

RESEARCH ARTICLE

Acoustic behaviour of male European lobsters (*Homarus gammarus*) during agonistic encounters

Youenn Jézéquel^{1,*}, Jennifer Coston-Guarini¹, Laurent Chauvaud¹ and Julien Bonnel²

ABSTRACT

Previous studies have demonstrated that male European lobsters (*Homarus gammarus*) use chemical and visual signals as a means of intraspecific communication during agonistic encounters. In this study, we show that they also produce buzzing sounds during these encounters. This result was missed in earlier studies because low-frequency buzzing sounds are highly attenuated in tanks, and are thus difficult to detect with hydrophones. To address this issue, we designed a behavioural tank experiment using hydrophones, with accelerometers placed on the lobsters to directly detect their carapace vibrations (i.e. the sources of the buzzing sounds). While we found that both dominant and submissive individuals produced carapace vibrations during every agonistic encounter, very few of the associated buzzing sounds (15%) were recorded by the hydrophones. This difference is explained by their high attenuation in tanks. We then used the method of algorithmic complexity to analyse the carapace vibration sequences as call-and-response signals between dominant and submissive individuals. Even though some intriguing patterns appeared for closely size-matched pairs (<5 mm carapace length difference), the results of the analysis did not permit us to infer that the processes underlying these sequences could be differentiated from random ones. Thus, such results prevented any conclusions about acoustic communication. This concurs with both the high attenuation of the buzzing sounds during the experiments and the poor understanding of acoustic perception by lobsters. New approaches that circumvent tank acoustic issues are now required to validate the existence of acoustic communication in lobsters.

KEY WORDS: Passive acoustics, Accelerometer, Buzzing sound, Carapace vibration, Tank, Acoustic communication, Dominance, Sound attenuation

INTRODUCTION

Sounds can be used by marine organisms to convey information. Numerous studies have demonstrated that marine mammals and fish use sounds to navigate, find food, communicate with conspecifics or even deter predators (e.g. Tyack and Clark, 2000; Ladich, 2015). By comparison, the potential role(s) of sounds amongst marine invertebrates is poorly described (Taylor and Patek, 2010; Edmonds et al., 2016).

For instance, only a few crustacean species have been shown to produce sounds during behavioural interactions. The tropical spiny lobster (*Panulirus argus*) produces antennal rasps when attacked by predators (Bouwma and Herrnkind, 2009). Mantis shrimp (*Hemisquilla californiensis*) rumble to maintain their territories against conspecifics (Patek and Caldwell, 2006; Staaterman et al., 2011). Semi-terrestrial crabs (the Ocypodidae) are known to produce stridulations that attract females to their burrows for mating (Popper et al., 2001). Other crustacean species have also been shown to produce sounds, but the lack of relevant behavioural studies does not yet permit validation of potential ecological roles for these sounds. In the temperate coastal waters of Brittany (France), several crustacean species produce a large diversity of sounds, but their ecological roles, if any, are unknown (Jézéquel et al., 2018, 2019).

Lobsters, particularly the American lobster (*Homarus americanus*), have been identified as a good study model for analysing complex behaviours (Scrivener, 1971; Atema and Voigt, 1995; Huber and Kravitz, 1995). Male *H. americanus* lobsters exhibit highly aggressive behaviours towards each other. Indeed, they use agonistic encounters to establish and maintain their dominance within a group to gain better access to shelters and females for reproduction (Scrivener, 1971; Atema and Cobb, 1980; Atema and Voigt, 1995). When two individuals meet, they exhibit an array of agonistic behaviours ranging from visual displays to physical contact (Scrivener, 1971; Huber and Kravitz, 1995; Breithaupt and Atema, 2000). The main factor influencing the outcome of an agonistic encounter is body size: larger individuals have a greater chance of winning an encounter (Scrivener, 1971). This results in shorter behavioural sequences compared with those for size-matched lobsters where their aggressive behaviours lead to highly stressful conditions (Atema and Voigt, 1995). The loser of an encounter avoids the winner afterwards, and dominance is maintained through a variety of signals. Chemical signals (i.e. pheromones) released in urine appear to be the main means of preserving the memory of the outcome between pairs of individuals, post-encounter (Breithaupt and Atema, 1993; Karavanich and Atema, 1998; Breithaupt et al., 1999). Recently, Gherardi et al. (2010) and Bruce et al. (2018) showed that visual recognition of specific individuals also plays a role. The ability to recall the outcome of past encounters may help individual lobsters to avoid additional fights and lower their future risk of injury (Breithaupt and Atema, 2000).

A recent study has shown that, similar to *H. americanus*, the European lobster (*Homarus gammarus*) also emits buzzing sounds when stressed (Jézéquel et al., 2018). These sounds are produced through the rapid contraction of internal muscles located at the base of their second antennae, which causes the carapace to vibrate (Mendelson, 1969). These ‘buzzing’ sounds are characterized by low frequencies (~100 Hz) and have a relatively long duration (~200 ms; Henninger and Watson, 2005; Jézéquel et al., 2018).

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Ward et al. (2011) suggested that *H. americanus* may only use these sounds to deter predators. Interestingly, earlier studies indicated that few buzzing sounds were produced during agonistic encounters in male *H. americanus* and it was then concluded that these sounds do not have a role for intraspecific interactions (Scrivener, 1971; Atema and Voigt, 1995; Atema and Cobb, 1980). Hence, no study has examined the ecological role of these buzzing sounds and only one has described the behavioural patterns in *H. gammarus* during agonistic encounters (Skog et al., 2009).

The primary aim of the present study was to: (1) test whether male *H. gammarus* emit buzzing sounds during agonistic encounters, and (2) test the potential role of these sounds as acoustic communication between lobsters. For this purpose, we designed an experimental laboratory set-up whose main feature was a tank containing the lobsters under study. The set-up also combined hydrophones to record their buzzing sounds in the tank, accelerometers on the lobsters to record their carapace vibrations (i.e. the source of the buzzing sounds) and cameras to record animal behaviour. Firstly, we developed a detailed ethogram based on the video recordings of the encounters. Secondly, we analysed the behavioural sequences between dominant and submissive individuals. Lastly, we examined whether the sequences of buzzing sounds produced by two individuals depended on their relative size differences. We then analysed these as call-and-response signals to explore their potential role for the communication of dominance.

MATERIALS AND METHODS

All laboratory experiments were carried out at the research facilities of the Océanopolis public aquarium located in Brest (France).

Animal collection, characteristics and care

For these experiments, a total of 24 *H. gammarus* (Linnaeus 1758) male individuals, with carapace length (CL; measured from the eye socket to the posterior carapace margin for lobsters) between 8.7 and 13 cm, were used. They were collected carefully by hand while snorkelling in the Bay of Plougonvelin (Brittany, France) at water depths of between 1 and 10 m. Two samplings were done in May and July 2018; 12 individuals were collected during each session. Only intermoult individuals (following the description in Aiken, 1973) with full sets of undamaged appendages were collected and used for this study.

After capture, lobsters were separated randomly into two groups of 6 individuals each, and then transferred to different holding tanks. One group was held in a large shaded, polyester circular tank (radius 4 m, effective height 1.13 m, seawater volume 14.2 m³). The second group was held in two identical plastic rectangular tanks (1.50 m×1.00 m×0.5 m length×width×effective height; seawater volume 0.75 m³) with 3 individuals per tank, separated by plastic

dividers. In the communal tanks, the lobsters' claws were bound with numbered rubber bands to avoid injury. These also identified each individual lobster. All holding tanks were continuously supplied with sand-filtered, UV-sterilized seawater pumped from the Bay of Brest. Temperature, salinity and animal condition were controlled twice a day. During holding, temperature varied between (mean±s.d.) 14.8±1°C (in May and June) and 17.5±0.5°C (in July and August) and salinity between 34.4±0.3 and 34.9±0.1. Animals were fed with fresh pieces of fish (mackerel) and cephalopod (squid) *ad libitum*. They were kept under the natural photoperiod in the large circular tank, and under a 12 h:12 h photoperiod in the smaller tanks, the daylight condition being simulated by fluorescent light tubes above the tanks. Sections of rigid PVC drainage pipes were provided in abundance as shelters. Animals were acclimatized for at least 1 month in these conditions before they were used in the experiments.

Experimental set-up

All experiments were done in a dedicated plastic tank (1.13 m×0.73 m×0.5 m; 0.4 m³) placed in a quiet room, isolated from the main activities of the aquarium facilities (Fig. 1). The bottom was covered with a thin layer of sand, 5 cm deep, to provide a foothold for the animals. Two LED light strips (B0187LXUS2, colour temperature 4500 K) were placed 50 cm above the tank to ensure good visibility for video recording by the cameras. The experimental tank was divided into two equal volumes by a removable, opaque, Plexiglas divider (6 mm thick) installed in the middle of the tank prior to introducing the animals (Scrivener, 1971; Huber and Kravitz, 1995; Skog et al., 2009). To do this, plastic gutters were epoxy glued on the vertical sides and along the bottom of the tank. This permitted the divider to easily slide up at the start of each experiment. The edges of these gutters were silicone sealed to eliminate any water exchange while the divider was in place. The barrier prevented the exchange of chemosensory and visual cues between the two lobster opponents before the agonistic encounter was started by removal of the divider.

