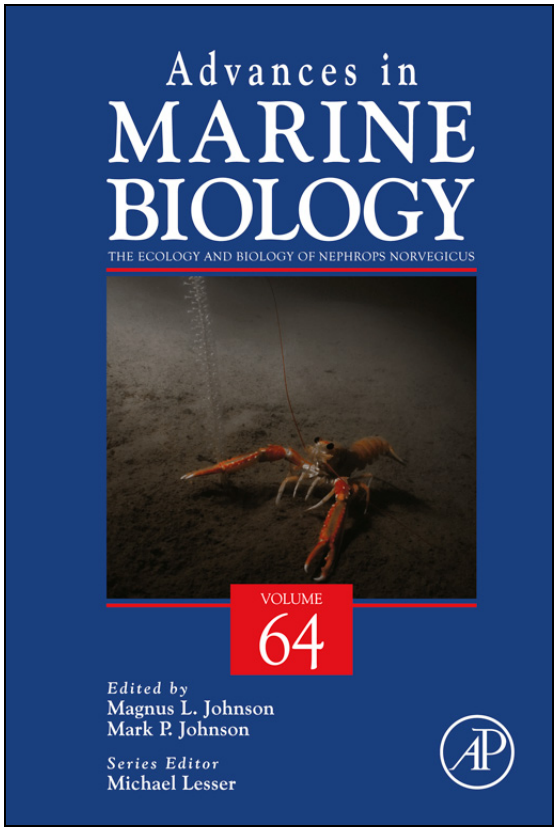

From: Emi Katoh, Valerio Sbragaglia, Jacopo Aguzzi, Thomas Breithaupt, Sensory Biology and Behaviour of *Nephrops norvegicus*. In Magnus L. Johnson and Mark P. Johnson, editors: Advances in Marine Biology, Vol. 64, Burlington: Academic Press, 2013, pp. 65-106.
ISBN: 978-0-12-410466-2

CHAPTER THREE

Sensory Biology and Behaviour of *Nephrops norvegicus*

Emi Katoh*, Valerio Sbragaglia†, Jacopo Aguzzi†, Thomas Breithaupt*,1

*School of Biological, Biomedical and Environmental Sciences, University of Hull, Hull, United Kingdom
†Marine Science Institute (ICM-CSIC), Passeig Marítim de la Barceloneta, Barcelona, Spain
1Corresponding author: e-mail address: t.breithaupt@hull.ac.uk

Contents

Abstract

The Norway lobster is one of the most important commercial crustaceans in Europe. A detailed knowledge of the behaviour of this species is crucial in order to optimize fishery yields, improve sustainability of fisheries, and identify man-made environmental threats. Due to the cryptic life-style in burrows, the great depth and low-light condition of their habitat, studies of the behaviour of this species in its natural environment are challenging. Here, we first provide an overview of the sensory modalities (vision, chemoreception, and mechanoreception) of *Nephrops norvegicus*. We focus particularly on the role of the chemical and mechanical senses in eliciting and steering spatial

Advances in Marine Biology, Volume 64
ISSN 0065-2881
http://dx.doi.org/10.1016/B978-0-12-410466-2.00003-0

orientation behaviours. We then concentrate on recent research in social behaviour and biological rhythms of *Nephrops*. A combination of laboratory approaches and newly developed tracking technologies has led to a better understanding of aggressive interactions, reproductive behaviours, activity cycles, and burrow-related behaviours. Gaps in our knowledge are identified and suggestions for future research are provided.

Keywords: Chemoreception, Mechanoreception, Vision, Rhythms, Burrowing, Actograph, Video-image analysis, Pheromone, Aggression, Mating

1. INTRODUCTION

Ethology, the study of animal behaviour, encompasses several aspects of animal biology and hence requires a multidisciplinary approach (Davies et al., 2012). Ethologists are interested in the causes of behaviour. Questions about animal behaviours can be subdivided into two major categories: questions about *proximate* (physiological) causes address 'how' an individual comes to behave in a determinate way; questions about *ultimate* (evolutionary) causes address 'why' the individual has evolved that behaviour (Tinbergen, 1963). For any putative behavioural trait, the first category of questions is usually addressed through laboratory experiments, while the second one requires the measurement of the fitness value.

Behavioural studies of the Norway lobster (*Nephrops norvegicus* L.; in the following referred to as *Nephrops*) started in the 1970s both in the field and in the laboratory, driven by fishery management issues in relation to population size, and overall exploitability of lobster stocks (Farmer, 1975). The first experiments were performed in order to relate the temporal variation in catchability with the behaviour of individuals in the laboratory (Chapman, 1980). That comparison was sustained by the assumption that the locomotor behaviour in the laboratory is a reliable proxy of burrow emergence behaviour in the field (and hence of overall catchability). Since the mid-1980s, *Nephrops* has also been used to answer fundamental neuro-ethological questions addressing the control of simple behaviours by the nervous system (e.g. Neil and Miyan, 1986; Neil and Wotherspoon, 1982; Newland and Neil, 1987). Over the past two decades, technical innovations both in monitoring *Nephrops* in the field and in studying their physiological parameters in the lab allowed insight into the proximate causes of rhythmic behaviour (e.g. Aguzzi et al., 2011a,b; Sardà and Aguzzi, 2012). These aim to provide better predictability of catch rate and more accurate population estimates. Only recently, basic biological questions about the social behaviour (aggressive interactions, reproductive behaviour) have been addressed (Katoh, 2011;

Katoh et al., 2008) targeting a better understanding of the ultimate causes of *Nephrops* behaviour.

This chapter reviews current knowledge of the behaviour of the *Nephrops*. We will start with a description of the sensory equipment of *Nephrops* and its role in triggering behaviour. We will then concentrate on two current research areas: social behaviour and biological rhythms.

2. SENSORY BIOLOGY AND THE CONTROL OF ORIENTATION RESPONSES

In common with other decapod crustaceans (Atema and Voigt, 1995), Norway lobsters possess a comprehensive set of mechanosensory, chemosensory, and visual receptors. The compound eyes are the main visual receptors (see Chapter 4) but decapods also have extraretinal light detectors such as the caudal photoreceptor (Figure 3.1). Chemoreceptors are on the antennules (olfactory receptors) and on the body appendages including second antennae, mouthparts, and walking legs (bimodal receptors; Figures 3.1 and 3.2). Mechanoreceptors include cuticular setae that are distributed over the whole exoskeleton of *Nephrops*, proprioreceptors in the joints of the appendages including the flagellae of the antennae, and the statocysts located in the basal segment of the antennules (Figure 3.2). While not all the receptors of *Nephrops* have been subject to detailed investigation, morphological similarities suggest functions that are similar to the receptors of the better investigated American lobsters *Homarus americanus*, spiny

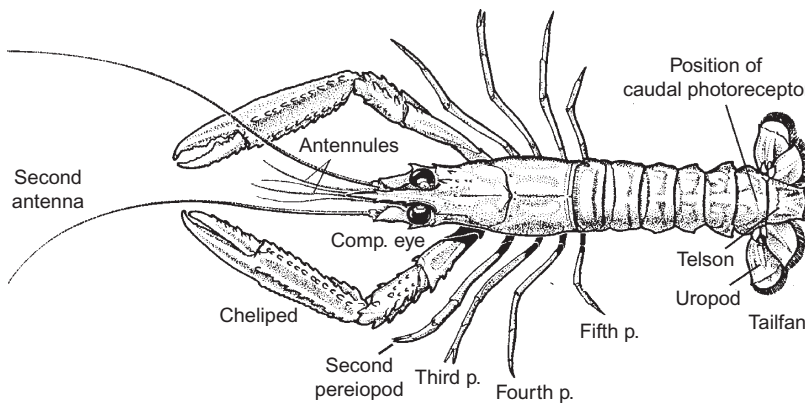

Figure 3.1 The Norway lobster *N. norvegicus*. Second to fifth pereiopod constitute the walking legs. *Drawing modified after Howard (1989) with permission from publishers.*

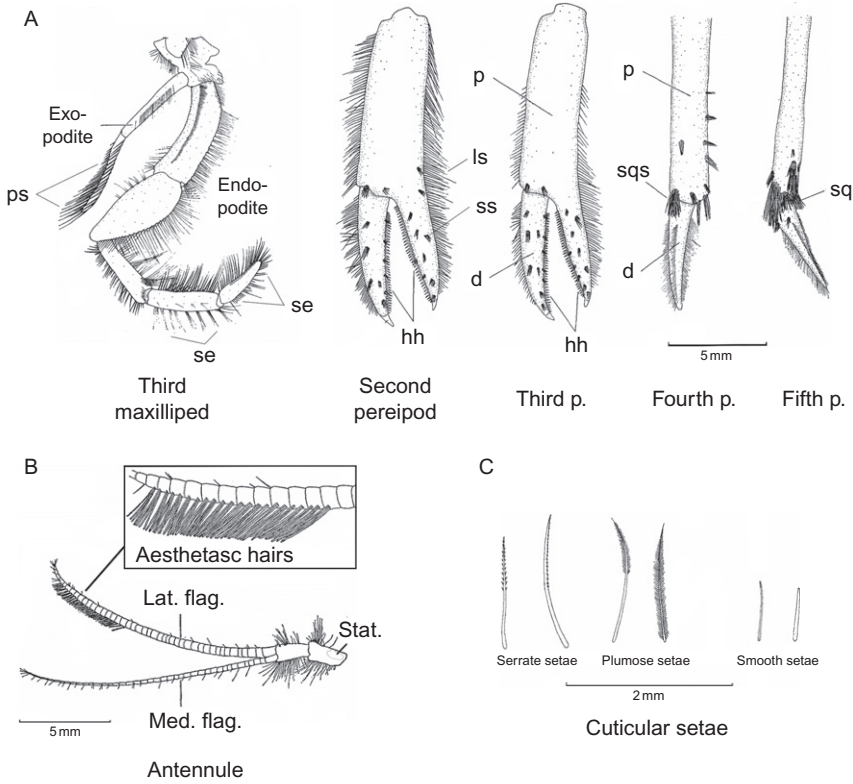

Figure 3.2 Cuticular setae of *N. norvegicus*. (A) Third maxilliped and walking legs (pereiopods 2–5) showing distribution of setae: hh, hedgehog hairs; se, serrate setae; ls, long smooth setae; ss, smooth setae; sqs, squamate setae; ps, propodite; d, dactylopodit; (B) antennule with aesthetasc hairs. Notice position of statocyst (stat.); (C) types of cuticular setae found on *N. norvegicus*. *(A) Modified after Farmer (1974a)—reprinted by permission of the publisher Taylor & Francis Ltd. (B) Modified after Farmer (1973, Figure 3)—with kind permission from Springer Science+Business Media. (C) Modified after Farmer (1974a)—reprinted by permission of the publisher Taylor & Francis Ltd.*

lobster *Panilurus* sp., or crayfish (e.g. *Pacifastacus leniusculus*, *Procambarus clarkii*) (see Atema and Voigt, 1995; Schmidt and Mellon, 2011).

2.1. Vision

Norway lobsters have large kidney-shaped ('reniform') compound eyes of the 'superposition type' that are typical of nocturnal crustaceans (Figure 3.1; Aréchiga and Atkinson, 1975). In contrast to other receptor organs, the compound eyes have been well investigated. They are reviewed in depth in Chapter 4. While vision can provide an accurate and instantaneous image

of the external environment in daylight conditions (Dusenbery, 1992), the low light availability at the spatial and temporal activity range of Norway lobsters limits the utility of this modality. Norway lobster populations that live in shallow waters are active out of the burrow only at night; at intermediate depth they are active at dawn or dusk and in deep water they are active at daytime (Bell et al., 2006; see also Section 4.4). Long-term capture–recapture experiments in the field have shown that lobsters with light-induced eye damage are still able to survive and reproduce and do not suffer reductions in growth (Chapman et al., 2000; Shelton et al., 1985). While the compound eyes are still important sensory organs facilitating spatial orientation and biological rhythms, they do not appear to be crucial in mediating important behaviours such as foraging, predator avoidance, and courtship. Some rhythmic behaviours and burrow-related behaviours may be mediated by the caudal photoreceptor, a multimodal interneuron situated in the sixth abdominal ganglion that responds to mechanical stimuli as well as to changes in light intensity (Chapman et al., 2000; Simon and Edwards, 1990).

2.2. Chemoreception

Decapod crustaceans including *N. norvegicus* have two types of chemosensory organs: unimodal olfactory sensilla and non-olfactory bimodal sensilla (Hallberg and Skog, 2011). The olfactory sensilla named aesthetascs are located on the distal end of the lateral flagellum of the antennules (Figure 3.2; Farmer, 1973). Each aesthetasc sensillum typically contains many olfactory neurons (hundreds of olfactory neurons in some species such as spiny lobsters; Caprio and Derby, 2008) that all project into the olfactory lobe in the brain. Non-olfactory bimodal sensilla are found on almost all appendages. These sensilla contain both chemo- and mechanoreceptors. The chemoreceptors do not project into the olfactory lobe but to other centres in the brain and in the ventral nerve chord (Schmidt and Mellon, 2011). Typical bimodal sensilla that are found in decapod crustaceans including *Nephrops* are the hedgehog hairs, the smooth and squamous setae, and the serrate setae (Derby, 1982; Farmer, 1974a; Goodall, 1988; for a recent review of types of setae see also Garm and Watling, 2013). The hedgehog hairs (named 'teeth' chemoreceptors in Farmer, 1974a) are stout conical structures organized in a row lining the inner cutting edge of the chelae of the second and third walking legs (Figure 3.2A; Derby, 1982; Farmer, 1974a). The smooth setae (named 'fine simple setae' in Farmer, 1974a) and the squamous setae ('large serrate setae with scales' in Farmer, 1974a)

are arranged in small groups ('tufts') rising at intervals out of small depressions along the propodit and dactylopodit of the walking legs (Figure 3.2A). Serrate setae are found on the mouthparts, including the maxillipeds (Figure 3.2A) and on the fourth and fifth pereiopods. Using electrophysiology, Derby (1982) confirmed that hedgehog hairs, smooth setae and squamous setae respond both to mechanical and chemical stimuli.

