

The role of controlled propagation on an endangered species: demographic effects of habitat heterogeneity among captive and native populations of the Socorro isopod (Crustacea: Flabellifera)

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Abstract. The Socorro isopod, *Thermosphaeroma thermophilum*, became the focus of a novel conservation strategy when apparent extirpation of the species from the wild prompted construction of the Socorro Isopod Propagation Facility (SIPF) near the native spring in Socorro, New Mexico, USA. We subjected captive populations to 4 habitat treatments over 2 consecutive 50-month experimental trials. Native populations of *T. thermophilum* remained significantly more abundant than captive subpopulations during the 100-month study. Population trends among artificial habitats differed slightly between the trials, but the magnitude of this difference was independent of linear flow within either pool series, suggesting that captive isopods responded to habitat quality. Isopod age structure was most heterogeneous in pools with plants suggesting that vertical structural diversity is necessary to maintain long-term viability of *T. thermophilum* in captivity. Observations of 'breeding huddles' in the SIPF pools implied that controlled propagation may affect the social basis of the species' mating system. This could be a behavioral response to selection on body size that may reduce predation risks from larger male cannibals, or to increase fitness of both sexes under spatially altered sex ratios of artificial environments. Our results accentuate the need for continued research on species-specific management practices for geographically restricted invertebrate taxa such as the endangered Socorro isopod.

Introduction

The conservation and management of rare species is a core theme of conservation biology (Soulé and Wilcox 1980; Caughley and Gunn 1996; Meffe and Carroll 1997; Primack 1998). Rarity itself imposes problems to managers not only in the long-term preservation of species and ecosystems, but also in the shorter-term evaluation of appropriate population management strategies where ecosystem degradation and loss have rendered native habitats unsuitable.

Under such circumstances, human intervention through captive breeding programs has been adopted as an emergency measure to prevent extinction. Captive breeding programs typically focus on genetic aspects of long-lived vertebrate taxa considered globally rare or 'endangered' (Conway 1980, Loftin 1995). Many of these endangered species are poorly suited to manipulative experiments designed to evaluate the most parsimonious management regime, since populations often are too small for suitable replication. Invertebrate species, however, lend themselves readily to experimental management due to their rapid turnover rates and small body size, which facilitate population and habitat manipulations under controlled conditions.

Isopods in the genus *Thermosphaeroma* occur in isolated thermal springs of North America (Richardson 1897; Bowman 1981, 1985; Shuster 1981a, b; Schotte 2001). Of the eight described species, *T. thermophilum* is the best known (Shuster 1981a, b; Davis 1996; Jormalainen and Shuster 1997, 1999; Jormalainen et al. 1999; Ketner et al. 2002, Shuster et al. 2005). This species is endemic to a single thermal spring near Socorro, Socorro County, New Mexico, representing the northwestern extent of the genus.

Iteroparous females reproduce year-round with reproductive peaks in spring and fall. Gestation in *T. thermophilum* lasts approximately 3 weeks and brood size is positively correlated with female body size; larger, longer-lived females produce up to 3 broods of 6–20 neonates. Juvenile *T. thermophilum* reach sexual maturity within 6–8 weeks; males mature more rapidly than females. Isopod longevity is estimated at < 1 year (Shuster 1981a, b).

Socorro isopods are crepuscular (Shuster 1981a). The more active mate-seeking males roam the substrata in search of, or while in breeding pairs with, pre-molt females (Shuster 1981b, Jormalainen and Shuster 1999). While males are larger than females in all *Thermosphaeroma*, dimorphism is most pronounced in *T. thermophilum* (Shuster, unpubl. data). The male-biased population structure of *T. thermophilum* (♂:♀ ratios of 4.44:1; Shuster 1981a) has a mating system characterized by isolated breeding pairs with intense male–male competition for mates (Jormalainen et al. 1999). Larger body size evidently confers increased reproductive fitness in both sexes by maximizing fecundity (Shuster 1981a, b) and minimizing precopulatory mate guarding time (Jormalainen and Shuster 1999, Jormalainen et al. 1999).

The omnivorous *T. thermophilum* feeds on detritus and algae (Shuster 1981a), but also preys on aquatic insect larvae (libellulid odonate nymphs), oligochaete worms (*Tubifex* sp.), and conspecifics. Compared to congeners, this species is highly cannibalistic (Shuster 1981a, b; Jormalainen and Shuster 1997; Shuster et al. 2005).

Jormalainen and Shuster (1997) documented age-, size-, and sex-specific microhabitat segregation in native and captive *T. thermophilum*. In their native spring, mancas (undifferentiated juveniles) occurred primarily on vegetation, whereas adult isopods were most common on benthic substrata; females frequented vegetation more often than males. In aquaria without a refuge chamber, males cannibalized females, adults of both sexes cannibalized man-

cas, and mancas cannibalized each other, even when alternative food was present. Such evidence of age-, size-, and sex-specific microhabitat segregation and predation risks associated with cannibalism implies that habitat heterogeneity may play a critical role in the viability of native and captive subpopulations of this endangered species.

Conservation efforts

The extremely limited range of this species and threats to its native habitat led to its listing as endangered in 1978 (Federal Register 1978). The primary objectives of Socorro Isopod Recovery Plan (USFWS 1982) were to prevent extinction of the species by stabilizing and enhancing the aquatic habitat of the native spring, and to initiate recovery of the species by maintaining captive populations.

In August 1988, *T. thermophilum* was apparently extirpated in the wild when diminished discharge of the native spring resulted in desiccation of the rheocrene. Spring flow was reestablished in September 1988, which likely flushed isopods from the underground plumbing system into the native spring system. The native population was augmented a month later from a captive population housed at the Department of Biology, University of New Mexico. This near extinction event prompted the City of Socorro and resource agencies (United States Fish and Wildlife Service, New Mexico Department of Game and Fish), ascribed with protection of this endangered species, to build the Socorro Isopod Propagation Facility (SIPF) near its native habitat. Upon completion of this facility in 1990, controlled propagation of *T. thermophilum* commenced to increase the available habitat.

Shuster et al. (2005) assessed the genetic consequences of multiple population bottlenecks (natural and induced) in this species. Although genetic divergence among captive subpopulations was not significant, the pattern of differentiation was consistent with the direction of downstream water flow through the SIPF, which was indirectly related to habitat heterogeneity in the experiment. Furthermore, body lengths of captive isopods increased nearly two-fold from the natural population, and over a shorter time period the rate of body size increase, evidently a selective response to avoid cannibalism, was inversely proportional to the type of physical structure added to artificial pools (Shuster et al. 2005).

Here we examine the demographic response of captive populations of *T. thermophilum* exposed to 4 artificial habitat treatments replicated over two 50-month experimental periods. We compare quantitative measures of population density and age structure among the managed subpopulations using the native population as a demographic baseline.

Material and methods

*The natural spring*¹

The natural spring system of *T. thermophilum* is supplied from deeply derived thermal waters associated with the Socorro Thermal Area (Summers 1976). Available habitat consists of 2 small, concrete pools and the plumbing system of an abandoned bathhouse. This spring system was variously modified in the early 1900's for use by local residents as a recreation site. The extant population of *T. thermophilum* occurs throughout the entire 50 m reach of the spring system. Habitat diversity is limited to a narrow (15–90 cm), shallow (0.5–15 cm) stream with an oval-shaped, concrete pool (0.9 w × 2.7 l × 0.2 d m) located in the upper third of the spring brook. Lotic habitat upstream of this pool is restricted to a small run (0.24 w × 0.75 l m) consisting of sand substrate ('valve' site) where groundwater discharges. Water then flows downstream from the valve site via a 10 m buried pipe that discharges to the concrete pool ('pool' site) where more lentic flows and greater cover (e.g., deep aqueous silt, rocks, an emergent monocot, *Distichlis* sp.) support higher abundances of isopods. Outflow from the pool is channelized into an open pipe (30 l m) open pipe that has filled with sand, gravel, and woody debris; discharge throughout this reach consists of broad, shallow flows interspersed within the channelized spring run ('run' site).

Socorro isopod propagation facility (SIPF)

The SIPF (Figure 1) consists of 2 series (North and South) of 4 rectangular pools (0.53 w × 1.63 l × 0.75 h m). These pools were designed to approximate dimensions of the natural habitat (pool site), and are supplied with groundwater from the natural spring at a rate of 0.02 m³/min. Each series of pools (North 1–4; South 1–4) is connected by PVC pipe (3.2 cm dia.) to create a through-flowing system that drains to a leach field. The lack of genetic differences among captive subpopulations suggests that isopods move between pools (Shuster et al. 2005).

