Chemical Communication and Social Behavior of the Lobster *Homarus americanus* and Other Decapod Crustacea

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Abstract and Keywords

The American lobster, *Homarus americanus*, is presented as a model organism of chemical communication in decapod crustaceans. Lobsters use chemical signals to form and maintain dominance hierarchies, to choose and locate mates, to determine reproductive receptivity, to recognize individual conspecifics, and perhaps to regulate their molt cycles. The chemical signals are carried primarily but not completely in the urine, and are dispersed into the environment by animal-generated currents. The chemical identity of the signals and their use under field conditions is little known. Many decapod crustaceans use chemical signals for purposes similar to those of *H. americanus*. The chemicals used by decapods to communicate sex, receptivity, dominance, etc., are likely to bear similarities between species. Advances made in...
pheromone identification will be of great consequence in understanding crustacean chemical communication, just as has been the case in insects.

*Keywords*: chemical signals, pheromones, sexual communication, mate choice, dominance hierarchies, individual recognition

(p.116)

Chemical signals are important to the behavior of nearly all organisms in which they have been investigated. Some chemical signals are known as pheromones: chemical communication signals among conspecifics. Pheromones evolve their communication function under natural and sexual selection. We use the broader term “chemical signals” to indicate cases in which there is no evidence that the signals are elaborated by the sender for communication purposes: such signals are released as metabolic waste products that are conveniently detected by anyone with the right receptors and interest, including predators, parasites, and conspecifics. Examples of intraspecific, nonpheromonal chemical signals include certain alarm substances (e.g., Atema and Stenzler 1977) and diet-related excretion (Bryant and Atema 1987).

Pheromones have been classified into four categories based on their biological consequences: * releasers of behavior and primers of (neuro)endocrine processes* (Wilson and Bossert 1963) and, recently proposed for humans, *signalers of information and modulators altering outcome probability* (Wysocki and Preti 2002, 2004). Marine pheromones are far less studied than are terrestrial pheromones, and most information we have is limited to behavioral evidence for their existence. The pheromones of decapod crustaceans are known mostly from behavioral evidence, which suggests that they can be classified as releasers of stereotyped behaviors such as agonistic responses, mate or gamete attraction, and larval release or settling. We also see signalers of sex, molt state,
receptivity, and individual identity. Primers are less known, but dominance regulation and female molt regulation provide examples worth investigating. Modulators have not been studied as such. Urine appears to be the most common vehicle for crustacean pheromones, but contact pheromones have also been suggested.

This review considers the role of chemical signals that regulate the social behavior of decapod crustaceans, primarily dominance and courtship. Reviews of this subject have been published (Dunham 1978, 1988). In the first section, we use the American lobster, *Homarus americanus*, as a model, because the social life of this often nocturnal animal is largely regulated by chemical signals, and there is a large behavioral, ecological and neurobiological database for context (Factor 1995). This includes lab and field studies, signal dispersal, and chemoreception (Atema and Voigt 1995). The lobster example suggests that in other species many more chemical signals will be discovered. In the second section, we review other species that provide both interesting examples of similar signaling and their own unique use of different pheromones. We recognize that the lobster story is by no means complete. Overall, the most glaring gap in knowledge is the lack of information on the chemical identity of the pheromones. The structure determination of bombykol, the major sex attractant of the silk worm moth, *Bombyx mori* (Butenandt et al. 1959) sparked a revolution in the field of chemical ecology. The current knowledge of crustacean pheromones shows that we can expect complexity rivaling that in insects and vertebrates (e.g., Duffy et al. 2002). But unless the chemistry catches up with the biology, we will remain ignorant about the true extent of chemical signaling in crustaceans.

**Lobsters as an Example of Complex Chemical Communication in Decapod Crustacea**
Chemical Signaling Behavior: Information Currents

To understand the use of chemical signals in the social behavior of any animal, it is important to appreciate the transport mechanisms that carry the signal from sender to receiver. Odor dispersal determines signal detectability. Often, this means understanding the invisible air or water currents, including animal-generated currents that disperse the odors. *Homarus americanus* is a good example of an animal that generates several multipurpose currents. These currents aid not only in locomotion, feeding, and metabolic functions, such as breathing and waste removal, but also in chemical information exchange. They may be thought of as a fluid extension of the animal itself. Juvenile and adult *H. americanus* generate three currents that can operate in isolation or in concert: gill current, fan current, and pleopod current (Fig. 6.1).

All three are implicated in chemical communication. In larval and early juvenile lobsters, the currents do not seem to be involved primarily in information transfer, but rather in locomotion and feeding (reviewed in Ennis 1995, Lavalli and Factor 1995).

The gill current is generated by the scaphognathites (leaflike outer branches of the second maxillae) beating inside the gill chambers. Their peristaltic pump action generates a powerful, rapidly pulsating current that jets forward from bilateral “nozzles.” This jet reaches distances of seven body lengths (BL) in adults (Atema 1985) (Fig. 6.2) and mean velocities of 3 cm/sec near the nozzle (T. Breithaupt, unpublished data). It is usually a bilateral current, carrying metabolites from the gills. Adult lobsters at warmer temperatures rarely cease producing this ventilating current; however, in winter the current stops for periods of several seconds (J. Atema, personal...
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Figure 6.1 Information currents used during lobster courtship as premolt receptive female (left) visits shelter of dominant male. Female jets gill current (a) into shelter. Male (right) retreats to opposite entrance, flicks antennules (b), fans exopodites (c) redirecting his gill current, and beats pleopods under raised abdomen (d) to create posterior “advertising” current outside shelter. From Atema (1986).

(observation), presumably reflecting lower metabolic rates. Urine can be released into the gill current from bilateral bladders, through small, ventrally directed nozzles (nephropores) at the base of the large antennae. Lobsters appear to release products of a pair of small nephropore glands into the urine (see “Nephropore Glands,” below).

A second current, the fan current, exerts further control over signaling. The stiff exopodite of the first maxilliped can be positioned directly in front of the nozzle, thus deflecting and redirecting the water flow sideways (T. Breithaupt, personal communication). The large, feathery exopodites of the second and third maxillipeds then fan
the deflected water backward. The water displaced by these outgoing currents draws incoming currents from around the head within a radius of about the length of the antennules (Atema 1985), which monitor chemical signals from the environment. The exopodite fan current can be bilateral or unilateral (Fig. 6.2).

The third and most powerful current is the pleopod current, which draws water from below the animal and moves it posteriorly by beating the pleopods—also known as swimmerets—underneath the raised abdomen (Atema 1985).

This behavior is seen in the “advertising” of cohabiting males.