Data recording

Buzzing sounds: hydrophones

Sounds were recorded using two pre-amplified hydrophones (HTI-92-WB, High Tech Inc., Long Beach, MS, USA), with a sensitivity of −155 dB re. 1 V μPa^{−1} and a flat response between 2 Hz and 50 kHz. Hydrophones were connected to a compact autonomous recorder (EA-SDA14, RTSys, Caudan, France) with a gain of 14.7 dB, and were powered by battery to limit electronic self-noise. Recordings were made with a sampling frequency of 156 kHz at 32-bit resolution. Even though buzzing sounds are characterized by low frequencies (~100 Hz; Jézéquel et al., 2018), we chose a high

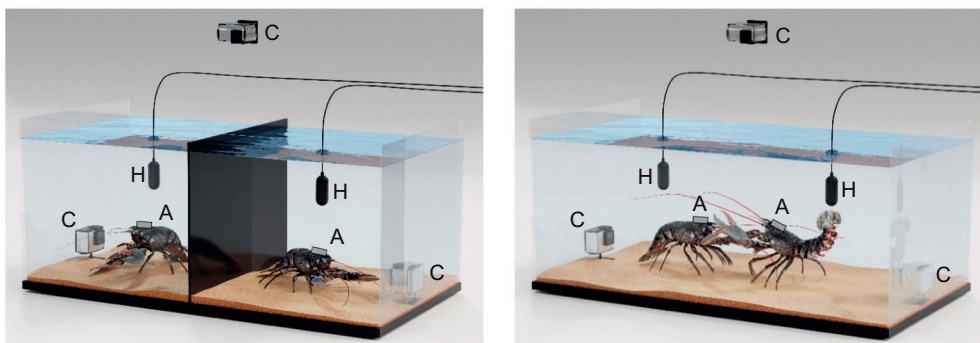


Fig. 1. Experimental set-up of the agonistic encounters performed with male European lobsters, *Homarus gammarus*. Individuals were first isolated for a period of 15 min on either side of the experimental tank (left), and then the divider was lifted and we recorded agonistic encounters for another 15 min. For these experiments, we used several recording devices: two hydrophones (H), two accelerometers (A) and three cameras (C).

sampling frequency because we wanted to cover a large frequency band, in case the lobsters produced new sounds during the experiments.

We used two hydrophones in the experimental tank to ensure most of the buzzing sounds emitted by individuals during the agonistic encounters could be recorded. One was placed in each compartment of the tank, 30 cm above the substrate, and they were separated by 55 cm from each other (Fig. 1). Based on our earlier work to determine the acclimation state of the animals used (Jézéquel et al., 2018), this installation did not perturb the individuals.

Carapace vibrations: accelerometers

During preliminary trials, we noted that very few buzzing sounds were recorded by the hydrophones during agonistic encounters. Lobsters emit buzzing sounds through rapid contractions of internal muscles located at the base of their antennae, which vibrate the carapace (Henninger and Watson, 2005); we therefore added accelerometers on their carapaces as a means to detect carapace vibration events, independently of the hydrophones.

One small AX-3 data logger (23×32.5×8.9 mm, mass 11 g; Axivity Ltd, Newcastle Helix, UK) was glued with 3 min underwater epoxy to the dorsal carapace of each lobster, near the eye sockets at the base of the second antennae (Fig. 1). The *x*-axis was oriented parallel to the longitudinal body axis, which is also parallel to the internal muscles responsible for the carapace vibration (Henninger and Watson, 2005). The accelerometers were set to record acceleration in all three axes (range $\pm 16\text{ g}$, 156.96 m s^{-2}) with a sampling frequency of 3200 Hz and a 13-bit resolution. The accelerometers had a 512 MB memory card onboard. Each accelerometer was waterproofed before attachment by encasing it in a polyethylene film sealed shut with heat-shrink tape. Air trapped inside the polyethylene film made the accelerometer loggers neutrally buoyant in seawater. All accelerometers were marked with unique numbers to associate them with particular individuals. This technique permitted us to link each carapace vibration recorded to an individual and also to validate the buzzing sounds recorded with the hydrophone recordings. As stated above for the hydrophones, we did not observe any evidence that the presence of the sensors perturbed their movements during the experiments.

Movements: video

Visual observations and video recordings were made during all experiments using three GoPro® HERO3 cameras. Two cameras were placed in the bottom of the tank at either end against the walls, and a third camera was placed 50 cm above the water surface of the tank (Fig. 1). Videos used a recording rate of $29.97\text{ frames s}^{-1}$ with an image resolution of 1920×1080 pixels.

Data synchronization

To ensure that all the data streams could be re-synchronized, we used a synchronization procedure at the end of the experiments. First, the accelerometers were gently taken off the lobsters and placed on the sand in the middle of the tank, and the two lobsters were returned to their holding tanks. Then, five sharp raps were made on the tank walls that could be used to synchronize all three types of recording device (hydrophones, accelerometers and GoPros).

Experimental design

Experiments were performed during June and August 2018 in the experimental tank described above. During each experiment,

seawater temperature was measured using a HOBO Pendant G data logger (UA-004-64, Onset Computer Corporation). Seawater temperature in the experimental tank was $17.11\pm 0.14^\circ\text{C}$ (mean \pm s.d.) in June and $18.44\pm 0.12^\circ\text{C}$ in August.

Agonistic encounters were set up between two categories of lobsters: size-matched male lobster pairs (difference in carapace length, $\Delta\text{CL}<5\text{ mm}$), and small and large male individuals ($\Delta\text{CL}>5\text{ mm}$). In fact, larger lobsters are more likely to win a fight if the ΔCL is more than 5 mm between the opponents, but at smaller size differences, the outcome is random (Scrivener, 1971). We formed pairs by taking one individual from each separately acclimated group to ensure that the individuals had no prior knowledge of each other (Karavanich and Atema, 1998). A total of 12 agonistic encounters (6 with $\Delta\text{CL}<5\text{ mm}$; 6 with $\Delta\text{CL}>5\text{ mm}$) were set up.

Because communal holding causes a general reduction of aggressiveness in lobsters (Breithaupt and Atema, 2000), we isolated the two selected individuals separately for 24 h in glass-sided rectangular tanks ($0.60\text{ m}\times 0.50\text{ m}\times 0.35\text{ m}$; 0.105 m^3) after the accelerometers were attached. This allowed the lobsters to recover from handling. For this step, the bands on their claws were also released. Lobsters were not fed during this period.

The next day, these same individuals were placed in the prepared experimental tank, one on either side of the divider (Fig. 1). Experiments were performed between 16:00 h and 20:00 h. Recordings started when the individuals were placed in the tank. We recorded the first 15 min as control observations of the individuals while they were in isolation in their respective compartments. Next, we lifted the divider and continued recording the agonistic encounters that ensued for another 15 min. This corresponds to the expected minimum time for determining the outcome, according to Scrivener (1971). After the experiment, the accelerometers were removed from both animals, and the lobsters were returned to their holding tanks. Then, the data synchronization procedure (described in 'Data synchronization', above) was followed. Afterwards, the experimental tank was drained completely, thoroughly rinsed and refilled with fresh seawater, and the sand was replaced. Each individual was used only once during the study.

Data analysis

Sound data

Sound files (.wav) from the two hydrophones (30 min recordings each) were archived at the end of each experiment. They were first carefully visualized over the entire frequency band (between 0 and 78 kHz) by using the spectrogram mode in Audacity® (v2.1.1; www.audacityteam.org) to check for potential biological broadband sounds emitted by lobsters during experiments. Next, sound data were subsampled between 0 and 500 Hz and spectrograms were visualized a second time using custom-written MATLAB scripts (v9.1; The MathWorks, Natick, MA, USA). The characterization of buzzing sounds has been detailed in our earlier study (Jézéquel et al., 2018). As the aim of the experiments in the present study was to understand when these sounds were produced within the behavioural sequences, here we only report the basic descriptive statistics of the buzzing events recorded during the agonistic encounters.

