-10°C, but were 6-7°C on most collection dates. This would indicate a predicted developmental time of about 80 days. Considering the fluctuations of water temperature that occur, the predicted time is remarkably close to that observed in nature.

Calculation of the maximum development time for the single reproductive period of Asellus sp. (pond) under natural conditions is relatively easy. If all the ovigerous females collected on 9 April became ovigerous the day after the preceding collection, i.e., on 7 March, and if all the young collected on 27 April entered the population at one time, on 26 April, then the maximum period of development would be 50 days (7 March to 26 April). However, it is more reasonable to assume that the first females to become ovigerous did so about mid-way between 6 March and 9 April, i.e., on 23 March and that the first young to enter the population did so mid-way between 9 April and 27 April, i.e., on 18 April. This gives a developmental time of about 26 days (23 March to 18 April). During this period of time, the water temperatures ranged from 10-13°C. This would indicate a possible incubation period of 24-37 days. This is reasonable in view of the fact that the "true" developmental time is probably somewhere between 26 days and 50 days.

Determining a field developmental time for A. intermedius is more

difficult because of the presence of ovigerous females and juveniles in almost all collections. However, it appears that females became ovigerous at Mile 1 on 1 January 1968. On 25 April, the first females with empty brood pouches were collected, so that the time of brood release is interpolated to be 15 April. Thus, the duration of the first winter brood is about 105 days. During this period, the water temperature varied from 1-12°C. It is assumed that females became ovigerous approximately mid-way between 10 August and 31 August 1967, i.e., on 20 August at Mile 1 Station. On 14 September, females with empty brood pouches were collected, indicating a probable release of young about 7 September. This gives a development time of 18 days for a mid-summer brood. During this period of time, the water temperature ranged from 10-26°C. Temperature variations of the magnitude encountered in both the winter and summer reproductive periods are too great to attempt to predict an appropriate developmental time from Fig. 14. It does seem that if more data were available, e.g., from continuous water temperature recorders, the laboratory-determined developmental times would give a fairly accurate indication of the duration of these phenomena occurring under natural conditions.

