

LIFE HISTORY CHARACTERISTICS OF *THERMOSPHAEROMA*
THERMOPHILUM, THE SOCORRO ISOPOD
(CRUSTACEA: PERACARIDA)

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ABSTRACT

The endangered species (Federal endangered species list), *Thermosphaeroma thermophilum*, or "Socorro Isopod," is endemic to a small spring near Socorro, New Mexico, that is thermally stable year-round. Isopods were observed in the field, and monthly samples were collected between March 1978 and February 1979 for laboratory examination. Males were larger than females, and sex ratio in the habitat was consistently biased toward males, particularly when sexually receptive females were abundant. Reproduction occurred primarily, although not exclusively, in spring and fall. Food seemed scarce, and intense predation by the omnivorous isopods appeared to exclude most invertebrate species, including predaceous aquatic insects, from the habitat. Fish do not inhabit the spring and avian predation is minimal or non-existent, perhaps permitting isopods to reach high densities and decreasing risks associated with male mate-searching behavior. Field and laboratory data indicated that isopods live less than 1 year. Males grow and reach sexual maturity faster than females. No evidence of hermaphroditism or sex-change was observed. Females were iteroparous and brood size increased with a female's age, but females were small and varied little in size, suggesting selection for an optimal female size.

INTRODUCTION

The "Socorro Isopod," *Thermosphaeroma thermophilum*, has received considerable popular attention as a result of its recently acquired status as an endangered species (Federal Register, 1977). The isopod has only briefly been mentioned in scientific literature, however, and all previous investigations have been primarily taxonomic (Richardson, 1897, 1900, 1904, 1905; Van Name, 1936; Rioja, 1950; Cole and Bane, 1978).

Thermosphaeroma thermophilum is one of four congeneric species of freshwater sphaeromatid isopods inhabiting thermal springs in the southwestern United States and in Mexico (Cole and Bane, 1978). Life history data on North American freshwater isopods are limited to a handful of papers concerning asellote species (Allee, 1914, 1927; Markus, 1930; Hatchett, 1947; Ellis, 1961), thus, the biology of the entire genus, *Thermosphaeroma*, is virtually unknown.

Thermosphaeroma thermophilum is endemic to a single effluent near Socorro, New Mexico, in which it is one of the few permanent macroscopic animal species. This unusual ecologic situation imposes selective pressures rarely encountered by most organisms. In addition, the habitat is small, isolated and stable, making it

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possible to collect life history information easily and accurately in the field and in the laboratory.

MATERIALS AND METHODS

The habitat of *T. thermophilum* consists of two concrete pools and the plumbing system of an abandoned bathhouse called Sedillo (Evergreen) Spring (see Shuster 1979 for details). These impoundments were constructed in the early 1900's when the spring was used by local residents as a recreation site. Before that time, the spring issued from an underground gallery and flowed eastward toward what is now the city of Socorro. The range of the isopod then is unknown, but is not likely to have extended much beyond a point where water temperature remained stable year-round (see discussion). Much of the isopod population is now confined to the larger of the two pools (2.69 × 0.94 m), whose flat bottom is covered with 1–4 cm of finely divided substrate. Isopods burrow into this material during the day and emerge at dusk, frequently reaching high densities (210 individuals/100 cm²). Vegetation throughout the habitat is limited to an almost indistinguishably thin film of blue-green algae that covers most surfaces. Cottonwood, juniper, and mesquite stand near the spring and contribute detritus. Fish do not inhabit Sedillo Spring, and water in the spring appears deep enough (15–25 cm) to minimize or prevent predation by local birds such as sparrows or quail. Birds were never seen feeding on isopods in over 300 hours of observation (Shuster, 1979).

Field studies

With authorization by the New Mexico Department of Game and Fish, isopods were collected from the larger pool in the 3rd week of each month (except September and November) beginning in March 1978 and ending in February 1979. Water temperatures from three locations within the habitat (Fig. 1a) were taken on each collection date, as was the water temperature of a swimming pool continuous with, though located 20 m southeast of, the habitat. Isopod samples were taken in three random sweeps along the pool bottom with a fine-mesh, 100 × 150 mm square net, immediately placed in an insulated jug containing spring water, and transported to the laboratory, where they were sexed. Females were identified by the presence of a ventral brood pouch (marsupium) and were classified by reproduction condition as (1) gravid (females carrying young in the marsupium), (2) undifferentiated (females possessing marsupial lamellae but with little ovary or hepatopancreas development), or (3) mature (females with large yellow ovaries and a dark distinct hepatopancreas). Both ovaries and hepatopancreas were clearly visible through the ventral cuticle. Males were often larger than females, and possessed a bifurcate penis located medially on the seventh pereopodal segment. Testes were frequently visible through the cuticle in segments 5–7. Individuals less than 4.0 mm in length usually lacked sexual characters and were classified as immature. All mature individuals were measured (length × width) with calipers to the nearest 0.5 mm. This procedure gives a more accurate estimation of individual body size than merely measuring length or width (Thornhill, 1977, 1978, 1979), and accounts for slight differences in body size among individuals. While it may be argued that the use of area compounds the variance of the two measurements, the sizes of males and females were compared using a non-parametric Mann-Whitney *U* test, which does not consider assumptions about parameters such as variance (Zar, 1974).