Accelerometry data

Data from the accelerometers were downloaded using Open Movement GUI software (v1.0.0.37). Accelerometers record movements simultaneously on three axes as the relative change detected in gravitational acceleration, *g* ($1\text{ g}=9.81\text{ m s}^{-2}$), and

carapace vibrations are known to have the same frequency as their associated buzzing sounds (~100 Hz; Henninger and Watson, 2005). After examination of the data on all three axes, we observed the strongest signals of the carapace vibrations were recorded on the *x*-axis, as expected. We thus used only the *x*-axis data to facilitate their detection among all the other high-amplitude signals related to the lobster movements (e.g. tail flips) by treating the data using a custom-written MATLAB script. We report here the number and timing of carapace vibration events recorded during each agonistic encounter for each individual. We also measured their duration (in ms) and peak frequency (in Hz).

Video annotation of movements during encounters

Video analysis consisted of annotating the visible movements performed by each individual during the encounters. Based on the extensive *H. americanus* literature (see Table S1) and preliminary tests, we built a description of movements (also termed ethogram) by annotating 30 associated movements for five different body parts (antennae, claws, legs, carapace, tail; Table 1). We focused on movements or actions initially instead of 'behaviours' because it allowed us to avoid subjective choices related to the sometimes ambiguous behaviours defined in the literature. Movement directions like 'walking away' and 'walking backward' were identified according to the direction of the body axis relative to the other individual. For example, 'walking away' for a lobster was defined as the direction of its rostrum that pointed away from its opponent, but does not necessarily mean it was escaping from its opponent. These 30 movements were annotated for each individual

and for all 12 agonistic encounters using the tools in BORIS (v6.3.9; Friard and Gamba, 2016).

Video data from each agonistic encounter comprised video recordings (30 min each) from each of the three cameras used in the experiments. We chose to annotate primarily videos from the plan view camera because this covered the entire experimental area and most of the movements were visible. We completed these observations by analysing the recordings from the two cameras placed in the bottom of the tank. This permitted us to visualize more precisely certain vertical movements made by the lobsters (e.g. high on legs, meral spread). All these annotations were then integrated with the annotation from the plan view camera for subsequent data treatment. Time energetic budgets were made for each movement and each individual (submissive and dominant) as percentages of the total length of the agonistic encounters (15 min).

Statistical analyses

Statistical analyses were performed using R v3.5.1 (<http://www.R-project.org/>). The mean percentage total time for each movement was tested for significant differences between dominant and submissive individuals in all 12 encounters. As these data were not distributed normally (Shapiro–Wilk test, $P < 0.05$), the non-parametric Mann–Whitney test (*U*-test) was used to determine whether their probability distributions were equal. The significance level for null hypothesis rejection was $\alpha < 0.05$. These results permitted us to associate sequences of movements typically shown by dominant and submissive individuals to particular behaviours based on the conventions used in the *H. americanus* literature (see Table S1).

Table 1. Ethogram of adult male European lobsters (*Homarus gammarus*) during agonistic encounters

Appendage	Movement	Description
Antennae	Antennae backward	Both antennae are positioned backward along the main body axis
	Antenna pointing	One, or both, antennae directed forward, toward opponent
	Antenna sensing	One, or both, antennae directed at opponent with lateral movements
	Antenna touching	One, or both, antennae continuously touching opponent
	Antennae up	Antennae pointing directly up, perpendicular to main body axis
Claws	Antenna whipping	Lashing of opponent's body with antenna(e) in a sweeping motion
	Claw boxing	One claw is pulled backward and then makes a quick 'hook' type strike directed toward the opponent's claw(s) or body
	Claws extended	Claws rest on substrate (in front of animal) and are stretched forward so that merus-carpus-propodus of both claws are aligned with body axis
	Claw forward	One claw is stretched forward (as a weapon) while the other is held close to the body (as a shield)
	Claw grasping	Clamping of claws onto opponent's claw(s) or body
	Claw locking	Crusher claws interlocked; resembles 'handshaking'
	Claws lunging	Thrusting claws forward
	Claw open	The dactyl of either, or both, claws fully open; generally crusher claw
	Claw pushing	Continuous pushing with claws on opponent's body
	Claw ripping	Rapid grasp and pull motion, with either claw, of opponent's claw(s) or body
	Claw scissoring	Both claws pulled backward and rapidly crossed in front of opponent's claw(s) or body in a scissor-like motion
	Claw snapping	Rapid opening and closing of seizer claw in direction of opponent
	Claws touching	Continuous touching of opponent with claws
	Meral spread	Both claws held wide apart above substrate facing opponent
Legs	High on legs	All legs are fully extended raising body high above substrate
	Sand removing	Legs are used to remove sand, causing back and forth rocking movements of the body
Carapace	Facing	Body not moving and rostrum directed towards opponent
	Resting	Body not moving and rostrum not directed towards opponent
	Turning away	Body turns so rostrum points away from opponent
	Turning toward	Body turns so rostrum points toward opponent
	Walking away	Walking with rostrum pointing away from opponent
	Walking backward	Walking backward with rostrum directed toward opponent
	Walking parallel	Walking with rostrum parallel to opponent's body axis
Tail	Walking toward	Walking with rostrum pointing toward opponent
	Tail flipping	Rapid abdominal contractions which propel the lobster backward

The terms are described with respect to the direction of the movement performed by body appendages, and are not related to behaviours or ranks of aggression used in the *Homarus americanus* literature (see Table S1). The description was used to annotate movements from lobsters in videos of agonistic encounters.

Analysis of carapace vibration sequences

As our experiments were necessarily brief to avoid injury (15 min long; Scrivener, 1971) and each experiment was also unique, the carapace vibration sequences did not meet the criteria for classical statistical tests (Guarini et al., 2019). Because the development of a behavioural model was beyond the scope of the present work, we only considered whether the sequences of carapace vibrations recorded by the accelerometers on each individual during the agonistic encounters could not have been produced by a random process. Instead of classical tests, we used a definition of randomness for algorithmic complexity that was recently formalized for short series of fewer than 100 characters that are common in behavioural studies (Soler-Toscano et al., 2014; Zenil et al., 2015preprint; Gauvrit et al., 2016).

Algorithmic complexity offers an alternative means to evaluate the existence of ordered patterns in short sequences by assessing the computing effort needed to stimulate them (Zenil et al., 2018). The approach compares a given string with results from randomly selected Turing machines calculating the likelihood that the string could be reproduced by these algorithms. In this definition, a low-complexity string has a higher probability of being generated by a randomly selected Turing machine, and therefore is less likely to have been produced by a random process (see development in Gauvrit et al., 2016). This has the double advantage of producing invariant estimates of complexity for a given observed sequence and that each experiment is treated as unique. In other words, each sequence is only compared with its own realization relative to the Turing machine algorithm. This method does not use thresholds to infer randomness (Zenil, 2015). Instead, it estimates the algorithmic complexity (AC) and an indicator of the computing time required to compress the sequence structure, called the logical depth (LD; Zenil et al., 2018). A longer LD means a non-trivial structure has been found in the sequence.

To apply this method, carapace vibration sequences produced by individuals during the same agonistic encounter were transformed to time-ordered, discrete binary series. Carapace vibrations were assigned to 1, if produced by the dominant individual, or 0 if produced by the submissive individual (e.g. 1000000001010010); the rhythm of the carapace vibrations (i.e. the time between vibrations) and their duration were not represented. This also means we considered that two individuals produced carapace vibrations sequentially (i.e. as 'call-and-response') and not simultaneously. Because of the short length of our strings (from 14 to 98 characters), we used the block decomposition method made available through an online tool to access the necessary range of Turing machine states (Soler-Toscano et al., 2014; Zenil et al., 2018; <http://complexitycalculator.com/index.html>, v3.0). The most conservative settings were used: the largest available maximum block size (12), with no overlap and a two-character alphabet. As the AC and the LD both depend on string length, we report normalized values (as bits per character and steps per character, respectively). Hence, a standardized AC value of 1 or higher would be considered as not differentiable from random. Using a two-character alphabet, when the standardized LD is about 2 or higher, then the process that generated the sequences cannot be distinguished from a random one (Zenil et al., 2018).

Ethical note

Experiments with *H. gammarus* are not subject to restriction for animal scientific research according to the French legislation and the European Community Council Directive of September 2010 (2010/63/UE). We nonetheless followed the ARRIVE guidelines (Kilkenny et al., 2010) for all the experiments. The animals' health state was

checked daily by the authors and the aquariology team of Océanopolis. During experiments, we planned to stop the agonistic encounters between two lobsters before any injury occurred to the animals; this never happened and no lobsters were injured or died during the study. At the end of the experiments, all animals were released back into the area from where they were collected.