To contrast the function of olfactory unimodal and non-olfactory bimodal sensilla, the latter have been attributed as taste or gustatory receptors (Atema and Voigt, 1995; Derby and Sorensen, 2008). For terrestrial animals, olfaction and taste are clearly distinguished based on the physical medium in which they are received. Olfaction is the detection of air-borne molecules whereas taste detects water-soluble molecules. For aquatic animals, the distinction between olfaction and taste is unclear as both modalities detect water-soluble molecules. In current discussions, the distinction is based on the organization of the first order interneurons (olfactory processing is localized in the olfactory lobe, non-olfactory processing is distributed across different areas of the central nervous system; Caprio and Derby, 2008) and on functional characteristics (Schmidt and Mellon, 2011). Taste mediates simple reflexive behaviours such as grabbing, biting, and swallowing, whereas olfaction mediates more complex behaviours such as search for odour sources from a distance, courtship behaviour and learning about odours (Caprio and Derby, 2008). Ablation experiments in spiny lobsters (Reeder and Ache, 1980) and American lobsters (Devine and Atema, 1982) showed that antennular receptors are involved in detection and initial tracking of odour plumes. Weissburg (2011) suggests that in blue crabs chemoreceptors on the walking legs are involved in odour plume tracking. Once near the food source the taste receptors are important in selecting and ingesting edible food. The first and second walking legs probe the ground and use the small chelae to pick up food items detected by leg chemoreceptors (Derby and Atema, 1982). Food is transferred to the maxillipeds where it is further checked by taste receptors and passed on to the mouth (Derby and Atema, 1982). Norway lobsters are predators and scavengers feeding on polychaetes, crustaceans, molluscs, and echinoderms (Bell et al., 2006). They rely on chemoreception in their food search (Krang and Rosenqvist, 2006). First responses to food include antennule 'flicking' (a behaviour that is analogue to sniffing in mammals as it enhances sensitivity to chemical stimuli; Schmitt and Ache, 1979) and antennal sweeps, followed by olfactory tracking (Krang and Rosenqvist, 2006). Little is known about the role of bimodal receptors in food detection and selection.

Olfactory sensilla on the antennules are important in mediating social interactions. Fighting behaviour in *Nephrops* is accompanied by increased flicking (Katoh et al., 2008) and chemical signals appear to play an important role both in aggressive and in courtship interactions (Katoh et al., 2008; see below). Olfactory detection and chemical signalling are facilitated by generation of 'information currents' (Atema and Voigt, 1995). The anterior location of the urinary pores ('nephropores') in the basal segments of the second antennae allows urine-borne molecules to be introduced into the frontal water currents emanating from the gill chambers. The gill currents serve as information currents by delivering urine-borne chemical messages towards conspecific receivers (Breithaupt, 2011). A second source of information currents is generated by beating of the maxilliped-flagellae (exopodites; see Figure 3.2A). The concerted action of the exopodites of all three maxillipeds act like a fan organ producing water currents that draw odour molecules towards the antennules. This fanning behaviour enhances the perceptive range of odour detection (Denissenko et al., 2007). Olfaction is also used to sense chemicals released by predators or by injured or disturbed conspecifics (Derby and Sorensen, 2008; Hazlett, 2011). This can mediate adaptive responses to elevated predation risk mostly by reducing locomotion (Hazlett, 2011).

2.3. Mechanoreception

Mechanoreceptors can be used for tactile exploration, for the perception of water movement (hydrodynamic stimuli), and for the detection of acoustic stimuli (Breithaupt, 2002; Breithaupt and Tautz, 1990; Goodall et al., 1990). The mechanoreceptor equipment of *N. norvegicus* is similar to that of other decapod crustaceans such as crayfish and lobsters (Farmer, 1974a; Goodall, 1988). Mechanosensory structures include short cuticular setae that are distributed over the entire surface of the body, the first antennae (antennules; Figures 3.1 and 3.2), second antennae, and the statocysts located in the basal segment of the antennules (Atema and Voigt, 1995; Breithaupt and Tautz, 1990; Goodall, 1988).

Mechanosensory setae of crayfish are innervated by two mechanoreceptive neurons that respond to movements of the seta in opposite direction providing the sensory hair with a directional sensitivity (Wiese, 1976). The cuticular setae respond to tactile stimuli as well as to hydrodynamic stimuli. Some of the hairs were shown to respond to water movements as slow as 0.1 mm/s (Breithaupt and Tautz, 1990).

Mechanoreceptive interneurons in the last abdominal ganglion integrate flow information from many different setae and respond to complex flow pattern moving over the tailfan (Tautz and Plummer, 1994). This enables crayfish to recognize vortices created by fish passing behind their tailfan (Breithaupt et al., 1995). The flow stimulus elicits a turning response in crayfish that can lead to capture of small prey fish (Breithaupt et al., 1995). Norway lobsters possess mechanoreceptive setae (plumose setae, long setae; Figure 3.2C; Farmer, 1974a) on their tailfan similar to those of crayfish (Goodall, 1988).

Mechanosensory hairs also trigger escape responses of Norway lobsters. The escape response involves rapid flexion and extensions of the abdomen (i.e. tail flips; Newland and Neil, 1990). The tail flip response and its underlying neuronal circuitry has been extensively studied in crayfish and in Norway lobsters and is one of the best-known examples of a stereotyped motor pattern (Newland and Neil, 1990; Newland et al., 1992; Wine, 1984). The initial tail flip is mediated by giant nerve fibres. Mechanical stimulation of the anterior cephalothorax is mediated by the median giant fibre and leads to a tail flip that is directed backwards, away from the point of stimulation. Stimulation of the abdomen recruits the lateral giant fibre and produces an upward, forward pitching tail flip. The initial giant fibre-mediated tail flip is followed by many swimming tail flips not mediated by the giant fibres (Newland et al., 1992). The trajectories of the swimming tail flip also take into account the laterality of the stimulation. Field experiments have shown that asymmetrical stimuli to the chelipeds elicit swimming trajectories directed away from the point of stimulation (Newland and Chapman, 1989). These escape behaviours are adaptive and can be used to escape rapidly approaching predatory fish. Cod (*Gadus morhua*) has been identified as the most important predator of Norway lobsters in the Atlantic Ocean (Farmer, 1975). In the Mediterranean Sea, major predators include angler fish (*Lophius* spp.), various elasmobranchs, hake (*Merluccius merluccius*) scorpionfish (*Scorpaena* spp.), and small gadoids (e.g. *Trispoterus minutus capelanus*) (Bell et al., 2006; see also Chapter 2). Swimming behaviour also plays a role in the process of capture of *Nephrops* in trawl nets (Newland et al., 1992). Lobsters stimulated to swim by ground gear generally escape approximately parallel to the direction of tow. However, lobsters facing away from the oncoming ground gear swim up into the water column (Newland et al., 1992). In both situations, approach of predatory fish or of a trawl net, the bow wave may provide the stimulus for the mechanoreceptors that triggers the directional escape response.

Sweeping movements of the long second antennae are a common behaviour of Norway lobsters during spatial exploration (e.g. Krang and Rosenqvist, 2006). In crayfish, the second antenna is equipped with sensory setae and specialized receptors that detect when the antennal flagellum is deformed (Sandeman, 1989; Tautz et al., 1981). These receptors together with proprioreceptors in the joint of the basal segment (Taylor, 1967) can serve the animal to register movement of the flagellum and deformation due to contact with objects. Similar to other decapod crustaceans, Norway lobsters sweep the antennae to create physical contact with objects in the environment. Behavioural experiments on the crayfish *Cherax destructor* have demonstrated that in the absence of visual stimuli the antennae are used to detect and learn topographic changes in the environment (Basil and Sandeman, 2000). It was suggested that during exploration behaviour they compare the input of the bilateral antennae to make orientation decisions (McMahon et al., 2005). Crayfish can retain information about the configuration of their environment for up to 24 h (Basil and Sandeman, 2000).

The statocyst, positioned in the basal segment of the antennules (see Figure 3.2), is a fluid-filled chamber that contains a mass of sand grains that act as statolith. Hair sensilla are arranged in a crescent around the statolith mass and are in contact with the sand grains (Atema and Voigt, 1995). Due to the higher inertia of the statolith, a tilt in one of the three body axis causes a relative movement between statolith and the wall of the statocyst thereby stimulating specific groups of cuticular hairs. Statocysts are primarily involved in maintaining equilibrium by triggering righting movements of walking legs, swimmerets, and uropods (Newland and Neil, 1987; see Figure 3.1). Analogue to the fish otocyst which is used in equilibrium responses and hearing, the statocyst has been suggested as an acoustic detector in crustaceans (e.g. Popper et al., 2001). Field experiments were carried out by Goodall et al. (1990) to test hearing abilities of the Norway lobster under appropriate acoustical conditions. They found that while Norway lobsters do not respond to the pressure component of sound (i.e. the sound component that the human ear detects) they show behavioural reactions to water vibrations (hydrodynamic stimuli) in the frequency range of 20–180 Hz. Bulk movement of water, such as the bow wave created by larger fish, tidal currents, or seismic waves will cause sudden displacements of the lobster's body which, due to the statolith's higher inertia, will be detected by the statocyst organ. It may be these hydrodynamic stimuli, rather than acoustic stimuli, that the crustacean statocyst is adapted to detect in its natural environment (Breithaupt, 2002).

3. SOCIAL BEHAVIOUR

3.1. Agonistic interactions

Many animals including the Norway lobsters display aggressive behaviour and fighting occurs between individuals over limited resources such as food, shelter, and mating opportunities (Chapman and Rice, 1971; Dissanayake et al., 2009; Moore, 2007). Fighting can cause injuries such as limb loss or even death which is an issue when keeping them communally (Briffa and Sneddon, 2007; McVean, 1982; Norman and Jones, 1991; Smith and Hines, 1991). Chapman and Rice (1971) noticed that a high proportion of *Nephrops* that were caught by creels in the field have circular indentations or holes in the propodits of their great claws. Due to the nature of these wounds, they were likely inflicted by claws of conspecifics suggesting that fighting is a common event in natural populations (Chapman and Rice, 1971). The level of aggression in fights and the method of forming a dominance hierarchy are affected by intrinsic and extrinsic factors (Moore, 2007). Intrinsic factors are features inherent to the individual such as size, sex, reproductive status, and winner/loser history (Mesterton-Gibbons, 1999; Moore, 2007). The fighting ability in terms of physical prowess (i.e. its resource holding potential; Parker, 1974) is correlated with the size of an animal. Larger animals usually dominate smaller ones and the subordinate animal usually positions itself as far as possible from the dominant animal (Lee and Fielder, 1982). Extrinsic factors include chemical signals from the opponent or the value and type of the resource that is contested (McGregor and Peake, 2000; Moore, 2007). In *Nephrops*, fighting has been observed in the field by video cameras and direct observation of divers (Chapman and Rice, 1971). These recordings suggest that fighting is often caused by territorial interactions over a burrow and start with one animal approaching a burrow defended by a conspecific. In the laboratory, aggressive behaviour can be elicited by placing two animals together in a small tank. Individuals that are initially separated by a divider will start interacting as soon as the divider is lifted. Aggressive behaviours are categorized based on stereotypical agonistic behaviours (Table 3.1). Fights sometimes involve more than one bout of aggressive displays. Fight duration is analysed as the sum of bout durations. A bout ends with one animal (the loser) showing avoidance (level −1) or escape behaviour (level −2). The loser of the fight is the combatant that loses the last bout and does not show any aggression exceeding level 3 for the remaining time of the interaction. Agonistic level

Table 3.1 Definition of agonistic levels for fighting *N. norvegicus*

Level	Behaviour	Definition
−2	Fleeing	Walking backwards, walking away, or turning away, tail flipping
−1	Avoidance	Walking around but avoiding opponent, body pressed to the ground
0	Separate	No activity
L	Separate	Locomotion, cleaning
1	Approach	Animals within reach of claws, facing approaching, turning towards, following
2	Touching	Some body parts (e.g. abdomen, pereiopods) touch for extended time without any higher levels of aggression
3	Threat display	High on legs, meral spread (horizontally spread chelipeds without display physical contact)
4	Cheliped pushing	Combatants push each other face to face in meral spread position pushing
5	Wrestling	Smacking, pushing, antennal touching claw grabbing, punching

Adapted from Atema and Voigt (1995).

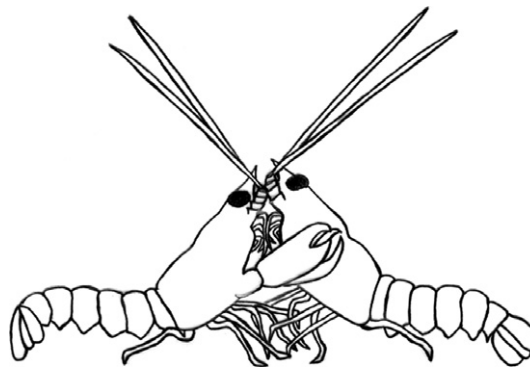

Figure 3.3 Fighting *Nephrops* using cheliped pushing behaviour (Katoh et al., 2008). Copyright 2008 by N.V. Koninklijke Brill, Leiden, The Netherlands.

4 is a *Nephrops*-specific behaviour called 'cheliped pushing' (Figure 3.3), where combatants are face-to-face making contact between the laterally outstretched chelipeds (Katoh et al., 2008).