Figure 6.2 Lobster-generated currents. (A) Gill currents with mean and standard deviations: top view of three different-sized animals (1–3; 15, 55, and 80 mm carapace length [CL]) and side view of adult (4; 80 mm CL) animal (broken line: vertical expansion of plume limited by stratification of water). AL: animal body length. (B) Exopodite “fan” current. Top, Small anterior arrows indicate region and direction of water flow drawn toward the lobster. “Wings” indicate areas of turbulent directional current: 1 is most common bilateral; 2 and 3 indicate increasingly unilateral flow fields. Bottom, Arrows in side view indicate ventral water uptake into gill chamber.
A good example of the use of these currents in chemical communication is seen in courtship (Fig. 6.1). Much of the information exchange between potential mates occurs when the female approaches the shelter of a male, where both increase urine release (Bushman and Atema 2000). Females visiting a shelter stand still at its entrance for many seconds (Atema et al. 1979, Karnofsky et al. 1989a, Cowan and Atema 1990). They alternate between fanning and not fanning. Although the current itself is, of course, invisible, the human observer can conclude that without fanning the continuous gill current blows into the male shelter. At the time of female visits, the male stands inside and often moves away from the entrance, flicking his antennules (i.e., "sniffing"), fanning his exopodites (thus drawing water toward his antennules and redirecting his gill current backward), and occasionally fanning his pleopods, drawing a large current into his shelter and blowing it out into the environment. Together, male and female currents result in mutual odor signaling. It is not known why, during copulation, both partners beat their pleopods so vigorously and thus disseminate their joint chemical signals into the surrounding environment.

Chemoreception

Lobsters have at least five different major chemoreceptor organs that could be involved in detecting pheromones: the lateral and medial flagella of the antennules; the antennae; the dactyl and propodus segments of the walking legs, particularly the chelated first two pairs; and the endopodite of the third maxillipeds. The antennules and antennae can be grouped as the cephalic receptor organs with neural connections into anterior brain centers, and the others as thoracic receptor organs projecting to centers in the posterior brain and thoracic ganglia (Sandeman et al. 1992). Cephalic chemoreceptor organs function primarily to sample odors in the free stream around the animal’s head; the thoracic chemoreceptor organs appear to be primarily involved in feeding behavior. This corresponds roughly to the smell and taste division in vertebrates (Atema 1977). The lateral filament of each antennule flicks (Shepheard 1974, Schmitt and Ache...
1979, Berg et al. 1992) and thus samples odor directly in front of the animal. It is the functional equivalent of sniffing and demonstrates again the importance of fluid flow for chemoreception. This organ is involved in the detection of at least some pheromones (Johnson and Atema 2005) and in the tracking of food odor plumes. One of the reasons that more is not known about pheromone receptors is that the compounds are not known. Details on lobster chemoreception have been reviewed elsewhere (Atema and Voigt 1995).

Social Behavior: Dominance, Courtship, and Mating

The courtship and mating of the American lobster are, as in so many animals, based on male dominance and female choice. The necessary information for establishing and maintaining dominance and pair bonds is based largely on chemical signals. Males (p.120) broadcast their sex, status, identity, and location both to rival males and to potential mates. Females convey their sex, identity, and state of receptivity and may exert chemical control over each other's molt cycles (reproductive suppression), allowing for female molt staggering.
Dominance and Individual Recognition

For lobsters, shelters and mating opportunities are limiting resources. Dominance serves to secure priority access to these resources. Individual recognition and the winning and losing of encounters determine an animal's status within a social group (Dugatkin and Earley 2004). Dominance is established by behavioral displays, generally followed by physical fights. The more closely matched the opponents are, the further the fight escalates. Once established, dominance is maintained mostly by displays and rarely by continued fights. These displays have an important chemical component, perhaps coupled with tactile, hydrodynamic, and visual cues. There appear to be two different kinds of chemical signals that help maintain dominance: status signals and individual recognition signals. We present experimental evidence from behavioral tests for these chemical signals.

We should point out that, although most experiments on dominance involve males, females also have dominance relationships and individual recognition. But, where the function of male dominance seems clear (securing the best shelter and attracting females), the function of female dominance is not as clear. We suggested priority in securing shelters perhaps close to the dominant male, but the expected priority for mating with the dominant male was not found (Cowan and Atema 1990).

Much of the evidence for chemical signals in dominance encounters is based on a simple assay: the forced encounter or “boxing match.” The first detailed analysis of lobster agonistic behavior comes from Scrivener (1971). Similar results have been obtained under more natural conditions (Stein et al. 1975, Atema et al. 1979, Karnofsky and Price 1989, Cowan and Atema 1990) and in the field (Karnofsky et al. 1989a). Agonistic encounters follow a predictable sequence of escalation from displays such as “meral spread” (the extension and raising of the claws), to physical contact such as pushing with the claws and whipping with the antennae, to damaging behavior such as claw locking, jabbing, and ripping of antennae, antennules, and legs that can lead to limb loss, bleeding, and death. The latter is rare, but occasionally lobsters can be very aggressive, particularly naive animals raised in isolation (Huber and Kravitz 1995). Physical aggression observed in the field and among long-term aquarium residents tends to be infrequent and much less

The decrease in aggression among familiar animals appears to involve two different chemical signals: a generic dominance status odor combined with the memory of the individual odor of a recent opponent. In boxing matches between two size- and sex-matched adult lobsters, an initially small (if any) difference in aggressiveness develops into a clear winner-loser distinction generally within 15 minutes (although fights lasting hours have been recorded), resulting in a lasting dominant-subordinate relationship. An increasing number of winning or losing experiences affects subsequent fights against other opponents, which suggests a gain or loss in “confidence,” known as (p.121)

winner and loser effects. Accounting for effects of body size and claw size, experienced winners win and losers lose significantly more encounters than predicted by chance (Scrivener 1971). Dominance status (or “confidence”) appears to affect the rate and amount of urine output at the onset of an encounter: future winners release more in the early fight stages (Breithaupt and Atema 2000) (Fig. 6.3). Status may be signaled through unknown “dominance” compounds in the urine (see “Neuromodulators as Dominance Signals?,” below). The impact of a loss or a win on confidence increases until, after five consecutive losses or wins, the probability of a loss or a win, respectively, approaches 95%; winning and losing effects fade with time and future fight results (Morschauser 2002).

In addition to status recognition, there is individual recognition. If two adult lobsters meet for the first time and fight, are then separated for 24 hours (either in isolation or in communal tanks), and subsequently meet again, the previous loser will not challenge his former dominant opponent. However, the loser will challenge and can defeat an unfamiliar opponent, even if the new opponent is the recent winner of another fight (Karavanich and Atema 1998a). These results
indicate that lobsters are capable of individual recognition: they distinguish between familiar and unfamiliar dominants. Memory of a specific dominant individual can last for about one week without renewing the acquaintance, whether the week was spent in isolation or among many other individuals (Karavanich and Atema 1998a). This experiment also demonstrates that losing one fight does not turn the loser into a generic (p.122) subordinate: he or she can win the next fight. Individual recognition was similarly demonstrated in female–female (Atema et al. 1999) and male–female interactions (Berkey and Atema 1999). Male–female aggressive interactions can also change into mating attempts and intermolt mating, perhaps as a result of changing chemical signals.