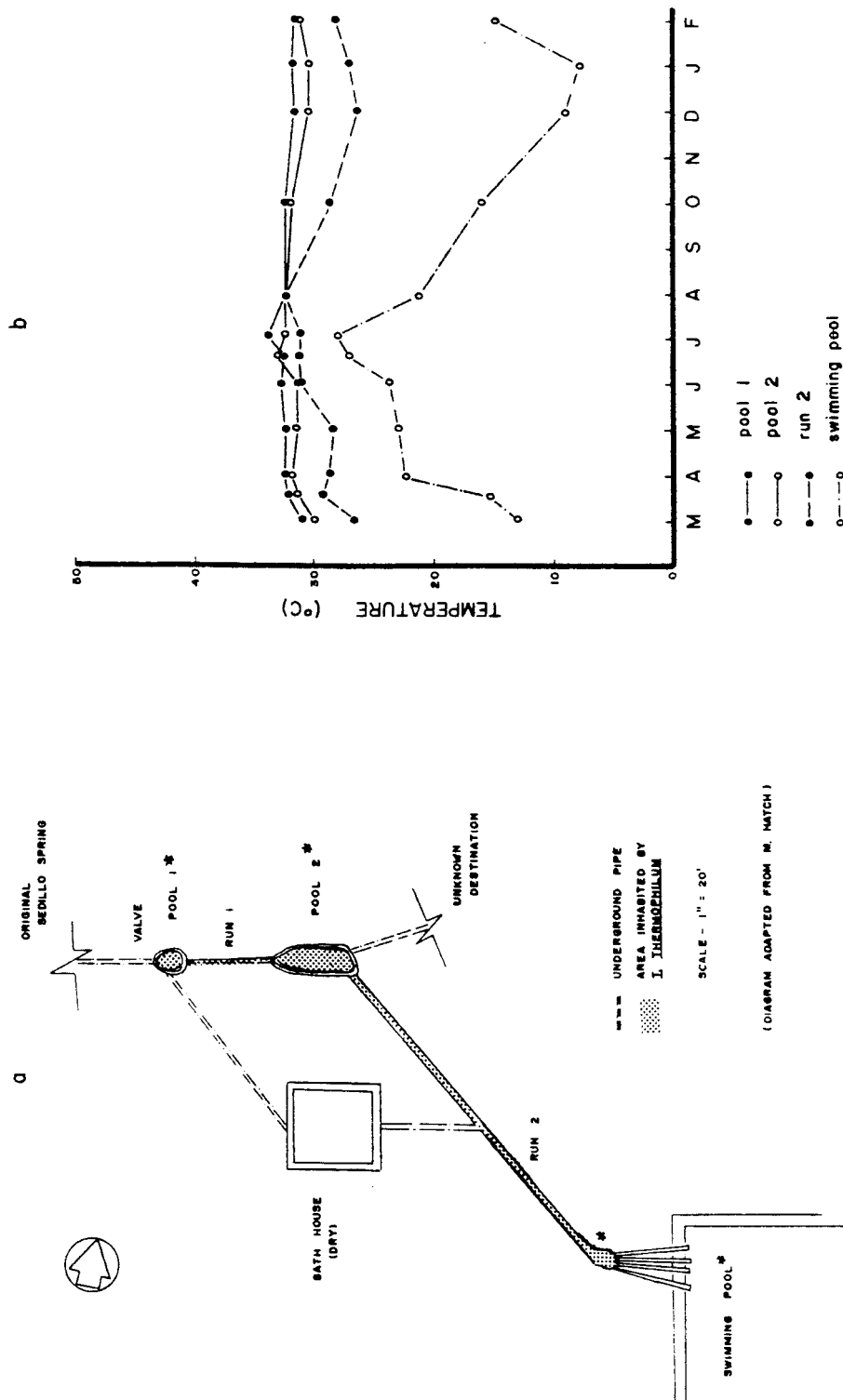


FIGURE 1. (a) The habitat of *T. thermophilum*. (*) indicate locations where water temperature was recorded. (b) Temperatures recorded at Sedillo Spring from March 1978 to February 1979.

