Sex and violence in lobsters - a smelly business

Skog, Malin

2008

SEX AND VIOLENCE IN LOBSTERS - A SMELLY BUSINESS

Olfactory-based communication in the European lobster

Malin Skog

Doctoral Thesis
Lund, September 2008

LUND UNIVERSITY

DEPARTMENT OF CELL AND ORGANISM BIOLOGY

Academic thesis in fulfilment of the degree of Doctor of Philosophy at the Faculty of Science at Lund University. The Thesis defence will take place in Högtidssalen, the Zoology Building, Helgonav. 3, Lund, at 10.00 am, September 12, 2008. Faculty opponent: Jelle Atema, Boston University Marine Program, Boston, USA.

Organization
LUND UNIVERSITY

Department of Cell & Organism Biology
Integrative Zoology
Zoologihuset, Helgonav.3
SE-223 62 Lund, Sweden

Author(s)
Malin Skog

Document name
DOCTORAL DISSERTATION

Date of issue
2009-09-12

Sponsoring organization

Title and subtitle

Sex and violence in lobsters – a smelly business. Olfactory-based communication in the European lobster

Abstract

The aim of this thesis was to study the chemical communication involved in aggressive and reproductive behaviours in the European lobster (*Homarus gammarus*).

Both male and female *H. gammarus* established and maintained dominance, but the sexes used different strategies for dominance maintenance. Male losers recognised individual fight opponents and avoided them but fought actively against unfamiliar dominants. In contrast, female losers avoided both familiar and unfamiliar dominants, indicating that they react to the dominance status of the opponent. Unexpectedly, females used more high-level aggression than males.

Blocking of the urine release in male lobster pairs with established dominance led to increased fight duration and increased aggression in a subsequent encounter, demonstrating the importance of urine signals for dominance maintenance in male *H. gammarus*.

Intruding American lobsters (*H. americanus*) have repeatedly been caught in European waters. Since the two species are closely related and have similar food and shelter requirements, aggressive and reproductive behaviours and communication signals may be similar and result in both competition for resources and possibly hybridisation. Aggressive interactions between male European and American lobsters showed that interspecific communication and dominance maintenance indeed occurs between the two species.

Lobsters often reproduce when the female is newly moulted, but mating can occur at any time during the female moult cycle. Intermoult courtship and mating behaviours were common in European lobsters, unless the sense of smell (olfaction) was blocked in the male, indicating the presence of a female pheromone that induces mating. Female olfaction was not important for these behaviours.

A morphological study of the European lobster antenna demonstrated unique sex differences in size and distribution of the olfactory aesthetasc hairs. Females had more antenna segments with aesthetascs than males, and also had longer aesthetascs. In contrast, males had more aesthetascs per antenna segment, possibly compensating for the fewer number of segments with this type of sensory hair.

Key words

Aggressive behaviours, chemical communication, dominance, recognition, urine signals, intermoult mating, sexual dimorphism, aesthetasc morphology, European lobster, *Homarus gammarus*

Classification system and/or index terms (if any)

Supplementary bibliographical information

Language
English

ISSN and key title

ISBN

Recipient´s notes

Number of pages
129

Price

Security classification

MAIN REFERENCES

This thesis is based on the following papers, which are referred to using their Roman numerals

I. Skog, M., 2008. Intersexual differences in the European lobster (*Homarus gammarus*): recognition mechanisms and agonistic behaviours. *Submitted for publication in Behaviour.*

II. Skog, M., Chandrapavan, A., Hallberg E. & Breithaupt, T., 2008. Maintenance of dominance is mediated by urinary chemical signals in male European lobsters, *Homarus gammarus. Submitted for publication in Marine and Freshwater Behaviour and Physiology.*

III. Skog, M., 2008. Male but not female olfaction is crucial for intermoult mating in European lobsters (*Homarus gammarus* L.). *Submitted for publication in Chemical Senses.*

IV. Skog, M., Hallberg, E. Chandrapavan, A. & Breithaupt, T., 2008. Dominance interactions between European and intruding American lobsters. *Manuscript.*

V. Skog, M. & Hallberg, E., 2008. The sexually dimorphic antennula of the European lobster (*Homarus gammarus*). *Submitted for publication in Journal of Crustacean Biology.*

List of contribution to papers II, IV and V:

In Paper II and IV, TB contributed with the original idea, most funding and laboratory equipment and AC and MS both performed the experiments. MS analysed the data and wrote the manuscript after consulting with the other authors.

In Paper V, both authors contributed equally to the idea and analysis. MS performed morphological preparations and microscopy and wrote the manuscript in consultation with EH.

CONTENTS

HUMRARNAS KEMISKA SPRÅK

Kemiska signaler är en av de äldsta formerna av kommunikation i djurriket. När djur av samma art kommunicerar med kemiska signaler kallas dessa feromoner, och används t.ex. som alarmsignaler, locksignaler och revirmarkeringar. Kommunikation är särskilt viktigt i samband med reproduktionen samt vid aggressiva beteenden inom arten. Aggression hör hos många djurarter ihop med dominans, där mer dominanta djur har företräde till t.ex. mat, boplatser eller partners.

Kemiska signaler kan bestå av både dofter och smaker, dessa skiljs bara genom vilken typ av sinnesorgan som uppfattar dem - luktsinnet eller smaksinnet. Lukter och smaker har inte någon inneboende rörelse (som t.ex. ljud eller ljus har) och därför krävs det att luften eller vattnet som den kemiska signalen befinner sig i rör sig för att den skall kunna spridas. Från en luktkälla bildar strömmen eller vinden en svajig ”plym” med avtagande koncentration längre bort från källan (tänk skorstensrök). Denna plym kan djur använda på olika sätt för att finna en luktkälla.

Mitt försöksdjur har varit den europeiska hummern, som trots att den är en kommersiellt viktig art har dåligt känd biologi. Mitt mål har varit att studera hummerns kommunikation genom kemiska signaler (feromoner) i samband med t.ex. reproduktion och aggression.

Humrar är aggressiva djur och när två jämnstora humrar träffar på varandra för första gången slåss de för att avgöra vem som är dominant. Status är nämligen viktigt i hummersamhället. Hög status innebär att hummern kan skaffa en bra boplats bland klippor och stenar där den kan ta skydd under dagen, eftersom humrar vanligen är nattaktiva. Troligen påverkar också hanens status hur många partners han kan få; dominanta vinnarhanar är mer populära bland honorna än förlorare. För en tidigare förlorare kan det vara bra att känna igen dominanta djur för att slippa förlora igen. Det kan antingen ske genom igenkänning av alla djur med en högre status än den egna (alla dominanta djur), eller genom igenkänning av de individer man har förlorat mot tidigare (bekanta).

Genom att anordna ”boxningsmatcher” för både hanar och honor undersökte jag dominans och igenkänning hos den europeiska hummern (**PAPPER I**). Både hanar och honor slåss, och honorna slåss faktiskt mer intensivt (med högre aggressionsnivåer) än hanarna! Båda könen etablerade dominansförhållanden som bibehölls vid ett andra möte mellan samma djur, något som visade sig genom kortare slagsmål och lägre aggressionsnivåer.

Hanarna kände bara igen andra hanar som de träffat förut (bekanta), och förlorande hanar undvek att slåss med vinnare som de kände, men slogs aktivt om de istället matchades mot okända dominanta hanar och kunde till och med vinna dessa möten. Oväntat nog visade sig honorna använda den andra typen av igenkänning (status). Förlorande honor undvek alltså alla vinnare, både dem de träffat på själva och okända dominanta honor. Man känner inte till något annat kräftdjur där könen har olika typ av igenkänningsmekanism. Ett annat oväntat resultat var att honornas slagsmål var mer aggressiva än hanarnas. Hos humrar, som hos många andra djur, anses annars hanarna vara det mer aggressiva könet.

Humrar och andra kräftdjur pratar inte med varandra som vi människor gör. Kräftdjur förlitar sig till stor del på en rad olika kemiska signaler och oftast kommunicerar de genom att släppa ut olika kemiska ämnen i urinen. En vuxen hummer kan spruta iväg urinen upp till 7 gånger sin egen längd, och eftersom urinen kommer ut framtill på djuret, under antennerna, så kommunicerar humrar alltså genom att ”kissa varandra i ansiktet”! Nu är det

inte riktigt lika illa som det kanske låter för oss. Humrarnas urin består till allra största delen av saltvatten, och istället för att använda ljud som bildar ord och meningar som vi gör använder humrarna istället olika kemiska ämnen som de släpper ut i urinen. Dessa ämnen kan till exempel tala om vilket kön hummern har, hur den mår, när den tänker ömsa skal, hur aggressiv den är och vilken status den har.

När humrarnas urinutsläpp hindrades genom att montera på specialkonstruerade katetrar (**PAPPER II**) kunde de inte längre känna igen varandra efter ett första slagsmål, och jag kunde alltså visa att urinsignaler är viktiga för upprätthållandet av dominansförhållanden hos europeiska humrar.

Humrarnas sexliv är lite komplicerat. Vanligen parar de sig under sommaren omedelbart efter det att honan har ömsat skal och fortfarande är helt mjuk. Äggen befruktas och läggs under honans bakkropp först på sommaren nästa år, och hon bär sedan äggen och sköter om dem i 9-11 månader innan de kläcks, nästan två år efter parningen! Honan kommer sedan att ömsa och para sig på nytt. Av olika anledningar parar sig dock inte alla honor när de är nyömsade, och riktigt stora honor kan lägga ägg två gånger mellan ömsningarna. Då finns en reservplan - nämligen att para sig även med hårt skal. Mellanrummet mellan parningen och äggläggningen kan då bli betydligt kortare.

Jag studerade de beteenden som är associerade till hårdskalsparningar hos europeisk hummer (**PAPPER III**), och genom att slå ut luktsinnet hos antingen honan eller hanen kunde jag visa att hanens (men inte honans) luktsinne är helt avgörande för att parning eller uppvaktning skulle ske. Hanen måste alltså kunna känna lukten av honan för att förstå att det är en hona, i annat fall sker ingen parning.

Då en hona och en hane träffade på varandra blev det vanligen slagsmål. Om honan gick vinnande ur detta försvann hanen snabbt från platsen. Om hanen däremot vann tillät honan att han uppvaktade henne och de kunde även para sig. Även honor som har parat sig tidigare kan ibland para sig igen med hårt skal - kanske träffar de på en ”bättre” hane än den de parade sig med ifrån början?

Den europeiska hummern är närbesläktad med den amerikanska, som på senare år har fångats vid upprepade tillfällen i europeiska vatten. De båda arterna har likartade födobehov och vill bo i samma typ av hålor. Dessa fakta tillsammans med möjligheten att både beteenden och kommunikationssignaler dessutom liknar varandra gör att de troligen kommer att konkurrera med varandra. Dessutom är hybridisering en möjlighet, liksom överföring av sjukdomar mellan arterna (ett närliggande exempel är ju kräftpesten).

Fighter anordnades mellan en amerikansk och en europeisk hummer (**PAPPER IV**), och resultaten visade att de båda arterna kan förstå varandra i någon utsträckning, och att dominans och igenkänning är möjligt över artgränsen.

Slutligen gjorde jag en morfologisk studie av hummerns luktorgan (”näsa”) (**PAPPER V**) - på det kortare av de två antennparen på hummerns huvud. På dessa antenner sitter en borste med tusentals små, tunna hår och det är här som doftämnen tas upp. Jag hittade unika skillnader hos dessa sinneshår mellan könen. Honorna hade fler segment med luktsinneshår på antennen och dessa hår var också längre än hos hanarna. Hanarna hade å andra sidan något fler hår per segment, vilket kanske kan kompensera för det lägre antalet segment och jämna ut könsskillnaderna. Könsskillnader hos antennerna är mycket ovanligt bland högre kräftdjur.

ABSTRACT

The aim of this thesis was to study the chemical communication involved in aggressive and reproductive behaviours in the European lobster (*Homarus gammarus*).

Both male and female *H. gammarus* established and maintained dominance, but the sexes used different strategies for dominance maintenance. Male losers recognised individual fight opponents and avoided them but fought actively against unfamiliar dominants. In contrast, female losers avoided both familiar and unfamiliar dominants, indicating that they react to the dominance status of the opponent. Unexpectedly, females used more high-level aggression than males.

Blocking of the urine release in male lobster pairs with established dominance led to increased fight duration and increased aggression in a subsequent encounter, demonstrating the importance of urine signals for dominance maintenance in male *H. gammarus*.

Intruding American lobsters (*H. americanus*) have repeatedly been caught in European waters. Since the two species are closely related and have similar food and shelter requirements, aggressive and reproductive behaviours and communication signals may be similar and result in both competition for resources and possibly hybridisation. Aggressive interactions between male European and American lobsters showed that interspecific communication and dominance maintenance indeed occurs between the two species.

Lobsters often reproduce when the female is newly moulted, but mating can occur at any time during the female moult cycle. Intermoult courtship and mating behaviours were common in European lobsters, unless the sense of smell (olfaction) was blocked in the male, indicating the presence of a female pheromone that induces mating. Female olfaction was not important for these behaviours.

A morphological study of the European lobster antenna demonstrated unique sex differences in size and distribution of the olfactory aesthetasc hairs. Females had more antenna segments with aesthetascs than males, and also had longer aesthetascs. In contrast, males had more aesthetascs per antenna segment, possibly compensating for the fewer number of segments with this type of sensory hair.

THE EUROPEAN LOBSTER

Crustaceans are common study organisms for investigations of aggressive and sexual behaviours, sensory systems and communication. They are common, relatively small-sized, easy to hold in the laboratory, have high activity, harmful weapons, large and sophisticated sensory organs and advanced sexual and aggressive behaviours (Dingle, 1983).

The European lobster (*Homarus gammarus*, *Fig.1*.) is a decapod crustacean belonging to the family Nephropidae (clawed lobsters), which also includes the American lobster (*H. americanus*) and the Norway lobster (*Nephrops norvegicus)*. The known maximum size of *H. gammarus* is 60-65 cm total length, corresponding to a weight of 8.4-9 kg (Wolff, 1978; Phillips et al., 1980) and possibly an age of 50-100 years. European and American lobsters are closely related (estimated genetic distance 0.11) and were geographically separated about 10 000 years ago (Phillips et al., 1980; Williams, 1995).

Fig.1. European lobster, *Homarus gammarus*. Photograph by M. Skog.

Distribution

H. gammarus occurs along most European coasts. Exceptions include areas where the distribution is probably restricted due to low temperatures (Iceland, Norway north of the Lofoten Islands and northern Russia) or by low salinity and temperature fluctuations (the Baltic Sea south of the Öresund strait parting Sweden and Denmark) (Cooper & Uzmann, 1980; Ulmestrand, 2005).

The distribution also includes low densities of lobsters along the Mediterranean coastline, and has a southern limit at ca 30° N on the Atlantic coast of Morocco. The depth distribution is not known, but thought to be down to about 60 m (Cooper & Uzmann, 1980; Ulmestrand, 2005).

Larvae need a salinity above 15-17 PSU while adults tolerate lower salinities, down to 10 PSU (Charmantier et al., 2001).

Adult lobsters

Despite being a commercially important fishery resource, the social biology, behaviours and communication of European lobsters has received far less attention than its well-studied American relative. Lobster adults are night-active and usually spend daylight hours in shelters (crevices in bedrock, hollows between rocks or boulders, burrows under rocks or tunnels dug in soft sediments like mud or clay). Water temperature also affects activity; when the water temperature is below 8°C, both the metabolism and activity decrease and the lobster can manage several months in winter without feeding (Cooper & Uzmann, 1980; Smith et al., 1999).

H. gammarus adults are capable of suspension feeding but are considered to be mainly scavengers and predators on fish and invertebrates (Hallbäck & Warén, 1972; Loo et al., 1993). Apart from cannibalism on newly moulted or injured animals at all stages in the life history, no predators on adult lobsters are known. Unlike the American lobsters, European lobsters seem very stationary and do not undertake any long migrations (Saila & Marchesseault, 1980; Smith et al., 2001), possibly with the exception of moving towards deeper water before winter and back towards shallower water before summer, a migration believed to occur by fishermen but never proven.

Large lobsters moult once per year or more seldom, males more often than females. The size increase at each moult is greater in younger animals than in older. Males and females differ in growth tactics; males moult more often, grow fast and develop large claws while females moult more seldom due to their reproductive cycle, gain less weight per moult and de-

velop broad abdomens that can accommodate more eggs. Thus there is a sexual dimorphism in *Homarus* with large males with very large claws, whereas females have smaller claws at a given carapace length and much broader abdomens than males (Aiken, 1980; Phillips et al., 1980).

Reproduction, larval & juvenile biology

Mating in lobsters is normally thought to take place within shelters shortly after the female moult in summertime, but lobsters can also mate in intermoult stages. The male transfers a sperm packet (spermatophore) to the female, which she stores in a 'pocket' on her ventral side, called spermatheca, until the eggs are laid and fertilised next spring-summer. The eggs are then incubated 9-11 months under the female's abdomen until hatching over several nights in July-August almost two years after the (softshell) mating (Templeman, 1934; Hewett, 1974; Atema, 1986; Waddy & Aiken, 1991; Ulmestrand, 2003).

The larvae go through four pelagic larval stages with a total duration of 1-2 months, mainly determined by water temperature (Cobb & Wahle, 1994; Ennis, 1995). The stage IV larvae settle in relatively shallow waters and presumably burrow under rocks on sandy and muddy bottoms (Berrill, 1974; Cobb & Wahle, 1994) (*Fig.2.*).

Next to nothing is known of juvenile *H. gammarus* biology, but juveniles are assumed to be highly cryptic. They might survive entirely on suspension feeding (Lavalli & Barshaw, 1989; Loo et al., 1993), or forage opportunistically outside their shelter as predators or scavengers more similar to the adult stage (Mehrtens et al., 2005). The habitat of juvenile European lobsters is not known.

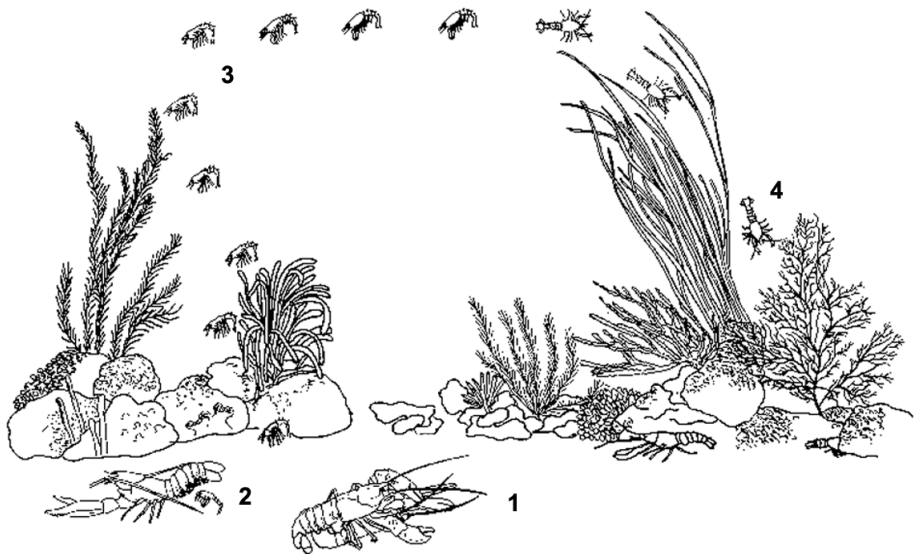

Fig.2. The life cycle of the American lobster (*H. americanus*): Mating (**1**) occurs either when the female is newly moulted or intermoult. Eggs are incubated for 9-11 months under the female's abdomen before first stage larvae are released (**2**). The pelagic larval phases last 1-2 months (**3**), after which the fourth larval stage settles to the bottom (**4**) and eventually mature to adults. From Atema & Voigt (1995).

Intruding American lobsters

Migration and larval dispersal are natural causes of introductions of species to new areas, often regulated by the survival of the individuals en route. Accidentally or deliberately, anthropogenic activities have drastically increased the rate of new establishments for example through trade and active introduction of commercial species, removal of natural barriers (e.g. the Suez Canal & the Panama Canal) and fast worldwide transports of living and resting stages of planktonic species in ballast water.

Most new species never establish, or are unable to reproduce in their new environment, but the ones that do may affect their new environment negatively in a number of ways. Some, like the European shore crab *C. maenas* invading South African, Australian and North American shores, and the American ctenophore *Mnemiopsis leidyi* in the Black Sea, cause changes in the biodiversity of their new ecosystem by out-competing native species or by constituting a heavy predation or grazing pressure on them (Kideys, 2002; Secord, 2003).

In other cases the biotope itself is changed by the alien species' actions. Such is the case with the Chinese mitten crab *Eriocheir sinensis* that has spread in European rivers where it excavates hollows in the riverbanks, causing large-scale erosion (Panning, 1939; Peters et al., 1933).