RESULTS

Description of the movements performed by male

H. gammarus during agonistic encounters

When isolated on either side of the divided tank, lobsters wandered freely around the space and did not show any particular movements related to the other individual. When the divider was lifted, the individuals quickly engaged physically in an agonistic encounter (e.g. Fig. 2). Initially, they made a short (<1 min) series of threat displays, typically consisting of: antenna pointing or antenna whipping, claw open, meral spread and high on legs movements. Next, they advanced rapidly with different types of physical claw contact to drive away their opponent. This stage was mainly dominated by claw pushing movements. In 6 of the 12 agonistic encounters (4 with $\Delta CL > 5$ mm, 2 with $\Delta CL < 5$ mm), the outcome was decided at this stage. In the six other trials, the lobster pairs increased the intensity of the fight by using a variety of claw movements to attack their opponents. These movements, such as claw boxing, claw ripping or claw snapping, were very short in duration and occurred in association with aggressive upward-directed tail flipping. Generally, after these actions, one individual withdrew and assumed the submissive role for the remaining time (Fig. 2).

After this first encounter, which determined the hierarchical status between the two lobsters, each dominant and submissive individual displayed typical groups of movements (Fig. 2, Table 2). Dominant individuals continued to perform physical displays (i.e. meral spread, high on legs and claw open), and often approached the submissive individuals (i.e. walking toward) to re-engage in physical contact (mainly antenna whipping and claw pushing). In contrast, submissive individuals always responded by escaping through physically demanding movements such as walking backward and tail flipping (Fig. 2, Table 2). In particular, submissive individuals used a characteristic submissive posture with the claws extended in front of the animal for much of the period following the first encounter. Finally, when individuals were not making claw contact, the dominant animals were moving actively around the tank such as walking or sand removing, while in contrast, the submissive ones were relatively immobile (i.e. resting) near the tank walls with their claws extended (mean: 44.9% of time; Fig. 2, Table 2).

Buzzing sounds and carapace vibrations produced during agonistic encounters

During the agonistic encounters, we did not record any particular sounds other than the buzzing sounds with the hydrophones. We identified a total of 65 buzzing sounds from 9 of the 24 lobsters tested. In marked contrast, the accelerometer data showed that 23 out of the 24 lobsters tested vibrated their carapace during the agonistic encounters. The only lobster that did not vibrate its carapace was a dominant individual. From these 23 lobsters, a total of 422 carapace vibrations were recorded, meaning that only 15% of the associated buzzing sounds were recorded by the two hydrophones in the tank. Fig. 3 shows an example where two lobsters produced three carapace vibrations during a short period (6 s), and the associated buzzing sounds were only recorded by the closest hydrophone (<20 cm from the animals). However, in most other cases when

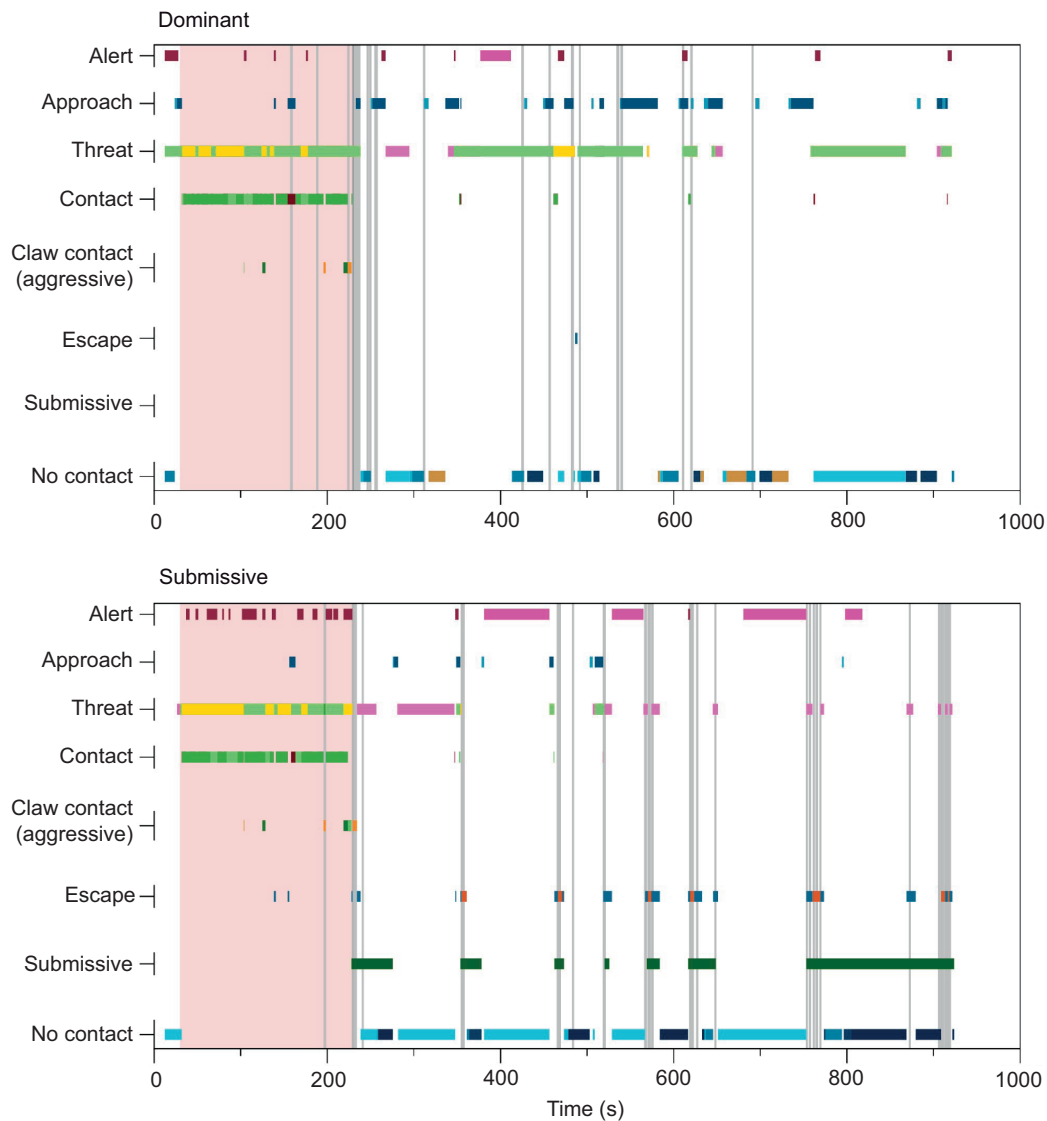


Fig. 2. Example chronology of movements (horizontal colour bars) performed by two lobsters during an agonistic encounter. Top, the dominant individual; bottom, the submissive individual (difference in carapace length, $\Delta\text{CL} < 5$ mm). The different bar colours refer to different movements performed by lobsters that are shown in Table 1 and Table 2. All movements were regrouped using the behavioural terms obtained in Table 2. The first encounter is shaded red. A total of 98 carapace vibrations (vertical grey bars) were produced by both lobsters during this experiment (dominant: 35; submissive: 63), whereas only 7 associated buzzing sounds (7.1%) were recorded by the two hydrophones. Note that most carapace vibrations were produced just after the first encounter and during episodes of approach/escape between dominant and submissive individuals.

lobsters vibrated their carapaces, the associated buzzing sounds were not recorded by the two hydrophones at the same time.

We therefore used the number of carapace vibrations as a proxy for the number of buzzing sounds produced by lobsters. No carapace vibrations were detected when lobsters were first separated from each other by the divider. Even though some first encounters were long (up to 3.38 min) with highly aggressive movements between lobsters (e.g. claw ripping), very few carapace vibrations (4.7%) were produced at this time (Fig. 2). In contrast, carapace vibrations were mostly (95.3%) produced after the first encounter (i.e. after hierarchical status was determined), during the stage of repeated approaches by the dominant individuals making threat displays towards the submissive individuals (Fig. 2).

Fig. 4 describes the distribution of all carapace vibrations detected by the accelerometers according to dominant or submissive outcomes. Overall, dominant individuals emitted about half as many carapace

vibrations as submissive ones (141 and 281, respectively). Carapace vibrations had durations that varied from about 50 ms to nearly 600 ms, and their peak frequencies varied between 100 and 200 Hz. No carapace vibrations were recorded that began at exactly the same time. These data were also plotted as time series for all 12 encounters (Fig. 5). There are few clear patterns in the series. The total number of carapace vibrations in an experiment between individuals of nearly the same CL (Fig. 5, left) tended to be higher than that in experiments where the ΔCL was > 5 mm (Fig. 5, right). Submissive individuals, which were also the only individuals to assume the 'extended claw' pose (Table 2), produced carapace vibrations in all encounters and mostly, but not always, while in this pose (Fig. 5). For most agonistic encounters, submissive individuals produced more carapace vibrations than did dominant ones; but in three experiments (Fig. 5C,H,L), the opposite pattern was obtained and the dominant animal vibrated more frequently. In one experiment, the dominant individual was silent (Fig. 5E).