The numbers, percentages, and size frequencies of males and females in each reproductive condition (gravid, undifferentiated, mature) were tabulated for each month, and sex ratios were calculated. The number of immatures was also recorded. Several individuals were then dissected and their gut contents microscopically examined, but most individuals were either placed in 35 l holding tanks or returned to the habitat. The feeding behavior of isopods was observed in the field.

Laboratory studies

Individual growth rates were investigated in the laboratory. Twenty-six gravid females were placed in separate chambers constructed of 75 × 100 mm square fish nets and suspended in 35 l aquaria. Water temperature was maintained at 31°C and several flakes of algae fish food (Tetra-min) were added to each chamber every 3–5 days. Algae usually began to grow on the nets within a week or two, and females fed on this growth. Thereafter, fish food was provided only if algae was sparse or absent. Broods were separated from females upon release and counted. Juveniles were measured (length × width) to the nearest 0.1 mm using an ocular micrometer and placed in 75 × 100 mm fish nets with siblings. Individuals were measured each week for 15 weeks, and the appearance of sexual characters was recorded as individuals matured. A logarithmic transformation was used to normalize body size data and growth rates for males and females were fitted to lines using multiple y-value linear regression. The slopes of these lines were compared with a *t* test.

After releasing a brood, each female was returned to her chamber with one mature male. Females were examined weekly for 20 weeks or until they died. Males were removed from chambers when females became gravid, and were returned after each brood was released. Broods were measured and counted as previously described.

RESULTS

Field studies

Temperatures in the portion of Sedillo Spring inhabited by *T. thermophilum* remained relatively constant throughout the year (27°–34° C, Fig. 1b). Temper-

TABLE I

Population demography of *T. thermophilum* collected between March 1978 and February 1979 (except during September and November.)

	Mar.	April	May	June	July	Aug.	Oct.	Dec.	Jan.	Feb.
<i>N</i>	84	162	68	78	147	148	90	80	121	66
No. males (%)	31(36)	128(79)	42(62)	53(68)	117(80)	110(74)	57(63)	47(59)	49(40)	44(67)
Mean male size (mm ²)	13.87	21.78	19.19	22.00	16.12	23.61	26.72	16.02	17.20	16.12
Variance	26.25	38.71	97.49	82.68	77.52	79.32	58.62	38.70	58.00	49.15
No. females (%)	25(30)	33(20)	17(25)	19(24)	23(15)	20(14)	30(33)	15(19)	26(22)	21(31)
Mean female size (mm ²)	10.77	11.27	12.03	12.62	13.87	13.84	15.36	12.47	10.68	8.53
Variance	1.87	6.57	3.79	3.12	2.85	4.18	2.61	7.10	10.68	8.53
No. gravid (%)*	6(24)	22(66)	3(18)	1(5)	2(9)	0(0)	11(36)	3(20)	3(12)	8(38)
No. undiff. (%)*	11(44)	5(16)	5(29)	8(42)	8(34)	4(20)	8(27)	8(53)	9(34)	4(19)
No. mature (%)*	8(32)	6(18)	9(53)	10(53)	13(57)	16(80)	11(37)	4(27)	14(54)	9(43)
No. immatures (%)	28(33)	1(1)	9(13)	6(8)	7(5)	18(12)	3(4)	18(22)	46(38)	1(2)
Sex ratio (m/f)	1.24	3.87	2.47	2.79	5.08	5.50	1.90	3.13	1.88	2.10

* Percentages of the total number of females in each sample.

