

Chemical Communication in Crustaceans

Thomas Breithaupt • Martin Thiel
Editors

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With drawings by Jorge Andrés Varela Ramos

 Springer

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To our families and friends.

Preface

Animal communication has fascinated biologists for centuries. This fascination has sustained many a scientific career as will be evident from the personal accounts by the contributors to this book. Chemical signaling is the most widespread form of communication in crustaceans. During the past two decades, there have been significant advances in our understanding of crustacean chemical ecology. Gathering this information in an edited volume was the next logical step.

This book covers a wide range of topics, including the identity, production, transmission, reception, and behavioral function of chemical signals in selected crustacean groups. The chapters are organized into five sections. The introductory section gives a brief overview of the main questions that are tackled in this volume and provides important definitions of signals, cues, and behavior. The next section on the transmission of chemical cues in the environment and on sensory biology is followed by a section on the behavioral contexts in which crustaceans use chemical communication, providing examples from the best studied taxa. Recent advances in the molecular identification of chemical signals are presented in the fourth section. The fifth and last section deals with the possible applications of pheromone research to aquaculture and pest management.

One of our goals as editors was to encourage contributors to identify similarities and differences in chemical communication by crustaceans and by other taxa and thereby address questions of general interest. We therefore invited experts on communication in insects, spiders, and fishes to contribute to this book. They readily and, at first perhaps, innocently accepted our invitation, unaware that we would ask them to integrate knowledge of crustaceans into their chapters. Thus, their tasks went beyond a synthesis of their own work and expertise and we feel that they all have done a marvelous job. We learned a lot from them and we now share some of their fascination for their favorite organisms and the excitement that comes from studying them. Within the same spirit, we hope that this book will attract readers who are interested in learning about crustaceans, but who study other taxa in their quest to understand the evolution and function of chemical communication.

There are several topics that we thought were ready for thorough review such as multimodal communication, deception, and pheromones in aquaculture and pest

management, but are still beyond the mainstream of crustacean research. Several of our colleagues had some experience in these areas, and they were thus “naturals” to be invited for these contributions. Though reluctant at first, they accepted the challenge and their enthusiasm grew as they wrote.

In order to make this volume accessible to a broad audience that spans scientific and applied fields, we asked the authors to include a personal statement briefly describing why they entered their respective research fields. Such statements are not generally accepted in scientific writing. But we are most grateful that many of our authors adopted a more informal style and expressed their enthusiasm for their particular study species or research questions. We hope that our authors’ enthusiasm is sufficiently infectious and that the scientific questions they raise in their contributions will stimulate future research. If only a few young scholars are infected by this excitement for crustacean chemical communication, this book has achieved its goal.

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We thank our teachers, collaborators, and students who have helped shape our understanding of crustacean communication during the past two decades. The contributors to this book deserve most of our gratitude – all this would not have been possible without their expertise and efforts. A very special thanks goes to the more than 80 reviewers for their time and suggestions, which were very helpful to us and the authors – we could not have done without their critical and constructive input. Iván A. Hinojosa provided expert help in the preparation of many of the figures in this book. Jorge A. Varela Ramos made many of the chemical interactions visible with his artistic drawings. TB would like to thank his wife Gabi and son Tobias for their endless patience during the many evenings and weekends when husband/daddy had to work on “the book” and was not available for family activities. MT thanks Taizhu for her continuous support and patience. His participation in this project would not have been possible without the unconditional support from Universidad Católica del Norte (UCN). Many of the chapters in this book were edited during a sabbatical stay at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland. MT wishes to thank A.H. Hines for supporting his stay at SERC.

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Part I
Introductory Section

Chapter 1

Chemical Communication in Crustaceans: Research Challenges for the Twenty-First Century

