Veijo Jormalainen · Stephen M. Shuster

Microhabitat segregation and cannibalism in an endangered freshwater isopod, *Thermosphaeroma thermophilum*

Abstract Intraspecific microhabitat segregation is expected to arise when there are age- or sex-specific differences in predation risk. The degree to which conspecific predation (cannibalism) can generate this risk, however, is poorly understood. In this paper, we examine microhabitat use, cannibalism, and individual responses to the presence of conspecifics in *Thermosphaeroma thermophilum*, an endangered isopod crustacean species that is endemic to a single, thermal spring in Socorro, N.M. USA. In samples from the natural habitat, juveniles (mancas) were found mainly on vegetation, whereas adults were found predominantly on bottom sediments. Females were found on vegetation more often than males. In laboratory containers without refuges, males cannibalized females, males and females cannibalized mancas, and mancas cannibalized each other, even in the presence of alternative food. When placed in containers provided with refuges, mancas actively avoided adults. We suggest, therefore, that cannibalism in *T. thermophilum* generates age-, size-, and sex-specific predation risks which are responsible for microhabitat segregation between mancas and adults, and between males and females. Since interspecific predation in the spring is negligible, cannibalism appears to play a significant role in population regulation and behavioral evolution in this species. We recommend, given the current "endangered" status of this species, that microhabitat heterogeneity be maintained in its native spring because it provides refuges from cannibalism and may support a larger and more viable natural population.

Introduction

Theoretical and empirical studies of habitat choice indicate that animals can assess habitat suitability in terms of the availability of food, shelter, or mates, and as a site of refuge from predators, competitors, or hazardous environmental conditions (Dill 1987; Holomuzki and Short 1988; Werner and Hall 1988; Lima and Dill 1990; Huang and Sih 1991; Milinski and Parker 1991; Hugie and Dill 1994). Microhabitat segregation between sexes (Jormalainen and Tuomi 1989; Anholt 1992; Dangerfield and Hassall 1994; Forsman and Shine 1995) or between age classes (Mittelbach 1981; Werner et al. 1983; Foster et al. 1988; Kurihara et al. 1989; Leonardsson 1991; Jormalainen et al. 1995) is expected to arise if profitability or risk within distinct parts of the habitat vary among particular intraspecific groups. Energetic demands for reproduction may differ between the sexes, for example leading to differential qualitative or quantitative feeding and habitat requirements (Trivers 1972; Slatkin 1984; Shine 1989). Moreover, predators may be selective with respect to the size and age of their prey (Polis 1981; Lima and Dill 1990).

The actual behavioral processes responsible for intraspecific microhabitat segregation are often unclear because there may be numerous interacting causal factors. Two isopod species exemplify such complexity. *Idotea baltica* inhabits structurally complex littoral habitats in the Baltic Sea. Males and females are found commonly on bladderwrack (*Fucus* sp.), their main food source, whereas juveniles occur primarily on filamentous green algae (Salemaa 1979) and are unable to consume bladderwrack (Jansson and Matthiesen 1971; Salemaa 1979). Moreover, intersexual differences in feeding behavior, different reproductive activities of males and females, and the differential predation risk between the sexes lead to sexual dimorphism in habitat use and adult

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coloration (Jormalainen and Tuomi 1989; Jormalainen et al. 1995; Merilaita and Jormalainen, in press). Another Baltic isopod, *Saduria entomon*, inhabits homogenous bottom sediments and shows little evidence of age-specific food preferences (Haahtela 1990). However, adults and juveniles exhibit spatial segregation as a consequence of active juvenile avoidance of cannibalistic adults (Leonardsson 1991; Sparrevik and Leonardsson 1995). Cannibalism has also been suggested to induce an age-specific predation risk that may lead to age-specific habitat segregation in some fishes (Foster et al. 1988), crabs (Kurihara et al. 1989), and aquatic insects (Robinson et al. 1991; Sih 1992).

In this study, we investigate microhabitat use and cannibalism in a freshwater isopod, *Thermosphaeroma thermophilum* (Cole and Bane) (Crustacea: Peracarida). Cannibalistic feeding behavior has been observed in the natural habitat of this species (Shuster 1981a), and several conditions appear to favor cannibalism (see Fox 1975): (1) an unusually small habitat, a thermal freshwater spring (< 20 m^2; Shuster 1981a) that makes dispersal impossible, (2) a high population density (up to 210 individuals/100 cm^2; Shuster 1981b), (3) apparent food shortages during peak densities ("feeding frenzies" occur when additional food is introduced or when isopods are injured; Shuster 1981a), and (4) structural simplicity of the habitat, which offers only limited shelter from conspecifics (Shuster 1981a, b). Interspecific predation on *T. thermophilum* is negligible, predators occuring only rarely (Shuster 1981a), and thus food limitation and/or intraspecific predation are most likely the main population regulation mechanisms. These conditions, combined with the endangered status of this species, (Federal Register 1977), make *T. thermophilum* an intriguing object for studying cannibalism and the selective forces this contributed form of predation.

