Chapter 14
Chemical Communication in Decapod Shrimps: The Influence of Mating and Social Systems on the Relative Importance of Olfactory and Contact Pheromones

Raymond T. Bauer

Abstract Interest in chemoreception of decapod shrimps has been stimulated by observations indicative of sex pheromones, such as frenzied male searching and copulatory activity in the presence of premolt or recently postmolt reproductive females. Review of previous studies on shrimp mating behavior led to the formulation of hypotheses about the variation of chemical communication with mating and social systems. Penaeoidean and many caridean species are highly mobile and live in dense aggregations, resulting in frequent contacts among individuals. In such species, males are usually stimulated to copulatory behavior by apparent contact pheromones on the newly molted female's exoskeleton, received by contact with the male's antennal flagella. In species with temporary mate guarding, males search for premolt reproductive females, which release water soluble substances received by olfactory receptors (aesthetascs). Males guard females for some days until the female molt, after which mating occurs, followed by male abandonment to search for other females. In "neighborhoods of dominance" mating systems, it is the premolt parturial female that seeks out a large dominant male, stimulated by his olfactory pheromones. She is then guarded by the male, which will mate with her after her molt. In monogamous mate guarding species, males and females form permanent pairs, with the initial pairing perhaps mediated by sex pheromones emitted and perceived by both sexes. Olfactory sex pheromones are given off by females in many caridean species just after the molt, stimulating nearby males and ensuring mate finding. Recognition of pair partners or social (agonistic) status of an individual is chemically mediated in various decapod shrimps. The exact source and chemical composition of olfactory sex pheromones is still unknown, but both cuticular hydrocarbons and glycoproteins have been implicated as contact sex pheromones. Comparative studies with additional species are required to test these hypotheses about the form of chemical communication in different mating systems. Isolation and chemical identification of sex and individual-recognition

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R.T. Bauer (✉)
Department of Biology, University of Louisiana,
Lafayette, LA 70504, USA
e-mail: rtbauer@louisiana.edu

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pheromones is a major avenue of future research. Results of such studies may not only result in a greater understanding of chemoreception per se, but also may lead to commercial applications in shrimp fisheries and aquaculture.

14.1 Introduction

Striking behavioral responses to waterborne odors by decapod shrimps ("natantians") indicate that they, like many other crustaceans, rely on chemical senses in food searching, mate recognition, and social interactions. My initial interest in this subject began in graduate school, stimulated by behavioral observations on small tidepool shrimps, *Heptacarpus sitchensis*, in aquaria. When food items were placed in the water, shrimps at some distance from the food responded within seconds. Their increased searching and probing of their surroundings indicated that an olfactory sense was at work. However, males did not become noticeably excited when a receptive (recently molted) female was placed at some distance from them in the aquarium. Only when the male wandered idly by and touched the female with one of its chemotactile antennal flagella did it react by frantically turning towards and grasping and copulating with the female. This began a research interest in the olfactory and chemotactile cues used by shrimps in their mating and social behaviors. Chemical communication in decapod shrimps is not surprising because most species are nocturnal or live in turbid environments in which visual cues are limited. However, this research area, although expanding, is still mainly limited to basic behavioral studies on relatively few decapod shrimps from a phylogenetically and ecologically diverse assemblage.

The purpose of this chapter is to briefly review the most important work done on sex pheromones (mate attraction and recognition) in relation to species mating system. Important gaps in our knowledge are presented and hypotheses are proposed that might be tested in future research. The form and role of chemical communication in intraspecific social interactions (dominance relationships and individual recognition) is a relatively unexplored but expanding field of interest in decapod shrimps. Comparisons of chemical communication with other decapods, especially crabs (Sneddon et al. 2003), lobsters (Atema and Steinbach 2007, Aggio and Derby, Chap. 12), and crayfishes (Breithaupt and Eger 2002; Breithaupt, Chap. 13) as well as other taxonomic groups, e.g., the insects (Howard and Bloomquist 2005; Wyatt 2003) will aid in proposing hypotheses for future testing.

Phylogenetic differences in basic ecology and life history impose both constraints and opportunities on reproduction that are reflected in the forms of chemical communication of decapod shrimps. Although "decapod shrimps" refer to an assemblage of taxa ("natantians") with a similar primitive body form ("caridoid facies"), this group is not phylogenetically homogeneous (Bauer 2004; Fransen and De Grave 2009). The carideans (~3,200 spp.) are especially diverse ecologically, with a variety of life styles in marine habitats at all depths and latitudes, and they have invaded freshwater habitats as well. The penaeoideans (over 400 spp.) are schooling shrimps in warm waters of soft-bottom shallow seas, while the sergestoids (~100 spp.) are planktonic. The stenopodideans (~70 spp.) are marine shrimps, often symbiotic with other invertebrates, occurring in male–female pairs. The decapod shrimps, with their diverse ecologies and life histories, show considerable variation in mating systems, and their chemical communication as will be discussed in this chapter.

14.2 Mating Behavior and Mating Systems

The adaptive value of sex pheromones, the most studied form of chemicals mediating communication in decapod shrimps, can be best understood in the context of their basic reproductive biology and mating systems. Penaeoid shrimps have two very different reproductive biologies (Bauer 1991). In the largest family (Penaeidae) "open thelycum" species mate without molting when the female is ready to spawn, at least in the commercially important genus *Litopenaeus* (Yano et al. 1988). "Closed thelycum" species have sperm-storage structures that are filled by the male just after a female molt, which is not closely tied to spawning. In caridean and stenopodidean shrimps, females with vitellogenic gonads mate just after a parturial (prespawning) molt. Spawning takes place soon thereafter, with the female attaching the fertilized eggs (embryos) below the abdomen for an extended incubation (Bauer 2004).

