

Chapter 5

Social Behaviour and Recognition in Decapod Shrimps, with Emphasis on the Caridea

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Abstract Common in most aquatic environments, shrimps occur in a wide range of social associations with conspecific and other species, and express various levels of social recognition. We review the mechanisms and forms of social recognition in shrimps, emphasizing the Caridea. Most research has been conducted on Alpheidae, Hymenoceridae, Hippolytidae, Palaemonidae and Stenopodidae. The olfactory first and chemotactile second antennae are important in perceiving waterborne cues/pheromones and contact pheromones. Potential distance and contact pheromones have been strongly suggested by behavioural studies in several species and even tentatively identified in a few species. All forms of social recognition and interspecific communication have been documented in shrimps, including recognition by mate, size, rank, kin and individual. Given the diversity of ecology, mating and social behaviour, and the previous research on social recognition in caridean shrimps, this group is a promising productive model taxon for studies in animal communication.

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Introduction

Shrimps are ubiquitous crustaceans in most aquatic environments (Bauer 2004). They occur in a wide range of social associations with conspecifics and also with other species (Fig. 5.1). Associations may consist of a minimum of two individuals (typically male and female), groups of several individuals (Baeza et al. 2010), and even reach aggregations of hundreds or more in commercially important schooling species of pandalid carideans and dendrobranchiate shrimps. Snapping shrimps (Alpheidae) are also the only marine invertebrate taxon with species that live in large eusocial groups (up to several hundred individuals), which are dominated by one or several queen-like females (Duffy 1996, 2007).

Given the diversity of group-association patterns in animal taxa, it is not surprising that a wide range of social associations and behaviours are reported for caridean shrimps (Bauer 2007), for example, dominance hierarchy among males (Ra'anan and Cohen 1985; Correa et al. 2003), coordinated defense by colony members in eusocial shrimps (Tóth and Duffy 2005), and pair living (Seibt and Wickler 1979; Knowlton 1980; Bauer 2004; Wong and Michiels 2011; Baeza et al. 2013). Since some species are known or supposed to cohabit for long time periods with conspecifics, it is to be expected that various levels of conspecific recognition have evolved.

Herein we review the existing literature on recognition in decapod shrimps, with emphasis on carideans, the group in which social recognition has been best studied. We present examples of the principal communication patterns currently

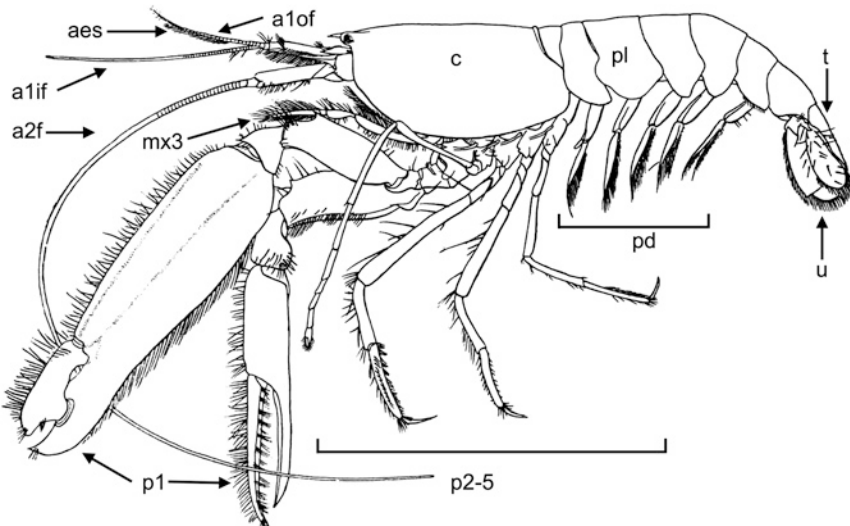


Fig. 5.1 External anatomy of a caridean shrimp, *Alpheus glaber*. The first pereopods (p1) are modified as specialized chelipeds. *a1if* inner flagellum of antennule (antenna 1); *a1of* outer flagellum of antennule; *a2f* flagellum of antenna (antenna 2); *aes* aesthetascs; *c* carapace; *mx3* third maxillipeds; *p1-5* pereopods (walking legs) 1-5; *pd* pleopod (swimming legs); *pl* abdominal pleuron; *t* telson; *u* uropod. Adapted from Holthuis (1955)

known in this group. We also highlight exciting cases for which more knowledge is urgently needed in order to understand the evolution of social behaviours in these beautiful crustaceans.

Shrimp Life Styles and Habitats

Most shrimps are medium-sized, being slightly larger than amphipods or isopods, but usually smaller than lobsters and many crabs. They have a well-developed abdomen and two pairs of chelipeds that can be morphologically quite variable (Fig. 5.1). These chelipeds may be used for food-processing, grooming, intra- and interspecific fights, and mating interactions. Females of caridean and stenopodidean shrimp species incubate their embryos under their abdomen and the eggs hatch into dispersing planktonic larvae in most species or benthic postlarvae or juveniles in some species (Bauer 2004).

Carideans are a taxonomically and ecologically diverse group (Bauer 2004) (Fig. 5.2). They are the most speciose of decapod shrimps, with at least

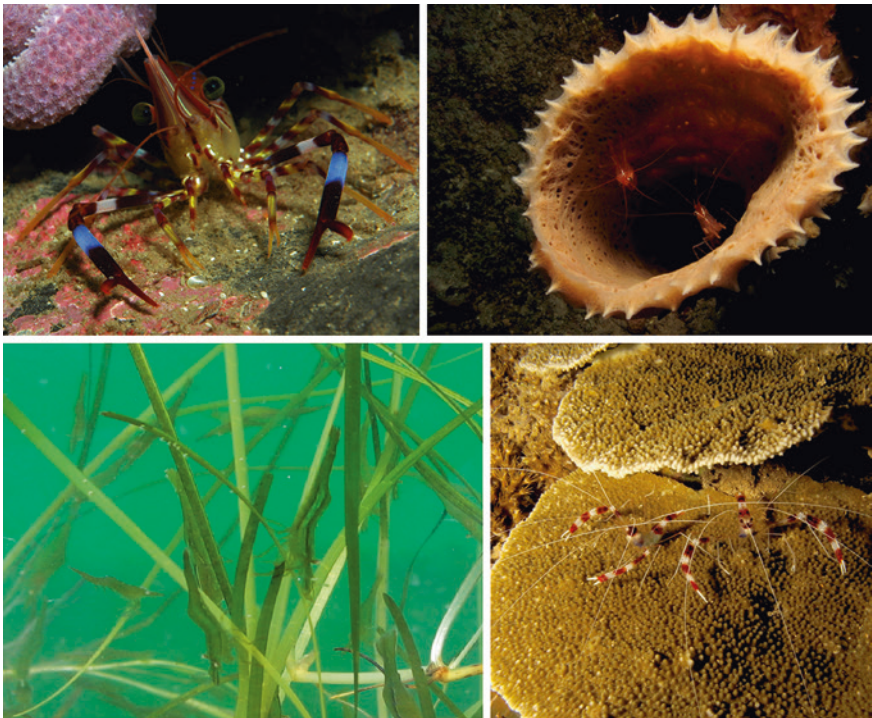


Fig. 5.2 Solitary caridean shrimp *Campylonotus vagans* (upper left), pair-living *Lysmata* sp. (upper right), gregarious *Hippolyte williamsi* (lower left), and monogamous stenopodidean shrimp *Stenopus hispidus* (lower right). Photographs courtesy of Dirk Schories (upper left) and Raphael Ritson-Williams (upper and lower right)