In September 1990, 600 isopods were introduced to the SIPF (75 isopods/pool). Monthly management began in December 1994 when efforts focused on stabilizing winter water temperatures of the SIPF pools to eliminate annual die-back of isopods in downstream (cooler) pools. By spring 1995, isopods in the South series had been extirpated, whereas those in the North series stabi-

¹In accordance with the private land owner's request not to release 'confidential data' regarding the specific location of the Socorro isopod population, and pursuant to the New Mexico Wildlife Conservation Act (Sections 17-2-37 through 17-2-46 NMSA 1978), section 19.33.4.8 ('Release of Confidential Data Regarding Endangered Species'), we refer to the species' type locality (Richardson 1897) as a 'thermal spring', 'native habitat', 'natural spring', or variant thereof (e.g., 'native population'), since some data presented here are from the native habitat which post-date passage of this regulation on 14 April 2000.

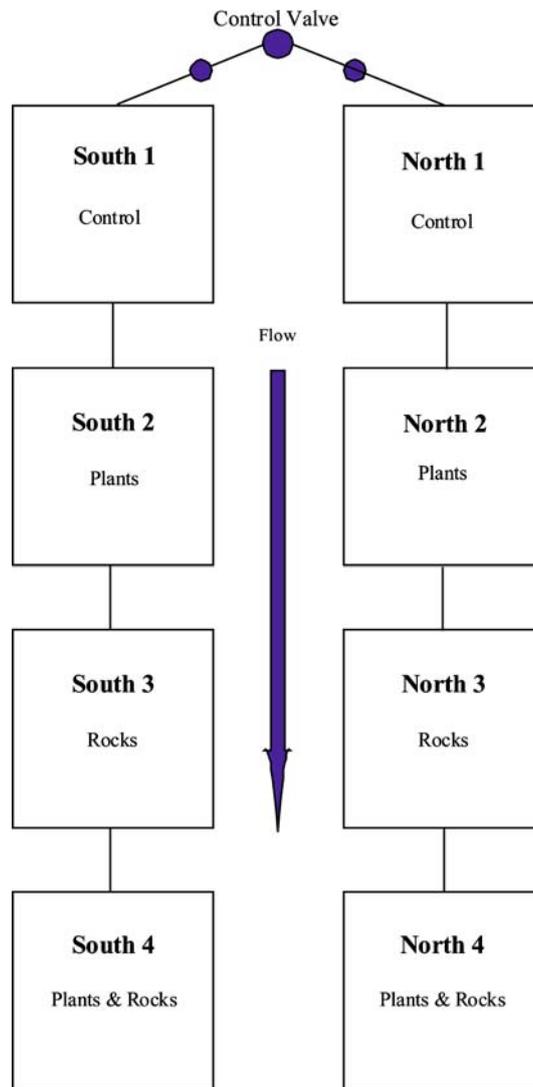


Figure 1. Socorro Isopod Propagation Facility (SIPF) design.

lized, and monthly demographic monitoring began there in July 1995. As part of an experiment to quantify the effects of habitat structure on isopod numbers in artificial habitats, 4 treatments were introduced in the SIPF North pools in April 1997; specifically, plants were added to North Pool 2 (N2), rocks added to North Pool 3 (N3), and both plants and rocks added to North Pool 4 (N4). No modifications were made to North Pool 1 (N1), which served as our experimental control. Monitoring was terminated in August 1999 when habitat degradation led to extirpation in the north series (Lang 2001).

We replicated this experiment in the SIPF South pools (S1–S4) with 400 isopods (100 individuals/pool) introduced from the native population over the period March–May 1999. Population monitoring in the South pools, without habitat treatments, started in August 1999. Within 6 months, the founding isopod populations of all South pools showed a marked decline in density, especially among manca, and evidence of increasing male and female body sizes (Lang pers. obs.). Habitat treatments were initiated in the South pools in November 1999 to salvage the experiment. We report population data from the South pools (August 1999 to September 2003) over a similar time period as in the North pools (50 months).

Thus, our study occurred over a 100-month period, evenly divided among North and South pools; an unanticipated die-off of the South pool populations during winter 1995 precluded simultaneous replication (*sensu* Hurlbert 1984) among pool systems. During the entire study (July 1995 to September 2003), we monitored the native population as a natural control using the sampling protocol described below.

Monthly sampling protocol

Densities of *T. thermophilum* were estimated by direct count of live individuals from 3 benthic samples and 3 sweep net samples per pool type (N1–4, S1–4, native pool). Due to indurate substrata of shallow lotic habitats in the native spring, we limited sampling to a single benthic grab at the valve and run sites from May 1997 to September 2003. In all samples, we recorded isopod age classes as either adult (> 2.1 mm total length) or manca (< 2.0 mm TL). Isopods were returned live to their site of origin following counts.

Sweep samples were effected by dragging a fine mesh aquarium net (10.4×12.7 cm) for 1.0 m throughout the water column. Isopods from each sweep sample were washed into a white tray and enumerated by age class.

Benthic samples were collected in a stratified random design from distinct areas in each SIPF pool and in the natural pool site: the first grab sample was taken from a corner of the pool (BG1), the second from the middle (BG2), and the third from one side of a pool (BG3). The benthic sampler consisted of a customized stainless steel basket ($5.08_w \times 7.62_l \times 2.54_h$ cm) lined with a fine screen (mesh: 0.69 mm; gauge: 0.58 mm) and a 6 mm groove welded on three sides. Benthic samples were collected by inverting the sampler, grooved-side down, into the substrate and sliding a stainless steel top into the groove. Organic material and substrate were washed from the basket, and isopods were flushed into a white tray for enumeration by age class.

Physicochemical conditions (water temperature, pH, salinity, specific conductance, total dissolved solids and dissolved oxygen) were measured monthly from 1996 to 2000 with a Hydrolab Recorder[®] at each sample site. Temperature loggers (Onset Optic StowAway[™]) were deployed for unattended hourly

measurements in pool habitat of the natural spring and pool 4 of the North and South series from 1996 to 2000.

Data analysis

Data were analyzed using fixed effects (Model 1) analysis of variance (ANOVA; Zar 1999) with sample type (benthic vs. sweep samples), pool series (North vs. South), pool (N1–4, S1–4, natural), and date as independent factors, and isopod density (benthic samples = no. isopods m^{-2} ; sweep samples = no. isopods m^{-3}) as dependent factors. Specifically, we examined age-specific microhabitat segregation of *T. thermophilum* in artificial and native habitats, short- and long-term demographic patterns of captive isopod populations in response to induced habitat manipulations, and overall experimental results of controlled propagation as an effective method for management of this endangered species.

Isopod habitat use

Because *T. thermophilum* has been reported to segregate habitat by age classes (Jormalainen and Shuster 1997), we examined age structure in benthic and sweep samples using one-way ANOVA with a priori contrasts (using least-squares means) of isopod age class (adult, manca) by sample type (benthic, sweep); north and south series were analyzed separately. For the native pool and for all pools in each series, we tested for microhabitat segregation within substrata using two-way ANOVAs to compare benthic sample site (e.g., corner, middle, side) and age class as independent factors with interaction. Within the native spring system, we assessed habitat segregation by age class using a two-way ANOVA comparing the effects of sample site (valve, pool, run) and age class with interaction from benthic samples.

Habitat treatments: demographic effects

With the initiation of habitat treatments in pools 2–4, pool 1 in each series (North, South) served as the experimental control during each 50-month study period. We assessed the short-term effects of the North series habitat manipulations on adult and manca isopods with a two-way ANOVA on ages vs. treatments. We quantified temporal variability in estimated population sizes with coefficients of variation (CV), and tested within pool series (North, South) with chi-square tests (Zar 1999).

Efficacy of controlled propagation

We evaluated the efficacy of habitat modification by combining age classes and testing for differences in total population size among treatment pools and the

native spring. We treated pool (N1–4, S1–4) and sample type (benthic grab vs. sweep sample) as fixed independent factors in one-way ANOVAs, and compared each pool series separately since these were not concurrent.

Results

Physicochemical environments

Physicochemical environments were similar in native and artificial pool habitats (see Appendix 1) throughout the study. Specific conductance varied within the native habitat sites because shallow lotic habitats (valve and run sites) required measurement with a calibration cup (no stirrer attached) rather than complete immersion of the instrument (stirrer attached) into the water column. Thermal profiles ranged narrowly within and among all pool habitats. The native pool was the coolest (mean $T = 28.93 \pm 0.0^\circ\text{C}$; $n = 20,544$ measurements) and most stenothermic (range = $24.52\text{--}32.51^\circ\text{C}$) of all habitats. The thermograph of pool N4 (mean $T = 30.80 \pm 0.02^\circ\text{C}$; range $T = 23.31\text{--}35.36^\circ\text{C}$; $n = 20,544$) closely tracked that of pool S4 (mean $T = 30.88 \pm 0.01^\circ\text{C}$; range $T = 24.52\text{--}32.74^\circ\text{C}$; $n = 7944$).