Individual recognition is critical to the maintenance of lobster social structure. Once the dominant male has established a “mating shelter” large enough for two lobsters, he regularly patrols other nearby shelters, temporarily evicting other animals without a physical fight (O’Neill and Cobb 1979, Karnofsky et al. 1989a). We conclude that this eviction routine must be based on blowing the gill current with urine into the subordinates’ shelters. Since memory lasts a week, it may be a
mechanism to remind them regularly of his individual odor and status.

Blocking or catheterizing nephropores to prevent urine release into the gill current and lesioning antennules to block olfaction demonstrate that individual odor memory is based on chemical signals in urine mediated by antennular olfaction (Karavanich and Atema 1998b). Olfactory lesions prevent the establishment of a stable hierarchy, and fighting can continue for weeks (Cowan 1991). Individual recognition signals are received specifically by the chemosensory aesthetasc sensilla on the lateral flagella of the antennules (Johnson and Atema 2005). Thus, individual recognition is processed in the olfactory lobe of the brain.

**Sex Identification**

Male and female sex pheromones are behaviorally evident (Atema and Engstrom 1971, McLeese et al. 1977, Atema and Cowan 1986, Cowan 1991; reviewed in Atema and Cobb 1980, Atema 1986) but, despite some early attempts (McLeese et al. 1977), have not been identified chemically. In laboratory experiments, urine and tank water from the opposite sex cause closing of the seizer claw, a nonaggressive gesture, whereas same-sex stimuli cause claw opening, an aggressive gesture (Atema and Cowan 1986). In choice flume assays, females are more attracted to any male-occupied shelter, dominant or subordinate, than to an empty shelter (Bushmann and Atema 2000). This suggests that males release their sex signal more or less continuously, causing females to be attracted from a distance. Males also attract other males, leading to fights between unfamiliar opponents. In contrast, males do not discriminate between female-occupied and empty shelters (Bushmann and Atema 1997). This suggests either that males are not responding to a continuously emitted female signal or that females do not release their sex signal continuously. If females control the release of their sex signal, they use it in male proximity and to enter male shelters (Bushmann and Atema 2000). At close range, males do discriminate between sexes and even between the receptivity states of females (see “Female Signals and Receptivity,” below). Restricted release of sex signals might allow females to conserve signaling compounds and to avoid interfemale aggression.
Generally, lobsters do not accept conspecifics into their shelters. However, when a female of any molt state approaches a male's shelter, she is met with little or no aggression and may be admitted into the shelter. In contrast, another male will be met aggressively, leading to expulsion of either one (Atema et al. 1979, Bushmann and Atema 1997). If the approaching female is catheterized (preventing release of urine (p.123) with its chemical signals), she is met with high aggression similar to that directed at another male (Bushman and Atema 2000). Even with normal urine release, not all females are treated equally, depending on their receptive state (see “Female Signals and Receptivity,” below).
Male Signals and Female Choice

Naturalistic studies in large aquaria (Atema et al. 1979, Karnofsky and Price 1989, Cowan and Atema 1990) supported by limited field observations (Karnofsky et al. 1989a) show that the dominant male occupies a shelter sufficiently large for two animals and that the shelter of a dominant male becomes a focus of social interactions, including frequent visits by adult, premolt females. These females stop at the male shelter entrance and appear to inspect him, probably chemically. The female's decision to enter seems to be based on information from the male and the female's own internal state (e.g., molt stage, sperm status). During shelter visits both males and females greatly increase urine release (Bushman and Atema 2000), suggesting an exchange of chemical signals. In odor choice tests, females prefer to associate with dominant males over subordinates (Bushman and Atema 2000). When the dominant male was catheterized (preventing urine release), females were less attracted to his shelter (Bushman and Atema 2000). Female lobsters may locate a dominant male by following a plume of dominant male odor to its source, and/or they may learn the location of his shelter from their frequent explorations of the local environment, its shelters, and lobster inhabitants. Lobsters are surprisingly quick in learning the details of their local geography and sociology (J. Atema, personal observation).

Once the female is allowed into the male's shelter, the two animals cohabit until the female molts, after which they mate. During cohabitation, whenever one of a mated pair enters the shelter, they fight mildly (typically “boxing”) for a few seconds (Cowan and Atema 1990) suggestive of the time it takes for a chemical signal to disperse and be recognized. This signal may include not only sex information but also an individual signature. Individual recognition in the context of mating has not been investigated. Over the premolt cohabitation period, the frequency of male pleopod fanning increases (see “Chemical Signaling Behavior: Information Currents,” above), reaches a maximum during the day of female molting, and wanes in the postmolt cohabitation days. This current carries with it all male and—inevitably—female metabolites (including chemical signals) released by the cohabiting pair (Fig. 6.1). This activity can be seen as male “advertising,” since it is positively correlated with visits of other lobsters to the shelter,
including premolt females (Cowan and Atema 1990). It is unlikely that the cohabiting female benefits from this advertisement.

Snyder et al. (1993) observed successful courtship and mating when either males and/or postmolt females were catheterized (preventing urine release); they questioned the presence of sex-identifying cues in the urine of *H. americanus* but mentioned that this may be the result of conducting their tests in small tanks. Indeed, in a large flume tank, catheterized males, particularly when their previously collected urine was played back, still attracted females, but with fewer approaches and entry attempts. Females were not attracted to an empty shelter emitting only the urine collected from a dominant male (Bushman and Atema 2000). This suggests that (p.124) females use both urine-based cues and other, non-urine-based cues to locate and mate with a preferred male (Bushman and Atema 2000).
Female Signals and Receptivity

Mating in lobsters can occur at any time throughout the female's molt cycle (Waddy and Aiken 1990). It appears that females can monitor their sperm load and molt state and solicit matings when they need sperm during a long intermolt period. However, long-term, naturalistic aquarium observations showed that nearly all matings occurred shortly (around 30 minutes) after a female molts in the middle of a prolonged cohabitation period (Atema et al. 1979, Cowan and Atema 1990). Females are more likely to be receptive after molting because during the molting process they lose the sperm they may have been storing from a previous mating (Cowan and Atema 1990, Bushmann and Atema 1997). In naturalistic tanks, dominant males allowed only premolt females into their shelter for cohabitation, although females of all molt stages were met with less male aggression than were males (Cowan and Atema 1990). Clearly, males can detect differences in female receptivity.