3400 species, compared to other shrimp taxa (Dendrobranchiata: 534 species; Stenopodidea: 70; DeGrave and Franssen 2011). Their geographic and bathymetric distributions are quite broad, as they occur in freshwater, estuarine and marine habitats. In the oceans, carideans occur at all depths and latitudes from pole to pole. They are an important component of neritic, pelagic, and deep-sea communities, occurring epibenthically over rocky, coral and soft sediments (sand and mud). Commercially important carideans, mainly pandalids and crangonids, are schooling species that move over soft-bottom marine habitats where they can be fished by trawling (Bergström 2000; Bauer 2004). Many carideans dig themselves into soft sediments during the day to emerge at night, and other species occupy more permanent burrows, often with a sexual partner. Carideans are a key component of seagrass and coral reef communities, and many species live in symbiotic associations with invertebrate hosts (Bruce 1976; Bauer 2004).

The Dendrobranchiata comprises the pelagic sergestoid and epibenthic penaeoid shrimps (Dall et al. 1990; Tavares and Martin 2010). The only known type of social organization in these shrimps is schooling, i.e., occurrence in large mobile aggregations. Penaeoids are subtropical and tropical species which are the most important component of the world's shrimp fisheries (Bauer 2004; Tavares and Martin 2010). The Stenopodidea is a small group with two major families, one (Stenopodidae) with species in shallow rocky and coral reef habitats in warm waters (Chockley et al. 2008; Goy 2010), while members of the other family (Spongicolidae) are associates of deep-water invertebrate hosts, especially hexactinellid (glass) sponges (Saito and Takeda 2003; Goy 2010). Most Stenopodidean species (for which such information is available) are reported to live as adults in male-female pairs (e.g. Saito et al. 2001; Goy 2010).

Mechanisms of Recognition

Decapod shrimps use waterborne (olfactory), contact or visual signals, or a combination of these, for social recognition. Specialized setae on the antennal (second antenna) flagella, third maxillipeds, and anterior pereopods are used to detect contact pheromones (Bauer 2011). Similar to other decapods (e.g. clawed lobsters, spiny lobsters, and crayfish; Aggio and Derby 2011; Breithaupt 2011), the first and second antennae are the main sites to perceive olfactory and contact signals (Fig. 5.1). Putative candidates for distance olfactory pheromone and contact pheromones have been identified in some species (Bauer 2011).

Waterborne cues are used by many shrimp species to obtain information about other individuals; in some species, the sender could even direct specific currents towards a receiver. For example, female *Hymenocera picta* produce a pheromone that is perceived by their male partners, which recognize their female partners among several shrimps (Seibt 1973). In the big-clawed snapping shrimp *Alpheus heterochaelis*, waterborne cues are important to differentiate between familiar and unfamiliar individuals (Ward et al. 2004). Transfer of these waterborne cues

is facilitated by various behaviours of the emitting and receiving individuals. *Alpheus heterochaelis* produce various kinds of currents generated by the anterior appendages; some of these currents may be important in chemical communications (Herberholz and Schmitz 2001). A fast, strong, anterior-directed current is initiated after contact with a conspecific of either sex or with an interspecific shrimp. This current can likely reach the opponents' area of chemical perception. The frequency, duration, and range of the current are lower in encounters with interspecific individuals than in interactions with conspecifics. Moreover, the number of fast anterior gill currents is higher in winners than in losers of same-sex interaction, suggesting a role in hierarchy formation. Another current, the lateral gill current is produced by movements of the scaphognathites (the exopodites of the second maxillae), which is the most frequently observed current in *A. heterochaelis*; it has long intervals but has a short range and a low velocity. Lateral gill currents can likely improve the shrimps' ability to sense nearby chemical signals by constantly refreshing the area around its chemical receptors (Herberholz and Schmitz 2001).

The olfactory antennules and chemotactile antennae (first and second antennae) are important in perceiving the pheromones that permit differentiation of mates from non-mates, but the frequency of antennal exploration of other individuals may differ substantially between males and females, and also between different species (Vickery et al. 2012). In alpheid snapping shrimps, the antennae are used during initial contacts between individuals and the antennules are important for pair formation. During initial contacts, mutual antennulation (contact of one or both chemotactile antennae between two individuals) is more frequently observed in heterosexual than in homosexual interactions in both *Alpheus heterochaelis* and *A. normanni* (Nolan and Salmon 1970). Mutual antennulation often led to threat postures with open chela in homosexual interactions of both sexes. Successful pairing, however, may require olfactory function of the antennules. In *Alpheus edwardsii*, ablation of the antennae only slightly reduced heterosexual pairing frequency (Jeng 1994). However, ablation of the olfactory antennules (especially the outer antennular flagellum bearing the aesthetasc tufts) strongly reduced heterosexual pairing and increased homosexual pairing frequencies.

In *Macrobrachium rosenbergii*, the anatomy of the olfactory receptors, aesthetascs, and neural pathway to the brain have been examined (Kruangkum et al. 2013). Ablation of the lateral antennule (bearing aesthetascs) in males significantly reduced the mating success, but ablation of the antenna also caused a reduction in success. These results suggest that both olfaction (aesthetascs) and contact (antenna) may be involved in detection of olfactory or contact pheromones, respectively, and mate recognition in this species.

Potential candidates of distance and contact pheromones have been identified in two species of caridean shrimps, respectively. In the peppermint shrimp *Lysmata wurdemanni*, distance and contact pheromones operate together for successful copulation. Distance pheromones led to pre-copulatory approach and following behaviour for 5–120 min before the female moulted, while contact pheromones induced copulatory behaviour (Zhang and Lin 2004). Males tracked and located premoult females but not premoult males, presumably using distance pheromones

specifically released by premoult females (but visual cues were not excluded) (Zhang and Lin 2006). “Washed” receptive females, which had insignificant amounts of distance pheromones, were not followed by males, but copulation still occurred after the male contacted the female with his antenna/antennules. Ablation of both antennae and antennules inhibited detection of distance and contact pheromones and resulted in no mating between males and receptive females. However, ablation of the outer flagella of the antennules inhibited only the detection of distance pheromones. A compound similar to the shore crab sex pheromone Uridine-di-phosphate was identified as the potential distance pheromone (Zhang et al. 2010). Aesthetascs on the outer flagella are likely the site of detection for distance pheromones, since they are innervated by olfactory receptor neurons and can possibly detect distance sex pheromones (Zhu et al. 2012b). Male-phase individuals of *L. wurdemanni* and several congeners have higher numbers of aesthetascs than those in the female (euhermaphrodite) phase, but this may be caused by delayed sex change in some males that attain larger sizes (Zhang et al. 2008; Zhu et al. 2012b). Moreover, the number of aesthetascs are also much higher in group living species (*L. wurdemanni* and *L. boggei*) than in pair-living or low density species, suggesting the importance of aesthetascs in social interaction (Zhang et al. 2008; Zhu et al. 2012b). Despite the demonstration of waterborne pheromones, the production and source of these pheromones are still unknown. However, as in other crustaceans, waterborne signals are likely contained in urine released anteriorly through a pair of nephropores (Breithaupt 2011).