Martin Thiel and Thomas Breithaupt

Abstract Chemical signals play an important role during various life stages of crustaceans. Settling of larvae, parent–offspring communication, mate finding, mate choice, aggressive contests, and dominance hierarchies are all mediated by chemical signals. Enormous advances have been made on understanding the function of chemical signals in crustaceans and we are on the doorstep of major advances in chemical characterization of pheromones. In many species urine is the carrier of chemical signals. Crustaceans control release and transfer direction of urine, but it is unknown whether crustacean senders can manipulate the composition of urineborne pheromones. Chemicals contained in the urine effectively convey information about conspecific properties such as sex, sexual receptivity, species identity, health status, motivation to fight, dominance, individual identity, and molt stage. In larger species (shrimp, crabs, lobsters, crayfish) signal delivery is often aided by self-generated fanning currents that flush chemicals towards receivers, which themselves might actively pull water towards their sensory structures. Antennal flicking also supports molecule exchange at the receptor level. Contact pheromones play a role in sex recognition in several crustacean taxa and in settlement of barnacles. Large crustacean species show little or no sexual dimorphism in receptor structures, but in smaller taxa, e.g. peracarids and copepods, males often have larger antennae than females. Whether differences in sexual roles have also resulted in sex-specific brain centers is not known at present. While pheromones play an important role in mate finding and species recognition, there are numerous examples from peracarids and copepods where males pursue or even form precopulatory pairs with females of closely related congeners. Differentiation of chemicals often appears to be insufficient to guarantee reproductive isolation. In many freshwater and coastal habitats, pollutants may also disrupt chemical communication in crustaceans, but the specific mechanisms of interference are not well understood. The chemical characterization of crustacean pheromones is viewed as a major step in improving our understanding of chemical communication.

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Knowing the chemical nature of pheromones in freshwater species will boost research on aquatic crustaceans. Interdisciplinary work between chemists (metabolomics), behavioral ecologists (bioassays), neurobiologists (chemoreception), and molecular biologists (genomics) promises to produce significant advances in our understanding of crustacean chemical communication during the coming decade.

He drew up plans, made lists, experimented with smells, traced diagrams, built structures out of wood, canvas, cardboard, and plastic. There were so many calculations to be made, so many tests to be run, so many daunting questions to be answered. What was the ideal sequence of smells? How long should a symphony last, and how many smells should it contain? What was the proper shape of the symphony hall? . . . Should each symphony revolve around a single subject – food, for example, or female scents – or should various elements be mixed together? ...What difference did it make if he didn't fully understand? . . . It might not have served any purpose, but the truth was that it was fun.

From *Timbuktu* by Paul Auster (1999)

1.1 Introduction

Crustaceans are found in all major environments in the oceans and on land. Given the diversity of habitats, they face numerous challenges in communicating with conspecifics. How does a female crab that is ready to reproduce find a male in the murky waters of a shallow estuary? She could roam in search of a male or she could stay put and wait for a male to find her. In both cases, her success in finding a mating partner would be enhanced by a chemical guidance system. If she searches for a male, it would be advantageous to sniff out the environment for chemical cues that would indicate the presence of a male. And if she waits for a male to find her, she could guide him towards her by releasing attractive chemicals. Regardless of the strategy, chemical stimuli enhance the probability of mate finding which is only one of many benefits offered by chemical communication.

Chemical signals play an important role during various life stages of crustaceans. Settling of larvae, parent–offspring communication, mate finding, mate choice, and aggressive contests are all mediated by chemical signals. Chemicals are ubiquitous messengers because they can effectively convey information about conspecific properties such as sex, sexual receptivity, species identity, health status, motivation to fight, dominance, individual identity, and molt stage. Not surprisingly, many crustaceans employ chemical communication to coordinate important life processes. At first glance, crustaceans do not seem to differ from many other animals such as insects or mammals in which chemical communication plays an important role. However, crustaceans have conquered a wider range of habitats than most other animals, inhabiting the deep abyss of the oceans, wave-battered shores, calm freshwater lakes, dark forests, and even dry deserts. Furthermore, the range of crustacean body sizes and shapes is unparalleled in many other animal taxa. And finally, the diversity of crustacean life styles is mind boggling even to well-seasoned crustacean researchers; tiny planktonic species share a common