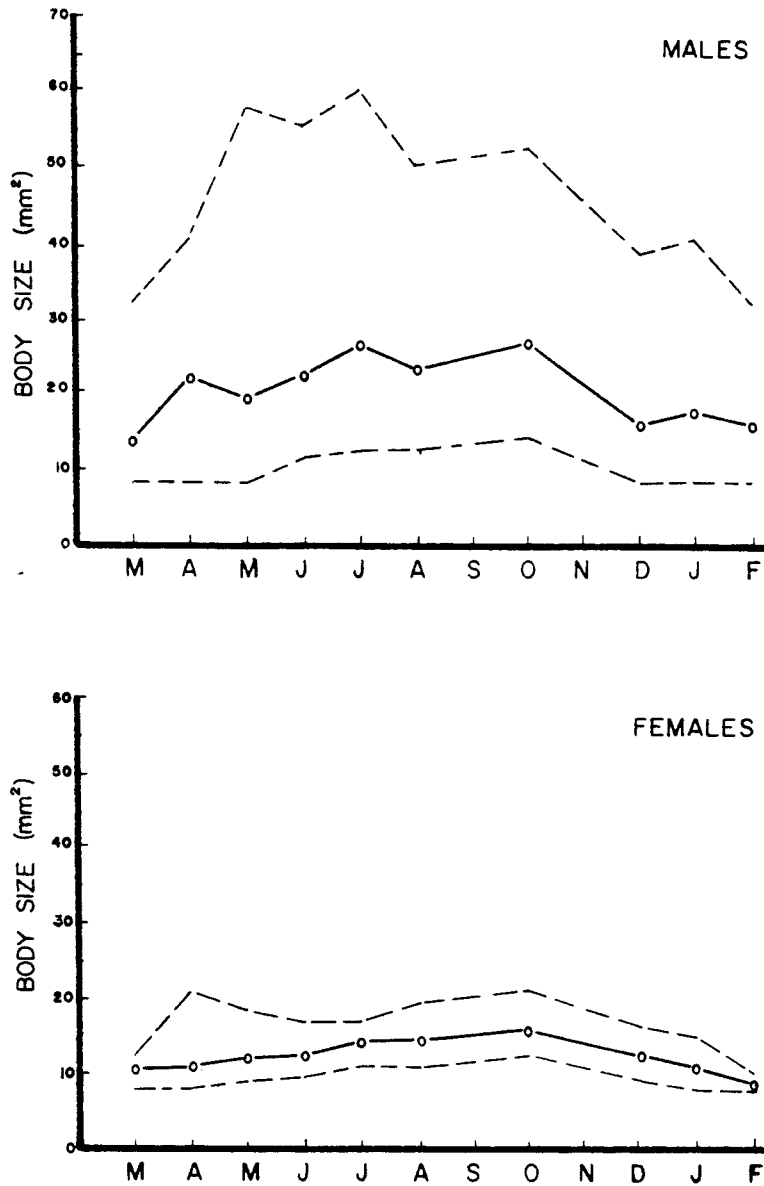


FIGURE 2. Maximum, minimum, and mean sizes of *T. thermophilum* males and females in field-collected samples from March 1978 to February 1979. Upper and lower dashed lines represent maximum and minimum size, respectively. The solid middle line represent mean size.

atures fluctuated considerably, however, in the swimming pool, which was not inhabited by isopods.

Table 1 summarizes data obtained from monthly samples. Males were consistently more abundant, and significantly larger, than females (males: range = 8.0–60.0 mm², median = 19.5 mm², $N = 678$; females: range = 8.0–21.0 mm², median = 11.9 mm², $N = 229$, Mann-Whitney U test, $P < 0.005$). Mean body size for both sexes increased from March to October, then decreased rapidly until February.