Contact signals/pheromones have been suggested in many shrimp recognition systems because contact by the antennae appears to initiate specific behaviours (e.g. snap or courtship). In the grass shrimp *Palaemonetes pugio*, males respond to postmoult parturial (sexually attractive) females only after touching them with the antennal flagella or the pereopods (Bauer and Abdalla 2001). Comparison of visual, tactile and behavioural cues as sexual signals pointed to the presence of a contact sex pheromone (Caskey and Bauer 2005) and further experiments identified glucosamine or a glucosamine-containing glycoproteins as the likely candidates (Caskey et al. 2009). Males can discriminate between reproductive (postmoult, parturial) and nonreproductive (nonparturial) females on the basis of contact chemoreception mediated through chemoreceptors on their antennae (Bauer 2011). Similar mechanisms are probably involved in mating behaviour and recognition of conspecifics in other aggregated and schooling species.

The contact recognition described for *Palaemonetes pugio* may be typical of shrimps with the pure-searching mating system (Wickler and Seibt 1981; Bauer 2004, 2011). These species generally live in aggregation with small males and larger females where frequency of contact is high. Females “hide” their reproductive condition as much as possible until after the moult, perhaps to prevent male harassment of females before they are receptive (Bauer and Abdalla 2001). Across caridean shrimps, at least 11 species are known to have pure-searching mating system (Correa and Thiel 2003) where the use of contact pheromones may play a crucial role in mate recognition. Pure search is the only known mating system for penaeoid shrimps (Bauer 1996), a group composed of aggregated or schooling species.

A potential mechanism for contact signal recognition is the ability of lectins to bind to specific carbohydrates on cell surfaces. Most studies on lectins in shrimps have focused on non-self-recognition for immune defense against microorganisms (Marques and Barracco 2000). Interestingly, N-acetyl-glucosamines (and mannose) are also found on the oocyte envelopes of *Rhynchocinetes typus*, which play an important role in spermatozoon recognition prior to the onset of penetration (Dupré et al. 2012). This suggests that similar chemical mechanisms may be employed for different recognition conditions in shrimps. Different sugar specificity and structural diversity have been observed for some species of crustaceans. In copepods, surface glycoproteins that can be targeted by lectins were shown to be important in mate recognition (Lonsdale et al. 1996, 1998). In grass shrimp *Palaemonetes pugio*, gas chromatography-mass spectrometry analysis of extracts from the cuticle also showed that cuticular composition of postmoult parturial females is very different from that of nonparturial females, males, and intermoult females (Caskey et al. 2009). The exact receptor and contact pheromone for social recognition have yet to be identified in caridean shrimps.

Felgenhauer and Abele (1982) suggested that also visual cues are involved in the recognition of mating partners in *Atya innocuous*. Similar observations have been reported by Díaz and Thiel (2004) who showed that in the rock shrimp *Rhynchocinetes typus* males recognize the presence of a reproductive female by visual cues from aggregations of males attempting to mate with the female. Although colouration is seldom sexually dimorphic in shrimps, Knowlton (1980) showed that males of *Alpheus armatus* had more colourful uropod spines (and larger snapping chelae) than females, and the mating system was polygynous. However, the mating system of the related *A. immaculatus*, from a nearby area with higher predation pressure, was more monogamous, and sexual dimorphism in colouration and chela size was absent and slight, respectively. Thus, visual cues in species with sexual differences in colouration may be important in mate recognition and should be investigated further. Visual cues also play a role in mate recognition in the stenopodidean *S. hispidus*, but chemical pheromones are much more important, with the strongest reaction when shrimps perceived both types of cues (visual and contact pheromone) in combination (Johnson 1969). Male *Alpheus heterochaelis* also modulate their behaviours in response to both pheromones and visual (open chela) signals (Hughes 1996a). Overall, visual signals have not received much investigation in caridean shrimps, but such cues may be important since shrimps have well developed compound eyes. However, chemical and contact pheromones may be a more efficient means of communication in complex habitats or for secretive and nocturnal species.

Familiar Recognition: Met Before?

As in other crustaceans, in some shrimp species the probability of meeting repeatedly is high. For example, this could be the case in burrow-living shrimps that defend burrows and forage in the vicinity of their home burrow, or in species that

live in comparatively persistent aggregations, e.g. in crevices or on large hosts. Under these circumstances it may be advantageous for shrimps to recognize individuals they have interacted with before, for example to prevent potential injury by aggressive interactions. While recognition of familiar conspecifics has been described for various decapod crustaceans (e.g. Karavanich and Atema 1998; Gherardi et al. 2012; Tierney et al. 2013), this has not been explicitly tested for shrimps. Given that some shrimp species have evolved mechanisms to distinguish particular classes of individuals (see below) it is not unlikely that they also can recognize conspecifics they have met before.

There are intriguing reports that suggest that familiar recognition may not be uncommon among shrimps. For example, in the pair forming clown shrimp *Hymenocera picta* (Wickler and Seibt 1970), males guard their mates continually by fighting off rival males; observation of their behaviour suggests individual recognition ability (Seibt 1974; Seibt and Wickler 1972). In the cleaner shrimp *Lysmata debelius* from the tropical Pacific, an individual would spend significantly more time near its familiar mate than near a stranger in an experimental chamber (Rufino and Jones 2001).

In the big-clawed snapping shrimp *Alpheus heterochaelis*, an individual can discriminate between its mate and a stranger after separation for 24 h: the interaction with a stranger is more aggressive and less pairing behaviour was observed (Rahman et al. 2001). When pairing did occur between a resident female and a strange male, the latency to pairing was similar to pairing between familiar mates. However, when pairing occurred between a resident male and a strange female, the latency to pairing was much longer. Thus, there is potentially an interaction between sex and familiar recognition. Similar discrimination was also found between familiar and unfamiliar same-sex individuals based on waterborne cues alone (Ward et al. 2004).