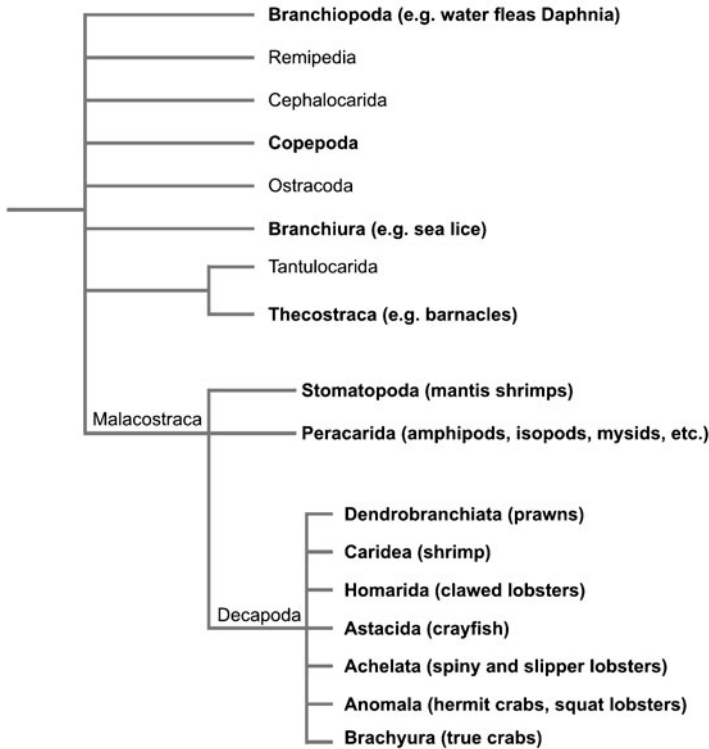


Fig. 1.1 Phylogeny of crustaceans, highlighting in bold the taxa that have been subject to research on chemical communication. Only those subtaxa of Malacostraca and Decapoda are shown that have been subject to chemical communication research. Phylogeny was modified after Tree of life (<http://tolweb.org/Crustacea>), and Dixon et al. (2003)

history with bulky crabs, colorful shrimp, and strange parasitic forms that can only be recognized as crustaceans during their larval stages.

Many of these species, regardless of habitat or morphology, communicate with their conspecifics via chemical substances. The crustacean species that have been subject to chemical communication research were drawn from six of the 12 classes of crustacea including Branchiopoda (water fleas), Copepoda, Branchiura (including fish lice), Thecostraca (including barnacles), and Malacostraca (the largest class including stomatopods, peracarids, and decapods) (Fig. 1.1). By far the greatest contribution to our understanding of chemical communication comes from research on decapod crustaceans including crabs, lobsters, and shrimps.

Many species from these groups employ chemical signals throughout or during parts of their lives. How do they do it and how have their phylogenetic histories and current environmental conditions shaped their communication systems? The contributions in this book offer answers to these questions and they also highlight fascinating challenges for the future.

1.2 Chemical Communication in Crustaceans – A Brief Literature Survey

1.2.1 Pheromone Signaling in Marine Invertebrates

In crustaceans, communication is mainly through the visual, chemical, and mechanical channels (see e.g., Mead and Caldwell, Chap. 11; Christy and Rittschof, Chap. 16; Clayton 2008). Whereas visual communication is mainly limited to species from terrestrial and clear-water environments, chemical communication can occur under most environmental conditions. Not surprisingly, studies on chemical communication dominate the literature. Of a total of 76 publications on crustacean communication (with the keywords *communicat** and *crustacea**) published between 1990 and 2010, 43 were on chemical communication, 24 on visual communication, and only 9 on mechanical/acoustic communication (Web of Science 2010).

Chemical communication may be prominent not only because it works under almost any environmental condition, but also because it may be subject to rapid evolutionary change (Symonds and Elgar 2008), possibly much more so than visual or mechanical communication, as was recently highlighted by Bargmann (2006): “The visual system and auditory system are stable because light and sound are immutable physical entities. By contrast, the olfactory system, like the immune system, tracks a moving world of cues generated by other organisms, and must constantly generate, test and discard receptor genes and coding strategies over evolutionary time.” The high potential for specificity has been one of the main reasons that many species communicate via chemical signals. These are often employed to attract conspecifics or to convey particular messages.

The first unequivocal demonstration of pheromone use by a crustacean was presented by Ryan (1966) who showed that male Pacific crabs *Portunus sanguinolentus* display a typical courtship response when stimulated with female premolt water. Males did not display when the female’s excretory pores were sealed. This paper was followed by several other studies confirming that crustaceans employ pheromones during mating interactions (e.g., Dahl et al. 1970, for amphipods; Atema and Engstrom 1971, for lobsters; Ameyaw-Akumfi and Hazlett 1975, for crayfish). Surprisingly, the first marine invertebrate for which the sex pheromone was chemically identified was the polychaete *Platynereis dumerilii* from the North Atlantic (Zeeck et al. 1988). Since then the chemical structure of pheromones has also been characterized for molluscs (Painter et al. 1998). Only during the past decade pheromones have been purified in several crustacean species (Kamio and Derby, Chap. 20; Hardege and Terschak, Chap. 19; Clare, Chap. 22; Rittschof and Cohen 2004).