Here we report (1) the distributions of *T. thermophilum* adults and mancas (= juveniles) in their natural habitat, (2) the results of experiments examining sex- and age-specific cannibalism under laboratory conditions, and (3) observations of the behavioral mechanisms used to avoid cannibalism, which are likely to influence the spatial distributions of individuals found in nature. These results have important implications for understanding the evolutionary ecology of cannibalism in this species, and for the conservation of endangered species such as *T. thermophilum*.

Material and methods

General *Thermosphaeroma* ecology

Thermosphaeroma (Sphaeromatidae, Dynameninae; Harrison and Ellis 1991) species inhabit isolated thermal springs in New Mexico and Texas in the U.S.A., and in Chihuahua. Coahuila, Durango, and Aquascalientes in Mexico (Rioja 1951; Cole and Bane 1978; Shuster 1981a, b, personal observations; Bowman 1981, 1985). These habitats consist of small, uniform, thermal (28–35°C) environments that are separated by hundreds to thousands of kilometers.

Of the seven described *Thermosphaeroma* species (Bowman 1985), the ecology and life history of *T. thermophilum* are the best known. The habitat of this species represents the northwestern limit of the range of the genus, and comprises of a single, thermally stable spring within an abandoned bathhouse near Socorro N.M. (for a figure of the habitat, see Shuster 1981a). The spring consists of two pools and a small stream that connects and extends below the pools. The main pool (pool 2 in Fig. 1 in Shuster 1981a) is small (2.69 m × 0.94 m) and shallow (15–26 cm), the bottom is covered with a few centimeters of finely divided substrate, and grasses (*Glyceria borealis* or *G. striata*) grow within and along the western wall of the pool. Decaying grasses are found on the bottom of both pools and in the stream leading away from them.

T. thermophilum reproduces all year, although reproductive peaks occur in the spring and fall. Females are iteroparous and sexual size dimorphism is pronounced (Shuster 1981a). Isopods feed on detritus and algae, but are facultatively carnivorous, preying on aquatic insect larvae that occasionally occur in the pool and on each other. Isopod activity is largely crepuscular and males are the most active individuals, wandering the bottom of the spring in search of, or in precopula with sexually receptive females (Shuster 1981b). Males guard females before mating and prefer large females that are close to a reproductive molt as precopulatory partners (Shuster 1981b).

Its extremely limited range and small population size (< 3,000 individuals) has led to the status of *T. thermophilum* as an "endangered" species (Federal Register 1977), although populations are presently maintained in accessory habitats near the natural spring in Socorro, N.M. in aquaria at the U.S. Fish Service offices in Albuquerque, N.M. (N.M. Department of Game and Fish, personal communication) and at the Department of Biological Sciences in Flagstaff, AZ.

Field sampling

Isopods were collected under permits authorized by the New Mexico Department of Game and Fish (NMGF permit 2829) and the U.S. Fish and Wildlife Service (USFWS permit PRT-676811) on 20–21 June 1995. We collected our specimens at dusk and at dawn from the main pool of the spring. On the first date, between 1830 and 1945 hours, three different sampling procedures were used to assess the distribution of individuals within the natural habitat. (1) A 7 × 7 cm wire square was placed on the substrate and all individuals entering this area during 3 min were removed using plastic pipettes; the procedure was replicated five times in other undisturbed locations within the pool (hereafter "on substrate 1," Table 1). (2) A 7 × 7 cm fine-mesh net was swept along each of these same five cleared bottom surface areas at a depth of < 5 cm for a distance of approximately 7 cm to collect all individuals below the surface of the substrate (hereafter "below substrate," Table 1). (3) A 15 × 12 cm fine-mesh net was swept through the open water among the erect grasses in the pool for 1 min, taking care to avoid touching or otherwise disturbing the substrate; this procedure was replicated three times (hereafter "on vegetation," Table 1). Similar sampling procedures were repeated on 21 June between 0530 and 0630 hours to provide a dawn collection. In addition to the three described sampling schemes, an additional sample of animals on the substrate was taken by sweeping a net (15 × 12 cm) along the surface of the substrate three times (hereafter "on substrate 2").

Animals from each replicate sample were separated into containers and classified within 48 h for sex (males by the presence of penes located at the ventral pereonal midline anterior to the first pleopods, females by the presence of a brood pouch or developing ovaries, mancas by the lack of any recognizable reproductive structures), reproductive condition (following Shuster 1981b), and body length to the nearest 0.125 mm.

Because there tended to be no differences in the proportions of mancas, males, and females between the replicate samples (Table 1), the replicates were pooled in the final analyses. However,

Table 1 Numbers of males (*m*), females (*f*), and mancas (*j*) found in each replicate sample taken from different microhabitats (below or on the substrate, or on vegetation; see text for a detailed explanation of the sampling procedure) on two sampling dates. The G-statistic tests for differences in the numbers of males, females, and mancas between replicate samples within each microhabitat category, i.e., the zero hypothesis is the independence of the frequencies of different animal groups on replicate (*Repl.*) samples

Date and location	Repl. 1			Repl. 2			Repl. 3			Repl. 4			Repl. 5			df	G	P
	m	f	j	m	f	j	m	f	j	m	f	j	m	f	j			
June 20																		
Below substrate	1	0	0	6	4	0	2	1	0	3	0	0	2	0	0	4	4.62	0.32
On substrate 1	8	7	0	6	3	1	11	5	0	12	0	0	5	2	2	8	18.4	0.02
On vegetation	7	8	15	18	13	7	4	5	4							4	8.55	0.07
June 21																		
Below substrate	1	0	0	0	0	1	2	1	2	1	0	1	1	0	0	8	5.54	0.70
On substrate 1	15	3	0	16	2	1	24	4	5	10	2	0	14	4	1	8	8.03	0.43
On substrate 2	40	13	8	2	2	2	5	2	3							4	3.78	0.44
On vegetation	4	3	26	5	5	35	4	2	31							4	0.94	0.92

the samples of 20 and 21 June were analyzed separately due to the slightly different sampling regimes.

In the laboratory, animals were placed in individual 55-cm^3 cylindrical plastic containers equipped with removable net walls at both ends. The containers were stacked within 40-l aquaria maintained at 30°C with aeration, and water was circulated through the cylinders. Isopods were fed with both vegetarian fish food and brine shrimp flakes. Progeny born in the laboratory were maintained as described below. All animals not used in laboratory analyses were returned to the spring.

Age- and sex-specific cannibalism

In the laboratory, we studied the occurrence and intensity of age-specific cannibalism by maintaining individual mancas under four experimental treatments: (1) alone ($n = 30$), (2) with a female ($n = 30$), (3) with a male ($n = 27$), and (4) in groups of four mancas ($n_{group} = 9$, $n_{mancas} = 36$). These experiments were performed in two subsets: in the first, laboratory-born mancas experienced treatments 1 and 3, in the second, newly born, field-collected mancas experienced treatments 1, 2, and 4. Vegetarian fish flakes were provided as food, and manca survival was recorded daily. During the daily observations, food was added and the fate of dead individuals (eaten or not) was noted.

We also reared male-female pairs in order to study their mating behavior, but because cannibalism occurred in these assays, we report here our data on intersexual cannibalism. Pairs were reared under similar conditions as juveniles, except that dried brine shrimp were offered as alternative food together with vegetarian fish food. The rearing duration of these male-female pairs varied from less than 1 day up to 21 days (mean = 7.4 days, SD = 5.0).

Responses of individuals to conspecific cues

Experiments with mancas

We studied the behavioral reactions of mancas to the physical proximity of adult males and females in a specially designed experimental setup (cf. Sparrevik and Leonardsson 1995). A 11 × 21 × 7 (width × length × height) cm Plexiglas chamber was divided into equal halves with a 1.5-mm mesh net through which mancas could easily swim but adults could not. For each trial, we placed 20 newly born mancas on one side of the chamber, and recorded their movement to the unoccupied, "refuge" side of the chamber at 10-min intervals for 90 min. We used a total of seven sets of 20 mancas, running a total of six trials with each of these sets: two control trials with no adults, two trials with six males,

and two trials with six females. The left or right side was randomly selected as the starting side for the first of the two replicates, with the opposite side used in the second replicate. The order of the different trials was also randomized. To control for possible biases due to external (e.g., lighting, noise) conditions, the test chamber was always kept in the same position in the laboratory.

Experiments with adults

To study the reactions of males and females to olfactory cues from the opposite sex, we placed an individual male or female into a modified Y-maze apparatus that allowed each experimental individual to choose between a control compartment and a compartment with odors from a group of adult isopods of the opposite sex. The test chamber consisted of a rectangular Plexiglas aquarium divided into three compartments and equipped with a stand-tube that maintained the water level at 3 cm depth (Fig. 1). The "neutral" area was a 10 × 10 cm square at the lower end of the aquarium; the other end was divided into two 5 × 10 cm compartments, both separated from the neutral area by two sets of baffles (Fig. 1), whose purpose was to enhance the chemical gradient within the apparatus. The 1-cm opening between the baffles allowed an animal to swim from the neutral compartment to the smaller compartments and back, but the baffles made it easier to leave the neutral compartment than to leave the small compartments. A current of water from separate reservoirs was arranged through an input in the upper end of each experimental chamber (Fig. 1). Water flowed out of the apparatus through the stand-tube at the lower end of the "neutral" compartment (Fig. 1). Input lines were equipped with quick-disconnect junctions allowing alternation of water sources to each experimental compartment. A water flow of 70 ml/min was directed through each input. Preliminary tests with colored water showed that a distinct gradient between the two smaller compartments formed within 10 min after flow was initiated and remained for over 30 min.