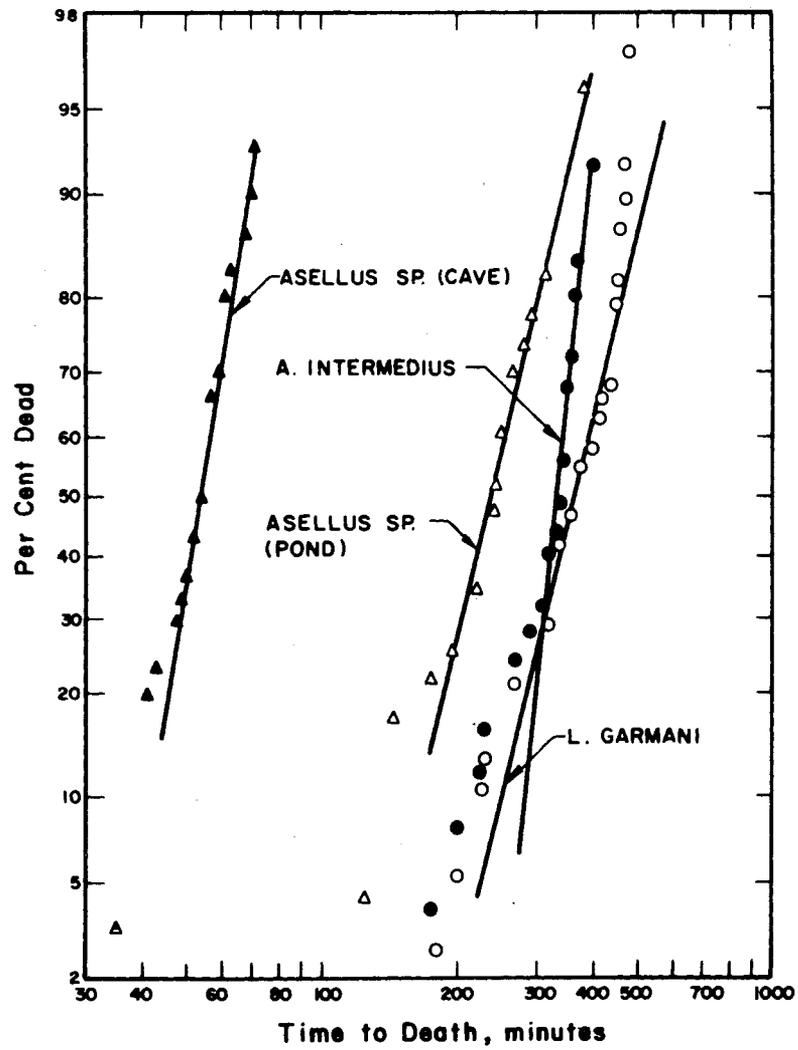
Thermal Tolerance

The results of these experiments are presented in Table 4 and Fig. 15. All of the LT_{50} values are significantly different from each other. The LT_{50} values of Asellus sp. (pond), A. intermedius, and L. garmani are close enough to each other that there may not be any ecological significance attached to the statistical differences. Birstein (1964) indicated that 28°C was the upper temperature limit of tolerance of A. aquaticus. Williams

Table 4. Thermal tolerance of 25°C-acclimated isopods tested at 35.0°C.

Species	Size Range Tested, mm	Sample Size	LT ₅₀ ± S.E. min
<u>A. intermedius</u>	6.0-10.1	25	343.2 ± 6.6
<u>Asellus</u> sp. (cave)	9.3-13.0	30	54.0 ± 1.0
<u>Asellus</u> sp. (pond)	5.2-7.0	23	242.5 ± 8.1
<u>L. garmani</u>	7.1-10.2	28	365.3 ± 7.2

Fig. 15 Mortality of 25° C-acclimated isopods tested at 35° C



(1962) found this to be true of both A. meridianus and A. aquaticus, although some could survive 5 days at 30°C (acclimation temperature = 20°C). Sprague (1963) found that the LT₅₀ of 25°C acclimated A. intermedius was about 200 minutes when tested at 35°C. Since an experimental temperature of 34°C produced a LT₅₀ value of about 500 minutes, slight differences in experimental procedure and temperature control may account for the differences between the values he reported and those reported here.

The most obvious difference in the results presented here is the relatively low tolerance of Asellus sp. (cave) to the experimental conditions. There does not appear to be much literature available comparing epigeal and troglobitic organisms with respect to their temperature sensitivity differences. The little work that has been done on this subject has been reviewed by Poulson (1964) and Vandel (1965).

Survival Out of Water

At 95% R.H., all the LT₅₀ values for survival out of water are significantly different from each other except Asellus sp. (pond) and Asellus sp. (cave) (Table 5). The longest survival time and largest LT₅₀ value at 95% R.H. was shown by L. garmani. This was also the largest species tested at 95% R.H. Their greater survival may be due to a smaller surface:volume ratio in the larger L. garmani, as Williamson (1951) and Naylor (1955a) suggested to explain their results.

The 100% R.H. LT₅₀ values for A. intermedius and L. garmani are statistically indistinguishable from each other; all others are significantly different from each other. There is a striking difference in survival time between young and old Asellus sp. (pond). This might have some adaptive value for the population during the summer dry period.

Table 5. Survival of isopods out of water at different controlled humidities at 15°C.

Species	95% Relative Humidity			100% Relative Humidity		
	Size Range Tested, mm	Sample Size	LT ₅₀ ± S.E. hours	Size Range Tested mm	Sample Size	LT ₅₀ ± S.E. hours
<u>Aseillus</u> sp. (cave)	9.0-11.0	32	13.0 ± 0.9	9.0-10.4	24	2042.5 ± 57.7
<u>Aseillus</u> sp. (pond)	8.4-10.8	21	12.4 ± 0.5	8.4-11.0	36	44.9 ± 4.1
<u>A. intermedius</u>	8.4-10.5	33	15.3 ± 0.7	5.6- 6.4	34	1660.5 ± 276.5
<u>Lirceus garmani</u>	11.6-14.3	56	28.8 ± 0.8	8.4-11.2	51	162.5 ± 7.9
				11.3-14.1	52	162.5 ± 7.0

While most of the individuals probably follow the descending water table and survive the dry period in an aquatic environment, some may be caught in moisture-filled subsurface spaces. Clifford (1966) collected L. fontinalis during the dry periods in both the "deep subsurface seepage and moist interstitial spaces". As he noted, these small spaces may be selective for smaller organisms. While the size of the space may be important, it is suggested here that the greatly increased probability of survival of the small Asellus sp. (pond) compared to larger individuals has adaptive significance since only small individuals occur in the population at the time the habitat dries up.