Despite these advances, our knowledge about pheromone structure, production, and effects in marine invertebrates is scarce. A Boolean literature search from the past 20 years (1990–2009) showed that most pheromone studies with marine invertebrates have investigated crustaceans, polychaetes, and molluscs (Fig. 1.2). Especially during

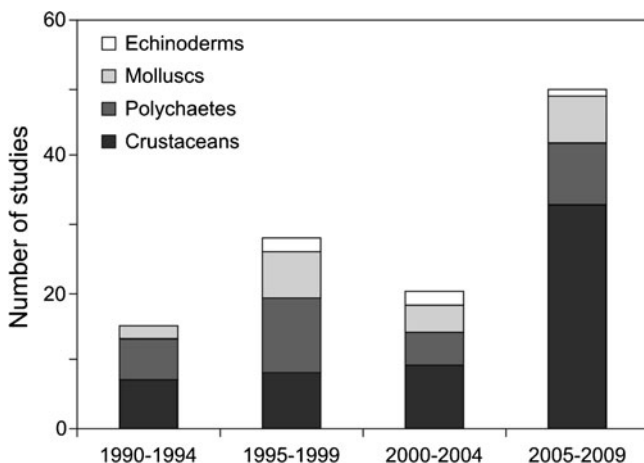


Fig. 1.2 Number of studies in pheromones in marine invertebrates during the period 1990 and 2009. Results based on Web of Science, Boolean search for pheromon* AND taxon*; freshwater and terrestrial taxa excluded

the pentad 2005–2009, there has been an increasing number of studies on crustacean pheromones, which most likely has been fostered by the beginning of the chemical characterization of pheromones in several species. Given recent advances in this field, it can be expected that this trend will continue in the future.

1.2.2 Crustaceans, Fish and Insects

Since most research on pheromones has been conducted in other taxa (e.g. insects, fish, and mammals), it is not surprising that crustacean researchers studying pheromones rely on this rich literature. Interestingly, not only do crustacean researchers cite a comparatively large number of studies on other taxa, but their own studies are also cited by researchers studying a diverse range of other taxa (Fig. 1.3). Traditionally, crustacean researchers studying pheromones have been inspired by research on fish (living in water) and insects (arthropod relatives of the crustaceans). Whereas crustacean studies often integrate information from studies on other taxa, the corresponding proportion in fish and insect studies is <10% (Fig. 1.3). Also, reciprocally, fish and insect studies are only rarely cited by pheromone studies on other taxa. Most likely, these differences between studies on crustaceans, fish, and insects are due to the fact that much more is known about pheromones in fish and insects than in crustaceans. Crustacean researchers might also cite studies on both aquatic (fish) and terrestrial (insects) taxa frequently because crustaceans have conquered both these environments. This integrative approach has always characterized studies on crustacean chemoreception (e.g., Weissburg 2000; Vickers 2000; Koehl 2001) and promises to do so in the future (see contributions in this volume).