Isopod habitat use

Benthic and sweep samples yielded different proportions of adults and mancas (Figure 2). Adult isopods were significantly more abundant than mancas in benthic substrata of the North pools ($F_{[1,1199]} = 9.11$, $p < 0.003$) and the native pool ($F_{[1,581]} = 321.65$, $p < 0.0001$), but not in the South pools ($F_{[1,1199]} = 3.17$, $p = 0.753$; Figure 2a). In contrast, sweep samples were dominated by mancas in both the North ($F_{[1,1199]} = 53.83$, $p < 0.0001$) and South ($F_{[1,1199]} = 69.94$, $p < 0.0001$) pools, but adults were more abundant in sweep samples from the native pool ($F_{[1,581]} = 208.36$, $p < 0.0001$, Figure 2b).

Within the SIPF, adults and mancas segregated benthic microhabitats of the pools in predictable patterns, with the highest densities in corner benthic samples of all North ($F_{[2,1199]} = 5.85$, $p = 0.003$) and South pools ($F_{[2,1199]} = 33.47$, $p < 0.0001$, Figure 2c). The age structure in these high-density sites was significantly ($p < 0.05$) dominated by adults that were concentrated in large aggregations (i.e., range = $75\text{--}227$ isopods/ 38.71 m^2) of isopods ('breeding huddles') consisting of breeding pairs admixed with single males and gravid or ovigerous females. In contrast, isopods in native habitat were significantly more abundant ($F_{[2,581]} = 4.90$, $p = 0.0078$, Figure 2c) in the middle and side of the pool than in the pool corner; this was true for adults but not for mancas.

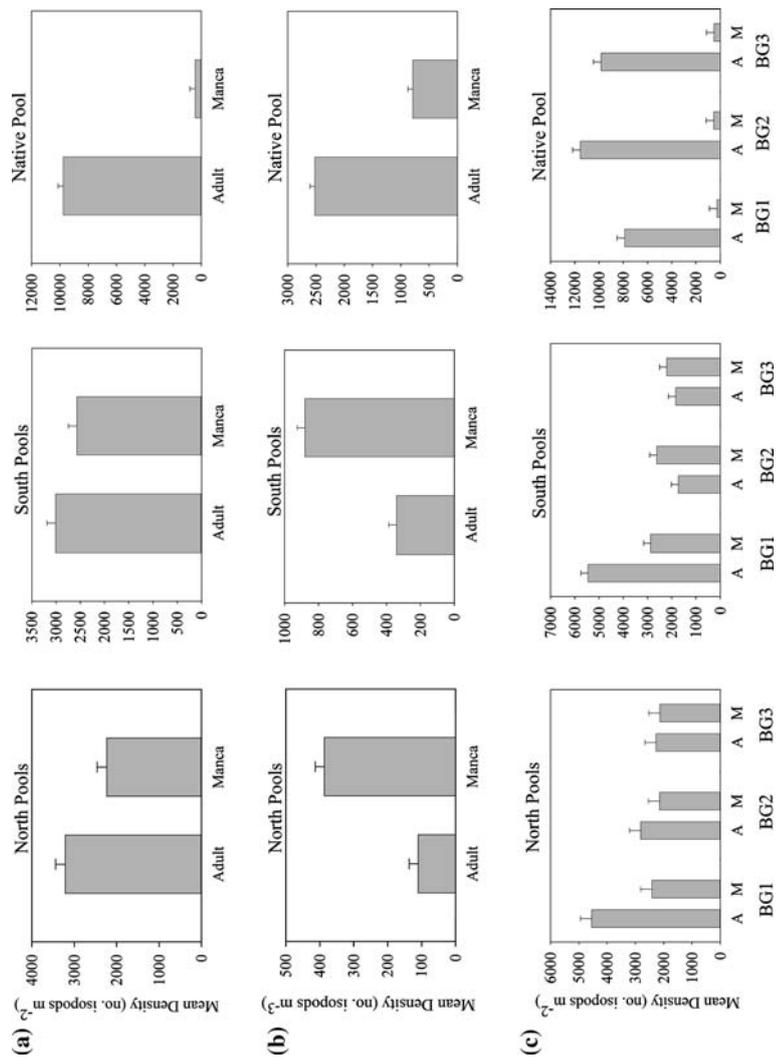


Figure 2. Age structure (A = adults, M = mancas) of *T. thermophilum* (mean density \pm SE) in the SIPF north and south pools (all pools combined within a series) and native pool by (a) benthic sample (no. isopods m⁻²), (b) sweep sample (no. isopods m⁻²), and (c) benthic grab location within a pool (BG1 = corner, BG2 = middle, BG3 = side).

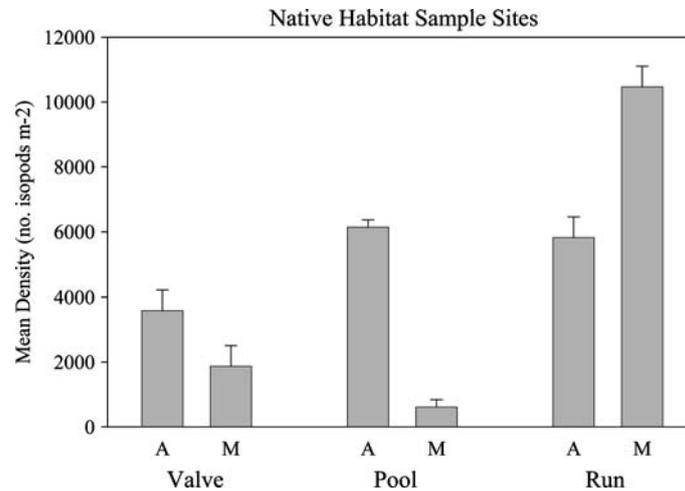


Figure 3. Age-specific habitat segregation represented as mean density \pm SE (no. isopods m⁻²) of adult (A) and manca (M) *T. thermophilum* among benthic sample sites (Valve, Pool, Run) in the natural spring system.

Within the natural habitat, the three sites (valve, pool, run) differed significantly in isopod density ($F_{[2,1463]} = 52.73$, $p < 0.0001$, Figure 3) and age structure ($F_{[1,1463]} = 3.91$, $p < 0.05$, Figure 4), with a highly significant interaction of these factors ($F_{[2,1463]} = 60.25$, $p < 0.0001$). Abundances of *T. thermophilum* were greatest at the pool and run sites ($p < 0.05$, Figures 3, 4); mancas were significantly more abundant than adults at the latter site, whereas adults were significantly more abundant than mancas at the pool site (both $p < 0.0001$), and adults tended to be more abundant at the valve site ($p < 0.06$). We found no significant differences of overall densities between the valve and pool sites.

Habitat treatments: demographic effects

Prior to introducing habitat complexity to the North pools in April 1997, the age structure was not significantly different among pools using benthic sampling, whereas sweep samples yielded significantly greater numbers of mancas in pools 2–4 (Table 1, Figure 5). With the application of habitat treatments, however, we observed significant short-term changes in age class representation in both benthic and sweep samples, although these were not similar in all treatments (both interactions $p < 0.05$, Table 1). Specifically, benthic samples from pools with vegetation (N2 and N4) yielded dramatic increases in the number of adults (Figure 5a), whereas sweep samples from these pools were dominated by mancas (Figure 5b). Addition of rocks (N3) did not differentially favor adults or mancas with either sampling method.