Since 1992, American lobsters have been caught relatively frequently in European waters (e.g. in England, Denmark & Norway), causing concern that their presence may affect the native European lobster populations and their habitat (van der Meeren et al., 2000). The wild-caught American lobsters were probably originally imported and escaped from illegal live cages in the sea or were deliberately released into the North Sea and Skagerrak in various countries.

H. americanus grows faster than *H. gammarus*, reaches a larger body size and has proportionally larger claws for a given carapace length (Wolff, 1978) (*Fig.3.*). It is uncertain if these properties give the American species a competitive advantage compared to its European relative. A shelter eviction study performed in the public aquarium in Bergen gave the impression that both male and female American lobsters in most cases could remove weight- and sex-matched European lobsters from their shelters, but not the other way around (van der Meeren & Ekeli, 2002).

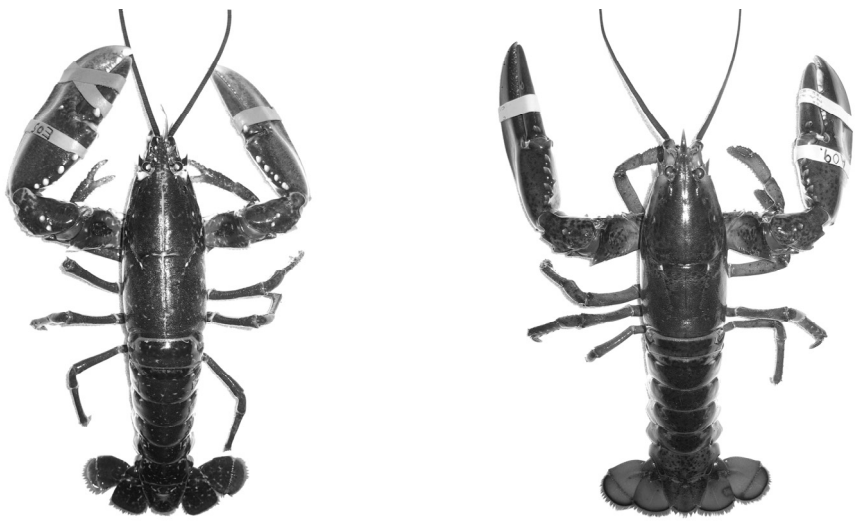

Fig.3. Comparison between a European (left) and an American (right) lobster. Photographs by M. Skog.

Introduced species may spread a number of parasites and diseases to new areas and other species. A well-known example is the fungus *Aphanomyces astaci* being transferred from American crayfish species (e.g. *Pacifastacus leniusculus*) to European crayfish like *Astacus astacus* and *Austropotamobius pallipes,* where it causes crayfish plague. Due to the crayfish plague and the deliberately introduced *P. leniusculus*' competitive advantages of larger size and higher aggressiveness, *A. astacus* is presently extinct from or highly threatened in many of its former habitats (Söderbäck, 1991, 1995; Westman et al., 2002).

American lobsters may act as vectors for two serious diseases currently not present in European lobsters; gaffkemia and shell disease. Gaffkemia is 100 % lethal in *H. gammarus* (Gro van der Meeren, personal communication) but does not kill American lobsters, which thus may become a reservoir for this disease if they establish in European waters (van der Meeren et al., 2000). Although shell disease is rarely lethal, it severely lowers the market value of affected animals (Martin & Hose, 1995; Castro & Angell, 2000).

In laboratory cross-matings (mostly *H. americanus* males x *H. gammarus* females), the two species produced fertile female offspring but sterile males (Carlberg et al., 1978; Talbot et al., 1984; Mangum, 1993). Unfortunately, none of these studies tell if the hybridisations were the result of natural or forced matings or artificial insemination. Competition between native offspring and either introduced or hybrid offspring can threaten the recruitment and in time cause the extinction of entire native populations (Söderbäck, 1995).

Even if no offspring is produced, cross-matings will make many females unavailable for normal mating, thus decreasing the number of native animals reproducing successfully per season. Chemical communication by pheromones in the introduced species may be also disturb reproduction in the natives, assuming that they can detect the substances used and react to them in some way (Tierney & Dunham, 1983).

AGGRESSION AND REPRODUCTION

Animal aggression, social conflicts, reproduction and sexual selection are closely linked. Since Darwin, the theory of sexual selection and the evolution of animal aggression and social conflicts through competition within each species for limited or favoured resources such as food, territory, shelters or mates have fascinated ethologists. Classical game theory has also successfully been applied to model and understand animal conflict situations (Riechert, 1998).

Aggression can be defined as hostile, threatening and/or destructive behaviours against another individual whereas agonistic behaviours include aggressive, appeasement, avoidance and defensive behaviours (Drews, 1993). A fight usually refers to an agonistic interaction between two conspecifics and is most often associated with competition for limiting (defendable) resources; e.g. mates, territory, food or shelters (Drews, 1993). Aggressive interactions are found in most higher animal taxa and the absence of intraspecific aggression is almost certainly a primitive trait (Huntingford & Turner, 1987).

Agonistic contests often start with threatening behaviours or ritualised (exaggerated, stereotyped, conspicuous and/or repetitive) displays; acts which may alter the behaviour of another animal without any direct physical contact (Huntingford & Turner, 1987). If the interaction escalates past displays, these low-key, energetically cheap movements performed at a distance are followed by more energetic behaviour including non-injurious physical contact (e.g. wrestling, pushing) and may in rare cases escalate to high-energetic and highly dangerous actions using weapons such as teeth, claws or horns (Riechert, 1998).

The conflict may be resolved by the retreat of one participant at any point during the escalation scale (Huntingford & Turner, 1987). Large size differences between individuals often resolve potential conflicts at an early stage, while escalation of the fight is most likely when opponents are similar in

size and the resource in dispute is valuable (Riechert, 1998).

During all stages of aggressive interactions, the contestants try to assess the fighting ability and motivation of the opponent and compare it to their own internal state or to a population average (Huntingford & Turner, 1987; Riechert, 1998). The exchange of information between contestants becomes more and more refined as the fight escalates (sequential assessment model)(Maynard Smith & Harper, 2003).

When there is a conflict of interest between signaller and receiver, signals are likely to be costly to avoid cheating (Riechert, 1998). Still, newly moulted stomatopods often display aggressively toward individuals approaching their shelter, despite their inability to follow up the threat if the bluff is called (Steger & Caldwell, 1983; Adams & Caldwell, 1990; Adams & Mesterton-Gibbons, 1995).

Weapons are physical structures used in fights to maintain contact between opponents and are used to push, pull and injure the opponent (Huntingford & Turner, 1987). Lethal weapons, injury and death in contests are not uncommon but contests are most often harmless, ritualized trials of strength (Huntingford & Turner, 1987; Maynard Smith & Harper, 2003). Ritualised behaviours help minimising events of extreme violence and thus the potential damage to animals, especially in contests where the opponents are likely to injure each other due to dangerous weapons (Huntingford & Turner 1987; Maynard Smith & Harper 2003).

Cost-benefit analysis of contests has shown that the potential costs of aggressive interactions include the development and maintenance of weapons and armour, energy expenditure during the fight, risk of injury and death from fighting and increased exposure to predators during contests. The benefits of winning a fight comprise of the exclusive use of resources and mating rights etc. Thus, in every aggressive interaction there is a theoretical optimum level of aggression for each individual depending on the costs and benefits (Huntingford & Turner, 1987).

Since eggs are generally more expensive to produce than sperm, sexual selection pressures act differently on males and females. As a result, males fight particularly fiercely over access to mates. Male conflicts lead to larger males, the development of weapons and to male colouration and/or ornaments (classical sexual selection). Successful males often mate more often than others (Huntingford & Turner, 1987).

Females often behave very aggressively in the defence of their young, but may also reject unwanted mates aggressively or fight each other over various resources, like food, shelters, nesting sites, etc. or compete over mates. Like in males, female conflict leads to larger body size, which is closely linked to increased ability to produce more, larger or more competitive offspring (Huntingford & Turner, 1987).

Dominance hierarchies & recognition

A common phenomenon throughout the animal kingdom is dominance hierarchies, where more dominant individuals most often gain priority of access to e.g. mates, food or shelter resources. Dominance is thus important for reproductive success, since more dominant individuals are often preferred by the opposite sex for mating, either because their larger resource holding potential (big size and/or weapons, ornaments, etc.) and/or for the attractiveness of the resource that they possess. The resource may not be in dispute at the time of the fight, however, since status may be competed for in anticipation of a conflict over resources at some other time (Huntingford & Turner, 1987; Drews, 1993).

Dominance can be defined as a persistent winner-loser relationship between two individuals that meet in repeated agonistic interactions with almost no need for actual fighting since the subordinate dyad member yields rather than escalating the fight. The dominance relationships in a hierarchy are not static, however, due to migration, death and changes in e.g. hormonal, reproductive

or moult status of individuals. Very little fighting is needed to maintain the hierarchy after the first aggressive resolving of dominance status, and each individual 'knows its place' in a stable dominance hierarchy.

Several mechanisms may contribute to the stability of the hierarchy and induce changes in dominant and subordinate behaviour; including winner and loser effects, status recognition and individual recognition (Barnard & Burk, 1979; Drews, 1993; Dugatkin & Earley, 2004).

In many species, recent winners become more likely to win in subsequent encounters, whereas recent losers become more likely to lose. Previous winning or losing experiences modify the individual's internal state and alters its aggressive motivation or 'confidence' in following fights (Barnard & Burk, 1979; Goessmann et al., 2000; Bergman et al., 2003; Hsu et al., 2006). Loser effects acting alone produce a clear alpha individual ('super-dominant') but other positions in the hierarchy may be more unclear, while winner effects instead create a stable linear hierarchy where every position is clear (Dugatkin, 1997; Issa et al., 1999; Dugatkin & Earley, 2004).

The recognition of dominance rank, status or aggressive state in opponents through some cue reflecting the individual's status or internal state (Winston & Jacobson, 1978) will result in lowered aggression in previous losers when encountering any previous winner than in interactions with inexperienced animals. Animals need no previous experience with the particular individual encountered to determine its rank or aggressive state.

In contrast, individual recognition of familiar opponents depends on association of a previous fight experience to a certain individual, which is recognised through one or more identifying cues. In this system, animals will differ in their response to familiar and unfamiliar individuals, and former losers will show high aggression towards all unfamiliar individuals, regardless of their previous fight history, but low aggression towards familiar winners (Barnard & Burk 1979, Drews 1993; Dugatkin & Earley 2004).

In most animal phyla, some discrimination between conspecifics takes place. It can be based on characters like sex, kinship, group membership, dominance status, reproductive state, familiarity or individual identity. True individual recognition implies the ability to differentiate between several familiar individuals, but most often the discrimination will create categories of conspecifics that will contain more than one animal. 'Binary' discrimination is based on a choice of only two options; e.g. male-female or familiar-unfamiliar (Thom & Hurst, 2004). However, the distinction between true individual recognition and the discrimination of familiar from unfamiliar individuals is very hard to test and prove and not always very interesting biologically (Barnard & Burk, 1979).

Both recognition of familiar individuals and true individual recognition are most certainly based on phenotypic traits typical for each individual or a unique set of cues (an auditory, electrical, visual, olfactory and/or tactile 'fingerprint') that provides information on species, age, sex, social and reproductive status, fighting ability, motivational state and individual identity. The individuality cue must be stable over time or change only slowly e.g. with age and have a high degree of diversity between individuals (Barnard & Burk, 1979; Huntingford & Turner, 1987; Thom & Hurst, 2004).

The mechanism for recognition of dominance status is less complex and may simply reflect the internal aggressive state of the animal. Categories of conspecifics can thus be created due to e.g. the presence/ absence or differences in volume or concentration of a specific chemical or mixture (e.g. dominance pheromone/agonistic pheromone or stress hormones) (Barnard & Burk 1979; Thom & Hurst 2004). In many birds, status is correlated to patches of colour, called badges of status, that vary in size - small in subordinates and more conspicuous in dominants (Maynard Smith & Harper, 2003).

Recognition of familiar, highly aggressive or high-status individuals benefits primarily the loser that avoids an unnecessary second fight and thus possible injury against a known superior opponent (Barnard & Burk, 1979). Individuals assess their own and the opponent's aggressive state, fighting ability and/or dominance rank before each interaction (Barnard & Burk, 1979). Rank signals must be costly to avoid cheating, since low-quality individuals would otherwise benefit from pretending to be dominant (Johnstone, 1998; Maynard Smith & Harper, 2003).

Different animals use different cues for recognising individuals or distinguishing between e.g. dominant and subordinate status. In insects, both odour differences and visual features may be used in individual or nestmate recognition (Barrows et al., 1975; Lenoir et al., 2001; Tibbets, 2004). Fish are often able to distinguish between relatives and non-relatives and many use chemical cues for this recognition (Olsén, 1992) but some electric fish can use the electric discharges of others for individual recognition (Paintner & Kramer, 2003).

Some birds rely on visual signals (Rohwer, 1975; Whitfield, 1987; Dale et al., 2001), others on vocal recognition (Mundinger, 1970; Godard, 1991) and still others on odour cues (Nevitt, 2008) for individual and/or status recognition. Reindeer, bats and fur seals also rely on vocal calls for individual recognition between mother - offspring (Espmark, 1971; Turner et al., 1972; Petrinovich, 1974; Pfalzer & Kusch, 2003), whereas many other mammals rely more on social odours, both for recognition of kin, individuals and dominance as well as for territorial markings. Best studied are the chemical signals in rodents, where chemical discrimination of individuals is thought to make use of highly variable proteins, e.g. those coded for by the major histocompatibility complex (MHC) genes (Ralls, 1971; Johnston, 2003; Bielsky & Young, 2004; Brennan, 2004; Brennan & Kendrick, 2006).

Crustacean dominance & recognition

Although agonistic behaviours and their regulation are probably best understood in rodents, many crustaceans (e.g. stomatopods, hermit crabs, crayfish and lobsters) have also become model organisms for this type of studies. Dominance hierarchies involving both status and individual recognition are common in crustaceans of different taxa. Only a few investigations have addressed true individual recognition in crustaceans (Gherardi et al., 2005) but this has not been demonstrated so far.

Dominance status recognition occurs in the crayfish *Astacus leptodactylus*, *Procambarus clarkii*, *P. acutus* and *Orconectes rusticus* (Copp, 1986; Zulandt Schneider et al., 1999, 2001; Breithaupt & Eger, 2002; Bergman et al., 2003; Gherardi & Daniels, 2003) and in the snapping shrimp *Alpheus heterochaelis* (Obermeier & Schmitz 2003a), while individual recognition or discrimination between familiar and unfamiliar opponents or partners has been shown in the stomatopod *Gonodactylus festae* (Caldwell, 1979, 1985, 1992), the banded shrimp *Stenopus hispidus* (Johnson, 1977), the cleaner shrimp *Lysmata debelius* (Rufino & Jones, 2001), the hermit crabs *Pagurus longicarpus* and *P. bernhardus* (Hazlett, 1969; Gherardi & Tiedemann, 2004; Gherardi & Atema, 2005; Gherardi et al., 2005) as well as both male and female American lobsters (Karavanich & Atema, 1998a; Atema et al., 1999; Berkey & Atema, 1999).

Both types of recognition involve chemical cues, possibly in the urine, and are received by chemoreceptors on the first antenna (Caldwell, 1979, 1985; Karavanich & Atema, 1998b; Zulandt Schneider et al., 1999, 2001; Breithaupt & Eger, 2002; Obermeier & Schmitz, 2003b; Gherardi & Tiedemann, 2004; Gherardi et al., 2005; Johnson & Atema, 2005). Information about an individual's internal state may be conveyed to others through metabolites of e.g. neurohormonal amines or hormones like ecdysteroids or through the use of pheromones like a 'dominance pheromone'

or 'agonistic pheromone', proposed by Thorpe & Ammerman (1978) in crayfish.

Most work on crustacean dominance and recognition has been conducted on the American lobster. Dominant *H. americanus* males acquire the best shelters, and are preferred as mates by females that can evaluate male dominance status by urine-borne chemical cues from outside the male shelter (Atema et al., 1979; Atema, 1986; Bushmann & Atema, 2000; Atema & Steinbach, 2007). Thus, the benefit of being a dominant male in the lobster hierarchy is increased reproductive potential by access to many partners (Atema, 1986; Karnofsky & Price, 1989; Cowan & Atema, 1990; Waddy & Aiken, 1991).

The possible advantages of female dominance are not well-known in lobsters. Likely they involve precedence to both food and shelter resources. Dominant *H. americanus* females do not get first access to mate with the preferred male (Cowan & Atema, 1990; Atema & Steinbach, 2007). Hypothetically, the timing of female moulting, mating and extruding eggs during the summer may affect the quality and survival of the offspring during brooding or after next season's hatching. In this case, a dominant female might be more likely than a subordinate one to get access to the dominant male during the optimal mating time in summer.

When two unfamiliar American lobsters meet, they will fight until the dominance is settled: the winner becomes dominant over the subordinate loser (Scrivener, 1971; Atema, 1986; Atema & Voigt, 1995; Atema & Steinbach, 2007). The loser subsequently avoids a second fight with a familiar winner, a chemical recognition mediated by compounds in the winner's urine that lasts one week without reinforcement (Karavanich & Atema, 1998a, 1998b). If the winner's urine release is blocked or if the loser's olfactory receptors are ablated or removed, the two lobsters will fight again during this time (Karavanich & Atema, 1998b; Johnson & Atema, 2005). When encountering an unfamiliar dominant, however, the *H. americanus* loser fights actively and may even win, demonstrating individual recognition of opponents (Karavanich & Atema, 1998a).

The claws of American lobsters are designed to catch and crush prey and can generate forces of over 350 kN/m^2 in large animals (Elner, 1981). These formidable weapons can be used to rip off legs or claws, and can inflict severe or lethal injuries to the opponent. Ritualised behaviours are common and important in *H. americanus* fights and help minimising events of extreme violence and thus the potential damage to animals in agonistic interactions (Atema & Voigt, 1995).

Ritualised threat displays like meral spread, high-on-legs and antenna whipping and 'arm wrestling' (claw lock), a low-key physical contact behaviour, *Fig.4.*) are the most frequent agonistic behaviours in both juvenile and adult American lobster fights. Unrestricted violence occurs only very seldom and only in well-matched fights (Atema & Voigt, 1995; Huber & Kravitz, 1995; Huber et al., 1997a). Fights escalate in a strict order from threats to low-key physical contact such as pushing and boxing to strength assessment through mutual claw lock and, finally, to unrestrained violence aimed to injure the opponent (Atema & Voigt, 1995).

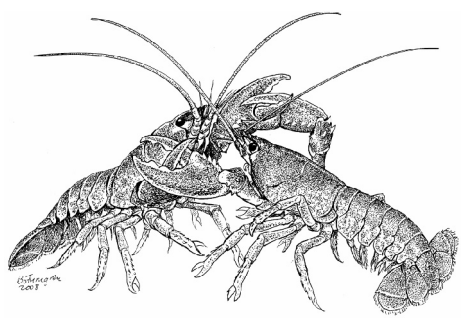

Fig.4. Aggressive interaction between two European lobsters, showing mutual claw lock. Drawing by Bo Furugren.

PAPER I demonstrates that both males and females in the European lobster establish dominance relationships. However, the sexes use different strategies for dominance maintenance, which is unique among the crustacean species studied so far. Like e.g.

American lobsters, *H. gammarus* males recognise individual familiar opponents, but fight actively against unfamiliar dominant animals. In contrast, females (that often fight more aggressively than males) show equally low aggression toward both familiar and unfamiliar dominant animals, demonstrating status recognition, similarly to e.g. crayfish. In **PAPER II**, urine was shown to be crucial for dominance maintenance in European lobster males.

Crustacean reproductive behaviours

Crustacean mating systems are many and varied. The reproductive cycle may be very short and completed several times per year or much longer, the extreme being clawed lobster females that need two years or more to complete a single reproductive cycle (Aiken & Waddy, 1980). Many crustaceans, like crayfish, spiny lobsters and some shrimp species pair only for the actual copulation (Lipcius et al., 1983; Yano et al., 1988; Reynolds, 2002) whereas other species form longer pair-bonds, often in the form of pre- and/or post-copulatory mate guarding by the male.

One form of prolonged pair-bond is the 'cradle-carry' shown by male crabs, which grasp and carry pre- and postmoult females for days - weeks, depending on species (Berrill & Arsenault, 1982; Gleeson, 1991; Sainte-Marie et al., 1997; Kamio et al., 2003). Likewise, male gammaridean amphipods carry the female in a precopulatory embrace for hours-days before her moult, when the copulation occurs (Holmes, 1903, Wellborn & Cothran, 2007).