Focal papers citing from studies on

Focal papers being cited by studies on

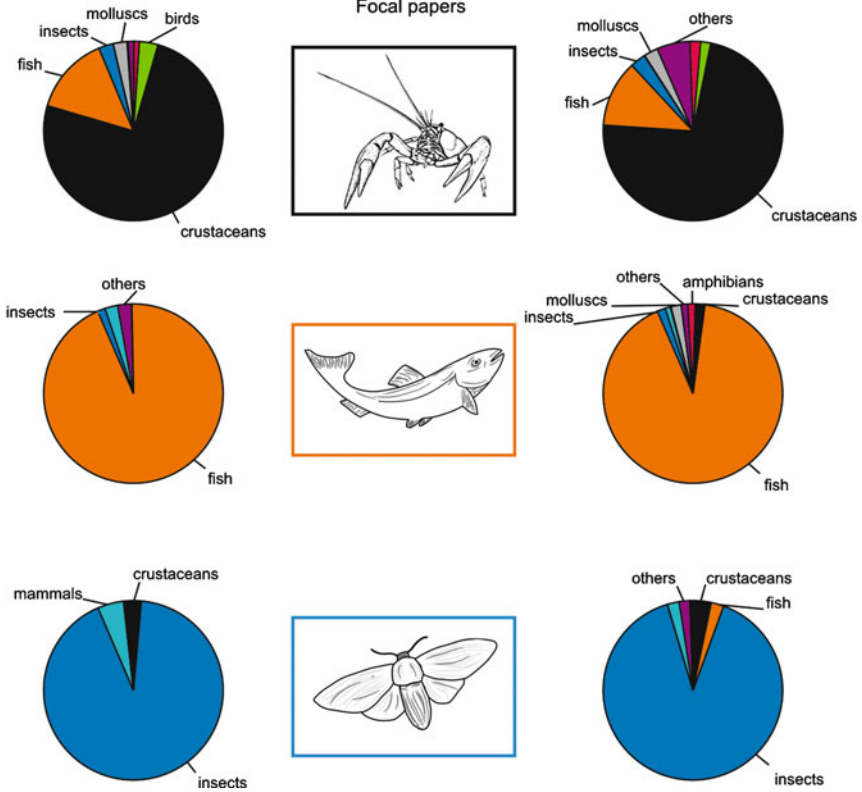


Fig. 1.3 Percentage of taxon-based studies cited by focal papers (*left column*) and citing the focal papers (*right column*). Results from Web of Science, based on the three most cited pheromone studies for each taxon (period 1990–2009)

1.3 Chemical Signals: Source and Identity

In crustaceans, chemical signals can be released to the surrounding liquid medium (soluble or volatile pheromones, “distance pheromones”) or bound to the body surface (“contact pheromones”; see e.g. Bauer, Chap. 14, and Snell, Chap. 23). In decapod crustaceans, the pheromones are released through the excretory pores (nephropores) located in the head region (Atema and Steinbach 2007; see also Kamio and Derby, Chap. 20; Hardege and Terschak, Chap. 19; Breithaupt, Chap. 13). Urine is often, but not always, the carrier of the chemical signal (see e.g. Kamio et al. 2002). Urine is predestined as a source of information molecules as it contains body metabolites that mirror the internal processes involved in sexual maturation, aggression, and illness. Many of the hormones underlying behavioral and developmental processes are well known in crustaceans

(Chang, Chap. 21). Numerous studies on fish have shown that hormones, once released, assume a pheromonal role (Chung-Davidson et al., Chap. 24). Although this is likely the case in other animals as well, there are only few studies providing examples of hormonal pheromones in crustaceans (Chang, Chap. 21). The larger decapod crustaceans should be ideal model organisms to close the gap between endocrinology and chemical communication research.

Urineborne chemicals reveal crucial information about conspecifics that can provide the receiver with distinct advantages over competitors in feeding, reproduction, and dominance interactions. Early during the evolutionary history of chemical communication, individuals might have obtained information by spying on urine chemicals from conspecifics. If emitters of these chemicals had adaptive advantages in revealing their status to others, this may have led to the evolution of complex urine release pattern (see Fig. 2.4 in Wyatt, Chap. 2). An example would be the release of chemicals that permit individual recognition within dominance hierarchies, where senders and receivers benefit from recognizing conspecifics (Aggio and Derby, Chap. 12; Gherardi and Tricarico, Chap. 15).

It is unknown whether crustacean senders can manipulate the composition of urineborne pheromones. They do, however, have control over the timing of urine release (Breithaupt, Chap. 13) and are therefore able to adjust the signaling to their own benefit. This may include opportunities to manipulate the receiver by either falsely reporting or by withholding information (Christy and Rittschof, Chap. 16). Only in few examples has the chemical nature of distance pheromones been characterized. These studies employed behavioral assays that used a specific behavioral response in the receiver as an indicator for pheromonal activity (Kamio and Derby, Chap. 20; Hardege and Terschak, Chap. 19).

The slow progress in crustacean pheromone identification is due (1) to difficulties in designing appropriate bioassays for animals that are under conflicting motivational regimes such as fighting, mating, or escape (Breithaupt, Chap. 13; Hardege and Terschak, Chap. 19), (2) to the quick alteration and degradation of the chemical components by aquatic bacteria (Hay, Chap. 3; for a terrestrial example see Voigt et al. 2005), and (3) to analytical challenges particular to identification of marine pheromones such as the difficulty in extracting and separating small molecules from a salty medium (Hay, Chap. 3; Hardege and Terschak, Chap. 19).