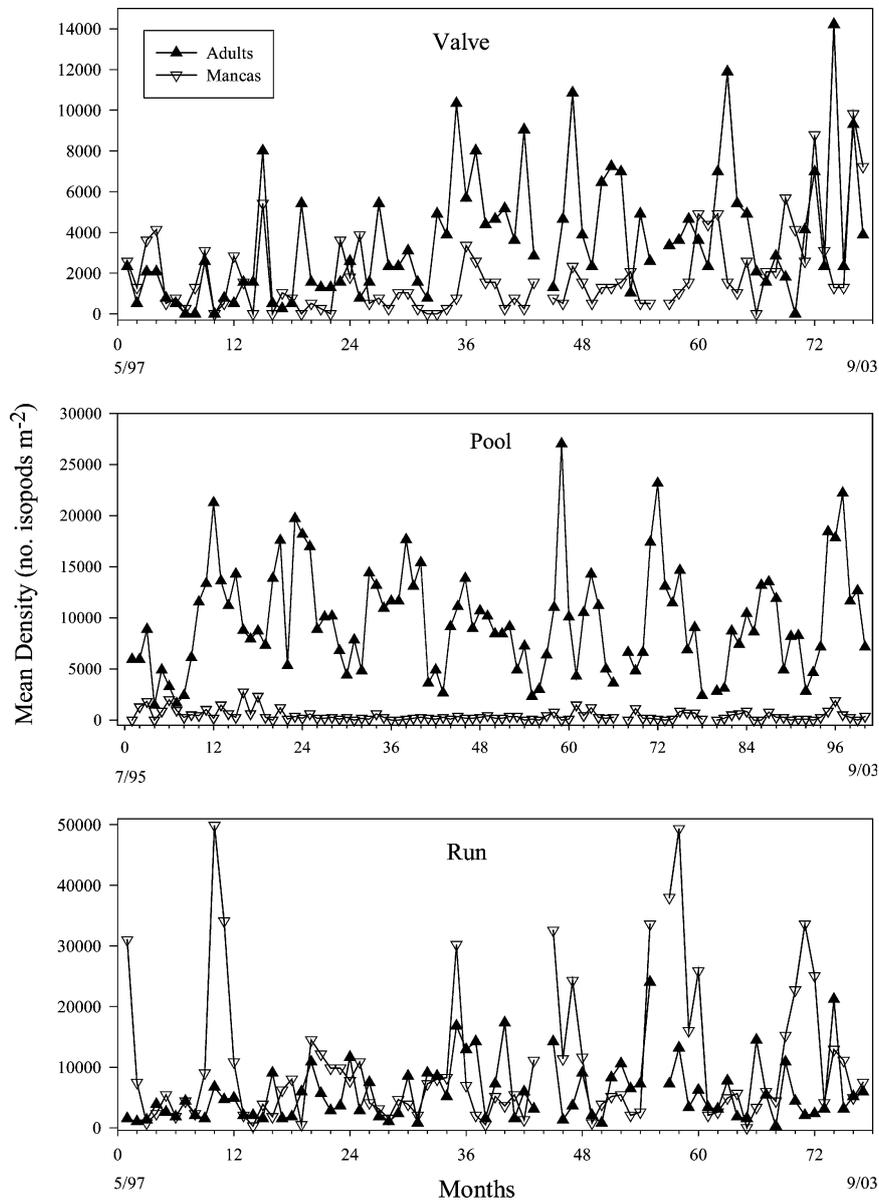


Figure 4. Monthly mean densities (no. isopods m⁻²) of *T. thermophilum* age classes in benthic samples collected from the Valve, Pool and Run sites in the natural spring from July 1995 to September 2003.

Population age structure varied over the 50-month series in both North and South pools (Figures 6–9). Apparent demographic pulses, generally dominated by adult *T. thermophilum* in most North and South pools, can

Table 1. One-way ANOVAs results by sample type comparing *T. thermophilum* (age classes combined) population response to pre-and post-habitat treatment periods among the SIPF North pools (N1–N4).

Source	DF	Mean Squares	F Ratio	Prob > F
Benthic Sample				
Pre-treatment				
Model	7	2.32×10^7	2.04	0.0489
Age	1	1.48×10^7	1.30	0.2554
Habitat	3	4.83×10^7	4.23	0.0057
Interaction	3	9.86×10^5	0.09	0.9675
Error	520	1.14×10^7		
Post-treatment				
Model	7	1.91×10^8	4.13	0.0002
Age	1	6.80×10^8	14.74	0.0001
Habitat	3	8.40×10^7	1.82	0.1423
Interaction	3	1.34×10^8	2.91	0.0341
Error	664	4.62×10^7		
Sweep Sample				
Pre-treatment				
Model	7	4.36×10^5	2.97	0.0046
Age	1	1.98×10^6	13.48	0.0003
Habitat	3	1.82×10^5	1.24	0.2952
Interaction	3	1.76×10^5	1.20	0.3093
Error	520	1.47×10^5		
Post-treatment				
Model	7	2.17×10^7	49.63	< 0.0001
Age	1	2.66×10^7	60.83	< 0.0001
Habitat	3	3.02×10^7	69.14	< 0.0001
Interaction	3	1.15×10^7	26.40	< 0.0001
Error	644	4.37×10^5		

be attributed to corner benthic samples where we observed isopods in breeding huddles. Using chi-square contrasts of age class CVs by sample type among pools in the North and South series, we observed differences in age structure heterogeneity between each 50-month replicate. Based on benthic sample data, the overall density of isopod populations remained substantially more stable in pools of the South series than in the North series ($\chi^2 = 2.43$ and 9.37 , respectively; $p > 0.25$ and < 0.025 , respectively). This may be deceptive, however, as variation in both adults and mancas was significant across pools of the South series ($\chi^2 = 8.25$ and 11.10 , respectively; $p < 0.05$ and < 0.025 , respectively) but neither were significantly different across pools of the North series ($\chi^2 = 3.71$ and 2.56 , respectively; both $p > 0.25$). Sweep samples yielded significant variation across pools for all age classes and in both North and South series (Figures 7, 9).

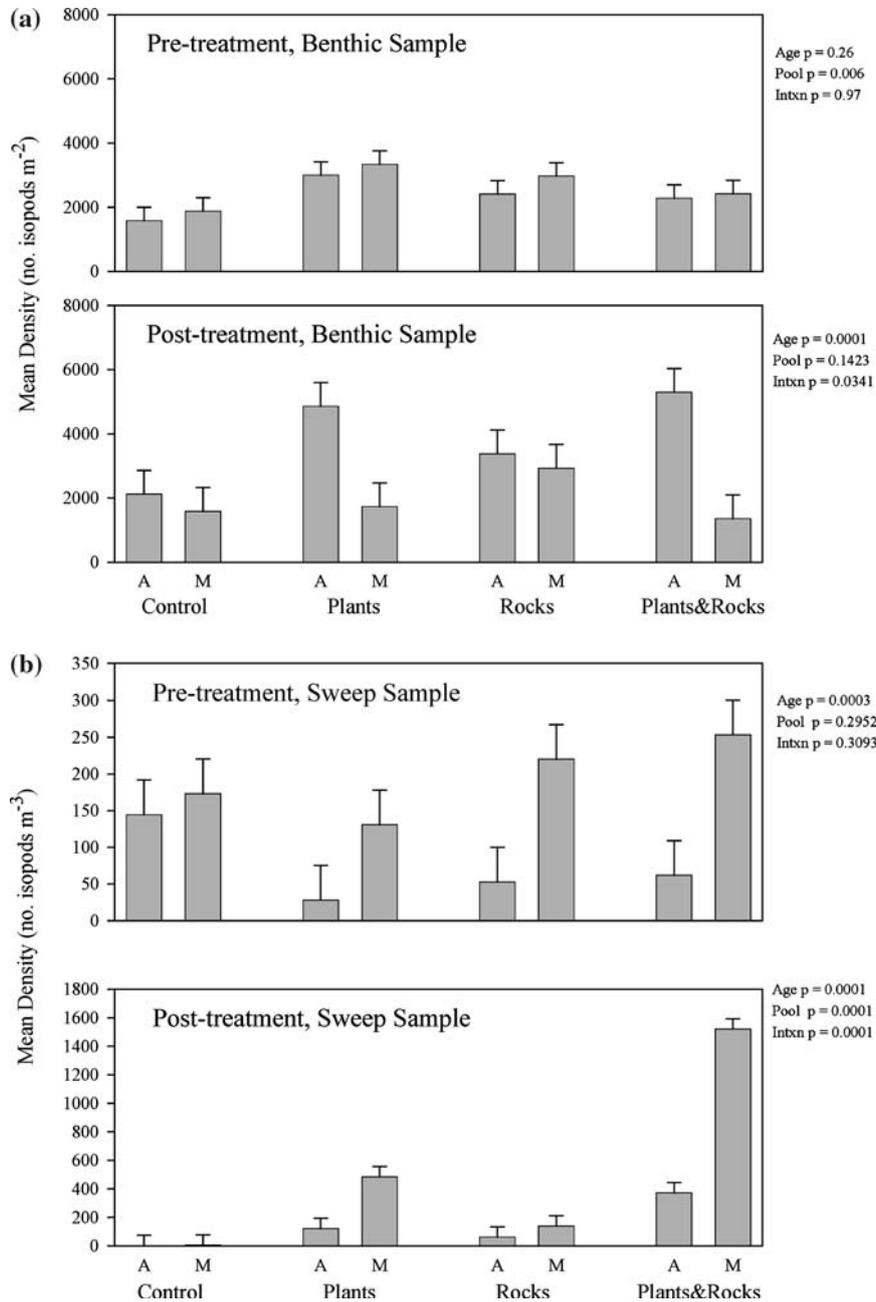


Figure 5. Pre-treatment and post-treatment mean density \pm SE of *T. thermophilum* age classes (A = adults, M = manca) by (a) benthic sample (no. isopods m⁻²) and (b) sweep sample (no. isopods m⁻³) in response to habitat treatments initiated in the SIPF north pools (N1 = Control, N2 = Rocks, N3 = Plants, N4 = Plants and Rocks) following the April 1997 census.

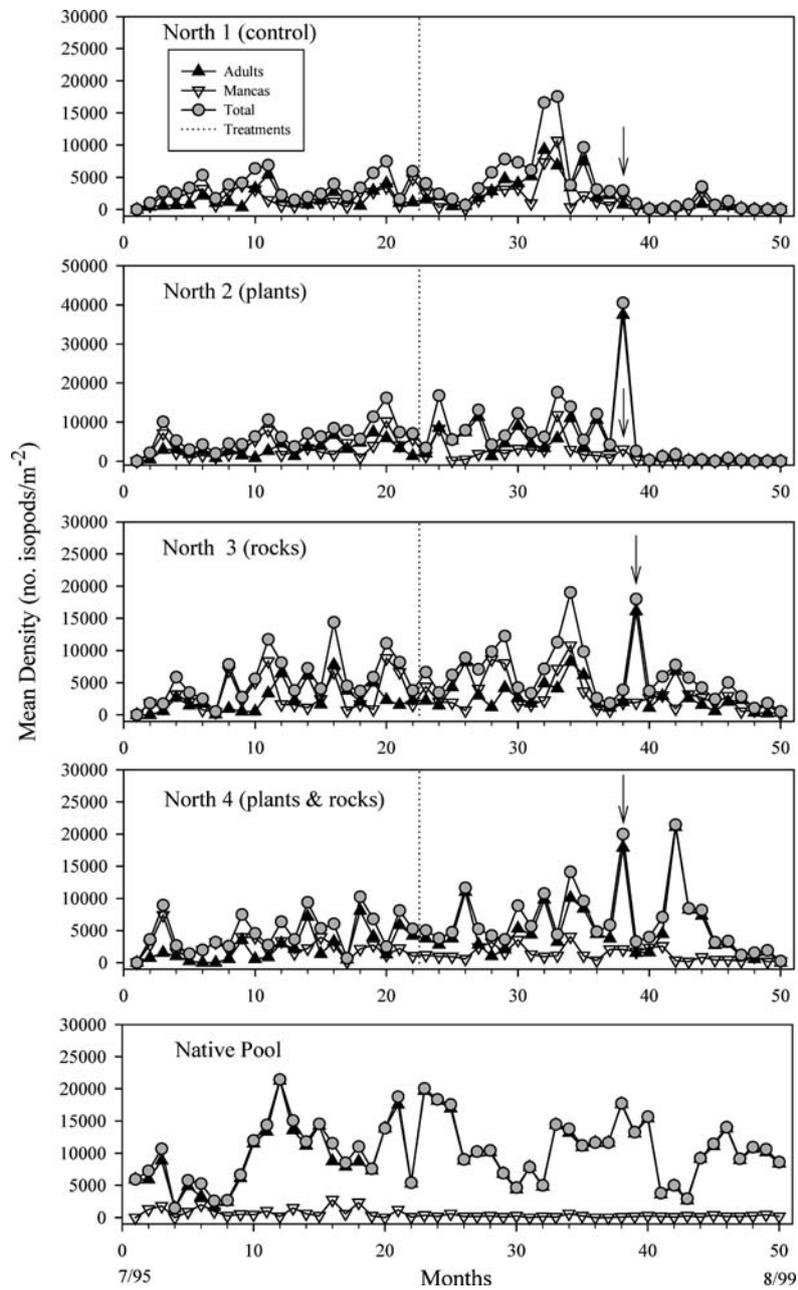


Figure 6. Monthly mean densities (no. isopods m^{-2}) of *T. thermophilum* age classes from benthic samples in the SIPF North pools 1-4 and native pool from July 1995 to August 1999. Dotted reference line represents initiation of habitat treatments in the pools as North 1 (control, no treatment), North 2 (plants), North 3 (rocks) and North 4 (plants and rocks). Arrows indicated impoverished habitat conditions (see Results).

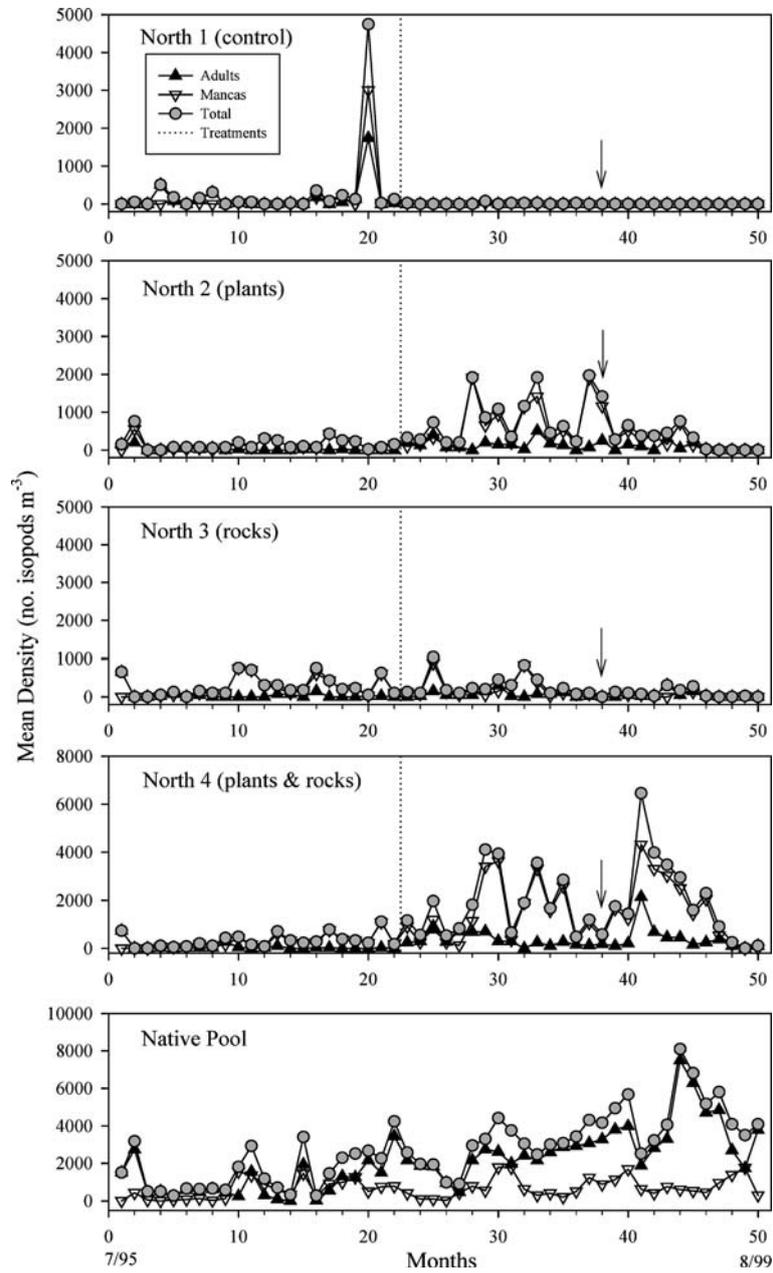


Figure 7. Monthly mean densities (no. isopods m⁻³) of *T. thermophilum* age classes from sweep samples in the SIPF North pools 1–4 and native pool from July 1995 to August 1999. Dotted reference line represents initiation of habitat treatments in the pools as North 1 (control, no treatment), North 2 (plants), North 3 (rocks) and North 4 (plants and rocks). Arrows indicated impoverished habitat conditions (see Results).

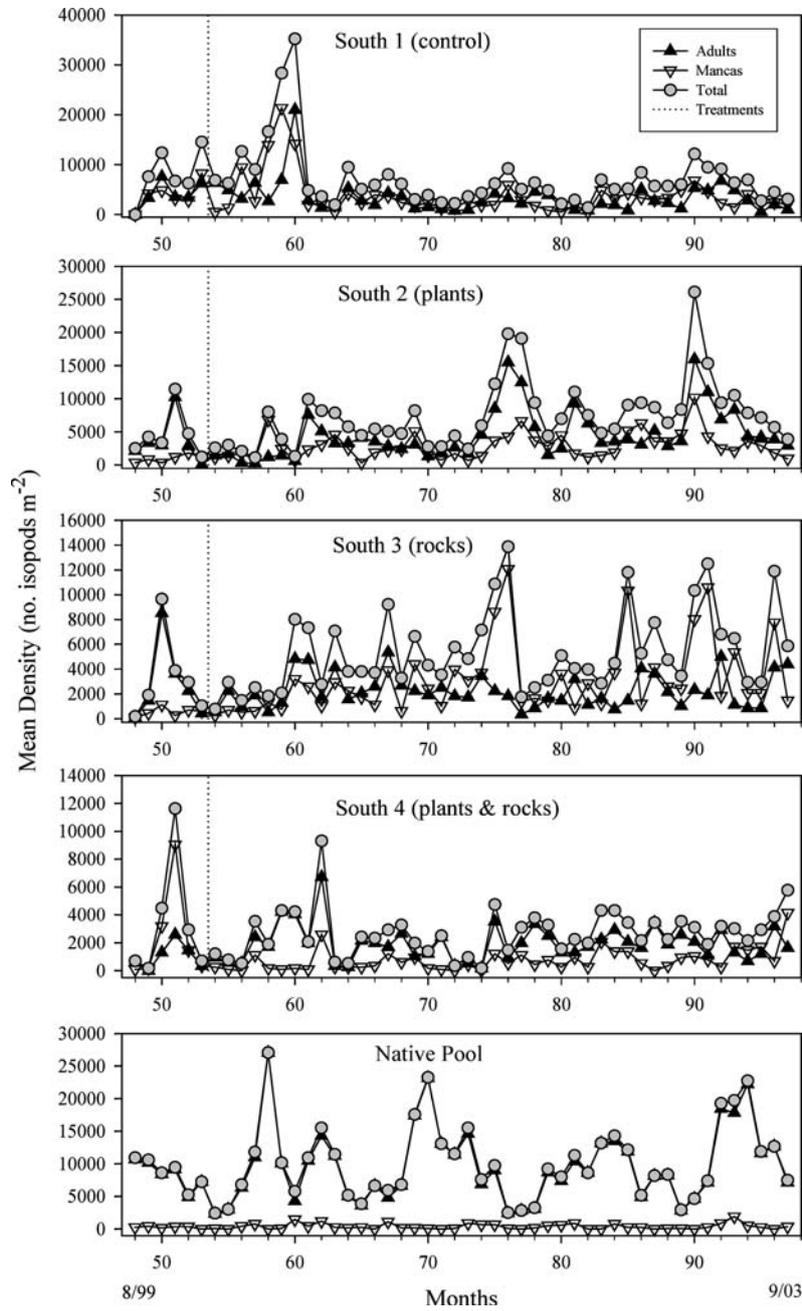


Figure 8. Monthly mean densities (no. isopods m⁻²) of *T. thermophilum* age classes from benthic samples in the SIPF South pools 1–4 and native pool from August 1999 to September 2003. Dotted reference line represents initiation of habitat treatments in the pools as South 1 (control, no treatment), South 2 (plants), South 3 (rocks) and South 4 (plants and rocks).

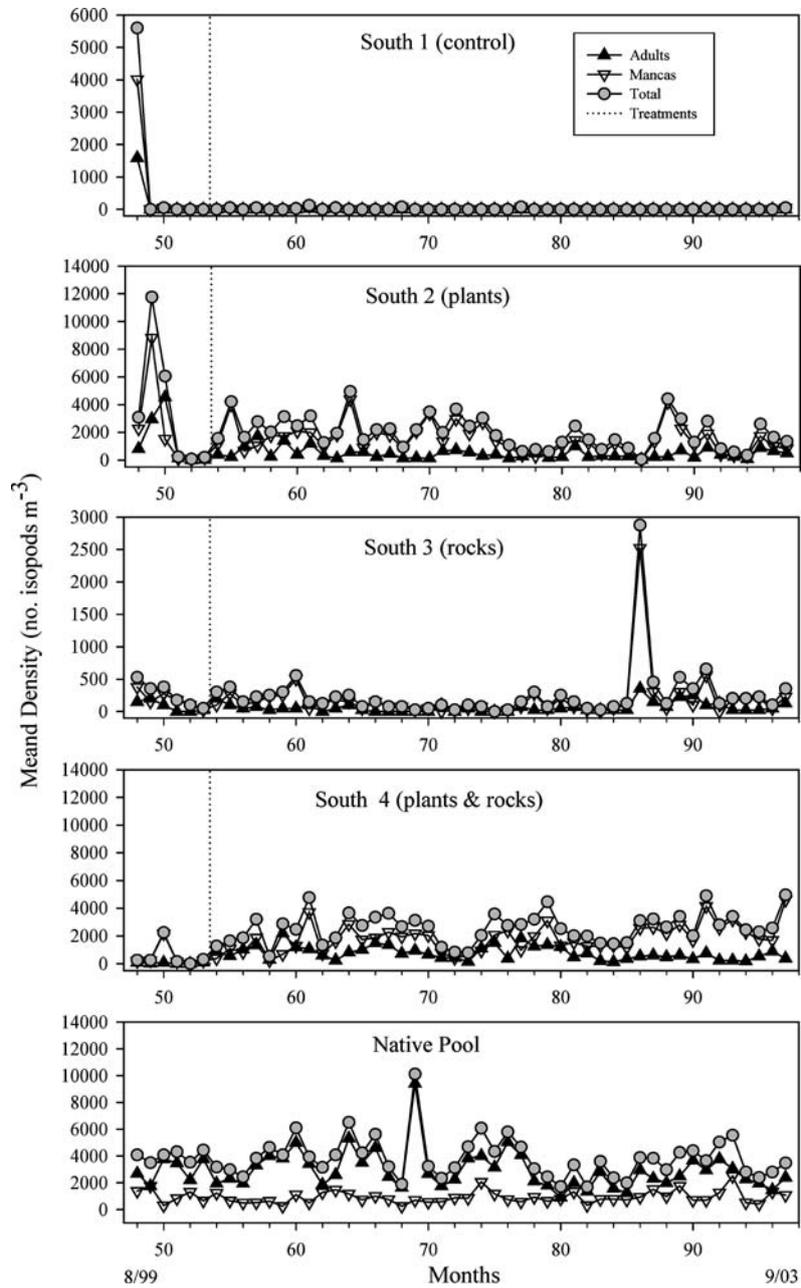


Figure 9. Monthly mean densities (no. isopods m^{-3}) of *T. thermophilum* age classes from sweep samples in the SIPF South pools 1–4 and native pool from August 1999 to September 2003. Dotted reference line represents initiation of habitat treatments in the pools as South 1 (control, no treatment), South 2 (plants), South 3 (rocks) and South 4 (plants and rocks).

Efficacy of controlled propagation

In general, native *T. thermophilum* populations maintained significantly higher densities than artificial populations (one-way ANOVAs, $p < 0.0001$ for separate analyses on total densities (age classes combined) for benthic and sweep samples; see Figure 2). Although we observed inconsistent patterns of demographic response to artificial habitat conditions between the North and South experimental periods based on benthic samples, sweep sample data indicated statistically consistent and nearly identical experimental response between each 50-month replicate, with the exception that plants alone (pool 2) yielded much greater populations in sweep samples in the second replicate (S2) than in the first (N2).

During the first 50-month experiment, benthic populations were significantly greater in pools N2 (plants), N3 (rocks), and N4 (plants and rocks) than the experimental control N1 ($p < 0.05$), whereas there were no significant differences in benthic isopod densities among treatment pools (N2–N4; Figure 10a). However, sweep samples in pool N4 yielded significantly ($p < 0.05$) more isopods than those from pools N1–N3 (Figure 10b).

Based on these findings, we predicted similar demographic responses in the second iteration of this experiment. Whereas we observed similar statistically significant patterns of population response from analysis of the South pool sweep sample data (Figure 10b), benthic sampling indicated a dramatic change in demographic response to habitat treatments (Figure 10a). Benthic populations in pools S1 (control) and S2 (plants) were significantly greater ($p < 0.05$) than those in S3 (rocks), which in turn were significantly greater than in S4 (plants and rocks; Figure 10b). The magnitude of this response, as noted in the North series experiment, appeared directly related to the type of vertical habitat structure afforded primarily by plants.

Discussion

Design of the SIPF provided a unique opportunity to assess the effects of habitat heterogeneity on the age structure of captive subpopulations of *T. thermophilum* over two consecutive 50-month experimental trials. Simultaneous monitoring of the species in its native habitat allowed for demographic comparisons among captive and native populations over a 100-month period.

Our experiment in the North pools was compromised around June 1998 (see Figure 5) when a series of complications resulted in impoverished habitat conditions. The SIPF leach field clogged, forcing us to reduce flow through the facility to prevent pool overflow. Additionally, a dog drowned in pool N2, disrupting physicochemical equilibrium in downstream pools, and leading to nutrient enrichment, thereby supporting blooms of filamentous blue-green algae. Finally, odonate nymphs appeared in pools N1 and N2 and gradually

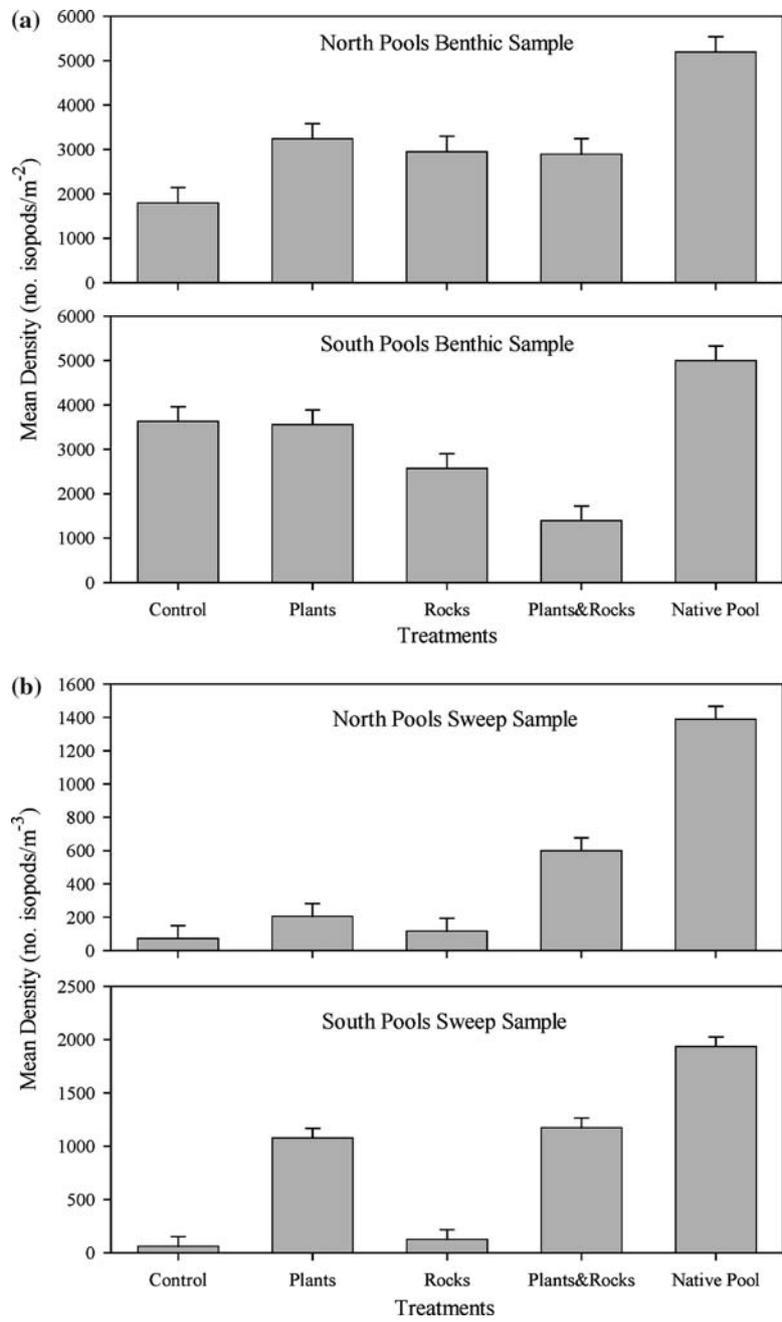


Figure 10. Overall experimental response of *T. thermophilum* (mean density \pm SE, age classes combined) to habitat treatments (Control = pool 1, Plants = pool 2, Rocks = pool 3, Plants and Rocks = pool 4) in the SIPF North (July 1995–August 1999) and South (August 1999–September 2003) pools relative to the native spring pool habitat.

dispersed to downstream pools. Under these conditions, all captive populations in the North series went extinct within 12 months.

Habitat heterogeneity

During both experimental trials (North and South), the native population of *T. thermophilum* consistently remained at significantly higher density (all $p < 0.0001$) than captive populations. We attribute these differences to the following abiotic and biotic factors. Habitat diversity with the SIPF is limited to deep lentic pools with eutrophic substrate conditions, whereas the native spring system is more heterogeneous, and includes substrates ranging from aqueous silts to small gravels. Input of allochthonous food sources (vegetative detritus, insects, etc.) from the adjacent riparian corridor of the natural habitat likely is greater than in SIPF pools, which are covered with screened tops to prevent oviposition from odonates. Additionally, efforts to increase the intrinsic rate of population growth under artificial habitat conditions of the SIPF pools may be limited by apparently higher rates of cannibalism in captive subpopulations compared to the natural population (Shuster et al. 2005).

The greatest overall response of *T. thermophilum* populations occurred in pools with plants, suggesting that qualitative features of habitat heterogeneity may play an important role in captive propagation of this species. In general, our results indicate that the magnitude of this interaction was consistently independent of linear flow within either pool series of the SIPF, and that captive isopod populations responded directly to the quality and quantity of habitat structure afforded primarily by plants, i.e., plants and rocks (N4, S4) > plants (N2, S2) > rocks (N3, S3) > control (N1, S1). Plants offer more surface area than rocks, providing both greater structural diversity throughout the water column than rocks, as well as favoring geotaxis of *T. thermophilum* while feeding and facilitating predator avoidance behavior by small adults and manca (Jormalainen and Shuster 1997). Additionally, plants provide a detrital food source for the omnivorous *T. thermophilum* (Shuster 1981a). In contrast, the flat surfaces of rocks likely provide limited refuge from predation risks attributed to smaller isopod life stages (Shuster et al. 2005), since rock facies are easily traversed by the more cannibalistic male isopods. Our experimental results underscore the findings of Jormalainen and Shuster (1997) and Shuster et al. (2005) that structural diversity provided by plants plays a major role in the survival of smaller-sized isopods as protective cover from larger cannibals.

Thermosphaeroma thermophilum is remarkably sensitive to changes in habitat condition. In several instances, the population response to stochastic perturbations during the experimental study period was nearly immediate. Impoverished aquatic conditions in the North series due to leach field drainage problems and the ill-fated dog were followed by a concurrent

infestation of libellulid odonate nymphs first observed in pools N1 and N2 in June 1998 (Month 38). Population declines, especially in benthic habitats, commenced in these two pools and spread quickly downstream to pools N3 and N4 (Figure 5). During this period, odonate densities in all North pools exceeded $645 \text{ nymphs m}^{-2}$, and within 12 months all populations in the North series were extirpated. Interestingly, we found only two odonate nymphs in the native habitat during the 100-month study period. Shuster (1981a) reported similar sporadic occurrence of libellulid nymphs in the native spring. Bowman (1981) suggested that the Flabellifera are excluded from most freshwater habitats due to their inability to compete successfully with aquatic insects and their larvae. It appears that *T. thermophilum* has successfully adapted to the delicate balance of this predator-prey relationship in its native spring habitat, whereas in captivity isopod densities may be insufficiently low to out-compete predatory odonates.

Habitat use

Within the native spring system, we observed significant segregation by age classes ($p < 0.0001$) among benthic samples collected from the valve, pool, and run sites. Overall isopod density was greatest at the pool and run sites, and mancae were significantly ($p < 0.05$) more abundant than adults at the latter site. These results support our observation that downstream dispersal of isopods may play an important role in relaxing predation risks from cannibalistic individuals associated with age- and sex-specific life stages of *T. thermophilum* in the native pool. Additionally, the relative density of mancae at the run site was ca. 5.6 and 17 times greater than at the valve and pool sites (Figure 3), respectively, suggesting that this area may not only represent an important migration corridor linking up- and downstream habitats, but may also serve as a critical reach for isopod reproduction. Further support for this hypothesis is that ovigerous or gravid females and mating pairs are most commonly encountered in run habitat downstream of the pool (Lang, unpubl. data). Thus, protecting the integrity of this portion of the native spring system likely is critical to perpetuate the long-term viability of *T. thermophilum* in nature.

The mating system of *T. thermophilum* is characterized by isolated male-female pairs and pronounced intra-male mate competition (Shuster 1981a). The duration and intensity of male pre- and post-copulatory guarding behavior apparently is affected by patterns of female sexual receptivity, spatial sex ratios, male-male competition for a mate, and by the males' chemoreception of near-molt females (Shuster 1981b; Jormalainen and Shuster 1999, Jormalainen et al. 1999). Our observations of significantly ($p < 0.0001$) dense aggregations (breeding huddles) of adult isopods in the corners of all SIPF pools (Figure 2c), and lack thereof in the native pool, may reflect a behavioral shift in the mating system under artificial conditions;

such social behavior has not been reported in *Thermosphaeroma* (S. Shuster, *pers. obs.*, V. Jormalainen, *pers. com.*). These social aggregations may simply be a consequence of physical attributes of the SIFP pools, as we have observed similar groupings in glass aquaria. However, it might also reflect a true shift in the mating system of *T. thermophilum* in response to increased rates of cannibalism (Shuster et al. 2005), or possibly a behavioral response to spatially altered sex ratios (Jormalainen and Shuster 1999) under artificial habitat conditions compared to the natural habitat.