Familiar recognition is also found in other decapod shrimps. In the stenopodidean banded shrimp *Stenopus hispidus* from Hawaiian reefs, mating pairs are thought to persist for repeated reproductive events despite frequent short-term separations at night. In encounters staged between previous mating partners, the individuals showed less aggression and courtship interactions than in encounters between heterosexual individuals that had never met before (Johnson 1969, 1977). Individuals can differentiate their mates from strangers, after having being separated for as much as 6 days (Johnson 1977).

Social Recognition

Social Environment

In some species, individuals appear capable of recognizing the social environment, translating this information into behavioural decisions or developmental processes. For example male-phase *Lysmata wurdemanni* delay sex change if they are

maintained with female-phase (simultaneous hermaphrodite) individuals, which offers them ample opportunities to mate with the latter, which can breed both as male and female. Most likely males recognize the social environment via their successful mating investments (Baeza 2007a). The frequent and complex interactions within large groups may represent important stimuli for adaptive sex-change (Baeza and Bauer 2004). In *L. amboinensis*, which breed in pairs of simultaneous hermaphrodite individuals, Wong and Michiels (2011) observed that moulting frequency was higher in these pairs than in groups of 3 or 4 individuals—they suggested that the risk of cannibalism after moulting leads to moult suppression in groups. Moulting is necessary for simultaneous-hermaphrodite individuals to mate and spawn as females. In pairs, the risk of cannibalism is reduced because individuals take turns moulting and reproducing as females, and the individual acting as male does not attack and eat its pair partner.

In *Hymenocera picta* females reached sexual maturity much faster when maintained with males than when kept in isolation, but solitary females reached larger body sizes (Fiedler 2002). In male river shrimp *Macrobrachium rosenbergii*, maturation to the next sexually mature morphotype is accelerated when males of that morphotype are lacking from the social groups (Ra'anana and Cohen 1985). In the snapping shrimp *Alpheus angulatus*, males abandoned recently mated females more often when held in groups with female-biased sex ratio than in groups with equal sex ratio (Mathews 2002).

These reports suggest that shrimps are capable of detecting the size and composition of groups, resulting in group-dependent variations in moulting and development: individuals remain in (or proceed to) the developmental stage that is most favorable in the respective social environment. This is also indirect evidence that these species can recognize conspecifics of certain class in their social environment (e.g. sex and morphotype). The mechanisms of how social cues translate into physiological processes are not well understood.

Class-Level Recognition: Which Gang Do You Belong to?

Recognition of Conspecifics

In many marine systems, closely related species of caridean shrimps live within the same habitats. Consequently, it is important for individuals to discriminate against shrimps from other species. The antennae are commonly employed in recognition of conspecifics, most likely via chemical cues that can be transported with water currents (Herberholz and Schmitz 2001) or via contact chemicals on the body surface of the shrimps (Vickery et al. 2012).

The two peppermint shrimps *Lysmata wurdemanni* and *L. boggei* are closely related, have partially overlapping distributions, but live in different habitats (Rhyne and Lin 2006). Both species are protandric simultaneous hermaphrodites in which juveniles mature as males (male phase) and later become simultaneous

hermaphrodites that resemble and function as females (female phase) but have male function; we will refer to these two phases simply as MP and FP, respectively. Zhang et al. (2009) and Zhu et al. (2012a) found that reproductive isolation of the two species are due to differences in the molecular composition of sex pheromones leading to asymmetric mate recognition. MP *L. boggei* rarely mate with FP *L. wurdemanni* because males cannot recognize the soluble sex pheromones from those FPs. In contrast, MP *L. wurdemanni* can recognize sex pheromones from moulted FP of *L. boggei* and displayed pre-copulatory behaviour, but FP *L. boggei* repelled MP *L. wurdemanni* likely by visual cues. Regardless of these FP behaviours, heterospecific matings between MP *L. wurdemanni* and FP *L. boggei* occurred but only in the dark and not under light. Since moulting and mating of *L. wurdemanni* primarily occurred at night (Bauer and Holt 1998), it is unclear whether the observed asymmetric mate recognition between the two species translates into pre-zygotic isolation.

Eusocial colonies of *Synalpheus regalis* live in canals of marine sponges in the Caribbean, where the same species of sponge may be host to more than one *Synalpheus* species (Macdonald et al. 2006). Colony members reacted differently to conspecific nest-mates and congeners (Duffy 1996; Duffy et al. 2002). Conspecific nest-mates that were isolated overnight were accepted peacefully into the colony with very little aggression. In contrast, congeneric intruders induced elevated aggression and were sometimes killed. Immediately after antennal contact, residents usually snap at the interspecific intruder with its enlarged major chela (first pereopod), suggesting the presence of a contact chemical cue.

Many shrimps live in large, often mixed-species, aggregations or schools (Butler 1980; Bergström 2000). In large-bodied species, this behaviour makes them susceptible to fishing by trawling or other large netting devices, and thus considerable attention has been given to them by fisheries and aquaculture biologists. Although their social behaviour is little known, their mating behaviours have been studied sufficiently so that their mating system can be identified as “pure search” (Wickler and Seibt 1981; Bauer 1996, 2004). In this mating system, typical of species with small males and larger females, males are able to make frequent contact with females because of the aggregated or schooling behaviour of the species. Such aggregations are mobile and thus males have little opportunity to defend or guard a female. Recognition of conspecifics must be important to the maintenance of these large mixed-species schools so that the aggregation does not scatter below a critical density. Both contact and distance chemoreception may be involved in both remaining near conspecifics as well as recognition of an appropriate mating partner. Little work has been done in this area but should be a fruitful topic of future research.

Recognition of Potential Mates and Their Reproductive Status

In caridean shrimps, the female receptive period is always confined to a short period after moulting. Therefore, the selective pressure for males to detect a female when she is approaching a moult and receptivity to mating is high. Accordingly, many

cases of recognition of potential mates and their reproductive status are documented in caridean shrimps, making use of chemical, contact and visual signals Table 5.1. Potential candidates of distance and contact pheromones have been identified in *Lysmata wurdemanni* and in *Palaemonetes pugio*, respectively (section “Mechanisms of Recognition”).

Male and female *Hymenocera picta* were capable of distinguishing between non-moulting male and female conspecifics but only if they could touch them with their antennules (Seibt 1974). Males used distance pheromones to recognize recently moulted females (Seibt 1973, 1974). Small amounts of water conditioned by a moulted female seem sufficient to attract males from different parts of a large (0.7 m²) holding tank (Seibt 1974). In experimentally formed pairs of *H. picta*, the physical distances between individuals decreased in heterosexual pairs as soon as both partners had attained sexual maturity, but the members of homosexual pairs maintained substantial distance to each other throughout the experiment (Fig. 5.3) (Fiedler 2002). Similarly in the freshwater shrimp *Atya innocuous*, the moulted females are recognized by males that are a few cm away from them (Felgenhauer and Abele 1982). In *Palaemon paucidens*, searching behaviour of males was only initiated when a postmoulted parturial female (with mature ovaries) or water conditioned by her was present (Kamiguchi 1972). In the latter case, some males would even attempt to copulate with a postmoult female without mature ovaries.