The latter problem may also explain the bias towards freshwater species in fish pheromone studies. Hormonal pheromones (see Chung-Davidson et al., Chap. 24) were identified in goldfish, round goby, African catfish, and Atlantic salmon that all release the pheromones into a freshwater environment (Sorensen and Stacey 2004). Even in sea lampreys, the chemical nature of larval migratory pheromone attracting adults and of male sex pheromones attracting females was identified for components that are naturally emitted into the freshwater spawning environment (Chung-Davidson et al., Chap. 24). The difficulties inherent in identifying marine semiochemicals suggest that freshwater crustaceans such as amphipods and crayfish may be better model systems for chemical characterization of pheromone components (Fig. 1.4).

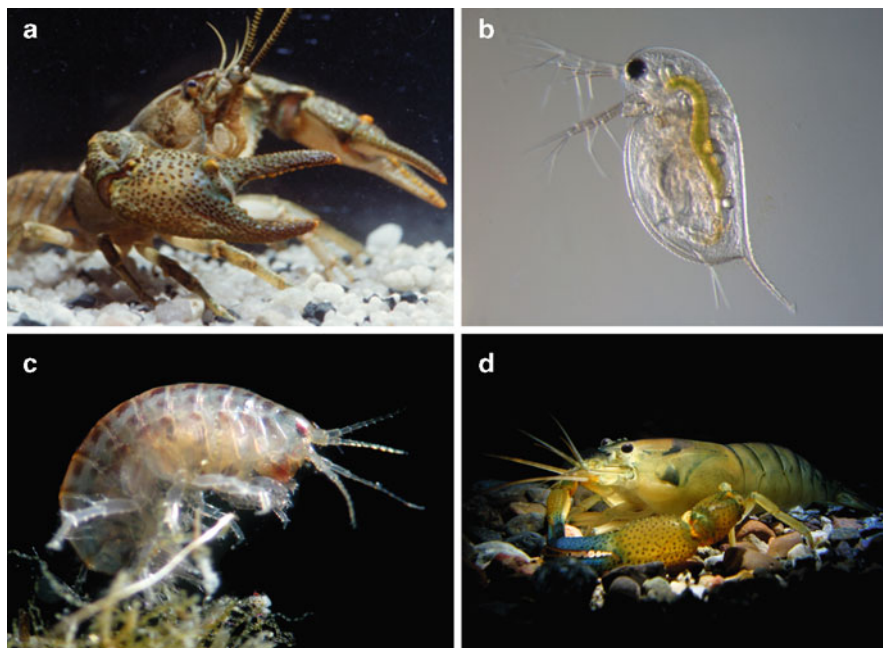


Fig. 1.4 Examples of crustacean species (in their natural environment) that are suited as models to address particular questions on crustacean chemical communication. **(a)** Crayfish *Austropotamobius torrentium* (photograph courtesy of Dr. Michael van der Wall); **(b)** water flea *Daphnia pulex* (photograph courtesy of Linda C. Weiss); **(c)** amphipod *Hyalella costera*; **(d)** freshwater shrimp *Cryphiops caementarius* (photographs **(c, d)** courtesy of Iván A. Hinojosa)

Despite these medium-specific problems, recent progress in pheromone characterization in crustaceans including hair crabs (Asai et al. 2000), helmet crabs (Kamio et al. 2000, 2002), blue crabs (Kamio and Derby, Chap. 20), green crabs (Hardege and Terschak, Chap. 19), peppermint shrimp (Zhang et al. 2010a), and barnacles (Clare, Chap. 22) highlights the fact that some of the initial difficulties in chemical purification have now been overcome and that the door is open towards rapid progress in structural identification.

While almost all insect pheromones are fatty-acid-derived hydrocarbons (Baker, Chap. 27), crustacean pheromones are more diverse. They belong to various substance classes such as peptides (Rittschof and Cohen 2004), nucleotides (Hardege and Terschak, Chap. 19) or other small polar molecules (Kamio and Derby, Chap. 20), small nonpolar molecules (Ingvarsdóttir et al. 2002), and possibly to ceramids (Asai et al. 2000). The higher diversity of waterborne pheromones again reflects the physical differences between the two media, with solubility in water being much less restrictive for the evolution of signal molecules than volatility in air.