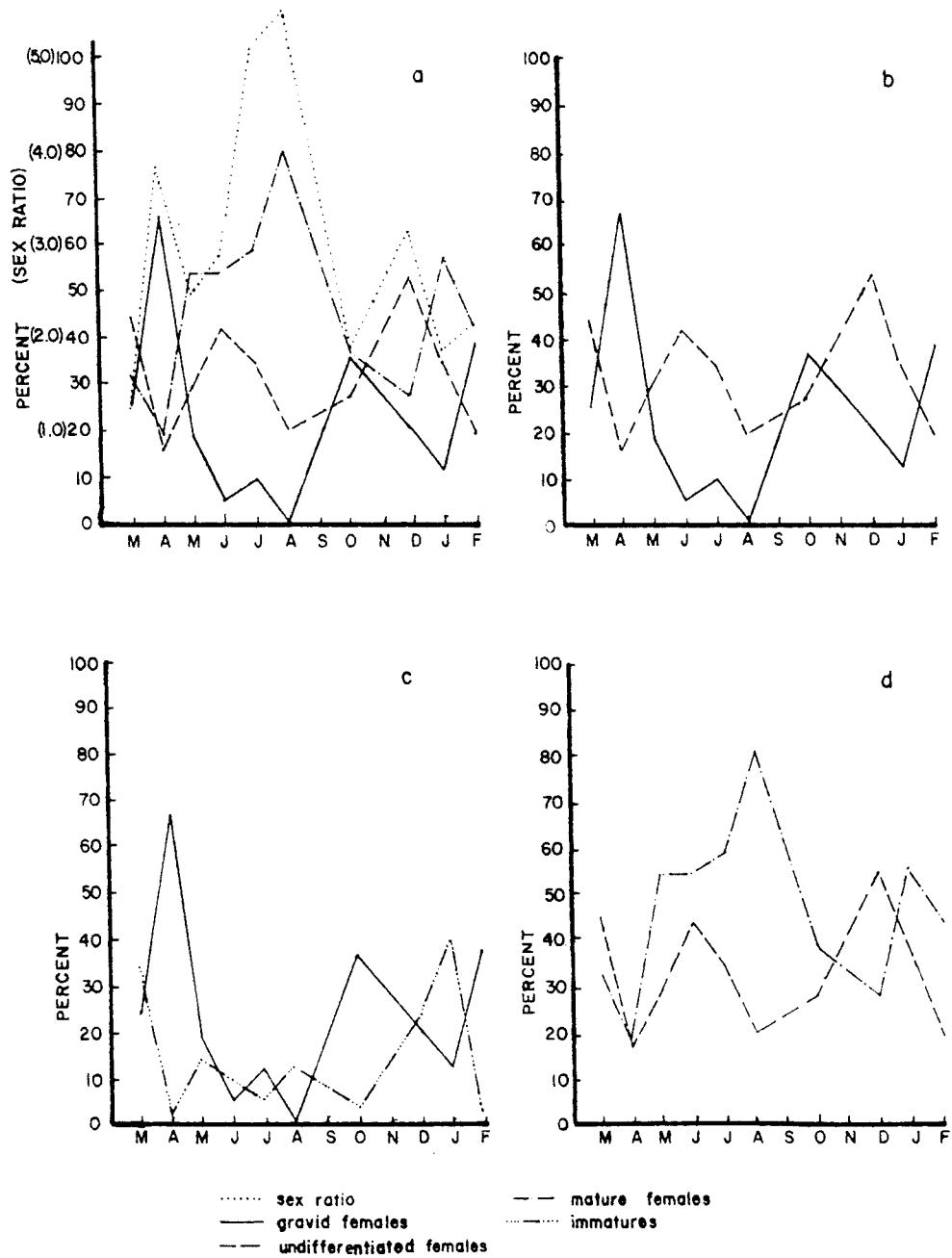


FIGURE 3. (a) Relationship between seasonal variation in sex ratio and seasonal abundance of mature, gravid, and undifferentiated females in field-collected samples from March 1978 to February 1979. Sex ratio is expressed as the number of males/the number of females. Each female type is expressed as a percentage of the total number of females in each sample. (b) Relationship between the seasonal abundances of gravid and undifferentiated females. (c) Relationship between the seasonal abundances of gravid females and immatures. Immatures are expressed as a percentage of the total number of individuals in each sample. (d) Relationship between seasonal abundances of mature and undifferentiated females.

This latter interval also included a conspicuous decrease in the maximum sizes of males and females (Fig. 2). Female size varied only slightly in all samples, but Male size varied considerably.

Sex ratio in the habitat fluctuated dramatically, yet, as mentioned, remained greater than 1:1 (Table I, Fig. 3a). The percentages of females in each reproductive condition also showed much variation. Percentages were used in the figure to represent the relative abundances of different groups, as sample sizes were somewhat unequal. Since percentage data may exaggerate certain relationships, the reader is urged to consult Table I for the actual numbers of individuals in each sample. Gravid females were present in all samples except August, and were particularly abundant in April and in October. As expected, peaks in gravid female abundance were followed by peaks in the abundances of undifferentiated females (Fig. 3b). The abundances of immatures, however, did not follow the abundances of gravid females as closely as expected (Fig. 3c). Mature females were particularly abundant between May and October, seemingly in excess of that expected, given the percentages of undifferentiated females prior to and during this interval (Fig. 3d).

The gut contents of field-caught isopods consisted of finely divided green material with fragments of what appeared to be arthropod cuticle. Two types of feeding behavior were observed in the field: (1) isopods dispersed across the walls and floor of the pool in late afternoon, apparently grazing on blue-green algae, or on bits of grass and other organic debris that had fallen into the water; (2) isopods inadvertently injured in sampling were consumed in "feeding frenzies" by conspecifics. Since injuries occurred on several occasions, I was able to observe such interactions fairly closely. Injured individuals were located within 1–2 min by other isopods, who immediately began feeding on the still-struggling casualty. As more isopods arrived, presumably cueing on blood diffusing into the water, a cluster of 10–30 isopods formed, all vigorously competing for access to the carcass. Individuals on the outside of the cluster would grasp the anterior end of established individuals and peel them backward and off the pile, then rapidly assume the position of the displaced individual. Larger isopods seemed most successful at this maneuver. All carcasses were stripped clean, and the feeders dispersed within 1 h.