Table 2. Overview of the movement assignments to behaviours and the time budgets for the 12 agonistic encounters

Behaviour	Movement annotated	Dominant (% time)	Submissive (% time)
Alert	Antenna sensing	4.2±6.2	17.3±14.2
	Antennae up	10.0±7.4	5.8±9.4
Approach	Turning toward	8.9±3.4	2.3±1
	Walking toward	25.7±7.3	3.8±2.5
Threat	Antennae backward	9.6±9.7	2.0±3.7
	Antenna pointing	20.2±8	21.9±16.9
	Claw forward	3.5±3.2	1.7±3.5
	Claws lunging	2.3±2	1.5±2.2
	Claw open	31.6±21.2	6.9±6.6
	High on legs	34.9±13.5	7.1±7.7
	Meral spread	35.3±11.3	2.8±9
Physical contact	Antenna touching	0.8±1.1	5.7±7.8
	Antenna whipping	11.7±7.8	2.1±3.2
	Claw pushing	7.8±6.5	3.9±5
	Claw touching	2.6±2.2	0.7±1.2
Aggressive claw contact	Claw boxing	0.1±0.2	0.1±0.1
	Claw grasping	0.3±0.9	0.2±0.4
	Claw locking	0.1±0.2	0.1±0.2
	Claw ripping	0.1±0.1	0.03±0.06
	Claw scissoring	0.1±0.1	0.1±0.2
	Claw snapping	0.02±0.06	0.05±0.1
Escape	Tail flipping	0.2±0.3	2.4±2
	Walking backward	1.0±0.8	18.9±5.6
Submissive	Claws extended	0.0±0	44.9±15.7
No contact	Facing	16.0±11.8	6.1±10.6
	Resting	12.3±6.7	44.8±11.7
	Sand removing	5.2±7.2	0.0±0
	Turning away	4.1±1.9	3.8±1.8
	Walking away	5.8±3.8	9.7±5
	Walking parallel	7.5±7.5	2.8±3

Mean (±s.d.) percentage of time in each movement is shown for the dominant and submissive individuals. Total time was 15 min for each encounter. Bold highlights significantly different means between dominant and submissive animals (U -test, $N_1=N_2=12$, $P<0.05$).

As described above, the carapace vibration series were then expressed as binary, ordered sequences and analysed for their AC and LD. The string standardized values of the AC and LD are given in Fig. 5, in bits per character and steps per character, respectively. The values of both measures ($1<AC<3$ and $2<LD<4$) indicate that the carapace vibration sequences were probably the product of a random process, and by themselves cannot be assimilated to call-and-response type signalling.

DISCUSSION

This study is the first report of male *H. gammarus* producing buzzing sounds during agonistic encounters. These sounds were produced by both dominant and submissive individuals during the experiments and were mainly emitted after the end of the first encounter (when claw contact stopped) up until the experiment ended.

Our agonistic encounters resembled descriptions of agonistic encounters published in earlier studies of male *H. americanus* (Scrivener, 1971; Atema and Voigt, 1995; Huber and Kravitz, 1995) and male *H. gammarus* (Skog et al., 2009). The initial stage consisted of a threat display between individuals that then quickly engaged in physical claw contacts, which could increase in aggressiveness (e.g. claw boxing) until the withdrawal of one individual (Fig. 2). This losing individual then exhibited submissive behaviours highlighted by a claws extended pose and was less active, while the winner remained active and continued to make approaches and threat displays. At the same time, both individuals produced buzzing sounds.

However, during these experiments, very few buzzing sounds were recorded by the two hydrophones even if they were placed close to the lobsters (<75 cm away). This is consistent with remarks made in previous studies on *H. americanus* (Scrivener, 1971; Atema and Cobb, 1980; Atema and Voigt, 1995; Ward et al., 2011). For example, Atema and Cobb (1980) stated that 'the biological significance of such vibrations is unknown; during high intensity fights in aquaria, these sounds were rarely recorded'. Ward et al. (2011) showed, with accelerometry and sound recordings (as in this study), that the presence of another lobster in a tank significantly increased the number of buzzing sounds produced, but that these events were also rare (mean of 3 sounds per lobster in a 30 min experimental period). Nonetheless, these authors did not perform experiments concerned with agonistic behaviours between male individuals, and in addition, the accelerometers used in Ward et al. (2011) required that the lobsters were immobilized.

In the present study, we used small accelerometers which could be attached directly on the carapace where sound production occurs (Henninger and Watson, 2005). This unobtrusive sensor permitted the lobsters to exhibit their full range of agonistic movements. In contrast to the earlier studies, we found that the number of carapace vibrations recorded with the accelerometers was very high during agonistic encounters. Indeed, we recorded a total of 422 carapace vibrations produced by 23 out of the 24 lobsters tested, with some individuals producing up to 70 carapace vibrations per experimental period (15 min total). In contrast, only 15% of these carapace vibrations were picked up by the two hydrophones (e.g. Fig. 3). This difference in detection between hydrophones and accelerometers is explained by the high attenuation of low-frequency sounds in tanks. Although low frequencies are less attenuated than high frequencies in open water, the situation is reversed in tanks when the wavelength of the sound is larger than the tank size (e.g. a 100 Hz sound has a ~15 m wavelength). This phenomenon is well known in the acoustic community (Gray et al., 2016; Rogers et al., 2016), but sometimes misunderstood in the bioacoustic community. Nonetheless, it was recently highlighted through numerical simulations and empirical measurements. Indeed, Duncan et al. (2016) illustrated that the attenuation in a tank at 100 Hz is 10 dB higher than in open water (note that the exact number depends on the specific tank size and the source/receiver configuration). Moreover, Jézéquel et al. (2019) performed an empirical illustration of this phenomenon by comparing spiny lobster sounds in a tank and *in situ*. Because the high attenuation of low frequencies has been ignored in previous bioacoustic tank studies that relied on hydrophones alone, we believe that the role and importance of buzzing sounds for lobsters during agonistic encounters have been underestimated.

The detection or determination of communication amongst individual animals is a fundamental challenge in behavioural ecology (Hebets and Anderson, 2018). Communication is defined most simply as a transfer of information from one or more individuals that is observed to change the behaviour of one or more receiving individuals. Information can be transmitted and perceived in many different ways (e.g. chemically, visually, acoustically) depending on the sensory capabilities of the organisms involved. Several studies have already shown that male *H. americanus* use chemical signals as a means of communication to both recognize individuals and maintain dominance (Atema and Engstrom, 1971; Karavanich and Atema, 1991; Breithaupt and Atema, 2000). These same mechanisms are also known for male *H. gammarus* (Skog et al., 2009). Studies have demonstrated that the volume of urine

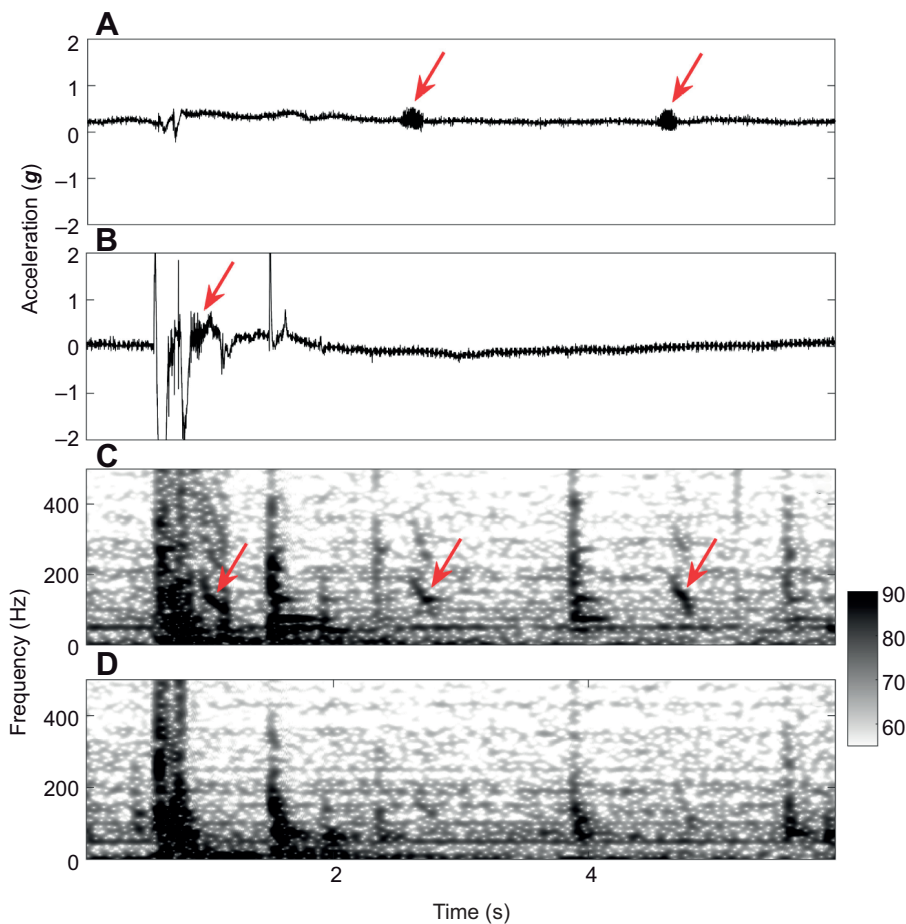


Fig. 3. Synchronized data of two accelerometers (top) and the two hydrophones (bottom) during an agonistic encounter. The red arrows highlight the carapace vibrations and the associated buzzing sounds. The dominant lobster (CL=13 cm) used claw contact and produced two carapace vibrations (A) toward the submissive lobster (CL=11.3 cm), which escaped by tail flipping (large negative peaks) and produced one carapace vibration (B). The three associated buzzing sounds were recorded by the hydrophone located at <20 cm from the animals (C) while the other more-distant hydrophone (D) did not record them. The vertical colour bar scale of the spectrograms is in dB re. $1 \mu\text{Pa}^2 \text{Hz}^{-1}$.