Intermolt females with depleted sperm stores solicit males, who recognize them and mate with them immediately (Waddy and Aiken 1990, Bushmann and Atema 2000). Even when a group of lobsters is introduced into a new tank, the males take time off from the initial dominance fights to mate with such a female (J. Atema, personal observation). Presence of a sperm plug in the female indicates nonreceptivity. In laboratory experiments, all receptive females that entered male shelters were mounted, and half were mated, whereas nonreceptive females were not mated and few were mounted (Bushman and Atema 1997). Tank water from freshly molted, isolated (and thus not mated) females is attractive to isolated males, who start searching for the source; it reduces male aggression, including reflexive closing of the seizer claw (Atema and Engstrom 1971, Atema and Cowan 1986).

Lobstermen have observed that if a recently molted female finds her way into a trap, the trap fills with males.

Female chemical signals may play a role not only in courtship and cohabitation but also in mating behavior itself. Just before molting, the female faces the male and places her claws on the male's "shoulders" (anterior carapace and claws) in a "knighting" gesture. This curious behavior may be accompanied by urine release as it puts the nephropores almost directly onto the male's antennules (Atema 1986). The signals transmitted through such positioning are unknown but
could indicate synchronization for imminent molting and copulation ("Don't leave me now"). Chemical signals may also be transmitted to the male during copulation when he turns over the recently molted female to insert his gonopodia into her seminal receptacle. The appendages the male uses to turn over the female (first two pairs of periopods, and third maxillipeds) are supplied richly with chemo- and mechanoreceptive sensilla (Derby 1982). Contact pheromones have not been studied in *Homarus americanus*.

**Female Molt Regulation**

The only long-term observations of lobsters in the field (Karnofsky et al. 1989a, 1989b) show that a small group of residents interact with a large number of transient animals. The social interactions between residents and transients are not known. (p.125) Almost all of our knowledge concerning molting, mating, and cohabitation comes from laboratory observations in which sex ratios are enforced and immigration and emigration are restricted. Adult female molt staggering is seen in such closed systems—one female at a time cohabits and—directly after molting—mates with the dominant male (Cowan and Atema 1990, Cowan et al. 1991). The mechanism causing molt staggering among females is unknown, but chemical signals (primer pheromones) are known to regulate female reproductive physiology in other animals. In mammals, primer pheromones in male urine can cause estrus synchronization (Ma et al. 1999) and the onset of puberty in females (Novotny et al. 1999). Estrus synchrony (McClintock 1983) and reproductive suppression (e.g., Barrett et al. 1993) can also occur with exposure to female urine. Most dramatically, in social insects such as the honeybee, *Apis mellifera*, chemical signals produced by the queen prevent ovary development in workers (Hoover et al. 2003), producing an effectively sterile worker class. Female reproductive suppression by dominant females has also been observed in zebrafish (Gerlach 2006) and may be more widespread in other fishes. Thus, since female lobsters molt shortly (days) after entering into cohabitation with a dominant male, it seems that his primer pheromones could be accelerating her molting. This would benefit both male and female mating partners. But what prevents the other females from molting and thereby removes their chance to mate with the dominant male? We hypothesize that female lobsters, while not cohabiting with a male, mutually suppress through primer
pheromones the final stage of each others’ endocrine molt preparation, specifically the well-known premolt ecdysterone peak (reviewed in Hopkins 1983, Quackenbush 1986). The female who then enters the male’s shelter, would be released from this inhibition by the absence of the putative female molt-inhibiting pheromone and the exclusive exposure to the putative male molt-accelerating pheromone, allowing her to continue rapidly toward molting and mating. Such a hypothesized mechanism (Atema 1986) would benefit both males and females and result in the observed molt staggering. It could operate equally well in other crustaceans where female molt regulation is important.

Chemical Signals

To date, no lobster pheromone has been identified. We do know, however, that many chemical signals produced by the lobster are released in the urine. A possible source of some of these signals may be the nephropore gland. Logical candidates for female courtship pheromones are compounds related to molt hormones; metabolites of neuromodulators linked to aggression may be connected with dominance. As yet, there is no evidence for these suggested chemical connections.
Urine and Urine Release
Urine is stored in bilateral bladders. A typical 400 gram lobster, when taken out of a tank, can release up to 10 milliliters of urine, 6 milliliters on one side, in one fine stream under considerable pressure (J. Atema, personal observation). Urine is released through paired nephropores on the ventral sides of the basal segments of the antennae. Sphincter muscles suggest control over release (Bushman and Atema 1996), and behavioral experiments demonstrate this. Urine release increases somewhat in the hours following feeding. It is particularly prominent in social behavior and not due to physical activity; for example, urine is not released when lobsters are chased around the tank (Breithaupt et al. 1999). Male lobsters produce significantly more urine when a second male is introduced into their tank (Breithaupt and Atema 1993, Breithaupt et al. 1999) and also when visiting male and female shelters (Bushman and Atema 2000). At rest, urine is typically released in occasional approximately 5-second-long squirts of about 1 microliter per second; during fights the release can go up to 10 microliters per second for minutes at a time (Breithaupt and Atema 2000) (Fig. 6.3). Release probability increases with increasing fight intensity; (future) winners but not losers tend to release some urine at the start of a fight. This early release seems to anticipate winning success and may indicate confidence gained from previous winning experience (see “Dominance and Individual Recognition,” above). At the end of the fight, losers but not winners stop releasing urine (Breithaupt and Atema 2000) (Fig. 6.3). This urine release behavior strongly suggests its importance in communication.

Of course, urine is a common solvent for chemical signals in many animals. Its metabolic waste disposal function can serve many signaling functions, both for social communication and for discovery by predators. As a waste disposal system, urine could be considered a rather honest signal reflecting the internal state of the animal. As such, metabolites of neuromodulators and molt hormones have been suspected as chemical signals (see below).
Nephropore Glands

The nephropore glands, first described in crabs (Fontaine et al. 1989), are composed of masses of rosette glands located lateral and medial to the ureter, approximately 100 micrometers inside the nephropore (Bushman and Atema 1993). The glands with their ducts and surrounding muscle tissue appear designed to control release of gland product into the urine. The valve of the nephropore, in turn, controls release of urine, with or without glandular secretion added (Fig. 6.4). Although nephropore glands structurally resemble the rosettes of ubiquitous tegumental glands (Yonge 1932), their large size, highly organized structure, pathway of product release, continuous activity cycle, and histological staining pattern make nephropore glands different from adjacent tegumental rosettes. This suggests a novel function: the nephropore glands are present and active in both males and females, at all molt stages and at all times of the year. Histochemical results indicate that they contain proteinaceous material and mucopolysaccharides (Bushman and Atema 1996).