I also observed two apparently uninjured isopods and two libellulid dragonfly nymphs attacked and consumed in aggregations similar to that described above. Only one intact nymph was ever obtained from sweep samples, although pieces of arthropod cuticle were often found. Other live invertebrates collected in samples were one dytiscid beetle, one belostomatid bug, and numerous oligochaete worms. The five arthropods collected or observed, other than isopods, were less than 5.5 mm in length.

Laboratory studies

A survivorship curve for lab-reared individuals is shown in Figure 4. Nearly 95% died within 15 weeks. Individuals reached sexual maturity between 4 and 11 weeks, and males seemed to mature more rapidly than females (Fig. 5). Males also grew more rapidly than females (*t* test, $P \ll 0.001$, Fig. 6). No evidence of hermaphroditism or sex-change was observed in this species.

Females are iteroparous and all gravid females (26 original females plus 4 producing more than one brood) released broods between 18 and 51 days after isolation ($\bar{X} \pm SD = 27.30 \pm 7.19$ days, $N = 30$). Of the 26 gravid females first isolated, four died after releasing young. The ovaries of all remaining females (22) became secondarily mature between 18 and 50 days ($\bar{X} \pm SD = 35.0 \pm 12.71$

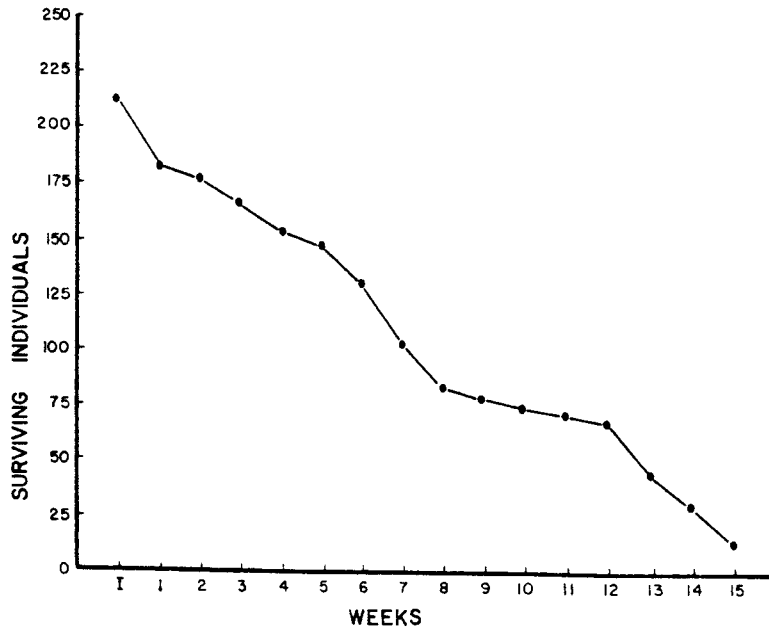


FIGURE 4. Survivorship curve for lab-reared *T. thermophilum*.

days). A heater malfunction killed 5 females, leaving 17, and 4 of these 17 were removed for use in another experiment (Shuster, unpublished). Five of the remaining 13 females became gravid, and 3 of these 5 released a second brood. In all cases, the second brood was larger than the first (Table II).

The ova of females not becoming gravid were apparently resorbed, as were the broods of the two gravid females which did not release offspring. The latter two