released is closely linked with aggressive behaviours (Breithaupt et al., 1999) and, after the first encounter, only dominant individuals continue to release urine to maintain their dominance (Breithaupt and Atema, 2000). There is also evidence that lobsters rely on visual signals to recognize each other (Gherardi et al., 2010; Bruce et al., 2018). All these means of communication emphasize the importance of individual-level recognition of submissive and dominant individuals. For example, this would be an advantage for avoiding additional aggressive claw contact incidents that could lead to injuries and even loss of an appendage (Breithaupt and Atema, 2000).

Dominance among male lobsters also relies on their relative size differences (Scrivener, 1971). In our study, 6 out of the 12 agonistic encounters were performed with closely size-matched pairs ($\Delta\text{CL} < 5 \text{ mm}$). As the encounters studied here represent examples of possible outcomes of new arrival dominance contests and not repeat encounters, the conditions should be suitable for a more important role of other signals conditioning the outcome, particularly for the encounters with closely size-matched pairs. In accordance with this, there were some intriguing patterns in the production of carapace vibrations. Indeed, we observed that

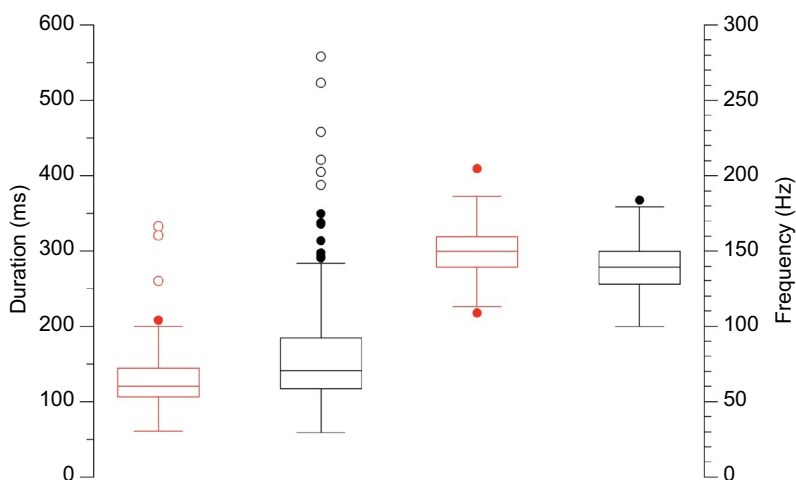


Fig. 4. Box plots of carapace vibration features produced by dominant (red) and submissive (black) animals during agonistic encounters. Median values for each group are indicated by the horizontal lines. Left: duration; right: frequency.

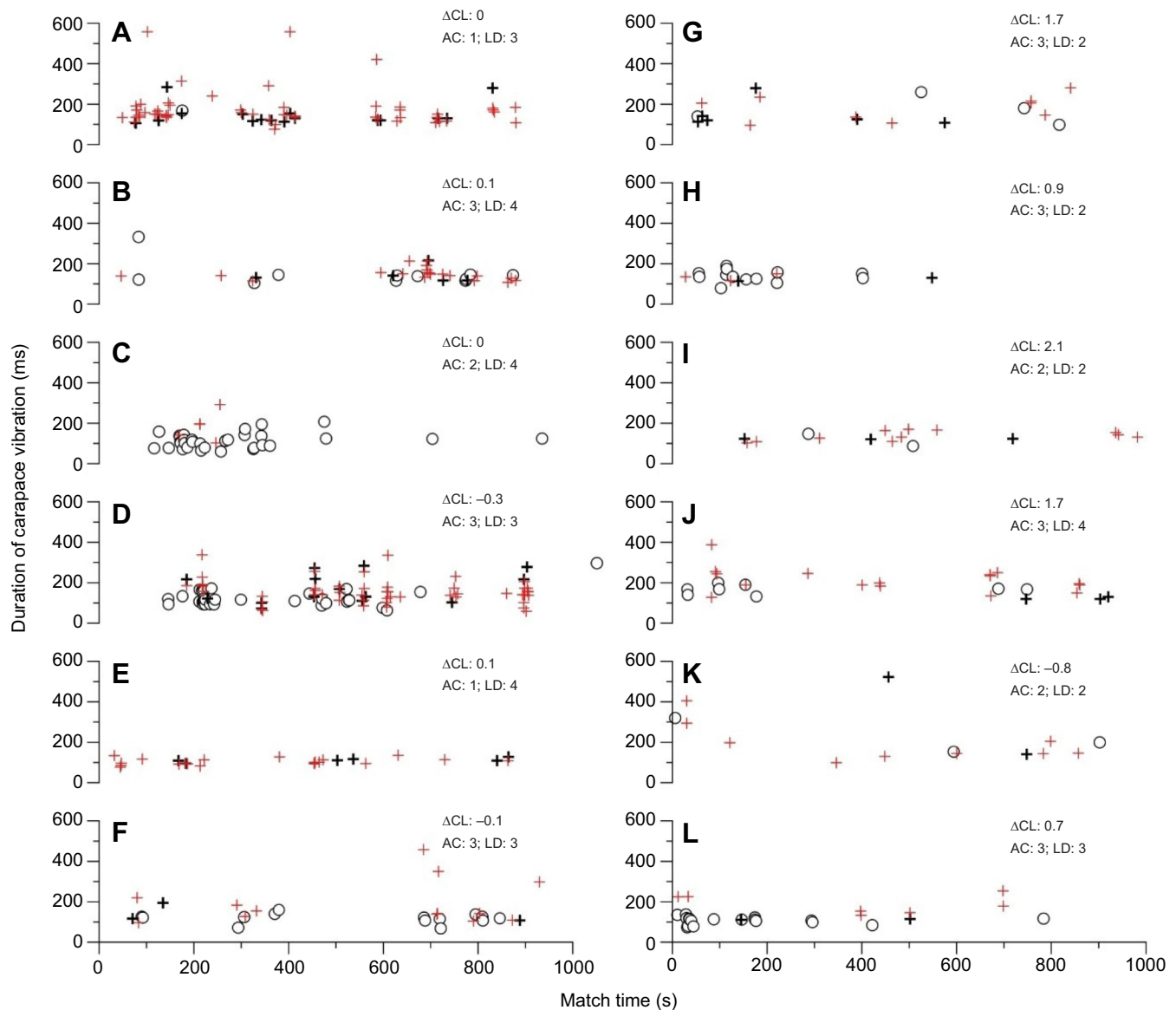


Fig. 5. Emitted carapace vibrations and their duration for all 12 agonistic encounters. Dominant animals (open circles) mostly vibrated less than submissive ones (crosses). Red crosses indicate when the submissive individuals vibrated while in extended claw pose. On each plot, the relative difference in CL (ΔCL) is indicated for each pair (estimated as the difference in length of the dominant and submissive individual); the left column of plots is for the $\Delta CL < 5$ mm size class and the right column is for the $\Delta CL > 5$ mm size class. The ratios of the algorithmic complexity (AC) and logical depth (LD) standardized by the string length are also given. In our analysis, all the values indicate that the pattern of vibrations emitted by the two individuals during the encounters cannot be differentiated from a random process.

submissive individuals always produced carapace vibrations, and these mostly occurred while in the claws extended pose, as well as having a broader range of duration and a higher number of carapace vibrations produced (Figs 4 and 5). In contrast, dominant individuals did not always produce a carapace vibration (e.g. Fig. 5E). We also noted that no carapace vibrations were produced by lobsters while isolated before agonistic encounters. However, examination of the carapace vibration sequences using the paradigm of AC (Gauvrit et al., 2016; Zenil et al., 2015preprint, 2018) indicated that these sequences cannot be differentiated from a random process. As stated earlier, this could be due to their non-detection by lobsters because of the high attenuation of these low-frequency sounds in the tanks (Gray et al., 2016; Rogers et al., 2016).