Katoh et al. (2008) showed that the duration and intensity of dyadic contests decreases when the fight is repeated (Figure 3.4; control) suggesting the formation of a dominance relationship. However, the mechanisms

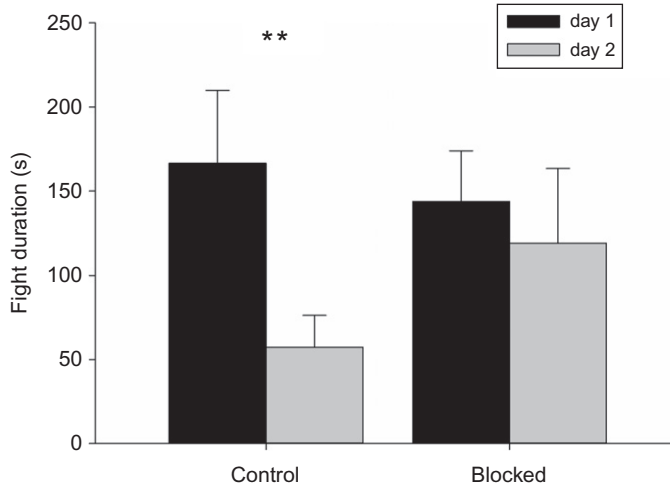

Figure 3.4 Duration (mean + SEM) of repeated fights between size-matched individuals. Animals had their urine release blocked on day 2 by catheter tubes diverting the urine to a syringe floating at the water surface (blocked) or were sham-catheterized (control, days 1 and 2; blocked, day 1) not restraining the urine output. Asterisks indicate significant difference in fight duration ($p < 0.01$). *Data from Katoh et al. (2008).*

responsible for the maintenance of dominance in *Nephrops* are unknown. There are three possible mechanisms to maintain an established dominance relationship: winner/loser effects, individual recognition, and recognition of social status (see Breithaupt, 2011, for a detailed discussion of the three mechanisms). Winner/loser effects are intrinsic factors based on the winning/losing history of an individual. Winners of previous fights tend to win again and losers are more likely to lose in future fights (Hock and Huber, 2005; Hsu and Wolf, 2001). Individual recognition has been demonstrated to mediate maintenance of dominance in some species of hermit crabs (Gherardi and Atema, 2005; Gherardi and Tiedemann, 2004; Gherardi et al., 2005; Hazlett, 1969), in mantis shrimps (Caldwell, 1979, 1985), and in lobsters (Johnson and Atema, 2005; Karavanich and Atema, 1998). Males in these species have the ability to remember the individual opponents they had fought in a previous encounter. The recognition of social status refers to sensory assessment of the winning/losing history of the opponent. A loser of a recent fight can recognize an unknown winner of a different fight. Status recognition has been demonstrated in some species of crayfish (Breithaupt and Eger, 2002; Copp, 1986; Gherardi and Daniels, 2003) and hermit crabs (Winston and Jacobson, 1978). In Norway lobsters, winner/loser effects to not appear to play an important role. Extrinsic factors (individual or status

recognition), based on chemosensory assessment of the opponent, appear to be more important in dominance relationships. Experiments blocking the urine release of fighting Norway lobsters indicate that assessment of the opponent's chemical signals is crucial in the maintenance of dominance (Katoh et al., 2008). Two *Nephrops* males that had interacted in a previous fight were paired again 24 h later. In the second fight, the urinary pores located frontally in the basal segments of the second antennae were blocked by connecting catheters to the cuticle surrounding the nephropores. Urine was released into the catheters rather than into the water. In the first fight, lobsters were sham catheterized (Katoh et al., 2008). In control animals that were sham catheterized in both fights, second encounters are generally shorter than first fights indicating the formation of a dominance relationship (Figure 3.4). However, when nephropores were blocked in the second encounter, these fights were as long as the initial encounter indicating that dominance was not maintained (Figure 3.4). This finding suggested that chemical communication is necessary for maintaining dominance (Katoh et al., 2008). It is likely that it is the subordinate who recognizes the chemical identity or status of the dominant. The subordinate *Nephrops* showed significantly more antennule flicking in first and second day fights than the dominant (Katoh et al., 2008).

In order to investigate whether *Nephrops* uses individual or status recognition, two rounds of dyadic encounters were staged (Katoh, 2011). For the interactions, only males with size-matched carapace length (less than 5% difference) were used to exclude size effects influencing the outcome of interactions. Males were isolated in 3-l individual tanks for 7–10 days prior to the first fight to remove any memory of previous encounters (e.g. in lobsters; Karavanich and Atema, 1998). Fights were staged at temperatures between 10 and 12 °C in a 70-l tank with three sides darkened by a black sheet and the bottom filled with 1 cm of black sand. The tank was illuminated with dim red light (25 W). Opponents were given 30-min acclimatization time on opposite sides of a divider. The fight was started by lifting the divider. The second fight followed 24 ± 1 h after the first fight allowing for sufficient time of physical recovery and restoring of urine resources after the first fight. The first fights enabled *Nephrops* to assess the opponent. The second fights were designed as either familiar or unfamiliar treatment. In familiar treatments (14 replicates), *Nephrops* encountered the same opponent they had fought in the first fight. In the unfamiliar treatment (14 replicates), individuals fought an unknown opponent with contrasting fighting experience (i.e. dominants were paired with subordinates; Karavanich and Atema, 1998;

Katoh, 2011). In Norway lobsters, if dominance was based on individual recognition the second fights would only be shorter in the familiar treatment but not in the unfamiliar treatment.

There was a significant effect of day of fight ($F=14$, $p<0.001$, two-way repeated measure ANOVA) but not of the treatment ($F=0.05$, $p=0.824$). In both treatment groups, second fights were shorter than first fights (Figure 3.5; *post-hoc* Tukey tests, $p<0.05$) but there was no difference between treatments. The result suggests that in *Nephrops* it does not make a difference whether the opponent is familiar or unfamiliar from previous fights. Norway lobsters appear to recognize the social status of the opponent rather than the individual identity (Katoh, 2011). This is surprising as Norway lobsters are similar to American lobsters (Atema and Voigt, 1995) in displaying some site fidelity even though they not always occupy the same burrow (Chapman and Rice, 1971; see also Section 4.2). American lobsters remember for up to 2 weeks the identity of previously fought conspecifics (Karavanich and Atema, 1998). Future field studies are necessary to understand the ecological significance of status recognition versus individual recognition in the Norway lobster.

A better understanding of the mechanisms of fighting behaviour is important to understand the relationship between population density and average body size found during the analysis of *Nephrops* stocks (see Chapter 2). Norway lobsters appear to grow less at high population densities. One

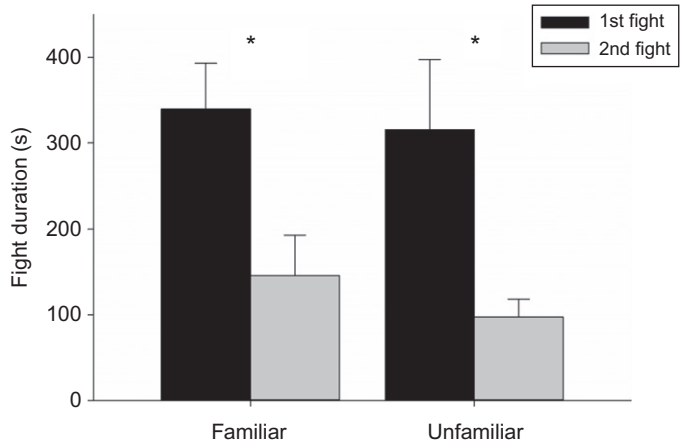

Figure 3.5 Fight duration (mean + SEM) of second encounter was lower than first day encounters, no matter if the same pair of animals fought twice (familiar) or the winner of the first fight met an unfamiliar loser (unfamiliar). Asterisks indicate significant differences ($p<0.05$, *post-hoc* Tukey test).

explanation of this could be that higher densities lead to more encounters and more territorial aggression. This increase in territorial behaviour may reduce the time for foraging and lead to a reduced growth of individuals (Chapter 2).

Experiments on Norway lobsters with disabled urine release indicated that chemical signals are important for the formation of a dominance relationship by reducing the aggression of the subordinate (Katoh et al., 2008). Based on this finding, one could expect that adding a chemical, such as dominance odour, into a tank with fighting *Nephrops* may further reduce aggression of the competitors. In contrast, Sneddon et al. (2003) found that male shore crabs *Carcinus maenas* would increase the fighting effort when female pheromone was added but not when male water or untreated seawater was added. To test the effect of conspecific odour on male competition in *Nephrops*, experiments were conducted by adding dominant odour, female odour, or sea water, as a control, to a tank with two fighting males. In the dominant odour treatment, a dominant male of a different fight was kept for 12 h in the experimental tank to condition the water with dominant male odour. After the conditioning period, the dominant male was replaced by two unfamiliar size-matched males. The males were allowed to interact immediately for 30 min. In the second treatment, water was conditioned for 12 h by an intermoult female (IF), and in the third treatment, water was left for 12 h without an animal (Katoh, 2011). The average fight duration decreased significantly when adding dominant odour compared to the control, where no conspecific odour was added to the experiment (Figure 3.6; $p < 0.05$, one-way ANOVA; Katoh, 2011). Although the dominant male was not present, the odour alone was enough to manipulate the agonistic behaviour of the two interacting males by decreasing fight durations. Female water did not have a significant effect on fighting behaviour. However, in contrast to the study of Sneddon et al. (2003), the females used in this experiment were not receptive (i.e. they were not post-moult) and therefore may have had less impact on the males as they may not have been considered a resource to fight for. This procedure of reducing aggressive behaviour by introducing odour from dominant males can possibly become a valuable tool in aquaculture by reducing aggression in communally held *Nephrops*.

3.2. Reproductive behaviour

Crustaceans have evolved a variety of mating strategies and behaviours (Duffy and Thiel, 2007). Various ways of communication including visual, tactile or chemical signals, or a combination of them plays a role in attracting

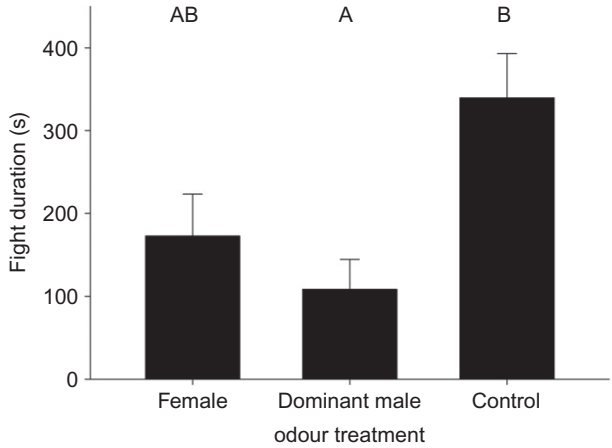

Figure 3.6 Fight durations (mean + SEM). Fight durations following the introduction of different stimuli: female odour, intermoult female conditioned seawater; male dominant odour, dominant male conditioned seawater odour; seawater, unconditioned seawater; $N = 14$. Dominant male odour significantly shortens fight duration in Norway lobster, *N. norvegicus* ($p < 0.05$; one-way ANOVA). Different letters above column indicates significant differences ($p < 0.05$).

mating partners (Duffy and Thiel, 2007). Depending on the species, the male or female initiates mating behaviour. In some species, it was observed that females initiate mating by approaching the male (Lipcius et al., 1983), visiting the males' shelter (Atema and Steinbach, 2007), or backing under the males' body (Jivoff and Hines, 1998). Females are usually selective with respect to the size of the male mate. This is seen when a female shore crab approaches and performs courtship behaviour to the largest available male (Sneddon et al., 2003). Female American lobsters (*H. americanus*) visit the males' shelters to assess the males' quality in order to choose a mating partner. Prior to their moult, *H. americanus* females enter the dominant males' shelter, cohabits with the male until it moults, after which mating occurs (Atema and Steinbach, 2007). In some species, when the female is in the pre-moult stage, she will back under the males' body to initiate his pre-copulatory mate guarding behaviour. The guarding behaviour of the male will protect the female from predators and other males during the moult stage, when the female is weak and vulnerable (Jivoff and Hines, 1998).

Ever since Farmer's classic paper on the reproduction of the Norway lobster (Farmer, 1974b), mating behaviour has not been subject to detailed investigation. Katoh's (2011) study provided the first in depth analysis of mating behaviour and the role of chemical signals in courtship of

N. norvegicus. Animals ranging in size from 31 to 45 mm carapace length were kept in individual tanks at 10°C in a 12–12-h light/dark cycle (with light dimmed down) and fed with polychaete worms once a week. Observations were made on size-matched male–female pairs ($N = 46$ pairs in total) in a 30-l tank illuminated by a 25-W red light with three sides darkened using black sheet and the bottom covered with black sand. Interactions were filmed for 12 h and recorded using time-lapse on a 3-h tape.

Mating behaviour can be divided into six stages (Table 3.2), altogether lasting between 28 s and 6.40 min. Six different behaviours were observed in 16 matings (Table 3.2). Mating generally starts with the 'male approaching' the female. The male then 'mounts' the female, 'turns' it onto her back or onto the side. This is followed by the male 'positioning' himself on top of the female so that his gonopods are close to the female receptacle. The male then 'rolls' the female to the side and deposits the spermatophores in the female receptacle using typical 'thrusting' movements (Table 3.2; Katoh, 2011). There were noticeable differences between the mating behaviours recorded in the study of Katoh (2011) compared to the study of Farmer (1974b). The males in Katoh's study did not have a specific approaching strategy, as mentioned in Farmer's study; they can approach from the front, side, or back and do not necessarily straddle the female from the rear. After 'penetration/thrusting', the pair separates and shows no interest in further interactions. In two cases, the pairs mated twice during the experiment. The observation of double mating in this experiment gives indication that females will mate more than once on occasions.

Decapod crustaceans either mate with hard shells (intermoult mating; e.g. crayfish; Berry and Breithaupt, 2008; squat lobster; Thiel and Lovrich, 2011), with soft shells shortly after moulting (post-moult mating; e.g. many Brachyuran crabs; Christy, 1987), or they sometimes mate hard-shelled, sometimes soft-shelled (e.g. *Homarus gammarus*; Skog, 2009). *N. norvegicus* has been described as a post-moult mater (Farmer, 1974b). Moreover, depending on the male guarding strategy, females can mate with more than one male. Streiff et al. (2004) discovered occurrence of multiple paternity in wild broods of Norway lobsters. Males can secure exclusive paternity only when they guard the female shortly before and after mating (post-copulatory guarding). In this situation, the male keeps other males away from the female for the short period of time during which the female is receptive. Such behaviour has been observed in other Nephropidae, such as the American lobster, *H. americanus* where the male cohabits with a female for up to 2 weeks in the mating shelter (Atema and Steinbach, 2007).

Table 3.2 Definition of courtship levels for mating *N. norvegicus*

Level	Behaviour	Definition
1	Male approach	The male approaches the female by walking towards her from the front ($N=6$), the side ($N=2$), or from the back ($N=8$)
2	Mount	The male climbs onto the females' carapace, from behind or from the side when they are parallel to each other, using his pereiopods. The female is usually passive during mounting and does not move unless she refuses to mate. In the latter case, the female tries to escape, which occurred 8 times out of 24 mounting attempts
3	Turn	The male turns the female using his walking legs (pereiopods) onto her back ($N=6$) or onto the side ($N=6$). During this procedure, the male often holds a claw or antenna of the female with one cheliped ($N=11$). In some cases, there was no reason for the male to turn the female, as in 4 out of 16 matings the female turned onto her back herself, while the male tried to climb on her
4	Positioning	The male positions himself on top of the female ($N=6$ out of 16 matings) so the ventral-to-ventral and face-to-face position can be maintained and the male gonopods are closest to the female seminal receptacle. This stage is skipped if the male has turned the female to the side directly instead of turning her onto her back
5	Rolling	The males who turned females on their backs and positioned themselves on top, will now turn with the females to the side while the hold on to the female with their pereiopods. Usually, at this point the males' claw lets go of the females' claw or antenna. The females are in a torpedo shape with outstretched chelipeds
6	Thrusting	The male moves his abdomen rapidly, while the uropods at the telson open and close (indication of spermatophore transfer and thus mating success; Skog, 2009)

Adapted from Skog (2009).

3.3. The role of pheromones in *Nephrops* mating

Post-moult mating is often triggered by sex pheromones released by the female around the time of moulting (Aggio and Derby, 2011; Hardege and Terschak, 2011). In order to explore whether chemical signals play a role in the courtship and mating of the Norway lobsters, male–female pairs were exposed to water from intermoult (IW in Figure 3.7) or from post-moult females (PW; Katoh, 2011). Freshly moulted females were used within 3 days after moult. These females were used to condition the water

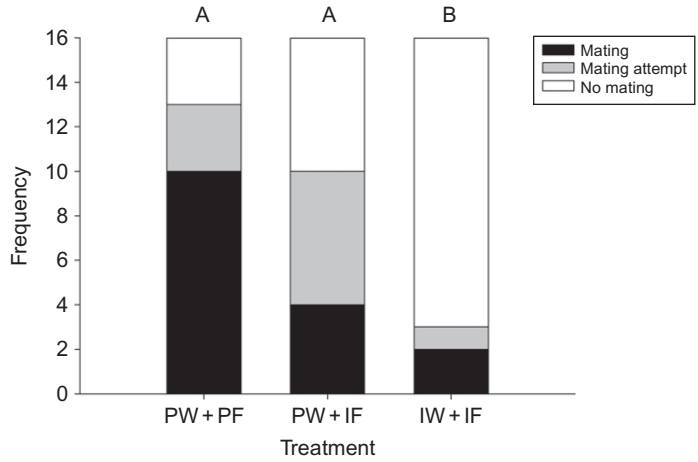

Figure 3.7 The total number of matings, mating attempts, and non-matings in *N. norvegicus* male–female pairs ($N = 16$) exposed to different treatments. PW, post-moult female water; PF, post-moult female; IW, intermoult female water; IF, intermoult female. The male was always in the intermoult stage. The letters indicate differences between the treatments. Columns with different letters are significantly different from each other with respect to the ratio between 'matings + mating attempts' and 'no-matings' ($p < 0.05$; Fisher's exact test). Different letters above column indicate significant differences ($p < 0.05$).

for 12 ± 1 h prior to staging male–female interactions in the observation tank, a glass tank ($45.5 \times 25.5 \times 25.5$ cm) filled with 30-l still water which had three sides darkened with black sheet. After the conditioning period, the female was replaced by another female which was either freshly moulted (PF in Figure 3.7; 16 trials) or intermoult (IF; 16 trials). Introduction of the second female was complemented by introduction of an intermoult male. Control experiments used an IF to condition the water (IW) which was then replaced by an IF paired with an intermoult male (16 trials; Katoh, 2011). The pairs were allowed to interact for 12 h. Behaviours were analysed by recording the presence and timing of the different elements of mating behaviours (Table 3.2). Interactions were scored as 'mating attempts' when males grabbed females from behind and tried to turn her over but did not proceed to thrusting (i.e. spermatophore transfer; Table 3.2). Interactions were scored as 'matings' when thrusting was observed.

The highest numbers of matings occurred when the water was conditioned with a freshly moulted female and interaction were staged between a post-moult female and an intermoult male (PW + PF; Figure 3.7). Out of 16 experiments, 10 pairs mated and three males attempted mating.

In the second treatment, testing intermoult mating in post-moult female conditioned water (PW + IF) 10 out of 16 males attempted to mate, with only four of these being successful. The number of matings and mating attempts was not significantly different from that of the first treatment ($p = 0.433$; Fisher's exact test). The third treatment tested whether mating takes place between an IF and male in water conditioned by an IF (IW + IF). Two of the 16 pairs mated under these conditions and there was one mating attempt. This was significantly different to the number of 'matings + mating attempts' in the first and second treatment ($p = 0.004$; Fisher's exact test; Figure 3.7). This outcome indicates that the odour of moulted female contains sex-specific substances that entice males to mate. The duration of matings was significantly longer (mean ± SEM = 246 ± 104 s) when IFs were involved than between post-moult females and intermoult males (134 ± 71 s; $t = -2.6$, df = 14, $p = 0.022$, t-test) reflecting the observation that females were less resistant to mating when they were in post-moult than in intermoult.

Male *Nephrops* clearly were attracted to females and initiated courtship behaviour when odour from a freshly moulted female was present. Mating attempts were displayed towards post-moult female and IFs, indicating that the presence of the odour was more important than the current moult stage of the female. Odour from IFs rarely (2 out of 16 matings, 12.5% of all matings) initiated male mating attempts suggesting that the odour from post-moult females rather than from IFs contained sex pheromones. The presence of sex pheromone has been demonstrated in many other decapods crustaceans (Atema and Steinbach, 2007), including American and European lobsters and spiny lobsters (Aggio and Derby, 2011), some species of crayfish (Breithaupt, 2011), shore crabs *C. maenas* (Hardege and Terschak, 2011), blue crabs *Callinectes sapidus* (Kamio and Derby, 2011), and Caridean shrimps (Bauer, 2011). In all these examples, sex pheromones were released by the female and initiated male courtship behaviour.

It is questionable whether female *Nephrops* conduct mate choice. In shore crabs (*C. maenas*), for example, the female approaches and mates with the largest male, selecting males based on size (Sneddon et al., 2003). In blue crabs, the female is attracted by males displaying courtship 'stationary paddling' (rhythmically waving the last pair of legs; Kamio and Derby, 2011). This allows the females to assess quality of the male based on mechanical and chemical signals produced by the display (Kamio and Derby, 2011). In American lobsters and in spiny lobsters, it was shown that pre-moult females choose a mating partner by repeatedly visiting the shelter of the chosen mate (Atema and Voigt, 1995; Lipcius et al., 1983). However, similar behaviour

from female *Nephrops* was not observed. In the first treatment where the female was freshly moulted, only two females managed to escape the mating attempt of the males. The vulnerable and fragile condition of the moulted females indicates that they do not have a choice whether they want to mate or not. Mating with post-moult females was significantly shorter than mating with IFs, probably due to higher resistance of the IF. Berry and Breithaupt (2010) showed that following release of female sex pheromone male signal crayfish have to overcome the resistance of the female. Female may display variation in resistance to conduct selection of particular males (Berry and Breithaupt, 2010). In *Nephrops*, it could also be that a female's willingness to mate may be higher when she is freshly moulted. Female blue crabs and female rock shrimp *Rhynchocinetes typus* demonstrated a willingness to mate by backing under the males' body to initiate pre-copulatory mate guarding (Díaz and Thiel, 2003; Jivoff and Hines, 1998). Yet, the moulted female *Nephrops* showed no such behaviour. Furthermore, males did not show any form of guarding behaviour towards the moulted females. In the experiments where the water was conditioned by a freshly moulted female, which was then replaced with an IF, only four matings were successful. Of the six males that attempted to mate, three showed repeated attempts but were not successful; in all six cases, the female managed to escape before spermatophore transfer took place (Katoh, 2011).

The source of sex pheromone in *N. norvegicus* is unknown. Where investigated in other decapods crustaceans, sex pheromones were always released in the urine (see Breithaupt and Thiel, 2011). The chemical identity of sex pheromone has been revealed as a nucleotide uridine diphosphate in the shore crab *C. maenas* (Hardege et al., 2011). Other crustacean sex pheromones have been preliminary characterized (e.g. the blue crab *C. sapidus*; Kamio and Derby, 2011). Future studies of *Nephrops* need to concentrate on identifying the source and chemical identity of the sex pheromone.

We have only begun exploring the possible existence of pheromones in *Nephrops*. It is still a long way towards a better understanding of the role that chemical signals play in the behaviour of the Norway lobster. The potential benefits of such knowledge are manifold (Thiel and Breithaupt, 2011). Chemical signals can provide efficient tools in manipulating and controlling species (e.g. by trapping invasive lampreys in the Great Lakes of the United States, Johnson et al., 2009; in insect pest management, Baker, 2011). Knowledge of the chemical identity and responses elicited by sex pheromones could benefit fisheries and aquaculture of *Nephrops*. Using concentrated female sex pheromone as bait in creels may provide a powerful and

selective way of capturing males (Hardege and Terschak, 2011). Likewise, compared with other bait it would be a useful means of protecting females during the reproductive season. Sex pheromones could provide powerful tools to enhance the success of *Nephrops* aquaculture. They may be useful for selective brood-stock acquisition or to stimulate and time reproduction in captivity (Barki et al., 2011).

4. BIOLOGICAL RHYTHMS

4.1. The general concept of biological rhythms

Evolution shapes the temporal functioning of all living organisms favouring organism that adapt their behaviour to a changing world (Hochachka and Somero, 2002). Periodic habitat changes (e.g. photoperiod, temperature, tides) are driven by the rotation of the earth on its axis and in relation to its positioning respect to the sun and the moon. In response, species evolved a complex system to synchronize their biological activity within the framework of deterministic habitat changes. Such tuning is required in order to anticipate the onset of unfavourable conditions (reviewed by Naylor, 2010). As a result, all species show marked diurnal, nocturnal, crepuscular, or tide-related adaptations to their respective ecological niches (Kronfeld-Schor and Dayan, 2003).

Biological rhythms are governed by the biological clock through a three-step mechanism (Tosini and Aguzzi, 2005): (1) input pathway, (2) processing system, and (3) output pathway. The first is the sum of all the sensory processing environmental information. The second is represented by the circadian pacemaker, a group of neuronal cells that are capable to generate a self-sustained oscillation, the functioning of which can be adjusted (i.e. entrainment) to the periodic environmental fluctuations. The third compartment is represented by the rhythm itself at the level of the soma (Dunlap et al., 2004; Refinetti, 2006). The entrainment permits to distinguish endogenous (biological clock-driven) rhythms from exogenous ones (Aschoff, 1960). Endogenous rhythms persist with only slight modification of phase and period when the specimen under study is exposed to constant conditions (e.g. darkness). Such rhythms displaying a 24-h-based fluctuation are defined as circadian (from the Latin: *circa*—around and *dies*—days). Other rhythms are circatidal, when approximating the tidal periodicity (12.4 h) in their fluctuation, while we refer to ultradian or infradian when the period is shorter or longer than 24 h, respectively. In this context, the term 'masking' refers to any modification of overt rhythms that is not controlled by the

pacemaker. Masking is of importance when trying to define the diurnal or nocturnal character of an animal (Mrosovsky and Hattar, 2005). In some terrestrial species (e.g. rodents), individuals show a nocturnal behaviour in the field that reverts to diurnal (i.e. locomotion peaks at subjective daytime), when animals are exposed to constant laboratory conditions.

The nature and location of the pacemaker is a current theme of investigation in many marine species. That structure is of neural nature and in vertebrates is located in the suprachiasmatic nucleus of the brain (Stephan and Zucher, 1972). In invertebrates (e.g. the fruit fly, *Drosophila melanogaster*), it is located in the brain hemispheres. In crustaceans, no master clock has been yet identified, but a model of distributed clockworks has been proposed as made by different oscillators (e.g. retinular cells, neurosecretory systems in the optic lobes; Aréchiga and Rodriguez-Sosa, 2002; Strauss and Dircksen, 2010). The circadian system of *N. norvegicus* seems to fit within this dispersed model (Aréchiga et al., 1980; Naylor, 1985).

On land, day–night cycles and seasonal photoperiod length variations are pervasive (with some exceptions such as caves). In the sea, the depth gradient and differences in water quality introduce an additional and vertical complexity to the light cycle (reviewed by Aguzzi and Company, 2010; Mercier et al., 2011). Light intensity and spectral quality strongly diminish with depth, to an extent that locally depends upon the primary productivity and overall turbidity (Herring, 2002; Jerlov, 1968; Kirk, 1996). The narrowing of the spectral diversity means that only blue light (480 nm) penetrates to deeper water. Biological clocks of marine species that inhabit a wide range of depths rely on the measurement of this wavelength, since it is the only one invariantly present all over the water column down to the twilight zone end (i.e. the theoretical depth limit of light presence). Blue light seems to be a good candidate for biological clock entrainment also in *N. norvegicus* (Aguzzi and Company, 2010) that is demonstrated to have a blue sensitive rhabdomere (Johnson et al., 2002; for more specific details on eye structure and sensibility, see Chapter 4). Furthermore, the regulation of blue light on animals' biological clocks seems to be an ancient evolutionary achievement, being present in species of several phyla (Sancar, 2003).