Other species cohabit for shorter or longer periods. For example, male rock shrimp (*Rhynchocinetes typus*) guard the female for up to three hours after the copulation during the subsequent spawning (egg deposition) (Correa et al., 2000). Shelter sharing in the female tube in the amphipod *Microdeutopus gryllotalpa* starts about 12 hours before the female moult (Borowsky, 1980, 1983) and likewise, male fiddler crabs of the species *Uca paradussumieri* enter the female burrow about half a day before the female spawns to copulate with and guard the female (Murai et al., 2002). American lobsters cohabit in the male shelter for several days to weeks before and after the female moult. Snapping shrimp (*Alpheus sp.*) and some other caridean shrimp (e.g. harlequin shrimp *Hymenocera picta*, anemone shrimp *Periclimenes ornatus*) are monogamous, i.e. they form long-lasting, stable male-female pair bonds (Seibt & Wickler, 1979; Knowlton, 1980; Omori et al., 1994; Correa & Thiel, 2003).

Sperm competition may occur in crustaceans where 1) there is a delay between insemination and spawning 2) the female has opportunity to mate with several males before spawning and 3) the sperm is retained in a storage organ (the spermatheca) (Snedden, 1990; Villanelli & Gherardi, 1998; Sainte-Marie, 2007).

Reproductive behaviours in lobsters

Lobster matings usually start by the male touching the female carapace or abdomen with his mouthparts (maxillipedes), after which he mounts the female. He then directly uses his maxillipedes and walking legs to grasp the female and attempts to turn her around, dorsal side down. During the copulation that follows, the male inserts his gonopods (specialised mating organs) into the females' spermatheca and transfers a sperm packet (spermatophore) to her. Copulation usually takes place with the female lying on her back, the male on top and the animals facing in the same direction (Atema et al., 1979; Aiken & Waddy, 1980; **PAPER III** & pers. obs.) (*Fig. 5*.).

Lobsters most often mate shortly after the female moults in summer. In *H. americanus*, males probably broadcast their presence and dominance status, which are evaluated by females through frequent shelter visits to neighbouring lobsters (Atema et al., 1979; Atema, 1986; Bushmann & Atema, 2000). A few days before the female moults, she enters the shelter of the locally dominant male to cohabit with him. Copulation usually takes place ca 30 minutes after the moult, and the female continues her cohabitation with the male

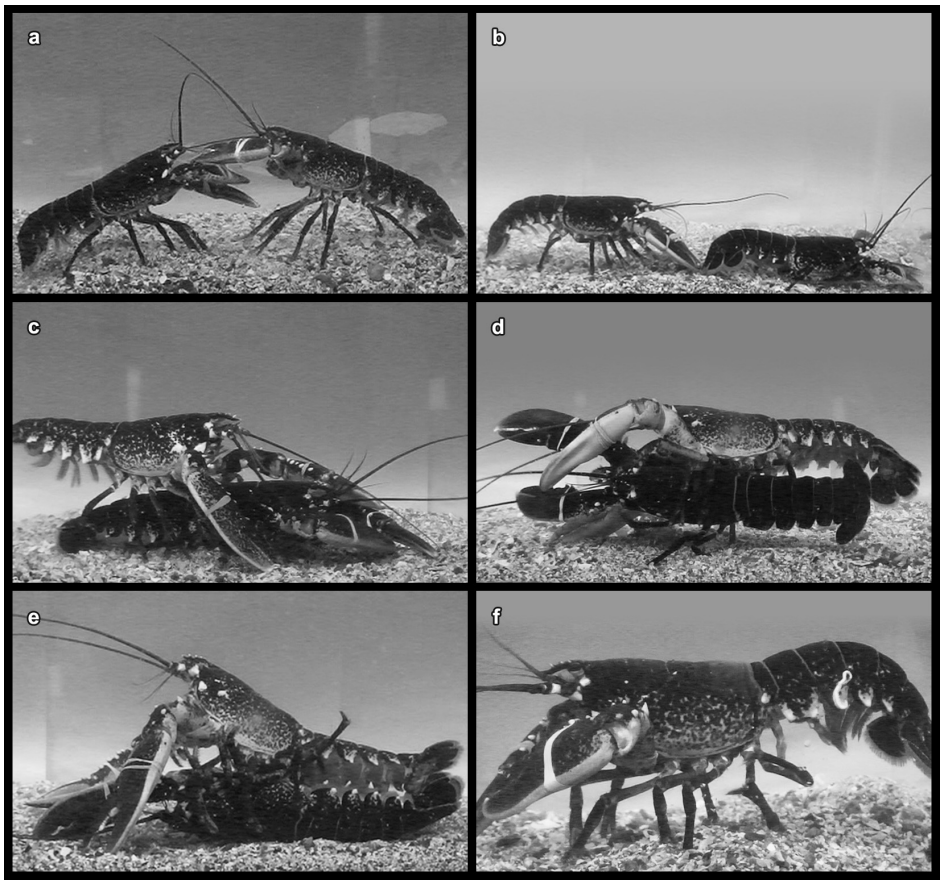

Fig.5. Intermoult mating in the European lobster. **a.** Initial aggressive interaction between male and female **b.** Female (right) submissive posture **c.** Mounting (female below) **d.** Turning (female below) **e.** Copulation (female below) **f.** Postcopulatory grooming by the male. See also *Tab. 2.* Photographs by M. Skog.

for a further couple of days after the moult and mating. This short-term pair bond and cohabitation in the male's shelter usually lasts 1-2 weeks (Atema et al., 1979; Atema, 1986; Atema & Steinbach, 2007).

Other females may wait their turn to cohabit and mate with the dominant male in succession, rather than mate with a subordinate male. Thus, the dominant male may cohabit and mate with several females sequentially (serial monogamy) (Cowan & Atema, 1990). Waiting females may be affected to postpone their moulting date (moult staggering) by chemical signals released by the cohabiting male and/or female 'advertised' by the male through extensive pleopod fanning (Atema, 1986, 1995; Cowan & Atema, 1990; Atema & Steinbach, 2007). However, since female moult stages was not monitored before or during the study by Cowan and Atema (1990), the theory of female moult staggering has been disputed (Waddy et al., 1995).

Mating in *H. americanus* is not restricted to postmoult females, but can occur throughout the female's moult cycle (Dunham & Skinner-Jacobs, 1978; Waddy & Aiken, 1990, 1991; Atema & Steinbach, 2007). Intermoult matings is an alternative strategy for females that failed to mate at the time of moulting, that were inseminated with a very small amount of sperm, or for very large females that spawn twice between moults that need to replenish their sperm store to fertilise two consecutive broods (Waddy & Aiken, 1990, 1991). Intermoult females may

enter the shelter of males, cohabit briefly with them and receive mating attempts (Bushmann & Atema, 1997, 2000).

Both male and female lobsters may mate several times in rapid succession (Templeman, 1934; Waddy & Aiken, 1991), but previously inseminated females are believed to be less attractive to males. Still, they may enter male shelters and receive mating attempts like other females (Waddy & Aiken, 1990, 1991; Bushmann & Atema, 1997).

Females are believed to be able to monitor their own sperm load, and uninseminated females that are soon about to spawn become 'desperate'; they become very active during their nightly forays, presumably searching for a suitable male (Waddy & Aiken, 1991; Flight et al., 2004). Wild females have been shown to spawn broods with multiple lobster fathers, showing that multiple inseminations by several males are not a by-product of laboratory studies (Nelson & Hedgecock, 1977; Gosselin et al., 2005).

Not much is known about the reproductive behaviour of European lobsters. Anderton (1909) described matings between intermoult males and recently moulted females and Debuse et al. (2003) regarded the courtship behaviour of *H. gammarus* as 'similar to that of the American lobster'.

However, in the study by Debuse *et al.*, advanced courtship interactions often took place outside shelters, and shelter-owning European lobster males were not involved in courtship interactions more often than those lacking shelters, demonstrating differences the importance of shelters for courtship and mating between the two species. Courtship outside shelters is not reported in naturalistic settings for American lobsters, unless the provided shelters were too small for two animals (Atema, 1986; Karnofsky et al., 1989; Karnofsky & Price, 1989).

Intermoult matings had not been investigated in *H. gammarus* previous to **PAPER III**, which gives an indication that such interactions may be a common reproductive strategy in *H. gammarus* as well as in *H. americanus*. Male olfaction was shown to be crucial for intermoult courtship and mating behaviours in European lobsters, whereas the ablation of the female's olfactory sensilla did not affect these behaviours in any way.

CHEMICAL COMMUNICATION

Communication can be defined as transmission of signals between organisms, where selection has favoured both the production and the reception of such signals as well as the behavioural response in the receiver (Lewis & Gower, 1980; Maynard Smith & Harper, 2003). According to this definition, predator-prey interactions for example are regarded as non-communicative; even if the predator receives sensory information about the presence of the prey, this is not a signal that has evolved in the prey to alert the predator to its existence and availability.

Any chemicals in the environment that carry information, like flower and plant scents, body odours, vapour rising from a rotten corpse, territorial markings and the smell of a newly painted wall or burned cookies, can be defined as infochemicals. When chemical signals are used in communication contexts, these signals are often called semiochemicals (Wyatt, 2003).

Communication is used in a number of contexts, both within and between species. Intraspecific chemical communication (within the species) involve aggregation signals, alarm signals, food signals, aggressive, appeasement, courtship and mating signals, territory markings, displays, recognition of social group members, kin, species, sex and status among other things. Chemical signalling is one of the oldest forms of communication in the animal kingdom and is used both by aquatic and terrestrial organisms.

Within-species chemical communication is mediated by pheromones, defined as "substances that are released to the outside of the animal, often in minute amounts, and are detected by specialised sensory structures in another member of the species, where they induce a specific reaction"

(Karlson & Lüscher, 1959). Pheromones can be further divided into primer pheromones, which initiate changes in the physiological (neuroendocrine) state of the receiver and releaser pheromones that induce an immediate behavioural change in the receiver (Wilson & Bossert, 1963).

Most well-known are the sexual pheromones that aid individuals in finding a partner for reproduction and/or evaluating the reproductive state of another individual, but other signals may involve e.g. aggregation pheromones, social relationship pheromones, larval release pheromones, alarm pheromones and territory markings. Bombykol, the major sex pheromone of the silkmoth *Bombyx mori*was the first to be fully characterised (Schneider, 1957; Butenandt et al., 1959). Insect and rodent pheromones are the best studied and understood chemical communication signals today, but pheromones are found in most animal taxa studied (Wyatt, 2003).

Sex pheromone research in crustaceans has focused on decapods such as crayfish (Ameyaw-Akumfi & Hazlett, 1975), lobsters (Atema & Engstrom, 1971; Dunham, 1979; Bushmann & Atema, 1996) and several crab species, i.e. shore crab, *C. maenas* (Eales, 1974; Hardege et al., 2002; Ekerholm & Hallberg, 2005); blue crab, *Callinectes sapidus* (Gleeson et al., 1984; Gleeson, 1991) and helmet crab *Telmessus cheiragonus* (Kamio et al., 2000, 2002). So far, only one putative crustacean sex pheromone has been purified, revealing a ceramide structure (Asai et al., 2000).

Interspecific chemical communication

Understanding and communication between species (interspecific) is not uncommon. For example, animals will benefit from perceiving and reacting to another species' warning calls or alarm pheromones meant to notify conspecifics e.g. of the presence of a predator (Seyfarth & Cheney, 1990; Chivers et al., 1997; Rainey et al., 2004). However, this does not qualify as communication according to the definition used previously, since the signal was not evolved for this purpose.

In contrast, flower scents that attract pollinators are clearly an example of communicative semiochemicals. Likewise, in commensal cleaning relationships, interspecific communication is important and has evolved for mutual understanding of the context. Cleaner fish and cleaner shrimp often enter the mouth of their larger host fish without being eaten, while the hosts (clients) in return expose their vulnerable gills for cleaning, risking deception and injury by false cleaner-mimicry fish (Floeter et al., 2007). Typical colour patterns in the cleaner fish and shrimp and other visual signals like stereotyped behaviour and tactile stimulation through specialised 'dancing' are important communication signals in this type of relationship (Grutter, 2004; Stummer et al., 2004).

Some closely related species may detect and react to each other's sexual signals or pheromones. For example, both male and female fiddler crabs of the genus *Uca* have shown courtship-related displays toward members of the opposite sex of another species (Zucker & Denny, 1979). In moths of the genera *Yponomeuta* and *Eriocrania* among others, the sexual pheromone consists of blends of different chemicals. Males respond to chemical signals from females of several species and the different species can hybridise in lab conditions (Löfstedt & van der Pers, 1985; Kozlov et al., 1996).

Normally, such closely related species are prevented from hybridisation through reproductive isolation in two or more 'niche dimensions' like the ratio of pheromone components; additional pheromone compounds; different spatial niches or temporal factors in reproductive behaviour e.g. diel and seasonal activity (Löfstedt & van der Pers, 1985; Löfstedt, 1990).

In evolutionary terms, the separation of the two *Homarus* species (10 000 years) is short and maybe not sufficient to change pheromones and behaviours enough for reproductive isolation barriers to be in place; especially since the two species have had no contact during this time. If the two species use the same or similar chemical 'language' (pheromones) and reproductive

behaviour, hybridisation may occur spontaneously in natural conditions after the introduction of American lobsters to Europe. **PAPER IV** shows that some interspecific communication and dominance maintenance occurs in aggressive interactions between male *H. gammarus* - *H. americanus*.

Chemical signals

All sensory stimuli are perceived by animals via specific sensory receptors, usually arranged together in sensory organs. Chemical stimuli can be defined as any chemical or mix of chemicals detected by the chemoreceptive sensory systems or organs in an organism, most commonly the organs of smell (olfaction) and taste (gustation).

As opposed to the continuous wavelength spectra of light and sound stimuli, chemical stimuli represent a highly discontinuous spectrum of molecules of every size, shape, charge and combination of active groups (Atema, 1988; Derby & Atema, 1988). Further, odours and tastes possess no inherent directionality, and depend on the processes of molecular diffusion and water or air movements for transport.

All signals need to stand out from the background noise (signal-to-noise ratio), i.e. to have contrast either in quality or quantity. Qualitative contrast ('spectral contrast' Atema, 1985, 1995) is provided by rare or unique chemicals as well as unique mixtures of (rare or common) chemicals that stand out from the local chemical environment. Contrast in quantity ('dynamic temporal contrast') means that the chemical occurs in pulses of 'unusual' concentration, different from the background level of the compound (Atema, 1995).

The properties of the chemical stimulus - volatility, solubility, polarity, size, biochemically active groups, chirality, concentration, etc. - combined with its chemical surroundings (mixture, background noise) and the receptor's properties all affect whether a stimulus is detected and what response it elicits in the animal. Different species react to different substances at different concentrations, and the response to the same chemical may be opposite in two different species, or in the same species under different circumstances (Derby & Atema, 1988). Mixtures of different chemicals are common as signals and are in some cases more stimulatory than any of the constituent compounds (Bardach, 1974; Atema, 1985).

Airborne chemical signals must be volatile (gaseous) to stay in the air and can be transported for long distances by winds and other air movements. The noise level of volatile compounds is very low, and most terrestrial animals can detect minute concentrations of different volatile compounds. In water, noise levels of chemical substances are extremely high. Animals are immersed in a 'soup' of more or less soluble chemicals at different concentrations.

Since almost all chemicals may be dissolved or mixed with water, or may be present in suspended lipophilic droplets, gas bubbles or adsorbed to surfaces of particles present in the water (Atema, 1985), very little is known of the chemical properties of odours under water. Not all chemical signals in water share the same chemical properties, like volatility of odours in air, something that makes chemical analysis of waterborne odours difficult at best.

Chemical communication stimuli in aquatic animals are very hard study and to date only very few active compounds are known. Water-born pheromones usually belong to one of two classes: steroid-based pheromones or large, polar molecules like polypeptides (Wyatt, 2003) They are believed to be highly potent (responses may be elicited at very low concentrations, e.g. 10^{-10} M) and often present in unique mixtures (Ache, 1982, 1985; Carr, 1988).

Chemicals that stimulate feeding behaviour often contain elements from the animal's natural food objects. For aquatic predators and scavengers, this means water-soluble common metabolites of low molecular weight, like amino acids, ammonium compounds, nucleotides, nucleosides and organic acids. Many of these are strongly polar molecules and they are relatively soluble in water (Bardach, 1974; Ache, 1982; Ache & Derby, 1985; Carr, 1988).

Fig.6. A stylised turbulent odour plume. From Zimmer & Butman (2000).

Odour plumes & dispersal of chemical stimuli

Since chemical stimuli have no inherent motion, they rely on movements of the medium (air or water) for transportation. Molecular diffusion (i.e. semi-random movement of molecules from a higher towards a lower concentration) is a very slow process and is biologically useful only at very small scales (<10 μm) but is virtually the only effective mechanism of chemical transport in viscous boundary layers close to surfaces (Atema, 1985, 1988, 1995).

At larger scales, air and water movements (e.g. laminar flow, turbulent mixing and currents) disperse chemicals. From a stationary odour source, water or air movements will create an odour plume (*Fig.6.*) carrying the odour away, with average odour concentration decreasing further away from the source.

In the plume, small- and large-scale turbulence will break up the odour gradient and create eddies with very different chemical composition, as well as meanders involving the entire plume. Turbulent plumes are chaotic, unstable and irregular, and eddy structure and meanders change over time. Substrate structure and air/water flow velocity will affect the degree of turbulence in the plume and friction against the substrate will create a semi-laminar flow close to the substrate. The plume becomes gradually more homogeneous with distance and time, and eventually the signal value will have faded into the background noise (Atema, 1985, 1988; Weissburg & Zimmer-Faust, 1993).

Animals use several different search strategies to find an odour source. Some, like aquatic bacteria and tuna may use relatively random turn and search behaviour, whereas others use the chemical information the odour plumes to move toward (or away from) a higher concentration (chemotaxis). Other search strategies depend not only on the odour itself, but also on the ability of the animal to determine current or wind direction.

In moths, the animal flies upwind as long as is can smell the odour (chemically stimulated rheotaxis) and start casting cross-wind if it looses the odour (David et al., 1982). The tsetse fly monitors the average wind direction while stationary and then aims straight for the odour source. Frequently they overshoot and have to circle back downwind and start over (Bursell, 1984).

The turbulence of most odour plumes creates a complicated situation for the tracking animal regardless if it uses chemotaxis only or in combination with rheotaxis, since the signal will be perceived as a series of pulses of different concentration. Bilateral comparison between chemosensory organs or receptors situated on different parts of the body combined with turning behaviours and temporal analysis of concentrations allow animals to orient in such turbulent plumes with patched odour distribution (eddy chemotaxis) (Zimmer & Butman, 2000; Webster et al., 2001), a technique used by e.g. the American lobster (McLeese, 1973; Derby & Atema, 1982;

Devine & Atema, 1982; Moore & Atema, 1991; Moore et al., 1991; Atema, 1995).

Degradation of chemical stimuli

Signal life-time is limited, and most chemicals will be subject to turbulent mixing, molecular diffusion, adsorption, photolysis, chemical transformation and/or biological uptake and breakdown by bacteria, other micro-organisms and small invertebrates until finally all signals will fade into the background noise and be signals no more.

Degradation of signals is crucial to keep the signal-noise ratio high and allow a following signal to be received (Atema, 1985, 1995). Thus, in each signalling context, there is an optimal signal life-time; the signal must last long enough to be received, but 'disappear' as soon as the receiver has used it, so it does not interfere with later signals. Consequently, biologically and chemically stable compounds should be more common as signals over large time/space scales like territory markings and tracking substances, whereas less stable substances are more likely to be used in short-range communication (Atema, 1985).

Crustacean urinary signals

Chemical communication in crustaceans during mate evaluation, courtship and aggression commonly involve urinary (pheromone?) signals. For instance, precopulatory mate guarding is induced by female premoult urine in the shore crab, the helmet crab and the blue crab (Gleeson, 1980; Kamio et al., 2000; Hardege et al., 2002; Ekerholm & Hallberg, 2005) and normal courtship behaviour in the American lobster depends on the release of female urine (Bushmann & Atema, 2000).

The probability of urine release increases linearly with increasing aggression levels during fights in the crayfish *A. leptodactylus* and *H. americanus* and the urine possibly contains information about the fighting ability and/or aggressiveness of the signaller (Breithaupt et al., 1999; Breithaupt & Atema, 2000; Breithaupt & Eger, 2002).

Information about an individual's internal state may be conveyed to others through pheromones or metabolites of e.g. neurohormonal amines or hormones that are excreted in the urine (Kennedy, 1978; Snyder & Chang, 1991).

Urine release and perception

Decapods release urine intermittently through the bilateral nephropores; small apertures situated on the base of the second antenna. The urine is ejected into the powerful gill current and carried away from the animal. Perception of urine signals seem to be mediated by the olfactory sensilla (aesthetascs) on the first antenna in most species (Tierney et al., 1984; Cowan, 1991; Karavanich & Atema, 1998b; Raethke et al., 2004; Johnson & Atema, 2005). Lobsters therefore communicate by peeing each other in the face!

By fitting animals with catheters made of plastic tubing glued around the nephropores to prevent urine from reaching the environment as well as antenna ablations, urine signals and olfactory detection of signals have been studied in lobsters and crayfish (Cowan, 1991; Bushmann & Atema, 1997; Karavanich & Atema, 1998b; Zulandt Schneider et al., 2001).

Adjacent to the urinary tracts of *H. americanus* are the rosette glands, suggested to be involved in pheromone production. These glands have ducts both to the urine bladder and to the exterior of the animal, and may thus release their products into the urine or directly to the environment (Bushmann & Atema, 1996).

Information currents in lobsters

Crustaceans affect their local chemical environment through the generation of several water currents of different power and direction. Best-known are the tree currents generated by lobsters and crayfish: the gill current, the fan currents and the pleopod currents (*Fig.7.*).

The gill current is the continuous, powerful respiratory current generated by the scaphognatites of the second maxilla inside the gill chambers. Water is drawn in

through openings between the walking legs, passes over the animal's gills and exits under the antennae. In an adult American lobster, this current can project up to seven bodylenghts forward, away from the animal. The gills are in part excretory organs and this current will therefore contain waste products (Atema, 1985, 1988).

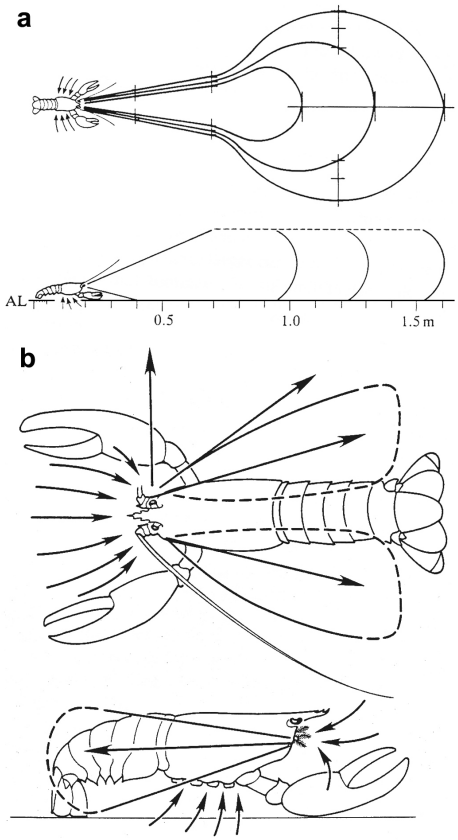

Fig.7. Information currents in *Homarus americanus.* **a.** Top and side view of the gill current of an adult lobster with mean gill current distance and standard deviations. **b.** The exopodite fan current can redirect the gill current in several ways (large arrows), drawing in water from around the animal (small arrows). Adapted from Atema (1985).

The asynchronous beating of the three maxillipede exopodites (fan organ) creates the exopodite fan current. This current can redirect the flow of the gill current backwards/upwards, and draws in a weak flow of water from around the animal's head where chemoreceptors are situated. The fan current is controlled by the animal, and may be bilateral or unilateral on either side or shut off entirely. It is used in social contexts, e.g. during fights and when the animal is investigating food odours (Atema, 1985, 1988; Breithaupt, 2001).

The most powerful lobster-generated current is the pleopod current. As the name suggests, it is produced by the beating of the pleopods, and draws water from under the animal backwards (Atema, 1985, 1988). This current is used in a number of contexts; in walking and climbing (Atema, 1995), in digging (Dybern et al., 1967; Dybern, 1973) and for 'advertising' in cohabiting males (Atema, 1985, 1988; Cowan & Atema, 1990).

Communication of dominance

As discussed above, crustaceans often use urinary chemical communication cues during fights, but less is known about what these signals tell the opponent. Part of this communication has been linked to hormonal, neurohormonal and neuromodulatory substances such as amines, peptides and steroid hormones that serve as important modulators of aggression and the associated changes in social status in many animals, including crustaceans (Kravitz & Huber, 2003; Libersat & Pflueger, 2004).

Maximal levels of aggression occur about 2-4 weeks before moulting in the American lobster, and the moulting hormone crustecdysone and related steroid hormones are thought to be linked to aggressive behaviour in lobsters and many other crustaceans (Tamm & Cobb, 1978; Bolingbroke & Kass-Simon, 2001; Huber et al., 2001).

Crustecdysone and its metabolites are mainly excreted via the urine and can change the behaviour in an opponent lobster when released instead of urine during a fight. Electrophysiological recordings have shown that crustecdysone can be perceived by lobster olfactory receptors. Thus, crustecdysone might be used during fights as a chemical signal used in coordinating aggressive behaviour (Snyder & Chang, 1991; Coglianese et al., 2004; Cromarty et al., 2004).

In lobster and crayfish fights, winner and loser effects from previous social experiences may affect the likelihood of success in subsequent encounters (Scrivener, 1971; Dugatkin & Earley, 2004). These effects have been linked to the regulation of aggressive behaviour by the amines serotonin and octopamine. Injections of serotonin and octopamine in American lobsters or crayfish produce postures resembling those normally seen in dominant (serotonin posture) and subordinate (octopamine posture) animals during and after aggressive encounters (*Fig.8.*) (Livingstone et al., 1980). These posture changes result from the amines influencing muscle neurons in opposing ways (Kravitz, 1988).

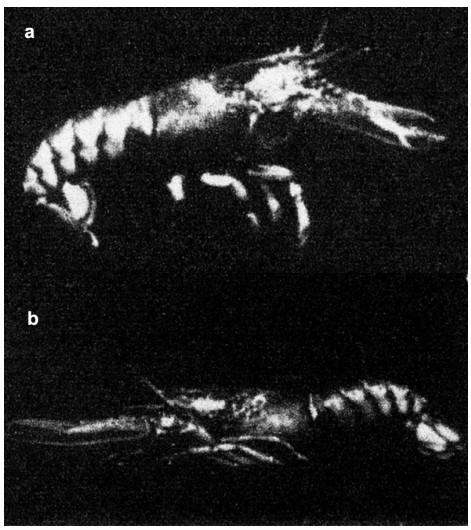

Fig.8. Rigid postures produced by amine injections in American lobsters. **a.** 'Dominant' or flexed posture after serotonin injection. **b.** 'Subordinate' or extended posture after octopamine injection. From Livingstone et al. (1980).

Low-concentration infusion with serotonin changes the willingness to fight and the frequency of withdrawal during fights. Normally, subordinate animals do not engage in aggressive interactions against known dominants for up to a week after loosing. Crayfish losers injected with serotonin, however, may engage much larger opponents in fights with prolonged bouts of fighting (Edwards & Kravitz, 1997; Huber et al., 1997a, 1997b; Huber & Delago, 1998).

'Expensive' metabolites (e.g. sulphate conjugates) of amines are released into the urine of lobsters (Kennedy, 1978; Huber et al., 1997a). If the excretion of amine metabolites is fast enough to mirror their use in the nervous system and if animals can detect these substances via chemoreceptors, each animal could evaluate the patterns of use of different amines in the nervous system of the opponent (and thereby its motivation to continue the fight?) by the pattern of metabolites released (Huber et al., 1997a; Kravitz, 2000).

The chemical senses of crustaceans

In terrestrial animals, the distinction between taste (gustation) and smell (olfaction) is quite straightforward. Gustation most often involves solid and/or dissolved chemicals (solutions) in high concentrations and is regarded as a contact sense, whereas olfaction involves airborne volatiles in low concentrations and is more of a distance sense (Laverack, 1988). In vertebrates, the organ of smell is the olfactory epithelium in the nose and gustatory receptors are found in taste buds on the tongue. Insect taste receptors are commonly found on the feet and mouthparts and olfactory receptors on the antennae.

In water, such a division of stimuli into gaseous/volatile versus solid/ fluid is not very useful. In crustaceans, the location and morphology of chemosensory structures are often used to separate olfaction and gustation. The olfactory chemoreceptive hairs are thought to be situated almost exclusively on the first antenna (antennula) (Ache, 1982; Hallberg et al., 1992, 1997), whereas hairs with gustatory chemoreceptors are found on the mouthparts, legs, claws, and spread diffusely over the entire body (Laverack, 1968; Ache, 1982; Atema, 1985).

Atema (1977) made a functional division between gustation and olfaction based on the behaviours governed by each sense. Thus, he connected gustation to basal behaviours such as feeding and olfaction to

more advanced behaviours such as searching for food or mates and social communication.

Laverack (1988) defined crustacean gustation morphologically as the sense of those organs where both chemical and mechanical receptors are present in the same sensilla (bimodal receptors). Stimulation of both receptor types is necessary for creating a response potential in the bimodal receptor cell, i.e. contact with the chemical is needed to trigger both chemo- and mechanoreceptors. In contrast, olfactory organs are unimodal with no mechanoreceptors, they perceive only chemicals and need no mechanical stimulation to do so. Henceforth, I will concentrate on the olfactory sense only, defined according to Laverack (1988), i.e. the unimodal chemosensory sensilla known as aesthetascs.

The crustacean olfactory system

The aesthetascs

In crustaceans chemoreceptor cells are situated in sensory hairs (also: sensilla or seta); hair-like cuticular structures that are spread unevenly over most of the body surface. Olfactory receptors are found in tufts of special sensilla called aesthetascs (*Fig.9, 10.*) on the outer/lateral branch (exopodite) of the antennula (Ache & Derby, 1985; Hallberg et al., 1992, 1997).

The aesthetascs are slender, unbranched hairs without visible pores in the cuticle, but a slightly 'spongy' appearance of the most distal cuticle at high magnification (Ache, 1982; Grünert & Ache, 1988; Hallberg et al., 1992, 1997; Derby et al., 1997).

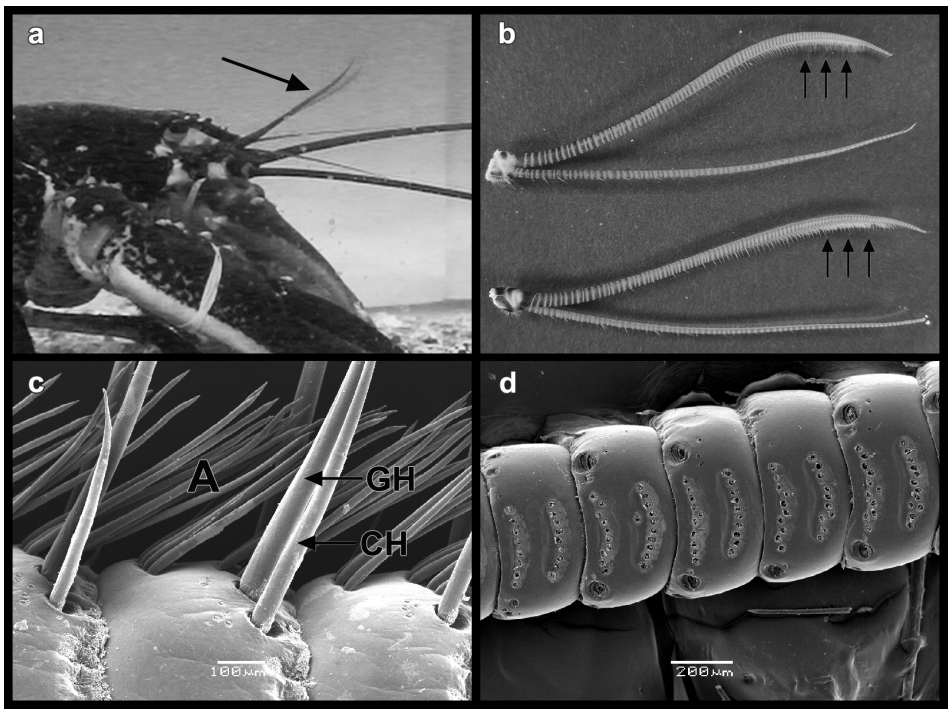

Fig.9. The morphology of the lobster antennula **a.** The front of a lobster showing the antennules (arrow). **b.** Excised antennules from a lobster showing the thinner inner/medial branch and the more robust outer/lateral branch bearing the aesthetasc tuft (arrows). **c.** SEM picture of aesthetasc hairs (A) that are arranged in two rows per annulus (antennule segment) and are surrounded by larger guard (GH) and companion hairs (CH). **d.** SEM picture of the aesthetasc sockets in two rows per annulus, surrounded by guard hair sockets. Photographs and SEM by M. Skog.

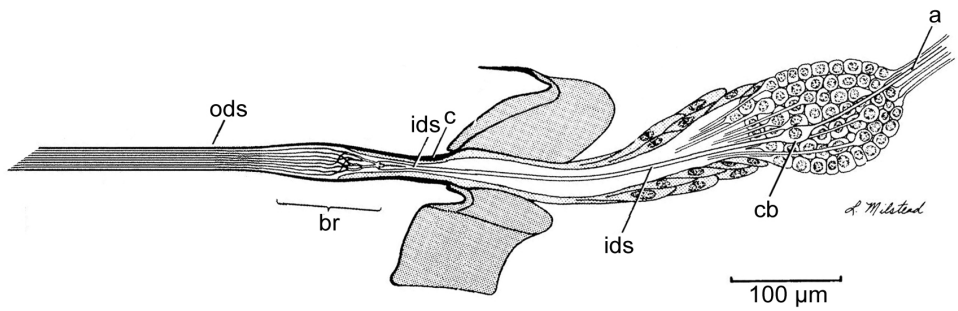

Fig.10. Schematic longitudinal section of the basal part of one decapod aesthetasc hair with a single sensory cell emphasised for clarity. **a**: axon; **br**: branching region **c**: cuticle; **cb**: sensory cell body; **ids**: inner dendritic segment; **ods**: outer dendritic segment. Adapted from Grünert & Ache (1988).

It has long been known that larger molecules have less effect than smaller on chemical receptors in crustaceans (Laverack, 1968) and this spongy part of the cuticle is believed to have mass sieving properties, i.e. very large particles cannot pass. In the spiny lobster *Panulirus argus* only molecules smaller than ca 8,5 kDa can pass the aesthetasc cuticle (Derby et al., 1997).

In decapod crustaceans the number of aesthetasc hairs varies widely with species. The shore crab has approximately 150-200 per antennula; *H. gammarus* has ca 600-900 (Skog, pers. obs.), and the spiny lobster *P. argus* has 1200-2500 aesthetascs present on each antennula depending on individual size (age) (Spencer & Linberg, 1986). The distribution and size of the aesthetascs also vary between taxa, but in European lobsters the aesthetasc tuft covers approximately 1/3 of the entire length of the antennula and aesthetascs are situated in two rows per annulus (antennule segment). *H. gammarus* aesthetasc hairs are about 700 µm long and 20 µm in diameter (**PAPER V**). In most species there is no obvious difference in antenna morphology between the sexes, but **PAPER V** reveals several differences between males and females in the European lobster.

In decapods, each aesthetasc is innervated by large numbers of bipolar olfactory receptor neurons. 350-500 receptor cell bodies may be present in each sensillum in decapods, each projecting one neuron to higher olfactory centra in the crustacean brain (Laverack, 1968; Ache, 1982; Ache & Derby, 1985; Hallberg et al., 1992, 1997).

Each receptor cell usually gives rise to two dendrites, and the inner dendritic segment projects from the cell body into the lumen of the sensillum where it branches into two outer dendritic segments, which in turn branch into multiple cilia (*Fig. 10.*). The cell bodies of each receptor cell in the aesthetasc hair lie gathered in a cluster below the base of the hair (Ache, 1982; Ache & Derby, 1985; Grünert & Ache, 1988; Hallberg et al., 1992, 1997).

The chemoreceptor cell

Different chemoreceptor cells (chemoreceptor neurons) respond to different stimuli depending on which odorant receptor (OR) protein they express. For each receptor type (protein), there is a 'best compound' and a few others that may also elicit a weaker response. More than one OR protein may be expressed on each neuron (ORN, odorant receptor neuron), and the ORNs with the same 'best compound' can have different 'second-best compounds'. They may also be inhibited by different compounds in different amounts and show different 'mixture interactions' (response to a mixture different from what would be expected from the responses to the components of the mixture) (Derby, 2000).

In decapods, it seems that different OR proteins are distributed evenly across all or almost all aesthetascs (Steullet et al., 2000). Odorant receptor proteins and odorant

receptor genes, coding for these proteins, have not been sequenced for crustaceans (Eisthen, 2002). In contrast, odorant receptor genes have been fully sequenced in e.g. the rat and the fruit fly (Buck & Axel, 1991; Vosshall et al., 1999).

Insect and mammal ORNs are not in direct contact with the environment, but rather surrounded by mucus in the olfactory epithelium (mammals) or the receptor lymph inside the sensilla (insects). Thus, airborne molecules would first have to dissolve in this watery environment and then rely on molecular diffusion as the only means for transportation to the receptor site, a very slow process. Instead, insects and mammals have specialised odorant binding proteins (OBPs) that probably help transport the chemical from the gaseous environment to the receptor site. No OBP has so far been reported for any aquatic animal, and one theory is that they are in fact not needed in an all-aquatic environment, but rather arose to transport airborne, hydrophobic compounds in terrestrial animals only (Eisthen, 2002).

Tuning and threshold levels

The range of compounds activating a given receptor can be termed the receptor's reaction spectrum or tuning. Receptors of low substrate specificity are said to have broad reaction spectra or broad tuning, whereas those with high substrate specificity have narrow reaction spectra or narrow tuning. Interesting is also the 'functional' specificity or tuning, since not all substances that potentially can be detected are behaviourally important for the animal (Ache, 1982).

In the lobster, all chemical receptors - both olfactory and gustatory - are predominantly narrow-tuned, i.e. they have very specific binding sites that respond to one or a few compounds only (e.g. taurine, L-glutamate, ammonium, AMP & ATP (Derby & Atema, 1988)). This finding was unexpected when compared to the better-studied insects where few receptors (predominantly those that react to pheromones) are narrow-tuned, whereas most other chemoreceptors have broad reaction spectra (Ache, 1982; Atema, 1985; Derby & Atema, 1988; Voigt & Atema, 1992). Specific tuning to the temporal parameters of the odour, i.e. the timing of odour pulses, also seems important in lobsters (Gomez & Atema, 1996a, 1996b).

Crustaceans as a group are extremely sensitive to their chemical environment. The threshold level (the lowest detected concentration of a given substance) depends on physiological adaptation of the receptor - previous exposure to the same stimulus may raise the receptor threshold and thus lower its sensitivity (Ache, 1982).

Generally, aesthetasc chemoreceptors have fast adaptation and disadaptation rates and low threshold values compared to e.g. the bimodal leg chemoreceptors that are considered gustatory (Atema, 1985). The threshold of aesthetasc chemoreceptors may be as low as 10^{-13} M, and they may have a working capacity of about 10 orders of magnitude, making self-adaptation of the receptor important to ensure a good signal-to-noise ratio in e.g. chemical gradients (Derby & Atema, 1988).

Different concentrations of the same chemical may elicit different behaviours in the same animal. For example can extracts from food organisms induce arousal at below picogram quantities, walking and searching behaviours at microgram levels and ingestion or food handling at milligram concentrations, when reception shifts from olfactory to gustatory sensory cells (Atema, 1988).

Central projection and signal processing

The number of neurons from each antennula (each projecting from and representing a single receptor cell) is enormous, reaching hundreds of thousands in large decapods. The neurons are packed in bundles of axons without individual glial sheaths, that join to form the antennular nerves (one from each antennula), which in turn project to the olfactory lobes in the brain (Ache, 1982; Ache & Derby, 1985).

The olfactory lobes of crustaceans are organised into a number of subunits called glomeruli; large tangles of nerve fibres that

receive input from groups of axons (=chemoreceptor cells), probably expressing identical OR protein genes. Decapod glomeruli are wedge- or cone shaped and stratified horizontally into three zones innervated by different interneurons. This is very different from the rounded glomeruli found in both vertebrates and insects, which show no stratification (Strausfeld & Hildebrand, 1999; Eisthen, 2002).

Neurons from the olfactory lobe project to two other centra (*Fig.11.*); 1) via the olfactory-accessory tract to the accessory lobe, and 2) via the olfactory-globular tract to the medulla terminalis and the associated hemiellipsoid bodies in the eyestalk which are supposed to be olfactory integrating centra of crustaceans, analogous to the insect mushroom bodies (Ache, 1982; Ache & Derby, 1985; Schmidt & Ache, 1997; Strausfeld & Hildebrand, 1999; Eisthen, 2002).

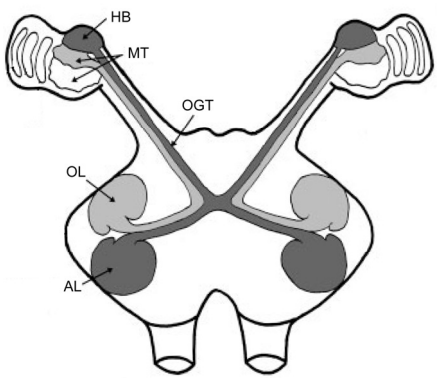

Fig.11. The morphology of the crustacean higher olfactory centra. The olfactory and accessory lobes are innervated by projection neurons, whose axons form the olfactory globular tract to the hemiellipsoid body and medulla terminalis. AL: accessory lobe HB: hemiellipsoid body MT: medulla terminalis OL: olfactory lobe OGT: olfactory-globular tract.

Sniffing in water - the importance of antenna flicking
The dense packing of the aesthetascs in tufts on the exopodite of the antennula inhibits water flow and embeds them in a viscous boundary layer of water. Exchange of this boundary layer water is obtained by flicking, a powerful beat of the entire antennula that allows rapid odour access to the lobster's aesthetasc tufts by splaying out the aesthetasc sensilla and forcing in 'new' water into the dense aesthetasc tuft (Schmitt & Ache, 1979; Ache, 1982; Atema, 1985).

Between flicks the olfactory receptors adapt to the chemical environment of the viscous layer and when the water is exchanged in the next flick, the receptors differentiate between the 'new' and the 'old' odour. These adaptations - olfactory receptor cells that adapt rapidly and high viscosity through dense packing of sensilla - are proposed as mechanisms to prevent odour reception between flicks as well as to enhance stimulus contrast during the flick and between flicks (Schmitt & Ache, 1979; Atema, 1985).

In lobsters, flicking is a very common behaviour especially when the animal is responding to external chemical stimuli (Schmitt & Ache, 1979; Atema, 1985) and it is possible to measure the number of antennula flicks in freely moving animals (Berg et al., 1992). The rate of flicking may vary, but the maximum flick rate is 4Hz (4 flicks per second) (Atema, 1995).

PROJECT DESCRIPTION

Aim

The aim of my PhD project has been to study the chemical communication system in the European lobster. Aggressive behaviours, dominance and recognition constitute a large part of the present thesis. Further, I have looked at the role of olfaction during intermoult mating and the morphology of the olfactory organ on the antennules.

PAPER I: Dominance & recognition: sex differences?

PAPER I investigated the establishment and maintenance of dominance relationships in male and female *H. gammarus* and compared fight behaviours between the sexes.

General fight procedure
Fights between pairs of same-sex size-matched lobsters were staged in a 200 l

glass aquarium filled with fresh seawater on two consecutive days. Three sides of the aquarium were covered with paper or black plastic sheets, preventing movements outside the tank from affecting the lobsters during the interaction. Video recording of interactions was made through the fourth side of the aquarium.

The two lobster opponents were allowed 10 minutes of acclimatisation to their new environment, separated by a removable opaque plastic divider. Video recording of interactions started just before the divider was lifted and continued until the consistent withdrawal of one animal confirmed the establishment or maintenance of a stable dominance relationship (or for maximum 20 minutes if no dominance was established). The animal consistently withdrawing is designated the *loser* or the *subordinate animal*, the other animal is thereby the *winner* or *dominant animal*. These descriptions are used even when referring to the first fight where dominance is not yet settled, indicating the eventual loser or winner of that fight.

Familiar/Unfamiliar opponent treatments

Each lobster was rematched in the second encounter (24±4 h later) against either the same individual as on the first day (familiar opponent) or against an unfamiliar lobster of the opposite dominance status. The unfamiliar interactions thus used four size-matched lobsters of the same sex that were randomly paired for the first fight, which followed the general fight procedure above. In the second interaction, these two lobster pairs were switched, so that the winner from one fight pair met the loser from the other equal-sized pair. This way, all four lobsters met a size-matched unfamiliar opponent of the opposite dominance status but unfamiliar individual identity on the second day (*Fig.12*.).

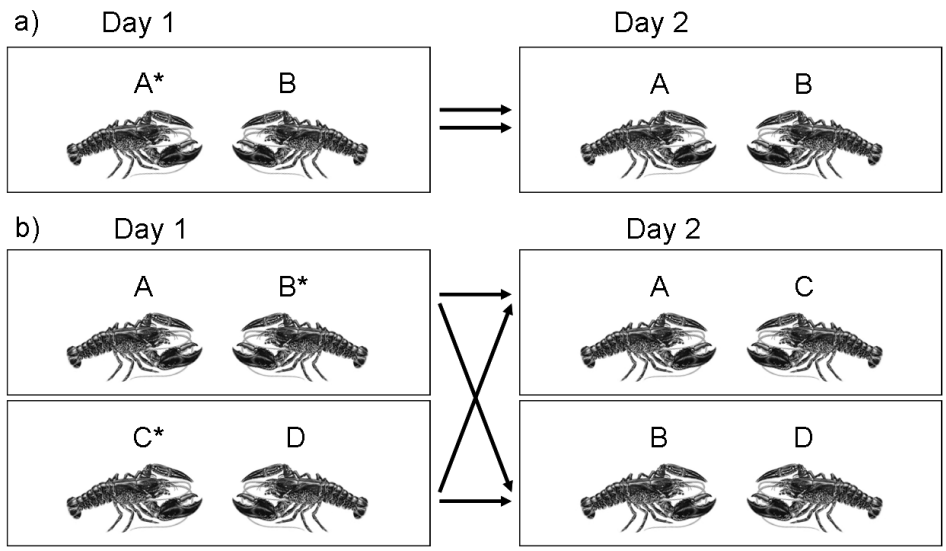

Fig.12. Procedure for familiar (a) and unfamiliar (b) opponent interactions. A, B, C & D indicate different lobster individuals and * indicate the lobster that won (i.e. became dominant) in the first fight. **a**. Familiar opponent treatment: the same lobster pair met on two consecutive days. **b**. Unfamiliar opponent treatment: four size-matched lobsters were paired randomly and allowed to establish dominance in a first interaction. Next day, the dominant animals from the two pairs were switched, so each first day loser met the winner from the other equal-sized pair. This way, all four lobsters met a size-matched unfamiliar opponent of the opposite dominance status but unfamiliar individual identity on the second day.

Tab.1. Definitions of agonistic intensity levels in lobster interactions

Intensity level [a]	Label	Behaviours involved [b]
-2	Fleeing	Tail flip away, jump away, walk away fast, run away
-1	Avoidance	Turn away, walk away slow
0	Separate	>1 body length apart, no activity
1	Approach	Face, turn towards, follow, walk towards
2	Threat display	High on legs, meral spread, claw open, claw forward, run towards
3	Physical contact	Antenna touch, antenna whip, claw touch, claw tap, claw push, claw box, claw scissoring
4	Claw lock	One or both claws held onto opponents body
5	Unrestrained	Claw snap, claw rip, aggressive tail flip

[a] Negative values signify defensive behaviours, whereas positive values indicate increasingly aggressive behaviours. [b] List of specific behaviours included in each intensity level, adapted from Karavanich & Atema (1998a). For definitions of behaviours, see Atema & Voigt (1995).

Analysis of duration and fight behaviours

The fight duration and use of different fight behaviours during the fight were analysed in all agonistic interactions. First day fights below 30 seconds were considered too short to ensure a stable dominance establishment, and were not continued with a second interaction. Likewise, first fights where no dominance was established after 20 minutes of aggressive interaction were also disqualified from analysis.

Agonistic levels (*Tab.1.*) and behaviour patterns defined previously for American lobsters were used, since these are easily recognised and can be quantified in real time or from video recordings of interactions (Atema & Voigt, 1995). The two closely related *Homarus* species presumably use similar behaviours.

These behaviours were always treated as mutually exclusive in the analysis, i.e. one animal could not perform several behaviours simultaneously. If behaviours could indeed coexist, high-level aggression outranked lower levels, and more defensive behaviours outranked less defensive behaviours. Emphasis in the analysis has been on the three highest (aggressive) and the two lowest (defensive) agonistic levels.

It is worth mentioning that I have looked only at agonistic behaviours occurring *during* each fight, not the behaviours preceding it or following it. The start of the fight was defined as *first approach by one animal followed by mutual agonistic behaviour above level 2* and the end of the fight as *start of withdrawal (avoidance or fleeing) by one animal followed by at least 5 minutes with no further aggressive behaviour above level 2 by that animal.*

Thus, 'normal' second day interactions with a subordinate animal moving away constantly from an intimidating dominant will have the fight duration zero and no aggressive or defensive behaviours scored in either animal, since these behaviours were not both preceded and followed by mutual aggressive behaviours.

Results

Both males and females established and maintained dominance. As expected for stable dominance relationships, second encounters against familiar opponents had shorter fight duration and less aggression than first fights in both sexes.

More unexpected was the finding that females used more high-level aggression than males and that the response to unfamiliar opponents differed between sexes. Male losers differentiated between familiar and unfamiliar dominant animals whereas female losers showed similar responses to both familiar and unfamiliar dominants. Thus, male-male unfamiliar interactions

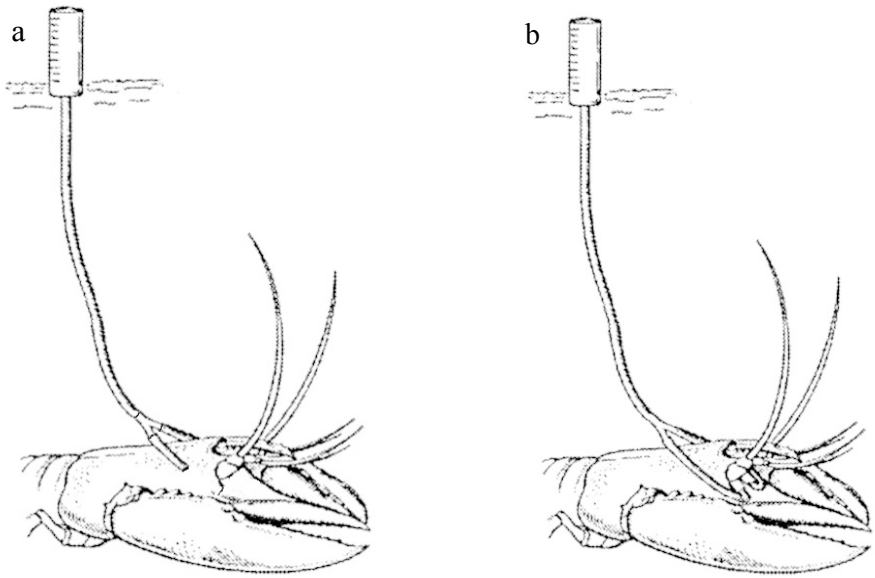

Fig.13. Attachment of catheters and collection vial to lobsters in urine blocked treatment fights. **a.** First day blocked fight: only collection tube and bottle attached, catheters were not attached to nephropores and do not block urine release. **b**. Second day blocked fight: catheters connect nephropores to the collection bottle and tubing, blocking urine release to the environment. Adapted from Breithaupt et al. (1999).

were as long and aggressive as other first day interactions and former losers won 1/3 of these fights. In contrast, female second day interactions were short and with very little aggression both when losers met familiar and unfamiliar winners and there were no dominance reversals. These results imply that male *H. gammarus* recognise familiar individuals, whereas females use status recognition rather than familiarity.

PAPER II: The role of urine in dominance maintenance

Together with co-workers at Hull University, the role of urine signals in male European lobster dominance maintenance was studied in **PAPER II**.

Blocked/Unblocked urine release treatment

The general fight procedure described for **PAPER I** was followed with slight alterations. Pairs of lobsters were allowed to establish dominance in a first interaction, then were rematched with free urine release (unblocked) or carrying special catheters that prevent urine release to the environment and thus remove all urinary signals. Unblocked treatment animals were completely unrestrained in both interactions. Blocked treatment animals carried tubing connecting to a bottle floating at the water surface during this first fight (*Fig.13a.*) and plastic tubing was glued around the animals' nephropores and connected to the collection bottle at the surface in the second interaction (Breithaupt et al., 1999) (*Fig.13b*). Durations and agonistic behaviours were analysed as in **PAPER I**.

Results

When urine release was blocked in second day interactions, the normal decrease in fight duration and aggression was absent. Instead, fight durations and aggression levels did not differ between days in interactions with blocked urine release, confirming the importance of urine signals for normal dominance maintenance in male *H. gammarus*.

PAPER III: Mating behaviours and the role of olfaction

PAPER III is a study of the behaviours and chemical communication associated with intermoult reproductive behaviours in *H. gammarus*, investigating the role of olfaction in males and females.

Intersexual interactions & antennule ablations

The procedure for the intermoult mating experiments was similar to the general fight procedure described in **PAPER I**, except that the lobsters were not same-sex, but a size-matched pair of one male and one female, and that most pairs met only once (though some met on two consecutive days).

To study the role of olfaction, either the male or the female in each pair had its antennules treated with distilled water for 10 minutes (olfactory ablation) to block the olfactory input from the antennules temporarily and reversibly, probably through osmotic shock (Derby & Atema, 1982; Gleeson et al., 1996, 1997; Karavanich & Atema, 1998b). All treated animals were allowed 30 minutes to recover from handling, followed by the normal 10-min acclimatisation of both animals to the interaction aquarium and a subsequent 30-min intersexual interaction according to the general procedure. The ablation procedure was repeated in other lobster pairs with seawater-treatment of the antennules (sham ablation/control) of either the male or the female.

Analysis of reproductive behaviours

Five different intersexual behaviours (*Tab.2.*) were used in the analysis of all male-female interactions. The number, latency (from lifting the divider to the first start of each behaviour), duration of the behaviour the first time it is performed (first duration) and total duration of each behaviour during the entire interaction (summed duration) were compared between treatments. Male mouthpart touching could coincide with mounting and turning, but all other behaviours were treated as mutually exclusive.

Tab.2. Definitions of intersexual behaviours

Sex [a]	Label	Intersexual behaviours [b]
F	Present tail	The female turns in front of the male, positioning her tail directly in front of him, and stops moving
M	Mouthpart touching	The male uses the maxillipedes to touch the female, usually on the tail/carapace before and during mounting and turning
M	Mount	The male climbs onto the females carapace, usually from behind
M	Turn	The male uses his walking legs and maxillipedes to turn the female after mounting is completed
F/M	Copulation	The female is on her back with outstretched claws, the male is on top of her. The male inserts his gonopods into the females spermatheca
M	Ejaculation [c]	Several rapid thrusting movements by the abdomen of the mail signify the ejaculation of his spermatophore and thus mating success

[a] The sex that performed each behaviour.
[b] Adapted from Atema et al. (1979).
[c] Not analysed statistically.

Results
17 matings and 25 additional mating attempts in 55 intermoult interactions between one male and one female European lobster indicate that this might be a common reproductive strategy in *H. gammarus*. Males that did not become dominant over the female rarely showed any courtship behaviours and never attempted mating. Previous insemination of the female did not affect subsequent courtship and mating, and individual lobsters (both males and females) mated 2-5 times with different partners.

Antennule ablations clearly demonstrate that male but not female olfaction is crucial for intermoult courtship and mating behaviours, since no mating behaviours and very few courtship behaviours were performed by olfactory ablated males, while the blocking of female olfaction did not affect these behaviours.

PAPER IV: Interspecific dominance and recognition

Interspecific communication and dominance maintenance between *H. gammarus* and *H. americanus* was studied in **PAPER IV.**

Conspecific and interspecific fights
The general fight procedure from **PAPER I** was followed, using either two European lobster males (conspecific/European-European) or one European and one American lobster male (interspecific/ European-American) that met the same opponent on two consecutive days. If both species use identical signals for dominance maintenance, there would be no differences between the conspecific and interspecific interactions. In contrast, species differences in the communication of e.g. dominance and subordinance would most probably result in differences in fight behaviours and/or fight duration. Behaviours and durations were analysed as in **PAPER I**.

Results
European lobsters won most interspecific fights (67%; EurW). Conspecific European interactions and EurW interspecific interactions both had shorter second fights with little aggression, normal for stable dominance relationships. Thus, dominance can be formed and maintained between a European and an American lobster, showing that interspecific communication occurs between these two closely related species (probably through urinary chemical cues).

American losers are possibly better at recognising European winners than vice versa, since interspecific interactions won by American lobsters (AmW) did not differ significantly in length or in the use of aggressive behaviours between the first and the second day. However, AmW fights were fewer than EurW interspecific fights and further replication may help interpreting these results.

PAPER V: Antenna morphology

PAPER V is a morphological study of the aesthetascs and their distribution on the antennula in male and female European lobsters.

Morphological preparations
Entire antennules were cut with sharp scissors and fixed in 70 % ethanol for SEM (scanning electron microscopy). The number of annuli (antennule segments) distal to, proximal to and within the aesthetasc tuft was counted in a preparation light microscope. For SEM, specimens dehydrated in alcohol were either air dried (for counting the number of aesthetascs per annulus) or critical point-dried (for measurements of aesthetasc lengths and diameters) before mounting and sputter coating the antennules and examination in a scanning electron microscope.

Results
The European lobster antennules demonstrated unique sex differences in size and distribution of the aesthetascs. Females had more annuli with aesthetascs than males at the same carapace length. Further, female aesthetascs were significantly longer (average 722 μm) than those in males (average

692 μm). In contrast, each annulus contains on average 22 aesthetascs in males and 20 in females, possibly compensating for the fewer number of annuli with this type of sensory hair in males. The median diameter (ca 18 μm) of the hairs did not differ between sexes (*Fig.9.*).

Discussion & future research

Until now, American and European lobster behaviour has been assumed to be very similar, even identical. When I started my thesis work there were only three previous studies on agonistic interactions in European lobsters (Debuse et al., 1999, 2003; van der Meeren & Uksnøy, 2000).

van der Meeren & Uksnøy (2000) studied the probability of winning in single aggressive interactions between wild and cultured male European lobsters. Cultivated lobsters often develop two scissor-type claws instead of the normal set of one crusher and one scissor claw. This study concluded that wild lobsters (with a crusher claw) or cultivated lobsters with very large claws became dominant in these fights.

Debuse *et al.* (1999, 2003) studied intersexual interactions and the influence of sex ratio and shelter abundance on competition in mixed-sex groups of six lobsters (85.0-104.9 mm CL). These interactions mostly involved only low levels of aggression as a result of the deliberate use of different-sized lobsters and, most importantly, of not starting observations until 1-2 days after introducing all animals into the experiment tank. Thus, initial interactions between closely size-matched unfamiliar animals that might normally involve high-level aggression during dominance establishment were not observed by Debuse *et al.*

PAPER I demonstrated high female aggression and low general levels of ritualisation in *H. gammarus*, deviating significantly from what is known for *H. americanus*. Escalation of fights in *H. gammarus* went from low-key physical contact directly to unrestrained violence, whereas both crayfish and American lobsters escalate from pushing etc to mutual claw lock as a strength assessment before rare instances of unrestrained violence (Atema & Voigt, 1995; Moore, 2007).

Further, highly ritualised behaviours like meral spread and mutual claw lock were uncommon in European lobsters. Threat behaviours instead mostly involved only 'high on legs' with the claws closed and held low. At the same CL, *H. americanus* always have bigger claws than same-sex *H. gammarus* (Phillips et al. 1980). Thus, possibly the need for ritualisation of fights is less pronounced in the European species than in the American due to its smaller weapon size.

Generally in crustaceans, males are regarded as more aggressive than females and fight more often (Scrivener, 1971; Moore, 2007) and no other study on crustaceans has shown higher aggression levels in females than in males. These findings may be the first of many important differences between the two closely related *Homarus* species, and may help us understand competitive interactions between invasive American lobsters and native European lobsters.

The sex difference shown in recognition mechanism and dominance maintenance is unique among crustaceans so far, but female aggression and dominance are generally poorly understood, and further studies may find unpredicted sex differences in these behaviours in other species as well. Dominance has mostly been studied in male crustaceans, but female *H. americanus* appear to establish dominance as well (Atema et al. 1999). Possibly, the establishment of dominance relationships and memory of former opponents is more important for male lobsters, where dominance is possibly correlated directly to reproductive success (Atema & Steinbach, 2007), than for females, where the benefits of being dominant might be less pronounced.

Not very surprisingly, **PAPER II** showed that urine communication is important in male *H. gammarus* dominance maintenance, as it is in both American lobsters and crayfish (Karavanich and Atema 1998b; Zulandt

Schneider et al. 2001). Not only the chemical components of the urine but also the mechanosensory component or the volume of urine released may be important during fights. In both *A. leptodactylus* and *H. americanus*, aggressive fight behaviours must be associated with urine release to be efficient. Furthermore, escalation of aggression to higher levels will increase the probability of urine release (Breithaupt & Atema 2000; Breithaupt & Eger 2002), and winning American lobsters released more urine early in the fights than eventual losers (Breithaupt & Atema 2000). It is not known if the quantity or the quality (e.g. the pheromone content) is more important in urine communication, and future studies should address this question.

These studies of urine release dynamics during fights used volume measurements of urine release by catheterisation in *H. americanus* (Breithaupt & Atema 2000) or dyeing the urine with fluorescein in *A. leptodactylus* (Breithaupt & Eger 2002); techniques that can be used in the future to reveal more about urine communication in *H. gammarus*. In late august 2007, I finally managed to visualise urine release in fighting males after many failed attempts, but that was unfortunately too late to use in any of my experiments. Further, reversible antennule ablations with distilled water, as in **PAPER III**, or removal of the olfactory sensilla on the first antenna through shaving could tell us if urinary recognition in European lobsters is mediated by the aesthetascs, as in American lobsters (Karavanich & Atema 1998b; Johnson & Atema 2005).

Reproductive behaviours in the European lobster have not received much interest previously, but Debuse et al (1999, 2003) studied how intersexual interactions were affected by different shelter abundances and sex ratios in groups of lobsters, and reported courtship behaviours and matings both inside and outside shelters. The moult stage of these animals was not determined.

In **PAPER III**, intermoult matings were found to be common in a laboratory setting, and this might be a common natural phenomenon in *H. gammarus*. Intermoult mating is now accepted as an alternative mating strategy in very large American lobster females that moult more seldom and therefore need to refill their sperm store since they must fertilise two broods (i.e. lay eggs twice) between moulting as well as for females that received very little sperm or failed to mate or at the time of their moult (Waddy & Aiken, 1990, 1991; Atema & Steinbach, 2007).

Further, intermoult females that were inseminated at their latest moult may encounter males that are superior to their former mate, and mate with them to replace the sperm stored from the inferior male. This hypothesis assumes that sperm competition with last male sperm precedence occurs in lobsters, as in some other crustaceans (Sevigny & Sainte-Marie, 1996; Galeotti et al., 2007).

For the future, long-term studies of European lobsters in large, naturalistic settings will be useful to better understand the context of aggressive behaviours, dominance maintenance and both postmoult and intermoult mating behaviours. In the summer of 2004, I did one such study, but only a few male-male aggressive behaviours and no reproductive behaviours were seen at that time.

Chemical communication is an important part of the reproductive behaviours in American lobsters. Female *H. americanus* are attracted chemically to male shelters from a distance by substances in the male urine (Bushmann & Atema, 1997, 2000), are able to distinguish male status from chemical cues in the urine and prefer to associate with dominant males (Cowan & Atema, 1990; Bushmann & Atema, 2000). Males, on the other hand, show no distance attraction to female shelters, but investigate them once nearby (Bushmann & Atema, 1997).

Both male and female American lobsters often visit shelters of resident (dominant) males. Females of all moult stages are allowed to enter the male shelter after only mild aggression from the resident whereas visiting males are met with high aggression

and only enter the shelter if the resident is evicted (Bushmann & Atema, 1997, 2000). Both sexes release more urine when visiting a male shelter than in isolation, and if female urine release is blocked by catheters, she is met with as much aggression as a visiting male and mating attempts become few. Thus, female urine signals are believed to reduce male aggression and facilitate mating in *H. americanus* (Bushmann & Atema, 1997).

However, in groups of American lobsters studied in naturalistic aquaria, the removal of the male antennules (olfactory ablation) did not affect normal cohabitation and (softshell) mating behaviours. In contrast, when the female antennules were removed, pair formation and cohabitation became rare and of very short duration, and moulting females were injured or even killed (Cowan, 1991). Olfactory-ablated males could possibly use contact-chemosensory receptors on the mouthparts and legs instead of olfaction; these appendages were used more than normally during the female moult in treatment males. Female olfaction thus seems to play a critical role in *H. americanus* reproductive behaviour.

The olfactory ablation experiments on European lobster males or females in **PAPER III** demonstrated that male but not female olfaction is crucial for normal intermoult courtship and mating behaviours. This dependence on male olfaction may indicate the presence of a female sex pheromone that is needed for intermoult courtship and copulation. It seems that this female pheromone is produced throughout the female moult cycle, as opposed to the moulting pheromones released by female crabs (Gleeson, 1991; Bamber & Naylor, 1997; Hardege et al., 2002; Kamio et al., 2000). The presence of this pheromone seems enough to reduce aggression and induce mating in *H. gammarus*, and possibly in *H. americanus* as well, since female urine signals are very important in American lobster courtship (Bushmann & Atema, 1997).

Female sex discrimination, on the other hand, seems to depend on non-olfactory cues, and may be based on visual, tactile or other (contact) chemosensory cues from the male, combined with characteristic male behaviours like mouthpart touching and mounting.

With *H. americanus* being introduced into European waters, transfer of disease, competition and hybridisation between the two species pose threats to the native *H. gammarus* populations. In evolutionary terms, the geographical separation of the two *Homarus* species has been short (Phillips et al., 1980; Williams, 1995). Thus, pheromones and behaviours may not have changed enough for reproductive isolation barriers to be in place; especially since the two species have had no contact during this time. If the same or similar chemical 'language' (pheromones) and reproductive behaviours are used by the two species, hybridisation may occur spontaneously in natural conditions, resulting in partly sterile offspring (Carlberg et al., 1978; Talbot et al., 1984; Mangum, 1993).

In evolutionary terms, the separation of the two *Homarus* species (10 000 years) is short and maybe not sufficient to change pheromones and behaviours enough for reproductive isolation barriers to be in place; especially since the two species have had no contact during this time. If the two species use the same or similar chemical 'language' (pheromones) and reproductive behaviour, hybridisation may occur spontaneously in natural conditions.

In small heterospecific groups of lobsters consisting of one premoult European lobster female and a pair of one American and one European lobster males, the females seemed to prefer to mate with the conspecific male even when he was subordinate to the American male. There were no sexual interactions between species and no sexual response to *H. gammarus* females by *H. americanus* males. These findings suggest that there are pre-mating barriers that prevent natural hybridisation between the two species (van der Meeren et al., 2008).

In contrast, **PAPER IV** showed that interspecific communication during agonistic interactions occurs between *H. gammarus* and *H. americanus* males, since dominance is both established and maintained through either recognition of familiar individuals or of dominance status between species.

In an interspecific lobster study by van der Meeren & Ekeli (2002), American lobsters of both sexes dominated over and successfully evicted same-sex European lobsters from shelters, while **PAPER IV** found that European lobsters won a majority of the staged 'boxing matches'. The two experimental situations are not entirely comparable, since the two species may behave differently when competing for shelters in a relatively large arena (van der Meeren & Ekeli, 2002) than when fighting each other in a relatively confined space (**PAPER IV**). Similarly, Jensen et al. (2002) found that in two competing crab species in the US (*C. maenas* and *Hemigrapsus sanguineus*), *C. maenas* compete harder for food while *H. sanguineus* compete harder for shelters.

Even if natural hybridisation between the two species is unlikely if European lobster females prefer to mate with same-species males, aggressive competition for food and shelter resources may be further complicated by social recognition between the species as shown in **PAPER IV** as well as other forms of interspecific communication yet to be found.

Studies of both European-European and European-American communication during agonistic interactions using catheters or antennule ablations (Karavanich & Atema, 1998b) as well as urine dyeing (Breithaupt & Eger, 2002) would provide further information about how and when this communication takes place.

Sexual dimorphism of the sensory organs is a very evident phenomenon in many insects, with well-developed male antennae and less prominent female antennae. However, in decapod crustaceans, sexual dimorphism of the antennules as shown in **PAPER V** is almost unknown, even if Marcus (1912) reported sexual dimorphism in some squat lobsters (galatheids), where males had longer aesthetascs and higher numbers of aesthetascs than females.

In other groups of crustaceans, sexual dimorphism of the olfactory apparatus is much more common. Copepods, amphipods, isopods, cumaceans and mysids often display obvious differences between the sexes, either in the number of aesthetascs per segment on the antennula, the size of aesthetascs, or the presence of male-specific sensilla or a chemosensory organ called callynophore. The typical pattern is enhanced male chemosensory structures, in most cases correlated to males locating females and/or putative male pheromone perception (Guse, 1983a; Lowry, 1986; Johansson & Hallberg, 1992, 1997; Johansson et al., 1996; Boxshall & Huys, 1998; Miller et al., 2005).

PAPER V, on the other hand, demonstrated more developed aesthetascs found on more annuli on the antennule in female, not male, lobsters. Reproductive communication is one likely cause of sex differences in the chemosensory organs. As discussed above, female olfaction is crucial during several phases of American lobster reproduction including mate location, evaluation and courtship (Cowan, 1991; Bushmann & Atema, 2000). Aggressive behaviours and the type of recognition used also differ between sexes (**PAPER I**), but these differences are less likely to result in sexual differences in the olfactory organ than reproductive communication.

The chemical structure of the pheromone substances used in lobster communication (sexual pheromones, dominance recognition, recognition of familiar individuals) is still an enigma. One problem is to develop a reliable, simple and cheap behavioural essay for testing urine fractions and putative pheromones. In crabs, the precopulatory embrace has been used successfully as such a bioassay, but unfortunately no behavioural essay in lobsters has been very reliable. When I presented a sponge soaked in the tank water of a recently moulted female to a

European lobster male, he showed no response whatsoever to the sponge.

Further, with a student I tried to use non-invasive IR-measurement of heart rate changes in lobsters while introducing different chemical stimuli. These measurements unfortunately produced no clear-cut results and had the problem of high noise levels and disturbances. Further, heart rate changes are not expected to be a specific pheromone response, but may still provide a measurement of lobster 'excitement' at different odours. Another non-specific measure that might be used to measure 'excitement' is the flicking rate of the antennules, which is thought to increase when the animal is more interested.

Electrophysiological methods have been employed very successfully in insect pheromone research, and with another student I have tried to use electrophysiology to find receptors in the antenna of the shore crab *C. maenas* (since getting enough animals proved hard in lobsters) that responded to female urine or a still unpublished putative artificial pheromone sent to us from Jörg Hardege et. al in Hull. This is a difficult technique, especially in seawater, and we ran into a number of technical problems with minimising noise levels. In one of the last weeks of this experiment, we found one single chemoreceptor that did respond to the putative pheromone but not to food stimuli; possibly a pheromone receptor?

The study of European lobster behaviours and communication presented in this thesis has provided several surprising results, both in the light of what is known about its closest relative *H. americanus* as well as crustaceans in general. Further comparative studies of males and females as well as between other closely related species pairs may prove useful in future behavioural and morphological investigations. The development of a reliable pheromone essay is a major issue for future crustacean communication studies, and electrophysiological methods can possibly be refined to find pheromone receptors.

REFERENCES

ACHE, B. W. (1982). Chemoreception and thermoreception. In: The biology of Crustacea (H. L. Atwood & D. C. Sandeman, eds.). Academic Press, New York, p. 369-398.

ACHE, B. W. & DERBY, C. D. (1985). Functional organization of olfaction in crustaceans. Trends Neurosci 8, 356-360.

ADAMS, E. S. & CALDWELL, R. L. (1990). Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. Anim Behav 39, 706-716.

ADAMS, E. S. & MESTERTON-GIBBONS, M. (1995). The cost of threat displays and the stability of deceptive communication. J Theor Biol 175, 405-421.

AIKEN, D. E. (1980). Molting and growth. In: The biology and management of lobsters. Volume I: Physiology and Behavior (J. S. Cobb & B. F. Phillips, eds.). Academic Press, New York, 91-136.

AIKEN, D. E. & WADDY, S. L. (1980). Reproductive biology. In: The biology and management of lobsters. Volume I: Physiology and Behavior (J. S. Cobb & B. F. Phillips, eds.). Academic Press, New York,. p. 91-163.

AMEYAW-AKUMFI, C. & HAZLETT, B. A. (1975). Sex recognition in the crayfish *Procambarus clarkii*. Science 190, 1225-1226.

ANDERTON, T. (1909). The lobster, *Homarus vulgaris*. Rept Mar Dept New Zealand 1908-1909, 17-23.

ASAI, N., FUSETANI, N., MATSUNAGA, S. & SASAKI, J. (2000). Sex pheromones of the hair crab *Erimacrus isenbeckii*. Part 1. Isolation and structures of novel ceramides. Tetrahedron 56, 9895-9899.

ATEMA, J. (1977). Functional separation of smell and taste in fish and Crustacea. In: Olfaction and taste VI. (J. Le Magnen & P. Mac Leod, eds.) Information Retrieval, London, 165-174.

ATEMA, J. (1985). Chemoreception in the sea: adaptations of chemoreceptors and behaviour to aquatic stimulus conditions. In: Physiological adaptations of marine animals. (M. S. Laverack, ed). Cambridge University Press, Cambridge, p. 387-423.

ATEMA, J. (1986). Review of sexual selection and chemical communication in the lobster, *Homarus americanus*. Can J Fish Aquat Sci 43, 2283-2290.

ATEMA, J. (1988). Distribution of chemical stimuli. In: Sensory biology of aquatic animals (J. Atema, R. R. Fay, A. N. Popper & W. N. Tavolga, eds.). Springer Verlag, New York, p. 29-56.

ATEMA, J. (1995). Chemical signals in the marine environment: Dispersal, detection, and temporal signal analysis. Proc Natl Acad Sci USA 92, 62-66.

ATEMA, J. & ENGSTROM, D. G. (1971). Sex pheromone in the lobster *Homarus americanus*. Nature 232, 261-263.

ATEMA, J. & STEINBACH, M. (2007). Chemical communication and social behavior of the lobster *Homarus americanus* and other decapod Crustacea. In: Evolutionary ecology of social and sexual systems. Crustaceans as model organisms (J. E. Duffy & M. Thiel, eds.). Oxford University Press, p. 115-144.

ATEMA, J. & VOIGT, R. (1995). Behavior and sensory biology. In: Biology of the lobster *Homarus americanus* (J. R. Factor, ed). Academic Press, p. 313-348.

ATEMA, J., JACOBSON, S., KARNOFSKY, E., OLESZKO-SZUTS, S. & STEIN, L. (1979). Pair formation in the lobster *Homarus americanus*: behavioral development, pheromones and mating. Mar Behav Physiol 6, 277-296.

ATEMA, J., BREITHAUPT, T., LEVAY, A., MORRISON, J., MALLIDIS, M. & EDATTUKARAN, M. (1999). Urine pheromones in the lobster, *Homarus americanus*: both males and females recognize individuals and only use the lateral antennule for this task. Chem Senses 24, 615-616.

BAMBER, S. D. & NAYLOR, E. (1997). Sites of release of putative sex pheromone and sexual behaviour in female

Carcinus maenas (Crustacea: Decapoda). Est Coast Shelf Sci 44, 195-202.

BARDACH, J. E. (1974). Chemoreception of aquatic animals. In: Olfaction and taste V (D. A. Denton & J. P. Coghlan, eds.). Academic Press, New York, p. 121-132.

BARNARD, C. J. & BURK, T. (1979). Dominance hierarchies and the evolution of 'individual recognition'. J Theor Biology 81, 65-73.

BARROWS, E. M., BELL, W. J. & MICHENER, C. D. (1975). Individual odor differences and their social functions in insects. Proc Natl Acad Sci USA 72, 2824-2828.

BERG, K., VOIGT, R. & ATEMA, J. (1992). Flicking in the lobster *Homarus americanus*: recordings from electrodes implanted in antennular segments. Biol Bull 183, 377-378.

BERGMAN, D. A., KOZLOWSKI, C. P., MCINTYRE, J. C., HUBER, R., DAWS, A. G. & MOORE, P. A. (2003). Temporal dynamics and communication if winner-effects in the crayfish, *Orconectes rusticus*. Behaviour 140, 805-825.

BERKEY, C. & ATEMA, J. (1999). Individual recognition and memory in *Homarus americanus* male-female interactions. Biol Bull 197, 253-254.

BERRILL, M. (1974). The burrowing behavior of newly settled lobsters *Homarus vulgaris* (Crustacea: Decapoda). Journal of the Marine Biological Association of the United Kingdom 54, 797-801.

BERRILL, M. & ARSENAULT, M. (1982). Mating behavior of the green shore crab *Carcinus maenas*. Bull Mar Sci 32, 632-638.

BIELSKY, I. F. & YOUNG, L. J. (2004). Oxytocin, vasopressin, and social recognition in mammals. Peptides 25, 1565-1574.

BOLINGBROKE, M. & KASS-SIMON, G. (2001). 20-hydroxyecdysone causes increased aggressiveness in female American lobsters, *Homarus americanus*. Horm Behav 39, 144-56.

BOROWSKY, B. (1980). The pattern of tube sharing in *Microdeutopus gryllotalpa* (Crustacea: Amphipoda). Anim Behav 28, 790-797.

BOROWSKY, B. (1983). Behaviors associated with tube-sharing in *Microdeutopus gryllotalpa* (Crustacea: Amphipoda). J Exp Mar Biol Ecol 68, 39-52.

BOXSHALL, G. A. & HUYS, R. (1998). The ontogeny and phylogeny of copepod antennules. Philos Trans R Soc Lond B Biol Sci353, 765-786.

BREITHAUPT, T. (2001). Fan organs of crayfish enhance chemical information flow. Biol Bull 200, 150-154.

BREITHAUPT, T. & ATEMA, J. (2000). The timing of chemical signaling with urine in dominance fights of male lobsters (*Homarus americanus*). Behav Ecol Sociobiol 49, 67-78.

BREITHAUPT, T. & EGER, P. (2002). Urine makes the difference: Chemical communication in fighting crayfish made visible. J Exp Biol 205, 1221-1231.

BREITHAUPT, T., LINDSTROM, D. P. & ATEMA, J. (1999). Urine release in freely moving catheterised lobsters (*Homarus americanus*) with reference to feeding and social activities. J Exp Biol 202, 837-844.

BRENNAN, P. A. (2004). The nose knows who's who: chemosensory individuality and mate recognition in mice. Horm Behav 46, 231-240.

BRENNAN, P. A. & KENDRICK, K. M. (2006). Mammalian social odours: attraction and individual recognition. Philos Trans R Soc Lond B Biol Sci 361, 2061-2078.

BUCK, L. & AXEL, R. (1991). A novel multigene family may encode odorant receptors: a molecular basis for odor recognition. Cell 65, 175-87.

BURSELL, E. (1984). Observations on the orientation of tsetse flies (*Glossina pallidipes*) to wind-borne odours. Physiol Entomol 9, 133-137.

BUSHMANN, P. J. & ATEMA, J. (1996). Nephropore rosette glands of the lobster *Homarus americanus*: Possible sources of urine pheromones. J Crust Biol 16, 221-231.

BUSHMANN, P. J. & ATEMA, J. (1997). Shelter sharing and chemical courtship signals in the lobster *Homarus ameri-*

canus. Can J Fish Aquat Sci 54, 647-654.

BUSHMANN, P. J. & ATEMA, J. (2000). Chemically mediated mate location and evaluation in the lobster, *Homarus americanus*. J Chem Ecol 26, 883-899.

BUTENANDT, A., BECKMANN, R., STAMM, D. & HECKER, E. (1959). Über den sexual-lockstoff des Seidenspinners *Bombyx mori* - Reindarstellung und Konstitution. Z Naturforsch Pt B 14, 283-284.

CALDWELL, R. L. (1979). Cavity occupation and defensive behavior in the stomatopod *Gonodactylus festai*: Evidence for chemically mediated individual recognition. Anim Behav 27, 194-201.

CALDWELL, R. L. (1985). A test of individual recognition in the stomatopod *Gonodactylus festae*. Anim Behav 33, 101-106.

CALDWELL, R. L. (1992). Recognition signalling and reduced aggression between former mates in a stomatopod. Anim Behav 44, 11-19.

CARLBERG, J. M., VAN OLST, J. C. & FORD, R. F. (1978). A comparison of larval and juvenile stages of the lobsters *Homarus americanus*, *Homarus gammarus*, and their hybrid. Proc World Maricult Soc 9, 109-122.

CARR, W. E. S. (1988). The molecular nature of chemical stimuli in the aquatic environment. In: Sensory biology of aquatic animals (J. Atema, R. R. Fay, A. N. Popper & W. N. Tavolga, eds.). Springer Verlag, p. 3-27.

CASTRO, K. M. & ANGELL, T. E. (2000). Prevalence and progression of shell disease in American lobster, *Homarus americanus*, from Rhode Island waters and the offshore Canyons. J Shellfish Res 19, 691-700.

CHARMANTIER, G., HAOND, C., LIGNOT, J. & CHARMANTIER-DAURES, M. (2001). Ecophysiological adaptation to salinity throughout a life cycle: a review in Homarid lobsters. J Exp Biol 204, 967-977.

CHIVERS, D. P., KIESECKER, J. M., WILDY, E. L., ANDERSON, M. T. & BLAUSTEIN, A. R. (1997). Chemical alarm signaling in terrestrial salamanders: intra- and interspecific responses. Ethology 103, 599-613.

COBB, J. S. & WAHLE, R. A. (1994). Early life history and recruitment processes of clawed lobsters. Crustaceana 67, 1-25.

COGLIANESE, D., CROMARTY, S. I. & KASS-SIMON, G. (2004). The perception of steroid molting hormones is involved in orchestrating agonistic interactions in the American lobster, *Homarus americanus*. Society for Neuroscience Abstracts, Program No. 414.15.

COOPER, R. A. & UZMANN, J. R. (1980). Ecology of juvenile and adult *Homarus*. In: The biology and management of lobsters (J. S. Cobb & B. F. Phillips, eds.). Academic Press, NY, p 97-142.

COPP, N. H. (1986). Dominance hierarchies in the crayfish *Procambarus clarkii* (Girard, 1852) and the question of learned individual recognition (Decapoda, Astacidea). Crustaceana 51, 9-24.

CORREA, C. & THIEL, M. (2003). Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. Rev Chil Hist Nat 76, 187-203.

CORREA, C., BAEZA, J. A., DUPRE, E., HINOJOSA, I. A. & THIEL, M. (2000). Mating behavior and fertilization success of three ontogenetic stages of male rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). J Crust Biol 20, 628-640.

COWAN, D. F. (1991). The role of olfaction in courtship behavior of the American lobster *Homarus americanus*. Biol Bull 181, 402-407.

COWAN, D. F. & ATEMA, J. (1990). Molt staggering and serial monogamy in American lobsters *Homarus americanus*. Anim Behav 39, 1199-1206.

CROMARTY, S. I., BOSEMANN, D. M. & KASS-SIMON, G. (2004). The physiological basis for olfactory perception of steroids in the American lobster, *Homarus americanus*: olfaction receptor

neuron recordings. Society for Neuroscience Abstracts, Program No. 414.14.

DALE, J., LANK, D. B. & REEVE, H. K. (2001). Signaling individuality versus quality: a model and case studies with ruffs, queleas, and house finches. Am Nat 158, 75-86.

DAVID, C. T., KENNEDY, J. S., R., L. A., PERRY, J. N. & WALL, C. (1982). A reappraisal if insect flight towards a distant point source of wind-borne odor. J Chem Ecol 8, 1207-1215.

DEBUSE, V. J., ADDISON, J. T. & REYNOLDS, J. D. (1999). The effects of sex ratio on sexual competition in the European lobster. Anim Behav 58, 973-981.

DEBUSE, V. J., ADDISON, J. T. & REYNOLDS, J. D. (2003). Effects of breeding site density on competition and sexual selection in the European lobster. Behav Ecol 14, 396-402.

DERBY, C. D. (2000). Learning from spiny lobsters about chemosensory coding of mixtures. Physiol Behav 69, 203-209.

DERBY, C. D. & ATEMA, J. (1982). The function of chemo- and mechanoreceptors in lobster (*Homarus americanus*) feeding behavior. J Exp Biol 98 317-328.

DERBY, C. D. & ATEMA, J. (1988). Chemoreceptor cells in aquatic invertebrates: peripheral mechanisms of chemical signal processing in decapod crustaceans. In: Sensory biology of aquatic animals (J. Atema, A. N. Popper, R. R. Fay & W. N. Tavolga, eds.). Springer Verlag, NY, p. 366-385.

DERBY, C. D., CATE, H. S. & GENTILCORE, L. R. (1997). Perireception in olfaction: molecular mass sieving by aesthetasc sensillar cuticle determines odorant access to receptor sites in the Caribbean spiny lobster *Panulirus argu*s. J Exp Biol 200, 2073-2081.

DEVINE, D. V. & ATEMA, J. (1982). Function of chemoreceptor organs in spatial orientation of the lobster *Homarus americanus*: differences and overlap. Biol Bull 163, 144-153.

DINGLE, H. (1983). Strategies of agonistic behavior in Crustacea. In: Studies in adaptation: the behavior of higher Crustacea (S. Rebach & D. W. Dunham, eds.). John Wiley & Sons, p. 85-111.

DREWS, C. (1993). The concept and definition of dominance in animal behaviour. Behaviour 125, 283-313.

DUGATKIN, L. A. (1997). Winner and loser effects and the structure of dominance hierarchies. Behav Ecol 8, 583-587.

DUGATKIN, L. A. & EARLEY, R. L. (2004). Individual recognition, dominance hierarchies and winner and loser effects. Proc R Soc Lond B 271, 1537-1540.

DUNHAM, P. J. (1979). Mating in the American lobster: stage of molt cycle and sex pheromone. Mar Behav Physiol 6, 1-11.

DUNHAM, P. J. & SKINNER-JACOBS, D. (1978). Intermolt mating in the lobster *Homarus americanus*. Mar Behav Physiol 5, 209-214.

DYBERN, B. I. (1973). Lobster burrows in Swedish waters. Helgoländ Wiss Meer 24, 401-414.

DYBERN, B. I., JACOBSSON, L. & HALLBÄCK, H. (1967). On the habitat behaviour of the lobster (*Homarus vulgaris*) in Swedish waters. Meddelande från Havsfiskelaboratoriet i Lysekil 36, 1-13.

EALES, A. J. (1974). Sex pheromone in the shore crab *Carcinus maenas*, and the site of its release from females. Mar Behav Physiol 2, 345-355.

EDWARDS, D. H. & KRAVITZ, E. A. (1997). Serotonin, social status and aggression. Curr Opin Neurobiol 7, 812-819.

EISTHEN, H. L. (2002). Why are olfactory systems of different animals so similar? Brain Behav Evol 59, 273-93.

EKERHOLM, M. & HALLBERG, E. (2005). Primer and short-range releaser pheromone properties of premolt female urine from the shore crab, *Carcinus maenas*. J Chem Ecol 31, 1845-1864.

ELNER, R. W. (1981). Force, function and mechanical advantage in the chelae of the American lobster *Homarus*

americanus (Decapoda: Crustacea). J Zool 193, 269-286.

ENNIS, G. P. (1995). Larval and postlarval ecology. In: Biology of the lobster *Homarus americanus* (J. R. Factor, ed). Academic Press, NY, p. 23-46.

ESPMARK, Y. (1971). Individual recognition by voice in reindeer mother-young relationship. Field observations and playback experiments. Behaviour 40, 295-301.

FLIGHT, P., GERLACH, G. & ATEMA, J. (2004). Sperm load impact on female courtship behavior in the American lobster (*Homarus americanus*). Biol Bull 207, 155.

FLOETER, S. R., VAZQUEZ, D. P. & GRUTTER, A. S. (2007). The macroecology of marine cleaning mutualisms. J Anim Ecol 76, 105-111.

GALEOTTI, P., PUPIN, F., RUBOLINI, D., SACCHI, P., NARDI, P. A. & FASOLA, M. (2007). Effects of female mating status in copulation behaviour and sperm expenditure in the freshwater crayfish *Austropotamobius italicus*. Behav Ecol Sociobiol 61, 711-718.

GHERARDI, F. & ATEMA, J. (2005). Memory of social partners in hermit crab dominance. Ethology 111, 271-285.

GHERARDI, F. & DANIELS, W. H. (2003). Dominance hierarchies and status recognition in the crayfish *Procambarus acutus acutus*. Can J Zool 81, 1269-1281.

GHERARDI, F. & TIEDEMANN, J. (2004). Chemical cues and binary individual recognition in the hermit crab *Pagurus longicarpus*. J Zool 263, 23-29.

GHERARDI, F., TRICARICO, E. & ATEMA, J. (2005). Unraveling the nature of individual recognition by odor in hermit crabs. J Chem Ecol 31, 2877-2896.

GLEESON, R. A. (1980). Pheromone communication in the reproductive behavior of the blue crab *Callinectes sapidus*. Mar Behav Physiol 7, 119-134.

GLEESON, R. A. (1991). Intrinsic factors mediating pheromone communication in the blue crab, *Callinectes sapidus*. In: Crustacean sexual biology (R. T. Bauer & J. W. Martin, eds.). Columbia University Press, New York, p. 17-32.

GLEESON, R. A., ADAMS, M. A. & SMITH, A. B., III. (1984). Characterization of a sex pheromone in the blue crab, *Callinectes sapidus*: Crustecdysone studies. J Chem Ecol 10, 913-922.

GLEESON, R. A., MCDOWELL, L. M. & ALDRICH, H. C. (1996). Structure of the aesthetasc (olfactory) sensilla of the blue crab, *Callinectes sapidus*: Transformations as a function of salinity. Cell Tissue Res 284, 279-288.

GLEESON, R. A., WHEATLY, M. G. & REIBER, C. L. (1997). Perireceptor mechanisms sustaining olfaction at low salinities: Insight from the euryhaline blue crab *Callinectes sapidus*. J Exp Biol 200, 445-456.

GODARD, R. (1991). Long-term memory of individual neighbors in a migratory songbird. Nature 350, 228-229.

GOESSMANN, C., HEMELRIJK, C. & HUBER, R. (2000). The formation and maintenance of crayfish hierarchies: Behavioral and self-structuring properties. Behav Ecol Sociobiol 48, 418-428.

GOMEZ, G. & ATEMA, J. (1996a). Temporal resolution in olfaction: stimulus integration time of lobster chemoreceptor cells. J Exp Biol 199, 1771-1779.

GOMEZ, G. & ATEMA, J. (1996b). Temporal resolution in olfaction II: time course of recovery from adaptation in lobster chemoreceptor cells. J Neurophysiol 76, 1340-1343.

GOSSELIN, T., SAINTE-MARIE, B. & BERNATCHEZ, L. (2005). Geographic variation of multiple paternity in the American lobster, *Homarus americanus*. Mol Ecol 14, 1517-1525.

GRUTTER, A. S. (2004). Cleaner fish use tactile dancing behavior as a preconflict management strategy. Curr Biol 14, 1080-1083.

GRÜNERT, U. & ACHE, B. W. (1988). Ultrastructure of the aesthetasc (olfactory) sensilla of the spiny lobster, *Panulirus argus*. Cell Tissue Res 251, 95-103.

GUSE, G.-W. (1983). Die Sensillen des Lobus masculinus von Mysidaceen (Crustacea): Ihre Ultrastruktur und mögliche Bedeutung als Pheromonrezeptoren. Verh Dtsch Zool Ges, 189.

HALLBERG, E., JOHANSSON, K. U. & ELOFSSON, R. (1992). The aesthetasc concept: structural variations of putative olfactory receptor cell complexes in Crustacea. Microsc Res Techniq 22, 325-335.

HALLBERG, E., JOHANSSON, K. U. I. & WALLÉN, R. (1997). Olfactory sensilla in crustaceans: morphology, sexual dimorphism, and distribution patterns. Internat J Insect Morph Embryol 26, 177-180.

HALLBÄCK, H. & WARÉN, A. (1972). Food ecology of lobster, *Homarus vulgaris*, in Swedish waters. Some preliminary results. ICES CM 1972/K:29, 1-5.

HARDEGE, J. D., JENNINGS, A., HAYDEN, D., MÜLLER, C. T., PASCOE, D., BENTLEY, M. G. & CLARE, A. S. (2002). Novel behavioural essay and partial purification of a female-derived sex pheromone in *Carcinus maenas*. Mar Ecol Prog Ser 244, 179-189.

HAZLETT, B. A. (1969). 'Individual' recognition and agonistic behaviour in *Pagurus bernhardus*. Nature 222, 268-269.

HEWETT, C. J. (1974). Growth and moulting in the common lobster (*Homarus vulgaris* Milne-Edwards). J Mar Biol Assoc UK 54, 379-391.

HOLMES, S. J.(1903). Sex recognition among amphipods. Biol Bull 5, 288-292.

HSU, Y., EARLEY, R. L. & WOLF, L. L. (2006). Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. Biol Rev Camb Philos Soc 81, 33-74.

HUBER, R. & DELAGO, A. (1998). Serotonin alters decisions to withdraw in fighting crayfish, *Astacus astacus*: the motivational concept revisited. J Comp Physiol A Sens Neur Behav Physiol 18, 573-583.

HUBER, R. & KRAVITZ, E. A. (1995). A quantitative analysis of agonistic behavior in juvenile American lobsters (*Homarus americanus* L.). Brain Behav Evol 46, 72-83.

HUBER, R., ORZESZYNA, M., POKORNY, N. & KRAVITZ, E. A. (1997a). Biogenic amines and aggression: experimental approaches in crustaceans. Brain Behav Evol 50 Suppl 1, 60-68.

HUBER, R., SMITH, K., DELAGO, A., ISAKSSON, K. & KRAVITZ, E. A. (1997b). Serotonin and aggressive motivation in crustaceans: Altering the decision to retreat. Proc Natl Acad Sci USA 94, 5939-5942.

HUBER, R., PANKSEPP, J. B., YUE, Z., DELAGO, A. & MOORE, P. (2001). Dynamic interactions of behavior and amine neurochemistry in acquisition and maintenance of social rank in crayfish. Brain Behav Evol 57, 271-282.

HUNTINGFORD, F. A. & TURNER, A. K. (1987). Animal conflict. Chapman & Hall.

ISSA, F. A., ADAMSON, D. J. & EDWARDS, D. H. (1999). Dominance hierarchy formation in juvenile crayfish *Procambarus clarkii*. J Exp Biol 202 Pt 24, 3497-3506.

JENSEN, G. C., MCDONALD, P. S. & ARMSTRONG, D. A. (2002). East meets west: Competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus spp*. Mar Ecol Prog Ser , 251-262.

JOHANSSON, K. U. I. & HALLBERG, E. (1992). Male-specific structures in the olfactory system of mysids (Mysidacea: Crustacea). Cell Tissue Res 268, 359-368.

JOHANSSON, K. U. I., GEFORS, L., WALLÉN, R. & HALLBERG, E. (1996). Structure and distribution patterns of aesthetascs and male-specific sensilla in *Lophogaster typicus* (Mysidacea). J Crust Biol 16, 45-53.

JOHNSON, M. E. & ATEMA, J. (2005). The olfactory pathway for individual recognition in the American lobster *Homarus americanus*. J Exp Biol 208, 2865-2872.

JOHNSON, V. R. J. (1977). Individual recognition in the banded shrimp

Stenopus hispidus (Olivier). Anim Behav 25, 418-428.

JOHNSTON, R. E. (2003). Chemical communication in rodents: from pheromones to individual recognition. J Mammal 84, 1141-1162.

JOHNSTONE, R. A. (1998). Game theory and communication. In: Game theory and animal behavior (L. A. Dugatkin & H. K. Reeve, eds.). Oxford University Press, p. 94-117.

KAMIO, M., MATSUNAGA, S. & FUSETANI, N. (2000). Studies on sex pheromones of the helmet crab, *Telmessus cheiragonus* 1. An assay based on precopulatory mate-guarding. Zool Sci 17, 731-733.

KAMIO, M., MATSUNAGA, S. & FUSETANI, N. (2002). Copulation pheromone in the crab *Telmessus cheiragonus* (Brachyura: Decapoda). Mar Ecol Prog Ser 224, 183-190.

KAMIO, M., MATSUNAGA, S. & FUSETANI, N. (2003). Observation on the mating behaviour of the helmet crab *Telmessus cheiragonus* (Brachyura: Cheiragonidae). J Mar Biol Assoc UK 83, 1007-1013.

KARAVANICH, C. & ATEMA, J. (1998a). Individual recognition and memory in lobster dominance. Anim Behav 56, 1553-1560.

KARAVANICH, C. & ATEMA, J. (1998b). Olfactory recognition of urine signals in dominance fights between male lobster, *Homarus americanus*. Behaviour 135, 719-730.

KARLSON, P. & LÜSCHER, M. (1959). 'Pheromones': a new term for a class of biologically active substances. Nature 183, 55-56.

KARNOFSKY, E. & PRICE, H. J. (1989). Dominance, territoriality and mating in the lobster, *Homarus americanus*: a mesocosm study. Mar Behav Physiol 15, 101-121.

KARNOFSKY, E., ATEMA, J. & ELGIN, R. H. (1989). Field observations of social behavior, shelter use, and foraging in the lobster, *Homarus americanus*. Biol Bull 176, 239-246.

KENNEDY, M. B. (1978). Products of biogenic amine metabolism in the lobster: sulphate conjugates. J Neurochem 30, 315-320.

KIDEYS, A. E. (2002). Fall and rise of the Black Sea ecosystem. Science 297, 1482-1484.

KNOWLTON, N. (1980). Sexual selection and dimorphism in 2 demes of symbiotic pair bonding snapping shrimp. Evolution 34, 161-173.

KOZLOV, M. V., ZHU, J., PHILIPP, P., FRANCKE, W., ZVEREVA, E. L., HANSSON, B. S. & LÖFSTEDT, C. (1996). Pheromone specificity in *Eriocrania semipurpurella (*Stephens) and *E. sangii* (Wood) (Lepidoptera: Eriocraniidae) based on chirality of semiochemicals. J Chem Ecol 22, 431-454.

KRAVITZ, E. A. (1988). Hormonal control of behavior: amines and the biasing of behavioral output in lobsters. Science 241, 1775-1781.

KRAVITZ, E. A. (2000). Serotonin and aggression: insights gained from a lobster model system and speculations on the role of amine neurons in a complex behavior. J Comp Physiol A 186, 221-238.

KRAVITZ, E. A. & HUBER, R. (2003). Aggression in invertebrates. Curr Opin Neurobiol 13, 736-743.

LAVALLI, K. & BARSHAW, D. E. (1989). Post-larval American lobsters (*Homarus americanus*) living in burrows may be suspension-feeding. Mar Behav Physiol 15, 255-264.

LAVERACK, M. S. (1968). On the receptors of marine invertebrates. Oceanogr Mar Biol Ann Rev 6, 249-364.

LAVERACK, M. S. (1988). The diversity of chemoreceptors. In: Sensory biology of aquatic animals (J. Atema, R. R. Fay, A. N. Popper & W. N. Tavolga, eds.). Springer Verlag, p. 287-312.

LENOIR, A., D'ETTORRE, P., ERRARD, C. & HEFETZ, A. (2001). Chemical ecology and social parasitism in ants. Annu Rev Entomol 46, 573-599.

LEWIS, D. B. & GOWER, D. M. (1980). Biology of communication. Blackie, Glasgow, UK.

LIBERSAT, F. & PFLUEGER, H.-J. (2004). Monoamines and the orchestration of behavior. Bio Science 54, 17-25.

LIPCIUS, R. N., EDWARDS, M. L., HERRNKIND, W. F. & WATERMAN, S. A. (1983). In situ mating behavior of the spiny lobster *Panulirus argus*. J Crust Biol 3, 217-222.

LIVINGSTONE, M. S., HARRIS-WARRICK, R. M. & KRAVITZ, E. A. (1980). Serotonin and octopamine produce opposite postures in lobsters *Homarus americanus*. Science 208, 76-79.

LOO, L.-O., BADEN, S. P. & ULMESTRAND, M. (1993). Suspension feeding in adult *Nephrops norvegicus* (L.) and *Homarus gammarus* (L.) (Decapoda). Netherland J Sea Res 31, 291-297.

LOWRY, J. K. (1986). The callynophore, a eucaridean/peracaridean sensory organ prevalent among the Amphipoda (Crustacea). Zool Scr 15, 333-349.

LÖFSTEDT, C. (1990). Population variation and genetic control of pheromone communication systems in moths. Entomol Exp Appl 54, 199-218.

LÖFSTEDT, C. & VAN DER PERS, J. N. C. (1985). Sex pheromones and reproductive isolation in four European small ermine moths. J Chem Ecol 11, 649-666.

MANGUM, C. P. (1993). Hemocyanin subunit composition and oxygen binding in two species of the lobster genus *Homarus* and their hybrids. Biol Bull 184, 105-113.

MARCUS, K. (1912). Über Geruchsorgane bei decapoden Krebsen aus der Gruppe der Galatheiden. Zeitschr Wiss Zool 97, 511-545.

MARTIN, G. G. & HOSE, J. E. (1995). Circulation, blood, and disease. In: Biology of the lobster, *Homarus americanus* (J. R. Factor, ed). Academic Press, Inc., p.465-495.

MAYNARD SMITH, J. & HARPER, D. (2003). Animal signals. Oxford University Press.

MCLEESE, D. W. (1973). Orientation of lobsters *Homarus americanus* to odor. J Fish Res Board Can 30, 838-840.

MEHRTENS, F., STOLPMANN, M., BUCHHOLZ, F., HAGEN, W. & SABOROWSKI, R. (2005). Locomotory activity and exploration behaviour of juvenile European lobsters (*Homarus gammarus*) in the laboratory. Mar Freshw Behav Physiol 38, 105-116.

MILLER, C. B., CRAIN, J. A. & MARCUS, N. H. (2005). Seasonal variation of male-type antennular setation in female *Calanus finmarchicus*. Mar Ecol Prog Se 301, 217-229.

MOORE, P. A. (2007). Agonistic behaviour in freshwater crayfish: the influence of extrinsic and intrinsic factors on aggressive encounters and dominance. In: Evolutionary ecology of social and sexual systems. Crustaceans as model organisms (J. E. Duffy & M. Thiel, eds.). Oxford University Press, p. 90-114.

MOORE, P. A. & ATEMA, J. (1991). Spatial information in the three-dimensional fine structure of an aquatic odor plume. Biol Bull 181, 408-418.

MOORE, P. A., SCHOLZ, N. & ATEMA, J. (1991). Chemical orientation of lobsters *Homarus americanus* in turbulent odor plumes. J Chem Ecol 17, 1293-1308.

MUNDINGER, P. C. (1970). Vocal imitation and individual recognition of finch calls. Science 168, 480-482.

MURAI, M., KOGA, T. & YONG, H.-S. (2002). The assessment of female reproductive state during courtship and scramble competition in the fiddler crab, *Uca paradussumieri*. Behav Ecol Sociobiol 52, 137-142.

NELSON, K. & HEDGECOCK, D. (1977). Electrophoretic evidence of multiple paternity in the lobster *Homarus americanus* (Milne-Edwards). Am Nat 111, 361-365.

NEVITT, G. A. (2008). Sensory ecology on the high seas: the odor world of the procellariiform seabirds. J Exp Biol 211, 1706-1713.

OBERMEIER, M. & SCHMITZ, B. (2003a). Recognition of dominance in the big-clawed snapping shrimp (*Alpheus heterochaelis* Say 1818). Part I: individual or group recognition? Mar Freshw Behav Physiol 36, 1-16.

OBERMEIER, M. & SCHMITZ, B. (2003b). Recognition of dominance in the big-clawed snapping shrimp (*Alpheus heterochaelis* Say 1818). Part II: analysis of signal modality. Mar Freshw Behav Physiol 36, 17-29.

OLSÉN, K. H. (1992). Kin recognition in fish mediated by chemical cues. In: Fish Chemoreception (T. J. Hara, ed). Chapman & Hall, p. 229-248.

OMORI, K., YANAGISAWA, Y. & HORI, N. (1994). Life history of the caridean shrimp *Periclimenes ornatus* (Bruce) associated with a sea anemone in southwest Japan. J Crust Biol 14, 132-145.

PAINTNER, S. & KRAMER, B. (2003). Electrosensory basis for individual recognition in a weakly electric, mormyrid fish, *Pollimyrus adspersus* (Günther, 1866). Behav Ecol Sociobiol 55, 197-208.

PANNING, A. (1939). The Chinese mitten crab. Smithsonian Institution annual report for 1938, Washington, D.C. In: Rudnick, D. A., Hieb, K., Grimmer, K. F., Resh, V. H. 2003. Patterns and processes of biological invasion: the Chinese mitten crab in San Francisco Bay. Basic Appl Ecol 4, 249-262.

PETERS, N., PANNING, A. & SCHNAKENBECK, W. (1933). Die Chinesische Wollhandkrabbe (*Eriocheir sinensis* H. Milne-Edwards) in Deutschland. Zol Anz, 59-155. In: Herborg, L.-M., Rushton, S. P., Clare, A. S. & Bentley, M. G. 2003. Spread of the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards) in Continental Europe: analysis of a historical data set. Hydrobiologia 503, 21-28.

PETRINOVICH, L. (1974). Individual recognition of pup vocalization by northern elephant seal mothers. Z Tierpsychol 34, 308-312.

PFALZER, G. & KUSCH, J. (2003). Structure and variability of bat social calls: implications for specificity and individual recognition. J Zool 261, 21-33.

PHILLIPS, B. F., COBB, J. S. & GEORGE, R. W. (1980). General biology. In: The biology and management of lobsters. (J. S. Cobb & B. F. Phillips, eds.). Academic Press, New York., p.1-82.

RAETHKE, N., MACDIARMID, A. B. & MONTGOMERY, J. C. (2004). The role of olfaction during mating in the southern temperate spiny lobster *Jasus edwardsii*. Horm Behav 46, 311-318.

RAINEY, H. J., ZUBERBÜHLER, K. & SLATER, P. J. B. (2004). Hornbills can distinguish between primate alarm calls. Proceedings of the Royal Society of London B 271, 755-759.

RALLS, K. (1971). Mammalian scent marking. Science 171, 443-449.

REYNOLDS, J. D. (2002). Growth and reproduction. In: Biology of freshwater crayfish (D. M. Holdich, ed). Blackwell Science, p. 152-191.

RIECHERT, S. E. (1998). Game theory and animal contests. In: Game theory and animal behavior (L. A. Dugatkin & H. K. Reeve, eds.). Oxford University Press, p. 64-93.

ROHWER, S. (1975). The social significance of avian winter plumage variability. Evolution 29, 593-610.

RUFINO, M. M. & JONES, D. A. (2001). Binary individual recognition in *Lysmata debelius* (Decapoda: Hippolytidae) under laboratory conditions. J Crust Biology 21, 388-392.

SAILA, S. B. & MARCHESSEAULT, G. (1980). Population dynamics of clawed lobsters. In: The biology and management of lobsters. (J. S. Cobb & B. F. Phillips, eds.). Academic Press, New York, p. 219-241.

SAINTE-MARIE, B. (2007). Sperm demand and allocation in decapod crustaceans. In: Evolutionary ecology of social and sexual systems. Crustaceans as model organisms. Oxford University Press, p. 191-210.

SAINTE-MARIE, B., SEVIGNY, J.-M. & GAUTHIER, Y. (1997). Laboratory behavior of adolescent and adult males of the snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) mated noncompetitively and competitively with primiparous females. Can J Fish Aquat Sci 54, 239-248.

SCHMITT, B. C. & ACHE, B. W. (1979). Olfaction: responses of a decapod

crustacean are enhanced by flicking. Science 205, 204-206.

SCHMIDT, M. & ACHE, B. W. (1997). Immunocytochemical analysis of glomerular regionalization and neuronal diversity in the olfactory deutocerebrum of the spiny lobster. Cell Tissue Res 287, 541-563.

SCHNEIDER, D. (1957). Elektrophysiologische Untersuchungen von Chemo- und Mechanorezeptoren der Antenne des Seidenspiners, *Bombyx mori*. L Z Vergl Physiol. 40, 8-41.

SCRIVENER, J. C. E. (1971). Agonistic behaviour of the American lobster *Homarus americanus* (Milne-Edwards). Fish Res Board Can Tech Rep 235, 1-113.

SECORD, D. (2003). Biological control of marine invasive species: cautionary tales and land-based lessons. Biol Invasions 5, 117-131.

SEIBT, U. & WICKLER, W. (1979). The biological significance of the pair bond in the shrimp *Hymenocera picta*. Z Tierpsychol 50, 166-179.

SEVIGNY, J.-M. & SAINTE-MARIE, B. (1996). Electrophoretic data support the last-male sperm precedence hypothesis in the snow crab, *Chionoecetes opilio* (Brachyura: Majidae). J Shellfish Res 15, 437-440.

SEYFARTH, R. & CHENEY, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. Anim Behav 40, 754-764.

SMITH, I. P., COLLINS, K. J. & JENSEN, A. C. (1999). Seasonal changes in the level and diel patterns of activity in the European lobster *Homarus gammarus*. Mar Ecol Prog Ser 186, 255-264.

SMITH, I. P., JENSEN, A. C., COLLINS, K. J. & MATTEY, E. L. (2001). Movement of wild European lobsters *Homarus gammarus* in natural habitat. Mar Ecol Prog Ser, 177-186.

SNEDDEN, W. A. (1990). Determinants of male mating success in the temperate crayfish *Orconectes rusticus*: chela size and sperm competition. Behaviour 115, 100-113.

SNEDDON, L. U., TAYLOR, A. C., HUNTINGFORD, F. A. & WATSON, D. G. (2000). Agonistic behaviour and biogenic amines in shore crabs *Carcinus maenas*. J Exp Biol 203, 537-545.

SNYDER, M. J. & CHANG, E. S. (1991). Ecdysteroids in relation to the molt cycle of the American lobster, *Homarus americanus*. II. Excretion of metabolites. Gen Comp Endocr 83, 118-131.

SPENCER, M. & LINBERG, K. A. (1986). Ultrastructure of aesthetasc innervation and external morphology of the lateral antennule setae of the spiny lobster *Panulirus interruptus* (Randall). Cell Tissue Res 245, 69-80.

STEGER, R. & CALDWELL, R. L. (1983). Intraspecific deception by bluffing, a defense strategy of newly molted stomatopods (Arthropoda: Crustacea). Science 221, 558-560.

STEULLET, P., CATE, H. S., MICHEL, W. C. & DERBY, C. D. (2000). Functional units of a compound nose: aesthetasc sensilla house similar populations of olfactory receptor neurons on the Crustacean antennule. J Comp Neurol 418, 270-280.

STRAUSFELD, N. J. & HILDEBRAND, J. G. (1999). Olfactory systems: common design, uncommon origins? Curr Opin Neurobiol 9, 634-639.

STUMMER, L. E., WELLER, J. A., JOHNSON, M. L. & CÔTÉ, I. M. (2004). Size and stripes: how fish recognize cleaners. Anim Behav 68, 145-150.

SÖDERBÄCK, B. (1991). Interspecific dominance relationship and aggressive interactions in the freshwater crayfishes *Astacus astacus* (L.) and *Pacifastacus leniusculus* (Dana). Can J Zool 69, 1321-1325.

SÖDERBÄCK, B. (1995). Replacement of the native crayfish *Astacus astacus* by the introduced species *Pacifastacus leniusculus* in a Swedish lake: Possible causes and mechanisms. Freshw Biol 33, 291-304.

TALBOT, P., THALER, C. & WILSON, P. (1984). Spawning, egg attachment and egg retention in captive lobsters (*Homarus americanus*). Aquaculture 37, 239-250.

TAMM, G. R. & COBB, J. S. (1978). Behavior and the crustacean molt cycle: changes in aggression of *Homarus americanus*. Science 200, 79-81.

TEMPLEMAN, W. (1934). Mating in the American lobster. Contributions to Canadian Biology and Fisheries VIII, 422-432.

THOM, M. D. & HURST, J. L. (2004). Individual recognition by scent. Ann Zool Fennici 41, 765-787.

THORPE, J. H. & AMMERMAN, K. S. (1978). Chemical communication and agonism in the crayfish *Procambarus acutus acutus*. Am Midl Nat 100, 471-474.

TIBBETS, E. A. (2004). Complex social behaviour can select for variability in visual features: a case study in *Polistes* wasps. Proc R Soc Lond B 271, 1955-1960.

TIERNEY, J. & DUNHAM, D. W. (1983). Behavioral mechanisms of reproductive isolation in crayfish of the genus *Orconectes*. Am Midl Nat 111, 304-310.

TIERNEY, A. J., THOMPSON, C. S. & DUNHAM, D. W. (1984). Site of pheromone reception in the crayfish *Orconectes propinquus* (Decapoda, Cambaridae). J Crust Biol 4, 554-559.

TURNER, D., SHAUGHNESSY, A. & GOULD, E. (1972). Individual recognition between mother and infant bats (*Myotis*). NASA SP 262, 365-371.

ULMESTRAND, M. (2003). Reproduction of female lobsters (*Homarus gammarus*) on the Swedish west coast. Can Tech Rep Fish Aquat Sci 2506, 35-39.

ULMESTRAND, M (2005). Hummern på svenska västkusten. In: Kräftdjur i hav och sjöar: kräfta hummer, krabba, räka (H. Ackefors & I. Gärsgård, eds.). Kiviksgården, p. 268-284.

WADDY, S. L. & AIKEN, D. E. (1990). Intermolt insemination, an alternative mating strategy for the American lobster (*Homarus americanus*). Can J Fish Aquat Sci 47, 2402-2406.

WADDY, S. L. & AIKEN, D. E. (1991). Mating and insemination in the American lobster, *Homarus americanus*. In: Crustacean sexual biology (R. T. Bauer & J. W. Martin, eds.). Columbia University Press, New York, p.126-144.

WADDY, S., AIKEN, D. E. & DE KLEIJN, D. P. V. (1995). Control of growth and reproduction. In: Biology of the lobster *Homarus americanus* (J. R. Factor, ed). Academic Press, p. 217-265.

VAN DER MEEREN, G. I. & EKELI, K. O. (2002). Samkvem mellom europeisk hummer (*Homarus gammarus*) og amerikansk (*Homarus americanus*); habitatutnyttelse; aktivitet; dominans og sosiale interaksjoner. In. Havforskningsinstituttet i Norge & Akvariet i Bergen, p. 1-17.

VAN DER MEEREN, G. I. & UKSNØY, L. E. (2000). A comparison of claw morphology and dominance between wild and cultivated male European lobster. Aquacult Int 8, 77-94.

VAN DER MEEREN, G. I., EKELI, K. O., JØRSTAD, K. E. & TVEITE, S. (2000). Americans on the wrong side - the lobster *Homarus americanus* captured in Norwegian waters. ICES CM U:20, 1-14.

VAN DER MEEREN, G. I., CHANDRAPAVAN, A. & BREITHAUPT, T. (2008). Sexual and aggressive interactions in a mixed species group of lobsters. Aquat Biol 2, 191-200.

WEBSTER, D. R., RAHMAN, S. & DASI, L. P. (2001). On the usefulness of bilateral comparison to tracking turbulent chemical odor plumes. Limnol Oceanogr 46, 1048-1053.

WEISSBURG, M. J. & ZIMMER-FAUST, R. K. (1993). Life and death in moving fluids: Hydrodynamic effects on chemosensory-mediated predation. Ecology 74, 1428-1443.

WELLBORN, G. A. & COTHRAN, R. D. (2007). Ecology and evolution of mating behaviour in freshwater amphipods. In: Evolutionary ecology of social and sexual systems. Crustaceans as model organisms (J. E. Duffy & M. Thiel, eds.). Oxford University Press, p. 147-166.

WESTMAN, K., SAVOLAINEN, R. & JULKUNEN, M. (2002). Replacement of

the native crayfish *Astacus astacus* by the introduced species *Pacifastacus leniusculus* in a small, enclosed Finnish lake: A 30-year study. Ecography 25, 53-73.

WHITFIELD, D. P. (1987). Plumage variability status signalling and individual recognition in avian flocks. Trends Ecol Evolut 2, 13-18.

VILLANELLI, F. & GHERARDI, F. (1998). Breeding in the crayfish, *Austropotamobius pallipes*: Mating patterns, mate choice and intermale competition. Freshw Biol 40, 305-315.

WILLIAMS. (1995). Taxonomy and evolution. In: Biology of the lobster *Homarus americanus* (J. R. Factor, ed). Academic Press, New York, p. 13-21.

WILSON, E. O. & BOSSERT, W. H. (1963). Chemical communication among animals. Recent Prog Horm Res 19, 673-716.

WINSTON, M. L. & JACOBSON, S. (1978). Dominance and effects of strange conspecifics on aggressive interactions in the hermit crab *Pagurus longicarpus*. Anim Behav 26, 184-191.

VOIGT, R. & ATEMA, J. (1992). Tuning of chemoreceptor cells of the second antenna of the American lobster (*Homarus americanus*) with a comparison of four of its other chemoreceptor organs. J Comp Physiol A Sens Neur Behav Physiol 171, 673-681.

WOLFF, T. (1978). Maximum size of lobsters *Homarus spp.* (Decapoda, Nephropidae). Crustaceana 34, 1-14.

VOSSHALL, L. B., AMREIN, H., MOROZOV, P. S., RZHETSKY, A. & AXEL, R. (1999). A spatial map of olfactory receptor expression in the *Drosophila* antenna. Cell 96, 725-736.

WYATT, T. D. (2003). Pheromones and animal behaviour. Communication by smell and taste. Cambridge University Press, Cambridge.

YANO, I., KANNA, R. A., OYAMA, R. N. & WYBAN, J. A. (1988). Mating behavior in the penaeid shrimp *Penaeus vannamei*. Mar Biol 97, 171-176.

ZIMMER, R. K. & BUTMAN, C. A. (2000). Chemical signaling processes in the marine environment. Biol Bull 198, 168-187.

ZUCKER, N. & DENNY, R. (1979). Interspecific communication in fiddler crabs: preliminary report of a female rejection display directed toward courting heterospecific males. Z Tierpsychol 50, 9-17.

ZULANDT SCHNEIDER, R. A., SCHNEIDER, R. W. S. & MOORE, P. A. (1999). Recognition of dominance status by chemoreception in the red swamp crayfish, *Procambarus clarkii*. J Chem Ecol 5, 781-794.

ZULANDT SCHNEIDER, R. A., HUBER, R. & MOORE, P. A. (2001). Individual and status recognition in the crayfish, *Orconectes rusticus*: The effects of urine release on fight dynamics. Behaviour 138, 137-153.

ACKNOWLEDGEMENTS - TACK!

Jag vill börja med att tacka min huvudhandledare **Eric** och min biträdande handledare **Per C** som förutom att ha stöttat och hjälpt mig under de här fem åren dessutom har lärt mig allt om kammaneter och varför lime ibland sjunker… Jag vill också tacka min biträdande handledare **Peter A**, som kom in i ett sent skede men som ändå har hjälpt mig enormt mycket!

I want to thank **Thomas Breithaupt**, his lab colleagues and the helpful personnel at **Hull Universit**y for letting me come to his lab to learn and participate in the urine and interspecific studies and for taking good care of me in and around Hull! I am also very obliged to **Jelle Atema**, his lab, students and personnel at the **Boston University Marine Program** for an interesting couple of weeks at the Marine Biological Laboratory in Woods Hole.

Jag vill självklart tacka mina **nuvarande och tidigare vänner och kollegor** både på **Zoologen i Lund** och **Marinbiologi i Helsingborg**; det är en glädje att gå till jobbet varje dag! Det är alltid liv och rörelse och en lagom blandning av skämt och vetenskap.

Särskilt vill jag tacka **Lina** för att du alltid ställer upp och för att du förgyller våra korridorer med dina melodier och ditt glada humör! **Linda** för allt skratt och alla tårar och för att du är en god vän. **Megan** for all the walks and all the talks. Mina roommates **Tim** (sedan dag ett på Zoologen!), **Marcus** och **Pertti** för alla glada stunder på kontoret som vi delat. **Yakir** för att du är en härlig vän. **Tony** och **Tessan**, nu är det ni som blir seniorer! Tusen tack till **Rita** för all din hjälp med allt från fixering till mikroskopering och alla pratstunder vi har haft däremellan. Tack **Anders G** för din tid och alla e-fys instruktioner till både mig och Patrik, och för din entusiasm och energi oavsett om det gäller att peta i små, små krabbantenner eller prata om obskyra b-filmer; du gjorde (och gör) Zootis så mycket roligare!

På **Campus** vill jag också tacka hela **fikarumsteamet** på våning 6 för alla konstiga, roliga och intressanta diskussioner vi har haft. Tack **Bo** för den fina hummerbilden. Tusen tack **Per-Erik**, min personliga statistik-guru, för att du har hjälpt mig med alla korkade och besvärliga statistikfrågor som jag har tampats med under åren. Tack till alla härliga **studenter** som jag har haft förmånen att få undervisa och vara på Klubban och i Kroatien med. Ett särskilt tack till mina exjobbare och projektarbetare **Jim**, **Totte**, **Agge** och **Patrik** för att de vågade sig på sina respektive projekt, och sedan hade så mycket entusiasm och tålamod att genomföra dem trots tidvis magra resultat, och till **Shabnam** för att du var min hummer-sexslav!

För mina härliga och givande, men jobbiga, somrar i Piggvarshallen vill jag tacka **ALLA** på **Kristinebergs Marina Forskningsstation** (numera **Sven Lovén Center för Marina Vetenskaper**) för all hjälp, för allt kul och för att ni gör stationen till en så skön plats att vara på! Tack **Kerstin, Tony och Bobbo Roysson** för ert eminenta hummerfiskande och alla intressanta pratstunder om allt möjligt som bor i havet!

Ett stort tack **Cissi** och **Annelie** för allt sällskap på Kristineberg och allt annat däremellan, och mina "**gamla vänner"** som gjorde studietiden i Göteborg till den bästa tänkbara, och för allt kul vi har haft sen dess: **Emma, Fredrik, Andreas, Patrik**, **Martin L, Martin B, Maria Å, Rasmus, Sara, Pelle, Jenny, Sofia C, Tina, Petri, …**

Tack till **mor** och **far**, **Cia** och **Johan**, som kanske inte alltid förstår vad jag håller på med och varför men ändå har stöttat mig. Nu är jag nog klar med "skolan" till slut! Slutligen tack **Lars** för ALLT och lite till!! För all hjälp och allt annat. Det är du som gör att jag orkar med även när jobbet har känts extra… jobbigt.