Contact pheromones were shown to play a role in sex recognition in copepods (Snell, Chap. 23) and in shrimp (Bauer, Chap. 14) as well as in inducing settlement

in barnacles (Clare, Chap. 22). In copepods and barnacles, the molecules were identified as surface-bound glycoproteins (Snell, Chap. 23). Glycoproteins were also found on the surface of caridean shrimp from the genus *Lysmata*, but behavioral experiments on the role of these molecules as mate recognition pheromone in shrimps revealed contradictory results (Caskey et al. 2009; Zhang et al. 2010b), calling for additional studies. Chemical characterization of contact and distance pheromones remains one of the main challenges in crustacean chemical ecology and promises the greatest progress in this field.

1.4 Signal Transmission, Reception, and Processing

1.4.1 Signal Delivery

Pheromones released in an aquatic environment will be carried downstream by the ambient flow (see Weissburg, Chap. 4). In stagnant environments such as some lakes and ponds, odor dispersal will be slow. Signalers that are walking or swimming leave a scented trail behind that facilitates detection as it can be used by receivers to track and find the signaler (Yen and Lasley, Chap. 9; Weissburg, Chap. 4). Stationary senders generate their own water currents by ventilating or by fanning maxillipeds or pleopods to disperse the chemical signals (for lobsters see Atema and Steinbach 2007, and Aggio and Derby, Chap. 12; for crayfish see Breithaupt, Chap. 13; for blue crabs see Kamio and Derby, Chap. 20; for shrimp see Bauer, Chap. 14; for stomatopods see Mead and Caldwell, Chap. 11).

Actively flushing signals towards conspecifics appears to be a general strategy in many crustaceans as they are equipped with specialized fanning structures to generate water currents (see e.g., Breithaupt 2001; Cheer and Koehl 1987). Some insects (e.g., bees; Agosta 1992) and mammals (e.g., bats; Voigt and von Helversen 1999; and ring-tailed lemurs; Bradbury and Vehrencamp 1998) are also able to direct their chemical signals by using their wings (bees, bats) or tails (lemurs), but this strategy of dispersing odors is much less common in terrestrial animals than in aquatic organisms.

Terrestrial animals often display chemical signals by depositing gland excretions, urine, or feces to the substratum. There are numerous examples of terrestrial animals marking their territories using scent marks. Common examples are mammals such as badgers and mice where defecating or urinating appears to serve a territorial function (Roper et al. 1993; Hurst 2005), or female spiders giving away their reproductive status via chemicals in their web's silk (Roberts and Uetz 2005). Interestingly, in terrestrial isopods, burrows or communal dwellings also carry kin- or species-specific scents, while observations of aquatic amphipods could find no evidence for the existence of scent marks on dwellings (Borowsky 1989). The lack of scent marks in aquatic environments may be a consequence of the high solubility of even large molecules such as proteins in water causing any scent marks to be rapidly diluted by water movements. In addition, the ubiquitous bacteria in water may quickly attack and degrade any scent marks.

1.4.2 *Reception and Processing of Pheromone Signals*

Crustaceans perceive chemical signals with olfactory receptors – limited to the aesthetasc hairs that only contain chemoreceptor neurons and are located on the antennae – or with other chemoreceptors situated in setae that are distributed over the body surface (“distributed chemoreceptors” including contact chemoreceptors, Schmidt and Mellon, Chap. 7; Hallberg and Skog, Chap. 6). “Contact chemoreceptors” contain both chemoreceptor neurons and mechanoreceptive neurons (Schmidt and Mellon, Chap. 7).

The evolutionary transition from water to land has resulted in an expansion of the chemoreceptor genes, most likely in response to the multitude of airborne odorants (Bargmann 2006). Organisms that frequently change between aquatic and terrestrial environments (e.g., amphibians) appear to have chemosensory systems for perception of both water-soluble as well as volatile odorants (Freitag et al. 1995). Soluble and volatile chemicals can also be perceived by aquatic and terrestrial crustaceans, respectively (e.g., Hansson et al., Chap. 8). However, at least in terrestrial peracarids, taste reception of odorants appears to be mediated by liquids (Seelinger 1983; Holdich 1984), just as food-smelling of terrestrial mammals under water is mediated by air bubbles (Catania 2006).