The mating systems of decapod shrimps can be summarized into relatively simple categories (generalizations) based on characteristics such as encounter rate between males and females, the duration of male–female interaction, and sexual dimorphism in body size and weaponry (major chelipeds and third maxillipeds). Bauer (2004) proposed three basic mating systems in carideans, based on those given by Wickler and Seibt (1981). In monogamy ("mate-guarding monogamy"; also considered as "extended mate guarding"), a male and female of similar size live in pairs that are permanent, at least within a single breeding season. The male continuously guards and defends the female from other males to ensure that when she molts, he will be at her side to mate. In temporary female guarding, the usually larger male with enhanced appendage weaponry seeks out females with maturing ovaries and guards her (24 h to a few days; Grafen and Ridley 1983; Ridley 1983) through the mating molt, after which he soon abandons her to seek other females. In pure searching, the usually smaller males guard neither females nor territories prior to mating. These shrimps occur in aggregations or schools, and individual mobility and population density are high. Males frequently encounter other members of the population, checking them for sex and receptivity. Newly molted females are quickly copulated and abandoned. Monogamy and temporary female guarding are characteristic of species with low encounter rates. In such species, males and females do not contact each other frequently because population density is low or their effective mobility is limited (species living in shelters or subject to high predation pressure). Correa and Thiel (2003) described another category of mating system, "neighborhoods of dominance," for shrimps such as *Rhynchocinetes typus* and *Macrobrachium rosenbergii*. In these species, morphologically distinct and aggressively dominant males control areas to which receptive postmolt females are attracted.

The basic form of chemical communication via sex pheromones might be expected to vary with the mating system of the species (Table 14.1 and Fig. 14.1). Females must ultimately advertise their reproductive condition and mating receptivity to males. Receptivity is limited to a brief period (a few hours to a day) after a parturial molt in all carideans, stenopodideans, and many penaeoids shrimps, or it occurs just before spawning in some penaeoids, e.g., *Litopenaeus* spp. (Yano et al. 1988). Females might advertise to attract males before becoming receptive when encounter rates with males are low or male assistance (defense, access to resources) is needed for successful reproduction. On the other hand, when contact with males is frequent as in schooling species (e.g., many pandalids, crangonids, and penaeoids), it might be advantageous for females to limit their advertisement prior to receptivity to prevent harassment from males. Advertisement over a distance is mediated by olfactory pheromones, whereas sexual condition at close range is accomplished by contact (gustatory and chemotactile) pheromones. Where male–female interaction is relatively brief, individual recognition is not predicted to evolve, but in monogamous mating systems it should be adaptive. In the following, I explore hypotheses about the form of chemical communication involved in sex attraction and mating behavior in various categories of decapod shrimp mating systems (Table 14.1), and I present the knowledge leading to these hypotheses.

Table 14.1 Hypotheses on the form of chemical communication in four different categories of decapod shrimp mating systems

	Mating systems			
	Pure searching	Temporary mate guarding	Monogamy "monogamous mate guarding"	Neighborhoods of dominance
Hypotheses				
Principal sex pheromone	Contact	Olfactory	Olfactory	Olfactory
Timing of pheromone advertisement	Upon female molting or ovulation	≥24 h Prior to female molting	Prior to pairing	Prior to female molting
Sex of pheromone advertises	Female	Female	Male or female	Male
Individual recognition	Absent	Low absent	Present	Low absent

These hypotheses have been derived from information on sex attraction and mating behavior in the published literature which is presented in the chapter

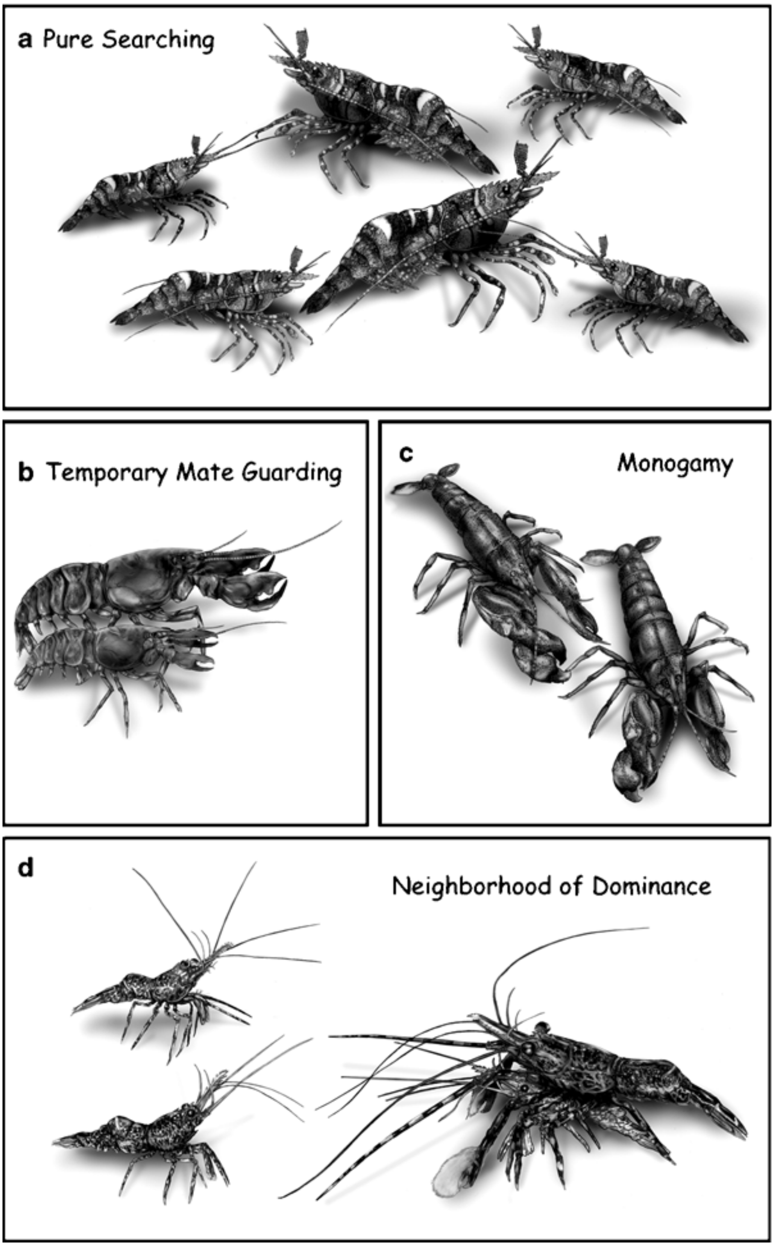

Fig. 14.1 Mating systems in decapod shrimps: sexual dimorphism in body size and weaponry, and pattern of male–female association. (**a**) Several small males searching for a larger receptive female (pure searching); (**b**) large male with hypertrophied chelipeds guarding smaller female (that he has been attracted to) prior to her mating molt (temporary mate guarding); (**c**) male and female of similar body size and weaponry in long-term pairing (monogamy); (**d**) large dominant male with hypertrophied weaponry guarding a receptive female (attracted to him) from smaller subordinate males (neighborhoods of dominance). Drawing by Jorge A. Varela Ramos

14.3 Female Olfactory Sex Pheromones

Behavioral observations on several caridean species (see earlier summary in Table 14.1 in Bauer 1979) as well as a few experimental studies indicate that female olfactory sex pheromones are often emitted *upon* or *after* the mating molt. Such pheromones stimulate obvious male search or courtship behavior in, for example, *Palaemon paucidens* (Kamiguchi 1972), *Hymenocera picta* (Seibt and Wickler 1979), or *M. rosenbergii* (in the small subordinate "sneaker" males; Karplus et al. 2000). On the other hand, careful Y-maze studies by Díaz and Thiel (2004; for Y-maze see Fig. 10.2 in Thiel, Chap. 10) revealed that males of the caridean *R. typus* were unable to locate receptive females using olfactory cues. However, females of this species apparently respond to and locate large dominant males using olfaction. In *Alpheus angulatus*, Mathews (2003) showed with a Y-maze experiment that males, which live paired with females in burrows, were attracted to water exposed to premolt females. However, males did not respond to premolt males and avoided water from intermolt males and females. Attraction of large males to premolt females is also indicated in another alpheid, *Athanas kominatoensis* (Nakashima 1987).

In some shrimp species, males enter into a frenzied search behavior upon detection of a water-soluble postmolt female substance. These males are more likely to respond to a conspecific with some sort of precopulatory behavior. The substance is not related to molting per se, because males do not respond to recently molted (soft exoskeleton) nonparturial females or males. In *H. picta*, the female olfactory pheromone is effective in attracting males for 3–5 h after her molt (Seibt and Wickler 1979). Males are induced to court any female when parturial female molt water is introduced into an aquarium (Seibt 1973). Kamiguchi (1972) showed with careful observations that a water-soluble substance was only effective in stimulating males of *P. paucidens* to search for ~30 min. However, males could recognize receptive females upon contact for a few hours after the female's parturial molt.

A postmolt rather than premolt release of pheromone may be viewed as adaptive in species living at high density aggregations with pure searching mating systems (e.g., many *Pandalus*, *Palaemon, Palaemonetes,* and *Lysmata* spp.), where advertisement by females to males long before the molt might to lead to their harassment and injury by males. The effect of the postmolt female pheromone has been shown in a rigorous experimental setup using *P. paucidens* as a model species by Kamiguchi (1972). Isolated males initiated searching behavior when water from an aquarium with a recently molted parturial female was pipetted into the male aquarium. Mating experiments (Fig. 14.2) showed that males primarily responded to postmolt parturial females. However, some males attempted to copulate with females in other reproductive states in the presence of postmolt female water, which presumably contained olfactory sex pheromone.

In the caridean *Heptacarpus paludicola*, Bauer (1979) was unable to detect obvious searching behavior by males for a receptive female in the same aquarium.

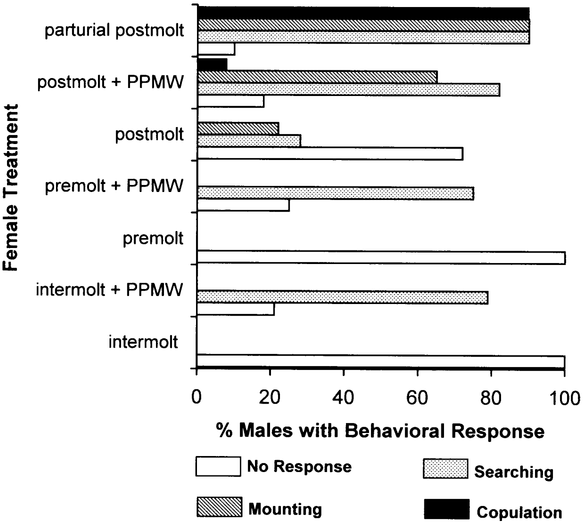

Fig. 14.2 Results of experiments by Kamiguchi (1972) showing effect of postmolt sexual pheromone given off by females of *Palaemon paucidens*. Males were exposed to females in different reproductive states, with or without "postparturial molt water" (PPMW), i.e., water from a tank containing a recently molted parturial female. Male responses (none, searching, mounting, and copulation) were recorded. Parturial postmolt: a recently molted female with mature ovaries; postmolt: a recently molted female without mature ovaries; premolt: female with mature ovaries nearing a parturial molt; intermolt: a female neither near molting nor spawning (from Bauer 2004)

To test for a more subtle response to such females, an "olfactometer" was devised. Males were kept downstream of an inlet chamber containing either an intermolt female incubating embryos (not sexually receptive) or a newly molted parturial (receptive female). Male response (swimming behavior) was recorded. First, however, the olfactometer was tested using a known stimulatory food item (positive control) and a nonstimulatory small rock (negative control) and found satisfactory to measure an olfactory response (Fig. 14.3a). Male response to receptive and nonreceptive females was then tested, resulting in a higher quantitative response toward the former (Fig. 14.3b). However, a striking qualitative response by males was not apparent, indicating that olfactory detection of females may not be important in this species. Postmolt contact pheromones are the primary means of sex attraction and recognition in this and other aggregated species. Perhaps females are not advertising with a pheromone but rather hiding their reproductive condition to avoid harassment, but they are not completely successful in doing so. Males, on the other hand, have evolved a method, albeit a relatively poor one, of detecting the upcoming female molt. Thus, a conflict of sexual interests between males and females may be occurring in such species.

A *premolt* "awareness" of a soon-to-molt female has been reported in some caridean species, perhaps indicative of a female olfactory pheromone. However, the period is rather short, approximately an hour or less before the molt. In *Palaemonetes*

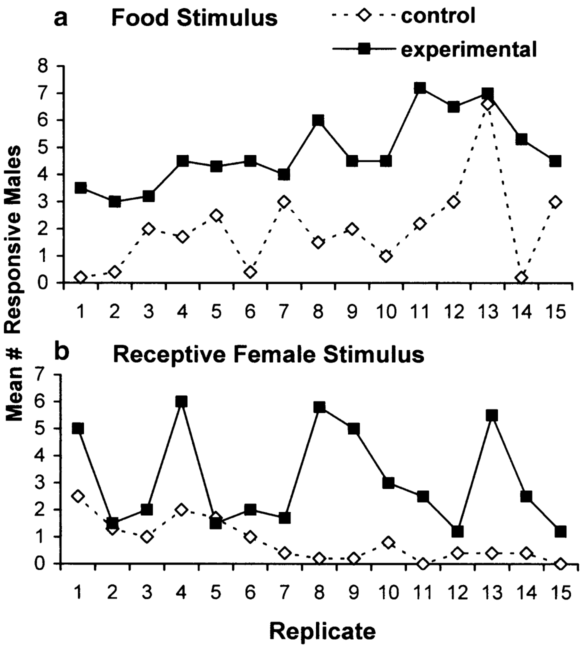

Fig. 14.3 Olfactometer experiments in *Heptacarpus paludicola* (data from Bauer 1979). In each replicate, waterborne stimuli were presented to a group of ten males located downstream of the stimuli. Five observations on the number of active males were made per replicate. (**a**) Experimental stimulus = food item, control = rock; (**b**) experimental stimulus = a newly molted parturial (receptive) female, control = an intermolt (nonreceptive) female (reproduced from Bauer 2004)

pugio, males made more frequent contact with females in the minutes just before the female's molt (Bauer and Abdalla 2001; Fig. 14.4). This does not result in a pairing with the female in *P. pugio* and might be interpreted as an increase in male searching behavior, enhancing the probability of encountering the soon-to-be molted female. In *Lysmata wurdemanni*, a protandric simultaneous hermaphrodite, male-phase individuals approach and remain in contact with a prespawning female-phase individual about an hour before the latter's molt, when mating occurs (Bauer 2002; Zhang and Lin 2006). In both *P. pugio* and *L. wurdemanni*, it may be that the male detects the female by a water-soluble substance. In both species, it is difficult to separate response to an olfactory vs. a contact pheromone. These studies on mating behavior were conducted within a small arena where physical contact (especially with the long antennal flagella) was probably frequent.

Bauer and Abdalla (2001) proposed an alternative hypothesis to explain the apparent male "awareness" within a short period of an upcoming female parturial molt in aggregating species. Females of such species are actually hiding their reproductive condition until the molt to prevent harassment from males. Males simply may be sensing a female metabolite, indicating her reproductive state that she can no longer control as the actual molt approaches.

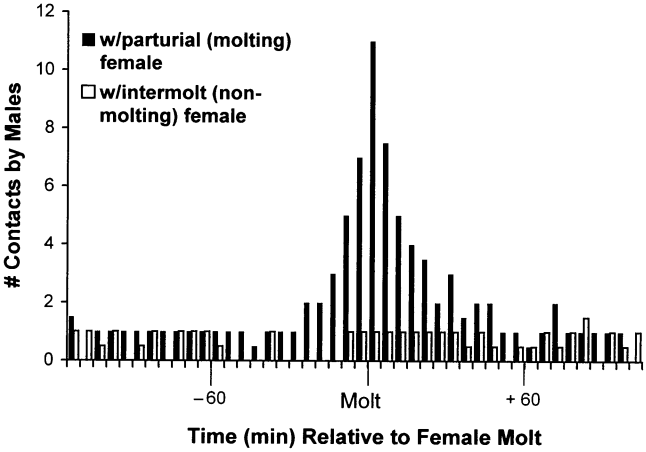

Fig. 14.4 Responses of males to parturial and intermolt females in *Palaemonetes pugio* (Bauer and Abdalla 2001). The graph shows the number of contacts per 5-min intervals by two males with a parturial female and a nonparturial (intermolt) female before and after the molt of the parturial female. Note that males recognized the parturial female (made significantly more contacts) starting about 25 min prior to the molt (reproduced from Bauer 2004)

Penaeoid shrimps characteristically live in aggregations ("schools") and have the expected pure search mating system of such species. Observations on mating behavior in penaeoidean species are limited, but suggest male responses to females similar to that of carideans with a similar aggregated life style (e.g., Hudinaga 1942; Bauer 1996). In *Litopenaeus vannamei*, Yano et al. (1988) cited unpublished observations, suggesting that males are stimulated to precopulatory chasing of other individuals (not necessarily females) when "female water" from a reproductively mature female is introduced into their environment. Thus, in the usually schooling penaeid species, as in similarly aggregated caridean species, males may be using water-soluble substances inadvertently released by females, which become attractive as her physiological state approaches receptivity.

Olfactory sex pheromones might be found in caridean species with mating systems involving temporary or extended (monogamous) male guarding of females before the parturial molt. In some carideans, males guard females by remaining near them (attendance) and defending them from the advances of other males. For example, Nakashima (1987) worked on the alpheid *A. kominatoensis*, which lives in association with sea urchins. In this nonmonogamous alpheid species, a large combative male guards an isolated parturial female prior to her molt but abandons her after mating. It would be advantageous for males to detect, find, and monopolize such females before other males do. Similar to the American lobster *Homarus americanus* (Atema and Steinbach 2007) and the shrimp *R. typus* (Díaz and Thiel 2004), premolt parturial females of *M. rosenbergii* (Karplus et al. 2000) and *M. australiense* (Lee and Fielder 1982) seek out dominant males. The male apparently attracts the female by regularly or continuously releasing his water-soluble pheromone. The dominant male may then recognize the female (and vice versa) by an interchange of olfactory and/or contact pheromone cues before allowing her into the mating nest.

14.4 Contact Sex Pheromones

In some caridean species, males are not noticeably stimulated at a distance by parturial (prespawning) females (e.g., *Palaemonetes vulgaris*, Burkenroad 1947; *H. sitchensis, H. paludicola*, Bauer 1976, 1979; *P. pugio*, Bauer and Abdalla 2001). It is only when males touch a newly molted parturial female with the long antennal flagellum that they react dramatically, seizing the female and copulating with her (Fig. 14.5). Burkenroad (1947) first proposed in *P. vulgaris* that a "nondiffusible" substance on the female exoskeleton was perceived by the male, which stimulated it to copulate. The duration of attractiveness was several hours, similar to that found by Caskey and Bauer (2005) for *P. pugio* (8 h; Fig. 14.6) in uninseminated newly molted females. As soon as spawning takes place (2–3 h after mating), the female becomes unattractive to males. The period of attractiveness of postmolt

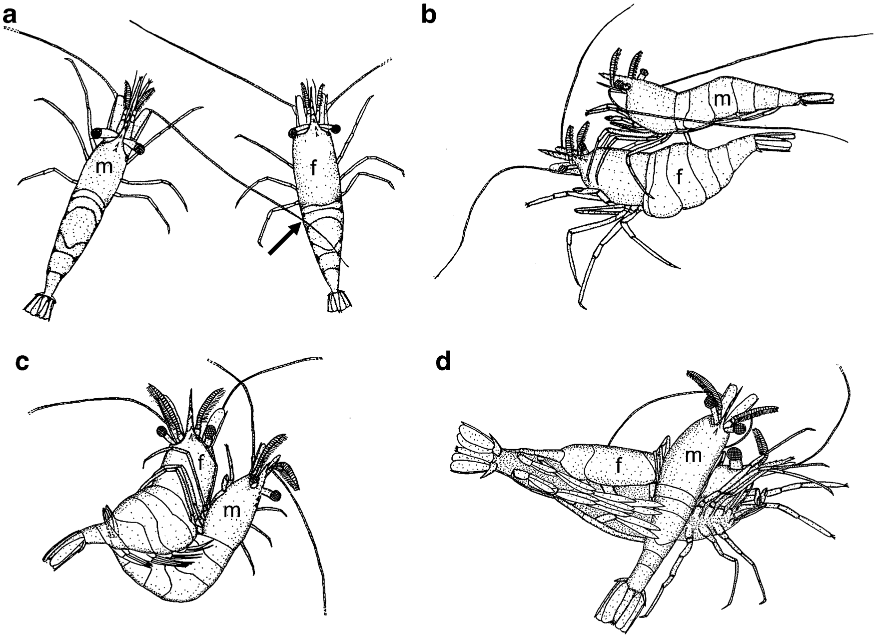

Fig. 14.5 Mating behavior of the caridean *Heptacarpus sitchensis* (Bauer 1976), a species with a pure searching mating system. (**a**) Male makes contact with female via antennal flagellum (*arrow*); (**b**) male mounts female; (**c**, **d**) copulation (male dips abdomen below that of female, which lowers pleopods to allow spermatophore deposition) (adapted from Bauer 2004)

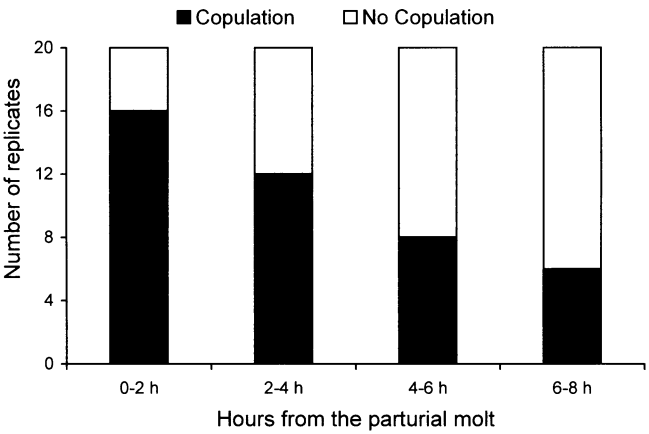

Fig. 14.6 Duration of female attractiveness to males after the female molt in the caridean *Palaemonetes pugio*. Females at varying intervals after the parturial molt were presented to males, and the presence or absence of copulation ("attractiveness") was recorded ($n = 20$ replicates per time interval) (reproduced from Caskey and Bauer 2005)

uninseminated females may be longer, up to 24 h (*Heptacarpus* spp., Bauer 1976, 1979; *R. typus*, Díaz and Thiel 2004).

Caskey and Bauer (2005) proposed that the "nondiffusible substance" is a contact sex pheromone perceived by receptors on setae borne by the antennal flagella and/or pereopods. The sexual condition of the female is thus perceived by "taste" rather than "smell," adaptive in the context of an aggregated species with a pure searching male mating strategy. The substances involved in chemotactile sex attraction and recognition must have little or no solubility and probably occur in relatively high concentrations on the exoskeleton compared with olfactory sex pheromones. Because the male receptors must make actual or very near contact with the surface bearing such substances, they can be termed "contact pheromones" (see Wyatt, Chap. 2; Snell, Chap. 23).

Experiments using individuals in different sexual and molting states have eliminated textural cues such as a soft postmolt cuticle or visual cues in sex attraction and recognition. For example, Bauer (1979: *H. sitchensis*) and Caskey and Bauer (2005: *P. pugio*) performed experiments in which males showed no mating response toward recently molted (soft) males and only a slight or no response to recently molted nonparturial females. Copulatory response was elicited only by newly molted females and only upon antennal or pereopod contact by the male.

In some high density species, visual cues may attract males to a receptive female once one or more males has contacted such a female and is attempting copulation. Díaz and Thiel (2004) used the term "tumult" to describe this situation which they documented with careful experiments. Once a male contacts a newly molted female, the jumping around and chasing of the female attracts the attention of other nearby males, presumably by vision. Similar tumults have also been observed in *L. wurdemanni* (pers. obs.). Response to tumults may be common in aggregating or schooling shrimps. It also occurs in response to other stimuli, e.g., discovery of large food items (pers. obs.). The rapidity with which these tumults develop underlines the importance for the female to hide its reproductive status in order to maintain some control of mating interactions and avoid male harassment (e.g., tumults) which might cause injury or death.

14.5 Chemically Mediated Recognition of Individual, Sexual, and Social Status

Recognition of particular or unique individuals may also be adaptive, e.g., identification of a male or female partner in pair-living species, or perhaps of individuals frequently or previously encountered in an individual's environment (winners or losers of previous agonistic encounters). Many stenopodidean shrimps live in pairs associated with other invertebrates, and there are numerous species of carideans, especially in the families Alpheidae, Palaemonidae (Pontoniinae), Hymenoceridae, and Hippolytidae that live in pairs. In such species, identification of the opposite sex and specific individuals (pair partners) at a distance might be important. In other carideans in which mating territories or colony homes are defended (e.g., *Macrobrachium* with large-bodied, large-clawed males; eusocial *Synalpheus* spp.), social or family group recognition is adaptive. In the eusocial *Synalpheus* spp. (Duffy 2007), chemical cues may mediate sterility of colony workers as well as communal colony defense, as in many of the social insects (Wyatt 2003).

Johnson (1969, 1977) used courtship and agonistic behaviors in the pair-living shrimp *Stenopus hispidus* to test the hypotheses that individuals could identify (a) members of the opposite sex (possible pair partners) and (b) a previous pair partner from among other individuals of the same sex. Members of the opposite sex could be identified by "touch" (presumably contact chemoreception) as shown by reduced agonistic interactions and courtship behaviors between previously unpaired males and females after a short period of physical contact (Johnson 1969). Individuals of the same sex, however, remained aggressive, often fighting to the death and showed no courtship behaviors (Johnson 1969). Olfactory cues allowed individuals to detect the presence of a conspecific but not their sex. In another set of experiments (Johnson 1977), "mates" (previously paired male and female) showed low levels of courtship when introduced to each other after a period of separation (Fig. 14.7a). On the other hand, individuals of the opposite sex that had never met before ("strangers") showed more intense courtship behavior (Fig. 14.7b). This demonstrated that previous mating partners recognized and "remembered" each other. They did not need to expend as much effort on courtship behaviors with previous mates as with strangers. Recognition of previous mates was possible after separations up to 6 days (a complete molt cycle). Contact chemoreception was considered the primary sensory mode involved in individual recognition.

In the pair-living caridean *H. picta*, the role of olfactory pheromones in individual recognition has been shown convincingly by simple behavioral observations and

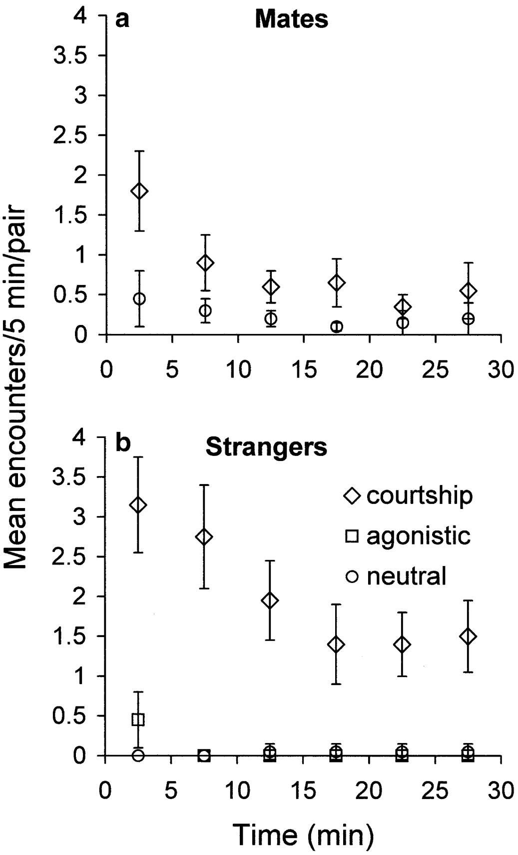

Fig. 14.7 Recognition of individual mating pair partners in *Stenopus hispidus* after a separation of 2 days (data from Johnson 1977). (**a**) Previous mating partners ("mates") exhibited low levels of courtship behavior when reintroduced compared to (**b**) individuals of the opposite sex which had never met ("strangers")

experiments by Seibt (1973). Variations in natural color markings allowed observers to distinguish between individuals of pairs in an aquarium microcosm. Male and female pair partners remained together for the period of observation. In one experiment, males were separated from their female partners, which were hidden from visual and physical contact by nets. After separation, males found and remained with their original partner from among several other similarly hidden females. Y-maze olfactometer experiments showed that *H. picta* could identify and choose water emanating from food vs. no food and from a conspecific vs. some other crustacean. Using olfactory cues, males could distinguish between males and females; a male could also identify its original female partner from other females. These tests were made on intermolt females so that the pre- and postmolt olfactory pheromones of parturial females mentioned earlier were not involved. Although members of this species can recognize other conspecifics visually, sex recognition from a distance can occur in the dark when visual cues are eliminated, and Y-maze tests indicated that olfaction was the sensory mode involved.

Dominance relationships among snapping shrimps (*Alpheus heterochaelis*) have been the focus of several studies. These shrimps live in burrows in female–male pairs. Both male and female defend the burrow and each other with the “snapping claw” which shoots a powerful jet of water in front of the animal (Bauer 2004). With same sex, Y-maze experiments and measures of aggressive activity, both Ward et al. (2004) and Obermeier and Schmitz (2003a) demonstrated that individuals can recognize dominants (individuals against which the focal individual has lost a previous agonistic encounter) from other individuals without previous fighting experience. The latter authors also showed that individuals do not distinguish (behave differently) between familiar and unfamiliar dominants. In experiments with *A. heterochaelis* on olfactory cues, Schein (1975) demonstrated with a Y-maze study that males can distinguish males from intermolt females, but Hughes (1996) found no such ability. However, Mathews (2003) found with similar techniques that males do recognize and are attracted to premolt females with olfactory cues. Rahman et al. (2001), measuring degree of aggressive behavior, found that both sexes can distinguish former mates from strangers. Recognition of mating partners, important in a socially monogamous species, has evolved in *A. heterochaelis*, as it has in *H. picta*, and perhaps will be found to be a common feature of pair-living species. Certainly, it is important for individuals of either sex to distinguish and avoid dominant individuals, which have previously defeated them in agonistic interactions. If individuals can detect and recognize conspecifics, either individually or by group (male vs. female, partner vs. nonpartner, and dominants vs. subordinates), a great deal of potentially injurious fighting can be avoided.

14.6 Transmission and Reception of Pheromones

The actual source and composition of olfactory sex pheromones in decapod shrimps is unknown. One can only speculate by comparison with other decapods (e.g., Atema and Steinbach 2007) that olfactory sex pheromones are contained in and emitted in the urine. However, the simple experiment of plugging nephrophores (antennal gland openings) has not been done in decapod shrimps, probably because of the small body size of most species. Given that the most striking attraction of males by female olfactory substances occurs after and not before the female mating molt in caridean shrimps, there is a good possibility that substances emanating from other sources (e.g., the newly molted exoskeleton) might also be involved.

Transmission of olfactory sex pheromones and odors involved in individual or group recognition is likely to be similar to those found in lobsters and crayfishes. In these decapods, gill and “fan-organ” currents are generated by the excurrent respiratory stream and its modification by beating of the maxillipedal exopods. Herberholz and Schmitz (2001) used plastic microparticles and ink to demonstrate similar currents in the shrimp *A. heterochaelis* and their role in intraspecific interactions. A rather slow “normal” anteriorly directed current is generated by the beating of the scaphognathites (gill bailers), which produces the respiratory currents. The anterior current can be directed laterally, either right or left, by the unilateral beating of the exopods of the second and third maxillipeds. It can also be accelerated anteriorly ("fast anterior gill current"), perhaps by faster beating of the scaphognathites. A posteriorly directed pleopod current produced by in-place beating of the abdominal swimmerets (pleopods) was not shown to be important in social interactions. The anterior fast current was implicated in carrying chemical information from one individual to an agonistic opponent and was produced most frequently by winners of agonistic encounters. The lateral current is a mechanism to remove an individual's own odor from in front of the olfactory antennules so that the individual can perceive the odor of its opponent.

Reception of olfactory cues in shrimps appears similar to that by other decapods, i.e., with specialized setae (aesthetascs) on the outer antennular (first antenna) flagella. This has been demonstrated by ablation of these flagella, a somewhat crude and traumatic technique but effective when coupled with similar trauma in control treatments, i.e., ablation of the medial (inner) flagella (Obermeier and Schmitz 2003b) and/or second antennae (Zhang and Lin 2006).

Behavioral observations (Burkenroad 1947; Bauer 1976, 1979; Caskey and Bauer 2005; Zhang and Lin 2006) indicate that setae on the antennal (second antenna) flagella, as well as those on the third maxillipeds and anterior pereopods, are the site of reception of contact pheromones. Aside from aesthetascs, the study of shrimp antennular (Obermeier and Schmitz 2004) and antennal setae (Bauer and Caskey 2006) is still in the morphological and ultrastructural stages with more to be done; the physiology of these setae is poorly known. The latter statement also applies to possible chemotactile ("taste" or gustatory) setae on the maxillipeds and pereopods. "Antennulation," i.e., mutual touching of antennular and antennal flagella during physical interactions between conspecifics indicates a complex interplay between olfactory and contact chemical cues.

14.7 Chemical Composition of Pheromones

Olfactory sex pheromones of decapod shrimps have not yet been identified. Water-soluble compounds involved in sexual or recognition behaviors are most probably metabolites excreted in the urine or by the gills. Contact pheromones, given their probable higher concentration and distinct localization on the exoskeletal surface, offer good possibilities for identification. Long-chained cuticular hydrocarbons (CH), a rich source of identified contact sex pheromones in insects (Howard and Bloomquist 2005), have been proposed as possible candidates in decapod shrimps (Caskey and Bauer 2005; Caskey et al. 2009a). In insects, these compounds evolved primarily to prevent water loss through the cuticle and have secondarily been used as contact sex pheromones. Although they are much less abundant in aquatic crustaceans, these and similar compounds can be extracted by hexane and other solvents used in gas chromatography/mass spectrometry (GC-MS). Using this technique in the shrimp *P. pugio*, Caskey et al. (2009a) found a variety or "blend" of CHs that differed significantly among parturial postmolt (PPM, recently molted, sexually attractive and receptive) females and intermolt females, as well as from that of postmolt nonparturial females and males. The particular CH mix on the surface of PPM females potentially could serve as a contact pheromone to stimulate male mating. A suitable bioassay needs to be devised to test this hypothesis. Substances on the surface of PPM females in a variety of caridean species lose their attractiveness within hours to a day of molting, indicated that the substances are modified or made unavailable to male receptors by the chemical changes that accompany cuticular hardening after the molt.

Alternatively, other classes of compounds incorporated into the exoskeleton or secreted onto its surface might serve as contact pheromones, e.g., glycoproteins (Kelly and Snell, 1998; "arthropodin hypothesis" of Dunham, 1988; Snell, Chap. 23). Using one technique from Kelly and Snell (1998), Caskey et al. (2009b) exposed PPM females of *P. pugio* to males in seawater with a 50 mM concentration of glucosamine, a glycan component of *N*-acetyl glucosamine glycoproteins in crustaceans. Mating in these pairings was significantly lower than those arranged in aquaria with 50 mM glucose or natural seawater. In other experiments, significantly greater increases in Ca^{2+} activity were recorded when isolated male antennae were touched to carapaces of anesthetized PPM females or exposed to glucosamine, but not when touched to carapaces of postmolt nonparturial and intermolt females or postmolt males, or when exposed to glucose. Other observations indicated that neurons within male antennal setae were stimulated by glucosamine, as they might be when touching the exoskeleton of a PPM female with such a surface moiety. The reduction in male copulatory behavior observed in the glucosamine treatment of mating experiments might be explained by the binding of glucosamine dissolved in the water to male antennal receptors. Thus, males with blocked or habituated receptors could not perceive a glucosamine-containing glycoprotein on the female exoskeleton, blocking the copulatory response. In sum, this study implicates surface glycoproteins as contact pheromones in *P. pugio*. On the other hand, Zhang et al. (2010), using the lectin-binding method by Kelly and Snell (1998), suggested that surface glycoproteins do not mediate male mating response. Thus, the possible role of glycoproteins, as well as surface CH, as contact pheromones remains unresolved and open to further study.

If contact sex pheromones in shrimps are CHs, changes in activity of surface tegumental glands in the hours after the molt might account for the decrease in female attractiveness. Similarly, sex-specific cuticular glycoproteins might become less stimulatory because of changes associated with quinone tanning during postmolt sclerotization of the exoskeleton. Males of at least some shrimp species lose interest in PPM females immediately after mating and spermatophore transfer (e.g., *P. pugio*, Bauer and Abdalla 2001; *L. wurdemanni,* pers. obs.). The rapid decline in female attractiveness after spermatophore transfer might be due to a number of factors such as change in emission or form of the contact pheromone, a change in female behavior, or perhaps even a male-repulsive substance released near or even deposited on the female by the mating male, e.g., contained within deposited spermatophores.

14.8 Future Directions and Applied Aspects

Future work on sex pheromones should be conducted and interpreted within the context of the species' mating and social systems. The hypotheses in Table 14.1 about the form of chemical communication in different mating systems are based on relatively few species. Future observations and experimental studies, both field and laboratory, on more species in each category are needed to adequately test these hypotheses. The caridean genus *Lysmata* would be a good test group. It contains both species in aggregations ("crowd" species) with pure searching mating system and apparently monogamous ("paired") species (Bauer 2000). Behavioral testing for suspected pheromones should follow as closely as possible the guidelines so clearly stated by Dunham (1978), i.e., use of negative and positive controls, blind observation procedures, and precise response definitions. Nephropore blockage experiments will help to identify whether urine contains possible pheromones. Precise sampling of urine and water generated from the respiratory stream, both possible sources of olfactory pheromones, is a necessary prelude to their chemical description. Isolation and chemical identification of contact sex pheromones, e.g., CHs, glycoproteins, or other substances, is just in the beginning phase. The cause of the very rapid decline in female attractiveness to males after mating also requires investigation. Identification of the setal and neuronal receptors of both olfactory and contact pheromones needs to go beyond the relatively crude technique of ablation experiments and on to more sophisticated physiological techniques.

Chemical communication in shrimps is of applied interest as well. Manipulation of male and female behavior with olfactory and contact pheromones to trap or attract a particular set of individuals (e.g., large-sized males or females, reproductive females) in fisheries or aquaculture might be accomplished with sex pheromones, once identified and synthesized (Barki, Jones, and Karplus, Chap. 25). Matings between preferred genotypes might be promoted using sex pheromones to increase attractiveness and stimulate matings of selected individuals with desired traits.

14.9 Summary and Conclusions

Olfactory and contact chemoreception is the principal means of communication during sexual and social interactions in decapod shrimps. The relative importance of one or the other type of pheromone appears to vary with the mating and social system of the species (Table 14.1). In all carideans and in the "closed thelycum" penaeoids, reproductive females are sexually receptive just after molting. In these aggregated or schooling species, female contact-sex pheromones, possibly cuticular CHs or glycoproteins, are perceived by the antennal flagella, stimulating the male to copulate. In some of these species, a possible olfactory pheromone may be released from the female during or just after the molt which stimulates nearby males to searching behavior. In other aggregated caridean species, males become aware of the female's reproductive state for only a short time prior to her molt. In such species, release of male-stimulating substances appears to be inadvertent and metabolically unavoidable on the part of the female, which may be hiding its reproductive status prior to molting to prevent harassment from the many nearby males. Olfactory pheromones, released by urine or in the anterior respiratory outflow, together with subsequent contact chemoreception, appear to mediate individual mate recognition in pair-living species and agonistic interactions in a number of species. The scant knowledge about the chemistry of decapod shrimp pheromones can be greatly expanded by the development of techniques for behavioral assays with rigorous protocols, leading to isolation and chemical identification of putative olfactory and contact pheromones. Sex pheromones, once characterized chemically, might be used to manipulate mating and social interactions in commercially important shrimp species to increase catch in fisheries, as well as to increase productivity and genetic quality in aquaculture species.

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