4.2. The burrow and the burrow emergence rhythm

Nephrops is a burrowing decapod inhabiting muddy bottoms of continental shelves and slopes of the Mediterranean and the European Atlantic (Bell et al., 2006; Sardà, 1995). Animals show a strict preference for a substratum

granulometry (i.e. silt and clays) that allows the building of tunnels of precise architecture (Chapter 2). A crater-like entrance opens with an approximately 45° onto the seabed and is connected to a tubular tunnel of a diameter adjusted to the animals' body size. That tunnel ends with one or multiple ventilator shafts (Rice and Chapman, 1971). The burrow can be considered the central place during the life of *Nephrops* individuals, since animals use it as centre for the expression of a strong territorial and aggressive behaviour (Chapman and Rice, 1971). Field studies showed that some animals changed burrows, while other individuals were observed in the same burrow for several days (Chapman and Rice, 1971). The mixed scavenger/predator life habits of the species are in accordance with the strong territoriality. Animals are capable of opportunistically feeding on a wide variety of items that are found close to their burrow (Farmer, 1975; Oakley, 1979).

The mechanisms driving the daily burrow emergence rhythm of the *Nephrops* population, at different shelf and slope depths, are observed by trawling at different time of day and night. The effect of population density and territoriality on burrow emergence is still unknown (Sardà and Aguzzi, 2012). *Nephrops* seem to respond mainly to light intensity variations (Chapman et al., 1975). This would explain the depth-related temporal shift of catch rates (representing *Nephrops* activity times) from night to daytime, when moving from shallow water to greater depth, respectively (see Section 2; Bell et al., 2006). The ultimate evolutionary causes for nocturnal or low light activity of *Nephrops* are unclear and await further research. Nocturnal activity is often seen as an adaptation to escape predatory pressure from diurnal visual hunters. For example, field studies investigating predation on tethered juvenile spiny lobsters (*Panulirus argus*) showed that predation risk in open habitat increased markedly from night to daytime, while there was little difference in predation risk between day and night in sheltered lobsters (Smith and Herrnkind, 1992).

Another important parameter controlling the timing of burrow emergence is the variation in the photoperiod length throughout the year. For example, in the Western Mediterranean area, *Nephrops* catches increase in spring-summer, when animals are engaged in moulting and reproductive activities (Aguzzi et al., 2004a). Moulting takes place outside the burrow and mating (i.e. the passing of spermatophores from males to females) generally occurs when the exoskeleton of the female is still soft (Farmer, 1975; see also Section 3.2). All these processes oblige lobsters to spend more time outside the burrow, which in turn provoke an increment of their catchability (see below). Synchronization of rhythmic behaviour between individuals within a population could also be achieved by stimuli such as

conspecific feeding behaviour, that in other crustaceans have been demonstrated to have an entraining effect (Naylor, 2010).

Novel scenarios of research on *Nephrops* entrainment concern the putative hydrodynamic modulation of burrow emergence. As depth increases, light fades out, especially in areas where water turbidity is elevated, so other geophysical cycles, such as periodical current flow, could modulate behavioural rhythms (Wagner et al., 2007). The Atlantic Ocean seabed is dominated by internal tides (12.4-h periodicity; Lorance and Trenkel, 2006), while in the Mediterranean Sea wind-driven inertial currents (18-h periodicity) are the only cyclic signal detected by moorings (Puig et al., 2000). Bell et al. (2008) observed an influence of tides on the catchability of *Nephrops*. In the Western Mediterranean, Aguzzi et al. (2009a) detected an 18-h patterning in the physiological activity of freshly collected animals, as indication that inertial current might control the burrow emergence behaviour. Hydrodynamic entrainment may occur via mechanoreception. The mechanoreceptors in the sensory setae, the first and second antennae, and the statocysts should be able to discriminate the direction and the strength of seabed currents (see Section 2).

There may be conflicting stimuli in those depth areas where animals are exposed to marked day–night and seabed current cycles. In the Atlantic shallow shelf areas, a tidal patterning was not reported to our best knowledge in the field or in the laboratory, as an indication that the day–night cycle may overwhelm any putative current modulation. In deeper areas, where light is almost absent and cyclical seabed currents are strong the effects on the entrainment of rhythms are still unknown. That question is currently under investigation with an appropriate actograph in the laboratory (Sbragaglia V. and Aguzzi J., unpublished data).

4.3. The laboratory-based research of locomotor activity

N. norvegicus can be considered a good model for laboratory studies of rhythmic behavioural and physiological modulation in marine species for the following reasons: it can be easily collected by trawling or creeling at any depth and a great fraction of fished animals survive capture induced stress quite well (Bergmann, 2001); it can be maintained in laboratory facilities for long periods of time (i.e. more than 1 year) if cool (12–13 °C) seawater is available; it displays a locomotor rhythmicity similarly to the diel burrow emergence pattern found in the field; finally, its burrowing behaviour is easy to track with the appropriate actographic technologies. In this sense, the species

can be compared to classic model organisms in chronobiology such as the golden hamster, the mouse, and the fruit fly (Aguzzi et al., 2011a), although it is still difficult and expensive to breed Norway lobsters in the lab.

The presence of a burrow is a very important element for the structuring of *Nephrops* locomotor activity rhythm into temporally coherent bouts (Aguzzi and Company, 2010). Withdrawal into the substratum for sheltering favours the development of temporal patterns of locomotor activity. This has also been reported in the American lobster (*H. americanus*; Jury et al., 2005) and the sand-burying penaeid shrimps (e.g. *Penaeus duorarum*, *P. monodon*, and *P. semisulcatus*; Huges, 1968; Honculada-Primavera and Lebata, 1995; Moller and Jones, 1975).

Nephrops can be captured by trawl hauling only when animals have emerged (Main and Sangster, 1985; Newland and Chapman, 1989; Newland et al., 1992). They are able to immediately retire into their tunnels when residing close to the entrance (Aguzzi and Sardà, 2008). As a consequence, research has focussed on the question whether trawl data provide reliable information on their population demography. Accordingly, several laboratory trials have experimentally studied the locomotor rhythms of *Nephrops*. Standard 12–12 light and darkness photoperiod regimes have been applied using white, green (530 nm; Aréchiga and Atkinson, 1975), or blue (480 nm) monochromatic lights (Aguzzi et al., 2009b). A period of acclimation to laboratory conditions is used prior the trials to minimize the effect of any potential stress from the capture process. Specimens are fed at random times during acclimation, but they starve during experiments to avoid possible feeding entrainment (Fernández de Miguel and Aréchiga, 1994).

Results of this research provided a reliable interpretation of *Nephrops* locomotor rhythms in relation to catch fluctuations. The 24-h behavioural rhythm of *Nephrops* can be subdivided into emergence, retraction, and residence at the burrow mouth (Figure 3.8) (Aguzzi and Sardà, 2008). This latter was described as 'door-keeping', with animals guarding the tunnel entrance, with their claws projected forward (Chapter 7). The duration of each of these behavioural components depends on size and reproductive state (Aguzzi et al., 2008). Seasonal variations in sex and size structures of catches have been reported in the Atlantic and the Mediterranean (Sardà, 1995), which could be caused by variations in emergence and door-keeping between genders and size classes (reviewed by Aguzzi et al., 2004a). Apparently, berried females do not emerge with the same frequency as adults males; in fact, females are rarely captured if they carry eggs (Aguzzi and Sardà, 2008). Presently, it is still unknown if the selective capturing of larger

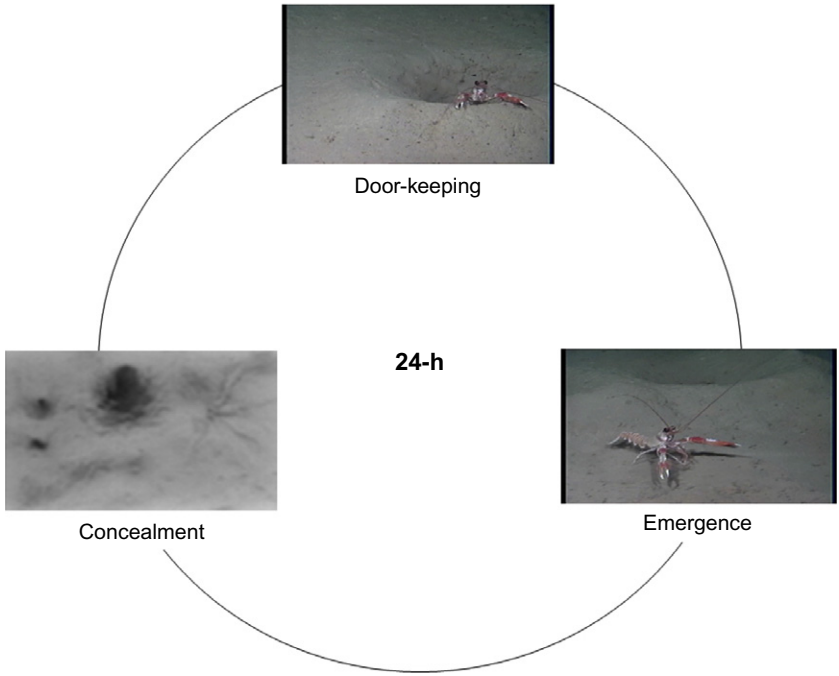

Figure 3.8 *Nephrops* images depict the behaviour of an individual portrayed at 665 m depth during the UE-funded EUROLEON survey by ROV in the Western Mediterranean. *Courtesy of Prof. M. Canals, University of Barcelona; Dr. J.B. Company, ICM-CSIC.*

quantities of males in relation to females is altering the population sex-ratio and consequently behaviour, as demonstrated in other crustacean fisheries (e.g. Van Son and Thiel, 2007). Also, juveniles are captured in lower proportions than adults suggesting different emergence behaviour. Both groups (berried females and juveniles) still do not starve, since they are capable of opportunistic food retrieval (i.e. when engaged in door-keeping, and collecting what is readily available in their close proximity; Aguzzi and Sardà, 2008). Intervidual variability was recently observed in burrow emergence of *Nephrops* under simulated light cycles (Sbragaglia V. and Aguzzi J., unpublished data). Laboratory experiments results did not match with catch fluctuations in the field. Food availability and social interactions might be the major exogenous factors interplaying with the circadian modulation of burrow emergence (the latter controlled by light intensity). Moreover, the effect of predators' presence remains to be tested (see Chapter 2). Taken together, these observations add other variables to the complex

scenario of endogenous and exogenous control of individuals' emergence behaviour. More systematic field studies of natural intra- and interspecific interactions using novel tracking technology are necessary to disentangle the impact of the different exogenous factors on *Nephrops*' emergence behaviour.

4.4. Our knowledge on physiological temporal patterning

Different physiological rhythms in *Nephrops* have been identified in relation to the burrow emergence behaviour. Modifications to the rate of cardiac activity, oxygen consumption, and haemolymph glucose concentration have been linked to the locomotor activity pattern (reviewed by Aguzzi and Sardà, 2008). These results pointed out the presence of two different components in the locomotor activity rhythm sustaining burrow emergence behaviour: these were door-keeping (activity at the burrow entrance related to territorial control) and active emergence (activity outside the burrow related to foraging and mating) (Chiesa et al., 2010). The light cycle could exert a masking effect on active emergence rhythm that disappears when the light stimulus is removed in laboratory constant darkness (Chiesa et al., 2010). Door-keeping and active emergence both occur during the night only in the shallower depth limits of the species distribution range (i.e. upper shelf; 10–50 m). As depth increases, the *Nephrops* locomotor pattern progressively dissociates into two components: one, door-keeping, invariantly nocturnal (as measured by constant darkness experiments in the lab) and the other, emergence, crepuscular (lower shelf; 100–200 m), or diurnal (slope; 200–400 m) (Chapman et al., 1972; Chiesa et al., 2010). Possibly, emergence is linked to light levels in order to avoid visual predators while maintaining residual light for individuals own foraging, whereas door-keeping relates to the activity of conspecifics depending on species–typical interactions.

Melatonin is an indolamine hormone that regulates the circadian cycle in animals within different phyla (Hardeland et al., 1995) by integrating the external photic information into the biology of the organism. Melatonin has been shown to be present at higher concentrations in the eyestalks of decapods, but its secretion is highly variable. In *Nephrops*, diel melatonin levels in haemolymph were studied in the laboratory, by simulating different depths (lower shelf and slope) through variable light intensity (10 and 0.1 lx, respectively) cycles. A daily increase was observed only at higher light intensity regimes (10 lx, lower shelf). Also, data indicated that levels of melatonin were two orders of magnitude higher at 10 lx than at 0.1 lx (Aguzzi et al., 2009c).

Even if melatonin is not strictly involved in the control of locomotor activity of *Nephrops* (Aguzzi et al., 2011a), its rhythmic secretion could be influenced by non-photic stimuli (periodical current flow) such as hypothesized for two species of demersal fish (Wagner et al., 2007).

4.5. The genetic control of rhythmic behaviour

The core of the biological clockwork was shown to be based on a set of genes (denominated 'clock genes') generating negative transcriptional–translational feedback loops (Dunlap et al., 2004). The clock genes have been extensively studied in the fruit fly and have been shown to regulate its circadian behaviour. Mutations in these genes cause dramatic modifications in the period and phase of activity rhythms (Peschel and Helfrich-Förster, 2011). Compared to insects very little is known about the presence and function of these genes in decapods. To date, only the gene *Clock* from the prawn *Macrobrachium rosenbergii* has been cloned (Yang et al., 2006). The characterization of the clock genes in *Nephrops* and their daily patterns of expression could speed up the research on biological rhythms in this and other marine species.

4.6. Future research insights and the new monitoring technological scenario

Studies on marine biodiversity should be linked to the concept of community functioning in the face of habitat changes through time (Smith et al., 2009). This should be carried out in a context where in the past decade, fishing effort has progressively moved to greater depths, impacting local communities in a poorly understood manner (Sheppard, 2000). The precise effects of this are unknown due to a general lack of knowledge on species distribution and their behavioural rhythms, which in turn influence our perception of local biodiversity (Aguzzi et al., 2012). The analysis of communities and biodiversity should take into account behavioural rhythms as a key parameter to fully understand the temporal dynamic.

The study of activity rhythms is of strategic importance for marine field research, especially in deep-water continental margin areas (Naylor, 2005). As the depth increases, the opportunities for conducting repeated observations decrease (Raffaelli et al., 2003). Technological limitations for direct observations are the reason for our scarce modelling capacity regarding population/stock and biodiversity assessments as well as overall ecosystem functioning in continental margin areas. The general problems with conducting repeated observations at greater depth set limitations to the study

of the activities of benthic populations (Aguzzi et al., 2012). Similarly, laboratory research on activity rhythms should follow a similar concomitant technological development in order to mix information on rhythmic patterns of individuals with those of population in the field (Naylor, 2005).

In relation to the field scenario, great efforts have been devoted to *Nephrops* population assessment by video imaging (reviewed by Sardà and Aguzzi, 2012). Video surveys have been conducted as parallel fishery-independent evaluation of demography of exploited stocks, to be compared with the outcomes of trawling. The number of burrows was counted as proxy of animals' density, assuming that one burrow would account for one animal (Bell et al., 2006; Morello et al., 2007). Underwater television observations have been conducted by towed benthic sledges in middle to lower shelf areas (Chapman, 1985; Tuck and Atkinson, 1995), while stills photography with tripod cameras was carried out on the slope (Aguzzi et al., 2004b). Where populations have a more shallow distribution (e.g. in the upper Atlantic shelf), more direct observations were possible and burrows have been manually counted by scuba divers (Chapman, 1979; Chapman and Howard, 1979). To the best of our knowledge, none of these studies was performed in a temporally scheduled fashion, in order to portrait the burrow emergence in the field and to assess, at the same time, how many individuals emerged over consecutive days. The study of the behaviour of *Nephrops* in the field could benefit from the most recent technological implementations in the field of deep-water marine exploration (Sardà and Aguzzi, 2012). Remote or autonomous operated vehicles, equipped with very efficient video-imaging systems, could be used to survey at hourly frequency the same and closely parallel transects. Also, cabled video observatory technology is revealing promising applications in the long-lasting and remote study of activity rhythms in the field at several different depths of the continental margins (Aguzzi et al., 2012).

Emergence behaviour in the laboratory has usually been studied using infrared actographs (Aguzzi et al., 2008; Naylor and Atkinson, 1972) and only recently using automated video imaging (Aguzzi et al., 2009b; Menesatti et al., 2009; Figure 3.9). Also, recent technological advancements in Radio Frequency IDentification (RFID) technology allowed the expansion of locomotor studies from isolated individuals to a group of four individuals, in order to study the social modulation of burrow emergence rhythms (Aguzzi et al., 2011b). Each individual was tagged with a different geometric form on the superior part of the carapace (Figure 3.10) and tracked through video imaging. At the same time, RFID transponders were

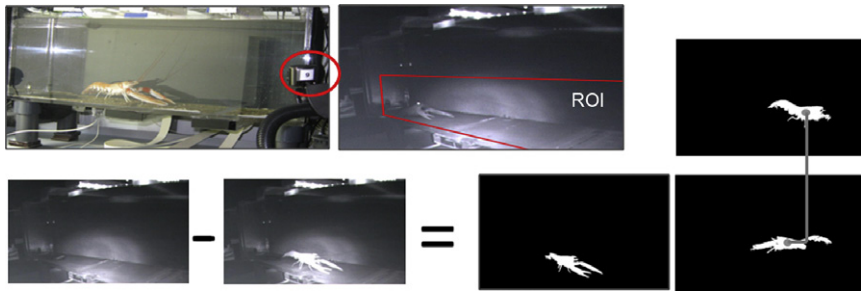

Figure 3.9 An example of actographic device used for the study of *Nephrops norvegicus* burrow emergence rhythm in the laboratory. The first two pictures in the upper row present an actograph where animals' movements are detected with a standard, low cost, mini-web camera through automated video imaging. On the left, the webcam is indicated by a grey (red) circle while on the right, the region of interest (ROI) used for the video imaging is framed by grey (red) lines. The lower row shows that subtraction of consecutive frames and binarization of images is used to extract the position of a lobster. Pictures on the right indicate displacement of the centre of the lobster body from one to the next frame. *Modified after Aguzzi et al. (2009b)—reprinted by permission of the publisher CSIC.*

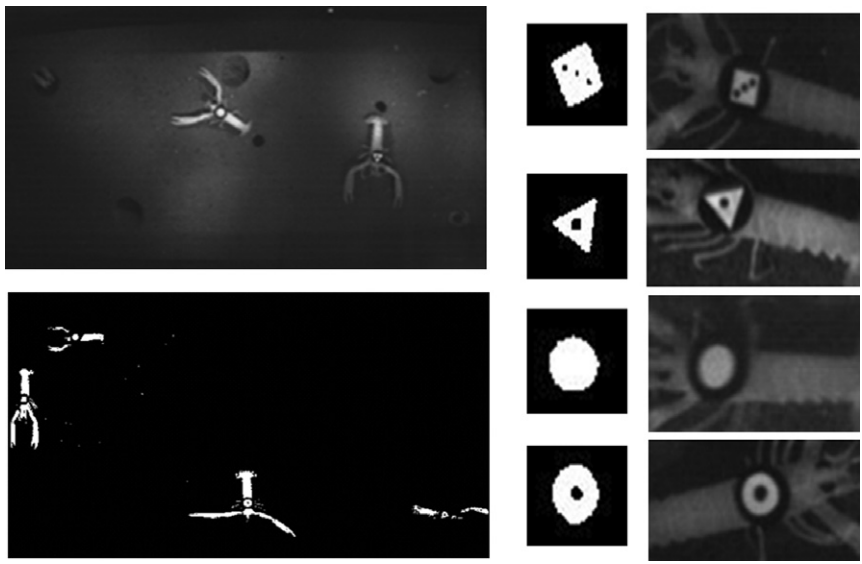

Figure 3.10 Two methods (RFID and video-imaging) are used in combination to track behavioural rhythms of four individuals of *N. norvegicus* in the same tank. On the left: (above) a video frame where dragged RFID transponders are visible as black dot behind the tails of both lobsters; (below) example of an image resulting from binarization of a video frame. On the right: the geometric tags used for the automated video imaging. *Modified after Aguzzi et al. (2011b)—reprinted by permission of the publisher MDPI.*

attached to lobsters' telson and receiving antennas at the bottom of the tank. Finally, results of both tracking methods were compared, showing similar results. In the future, these tracking technologies could be useful to study *Nephrops*' behavioural rhythms in relation to social interactions integrating different aspects of sensory biology.

5. CONCLUSION

A good understanding of the sensory biology and behaviour of an organism of such economical importance as the Norway lobster is crucial for better protection and sustainable exploitation of this species.

With respect to the sensory biology, thanks to the early work of Farmer (1973, 1974a), the morphology of the main mechano- and chemoreceptors is relatively well known and we have inferred the function of these organs by comparison with other, better studied crustaceans. This may not always be a valid comparison as the Norway lobster is adapted to its specific habitat conditions including low light, muddy sediment, and burrows with low oxygen. Our knowledge of the behavioural ecology of *Nephrops* is still very incomplete. Questions with respect to individual behaviour still await further exploration in depth studies. For example, our knowledge of the individual's activity in the field still does not go beyond anecdotal observations. Do individual defend one or several burrows? How does dominance status relate to size of territory or number of defended burrows, respectively? How far do individuals forage away from 'their' burrow(s)? How does individual behaviour change in the mating season? Do males (or females) increase activity in the mating season to find (and select) the mating partner? What are the mechanisms of mate choice in *Nephrops*? Some of the new monitoring techniques discussed above can provide insight into the behaviour of individuals by combining field and laboratory investigations. The results of such studies may eventually lead to better understanding of population parameters including sex-ratio and density/size relationships and facilitate management of natural *Nephrops* populations.

A better understanding of the chemoreceptor function and related behaviour would be important to foresee any specific threats to this species. For example, detailed investigations of the function of olfactory and gustatory receptors will be crucial to understand which specific senses *Nephrops* uses to find and select food (including bait offered in creels), to find and choose mating partners, and to avoid predators. The next step will be to identify

the impact of human-caused disruption of these receptors and behaviours by ocean acidification, global warming, and pollutants including heavy metals. Olsén (2011) reviewed the effects of pollutants such as pesticides, insecticides, and heavy metals on olfactory behaviours of crustaceans. Pollutants can disrupt olfactory receptor cells, parts of the central nervous systems, and the endocrine system. Only few studies have addressed the effect of pollutants on *Nephrops* behaviour. For example, Krang and Rosenqvist (2006) showed that increased Mangan concentration interferes with food search of *Nephrops*. As a benthic predator/scavenger pollutants accumulate in the body of *Nephrops* and may cause concern for its use in the food industry. Ocean acidification may be a particular problem in the future. Recent studies revealed that a lowering of pH has sublethal effects on chemoreception and impairs olfactory discrimination, homing abilities, and predator detection in some fish (Dixson et al., 2010; Munday et al., 2009).

Nephrops rhythmic behaviours could alter our perception of population dynamic. In spite of temporal limitations of sampling repeatability, two major research lines should be developed in the next future: a suitable technology to track behaviour in the laboratory and in the field and research focussed to understand molecular biological clock functioning. Regarding tracking technology of behaviour, great progress was made in the past years. In the laboratory, video-imaging analysis has shown to be the right candidate to improve our knowledge upon different aspects of the biology and ecology of Norway lobster considering also experiment trials with more than one individual in the same tank. This methodological approach when implemented in an automated way is not time consuming and generates a great quantity of data at the same time: (1) time series of lobsters movement, (2) the possibility to reprocess data acquired (frames) focusing on different selected areas in the experimental tank, and (3) the storing of high definition videos could be of valuable help at the moment to study different behavioural traits. Using the appropriate temporal resolution will be key to successful monitoring of individuals. In the field, cabled observatories might be used to track (Aguzzi et al., 2011a) a portion of a population in the natural environment over a long period of time (many years). These techniques will help us to better understand rhythmic behaviours and to correlate this area of research to other topics such as sexual interactions, response to predators, foraging behaviour, and aggressive interactions.

As reported at the beginning of the chapter, behavioural research is a multidisciplinary field. In future studies, an integrated multidisciplinary approach will be key to elucidate still unknown aspects of *Nephrops*

behaviour and ecology. Finally, as molecular sequencing technologies become less costly and more widely available (Wang et al., 2009), an important future direction will be to obtain more information upon genome and transcriptome of *Nephrops*. This will speed up our comprehension of the molecular mechanisms behind the behaviours described here.

ACKNOWLEDGEMENTS

We would like to thank the editors for inviting us to contribute to this volume; Dr. Magnus Johnson for his great support and constructive comments to the chapter; Dr. Martin Thiel for numerous valuable comments to a previous version of the manuscript that significantly improved its quality. Section 3 was part of a PhD project of E. K. and funded by Whitby Seafoods. Part of discussed findings was obtained within the framework of the RITFIM Project (CTM2010-16274; IP, J. A.). J. A. is a Postdoctoral Fellow of the *Ramón y Cajal* Program (Ministerio de Ciencia e Innovación, MICINN).

REFERENCES

Aggio, J., Derby, C.D., 2011. Chemical communication in lobsters. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 239–256.

Aguzzi, J., Company, J.B., 2010. Chronobiology of deep water continental margin decapods. Adv. Mar. Biol. Ann. Rev. 58, 155–225.

Aguzzi, J., Sardà, F., 2008. A history of recent advancements on *Nephrops norvegicus* behavioural and physiological rhythms. Rev. Fish Biol. Fish. 18, 35–48.

Aguzzi, J., Allué, R., Sardà, F., 2004a. Characterization of seasonal and diel variations in *Nephrops norvegicus* (Decapoda: Nephropidae) landings off the Catalan Coasts. Fish. Res. 69, 293–300.

Aguzzi, J., Bozzano, A., Sardà, F., 2004b. First records on *Nephrops norvegicus* (L.) burrows distributions from a deep-shelf population (100 m) in the Western Mediterranean by direct underwater survey. Crustaceana 77, 299–310.

Aguzzi, J., Sarriá, D., García, J.A., Del Rio, J., Sardà, F., Manuel, A., 2008. A new tracking system for the measurement of diel locomotor rhythms in the Norway lobster, *Nephrops norvegicus* (L.). J. Neurosci. Meth. 173, 215–224.

Aguzzi, J., Puig, P., Company, J.B., 2009a. Hydrodynamic, non-photic modulation of biorhythms in the Norway lobster, *Nephrops norvegicus* (L.). Deep-Sea Res. Pt. I 56, 366–373.

Aguzzi, J., Costa, C., Menesatti, P., García, J.A., Sardà, F., 2009b. Monochromatic blue light entrains diel activity cycles in the Norway lobster, *Nephrops norvegicus* (L.) as measured by automated video-image analysis. Sci. Mar. 73, 773–783.

Aguzzi, J., Sanchez-Pardo, J., García, J.A., Sardà, F., 2009c. Daynight and depth differences in haemolymph melatonin of the Norway lobster, *Nephrops norvegicus* (L.). Deep-Sea Res. Pt. I 56, 1894–1905.

Aguzzi, J., Company, J.B., Costa, C., Menesatti, P., Bahamon, N., Sardà, F., 2011a. Activity rhythms in the deep-sea crustacean: chronobiological challenges and potential technological scenarios. Front. Biosci. 16, 131–150.

Aguzzi, J., Sbragaglia, V., Sarriá, D., García, J.A., Costa, C., Del Río, J., Mànuel, A., Menesatti, P., Sardà, F., 2011b. A new RFID technology for the laboratory monitoring of behaviour in marine organisms. Sensors 11, 9532–9548.

Aguzzi, J., Company, J.B., Costa, C., Matabos, M., Azzurro, E., Mànuel, A., Menesatti, P., Sardà, F., Canals, M., Delory, E., Cline, D., Favali, P., Juniper, S.K., Furushima, Y., Fujiwara, Y., Chiesa, J.J., Marotta, L., Priede, I.M., 2012. Biorhythms challenge to stock and biodiversity assessments: cabled observatories video-solutions. Oceanogr. Mar. Biol. 50, 233–284.

Aréchiga, H., Atkinson, R.J.A., 1975. The eye and some effects of light on locomotor activity of Nephrops norvegicus. Mar. Biol. 32, 63–76.

Aréchiga, H., Rodriguez-Sosa, L., 2002. Distributed circadian rhythmicity in the crustacean nervous system. In: Wiese, K. (Ed.), The Crustacean Nervous System. Springer, Berlin, pp. 113–122.

Aréchiga, H., Atkinson, R.J.A., Williams, J.A., 1980. Neurohumoral basis of circadian rhythmicity in Nephrops norvegicus (L.). Mar. Behav. Physiol. 7, 185–197.

Aschoff, J., 1960. Exogenous and endogenous components in circadian rhythms. Cold Spring Harb. Symp. Quant. Biol. 25, 11–28.

Atema, J., Steinbach, M., 2007. Chemical communication and social behaviour of the lobster *Homarus americanus* and other decapods crustacean. In: Duffy, J.E., Thiel, M. (Eds.), Evolutionary Ecology of Social and Sexual Systems, Crustaceans as Model Organisms. Oxford University Press, Oxford, pp. 115–144.

Atema, J., Voigt, R., 1995. Behavior and sensory biology. In: Factor, J.R. (Ed.), Biology of the Lobster *Homarus americanus*. Academic Press, New York, pp. 313–348.

Baker, T.C., 2011. Insect pheromones: useful lessons for crustacean pheromone programs? In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 531–550.

Barki, A., Jones, C., Karplus, I., 2011. Chemical communication and aquaculture of decapods crustaceans: needs, problems, and possible solutions. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 385–506.

Basil, J., Sandeman, D., 2000. Crayfish (*Cherax destructor*) use tactile cues to detect and learn topographical changes in their environment. Ethology 106, 247–259.

Bauer, R.T., 2011. Chemical communication in decapods shrimps: the influence of mating and social systems on the relative importance of olfactory and contact pheromones. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 277–296.

Bell, M.C., Redant, F., Tuck, I., 2006. Nephrops species. In: Phillips, B.F. (Ed.), Lobsters: Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, Oxford, pp. 412–461.

Bell, M.C., Elson, J.M., Addison, J.T., Revill, A.S., Bevan, D., 2008. Trawl catch composition in relation to Norway lobster (*Nephrops norvegicus* L.) abundance on the farn deeps grounds, NE England. Fish. Res. 90, 128–137.

Bergmann, M., 2001. Survival of decapod crustaceans discarded in the Nephrops fishery of the Clyde Sea area, Scotland. ICES J. Mar. Sci. 58, 163–171.

Berry, F.C., Breithaupt, T., 2008. Development of behavioural and physiological assays to assess discrimination of male and female odours in crayfish, *Pacifastacus leniusculus*. Behaviour 145, 1427–1446.

Berry, F.C., Breithaupt, T., 2010. To signal or not to signal? Chemical communication by urine-borne signals mirrors sexual conflict in crayfish. BMC Biol. 8, 25.

Breithaupt, T., 2002. Sound perception in aquatic crustaceans. In: Wiese, K. (Ed.), The Crustacean Nervous System. Springer, Berlin, pp. 548–559.

Breithaupt, T., 2011. Chemical communication in crayfish. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 257–276.

Breithaupt, T., Eger, P., 2002. Urine makes the difference: chemical communication in fighting crayfish made visible. J. Exp. Biol. 205, 1221–1231.

Breithaupt, T., Tautz, J., 1990. The sensitivity of crayfish mechanoreceptors to hydrodynamic and acoustic stimuli. In: Wiese, K., Krenz, W.D., Tautz, J., Reichert, H.,

Mulloney, B. (Eds.), Frontiers in Crustacean Neurobiology. Advances in Life Sciences. Birkhäuser, Basel, pp. 114–120.
Breithaupt, T., Thiel, M., 2011. Chemical Communication in Crustaceans. Springer, New York.
Breithaupt, T., Schmitz, B., Tautz, J., 1995. Hydrodynamic orientation of crayfish (*Procambarus clarkii*) to swimming fish prey. J. Comp. Physiol. A 177, 481–491.
Briffa, M., Sneddon, L.U., 2007. Physiological constraints on contest behaviour. Funct. Ecol. 21, 627–637.
Caldwell, R.L., 1979. Cavity occupation and defensive behaviour 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.
Caprio, J., Derby, C.D., 2008. Aquatic animal models in the study of chemoreception. In: Basbaum, A.I., Kaneko, A., Shepherd, G.M., Westheimer, G., Firestein, S., Beauchamp, G.K. (Eds.), The senses: a comprehensive reference. Olfaction & Taste, vol. 4. Academic Press, San Diego, pp. 97–134.
Chapman, C.J., 1979. Some observations on populations of Norway lobster, *Nephrops norvegicus* (L.) using diving, television and photography. Rapports et Procés Verbaux des Reunions 175, 127–133.
Chapman, C.J., 1980. Ecology of juvenile and adult Nephrops. In: Cobb, J.S., Phillips, B.F. (Eds.), The Biology and Management of Lobsters. Academic Press, New York, pp. 143–178.
Chapman, C.J., 1985. Observing Norway lobster, Nephrops norvegicus (L.) by towed sledge fitted with photographic and television cameras. In: George, J.D., Lythgoe, G.I., Lythgoe, J.N. (Eds.), Underwater Photography and Television for Scientists. Science Publications, Oxford, pp. 100–108.
Chapman, C.J., Howard, F.G., 1979. Field observations on the emergence rhythm of the Norway lobster Nephrops norvegicus, using different methods. Mar. Biol. 51, 157–165.
Chapman, C.J., Rice, A.L., 1971. Some direct observations on the ecology and behaviour of the Norway lobster, *Nephrops norvegicus*. Mar. Biol. 10, 321–329.
Chapman, C.J., Priestley, R., Robertson, R., 1972. Observations on the diurnal activity of the Norway lobster, *Nephrops norvegicus* (L.). ICES 20, 254–269.
Chapman, C.J., Johnstone, A.D.F., Rice, A.L., 1975. The behaviour and ecology of the Norway lobster, *Nephrops norvegicus* (L.). In: Proceedings of the 9th European Marine Biology Symposium, pp. 59–74.
Chapman, C.J., Shelton, P.M.J., Shanks, A.M., Gaten, E., 2000. Survival and growth of the Norway lobster *Nephrops norvegicus* in relation to light-induced eye damage. Mar. Biol. 136, 233–241.
Chiesa, J.J., Aguzzi, J., García, J.A., Sardà, F., De la Iglesia, H., 2010. Light intensity determines temporal niche switching of behavioural activity in deep water *Nephrops norvegicus* (Crustacea: Decapoda). J. Biol. Rhythms 25, 277–287.
Christy, J.H., 1987. Competitive mating, mate choice and mating associations of Brachyuran crabs. Bull. Mar. Sci. 41, 177–191.
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.
Davies, N.B., Krebs, J.R., West, S.A., 2012. An Introduction to Behavioural Ecology. Wiley-Blackwell, Oxford.
Denissenko, P., Lukaschuk, S., Breithaupt, T., 2007. Flow generated by an active olfactory system of the red swamp crayfish. J. Exp. Biol. 210, 4083–4091.

Derby, C.D., 1982. Structure and function of cuticular sensilla of the lobster *Homarus americanus*. J. Crust. Biol. 2, 1–21.
Derby, C.D., Atema, J., 1982. The function of chemo- and mechanoreceptors in lobster (*Homarus americanus*) feeding behaviour. J. Exp. Biol. 98, 317–328.
Derby, C.D., Sorensen, P.W., 2008. Neural processing, perception, and behavioural responses to natural chemical stimuli by fish and crustaceans. J. Chem. Ecol. 34, 898–914.
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.
Díaz, E.R., Thiel, M., 2003. Female rock shrimp prefer dominant males. J. Mar. Biol. Assoc. U.K. 83, 941–942.
Dissanayake, A., Galloway, T.S., Jones, M.B., 2009. Physiological condition and intraspecific agonistic behaviour in *Carcinus maenas* (Crustacea: Decapoda). J. Exp. Mar. Biol. Ecol. 375, 57–63.
Dixson, D.L., Munday, P.L., Jones, G.P., 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. Ecol. Lett. 13, 68–75.
Duffy, J.E., Thiel, M., 2007. Evolutionary Ecology of Social and Sexual Systems: Crustacean as Model Organisms. Oxford University Press, New York.
Dunlap, J.C., Loros, J.J., DeCoursey, P., 2004. Chronobiology: Biological Timekeeping. Sinauer Associates Incorporated Publishing, Sunderland, Massachusetts.
Dusenbery, D.B., 1992. Sensory Ecology: How Organisms Acquire and Respond to Information. W.H. Freeman and Company, New York.
Farmer, A.S., 1973. Age and growth in *Nephrops norvegicus* (Decapoda: Nephropidae). Mar. Biol. 23, 315–325.
Farmer, A.S., 1974a. The functional morphology of the mouthparts and pereiopods of *Nephrops norvegicus* (L.) (Decapoda: Nephropidae). J. Nat. Hist. 8, 121–142.
Farmer, A.S.D., 1974b. Reproduction in *Nephrops norvegicus* (Decapoda: Nephropidae). J. Zool. 174, 161–183.
Farmer, A.S.D., 1975. Synopsis of data on the Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758). FAO Fish. Synop. 112, 1–97.
Fernández de Miguel, F., Aréchiga, H., 1994. Circadian locomotor activity and its entrainment by food in the crayfish Procambarus clarkii. J. Exp. Biol. 190, 9–21.
Garm, A., Watling, L., 2013. The crustacean integument: setae, setules, and other ornamentation. In: Watling, L., Thiel, M. (Eds.), Functional Morphology and Diversity. Oxford University Press, Oxford, pp. 167–198.
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.
Goodall, C.A., 1988. The sensory detection of water borne vibrational stimuli and their motor effects in the Norway lobster, *Nephrops norvegicus* (L.). PhD thesis, University of Glasgow, Faculty of Science, Glasgow.
Goodall, C., Chapman, C., Neil, D., 1990. The acoustic response threshold of the Norway lobster, Nephrops norvegicus (L.) in a free sound field. In: Wiese, K., Krenz, W.D., Tautz, J., Reichert, H., Mulloney, B. (Eds.), Frontiers in Crustacean Neurobiology. Advances in Life Sciences. Birkhäuser, Basel, pp. 106–113.
Hallberg, E., Skog, M., 2011. Chemosensory sensilla in crustaceans. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 103–121.

Hardege, J., Terschak, J.A., 2011. Identification of crustacean sex pheromones. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 373–392.

Hardege, J.D., Bartels-Hardege, H.D., Fletcher, N., Terschak, J.A., Harley, M., Smith, L., Davidson, L., Hayden, D., Müller, C.T., Lorch, M., Welham, K., Walther, T., Bublitz, R., 2011. Identification of a female sex pheromone in Carcinus maenas. Mar. Ecol. Prog. Ser. 436, 177–189.

Hardeland, R., Balzer, I., Poeggeler, B., Fuhrberg, B., Uria, H., Behrmann, G., Wolf, R., Meyer, T.J., Reiter, R.J., 1995. On the primary functions of melatonin in evolution: mediation of photoperiodic signals in a unicell, photooxidation, and scavenging of free radicals. J. Pineal Res. 18, 104–111.

Hazlett, B., 1969. "Individual" recognition and agonistic behavior in *Pagurus bernhardus*. Nature 222, 268–269.

Hazlett, B., 2011. Chemical cues and reducing the risk of predation. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 355–370.

Herring, P., 2002. The Biology of the Deep Ocean. Oxford University Press, Oxford.

Hochachka, P.W., Somero, G.N., 2002. Biochemical Adaptations: Mechanism and Process in Physiological Evolution. Oxford University Press, New York.

Hock, K., Huber, R., 2005. Modelling the acquisition of social rank in crayfish: winner and loser effects and self-structuring properties. Behaviour 143, 325–346.

Honculada-Primavera, J., Lebata, J., 1995. Diel activity patterns in Metapenaeus and Penaeus juveniles. Hydrobiologia 295, 295–302.

Howard, F.G., 1989. The Norway Lobster. Scottish Fisheries Information Pamphlet, 7, pp. 1–15.

Hsu, Y.Y., Wolf, L.L., 2001. The winner and loser effect: what fighting behaviours are influenced? Anim. Behav. 61, 777–786.

Huges, D.A., 1968. Factors controlling emergence of the pinks shrimp *Penaeus duorarum*, from the substrate. Biol. Bull. Mar. Biol. Lab., Woods Hole 134, 48–59.

Jerlov, N.G., 1968. Optical Oceanography. Elsevier, Amsterdam.

Jivoff, P., Hines, A.H., 1998. Female behaviour, sexual competition and mate guarding in the blue crab, *Callinectes sapidus*. Anim. Behav. 55, 589–603.

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, M.L., Gaten, E., Shelton, P.M.J., 2002. Spectral sensitivities of five marine decapod crustaceans and a review of spectral sensitivity variation in relation to habitat. J. Mar. Biol. Assoc. 82, 835–842.

Johnson, N.S., Yun, S.S., Thompson, H.T., Brant, C.O., Li, W., 2009. A synthesized pheromone induces upstream movement in female sea lamprey and summons them into traps. Proc. Natl. Acad. Sci. U.S.A. 106, 1021–1026.

Jury, S.H., Chabot, C.C., Watson, W.H., 2005. Daily and circadian rhythms of locomotor activity in the American lobster (*Homarus americanus*). J. Exp. Mar. Biol. Ecol. 318, 61–70.

Kamio, M., Derby, C.D., 2011. Approaches to a molecular identification of sex pheromones in blue crabs. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 393–412.

Karavanich, C., Atema, J., 1998. Individual recognition and memory in lobster dominance. Anim. Behav. 56, 1553–1560.

Katoh, E., 2011. Sex, pheromone and aggression in Norway lobsters (*Nephrops norvegicus*): for a better future of Scampi. PhD thesis, University of Hull, Hull.

Katoh, E., Johnson, M., Breithaupt, T., 2008. Fighting behaviour and the role of urinary signals in the maintenance of dominance of Norway lobsters, *Nephrops norvegicus*. Behaviour 145, 1447–1464.

Kirk, J., 1996. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge.