So far, in decapod crustaceans, the receptor-bearing structures have not been shown to display strong sexual dimorphism as is found in many insects (Hallberg and Skog, Chap. 6). In insects, particularly in moths, males generally have much larger chemoreceptor-bearing antennae than females (Lee and Strausfeld 1990; Baker, Chap. 27). This dimorphism reflects the direction of sexual communication, with females generally being the pheromone emitter and males being the pheromone receiver as reported or inferred for many species (Fig. 1.5). There is a strong selective pressure on the males to detect minor amounts of female pheromones and track down the female that usually remains stationary while signaling (Phelan 1997). Concordant with the dimorphism in olfactory organ morphology, the dimorphism extends to sex-specific differences in the brain. In most insect genera where adults are terrestrial, a sexual dimorphism was found in olfactory brain centers. In contrast to females, males often possess a system of sex-specific brain centers that make up the “macroglomerular complex”, which is involved in the processing of pheromone information (Strausfeld and Reisenman 2009). So far, no sexual dimorphism with respect to olfactory structures has been found in any decapod crustacean (Hallberg and Skog, Chap. 6). However, sexual dimorphism is evident in some peracarid crustaceans where males possess larger and more differentiated olfactory organs than females as well as exhibiting sex-specific olfactory centers (Johansson and Hallberg 1992; Hallberg and Skog, Chap. 6; Thiel, Chap. 10). It remains to be investigated whether the receptor dimorphism in peracarids is caused by sex-specific pheromones and whether it mediates sex-specific behaviors. In crustaceans with female sex pheromones and male-specific responses (Bauer, Chap. 14; Breithaupt, Chap. 13; Hardege and Terschak, Chap. 19; Kamio and Derby, Chap. 20; Yen and

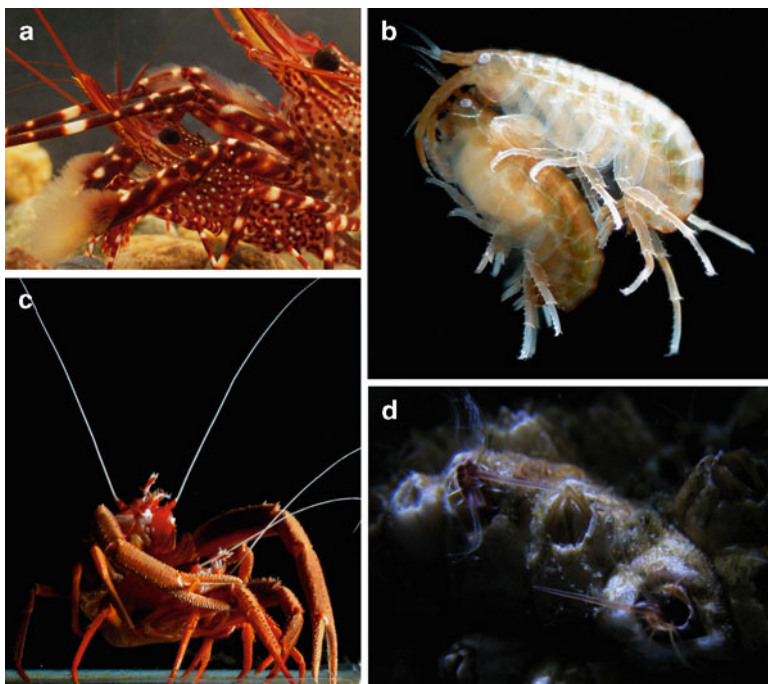


Fig. 1.5 Examples of mating interactions in several species of crustaceans where males are known or inferred to be receiver of female pheromones. (a) Rock shrimp *Rhynchocinetes typus*; (b) amphipod *Parhyalella penai*; (c) squat lobster *Cervimunida johni*; (d) barnacle *Balanus laevis*; (photographs courtesy of Iván A. Hinojosa)

Lasley, Chap. 9), males may have specific adaptations for neural processing of female chemical signals.

Sex recognition may also involve multiple sensory channels in some (many?) crustacean species (see Hebets and Rundus, Chap. 17), requiring more complex central processing of multimodal information. One of the future challenges to research on crustacean chemical communication is to enhance our understanding of the neuronal processing underlying pheromone perception (see Schmidt and Mellon, Chap. 7; Hansson et al., Chap. 8). Most importantly, the pheromone receptors need to be identified. This will then facilitate further investigation of the central neural pathways mediating chemical communication. Knowledge of pheromone receptor proteins will also open the door to sequencing of olfactory receptor genes.

1.4.3 Signal Enhancement

Crustaceans can actively enhance odor acquisition by creating water currents that draw the molecules towards them (in lobsters: Atema and Steinbach 2007; crayfish: