Sex Attraction and Recognition in the Caridean Shrimp *Heptacarpus paludicola* Holmes (Decapoda: Hippolytidae)

RAYMOND T. BAUER

Friday Harbor Laboratories, Friday Harbor, Washington, 98250, USA

Newly molted female *Heptacarpus paludicola* with full ovaries evoke a copulatory response from males upon contact. Males recognize a matable female for copulation by apparent contact chemoreception with the antennal flagellae. Observational evidence in this species and in several others cited in the literature did not strongly suggest distance perception of matable females by males. However, when tested in an experimental "olfactometer" evidence was obtained to indicate that matable females of this species emit a pheromone that increases activity of males, whereas hard-shelled, embryo-bearing females do not.

Although newly molted females with full ovaries were by far the most effective in evoking copulatory behavior from males, newly molted females without ovarian development (due to parasitization or food deprivation) showed varying degrees of attractiveness. Newly molted males were not attractive to other males. The duration of attractiveness to males was less than one day after matable females had molted. Chemicals associated with the hardening of the cuticle are suggested as a possibility for the apparent contact pheromone involved in sex recognition.

1 INTRODUCTION

It has become evident in recent years that distance perception of matable females by males through olfaction plays an important role in the sexual behavior of crustaceans. Both observational and experimental evidence indicate that behavioral changes in males prior to mating, such as searching or reduced aggressive behavior, are induced by water soluble substances released by the female. Such pheromones have been indicated in a variety of Crustacea, e.g., crabs (*Portunus sanguinolentus*, Ryan, 1966; *Carcinus maenas*, Eales, 1974; *Pachygrapsus crassipes, Cancer antennarius, C. anthonyi*, Kitteredge *et al.*, 1971), lobsters (*Homarus americanus*, McLeese, 1970;

Atema and Engstrom, 1971), crayfish (*Procambarus clarkii*, Ameyaw-Akumfi and Hazlett, 1975), amphipods (*Gammarus duebeni*, Dahl *et al.*, 1970) and copepods (*Labidocera jollae*, Kitteredge *et al.*, 1974).

In contrast, the literature on mating behavior in caridean shrimp is replete with reports strongly indicating a lack of distant perception of females by males. Chemotactile responses *via* second antennae or pereiopods appear to be the major process involved in sexual recognition (Table I; also see Carlisle, 1962 and Hazlett, 1975). This generalization is based primarily on observational evidence. Olfactory recognition between male–female pairs has been demonstrated experimentally in the caridean *Hymenocera picta* (Seibt, 1973).

The purpose of this study was to investigate distant perception of females by male *Heptacarpus paludicola* and the process of sexual recognition prior to mating. Reproductive parameters important to the understanding of mating behavior are reported.

2 METHODS

Heptacarpus paludicola is a small (approximately 1–3 cm total length) active shrimp inhabiting bay environments from British Columbia (Rathbun, 1904) to at least as far south as San Quintin Bay, Baja California (personal observation). Shrimp used in this study were collected by dipnet from algae in the Argyle Lagoon and Channel on San Juan Island, Washington, and maintained in the seawater system of the Friday Harbor Laboratories, where the laboratory table temperatures varied from 11–13°C. The work was conducted from June 15–July 23, 1978. Preliminary observations on this species had been done on individuals from San Quintin Bay, Baja California; Mission Bay, San Diego, California; and Morro Bay, California at intervals over the past several years. Shrimps were fed daily on a diet of tropical fish flakes and occasionally pieces of mussel (*Mytilus*). Hatching of embryos, molting and other pertinent activities were followed individually in females isolated in plastic cups (5 cm bottom diameter, water level 4 cm high) with many small holes drilled for water circulation. A small rock added to the cup seemed to aid in molting and provided habitat for the female.

Mating behavior and determination of contact attractiveness

Fifteen "formal" matings were conducted so that the sequence of events in mating could be determined. Females with ripe ovaries which had molted recently (i.e. within the previous 24 hours) were placed in a 26 cm long × 2 cm wide × 13 cm high plexiglass aquarium which had gravel strewn about on the bottom. A removable plexiglass partition divided the aquarium, and

TABLE I

Evidence of distance perception and/or contact recognition of females by male caridean shrimp: P, positive; N, negative; I, implied; U, unspecified; A, contact recognition via second antennae and/or pereiopods

| Species | Source | Olfactory perception | | Contact recognition |
		Observational evidence	Experimental evidence	
Alpheidae				
Athanas nitescens	Nouvel and Nouvel, 1937	U	None	I
Alpheus dentipes	Nouvel and Nouvel, 1937	U	None	I
Atyidae				
Atyaephyra desmaresti	Descouterelle, 1971	I	None	U
Crangonidae				
Crangon crangon	Nouvel, 1939	P	None	I
Crangon vulgaris	Lloyd and Yonge, 1947	N	None	A
Gnathophyllidae				
Hymenocera picta	Seibt, 1973	P	P	U
Hippolytidae				
Heptacarpus pictus	Bauer, 1976	N	None	A
Palaemonidae				
Palaemonetes vulgaris	Burkenroad, 1947	N	None	A
Palaemon squilla	Höglund, 1943	N	None	A
Palaemon squilla	Nouvel and Nouvel, 1937	U	None	I
Palaemon serratus	Forster, 1951	N	None	A
Typhlocaris galilea	Tsurnamal, 1978	N	None	A
Anchistus custos	Hipeau-Jacquotte, 1974	N	N	I
Pandalidae				
Pandalus danae	Needler, 1931	P	None	A
Pandalus borealis	Carlisle, 1959	N	None	A
Pandalus platyceros	Hoffman, 1973	I	None	I
Processidae				
Processa edulis	Nöel, 1976	I	None	I

male was placed in one side, the female in the other. After a ten-minute acclimation period, the partition was removed. Following mating the females were allowed to spawn. After spawning, females were replaced in individual containers to determine the period of embryo incubation.

Recently molted females and males, and females with embryos, were exposed to males to determine if they evoked a copulatory response. Test individuals were usually introduced into a container with several males. If any of the males showed a seizing response, but the test animal rebuffed the advance, then the latter was removed, anesthetized by chilling, and returned to the test chamber. Male response to the anesthetized animal was noted.

Duration of attractiveness of newly-molted, ripe females was tested by exposing them to a number of males at intervals of hours, after initially evoking a copulatory response from a male. It often happened that upon the second or third exposure, males were attracted, but the test female vigorously rejected the advance, making it difficult to determine objectively if a copulatory response had been evoked. Such females were anesthetized, as above, and re-exposed to males, often resulting in an undisturbed copulatory response.

Olfactory experiments

Male *H. paludicola* are small, highly active animals, easily agitated in aquarium situations. An olfactometer design which could overcome the problems of high intrinsic activity levels, individually variable behavior and ease of disturbance had to be used. Preliminary testing showed that olfactometer designs similar to that used by Ache (1975) or Y-maze set-ups like that of Evans *et al.* (1977) would not be appropriate for these shrimps. The final design (Figure 1) was a plastic aquarium in which a group of ten males were isolated individually in perforated plastic cups. Each cup had a small stone which, in addition to the isolation from other males, succeeded in making the males quiescent so that changes in behavior could be noted. Water flowing into the aquarium flowed first through an opaque plastic refrigerator jar with screened windows to allow water flow ("test chamber"). Dye tests showed that water flowing through the test chamber penetrated all the cups before exiting. Rate of water flow through the aquarium was 1 liter/minute.

A series of control tests using food stimuli were conducted prior to testing with matable females to ensure the effectiveness of the flow chamber.

In each test, there was a control and experimental run. In the control run, a small rock was placed in the stimulus chamber, whereas the test object was a piece of fresh mussel in experimental runs. Due to the variability and normal high level of male activity, it was necessary to compare the number of males active before and after the introduction of the test object. Thus, in any run,
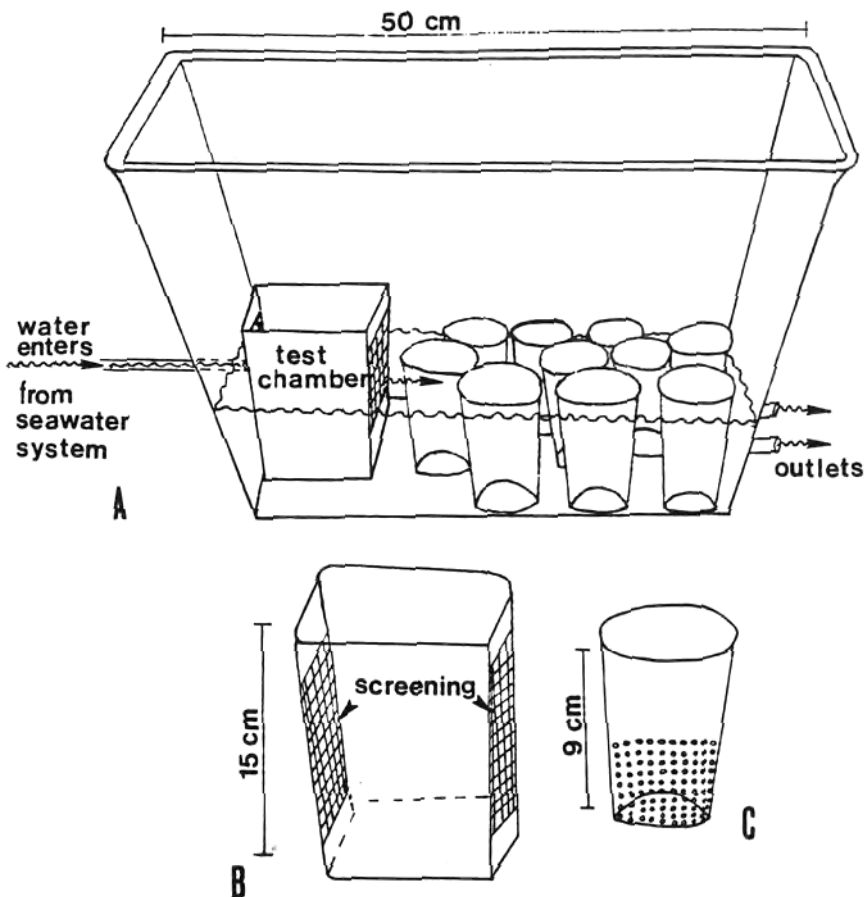
FIGURE 1   Apparatus used as an olfactometer in the distance chemoreception experiments. (A) entire olfactometer, showing position of test chamber and cups which contained males; (B) close-ups of test chamber giving position of the fine plexiglass screening; (C) cup showing perforations for water circulation.

five observations of the number of males (out of ten exposed) active, i.e., swimming or walking, were made at one-minute intervals ("before"), followed by a two-minute interval, introduction of the test object, followed by five observations ("after"). Ten minutes always separated control and experimental runs, with 30 minutes between new tests. Males were not fed during this set of experiments.

Distance detection of ripe females by males was tested for, with the control being a female brooding embryos, the experimental a newly molted female with ripe ovaries. The former type of individual never evoked a copulatory

response in interactions with males while the ripe females used in these tests were exposed to males after being used in a test, to ensure that they were indeed matable. Only one of 16 was not attractive to males upon contact, and the results of that test were discarded. In these tests, order of presentation of control and experimental subjects were alternated every test. Males used in these tests were well fed, as both McLeese *et al.* (1977) and Eales (1974) have indicated that food-satiated males show less variable response in such experiments.

Determination of reproductive parameters

Duration of embryo incubation, time interval between hatching of eggs and molting, and from molting to spontaneous spawning of eggs (in females deprived of mating) were measured by examining individually maintained females, three times daily. The time of occurrence of an event was set as midway between the two observations before and after the event occurred. Time between mating and spawning, and the duration of spawning were measured directly.

3 RESULTS

Mating behavior

The sequence of events and mechanics of mating in *Heptacarpus paludicola* are, qualitatively, indistinguishable from that described for the closely related *H. pictus* (Bauer, 1976). Recently molted females (with full ovaries showing through the carapace) evoke copulatory responses from males upon contact. Like *H. pictus*, *H. paludicola* females produce multiple broods each year, so that most females used in mating studies were carrying embryos which had to hatch before the pre-mating molt could take place. Table II shows the median time between hatching of embryos and the molt was 40 hours. Females which had ripe ovaries, molted but were not allowed to mate, spawned their eggs spontaneously, within a median time of 24 hours (Table II). The unfertilized eggs did attach to the female's pleopods, but were removed by the female by grooming within a few days.

As described for *Heptacarpus pictus*, the mating of *H. paludicola* can be divided into the following phases: *contact* (recognition), *climb*, *straddle*, *mount*, *dip*, *pleopod beat*, *disengagement*, *post-mating grooming*, and *spawning*.

The first obvious sign that a female has been recognized by the male is upon *contact* of the female by the male's antennal flagellae (usual) or pereiopods. The male abruptly changes its previous behavior and orients towards the

TABLE II

Time intervals of events associated with the reproductive cycle in *Heptacarpus paludicola* females

Event	Median	95% confidence limits on the median	Range	N
Time interval between embryo hatching and pre-mating molt	40 hours	33, 48	7–124	67
Time interval between molting and spontaneous spawning of eggs in females isolated from males	24 hours	18, 30	7–49	33
Time interval between copulation and spawning	5 minutes	3, 7	1–30	11
Duration of spawning	19 minutes	10, 60	9–90	10
Duration of embryo incubation (spawning–hatching at 12°C)	31 days	30, 31	30–31	11

female, attempting to seize her with the pereiopods. There is no consistent or obvious sign that the male recognizes the female's presence until this contact takes place. Introduction of a female into an aquarium with males or the converse does not bring about any qualitative difference in male behavior. I have observed on several occasions a male situated just outside of contact with a "matable" female with no sign of recognition or searching behavior. As soon as contact was established, the male attempted copulation.

Occasionally, after a male had responded to a female, the pair temporarily lost physical contact, in which case the male would orient to and track any nearby shrimp, apparently following movement visually, until antennal contact was re-established. If the male had contacted the matable female again, copulation would be attempted. If another male or non-matable female was contacted, it would be ignored. Not every male responded to a matable female; such males were removed and replaced by another in these matings.

No tactile behavior, e.g., stroking, prolonged tapping or palpation of the female by the male was observed. After contact, the male seizes the female, *climbs* to the dorsal surface of the female, orients his body along her dorsal midline (*straddle*), then lowers his body at right angles to hers (*mount*), swings underneath her (*dip*), deposits a spermatophore on the underside of her first abdominal segment (*pleopod beat*). *Disengagement* of the mating pair takes place, usually by a flight response of the female. Before a successful mating, the female is passive to the male, but just after the disengagement, she will flee any approach of a male. It was observed that if a female had

molted within a few hours of the attempted mating, she rejected male advances, but if reintroduced to males hours later, would copulate normally.

The female immediately engages in *post-mating grooming* just after copulation. Spawning takes place within a median time of five minutes, and the process lasted for a median time of 19 minutes in those females observed (Table II). Females brooded embryos for 30 or 31 days before hatching took place (Table II).

Olfactory experiments with males

Response to food Experiments were conducted to determine whether the olfactometer was appropriately designed to demonstrate distance chemoreception by males. The number of males active out of a group of ten exposed to stimuli was recorded at five one-minute intervals before and after the introduction of a test object. The test object was a small rock in the control runs, while a piece of mussel was used in experimental runs ($N = 15$ tests).

Results are presented graphically in Figures 2–4, while statistical comparisons of means between the various treatments are given in Table III. A comparison of activity before and after of food (Figure 2 and Table IIIA) shows a very significant increase after food introduction into the test chamber. Activity before and after the introduction of the control object (Figure 3,
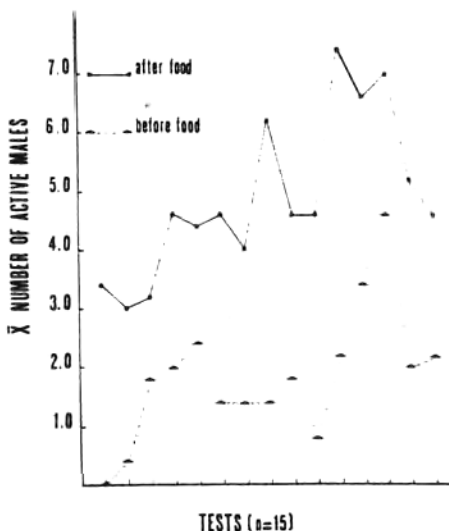

FIGURE 2 Comparison of male activity before and after introduction of food into the test chamber. Values of the ordinate axis are the mean number of males active out of a group of ten exposed to stimuli (each point on the graph is the mean of five observations).

TABLE III

Comparison of mean ($\bar{x}$) male activity in response to possible olfactory stimuli ($\bar{x} = \Sigma \neq$ males of ten exposed active in five observations/run divided by the number of tests (N = 15)· means of various treatments compared by one-way analysis of variance (ANOVA); S, means significantly different; NS, means not different

	Treatment	$\bar{x}$	vs	Treatment	$\bar{x}$	$F_{1,28}$ ratio from ANOVA	Probability that these two means are not different	
A.	"Before" experimental (*food*)	9.6		"After" experimental (*food*)	24.4	36.5	< 0.001	S
B.	"Before" control (*rock*)	9.8		"After" control (*rock*)	10.0	0.005	> 0.90	NS
C.	"After" control (*rock*)	10.0		"After" experimental (*food*)	24.4	26.3	< 0.001	S
D.	"Before" experimental (*matable female*)	3.0		"After" experimental (*matable female*)	15.5	26.1	< 0.001	S
E.	"After" control (*berried female*)	4.0		"After" experimental (*matable female*)	15.5	20.4	< 0.001	S
F.	"Before" control (*berried female*)	4.1		"After" control (*berried female*)	4.0	0.002	> 0.90	NS

Table IIIB) shows no significant difference, indicating that the test procedure itself did not stimulate an increase in male activity. Levels of activity "after" introduction of the control and "after" food emphasize the male perception of food at a distance (Figure 4, Table IIIC). It was concluded that the olfactometer design was satisfactory for demonstration of distance chemoreception in males.

Response to females   In these tests, females brooding embryos, which do not evoke copulatory behavior from males, served as controls. Newly molted females with full ovaries served as the experimentals. All the matable females were exposed to male contact after the tests and found to evoke copulatory behavior.

A comparison of male activity before and after the introduction of a matable female to the test chamber (Figure 5, Table IIID), and after the introduction of a control female (Figure 6, Table IIIE), show significantly higher levels induced by matable females. Figures 5 and 6 show that strong
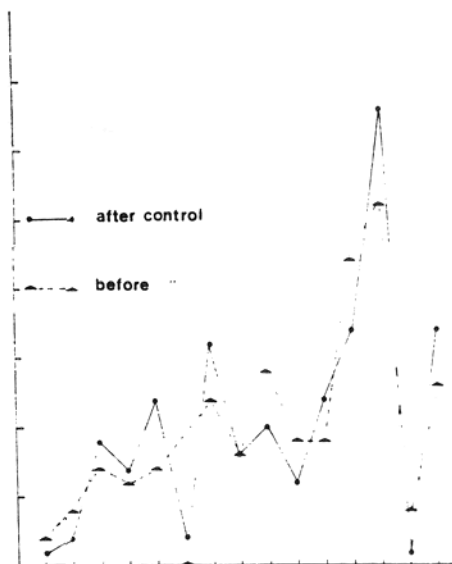
FIGURE 3   Comparison of male activity before and after introduction of the control object (rock) into the test chamber. (Axis labeling the same as Figure 2.)
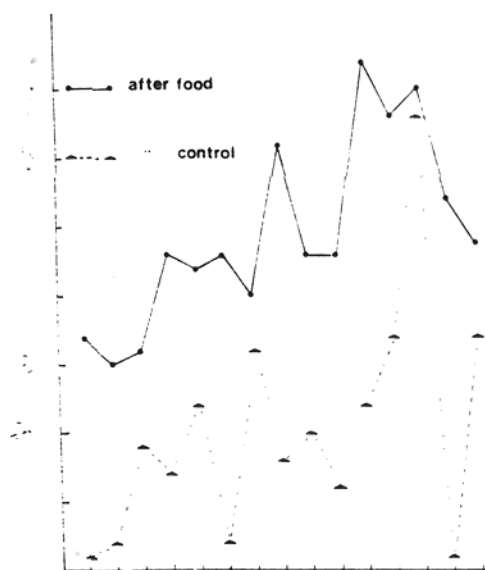

FIGURE 4   Comparison of male activity after introduction of food and after introduction of the control object (rock) into the test chamber. (Axis labeling the same as Figure 2.)
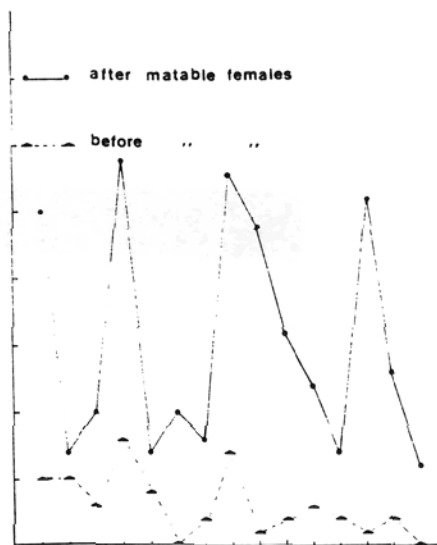
FIGURE 5 Comparison of male activity before and after introduction of a matable female into the test chamber. (Axis labeling the same as Figure 2.)
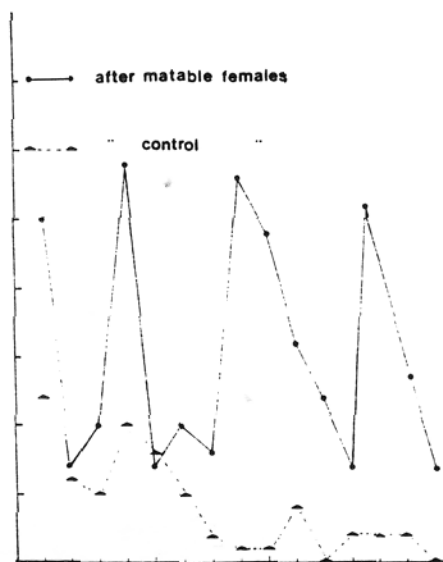

FIGURE 6 Comparison of male activity after introduction of a matable female and after introduction of a control (embryo-bearing) female into the test chamber. (Axis labeling the same as Figure 2.)

responses by the group of males was intermittent, although matable females nearly always induced at least slightly higher activity levels. Activity before and after introduction of control females (Figure 7, Table IIIF) indicate as in the food experiments, that the test procedure itself did not induce increased male activity. The evidence strongly indicates that males do respond at a distance to water flowing through a chamber containing a matable female.
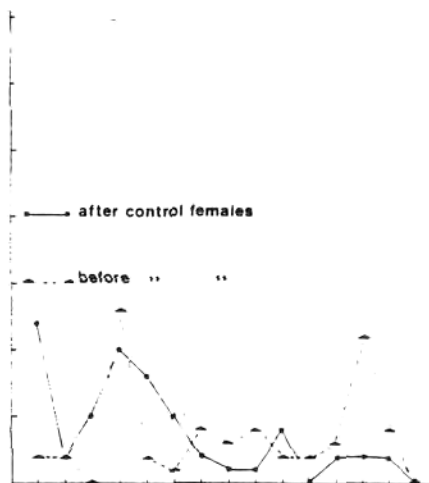

FIGURE 7   Comparison of male activity before and after introduction of a control (embryo-bearing) female into the test chamber. (Axis labels the same as Figure 2.)

Chemotactile responses

Preliminary observational evidence on *Heptacarpus paludicola* indicated that only newly molted females with ripe ovaries evoked copulatory behavior from males which touched them with antennae or pereiopods. Exposure of various types of individuals to males was conducted to determine more precisely which individuals evoked copulatory behavior. A positive response was recorded when one or more males to which the test individual was exposed showed a copulatory response on contact, i.e. at least seizure of the test individual, followed by an attempt to enter into the *mount* phase of copulation. Table IV shows the results of these tests. As expected, newly molted ripe females were nearly all attractive (95%), while hard-shelled females carrying embryos never were. No newly molted males were attractive in six tests. A high percentage (78) of newly molted females parasitized by the bopyrid isopod *Hemiarthrus abdominalis* were attractive. These females showed no ovarian development, although most elements of the "breeding

TABLE IV

Degree of copulatory response evoked from males upon physical contact with various types in the population

Type of individual	% positive responses	N
Newly molted females with full ovaries	95	42
Hard-shelled females carrying embryos	0	15
Newly molted females parasitized by bopyrid isopods	78	9
Newly molted females with empty ovaries	40	5
Newly molted males	0	6

dress" (see Bauer, 1976) were present. Newly molted females which were without ovarian development were obtained by having ripe females molt and spawn without mating. These females were used at their next molt, with ovarian development retarded by food deprivation. Two of five such females were attractive to males.

An attempt to determine the duration of contact attractiveness in matable females was made. Some females were exposed to males at intervals of hours, allowed to enter into the preliminary stages of copulation to establish attractiveness, but separated before a spermatophore could be deposited. In another group, mating and spawning was allowed on the first contact. When the female no longer evoked a copulatory response, the period of her attractiveness was considered at an end. In some females, even though no spermatophore was allowed to be deposited, spawning took place due to the shock of handling. Data on these females has been included with that of females allowed to mate and spawn.

Figures 8 and 9 give the results of these experiments. In the females which did not spawn, the median time at which attraction ended was 25 hours, while it was 16 hours for females which spawned during the course of the tests. However, a rank sum test supported the null hypothesis that these medians are not statistically different ($P > 0.20$). The data obtained in this study does not indicate that spawning has any effect on the duration of contact attractiveness in matable females.

4 DISCUSSION

Results of the olfactory experiments show that male *Heptacarpus paludicola* do respond to matable females from a distance with increased levels of activity (walking, swimming). Most observational evidence from the literature cited in Table I has given rise to the generalization that olfactory perception of females does not occur in the Caridea (e.g. Carlisle, 1962). Laboratory
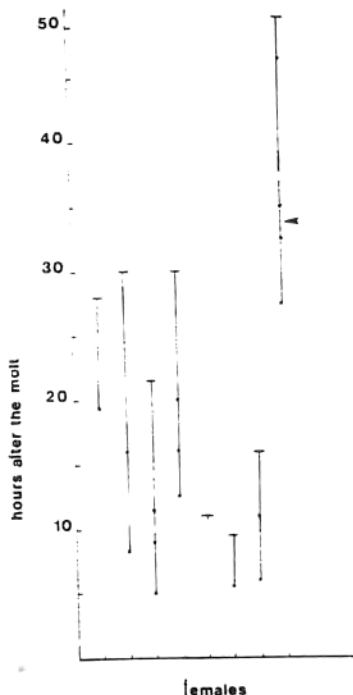
FIGURE 8   Duration of time after the molt females were attractive (evoked a copulatory response) to males on contact (no completed copulation or spawning in this group). Dots indicate exposure of a female to and a positive response from males; terminal bar indicates a negative response (end of attractiveness); arrow indicates time at which one female died.

situations which give rise to a strong olfactory response from males in other decapod crustaceans (presence of a matable female in the same aquarium, introduction of "female" water into an aquarium with males) do not give the same clear-cut results in this or previous studies (e.g. Bauer, 1976; *H. pictus*). Only in one experimental study (Seibt, 1973) has a caridean shrimp, *Hymeno-cera picta*, been shown to have an olfactory response to a mate.

Hamner and Hamner (1977) have pointed out that only under certain experimental conditions could chemosensory capabilities be observed and demonstrated in the sergestid shrimp *Acetes sibogae australis*. If the aquarium was too small or of the wrong shape, the capability could not be shown. Similar problems occurred in this study. Male *Heptacarpus paludicola* have a highly variable, easily disturbed behavior, and proper testing of olfactory sense could only be done under certain conditions. In this study, an olfac-tometer design was found which lowered male agitation in an aquarium, allowing quantitative observation of chemoreceptive abilities.
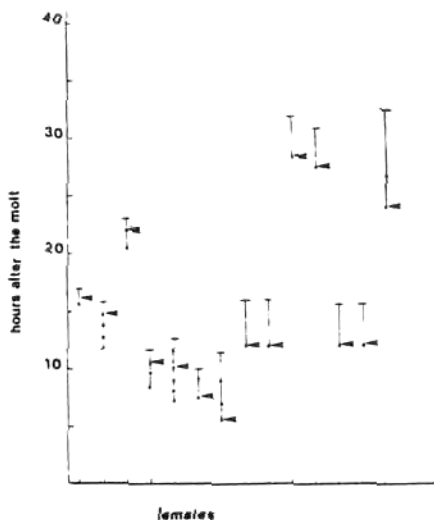
FIGURE 9 Duration of time after the molt that females which spawned were attractive to males. Same symbols as Figure 8, except arrows immediately after the first exposure indicate that a completed copulation followed by spawning took place; an arrow at any other time indicates spontaneous spawning without copulation.

Another factor which may have masked the qualitative observation of a male olfactory response to females was the apparent intermittent release of the water-soluble attractant or pheromone from the female. Males responded very strongly (as a group) to only five or six of the 15 matable females tested, although there was a higher level of response to the remaining matable females than to controls. Intermittent release of sex pheromones has been suggested by other studies, e.g., Ryan 1966; Eales, 1974; McLeese, 1970. Periodic release of urine by the female, with the pheromone being in the urine, has been suggested for this phenomenon.

This study has shown that matable females give off a water-soluble substance that increases male activity. It is suggested that other caridean species may exhibit such apparent pheromones, and that their presence in previous studies has been masked by rather non-specific male responses, high variable levels of activity in most species, as well as the intermittent release of the substance by females. Appropriately designed experimental studies could demonstrate sex pheromones in other caridean species.

Observations in this study and those in the literature on other species strongly suggest that actual recognition of a matable female by males is due to contact, usually with the long antennal flagellae. Although no experiments have been done with blinded males, observations suggest vision has little role in sexual recognition. Males walking next to, or standing near a matable

female, without actual contact, show no sign of recognition. The response is apparently chemotactile, with the change in behavior by the male very similar to that when he (or a female) can be quite near an item of food but only attempt to orient to it upon contact.

Results from this study do support the generalization from the literature that newly molted females with ripe ovaries evoke copulatory responses from males upon contact. In a series of test exposures, these "matable" females showed a very high level of attractiveness to males. Newly molted males were not attractive to other males upon contact, whereas, surprisingly, females parasitized and castrated by a bopyrid isopod were rather highly attractive to males. The bopyrid *Hemiarthrus abdominalis* is situated underneath the abdomen, where brooded embryos would usually be carried in a parasitized female. Such females still show elements of the breeding dress such as enlarged abdominal pleurities and broadened flanges on the protopods of pleopods. It could be that the parasite is mimicking a brood of embryos and that it induces a reproductive physiology similar to normal breeding females, accounting for the attractiveness of the parasitized females upon molting.

The fact that newly molted males do not evoke copulatory attempts from other males is an indication that a mechanical stimulus (soft cuticle) is not the primary or only stimulus involved in sex recognition. It is highly probable that a chemical substance adsorbed on the newly formed cuticle of the female serves as a pheromone perceived by contact chemoreception. Perhaps materials secreted through the tegumental glands involved in tanning the newly formed cuticle, with some substance specific to matable females, serve this purpose. Duration of attraction is about a day, and experiments in this study show that the end of attractiveness is simply due to a passage of time, rather than being tied to a specific event, such as spawning. Termination of attractiveness could be corresponding to the end of chemical changes taking place in the hardening cuticle. Hazlett (1970) has suggested that perhaps both tactile and non-diffusible chemical stimuli act synergistically in contact recognition of female *Pagurus bernhardus* by males. Alexander (1977) demonstrated electrophysiologically that sensory hairs on the antennae of the isopod *Ligia oceanica* could respond to both mechanical and chemical stimuli.

Résumé

Après la mue, les femelles avec ovaires mûrs provoquent une réaction copulatoire des mâles par contact. Les observations du comportement sexuel n'indiquent pas la perception olfactive des femelles par des mâles. Mais l'évidence expérimentale indique que les femelles émettent une substance soluble dans l'eau qui augmente l'activité des mâles. On a mis au point un olfactomètre qui réduit l'habituelle agitation des mâles dans les bacs de laboratoires. Des expériences avec de la nourriture, laquelle est un stimulant olfactif connu, ont confirmé que cet olfactomètre pourrait démontrer l'olfaction chez les mâles. Des ex-

périences semblables avec des femelles ont demontré que les femelles avec ovaires mûrs qui venaient de muer augmentent l'activité des mâles plus que les femelles de contrôle (les femelles avec des embryons).

Apparemment les mâles reconnaissent les femelles pour la copulation par chimio-réception de contact au moyen des fouets des deuxièmes antennes. Bien que les femelles avec ovaires mûrs qui venaient de muer furent le plus de succès en provoquant comportement copulatoire des mâles, les femelles sans développement des ovaires (à cause de parasites ou privation de nourriture) qui venaient de muer ont montré degrés variants d'attirance. Les mâles qui venaient de muer ne furent pas attirés par les autres mâles. La temps de l'attrait des femelles durait moins d'un jour après la mue. Les produits chimiques associés au durcissement de la cuticule pourraient être le pheromone de contact qui est impliqué dans la reconnaissance sexuelle.

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