In the snapping shrimp *Alpheus angulatus* males can discriminate pre-moult and post-moult females based on at least waterborne chemicals. Using a y-maze apparatus (Fig. 5.4), Mathews (2003) exposed males to untreated water (control) against water coming from a tank holding a male or female shrimp that were either (i) pre-moult (<3 days from moulting), (ii) inter-moult (7 days after moulting or >3 days from moulting), or (iii) post-moult (<24 h after moulting). The differences in time spent in the treatment arm versus the control arm of the y-maze showed that males were only attracted to water coming from pre-moult females, but rejected water conditioned by inter-moult females and males (Table 5.2). Mate choice experiments further confirmed male preference for pre-moult females rather than post-moult females (Mathews 2003). Thus, males use waterborne chemicals to recognize females of different reproductive status and choose ones that offer higher reproductive return.

In another snapping shrimp species, *A. heterochaelis*, Hughes (1996b) found that individuals of both sexes do not differentiate chemical signals from either sex. However, chemical signals appear to modulate an individual's response to an open chela, an aggressive display of snapping shrimps. Without chemical signals, males responded to an opened chela as a function of the presented chela size aggressively by opening their chelae (Hughes 1996a). In comparison, males responded less aggressively to an open chela with female chemical signals, but more aggressively with male signals (Hughes 1996b). When exposed to male chemical signals, males responded equally aggressively to an open chela regardless of the presented chela size; but males reduced aggressiveness to smaller chelae when female signals or no signals were present. Females responded equally to open or closed chelae and were not affected by chemical signals. Therefore, male *A. heterochaelis* can

Table 5.1 Current knowledge of social recognition in Caridean shrimps and other decapod shrimps (*)

Family	Species	Comments	Social organization	Duration (h)	Mechanism	References
<i>Class level recognition</i>						
Alpheidae	<i>Alpheus angulatus</i>	Males discriminate pre-moult and post-moult females	Heterosexual pair	NA	Olfactory pheromones	Mathews (2003)
	<i>Alpheus edwardsii</i>	Ablation of the antennular flagella reduced pairing	Heterosexual pair	NA	NA	Jeng (1994)
	<i>Alpheus heterochaelis</i>	Sex-specific chemical signals modulate an individual's response to an open chela	Heterosexual pair	NA	Olfactory pheromones and visual cues	Hughes (1996a)
		Females prefer larger or same-sized males than smaller males				
		Shrimp recognize the dominance status of an opponent				
<i>Synalpheus regalis</i>	Colony member discriminate between nest-mate and foreign conspecific (could be interpreted as familiar recognition)	Eusocial	~10	Olfactory and contact pheromones	Duffy (1996), Duffy et al. (2002)	
	Intruder discriminate between queen and other colony member					
Atyidae	<i>Atya innocous</i>	Males recognize recently moulted, reproductive females	NA	NA	Olfactory pheromones and possibly visual cues	Duffy et al. (2002) Feigenhauer and Abele (1982)

(continued)

Table 5.1 (continued)

Family	Species	Comments	Social organization	Duration (h)	Mechanism	References
Hymenoceridae	<i>Hymenocera picta</i>	Males recognize recently moulted females	Heterosexual pair	NA	Olfactory pheromones	Seibt (1973, 1974), Seibt and Wickler (1979)
		Males continually fight off rival males		NA		
Hippolytidae	<i>Lysmata pederseni</i>	Female-phase (FP) discriminate against male-phase (MP) individuals	Heterosexual pair	NA	Distance and contact pheromones	Baeza (2010)
		MP recognize recently moulted FP		NA		
Palaemonidae	<i>Lysmata wurdemanni</i>	FP preferentially mated with small rather than large mating partners	Aggregation	NA	NA	Baeza (2007b)
		Female actively seek dominant males but avoid intermediate and small males		NA		
Palaemonidae	<i>Macrobrachium rosenbergi</i>	Shrimps recognize the ranking of a conspecific	Aggregation	NA	NA	Barki et al. (1991)
		Water conditioned by receptive females induced male searching		30		
	<i>Palaemonetes pugio</i>	Males discriminate between reproductive and non-reproductive females	Aggregation	NA	Contact pheromones	Bauer and Abdalla (2001), Caskey et al. (2009)

(continued)

Table 5.1 (continued)

Family	Species	Comments	Social organization	Duration (h)	Mechanism	References
Rhynchocinetidae	<i>Rhynchocinetes typus</i>	Female prefer dominant male	Aggregation	NA	Olfactory pheromones	Diaz and Thiel (2004)
<i>Familial recognition</i>						
Alpheidae	<i>Alpheus heterochaelis</i>	Pair of mates and strangers behave differently	Heterosexual pair	24	NA	Rahman et al. (2001)
		Shrimp responded to reversed orientation of chemical cues from two familiar individuals (could be interpreted as true individual recognition)		0.05	Chemical cues	Ward et al. (2004)
	<i>Synalpheus regalis</i>	Colony member discriminate between nest-mate and foreign conspecific (could be interpreted as kin recognition)	Eusocial	~10	Olfactory and contact cues	Duffy (1996), Duffy et al. (2002)
Hymenoceridae	<i>Hymenocera picta</i>	Males continually fight off rival males		NA	NA	Wickler and Seibt (1970)
Hippolytidae	<i>Lysmata debelius</i>	Shrimp spend more time near its familiar mate than stranger	Heterosexual pair	NA	NA	Rufino and Jones (2001)
Stenopodidae*	<i>Stenopodus hispidus</i>	Pair of mates and strangers behave differently	Heterosexual pair	140	NA	Johnson (1977)
<i>True individual recognition</i>						
Alpheidae	<i>Alpheus heterochaelis</i>	Shrimp responded to reversed orientation of chemical cues from two familiar individuals (could be interpreted as familiar recognition)		0.05	Olfactory pheromones	Ward et al. (2004)

(continued)

Table 5.1 (continued)

Family	Species	Comments	Social organization	Duration (h)	Mechanism	References
Hymenoceridae	<i>Hymenocera picta</i>	Individual (heterosexual) partners recognize each other		NA	Olfactory pheromones	Seibt and Wickler (1972)
Hippolytidae	<i>Lysmata debelius</i>	Shrimp spend more time near its familiar mate than stranger	Heterosexual pair	NA	NA	Rufino and Jones (2001)
Stenopodidae*	<i>Stenopodus hispidus</i>	Pair of mates and strangers behave differently	Heterosexual pair	140	Unknown	Johnson (1977)

Durations are maximum times reported for the recognition; longer duration may not have been tested

Fig. 5.3 Intrapair distance (IPD) for three pair types of naive juveniles throughout a year of lab observation. Arrows indicate the onset of maturity (appearance of secondary sex characters). IPD decreased in heterosexual pairs after female sexual maturity, but remained high in homosexual pairs. Adapted from Fiedler (2002)