For trials using isopods, odor treatment and control inputs were established. The treatment input consisted of aged, aerated tap water flowing through a 250-ml chamber containing a group of 15 isopods. The control input consisted of aged, aerated tap water directed through an empty 250-ml chamber. When females were used as experimental animals, a group of 15 adult males was used as the "odor treatment," and when males were tested, the odor treatment group of 15 females included both gravid and nongravid females.

We began each trial by randomly selecting treatment and control sides for the apparatus and then allowing the odor and control reservoirs to flow for 10 min to form a chemical gradient within the apparatus. We then placed one individual, either a male ($n = 30$) or female ($n = 29$), into the middle of the neutral compartment. The
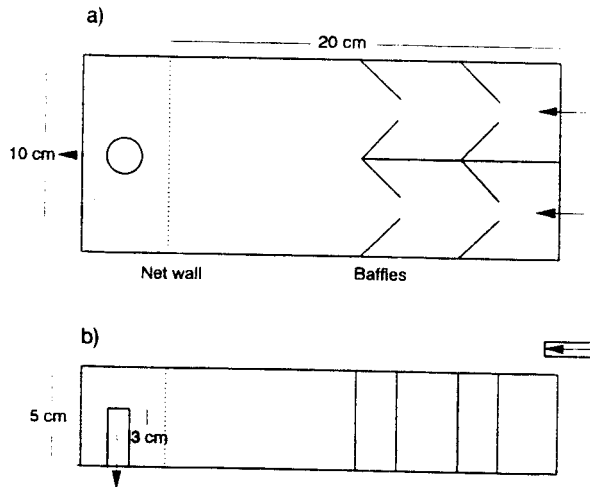
Fig. 1 The experimental chamber used to test adult responses to odors from the opposite sex in top view (a) and side view (b). The *arrows* indicate the direction of water flow

movements of each isopod were observed for 20 min, and the time each individual spent in each compartment as well as the time individuals spent moving or stationary were recorded. After at least 2 h but not more than 24 h after the first trial, the treatment and control input sides were changed and the same individuals were retested.

Results

Distribution of animals in the field

Male body length ranged from 4.1 to 9.4 mm (mean = 6.1, SD = 1.1, $n = 229$), and female body length from 3.4 to 5.6 mm (mean = 4.6, SD = 0.37, $n = 91$). Individuals smaller than 4.1 mm usually lacked ovarian development, brood pouches, or penes and were classified as mancas. Mancas ranged in size from 1.2 to 4.1 mm (mean = 2.2, SD = 1.0, $n = 145$).

Habitat segregation between adults and mancas was clear, their frequencies differing between the habitat categories (Figs. 2a, 3a). Adult and manca distribution showed similar tendencies in both the samples (Figs. 2a, 3a). Mancas were found mainly on vegetation. Furthermore, females were found more often on vegetation than below or on the substrate (Figs. 2b, 3b). This tendency existed in both samples, and was statistically significant in the later one (Fig. 3). Relatively few individuals were found burrowed below the substrate (Figs. 2, 3). The sex ratio was male biased below and on the substrate, but approached unity on the grasses (Figs. 2, 3).

No differences were found in the microhabitat distribution of virgin, gravid, or post-gravid females [2 × 2 contingency table (microhabitat × reproductive status)] – 20 June: $df = 4$, $G = 3.83$, $P = 0.43$; 21 June: $df = 6$, $G = 3.10$, $P = 0.80$).
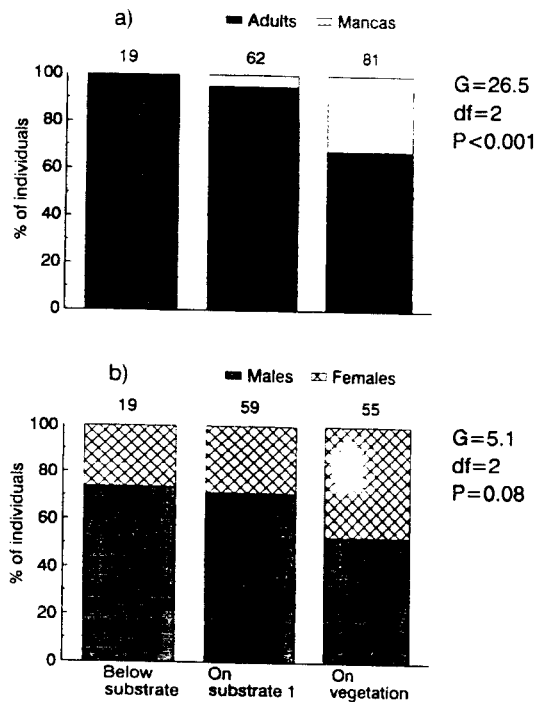