Lobster urine contains unusually large amounts of protein, commonly between 100 and 300 micrograms per milliliter (McLaughlin et al. 1999). Releasing such large amounts of protein may indicate a signal function. In addition, urine collected during a fight contained more protein than before or after a fight, and preliminary data show individually distinct patterns of three to six protein bands on gel electrophoresis (J. Atema, M. Mallidis, M. Edattukaran, unpublished observations). The source and function of lobster urine proteins are not known; however, proteins are thought to be excellent chemical signals in aquatic environments, due to their high solubility, potentially short half-lives, and resultant high signal-to-noise ratio (reviewed in Rittschof and Cohen 2004). Proteins mediate individual recognition in vertebrates,
Figure 6.4 Composite drawing of nephropore area of Homarus americanus, from horizontal histological sections. Single, large ducts travel from each gland complex and join to become a common duct terminating in the bladder. From Bushmann and Atema (1996).

for example, through the major histocompatibility complex (Apanius et al. 1997) and major urinary proteins (Benyon and Hurst 2004).
Molt Regulation Hormones as Pheromones?
The physiological role of crustecdysone in crustacean molt regulation is well understood; blood titers peak in the days before molting and drop precipitously on the day of molting (reviewed in Hopkins 1983, Quackenbush 1986). Since urine is the primary means of ecdysteroid removal, and since mating usually occurs in concert with molting, it was hypothesized that molting hormones could serve additionally as a crustacean sex pheromone (Kittredge et al. 1971). Several authors questioned this conclusion on theoretical grounds, primarily because crustecdysone would lack sex (p.128) and species specificity and provide only molt-timing information. This could be useful once the behavioral context of pairing has been accomplished by more specific signals. However, neither crustecdysone nor some of its metabolites elicited sexual behavior in male lobsters (Atema and Gagosian 1973, Gagosian and Atema 1973). Subsequent partial purification of two crab sex pheromones, Callinectes sapidus (Gleeson 1980) and Carcinus maenas (Hardege et al. 2002), showed that the cue was chemically distinct from crustecdysone. This supports the hypothesis that molting hormones and sex pheromones are not synonymous (Buchholz 1982, Gleeson et al. 1984, Hardege et al. 2002). It does not rule out that crustecdysone and its metabolites could be involved as additional molt timing signals or in other Crustacea (see also “Sex Pheromones,” below).

Neuromodulators as Dominance Signals?
As with crustecdysone, it is reasonable to speculate that metabolites of neuromodulators, such as the amines serotonin and octopamine might be excreted in the urine to serve as behavioral signals. Because serotonin has been implied as a regulator of aggressive behavior in lobsters, its metabolites might signal social status or confidence, and thus, serve as dominance pheromones. This link, however suggestive, has not been established despite several attempts. Kravitz (2000) reviewed the work on the connection between serotonin and dominance, using the lobster as a crustacean model. Following original studies of postural effects of serotonin (Livingstone et al. 1980, Kravitz 1988) subordinate lobsters (and crayfish) injected with serotonin showed increased tendency to instigate agonistic encounters with dominants, increased fight duration, and a decreased probability of retreating (Huber et al. 1997a). While such studies indicate a physiological link between the
neuromodulator and behavior, it does not indicate a pheromonal effect.

In high-performance liquid chromatography analysis of lobster urine, all radioactive metabolites of serotonin appeared as a single peak that coelutes with the serotonin-O-sulfate standard (Huber et al. 1997b); neither the metabolites nor the standard has been tested for pheromonal activity. Unlike in most vertebrate systems, the primary serotonin metabolite does not appear to be 5-hydroxyindole (Peeke et al. 2000).

It is worth mentioning that, in addition to amines such as serotonin and octopamine, other hormones and peptides are indicated in regulating lobster aggression (reviewed in Kravitz 2000). These include the molting hormone, ecdysone; its active form 20-hydroxyecdysone ( =crustecdysone); and a lobster stress hormone, crustacean hyperglycemic hormone (Chang et al. 1999). Crustecdysone levels peak just prior to ecdysis (Hopkins 1983, Quackenbush 1986, Snyder and Chang 1991), coincident with highest levels of aggression (Tamm and Cobb 1978, Atema et al. 1979, Cromarty et al. 1991) and affecting neuromuscular junction potentials in claw and abdominal muscles (Cromarty and Kass-Simon 1998). Crustacean hyperglycemic hormone peptides are produced by neurosecretory neurons, which are in turn influenced by both serotonin and octopamine (Chang et al. 1999).

In sum, despite sound reasoning and tantalizing clues from neurobiology, the chemical or functional links between neuromodulators, hormones, and pheromones are not clear at this point. We therefore do not add to further speculation.

Chemical Communication in Other Decapod Crustacea

Information Currents

The first description of what we now call information currents was given in great detail for Pagurus arrosor hermit crabs by Friedrich Brock (1926). He observed that the fan organs, feathery flagella of the exopodites of the maxillipeds, generate water currents that can be directed forward (by beating the exopodites of the maxillipeds bilaterally) and to either side (by unilateral fanning). In unilateral fanning the outgoing current is fed by an incoming current from the opposite side of the head. He then noted that both antennules move sideways to flick in parallel into the incoming current. Forward fan
currents are fed by an anterior counter current, and the antennules flick again into this incoming water. In this way, an animal can send and obtain directional chemical information.

Similar to hermit crabs, in the crayfish *Procambarus clarkii* fan organs generate a variety of well-described fluid flows, allowing the animal to send and receive chemical signals from the environment (Breithaupt 2001). These flows can be bilateral or unilateral, drawing fluid horizontally from nearly all directions toward the body, including the antennular chemoreceptors. For *Orconectes rusticus*, Bergman et al. (2005) described posterior currents (i.e., those generated by pleopods) and anterior currents (i.e., those generated by maxilliped fan organs) used in concert with urine release during agonistic behavior, particularly highly aggressive claw grasping, all remarkably similar to currents and behaviors in *H. americanus* (Breithaupt and Atema 2000).

It is interesting in a phylogenetic context that the currents of hermit crabs and crayfish are functionally similar to the ones of *H. americanus* (Atema 1985), but they are generated differently. In the lobster, the anterior currents are driven primarily by the powerful gill current and can be redirected by the exopodite fan organs. The gill current of hermit crabs and crayfish, including *Astacus astacus* and *A. leptodactylus* (J. Atema, unpublished observations), is not as powerful—perhaps as a result of smaller body size and related metabolic demands (see Fig. 6.2a)—and the anterior currents are mostly generated by the fan organs themselves. It would be interesting to see if large crayfish such as *Cherax destructor* or the Tasmanian giant crayfish, *Astacopsis gouldi*, use the fan organs to modulate the gill current as shown in lobsters.

**Nephropore Gland**

The earliest reference to a nephropore gland is in the green crab, *Carcinus maenas* (Fontaine et al. 1989), and we know of no other published accounts. From its presence in crabs and lobsters, we suspect it will be present in many decapod crustaceans and perhaps in crustaceans in general. The location and structure of the gland appear similar in *H. americanus* and *C. maenas*, and so are the speculations regarding its possible pheromonal function.

**Sex Pheromones**
The presence of a female sex pheromone in decapod crustaceans was first demonstrated in the crab Portunus sanguinolentus (Ryan 1966). Several other species of crabs have since been shown to utilize sex pheromones, but only one has been fully characterized.

Pre- and postmolt female hair crabs, Erimacrus isenbeckii, use a mixture of ceramides (lipid secondary messengers used in intracellular signaling systems) as a sex pheromone to elicit mating behavior from males; the compounds have been isolated, characterized (Asai et al. 2000), and synthesized (Asai et al. 2001, Masuda et al. 2002). The resultant synthetic compounds (Fig. 6.5) were identical to the natural pheromone. It is not clear if specific mixtures are required or whether any one of the compounds alone can elicit male mating behavior.

Studies on the blue crab, Callinectes sapidus, demonstrate that chemical signals are present in the urine of pre- and postpubertal molt females, inciting courtship and mate-carrying behavior in males (Gleeson 1980; reviewed in Gleeson 1991). Visual cues appear to have no effect on courtship or mating behaviors (Gleeson 1980, Bushmann 1999). Fractionation showed that although 20-hydroxyecdysone was present in this urine, it was not in the bioactive fraction (Gleeson et al. 1984), indicating that it is not the pheromone involved in signaling in this context as had been suggested (Kittredge et al. 1971). The active fraction has not been fully characterized.

The presence of a sex pheromone in the green crab, Carcinus maenas, was first demonstrated by Eales (1974). Male conspecifics responded to premolt female urine by displaying searching behavior. The pheromone causes male crabs to fight longer and more intensely than in the absence of the signal (Sneddon et al. 2003). Males attempt to mate even with inanimate objects such as stones conditioned with the chemical signal (Hardege et al. 2002). The pheromone may have dose-independent effects (searching for a female) and

**Figure 6.5** Ceramide structure of sex pheromones in the female hair crab, Erimacrus isenbeckii. From Asai et al. (2000).
dose-dependent effects (cradle carrying and stroking the female) (Ekerholm and Hallberg 2005). If antennular chemoreception is blocked, control of sexual behavior is disrupted (Bamber and Naylor 1996). The chemical identity of the female green crab sex pheromone is not known. Hardege et al. (2002) determined it to be a small molecule in premolt and postmolt female urine chemically distinct from 20-hydroxyecdysone. It has a molecular weight of less than 10 kDa, permitting it to cross the renal membrane.

The helmet crab, *Telmessus cheiragonus*, shows two female sex pheromones: a female precopulatory pheromone found in the urine of both pre- and postmolt females that induces male mate guarding (Kamio et al. 2000), and a postmolt female signal (not carried in the urine) that induces copulation (Kamio et al. 2002). Ultrafiltration showed the copulation pheromone to have a molecular size of less than 1 kDa (Kamio et al. 2002).

Studies on different species of crayfish have also indicated the use of sex pheromones. When exposed to the tank water of a conspecific female, male crayfish (*Procambarus clarkii*) behave submissively, displaying feeding behaviors, with lowered claws and curled abdomen. When exposed to male tank water, however, males behave agonistically, raising their claws. These disparate behaviors were seen only in the presence of chemical signals—visual stimulation had no effect (Ameyaw-Akumfi and Hazlett 1975). This sex-specific pheromone was determined to be a carbohydrate, but no further elucidation was done. These results were first questioned by Itagaki and Thorp (1981) but later reaffirmed by Dunham and Oh (1992). Tierney and Dunham (1982) demonstrated the use of pheromones in species recognition as well as sex recognition in the crayfish species *Orconectes propinquus* and *O. virilis*. The two species could perceive the signals of both conspecifics and heterospecifics but were attracted only to signals produced by opposite-sex conspecifics.

Preliminary evidence shows that mature female signal crayfish, *Pacifastacus leniusculus*, release a chemical signal that induces sexual behavior in males (Stebbing et al. 2003). In the crayfish *Austropotamobius pallipes*, males respond only to
chemical and visual cues in concert, not to chemical cues alone (Acquistapace et al. 2002).

Females of the New Zealand spiny lobster, *Jasus edwardsii*, prefer to mate with larger males and base their choice partially but not completely on male urine signals. In choice tests, females no longer expressed a clear choice when the urine output of a large male and a small male were exchanged so that the catheterized large male “emitted” the urine of the small male and vice versa. Mate choice was thus thought to be based on visual and tactile senses as well as olfaction (Raethke et al. 2004). However, the same result could also indicate the use of additional chemical signals not carried in the urine, as indicated in *H. americanus* (see “Male Signals and Female Choice,” above). Male *J. edwardsii* appear to depend more than do females on olfactory cues in order to mate successfully. Matings between anosmic (i.e., antennule-ablated) males and intact females increased mating delay after female molting and decreased female clutch size. Antennule ablation in females, which are known to use olfaction in mate choice, had no significant effect on fertilization success: it seems they can monitor their own receptivity and do not rely on chemical cues for timing information (Raethke et al. 2004). The female South African rock lobster, *Jasus lalandii*, appears to produce a chemical substance during the time of ecdysis that elicits courtship behavior from males (Rudd and Warren 1976).

In shrimp, early evidence of a dispersing sex pheromone came from the freshwater prawn *Palaemon paucidens*. Tank water from a female undergoing the parturial (i.e., adult) molt elicited searching behavior by males (Kamiguchi 1972). In choice tests, female rock shrimp, *Rhynchocinetes typus*, approached the dominant male significantly more than the subordinate and preferred to mate with dominant (“robustus”) males (Diaz and Thiel 2003, Thiel and Hinojosa 2003). To locate dominant males, females followed waterborne chemical cues. Males, however, did not follow a chemical trail to find a female. Rather, they used visual signals—“tumults” created by groups of subordinate males aggregating around the female—to find their mate; they needed physical contact to recognize the female’s state of receptivity (Diaz and Thiel 2004), an interesting example of a contact pheromone.
A female contact sex pheromone is also indicated in the grass shrimp *Palaemonetes vulgaris*. It was suggested to be a nondiffusible compound on the female integument detected by the male antennae (Burkenroad 1947). In the highly gregarious *P. pugio*, males recognize receptive females by contact but only during a brief period preceding the female’s parturial molt (Berg and Sandifer 1984, Bauer and Abdalla 2001). This close timing seems appropriate when animals already live in dense aggregations.