When looking at sequences of carapace vibrations between the two groups of encounters with different relative CLs, the more

closely size-matched pairs ($\Delta CL < 5$ mm) appeared to make a greater investment in countering the strategies of their opponents. Indeed, these encounters had more carapace vibrations, which implied more effort expended to counter the opponent's reactions (Fig. 5). These preliminary results are consistent with the hypothesis that carapace vibration sequences in pairs of nearly sized-match individuals contribute to the communication of dominance, but that when size differences are larger, other signals (i.e. visual) are sufficient to establish dominance (Scrivener, 1971; Atema and Voigt, 1995; Skog et al., 2009). Interestingly, such multimodal communication is well known in terrestrial arthropods (e.g. Elias et al., 2006). However, we caution that as stated above, the vibration sequences cannot be distinguished from a random process and that there is a potential bias due to sound attenuation in tanks, as well as a small number of observations.

Our results emphasize not only the numerous technical challenges in these experiments but also the absence of knowledge about how lobsters may perceive sounds. For instance, in our study, the lack of a call-and-response pattern with carapace vibrations between lobsters was surprising. Indeed, individuals only produced vibrations when in the presence of a potential opponent, strongly suggesting their emission is context dependent. If combinatoriality (that is, the property of constructing meaning from apparently meaningless elements) is present, then the acoustic production would be considered communication if it can be shown to provoke a predictable response (Engesser and Townsend, 2019). This highlights the need to better understand how animals perceive sounds to be able to design appropriate experiments.

Lobsters cannot directly detect pressure from buzzing sounds, but they may still be able to detect the corresponding particle motion (Breithaupt and Tautz, 1990; Breithaupt, 2001; Popper et al., 2001). Indeed, a large diversity of sensory receptors dedicated to this function is known in both *H. americanus* and *H. gammarus*, including statocysts and sensory hairs (Cohen, 1955; Laverack, 1962). By considering this, Breithaupt (2001) suggested that lobsters may only be able to detect these sounds in the near-field, i.e. at distances less than a few tens of centimetres from the source. This hypothesis is consistent with the close-range communication well described in terrestrial arthropods (Raboin and Elias, 2019). Here, we did not measure or model the acoustic particle motion field in the behavioural area as this was out of the scope of the study. As a result, if the lobsters were unable to detect the buzzing sounds using particle motion, we do not know whether this is due to the specificities of tank acoustics and/or because of biological reasons. Validating (or rejecting) this hypothesis would require further work, including model and/or measurement of near-field particle motion of lobster buzzing sounds (active and reactive intensity; e.g. Zeddies et al., 2012; Jones et al., 2019), and a better understanding of the lobster sound perception system (Breithaupt, 2001).

While some studies have confirmed experimentally the role of sound production in marine crustaceans to deter predators (Bouwma and Herrnkind, 2009; Ward et al., 2011), few studies have demonstrated these sounds are used for intraspecific communication. Interestingly, stomatopods produce low-frequency sounds termed 'rumbles' that are similar to the lobster buzzing sounds (Patek and Caldwell, 2006; Jézéquel et al., 2018). Mantis shrimps are territorial species living in burrows, like lobsters, and their sounds might help to send signals of their presence to conspecifics to maintain territory (Staaterman et al., 2011). Spiny lobsters have also been shown to emit antennal rasps during agonistic encounters in tanks (Mulligan and Fischer, 1977), suggesting that these sounds may be used as a threat display. Snapping shrimps may also use their powerful 'snaps' to deter other conspecifics from their territory (Schmitz and Herberholz, 1998). During agonistic encounters, male hermit crabs produce rapping sounds by rubbing their claws against their carapace, which may be a signal of stamina (Briffa et al., 2003). In marked contrast to other marine crustacean species where behavioural responses to sounds are not yet clear, semi-terrestrial crabs (Ocypodidae) have been shown not only to produce sounds (e.g. Taylor et al., 2019) but also to respond to these sounds during intraspecific interactions (Crane, 1966; Horch and Salmon, 1969; Horch, 1975).

In our earlier study (Jézéquel et al., 2018), we found that *H. gammarus* produced buzzing sounds when stressed by handling. In the present study, agonistic encounters led to stressful events for both dominant and submissive individuals that resulted in the production of buzzing sounds. Thus, these sounds may be used in a similar context to the spiny lobster antennal

rasps and the mantis shrimp rumbles to repel other organisms, whether conspecifics or heterospecifics (Mulligan and Fischer, 1977; Bouwma and Herrnkind, 2009; Staaterman et al., 2011). Taken together, these preliminary results suggest that male *H. gammarus* could use buzzing sounds, in addition to visual and chemical signals (Skog et al., 2009), as a means of intraspecific communication during agonistic encounters. However, we emphasize that our study should be repeated and include additional tests to evaluate whether these buzzing sounds really constitute communication. Other experiments should test behavioural reactions to emitted sounds as well as build an audiogram for the species associated with the quantification of particle motion (Goodall et al., 1990; Popper and Hawkins, 2018). As shown in this study, because small tanks highly attenuate buzzing sounds, these experiments should be done under controlled conditions or directly in the field (Gray et al., 2016; Rogers et al., 2016). This would also be expected to change the behavioural observations. Indeed, it is not yet known at what frequency and intensity lobsters fight for dominance under *in situ* conditions where escape is possible (Karnofsky et al., 1989). Finally, additional studies should address the acoustic behaviour of female lobsters during agonistic encounters, as they have also been shown to be aggressive towards conspecifics (Skog, 2009).

Conclusion

In this study, we have highlighted for the first time that male *H. gammarus* produce buzzing sounds during agonistic encounters. Notably, we showed that they only emitted sounds when placed in contact with each other, and that most of these sounds were produced after the first encounter (i.e. hierarchical status had been determined). However, we did not find clear evidence that these sounds could be used for communication between individuals. This may be due to the high attenuation of the buzzing sounds in tanks, which could prevent their perception by receivers. Other studies have suggested that these buzzing sounds could be a means of intraspecific communication in lobsters (Breithaupt and Tautz, 1990; Breithaupt, 2001). Further studies are now needed to validate this new hypothesis.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: Y.J., J.C.-G., L.C., J.B.; Methodology: Y.J., J.C.-G., L.C., J.B.; Software: J.B.; Validation: J.C.-G., J.B.; Formal analysis: Y.J.; Data curation: Y.J., J.C.-G., J.B.; Writing - original draft: Y.J., J.C.-G., J.B.; Writing - review & editing: Y.J., J.C.-G., L.C., J.B.; Visualization: Y.J., J.C.-G.; Supervision: J.C.-G., L.C., J.B.; Project administration: L.C.; Funding acquisition: L.C.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.211276.supplemental>