Breeding huddles were characterized by dense clusters of gravid and ovigerous females, breeding pairs, and small isopod life stages (manca, immature males and females). Such a heterogeneous mix of age classes and life stages is suggestive of spatially altered sex ratios in captivity where isopods may find refuge from cannibals in dense social aggregations, thereby reducing predation risks attributed to large cannibalistic males (Jormalainen and Shuster 1997). If ‘huddling’ reduces the threat of cannibalism, then the reproductive fitness of both sexes could be increased as a result of decreased predation risks evidently experienced among female and manca isopods (Shuster et al. 2005), increased frequency of receptive mate encounters, and decreased duration of pre- and post-copulatory mate guarding behavior (Jormalainen and Shuster 1999). Such a shift in social behavior could favor selection for large body size in captive populations of *T. thermophilum*, which in turn would confer reproductive advantages for larger-sized male and female isopods (Shuster 1981a, b; Jormalainen and Shuster 1999).

Additionally, evidence of intersexual conflict in *T. thermophilum* (Jormalainen and Shuster 1999) implies that behavioral plasticity within this species may play an important adaptive role in response to novel selection regimes in the context of altered mating strategies among captive subpopulations. Thus, the combined effects of population subdivision by controlled propagation and cannibalism-based selection can lead not only to rapid and marked genetic and morphological changes in populations experiencing genetic bottlenecks (Shuster et al. 2005), but also may affect the social basis of this species’ mating strategy.

During the entire 100-month study, breeding huddles have never been observed in the native pool habitat. In fact, adults were significantly more abundant ($p < 0.0001$) in the middle and side of the native pool than in corner benthic samples. These differences may simply be attributed to the lack of a true geometric corner in the irregularly ovoid native pool. More plausibly the absence of breeding huddles in the native pool may indicate that isopod life stages (small males, females, manca) at greatest risk to cannibals (Shuster et al. 2005) can escape predators by seeking protective cover on submerged leaves and stems of the emergent *Distichlis* sp. (Jormalainen and Shuster 1997) or amongst the irregular concrete surfaces of the pool wall, or alternatively that isopods can disperse downstream (upstream dispersal is likely limited) where habitat diversity is more heterogeneous.

Efficacy of controlled propagation

We conclude that controlled propagation of the *T. thermophilum* is an effective conservation management practice that not only has increased total population size, but also has ameliorated threats to the native population by establishing accessory populations at the SIPF and Albuquerque Biological Park. Perhaps most importantly, such recovery-oriented research actually prevented the global extinction of this species. We note that controlled propagation may affect the social basis of the species' mating system. This may reflect a behavioral response to selection on body size to avoid cannibalism, or adjustments to spatially altered sex ratios in artificial environments. Additionally, vertical habitat structure, especially plants, evidently is necessary to maintain age structure heterogeneity among captive *T. thermophilum*, thereby maximizing long-term population viability. Finally, habitat condition in controlled environments evidently plays a critical role, significantly affecting isopod body size and genetic affinities between captive and native population of *T. thermophilum* (Shuster et al. 2005).

Empirical data derived from our research form the basis for the development of a controlled propagation protocol and a genetic management plan for this species. These activities corroborate the intent of the Socorro Isopod Recovery Plan (USFWS 1982) and the Department of Interior's 'Policy Regarding Controlled Propagation of Species Listed Under the Endangered Species Act' (Federal Register 2000). While current research trends urge resource managers to adopt ecosystem-based management strategies, our results emphasize the need to continue research focused on species-specific management practices, which is particularly germane to conserve geographically restricted populations of non-charismatic invertebrates such as the endangered Socorro isopod.

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Appendix 1. Summary statistics of physicochemical conditions measured monthly (1996–2000) in the native habitat and Socorro Isopod Propagation Facility (SIPF) of *T. thermophilum*. Sample size is listed parenthetically.

Site	Statistics	Temperature (°C)	pH (units)	Sp. Cond. (μ S/cm)	Salinity (ppt)	TDS (mg/l)	DO (% sat.)	DO (mg/l)
Native Pool ($n = 41$)	minimum	22.7	7.6	126	0.1	0.2	29.8	2.4
	maximum	33.5	10.2	421	0.2	0.2	132.4	10.0
	\pm 1SD	29.6 ± 2.6	8.6 ± 0.8	340 ± 46	0.2 ± 0.0	0.2 ± 0.0	82.0 ± 24.3	5.7 ± 1.6
Valve ($n = 13$)	minimum	27.2	7.7	129	0.1	0.2	31.4	2.3
	maximum	33.2	9.9	502	0.3	0.3	108.0	7.0
	\pm SD	30.1 ± 1.8	9.0 ± 0.9	305 ± 96	0.2 ± 0.1	0.2 ± 0.0	66.9 ± 24.6	4.7 ± 1.6
Run ($n = 16$)	minimum	23.6	7.7	135	0.1	0.2	31.2	2.5
	maximum	33.2	10.4	367	0.2	0.2	132.4	10.0
	\pm SD	28.8 ± 2.6	9.4 ± 1.0	285 ± 90	0.2 ± 0.0	0.2 ± 0.0	68.8 ± 28.4	5.0 ± 1.9
SIPF North 1 ($n = 39$)	minimum	29.9	7.5	270	0.1	0.2	47.4	3.1
	maximum	32.9	10.1	419	0.2	0.2	119.9	8.2
	\pm SD	31.7 ± 0.8	8.3 ± 0.7	352 ± 24	0.2 ± 0.0	0.2 ± 0.0	95.6 ± 18.6	6.5 ± 1.3
North 2 ($n = 37$)	minimum	28.9	7.5	316	0.2	0.2	47.5	3.1
	maximum	32.7	10.2	400	0.2	0.2	171.9	11.1
	\pm SD	31.1 ± 1.0	8.4 ± 0.7	353 ± 16	0.2 ± 0.0	0.2 ± 0.0	103.0 ± 24.0	7.0 ± 1.7
North 3 ($n = 38$)	minimum	27.0	7.6	336	0.2	0.2	47.4	3.1

North 4 (<i>n</i> = 38)	maximum	32.6	10.2	385	0.2	0.2	144.1	9.4
	± SD	30.6 ± 1.4	8.4 ± 0.7	354 ± 13	0.2 ± 0.0	0.2 ± 0.0	102.2 ± 22.9	7.0 ± 1.7
	minimum	25.5	7.6	332	0.2	0.2	47.3	3.2
South 1 (<i>n</i> = 27)	maximum	32.3	9.9	383	0.2	0.2	142.1	9.5
	± SD	30.1 ± 1.7	8.4 ± 0.7	354 ± 114	0.2 ± 0.0	0.2 ± 0.0	102.3 ± 23.4	7.1 ± 1.7
	minimum	27.6	7.6	245	0.1	0.2	29.8	2.2
South 2 (<i>n</i> = 27)	maximum	32.9	10.0	427	0.2	0.2	118.4	8.8
	± SD	31.9 ± 1.0	8.6 ± 0.8	352 ± 29	0.2 ± 0.0	0.2 ± 0.0	81.8 ± 28.3	5.5 ± 1.9
	minimum	23.8	7.6	285	0.1	0.2	30.4	2.2
South 3 (<i>n</i> = 27)	maximum	32.7	10.1	383	0.2	0.2	118.4	8.6
	± SD	31.3 ± 1.7	8.6 ± 0.8	354 ± 18	0.2 ± 0.0	0.2 ± 0.0	83.1 ± 28.1	5.7 ± 1.9
	minimum	21.4	7.5	325	0.2	0.2	30.9	2.3
South 4 (<i>n</i> = 27)	maximum	32.6	10.1	381	0.2	0.2	120.1	8.8
	± SD	30.8 ± 2.2	8.6 ± 0.9	355 ± 12	0.2 ± 0.0	0.2 ± 0.0	83.2 ± 28.3	5.7 ± 2.0
	minimum	19.0	7.5	344	0.2	0.2	30.4	2.2
	maximum	32.4	10.2	397	0.2	0.2	120.2	8.8
	± SD	30.2 ± 2.8	8.7 ± 0.9	357 ± 12	0.2 ± 0.0	0.2 ± 0.0	82.9 ± 29.0	5.8 ± 2.1

Abbreviations: Sp. Cond. = specific conductance; TDS = total dissolved solids; DO = dissolved oxygen; SD = ± 1 standard deviation.

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