(p.132) Similarly, in the hippolytid shrimp *Heptacarpus paludicola*, only a weak male response to receptive females upstream could be observed under experimental conditions; males needed to contact females with their antennae to recognize their receptive state (Bauer 1979). Harlequin shrimp, *Hymenocera picta*, form pair bonds through chemical identification. This information is conveyed by pheromones produced only by females and detected only by males (Seibt 1973). Clearly, in order to form heterosexual pair bonds, sex identification is critical, and chemical signals are commonly used for sex discrimination. We would expect this to be the case in other, yet unstudied pair bonding species.

**Dominance and Individual Recognition**

Individual recognition is believed to have evolved to allow for stable dominance hierarchies, as well as to unmask individuals who may bluff about fighting ability when faced with an agonistic interaction (Barnard and Burk 1979). It occurs in species with a relatively complex social structure, including pair bonding, and highly aggressive interactions (Halpin 1980). The ability to recognize known individuals within a dominance hierarchy decreases the need to escalate aggressive encounters with known opponents. This strategy decreases costs to both individuals in time and energy expenditure, as well as risk of injury. In decapod Crustacea, individual recognition has arisen in multiple orders and families.

“True” individual recognition is a system in which an individual can identify another by “a unique set of cues defining that individual” (Beecher 1989) and can associate that set of cues with experiences related to that specific individual. This is in contrast to “binary discrimination” in which an individual can recognize a conspecific but is able
only to place that individual into a subgroup (dominant/subordinate or familiar/unfamiliar) rather than recognizing it individually (Barrows et al. 1975).

Two species of hermit crabs, *Pagurus bernhardus* and *P. longicarpus*, use individual recognition to establish dominance hierarchies. Hazlett (1969) observed small groups of *P. bernhardus*, noting steadily decreasing aggression between group members over several days of interaction. When an unknown crab was introduced, however, the number of fights observed between group members and the unknown crab increased significantly. Similarly, in *P. longicarpus*, interactions between unfamiliar individuals were more intense than between familiar animals; subordinates were more likely to initiate an interaction with a stranger than with a familiar dominant (Gherardi and Tiedemann 2004a). Carefully designed experiments showed that this individual recognition is chemically mediated—crabs reacted differently, taking longer to approach an empty gastropod shell in the presence of the odor of familiar versus unfamiliar conspecifics (Gherardi and Tiedemann 2004b). In this species, animals recognized individuals before a stable dominance hierarchy was formed, indicating that individual recognition is relatively unconnected with winning and losing experiences (Gherardi and Atema 2005). Initially, individual recognition in *P. longicarpus* was shown to be at least “binary,” indicating animals discriminate familiar from unfamiliar but do not distinguish between individuals based on a unique chemical “badge” (“true” individual recognition) (Gherardi and Tiedemann 2004a, Gherardi and Atema 2005). However, more detailed experiments reveal that this species can (1) chemically (p. 133) discriminate between larger crabs in high-quality shells from smaller crabs in lower quality shells as long as the odor donors are familiar to the receiver, (2) associate the odor of an individual crab with the quality of its shell, and (3) change this association when their shell quality changes (Gherardi et al. 2005). This implies that odor information of nearby individuals is fluidly associated with past and new experiences regarding their shell size and shell fit.

Individual recognition is essential in the formation and preservation of pair bonds. Harlequin shrimp, *Hymenocera picta*, almost always form pair bonds. The bonds are maintained by the male’s ability to distinguish (and prefer) the odor of his female mate over all other conspecifics (Seibt
1973). If the female of a pair is moved out of the male's territory and restrained elsewhere in a tank, the male will seek out his mate preferentially over remaining in his territory. If other females are available in the tank, he will bypass them, find his mate, and stay with her. The ability persists without visual cues (in darkness or in a Y-maze), confirming that chemical cues are responsible for recognition (Seibt 1973). Males do not distinguish among males, suggesting that individual recognition is not used in dominance interactions in this species, but only in pair bonds. The pheromone is generated only by the female and received only by the male (Seibt 1973). Female behavior was not studied as thoroughly but may contribute to the pair bond: in choice tests (Y-maze), they prefer the odor of their mate to all other conspecifics.

Banded coral shrimp, *Stenopus hispidus*, also display mate recognition in the context of a pair bond. If a pair is separated and placed back together after up to six (but not 33) days, they interact “neutrally” (i.e., at a low level). When separated and subsequently placed with a stranger, they show more intense interactions, indicating that they distinguish between familiar and unfamiliar conspecifics (Johnson 1977). No specific tests were done to show the involvement of chemical cues; however, this seems likely.

The cleaner shrimp *Lysmata debelius* forms pair bonds and can distinguish a partner from a stranger (Rufino and Jones 2001). Individual recognition allows animals to direct aggression toward strangers rather than toward mates. The modality of recognition in this species is not known, nor is the length of time recognition persists. Given the evidence in other pair bonding shrimp, it seems likely that chemical signals are involved.

Some evidence suggests that big-clawed snapping shrimp, *Alpheus heterochelis*, may be capable of individual recognition in pair bonding. Rahman et al. (2001) showed that animals could distinguish former mates from unfamiliar conspecifics. In Y-maze choice tests, individuals also preferred the odor of familiar same-sex conspecifics over the odor of an unfamiliar one. Animals can become conditioned to the odor of a specific individual if exposed to the tank water of that individual (Ward et al. 2004). Snapping shrimp do not, however, appear to use individual recognition in agonistic encounters. Subordinates who meet any dominant animal—familiar or unfamiliar—show
immediate escape responses, but subordinates who meet and lose to socially inexperienced animals require several days of daily fights to show gradually more subordinate behavior (Obermeier and Schmitz 2003a). The signal appears to be chemical: anosmic (i.e., aesthetasc-ablated) animals did not discriminate between dominant and inexperienced opponents (Obermeier and Schmitz 2003b). Thus, snapping shrimp can recognize by odor the dominance status of an opponent, but not the opponent's identity.

Male but not female snapping shrimp (*Alpheus heterochelis*) use chemical signals to reduce their aggressive response to an open chela display: male odor enhanced and female odor reduced the otherwise aggressive response to this visual signal; females always responded aggressively regardless of any conspecific odor (Hughes 1996).

The colonial, eusocial shrimp *Synalpheus regalis* may well be the crustacean answer to eusocial insects, including dependence on chemical signals. Although not studied yet in specific detail, observations suggest that antennal contact is critical in recognition of nest mates versus intruders; both contact chemicals and dissolved substances may be involved. Queen signals are also indicated (Duffy et al. 2002). In the future, this interesting social environment may well reveal a treasure of pheromone interactions.

Several species of crayfish display status recognition but not individual recognition. A male *Astacus leptodactylus* who has just lost a fight is just as likely to refuse escalating the next fight with a familiar or an unfamiliar dominant; the status signals are present in the urine (Breithaupt and Eger 2002). Similarly, urine carries status information in the crayfish *Orconectes rusticus*: individuals who lost their first fights engaged in much shorter second fights whether their opponent was familiar or unfamiliar (Zulandt Schneider et al. 2001). The same species has been shown to adjust its dominance status as a result of prolonged exposure to tank water from unfamiliar dominant or subordinate conspecifics: a five-day exposure to dominant male odor resulted in subordinate behavior against a new male; dominant behavior resulted from similar exposure to subordinate odor (Bergman and Moore 2005). This result has interesting implications for the study of physiological mechanisms of primer pheromones, but a natural context for such long odor exposure is not
known. *Procambarus clarkii* also determine dominance status through olfactory cues (Zulandt Schneider et al. 1999). Status recognition was shown in *Procambarus acutus acutus* (Gherardi and Daniels 2003).

Lowe (1956) showed evidence for individual recognition in *Cambarellus shufeldtii*. When one claw was removed from an established dominant, he would retain his dominant status in the hierarchy. However, when placed with unfamiliar individuals, he would often become subordinate. The large Australian crayfish *Cherax destructor* is both more likely to win fights against familiar than unfamiliar opponents and more attracted to familiar than to unfamiliar conspecifics. This “dear enemy” behavior was demonstrated even when using only visual or only chemical cues (Crook et al. 2004). See chapter 5 for additional information on crayfish social behavior.

Although belonging to the order Stomatopoda, rather than Decapoda, the work done on individual recognition in *Gonodactylus festae* and *G. bredini* requires mention here. Stomatopods are territorial animals that defend their rock crevices against conspecifics. Subordinate *G. festae* avoided crevices that smelled like familiar dominant conspecifics but readily entered and explored crevices without odor or with the odor of an unknown or subordinate animal (Caldwell 1979, 1985). *G. bredini* recognize former mates: males are less likely to evict a former female mate from her crevice, and females are less likely to defend their cavity against a former male mate (Caldwell 1992). This reduction of aggression was mediated by chemical signals and lasted approximately two weeks.

(p.135) Stress, Aggregation, Larval Release, and Maternal Signals

This section reviews chemical signals that are known in Decapoda, but not in *H. americanus*. Conspecific stress signals were observed and caused male aggressive responses in the crayfish *Procambarus acutus acutus* (Thorp and Ammerman 1978). Aggregation signals are used to form clusters of gregarious animals such as spiny lobsters (see chapter 13). One would not expect this to be the case for the solitary *H. americanus*. Larval release signals are known in some crabs and should be expected in all brooding crustaceans, including
**H. americanus.** Maternal signals should occur in species that extend brood care for hatched larvae, such as various crayfish species (see chapters 14, 15).

Starting in late juvenile stages and lasting through adulthood, Caribbean spiny lobsters, *Panulirus argus*, forage solitarily at night but exhibit gregarious shelter use during the day (Eggleston and Lipcius 1992). Shelter choice is often influenced by conspecific density and predator risk (Eggleston and Lipcius 1992). Aggregations are also formed through chemical signals. All but the earliest benthic stages of lobsters produce aggregation odors and are attracted to shelters by conspecific odors (Ratchford and Eggleston 1998). Lobsters produce these aggregation signals near dawn, when conspecifics return to shelters from solitary foraging expeditions. If foraging lobsters are experimentally kept on a different light/dark schedule than the animals producing the signal, they will respond to the signal even if temporally inappropriate; that is, they return to the shelter in the middle of the night rather than at dawn (Ratchford and Eggleston 2000). Field experiments on juvenile spiny lobsters support the use of chemical aggregation cues (Nevitt et al. 2000). Butler et al. (1999) demonstrated that late benthic juveniles of the New Zealand spiny lobster, *Jasus edwardsii*, increasingly strongly begin to aggregate and respond to the odor of larger conspecifics, facilitating gregarious behavior.

In some species, such as the mud crabs *Rhithropanopeus harrisii* (Rittschof et al. 1985) and *Neopanope sayi* (DeVries et al. 1991) and the blue crab, *Callinectes sapidus* (Tankersley et al. 2002), larval release pheromones are emitted by the hatching eggs themselves. These pheromones induce larval release behaviors in females such as compression of the egg mass to help break egg membranes, and abdominal pumping, which release the larvae into the water column (for an overview, see Forward 1987). In several species, for example, *R. harrisii* (Rittschof et al. 1985), the signals consist of a mixture of small peptides (molecular weight < 500 Da)

Early larval stages of several crayfish species, *Orconectes sanborni, Cambarus virilis*, and *Procambarus clarkii*, are attracted to chemical cues produced by a brooding female, normally their mother (Little 1975, 1976). The female cue appears at egg deposition, peaks at hatching, and starts disappearing as the larvae become independent. The larvae
are no longer attracted, and the female loses her inhibition to feed on them. This maternal pheromone may have originated as a mechanism to prevent cannibalism in brooding animals.

Summary
We have presented the American lobster, *Homarus americanus*, as a model organism of chemical communication in decapod crustaceans. Lobsters use chemical signals to form and maintain dominance hierarchies, to choose and locate mates, to determine reproductive receptivity, to recognize individual conspecifics, and perhaps to regulate their molt cycles. The chemical signals are carried primarily but not completely in the urine and are dispersed into the environment by animal-generated currents. These information currents are also vital for receiving chemical information from the environment, including conspecifics. In addition, the lobsters *H. americanus* and *Panulirus argus* are model organisms for chemosensory physiology, signal transduction, and receptor genetics as well as a number of nonsocial behavior studies such as odor plume tracking and biomimetic robotics. Lobsters and crayfish are important models for crustacean brain anatomy and physiology (see chapter 4). This multidisciplinary database makes them rich study subjects for our understanding of crustacean communication and the evolution of sociality.

However, this account of decapod crustacean behavior influenced by chemical signals also points out the gaping holes in our knowledge: the chemical identity of the signals and their use under field conditions. Many decapod crustaceans use chemical signals for purposes similar to those of *H. americanus*. We must now give high priority to chemical analysis and field studies. The amount of knowledge we possess of the social behavior, physiology, and utilization of chemical signals in *H. americanus* and some other decapod crustaceans is an excellent knowledge base from which to begin identifying the chemical composition of the pheromones. The chemicals used by decapods to communicate sex, receptivity, dominance, and so forth, are likely to bear similarities between species. We anticipate that advances made in pheromone identification will be of great consequence in understanding crustacean chemical communication, just as has been the case in insects. It will help us understand
evolutionary and ecological relationships; the neurobiology of signal processing; the costs of signal production, storage, and release; and the physical and chemical constraints on signal design imposed by different aquatic environments.

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