Fig. 2 The proportions of adults and mancas (a), and males and females (b) found below or on the substrate, or on vegetation in the 20 June sample. The contingency table statistics test for differences in habitat use between the respective groups
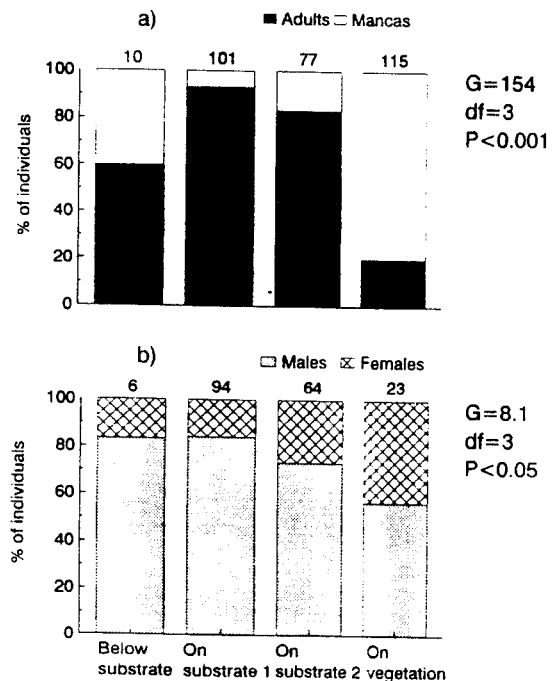

Fig. 3 The proportions of adults and mancas (a), and males and females (b) netted below the substrate, collected on the substrate using a pipette (*On substrate 1*), or netted on the substrate (*On substrate 2*), or netted on vegetation in the 21 June sample. The contingency table statistics test for differences in habitat use between the respective groups

Age and sex-specific cannibalism

Mancas maintained with adults and in groups

Adults clearly cannibalized mancas. Partly or completely consumed mancas were found in 13 out of 27 manca + male trials and in 23 out of 30 manca + female trials. Although we made no direct observations of adults attacking and killing mancas in these experiments, the lower survival of the mancas reared with males (Fig. 4a) or females (Fig. 4b) compared to controls indicated the direct adult predation of mancas. The mean longevity between mancas reared alone (mean = 5.04 days, SD = 3.12, $n = 28$) and with a male (mean = 3.37 days, SD = 1.73, $n = 27$) differed significantly (Fig. 4a: Mann-Whitney U-test, χ^2 approximation = 4.18, $df = 1.P < 0.05$).

In the second set of experiments, we found significant differences in survival between the mancas kept alone, in groups of four, or with a female (Fig. 4b: Kruskal-Wallis test, χ^2 approximation = 11.98, $df = 2.P < 0.01$). The mean longevity of the mancas reared with a female (mean = 10.3 days, SD = 8.17, $n = 30$) was slightly lower than that of the control (mean = 13.1 days, SD = 9.14, $n = 30$), but the difference was not statisti-
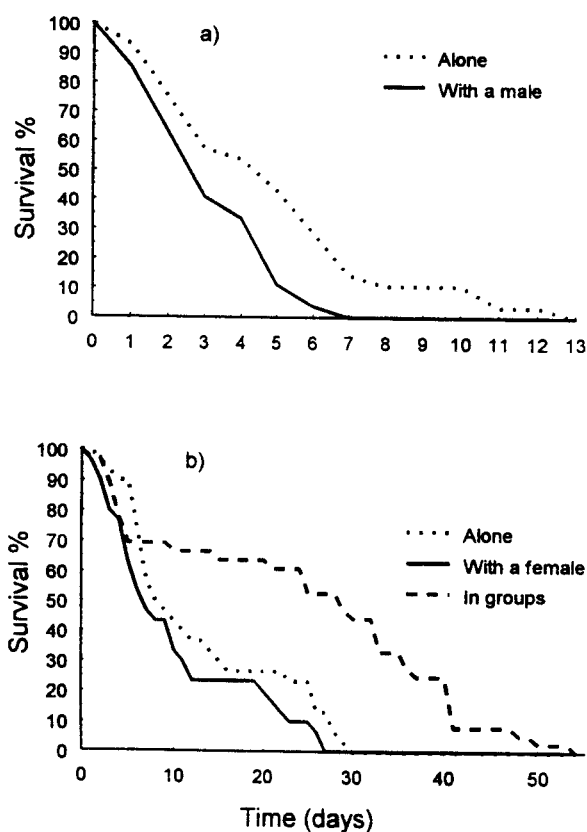
cally significant (Fig. 4b: nonparametric multiple comparison after Zar 1984: p. 200: $Q = 1.319$, NS). When mancas were maintained in groups of four, 18 out of 36 mancas were found partly or completely eaten. Interestingly, despite this considerable mortality, the survival in all-manca groups (mean = 24.69 days, SD = 16.53, $n = 36$) was better than that of mancas maintained alone or with a female (Fig. 4b: nonparametric multiple comparisons, alone vs. groups of four: $Q = 2.038$, NS: with a female vs. groups of four: $Q = 3.421.P < 0.01$).

Males and females maintained in pairs

Intersexual cannibalism also occurred in the laboratory. When the sexes were maintained in pairs, a female was eaten in 11 cases out of 59 (19%) while the male was never eaten. In 36 cases the female had given birth to a brood and was soon to undergo parturient ecdysis, before which males often guard females and during which copulation evidently takes place (Shuster 1981b). In 7 of these cases, the female was eaten either before or soon after copulation. In 23 cases, the female had undergone the parturient ecdysis before the male was introduced, and in 4 of these cases cannibalism occurred. Although the 11 females had been eaten, they may have died naturally and consumed afterwards. However, in 27 of 59 cases, the female was found dead and untouched by the male, showing that males do not necessarily feed on dead conspecifics. Furthermore, in 1 case, only small pieces of female exoskeleton were found 2 h after establishing the pair, suggesting that the female had indeed been attacked and rapidly consumed by the male.

Avoidance behavior

Manca response to adults

Mancas began to disperse to the unoccupied side of the partitioned test chamber immediately after each trial was initiated, and after 30 min the average number of mancas in the refuge remained relatively constant (Fig. 5). Therefore, we used the average number of mancas in the refuge 30 min after the start of each trial for comparisons. There were no differences in manca movement to the refuge between trials started from the left or right side (pairwise t-test – control, Fig. 5a: $t = 0.460$. $df = 6$, NS: with males. Fig. 5b: $t = 1.781$. $df = 6$. NS: with females, Fig. 5c: $t = 1.086$, $df = 6$. NS). Therefore the average of the left and right trials was used for further comparisons.

The average number of mancas that dispersed to the test chamber refuge was 5.55 (SD = 1.22, $n = 7$) for the control. 9.42 (SD = 1.62, $n = 7$) for mancas with males. and 8.80 (SD = 1.90, $n = 7$) for mancas with females. The difference between the treatments was statistically significant (Friedman two-way ANOVA: $r = 7.714$. $P < 0.05$). However, such a difference may arise if

Fig. 4 Survival curves for mancas reared with a male and alone (a), and for mancas reared alone, with a female, and in sets of four (b)
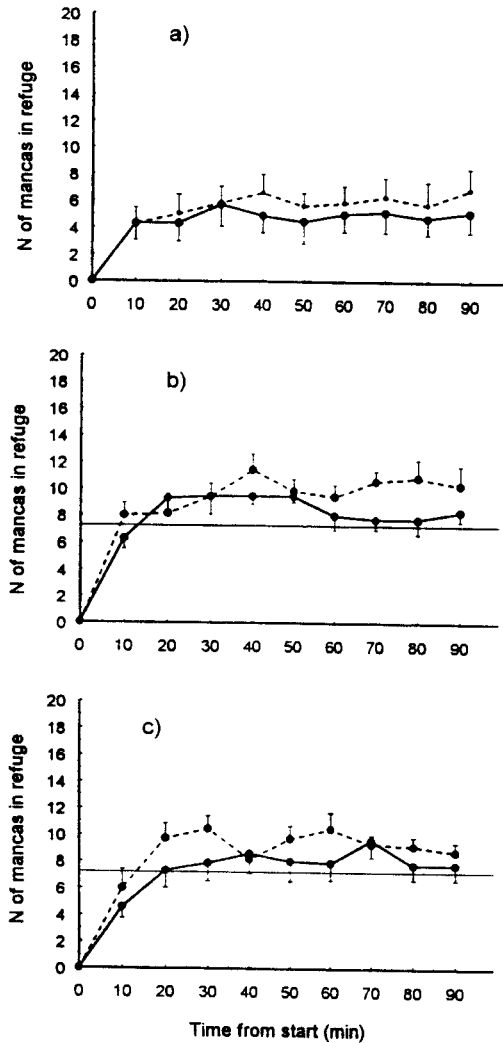
Fig. 5 Immigration of mancas to the refuge (initially empty) side of the test chamber after the start of the trial in a control test with 20 mancas only (a), in a test with six males and 20 mancas (b), and with six females and 20 mancas (c). The *solid and dotted lines* separate the cases where the starting side was either left or right. Means and SEs for seven sets of mancas are given. The *horizontal line* gives the expectation, calculated on the basis of control trials and the total number of animals in trials with males and females, for manca dispersal to the refuge as a response to density only

mancas only responded to the density of individuals regardless of age, size, or sex of the encountered conspecifics. Therefore, we calculated the mean percentage of individuals dispersed to the initially empty side in control trials, and used this as an expectation, or null hypothesis, for trials with males or females (Fig. 5b, c). When mancas were placed into the aquarium with males they dispersed to the refuge in greater numbers than expected if they had responded only to the density of individuals ($t = 3.601$, $df = 6$, $P < 0.05$), and they also tended to do so when with females ($t = 2.199$, $df = 6$, $P < 0.10$). Thus, mancas clearly avoided adult males, and to a lesser extent, also avoided adult females.

Adult responses to the opposite sex

When we tested the responses of males and females to olfactory cues from the opposite sex in the Y-maze apparatus, no avoidance or preference was found for either males or females (Table 2). The mean time spent in the treatment and control compartments did not differ significantly when the treatment input was either to the left or right compartment (Table 2). Neither were there any significant differences when the time spent in control and treatment compartments was combined from trials with treatment input from the left or right (pairwise *t*-test – males: $t = 0.323$, $df = 26$, $P = 0.75$; females: $t = 0.494$, $df = 28$, $P = 0.62$). There were no differences in the time spent stationary in different compartments, with the exception that females spent more time stationary in the left compartment when the odors from males came into right compartment (Table 2). However, when the time spent stationary in control and treatment compartments was combined from the trials of left and right odor input, no differences were found (pairwise *t*-test – males: $t = 0.058$, $df = 26$, $P = 0.95$; females: $t = 1.62$, $df = 28$, $P = 0.12$).

Discussion

Cannibalism and microhabitat segregation

The microhabitat segregation by *T. thermophilum* mancas and adults was unambiguous in their native spring. Mancas were mainly found above the substrate on the grasses on both sampling dates, whereas adults, especially males, were found mainly on the substrate. These observations are consistent with laboratory results indicating that mancas face a high risk of intraspecific predation when in the presence of adult males and females. Laboratory results also showed that mancas dispersed from the vicinity of adults, especially from males. Such behavioral avoidance of cannibalistic adults has been found in several species (Foster et al. 1988; Dong and Polis 1992; Sparrevik and Leonardsson 1995). For example, many gammarid adults prey on mancas (Hunte and Myers 1984; Dick 1995), and Hunte and Myers (1984) hypothesized that phototaxis of juveniles, leading to microhabitat segregation between juveniles and adults, is primarily an adaptation against cannibalism.

We have no data on the possible effect of food preferences on the distribution of individuals. Thus, we cannot exclude the possibility that subtle differences in food availability between grasses and substrate may generate microhabitat segregation. However, our demonstration of the avoidance of adults by mancas is sufficient to account for the nonrandom distribution of individuals within their habitat. Moreover, that females were vulnerable to predation by males and that females as well as mancas appeared to use pool vegetation as a refuge is consistent with this interpretation. Apparent

Table 2 Total time spent and the time spent stationary (*stop time*: mean and SE in seconds) in different compartments of the test chamber for males and females when the odors from the opposite sex were coming either into the left (*odor left*) or the right (*odor right*) compartment. The pairwise *t*-test statistics test for the difference in time spent in the left and right compartments

	n	Left Mean	SE	Right Mean	SE	Neutral Mean	SE	Test t	P
Odor left									
Males									
Total time	30	488	86	468	79	244	59	0.126	0.90
Stop time	30	135	52	130	40	81	42	0.074	0.94
Females									
Total time	29	547	89	492	87	161	41	0.319	0.75
Stop time	29	163	41	153	40	43	14	0.149	0.88
Odor right									
Males									
Total time	29	563	77	436	76	200	23	0.840	0.41
Stop time	29	119	29	124	45	51	15	0.078	0.94
Females									
Total time	29	584	89	422	83	194	46	0.983	0.33
Stop time	29	291	61	98	25	46	23	2.579	0.02

microhabitat segregation could be accentuated by the removal of mancas and females from the pool bottom by cannibalism. In addition, avoidance of cannibalism should act in opposition to dietary requirements of mancas and females if the refuge habitat is not as profitable as the adult habitat as a food source. In any case, we suggest that cannibalism and the attempts of individuals to avoid it are the primary causes of habitat segregation in this species.

Females were found more often than males above the substrate, a tendency which may have been underestimated because some of the largest individuals classified as mancas may actually have been small virgin females. By moving to microhabitats containing fewer males, females would avoid sexual harassment, as suggested by Shuster (1981a). Males continuously harass females while searching for mating partners, probably in order to assess female quality, and attempt to initiate precopulatory guarding (personal observations). Females usually respond by resisting guarding attempts (Shuster 1981b). Such female resistance is understandable if females face some cost due to prolonged guarding, a situation that could lead to sexual conflict over guarding duration (Jormalainen and Merilaita 1993, 1995; Jormalainen et al. 1994). One such cost was evident in this study: a female had a relatively high probability of being cannibalized by a male even if she was soon to become receptive for fertilization. Such 'reversed' intersexual cannibalism has been observed previously in gammarids and attributed to the larger size of males and hunger (Dick 1995). T. thermophilum males are larger than females, a common precondition determining the roles of cannibal and victim (Fox 1975; Polis 1981; Elgar and Crespi 1992), but the pairs were plentifully fed with both vegetarian and animal food, implying that hunger is not a necessary condition for intersexual cannibalism. Instead, the decision of males to mate with or eat females might result from a more complicated assessment of the quality of a female as a mating partner. Given the potential cost of becoming cannibalized, females can be expected to resist when encountered by a male and,

furthermore, to avoid unnecessary encounters before being ready for fertilization by hiding from the males (Clutton-Brock and Parker 1995; Jormalainen and Merilaita 1995).

Chemical communication using waterborne pheromones or molting hormones, especially for locating food and mating partners, is considered common, if not universal in aquatic crustaceans (Dunham 1978; Borowsky 1985; Dunham and Hurshman 1991). However, in this study, T. thermophilum females did not avoid water containing odors from males, and males neither preferred nor avoided water containing female odors. We suspect that the lack of responses to odors of the opposite sex in our experiments reflects a decreased reliance on waterborne chemicals in T. thermophilum. Their confined habitat and very dense population are likely to make chemical signaling either unnecessary or at least inefficient, and the trait may have been lost since the post-Cretaceous isolation of this species from its marine ancestors (Bowman 1985).

Cannibalism as a selective agent

Invertebrate predators occur only incidentally in the habitat of T. thermophilum since isopod predation effectively eliminates early stages of other predaceous invertebrates and there are no vertebrate predators in the spring (Shuster 1981a). The species shows tenacious cannibalistic habits in the laboratory even in the presence of alternative food, and cannibalism has been observed in field conditions (Shuster 1981a). Cannibals also appear to obtain nutritional benefits from eating conspecifics, since the survivorship of cannibalistic mancas was better than that of those reared with females. These facts suggest that cannibalism is a primary source of mortality in T. thermophilum. Thus, adaptations for cannibalism are likely to have evolved.

Cannibalism is likely to influence the duration of and activities associated with the molt cycle. Aquatic isopods and amphipods are especially vulnerable to predation

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during molts, when their cuticles are soft and their mobility is reduced (e.g., Dick 1995). In *T. thermophilum*, however, molting seems to constrain mobility very little, as half-molted animals can swim and crawl normally (personal observations). Furthermore, mancas, at the time of their release from brood pouches, stay attached below their mother for a day or two before leaving this shelter. Both of these traits are likely to enhance survival under conditions of heavy cannibalism.

The activity level of differently sized individuals may also be affected by cannibalism. In a cannibalistic population, the fitness consequences of differential activity depend on whether the individual is likely to be a victim or a cannibal (Crowley and Hopper 1994). High activity is beneficial for cannibals because it increases encounters with prey, but high activity increases the risk of mortality for potential victims. Interestingly, *T. thermophilum* males, who are the largest and most likely to cannibalize other isopods, are clearly the most active group (Shuster 1981a). This activity is understandable in terms of the male need to search for mates, but it may also enhance their cannibalistic foraging success.

Cannibalism directed at smaller size groups is likely to drive the sex ratio toward an excess of the larger sex. As expected, in *T. thermophilum*, the population sex ratio is male biased throughout the year (Shuster 1981a). This male bias may well arise as a consequence of intersexual cannibalism, and cannibalism among mancas is likely to further accentuate this effect, since sexual size dimorphism arises before individuals are fully mature (Shuster 1981a). Sexual size dimorphism is probably plesiomorphic in sphaeromatids and is certainly shared by all *Thermosphaeroma* species, but it is clearly most pronounced in *T. thermophilum* (S. Shuster and G. Davis, unpublished data). However, cannibalism is not prominent in other *Thermosphaeroma* species (personal observations). Therefore, we suggest that cannibalism, by biasing the sex ratio, intensifies sexual selection because a male-biased sex ratio strengthens intrasexual competition among males (Emlen and Oring 1977; Clutton-Brock and Parker 1992), which, in turn, increases the duration of male precopulatory guarding, and may affect patterns of female resistance to male mating attempts (Jormalainen et al. 1994). In mate-guarding crustaceans, intrasexual selection, and sometimes intersexual selection by means of female resistance, favors large male size and, thus, acts to increase the degree of sexual size dimorphism (e.g., Ridley and Thompson 1985; Jormalainen and Merilaita 1995).

Implication for species protection

Cannibalism may be the primary mechanism of population regulation in *T. thermophilum*. However, population extinctions are unlikely to result from cannibalism itself because the occurrence and intensity of cannibalism are usually density dependent (Polis 1981; Orr et al. 1990; Elgar and Crespi 1992; Hopper et al. 1996).

Cannibalism rates decrease as victims become rare, searching becomes more costly, and as alternative food resources become more available in low-density situations (Fox 1975; Lazzaretto and Salvato 1992; Crowley and Hopper 1994). *T. thermophilum* is an endangered species. Thus, the implication of our results for management and protection of this population is to ensure sufficient small-scale habitat heterogeneity both in the native spring and in the pools used as alternative habitats. Microhabitat heterogeneity creates the opportunity for habitat segregation and offers refuges from cannibalism, which, in turn, are likely to decrease cannibalism rates and allow a larger, more viable population.

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