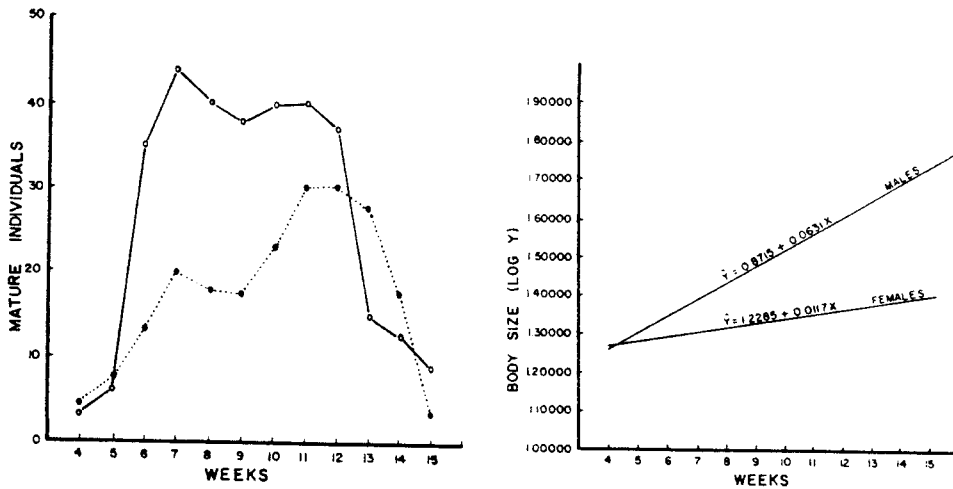


FIGURE 5. Maturation rates for lab-reared *T. thermophilum* males and females. Solid line represents males; dotted line represents females.

FIGURE 6. Growth rates for lab-reared *T. thermophilum* males and females. The slopes of these lines are significantly different (*t* test, $P \ll 0.001$).

TABLE II

Body sizes* (in mm²) and brood sizes of females that produced more than one brood in the laboratory.

Female	Initial size	1st brood (# ind.)	Size after next molt	2nd brood (# ind.)	Size after next molt	3rd brood (# ind.)
C1	12.5	6	16.5	15	—	—
D6	12.5	11	—	—	—	—
A3	12.5	10	—	—	—	—
A4	8.0	6	11.25	9	—	—
B2	11.25	9	15.0	14	19.25	20

females died before their ovaries matured again. The ovaries of two of the three females which released a second brood matured, and one of the two became gravid a third time and released a third brood. This brood was larger than the female's two previous broods (Table II).

DISCUSSION

Most of Sedillo Spring is thermally stable year-round. Temperature fluctuations in most areas inhabited by *T. thermophilum* were 30°–33° C, and water temperature never dipped below 27°C, even at the lower end of the habitat. Isopods do not inhabit a nearby swimming pool where water temperature was considerably lower than in the rest of the spring and varied with ambient air temperature. This suggests that *T. thermophilum* (and probably other *Thermosphaeroma* species) is adapted to thermally stable conditions, and that the range of this species was restricted long before the habitat was modified by man.

Sexual dimorphism in this species is pronounced. I demonstrated earlier (Shuster, 1981) that male-male competition in *T. thermophilum* is intense, and that large males are more successful at obtaining high-quality females (relative quality defined in terms of fecundity and proximity to a sexual molt) as mates than small males. Hence, large male size in this species may be considered a sexually selected attribute. Hansen (1906) states that sexual size dimorphisms are widespread among the Sphaeromatidae. Although behavioral ecology and sexual selection are not often the focus of most isopod research (but see Manning, 1975; Magniez, 1978; and Ridley and Thompson, 1979), I suggest that sphaeromatid sexual dimorphisms are largely, if not exclusively sexually selected (see Veuille and Roualt, 1980), and the family as a whole may provide numerous tests of present evolutionary and sexual selection theory.

Males were more abundant in the habitat than females, and were frequently observed roaming across the pool bottom. Trivers (1972) predicted that males may enhance their reproductive success by searching for mates, even when the costs of searching are high (see Thornhill, 1979; Gwynne and O'Neill, 1980). If such male behavior has been favored in this species, as is reasonable given a high degree of intrasexual competition and relatively low predation risks (see below), sweep samples are likely to have included a disproportionately large number of males.

The tremendous fluctuations in the abundances of females in various reproductive conditions (Figs. 3b–d) are puzzling and remain largely unexplained. One relationship, however, is clear: gravid females were present in all samples except one, and were particularly abundant in spring and in the fall. This suggests that while reproduction is somewhat seasonal, females reproduce year-round. As ex-

pected from laboratory data, peaks in the abundances of undifferentiated females followed peaks in gravid female abundance by about one month. Unexpectedly, however, the number of immatures in May was quite low, perhaps indicating a period of unusually high juvenile mortality. Unfortunately, I have no data to defend or refute this possibility.

Mature females occurred considerably more frequently in samples than expected between May and October, and sex ratios were periodically highly skewed (not merely biased) toward males. Since undifferentiated females become mature within 1-2 months, the dramatic August peak in mature female abundance should have been preceded by a similar peak for undifferentiated females, perhaps in June or July. While an increase in undifferentiated females was observed in June, it was numerically insufficient to account for the later boom of mature females.