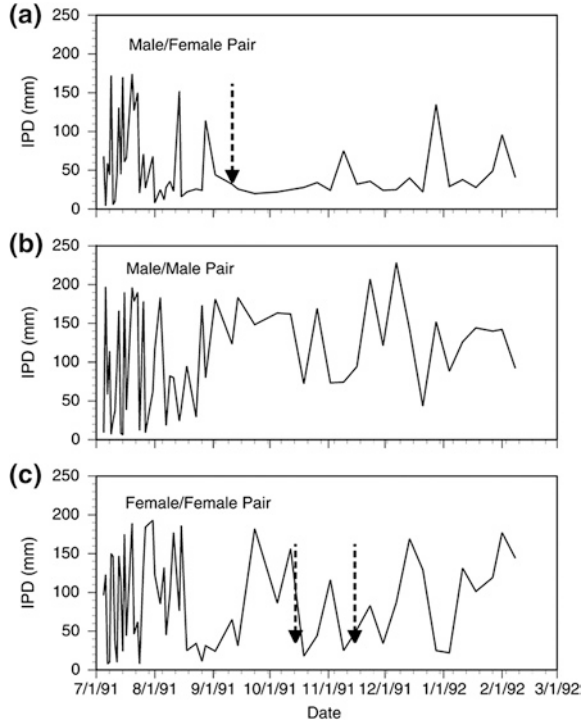
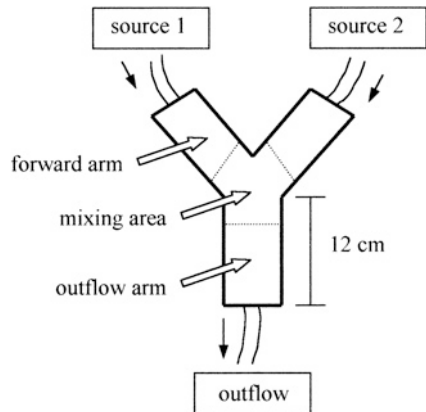


Fig. 5.4 A Y-maze apparatus to test for olfactory sex pheromones in *Alpheus angulatus*. Solid arrows indicate direction of water and pheromone flow. Times spent in the two forward arms were compared for significant differences. Adapted from Mathews (2003)



likely discriminate the sex of an individual by chemical signals, and modulate their responses according to the size of the opponent using visual cues.

In the eusocial snapping *Synalpheus regalis*, conspecific non-nest mate intruders contacted the queen (the only breeding female in the colony) more frequently than other colony members (a mix of non-reproductive females, males, and juveniles) in

Table 5.2 Testing for differences in time spent in the treatment arm (Source 1) against the control (Source 2)

Trial	Source 1	Source 2	<i>n</i>	Response	<i>p</i>
1	Intermolt female	Untreated	31	Negative	0.0052
2	Molted female	Untreated	30	–	0.4363
3	Premolt female	Untreated	32	Positive	0.0228
4	Intermolt male	Untreated	31	Negative	0.0002
5	Molted male	Untreated	28	–	0.1952
6	Premolt female	Untreated	29	–	0.3823
7	Untreated	Untreated	30	–	0.3210

Results show that *Alpheus angulatus* males can discriminate pre-moult females based on water-borne chemicals. Adapted from Mathews (2003)

lab experiments (Duffy et al. 2002). This also suggests that the reproductive female may produce pheromones that are detected by conspecifics.

Recognition of Size and Rank of Conspecifics

In many shrimp species there is substantial intrasexual variability in size and/or morphology. This opens the possibility that mates might choose among the individuals from the opposite sex. Moreover, when size or other phenotypic traits are correlated with fighting ability, rank-recognition may evolve (Gherardi et al. 2012). Potential physical cues include chela size in snapping shrimp (Hughes 1996b), chela colour and size differences between ontogenetic classes of *Macrobrachium rosenbergi* (Ra'anana and Cohen 1985), and strongly developed third maxillipeds and first chelae in dominant, male *Rhynchocinetes typus* (Correa et al. 2000).

Intersexual size-recognition has been observed in a few species. FP *Lysmata wurdemanni* preferentially mated with small rather than large mating partners (Baeza 2007b), but which stimuli they used to distinguish between mates (visual or chemical) is not known. Also, in *L. pedersoni*, large FP expelled small MP individuals from hosts, most likely because MP offered no return of female function (Baeza 2010). Small MPs were repeatedly struck with the third maxillipeds and/or the chelipeds.

In the big-clawed snapping shrimp *Alpheus heterochaelis*, which typically live in size-matched mating pairs, females would approach larger or same-sized males more often than smaller males and show more aggression (snapping) towards mates that are not size-matched (Rahman et al. 2002, 2004). This indicates that females recognize the sizes of a potential mate; such recognition is not observed in males. However, Obermeier and Schmitz (2003a) showed that both males and females may recognize the dominance status of an opponent. They exposed a loser in a first fight to (1) the winner of the first fight, (2) an unfamiliar winner, and (3) an inexperienced opponent for three consecutive trials. They found that losers showed immediate escape and less aggressive behaviour when encountering familiar and unfamiliar winners, but were more aggressive against an inexperienced opponent. At least for

the first trial, this submissive behaviour can be explained by the recognition of a winner's dominant signals. In subsequent trials, the aggressiveness of the loser against an inexperienced opponent gradually decreased after consecutive losses, which suggests a reduction of fighting motivation. Obermeier and Schmitz (2003b) performed a further treatment using a loser with ablated lateral antennular filaments against a familiar winner. Operated losers did not escape and showed the same aggressiveness as in their first fights (Fig. 5.5). This shows that without olfactory reception, an individual cannot recognize the pheromones from a dominant winner, even with intact antennae to detect potential contact chemical pheromones. Further examination confirmed that unimodal chemoreceptors (aesthetascs) are unique to the lateral antennular filaments (Obermeier and Schmitz 2004).

Males of *Macrobrachium rosenbergi* have three ontogenetic stages with different mating strategies: blue claw (dominant), orange claw (intermediate), and small (sneaker) males (Ra'anana and Cohen 1985). After establishment of hierarchy between males of different ranks, aggressive acts decreased and submissive

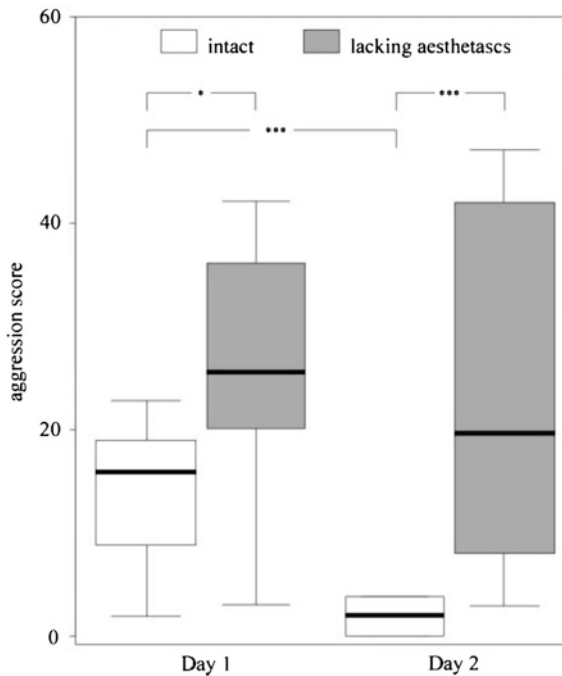
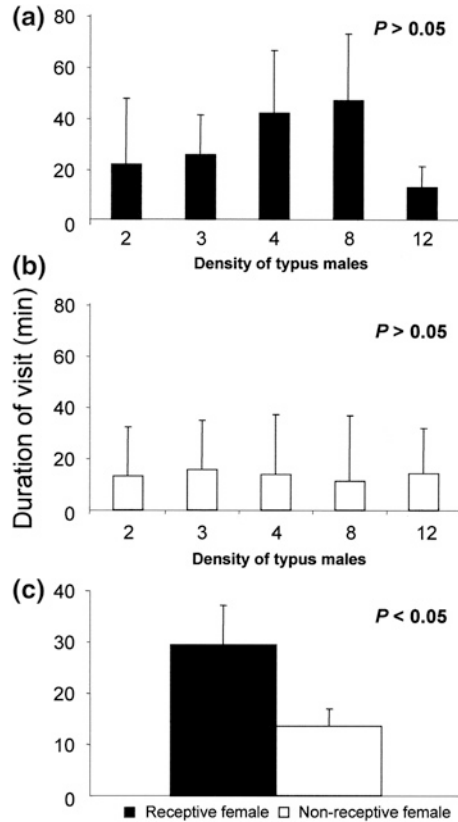


Fig. 5.5 Aggression scores of intact (aesthetascs present) and operated (aesthetascs ablated) *Alpheus heterochaelis* against a dominant opponent consecutively in two days. Intact shrimps recognized the dominant opponent in the encounter in the first day and reduced aggressiveness in the second encounter. However, shrimps with ablated aesthetascs did not recognize the dominant opponent and remain equally aggressive in the two encounters. Aggression scores were an estimate of fighting motivation involving the number of contact, snap, and fast anterior gill currents. Adapted from Obermeier and Schmitz (2003b)

Fig. 5.6 Total visit duration of robustus males *Rhynchocinetes typus* to the **a** receptive female and **b** nonreceptive female in respective treatments (no significant differences between treatments). **c** Total visit duration of robustus males to the respective females after pooling among all treatments (significant differences between visits to respective females). Bars and error bars are mean and standard deviation. Adapted from Díaz and Thiel (2004)



acts increased between group members (Barki et al. 1991). This suggests that an individual may recognize the ranking of a conspecific and modify its behaviour to reduce possible injury.

An important form of mate recognition occurs in species with a “neighborhoods of dominance” mating system (Correa and Thiel 2003) in which the females approach the males which emit a pheromone (Bauer 2004). In *Macrobrachium australiense* and *M. rosenbergi*, when females are near the moult, they seek out the dominant male who would guard an approaching female until she moulted and mating occurred (Lee and Fielder 1982; Ra’anan and Sagi 1985). Similarly, in rock shrimp *Rhynchocinetes typus*, females select dominant males using chemical but not visual cues, despite the fact that dominant males (called robustus) are larger than and morphologically different from subordinate (typus) males. In contrast, robustus males do not locate a receptive female via chemical signals, but likely become aware of receptive females by visual cues created by agitated aggregations of small typus males around the receptive females (Díaz and Thiel 2004) (Fig. 5.6).

Recognition of Kin

In a broad sense, kin recognition describes the discrimination between kin and non-kin, irrespective of mechanisms or functions (Penn and Frommen 2010). In the eusocial snapping shrimp *Synalpheus regalis*, resident colony members responded to foreign conspecifics with more aggression and less contacts than to nest-mate conspecifics (Duffy et al. 2002). In cases where an intruder ignored repeated snaps by multiple residents, escalated responses of coordinated snapping were carried out by at least 60 % of the colony (Tóth and Duffy 2005). Nest-mates are likely full-siblings and juveniles usually remain within the natal colony (Duffy 1996). Therefore, colony members may be distinguishing between kin and non-kin and this can be viewed as kin recognition in a broad sense. Alternatively, this could merely be a case of familiar recognition, if foreign conspecifics are distinguished from nest-mates by cues that are independent of relatedness, such as, for example, the scent associated with the host sponge's secondary metabolites or microbial composition. It is also possible that kin recognition has evolved in other shrimps with direct development in which females cohabit for extended time periods with their offspring (e.g. Huguet et al. 2011; Guay et al. 2011), but to our knowledge this has not been studied.

True Individual Recognition: Are You Special?

Tibbetts and Dale (2007) defined true individual recognition as recognition in which all processes involved (cues, internal recognition template, and response) are individual specific, even when a receiver learned the unique cues of one individuals and subsequently treat that individual differently from others (Tibbetts et al. 2008). There have been arguments that this definition is too restrictive (Steiger and Müller 2008) or that it is operationally difficult to understand for invertebrates (Gherardi et al. 2012). Despite the different opinions, these authors all agreed that monogamous mate recognition can be considered true individual recognition.

Some shrimp species seem to have monogamous mate recognition that fits the individual recognition criteria. These species live together in persistent heterosexual pairs, and mating partners can recognize each other even when the females are not sexually receptive. This has been experimentally confirmed for the clown shrimp *Hymenocera picta* (Seibt 1973, 1974; Seibt and Wickler 1979), the cleaner shrimp *Lysemata debelius* (Rufino and Jones 2001) and the banded shrimp *Stenopus hispidus* (Johnson 1977) (Fig. 5.7). Moreover, pairs of the clown shrimp recognized each other and within a group of >10 individuals, males rapidly identify "their" females and quickly associate with them (Seibt and Wickler 1972). Members of a pair occasionally share food, but only after the individual that secured the food had been satiated (Seibt and Wickler 1979).

A property of true individual recognition defined by Gherardi et al. (2012) is that a receiver would behave differently to two or more individuals belonging to

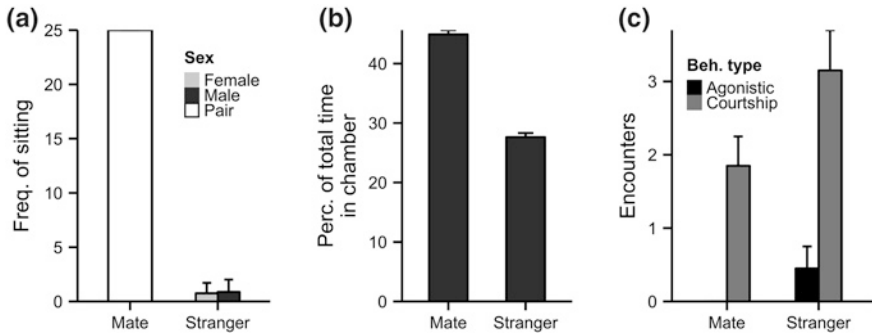


Fig. 5.7 Discrimination between mate and strangers in three monogamous decapod shrimps. **a** *Hymenocera picta*. Frequency of sitting with its mate or strangers in a mating pair of male and female (modified from Seibt 1974). Interactions with strangers is averaged from 8 individuals that were present in the same experimental tank and in which interactions were recorded separately for the male and female in the focal mating pair. **b** *Lysmata debelius*. Percentage of total time spent in each chamber where a mate or a stranger is present (modified from Rufino and Jones 2001). In a setup similar to a Y-maze, the test animals were allowed to choose from two chambers, each holding a mate or a stranger behind a filter, where chemical exchange and contact were allowed. **c** *Stenopus hispidus*. Frequencies of agonistic or courtship encounters between heterosexual mates and strangers within the first 5 min of contact after shrimps had been separated for two nights (modified from Johnson 1977). Note that courtship behaviour increased in encounters between strangers because it is used to establish new heterosexual pairing; this behaviour is generally lower between established pairs

the same familiar group. Ward et al. (2004) showed this in *Alpheus heterochaelis* by familiarizing a focal animal with the chemical cues of two size-matched, same-sex conspecifics for 3 h on two sides of a testing tank. Then they removed the sources of chemical cues and either repositioned them in the same (control) or opposite direction as before (treatment) for 30 min, followed by a final reposition of the cues for 30 min. Behaviours of the focal animal were compared between the first and last 30 min of the familiarization period, the control, and treatment periods. Antennal contact, leg poke and pull occurred more frequently in the experimental treatment than in the control, but did not differ between the two familiarization periods. The results show that the focal animal discriminated between two familiar chemical cues, thus being suggestive of true individual recognition.

Interspecific Associations and Communication

A number of snapping shrimps cohabit with other organisms. Many of these species commonly interact with their co-habitants, and sophisticated interspecific communication systems have been reported. For example, in the mutualistic, co-evolved partnership between gobies and alpheid shrimps, the shrimp maintains a

continuous antennal contact with its goby partner; through tactile communication the goby notifies the shrimp of any danger with different behaviours modulated to the kind of threat, location and responses of the shrimp (Karplus and Thompson 2011). Shrimps are attracted to their associated goby species by waterborne chemical cues but not visual cues (Karplus 1981). Chemical cues are also found in symbiotic associations between some shrimp species and anemones (Guo et al. 1996), for example the ectosymbiotic association between a snapping shrimp and a feather star (VandenSpiegel et al. 1998).

A special case is the heterospecific association between two different species of alpheid shrimps, *Alpheus inca* and *Alpheopsis chilensis* (Boltaña and Thiel 2001). Heterosexual pairs of these two species cohabit in stable burrows in deeper layers of intertidal cobble beaches. Males and females of each species live in size-assorted pairs, and furthermore within quartets there is a positive relationship between the mean body size of *A. inca* pairs and that of *A. chilensis* pairs. Interestingly, even the reproductive status of the two heterospecific females within a quartet seems to be synchronized. These observations are suggestive of heterospecific communication but no details of the heterospecific behaviours and recognition between these two shrimp species are available (Boltaña and Thiel 2001).

In most cases, the heterospecific partners appear to live together without major agonistic interactions. However, in the association between the snapping shrimp *Betaeus lilianae* and the crab *Platyxanthus crenulatus*, and between *Alpheus salmoneus* and a *Trapezius* crab, aggressive behaviours by the crab towards the shrimp have been observed (Baeza et al. 2010; Vannini 1985). Interestingly, *A. salmoneus* has evolved to use submissive behaviour in shrimp–crab interaction to alleviate the crab's aggressive behaviour, so that it can share the habitat with the crab.

Conclusion and Outlook

Caridean shrimps are diverse in their ecology, mating and social behaviour, so it is not surprising that all types of social recognition are observed in this group. Among the various forms of recognition in caridean shrimps, mate recognition is best documented, in which potential distance and contact pheromones have been strongly suggested by behavioural studies in several species and even tentatively identified in a few species. With the previous work on these candidate pheromones and the documentation of social recognition in many species, similar pheromones could be more easily identified in other shrimp species. This would further advance the study of communication and social recognition in this group.

Snapping shrimps (Alpheidae) appear to have great potential for future research on social recognition. All three types of social recognition (familiar, class-level, and true individual recognitions) have been demonstrated in snapping shrimps (*Alpheus* and *Synalpheus*). In particular, *Synalpheus* is the only group among crustaceans in which eusociality has evolved, a social system in which terrestrial eusocial counterparts usually have complex modes of communication (Costa and Fitzgerald 1996).

Living in a group of close kin, in which individuals may perform different tasks (e.g. defense) and aggressiveness within the colony is rare and evolutionarily non-adaptive, might be a precursor to true individual recognition in eusocial *Synalpheus* species. Moreover, this group is ideal for comparative analysis since eusociality has evolved independently at least three times, and other species of *Synalpheus* express varying degrees of sociality ranging from pair-cohabitation (like many other alpheidids) to communal living (Duffy et al. 2000). However, no formal experiment with any form of recognition has been performed in this genus and indications of mate recognition and kin recognition were only suggested from indirect evidence. Apart from eusocial species, many *Synalpheus* species live in multiple heterosexual pairs within the same sponge (communal species), in which the chance of encountering other conspecifics is expected to be high. This social system is intermediate between the typical pair-forming alpheidids and the aggregation-forming species. No studies have yet explored the recognition system in species in relation to varying social structures in shrimps, and the genus *Synalpheus* could be an ideal model system to study the evolution of recognition in shrimps.

Among decapod shrimps, all *Exhippolysmata* and *Lysmata* species examined, and one species of *Parhippolyte*, have been shown to be protandric simultaneous hermaphrodites, in which shrimps are initially males and later turn into functional simultaneous hermaphrodites (Baeza et al. 2009; Braga et al. 2009; Onaga et al. 2012). Protandrous sequential hermaphroditism has been found in a number of caridean species (Bauer 2000; Chiba 2007), e.g. *Rhynchocinetes uritai* (Bauer and Thiel 2011). Simultaneous hermaphroditism and protandry in shrimps present a unique opportunity to investigate the ontogenetic development of sensory systems pertaining to mate recognition. Since females and males have different needs in terms of mate recognition or attraction, how do such systems co-exist in the same individual?

In conclusion, we have a basic understanding of social recognition in caridean and stenopodidean shrimps, but much remains to be learned. The diverse ecology, mating, sexual, and social systems of this group offer unique opportunities for studying the mechanisms and evolution of animal communication.

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