Krang, A.S., Rosenqvist, G., 2006. Effects of manganese on chemically induced food search behaviour of the Norway lobster, Nephrops norvegicus (L.). Aquat. Toxicol. 78, 284–291.
Kronfeld-Schor, N., Dayan, T., 2003. Partitioning of time as an ecological resource. Annu. Rev. Ecol. Syst. 34, 153–181.
Lee, C.L., Fielder, D.R., 1982. Agonistic behaviour and the development of dominance hierarchies in the freshwater prawn, *Macrobrachium australiense* Holthuis, 1950 (Crustacea: Palaemonidae). Behaviour 83, 1–17.
Lipcius, R.N., Edwards, M.L., Herrnkind, W.F., Waterman, S.A., 1983. In situ mating behaviour of the Spiny lobster, *Panulirus argus*. J. Crust. Biol. 3, 217–222.
Lorance, P., Trenkel, V.M., 2006. Variability in natural behaviour, and observed reactions to an ROV, by mid-slope fish species. J. Exp. Mar. Biol. Ecol. 332, 106–119.
Main, J., Sangster, G.I., 1985. The Behaviour of the Norway Lobster *Nephrops norvegicus* (L.), During Trawling. Scottish Fisheries Research Reports, Vol. 34. pp. 1–23.
McGregor, P.K., Peake, T., 2000. Communication networks: social environments for receiving and signalling behavior. Acta Ethol. 2, 71–81.
McMahon, A., Patullo, B.W., Macmillan, D.L., 2005. Exploration in a T-maze by the crayfish *Cherax destructor* suggests bilateral comparison of antennal tactile information. Biol. Bull. 208, 183–188.
McVean, A.R., 1982. Autotomy. In: Bliss, D.E. (Ed.), The Biology of the Crustacea, vol. 4. Academic Press, New York, pp. 107–132.
Menesatti, P., Aguzzi, J., Costa, C., García, J.A., Sardà, F., 2009. Video-image analysis for microcosm experiments on activity rhythms with multiple individuals of Norway lobster, *Nephrops norvegicus* (L.). J. Neurosci. Methods 184, 161–168.
Mercier, A., Sun, Z., Sandrine, B., Hamel, J.F., 2011. Lunar rhythms in the deep sea: evidence from the reproductive periodicity of several marine invertebrates. J. Biol. Rhythms 26, 82–86.
Mesterton-Gibbons, M., 1999. On the evolution of pure winner and loser effects: a game-theoretic model. Bull. Math. Biol. 61, 1151–1186.
Moller, T.H., Jones, D.A., 1975. Locomotor rhythms and burrowing habits of *Penaeus semisulcatus* (de Haan) and *P. monodon* (Fabricius) (Crustacea: Penaeidae). J. Exp. Mar. Biol. Ecol. 18, 61–77.
Moore, P.A., 2007. Agonistic behaviour in freshwater crayfish: the influence of intrinsic and extrinsic factors on aggressive encounters and dominance. In: Duffy, J.E., Thiel, M. (Eds.), Evolutionary Ecology of Social and Sexual Systems: Crustacean as Model Organisms. Oxford University Press, New York, pp. 90–114.
Morello, E.B., Froglia, C., Atkinson, R.J.A., 2007. Underwater television as a fishery-independent method for stock assessment of Norway lobster (*Nephrops norvegicus*) in the central Adriatic Sea (Italy). ICES J. Mar. Sci. 64, 1116–1123.
Mrosovsky, N., Hattar, S., 2005. Diurnal mice (Mus musculus) and other examples of temporal niche switching. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. 191, 1011–1024.
Munday, P.L., Dixson, D.L., Donelson, J.M., Jones, G.P., Pratchett, M.S., Devitsina, G.V., Doving, K.B., 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. Proc. Natl. Acad. Sci. U.S.A. 106, 1848–1852.
Naylor, E., 1985. Tidally rhythmic behavior of marine animals. Symp. Soc. Exp. Biol. 39, 63–93.
Naylor, E., 2005. Chronobiology: implications for marine resources exploitation and management. Sci. Mar. 69, 157–167.
Naylor, E., 2010. Chronobiology of Marine Organisms. Cambridge University Press, Cambridge.
Naylor, E., Atkinson, R.J., 1972. Pressure and the rhythmic behaviour of inshore marine animals. Symp. Soc. Exp. Biol. 26, 395–415.

Neil, D.M., Miyan, J.A., 1986. Phase-dependent modulation of auxiliary swimmeret muscle-activity in the equilibrium reactions of the Norway lobster, *Nephrops norvegicus* L. J. Exp. Biol. 126, 157–179.
Neil, D.M., Wotherspoon, R.M., 1982. Structural specializations, fluid-flow and angular sensitivity in the statocyst of the lobster *Nephrops norvegi*cus. J. Physiol. (Lond.) 329, 26–27.
Newland, P.L., Chapman, C.J., 1989. The swimming and orientation behaviour of the Norway lobster, *Nephrops norvegicus* (L.), in relation to trawling. Fish. Res. 8, 63–80.
Newland, P.L., Neil, D.M., 1987. Statocyst control of uropod righting reactions in different planes of body tilt in the Norway lobster, *Nephrops norvegicus*. J. Exp. Biol. 131, 301–321.
Newland, P.L., Neil, D.M., 1990. The tail flip of the Norway lobster, *Nephrops norvegicus*. 2. Dynamic righting reactions induced by body tilt. J. Comp. Physiol. A 166, 529–536.
Newland, P.L., Neil, D.M., Chapman, C.J., 1992. Escape swimming in the Norway lobster. J. Crust. Biol. 12, 342–353.
Norman, C.P., Jones, M.B., 1991. Limb loss and its effect on handedness and growth in the velvet swimming crab *Necora puber* (Brachyura: Portunidae). J. Nat. Hist. 25, 639–645.
Oakley, S.G., 1979. Diurnal and seasonal changes in the timing of peak catches of Nephrops norvegicus reflecting changes in behaviour. In: Naylor, E., Hartnoll, R.G. (Eds.), Cyclical Phenomena in Marine Plants and Animals. Pergamon Press, Oxford, pp. 367–373.
Olsén, K.H., 2011. Effects of pollutants on olfactory mediated behaviours in fish and crustaceans. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 507–529.
Parker, G.A., 1974. Assessment strategy and the evolution of fighting behavior. J. Theor. Biol. 47, 223–243.
Peschel, N., Helfrich-Förster, C., 2011. Setting the clock—by nature: circadian rhythm in the fruitfly Drosophila melanogaster. FEBS Lett. 585, 1435–1442.
Popper, A.N., Salmon, M., Horch, K.W., 2001. Acoustic detection and communication by decapod crustaceans. J. Comp. Physiol. A: Sens. Neural Behav. Physiol. 187, 83–89.
Puig, P., Palanques, A., Guillén, J., García-Ladona, E., 2000. Deepslope currents and suspended particle fluxes in and around the Foix submarine canyon (NW Mediterranean). Deep-Sea Res. Pt. I 47, 343–366.
Raffaelli, D., Bell, E., Weithoff, G., Matsumoto, A., Cruz-Motta, J.J., Kershaw, P., Parker, R., Parry, D., Jones, M., 2003. The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic-pelagic coupling. J. Exp. Mar. Biol. Ecol. 285–286, 191–203.
Reeder, P.B., Ache, B.W., 1980. Chemotaxis in the Florida spiny lobster *Panulirus argus*. Anim. Behav. 28, 831–839.
Refinetti, R., 2006. Circadian Physiology. Francis and Taylor, New York, 667 pp.
Rice, A.L., Chapman, C.J., 1971. Observations on the burrows and burrowing behaviour of two mud-dwelling decapod crustaceans, *Nephrops norvegicus* and Goneplax rhomboides. Mar. Biol. 10, 330–342.
Sancar, A., 2003. Structure and function of DNA photolyase and cryptochrome blue-light photoreceptors. Chem. Rev. 103, 2203–2237.
Sandeman, D.C., 1989. Physical properties, sensory receptors and tactile reflexes of the antenna of the Australian freshwater crayfish *Cherax destructor*. J. Exp. Biol. 141, 197–217.
Sardâ, F., 1995. A review (1967–1990) of some aspects of the life history of *Nephrops norvegicus*. ICES Mar. Sci. Symp. 199, 78–88.
Sardâ, F., Aguzzi, J., 2012. A review of burrow counting as an alternative to other typical methods of assessment of Norway lobster populations. Rev. Fish Biol. Fish. 22, 409–422.
Schmidt, M., Mellon, D., 2011. Neuronal processing of chemical information in crustaceans. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 123–147.

Schmitt, B.C., Ache, B.W., 1979. Olfaction: responses of a decapod crustacean are enhanced by flicking. Science 205, 204–206.

Shelton, P.M.J., Gaten, E., Chapman, C.J., 1985. Light and retinal damage in *Nephrops norvegigus* (L.). Proc. R. Soc. Lond. B 226, 217–236.

Sheppard, C., 2000. Seas at the millennium: an environmental evaluation. Global Issues and Processes, vol. 3. Pergamon Press, Amsterdam and Oxford.

Simon, T.W., Edwards, D.H., 1990. Light-evoked walking in crayfish: behavioural and neuronal responses triggered by the caudal photoreceptor. J. Comp. Physiol. A 166, 745–755.

Skog, M., 2009. Male but not female olfaction is crucial for intermoult mating in European lobsters (*Homarus gammarus* L.). Chem. Senses 34, 159–169.

Smith, K.N., Herrnkind, W.F., 1992. Predation on early juvenile spiny lobsters Panulirus argus (Latreille): influence of size and shelter. J. Exp. Mar. Biol. Ecol. 157, 3–18.

Smith, L.D., Hines, A.H., 1991. The effect of cheliped loss on blue crab *Callinectes sapidus* Rathbun foraging rate on soft shell clams *Mya arenaria*. J. Exp. Mar. Biol. Ecol. 151, 245–256.

Smith, K.L., Ruhl, H.A., Bett, B.J., Billett, D.S.M., Lampitt, R.S., Kaufmann, R.S., 2009. Climate, carbon cycling, and deep-ocean ecosystems. Proc. Natl. Acad. Sci. 106, 19211–19218.

Sneddon, L.U., Huntingford, F.A., Taylor, A.C., Clare, A.S., 2003. Females sex pheromone-mediated effects on behaviour and consequence of male competition in the shore crab (*Carcinus maenas*). J. Chem. Ecol. 29, 55–68.

Stephan, F.K., Zucher, I., 1972. Circadian rhythms in drinking behaviour and locomotor activity of rats are eliminated by hypothalamic lesions. Proc. Natl. Acad. Sci. U.S.A. 69, 1583–1586.

Strauss, J., Dircksen, H., 2010. Circadian clocks in crustaceans: identified neuronal and cellular systems. Front. Biosci. 15, 1040–1074.

Streiff, R., Mira, S., Castro, M., Cancela, M.L., 2004. Multiple paternity in Norway Lobster (*Nephrops norvegicus* L.) assessed with microsatellite markers. Marine Biotechnol. 6, 60–66.

Tautz, J., Plummer, M.R., 1994. Comparison of directional selectivity in identified spiking and nonspiking mechanosensory neurons in the crayfish *Orconectes limosus*. Proc. Natl. Acad. Sci. U.S.A. 91, 5853–5857.

Tautz, J., Masters, W.M., Aicher, B., Markl, H., 1981. A new type of water vibration receptor on the crayfish antenna 1. Sensory physiology. J. Comp. Physiol. 144, 533–541.

Taylor, R.C., 1967. The anatomy and adequate stimulation of a chordotonal organ in the antennae of a hermit crab. Comp. Biochem. Physiol. 20, 709–717.

Thiel, M., Breithaupt, T., 2011. Chemical communication in crustaceans: research challenges for the twenty-first century. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 3–22.

Thiel, M., Lovrich, G.A., 2011. Agonistic behaviour and reproductive biology of squat lobsters. In: Poore, G.C.B., Ahyong, S.T., Taylor, J. (Eds.), The Biology of Squat Lobsters. CSIRO Publishing/CRC Press, Melbourne/Boca Raton, pp. 223–247.

Tinbergen, N., 1963. On aims and methods of ethology. Z. Tierpsychol. 20, 410–433.

Tosini, G., Aguzzi, J., 2005. Effects of space flight on circadian rhythms. In: Sonnenfeld, G. (Ed.), Experimentation with the Animal Model in Space, vol. 10. Elsevier, Amsterdam, pp. 165–174.

Tuck, I.D., Atkinson, R.J.A., 1995. Unidentified burrow surface trace from the Clyde Sea area. Neth. J. Sea Res. 34, 331–335.

Van Son, T.C., Thiel, M., 2007. Anthropogenic stressors and their effects on the behavior of aquatic crustaceans. In: Duffy, J.E., Thiel, M. (Eds.), Evolutionary Ecology of Social and

Sexual Systems, Crustaceans as Model Organisms. Oxford University Press, Oxford, pp. 413–441.
Wagner, H.J., Kemp, K., Mattheus, U., Priede, I.G., 2007. Rhythms at the bottom of the deep-sea: cyclic current flow changes and melatonin patterns in two species o demersal fish. Deep-Sea Res. Pt. I 54, 1944–1956.
Wang, Z., Gerstein, M., Snyder, M., 2009. RNA-Seq: a revolutionary tool for transcriptomics. Nat. Rev. Genet. 10, 57–63.
Weissburg, M.J., 2011. Waterborne chemical communication: stimulus dispersal dynamics and orientation strategies in crustaceans. In: Breithaupt, T., Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer, New York, pp. 63–83.
Wiese, K., 1976. Mechanoreceptors for near-field water displacements in crayfish. J. Neurophysiol. 39, 816–833.
Wine, J.J., 1984. The structural basis of an innate behavioural pattern. J. Exp. Biol. 112, 283–319.
Winston, M.L., Jacobson, S., 1978. Dominance and effects of strange conspecifics on aggressive interactions in hermit crab *Pagurus longicarpus* (Say). Anim. Behav. 26, 184–191.
Yang, J., Dai, Z., Yang, F., Yang, W., 2006. Molecular cloning of Clock cDNA from the prawn *Macrobrachium rosenbergii*. Brain Res. 1067, 13–24.