Males guard females before copulation in this species, and prefer females with mature ovaries (Shuster, 1981). Since males apparently determine the reproductive condition of females at close range (*i.e.* by grasping and manipulating them), males routinely grasp nearly every object that is about the same size and shape as a female isopod. Objects or individuals other than mature females are soon discarded, and the male continues searching. Parker (1974) suggested that male guarding behavior could be detrimental to females because of lost feeding time and possible injury, and therefore proposed that these costs should be incurred only by females that are ready to copulate. In turn, non-receptive females should leave areas of high male density. If mature (receptive) females in this species seek areas of high male density, they may have been sampled more frequently than expected, producing the anomalous relationship between undifferentiated and mature females in Fig. 3d. Concurrently, increased mature female abundance may have precipitated intensified male mate-searching behavior and skewed the August sex ratio sharply toward males (5.50:1, Table I).

The frequency of mature females in April and in December was low, and this, combined with emigration of undifferentiated and gravid females from areas of high male density (by burrowing or hiding in cracks) could also have skewed the sex ratio toward males. If this occurred, however, one might expect an overall decrease in the number of females contained in samples from April and December. This is not readily apparent in Table I. More intensive sampling, especially in potential refugia for non-mature females, may shed light on this matter.

Thermosphaeroma thermophilum is omnivorous. Gut contents consisted of vegetable and animal material, and isopods were observed feeding on both substances in the field. The paucity of vegetation in the spring, and especially the voracity with which isopods consumed their conspecifics and other animals, suggest that food is scarce, or at least that individuals able to obtain such resources gain sufficient fitness to justify vigorous contests for food. Brues (1932) reported considerable diversity of invertebrate species in thermal springs with physical characteristics similar to those in Sedillo Spring. That such diversity in this spring was lacking, suggests that colonizing invertebrates, including young predaceous aquatic insects, are rapidly extirpated via predation by isopods. This, combined with a lack of fish and avian predators, may reduce the costs of male mate-searching behavior. Low predation pressure may also permit isopods to reach high densities in the habitat, and limit surplus food.

That mortality among lab-reared individuals was nearly 95% in 15 weeks is by itself inconclusive. Isopods were maintained under somewhat unnatural conditions (in chambers). The proximity of other individuals could have depressed growth and maturation rates, or increased mortality. Alternatively, a predictable food source

may have enhanced growth and extended lifetimes, although this is doubtful. Field data, however, indicate an 8-month interval during which the mean and maximum sizes of males and females increased. This may represent the collective growth of a large group of individuals, perhaps a cohort produced by spring reproduction. The period of growth was followed by a 4-month interval in which mean male and female sizes, and numbers of large individuals, decreased. The rapid decrease in mean sizes could have resulted from recruitment of small individuals produced by fall reproduction alone, but the loss of large individuals indicates mortality. A longer study could elucidate a precise figure for longevity in this species, but it seems safe to state that most individuals live about 8 months or less, and certainly less than 1 year.

While confinement may have affected the longevity and overall growth rates of lab-reared individuals, the *relative* growth rates of males and females are not likely to have been significantly altered. Males grew more rapidly and reached sexual maturity sooner than females. Since male-male competition in this species is high, and since large size confers a reproductive advantage to males, the selective context for rapid growth and maturation rates among males is clear.

Hermaphroditism and sex-change have been reported in certain isopods (Cy-mothoidae; Richardson, 1905), but neither condition was observed in this species. Both hermaphroditism and sex-change are restricted primarily to parasitic species, or species with a history of reduced effective population size and/or highly skewed operational sex ratios (Ghiselin 1974). Such conditions are unlikely for *T. thermophilum*, or for that matter, for any other free-living, freshwater isopod species.

Female reproductive strategies in this species are likely to be complex given the array of female attributes that seem related to variable reproductive effort. Iteroparity and the ability to resorb developing young certainly indicate that females can reallocate reproductive resources when conditions (environmental and physiological) become unfavorable (see Lawlor 1976). Females produce larger broods as they age and grow, a relationship usually explained as a consequence of increased ovary and marsupium size, and one that implies selection for large females. Females in this species, however, are surprisingly small. In addition, variability in female size is low, and is considerably less than variability in male size. Downhower (1976) has indicated that in finches (Geospizinae), selection favors small females in habitats where food is scarce because small females accumulate sufficient resources for reproduction faster and more frequently than large females. If small female size is favored in *T. thermophilum*, females may place less energy into growth than other isopod species (Lawlor 1976) and may reproduce relatively continuously rather than seasonally. Although this seems to fit the data presented here, information on resource availability in Sedillo Spring, and on relationships between growth, energy storage and reproductive patterns in females are necessary to determine if the hypothesis is appropriate.

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