Poulson (1964) discussed the question of whether aquatic cave amphipods and isopods are more amphibious than episean forms. One of the physical factors of the cave environment is the occurrence of periodic floods (Poulson, 1964; Vandel, 1965, p. 382). Vandel (1965, p. 283) indicated that many aquatic cave organisms often leave the water. During the periods following flooding, aquatic organisms may be left stranded in small pools which dry up (Poulson, 1964) or may be left high and dry when the flood waters recede (Thomas C. Barr, Jr., personal communication). In either case, an organism that could tolerate a terrestrial, albeit near-saturated, environment would be at an obvious advantage. Steeves and Holsinger (1968) suggested that some species of subterranean isopods may inhabit "saturated crevices, fissures, and interstices". The data presented in Table 5 clearly show that Asellus sp. (cave) would be far more tolerant of such a situation than its epigeal relatives, and this would have considerable adaptive significance under the circumstances discussed.

SUMMARY

The isopod, Asellus intermedius, serves as an intermediate host of the acanthocephalan, Acanthocephalus dirus. The life cycle of the parasite has been studied in relation to its intermediate host. The isopod population first becomes infected with worm larvae in the summer. By the following March, as much as 60% of the isopod population is infected. Male and female isopods are equally susceptible to worm infection. The larger a female isopod is, the more likely it is that it will be infected, but for male isopods, the incidence of infection increased with increasing size of the isopod up to about 10 mm, after which the level of infection stabilizes at about 40%. Both male and female isopods carry significantly more worm larvae in the early part of the parasite's life cycle than in later months. Isopods that were heavily infected in the early part of the life cycle disappear from the population. It is suggested that the worm larvae cause a mortality of heavily infected isopods and this serves as an important means for the regulation of population density of the isopod population.

The presence of worm larvae affects the host's physiology. Infected isopods have a 31.3% higher metabolic rate than non-parasitized isopods. The thermal tolerance of uninfected isopods is significantly greater than parasitized isopods. Parasitized isopods survive longer out of water than non-parasitized isopods in 95% relative humidity conditions; the reverse is true in 100% relative humidity. The presence of worm larvae apparently causes a color change in the isopod host and increases the probability that the life cycle of the parasite will be completed.

Asellus sp. (pond) inhabits a vernal pond that becomes dry for a varying number of months each year. Its one reproductive period extends from March until May. This is the most fecund of the four species studied. This species has the fastest growth rate and shortest duration of embryonic development of the four species. These aspects of its physiology may be of considerable adaptive significance in enabling the population to complete its life cycle before the habitat dries up. Small individuals survive considerably longer out of water in 100% relative humidity than large individuals. This is thought to increase the probability of survival of individuals during the summer dry period.

Asellus sp. (cave) is a subterranean asellid which was collected from drain tile discharge. This species appears to breed only in the late spring and summer. It is a typical troglobitic organism exhibiting reduced fecundity, duration of development, growth rate, and greater sensitivity to temperature. This species survives out of water in 100% relative humidity considerably longer than the other species. It is suggested that this may be of considerable adaptive value after flood conditions in the subterranean environment.

Asellus intermedius inhabits a permanent creek. This species reproduces throughout the year. The young of spring and summer reproduce twice, but those that enter the population in autumn reproduce only once. Females reproducing in the summer are smaller than winter reproductive females. This has been shown to be due to a temperature effect on the time required to attain sexual maturity. There is a seasonal variation in the length-fecundity relationship of this species.

It is suggested that increased food supply in the autumn and winter underlies the increased fecundity seen at this time of the year.

Lirceus garmani was studied in a drainage ditch that dries up in the summer. It has one reproductive period each year, extending from January through July.

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