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Table S1

This study		Gherardi et al. 2010		Skog et al. 2007		Breithaupt and Atema 2000		Karavanich and Atema 1998		Atema and Voigt 1995		Huber and Kravitz 1995		Stein et al. 1975		Atema and Engstrom 1971		Scrivener 1971	
Species studied: <i>Homarus gammarus</i> (adults)		<i>Homarus americanus</i> (adults)		<i>Homarus gammarus</i> (adults)		<i>Homarus americanus</i> (adults)		<i>Homarus americanus</i> (adults)		<i>Homarus americanus</i> (adults)		<i>Homarus americanus</i> (juveniles)		<i>Homarus americanus</i> (adults)		<i>Homarus americanus</i> (adults)		<i>Homarus americanus</i> (adults)	
Appendages	Description	Behaviours (+ agonistic level)	Description	Behaviours (+ agonistic level)	Description	Behaviours (+ agonistic level)	Description	Behaviours (+ agonistic level)	Description	Behaviours (+ agonistic level)	Description	Behaviours	Description	Behaviours	Description	Behaviours	Description	Behaviours	Description
<i>Antennas</i>																			
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Antennule flicking (Neutral 0)	Rapid downstroke of lateral filament	NM	NM	NM	NM	NM	NM	NM	NM
Antenna sensing - searching (when separating/resting)	One antennae directed/ followed continuously opponent by the submissive lobster	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Antenna pointing (Investigative behaviour)	Stationary lobster demonstrated antenna pointing but then continued to follow its moving opponent with an antenna (2-5sec duration). It frequently occurred when lobsters were about 65 cm apart, either coming closer together or separating (gained or lost sensory contact).
Antenna pointing (during agonistic bout)	One or both antennae directed (forward) toward opponent	NM	NM	NM	NM	NM	NM	Antenna point (No physical contact threat display 2)	Holding antennae(s) parallel to body axis and directed towards opponent	Antenna pointing (Aggressive 3)	One or both antennae directed (forward) toward opponent	NM	NM	NM	NM	Antennal search (Alert)	NM	Antenna pointing (Investigative behaviour)	One or both antennae are moved from the normal resting posture (pointing 45° upwards from the tank bottom and away from the body axis), to a position pointing anteriorly, in the direction of the other combatant, and thus parallel to the bottom and the body axis. Short duration (1-2sec).
Antenna touching	One or both antennae continuously touching opponent body and/or antennae (can be continuous or very fast)	NM	NM	Antenna touch (Physical contact 3)	See Atema and Voigt (1995)	Antenna touching (Physical contact claws not used to grasp 3)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Antenna touching (Physical contact Claws not used to grasp 3)	Antennae(s) continuously touching opponent's body	Antenna touching (Aggressive 3)	One or both antennae continuously touching opponent	NM	NM	NM	NM	NM	NM	NM	NM
Antenna up	Antenna pointing directly up (perpendicular to body length)	Antennae up (Threat 2)	Both antennae are pointed straight up and away from the opponent	NM	NM	NM	NM	NM	NM	Antenna up (Neutral 0)	Antenna pointing directly up	Antenna up	Both antennae are pointed straight up and away from the opponent	NM	NM	NM	NM	NM	NM
Antenna whipping	Lashing of opponent body and/or antennae with antennae in sweeping motion	Antenna tap / whipping (Threat 2)	In a single motion, an antenna is rapidly swept downwards over the anterior portion of the thorax of the opponent / One or both antennae vigorously and repeatedly lash the opponent in rapid sequence	Antenna whip (Physical contact 3)	See Atema and Voigt (1995)	Antenna whipping (Physical contact claws not used to grasp 3)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Antenna whipping (Physical contact Claws not used to grasp 3)	Lashing of opponent with antennae(s) in sweeping motion	Antenna whipping (Aggressive 3)	Lashing of opponent with antennae(s) in sweeping motion	Antenna tap / whipping	In a single motion, an antenna is rapidly swept downwards over the anterior portion of the thorax of the opponent / One or both antennae vigorously and repeatedly lash the opponent in rapid sequence	Antenna fcl/whip (Social behaviour)	Quick successive movements of the antennae over another lobster – occurs in an aggressive encounter (i.e. face off or in mating)	NM	NM	Antennae whipping (Aggressive behaviour)	One lobster lashes another by sweeping its antennae back and forth in an horizontal plane. Often when an animal starts antennae whipping, its opponent reciprocates. Usually combined with pushing or meral spread. Duration = 1-10 seconds
Antenna backward (during claw contact)	Antenna directed backward, parallel to body length	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
<i>Claws</i>																			
Claw extended	Claws are lying forward, parallel to the body axis	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
Claw forward	Defensive body position where seizer claw is raised and extended and crusher claw is close to the body	NM	NM	Claw forward (Threat display 2)	See Atema and Voigt (1995)	Claw forward (No physical contact threat display 2)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw forward (No physical contact threat display 2)	Either chela extended directly forward and up	Claw forward (Aggressive 2)	One claw, usually seizer, extended up and out from body	NM	NM	En garde (social behaviour)	Defensive body position where seizer claw is raised and extended and crusher claw is close to the body	NM	NM	NM	NM
Claw open	Either or both claws completely open, usually seizer	NM	NM	Claw open (Threat display 2)	See Atema and Voigt (1995)	NM	NM	Claw open (no physical contact threat display 2)	Dactyl of either chela held wide open	Claw open (Aggressive 2)	Either or both claws completely open, usually seizer	NM	NM	NM	Claw open (Aggressive)	NM	NM	NM	NM
NM	NM	Claw down (Threat 2)	One or both claws are pointed straight down towards the substrate	NM	NM	NM	NM	NM	NM	NM	NM	Claw down	One or both claws are pointed straight down towards the substrate	NM	NM	NM	NM	NM	NM
Meral spread	Both claws extended up and out from body The crusher claws is raised up toward the oponent	Claw up - threat (Threat 2)	One or both claws are lifted high above the horizontal and extended laterally / Aggressive display, vclaws extended outwards and upwards	Meral spread (Threat display 2)	See Atema and Voigt (1995)	Meral spreading (No physical contact threat display 2)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Meral spread (no physical contact threat display 2)	Large chelae extended up and out, laterally away from body	Meral spreading (Aggressive 2)	Both claws extended up and out from body	Claw up	One or both claws are lifted high above the horizontal and extended laterally	Meral spread (social behaviour)	Claws raised and spread apart – usually a defensive posture	NM	NM	Meral spread (Aggressive behaviour)	Stands its legs with its body raised from 4-5 cm off the bottom. The abdomen is usually fully extended, with the cephalothorax angled slightly upwards from the horizontal. The chelae are held about 5cm off the bottom spread wide apart with their long axes pointing directly at the opponent. Some animals hold the claws fully extended, wide apart and as high off the bottom as possible. Pleopods are held against the abdomen and are not visible from a lateral view. The antennae are pointed at angles of 45° upwards and away the body axis. Max duration = 3min
Claw touching	Continuous touching of opponent body and/or claws with one or both claws	Claw touch closed/open (Strike 3)	A lobster touches the opponent with closed/open claws	Claw touch (Physical contact 3)	See Atema and Voigt (1995)	Claw touching (Physical contact claws not used to grasp 3)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw touching (Physical contact Claws not used to grasp 3)	Continuous contact of with chelae(s) to opponent's body	Claw touching (Aggressive 3)	Continuous touching of opponent with (closed) claw	Claw touch closed/open	A lobster touches the opponent with closed/open claws	NM	NM	NM	NM	NM	NM
Claw lunging	Thrust claw(s) forward	NM	NM	NM	NM	NM	NM	NM	NM	Claw lunging (Aggressive 3)	Thrust claw(s) forward	NM	NM	Lunge (social behaviour)	Fast extension of claws, usually accompanied by a run	NM	NM	NM	NM
Claw pushing	Continuous pressing of claw(s) on opponent's body and/or claws	Push (Strike 3)	A lobster attempts to displace an opponent through pushing and pulling using walking legs and pleopod and/or uses claws to push and/or punch claws or body of the opponent	Claw push (Physical contact 3)	See Atema and Voigt (1995)	Claw pushing (Physical contact claws not used to grasp 3)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw pushing (Physical contact Claws not used to grasp 3)	Pressing chelae(s) on opponent's body and walking forward, or extending chelae(s) in an attempt to displace opponent	Claw pushing (Aggressive 3)	Continuous pressing of claw(s) on opponent's body	Pushing - pulling	An animal attempts to displace the other through pushing or pulling using walking legs and pleopods	Push (social behaviour)	One animal extending claws against another and maneuvering him backwards	Claw push (Aggressive)	NM	Pushing (Aggressive behaviour)	When the animals raise their bodies as high as possible on their walking legs and push against each other chelae. The abdomen is fully extended with its tail fan open. The pleopods beat rapidly. Often the cephalothorax and abdomen form an arc, so that the long body axis becomes concave dorsally. The antennae are raised to a vertical position. Walking legs are raised to a vertical position. Walking legs three or four are extended posteriorly, thus producing a greater horizontal force component when the legs are straightened. The chelipeds are spread wide apart with the long axes of their palms pointing directly at, and making contact with, the other lobster. After prolonged pushing, the long axes of the palms are often turned perpendicularly to the long body axis and now face each other. The chelae are usually kept closed and only rarely did one animal actually grasp the other. Duration = 30 sec
NM	NM	Pull (Strike 3)	A lobster attempts to displace an opponent through pushing and pulling using walking legs and pleopod and/or uses claws to push and/or punch claws or body of the opponent	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
NM	NM	NM	NM	Claw tap (Physical contact 3)	See Atema and Voigt (1995)	Claw tapping (Physical contact claws not used to grasp 3)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw tapping (Physical contact claws not used to grasp 3)	Short, discontinuous touching of chelae(s) to opponent's body	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
Claw scissoring	NM	Scissor (Fight 4)	Rapid scissoring motion with both claws at opponent	Claw scissoring (Physical contact 3)	See Atema and Voigt (1995)	Claw scissoring (Physical contact claws not used to grasp 3)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw scissoring (Physical contact claws not used to grasp 3)	Bringing chelae from a laterally extended position rapidly inward in a scissor motion in front of opponent's body (may touch opponent in process)	Claw scissoring	Both claws rapidly crossing in front of body from meral spread	NM	NM	NM	NM	NM	NM	Scissoring (Aggressive behaviour)	Occurs when one lobster faces its opponent, with chelae in the meral spread posture (spread wide apart, long axes of the palms pointing at the adversary). The chelae are then rapidly brought together in a scissoring motion. As a result, they either strike or pass rapidly in front of the other animal. Simultaneously the lobster raises itself 7cm off the bottom which is about as far as its walking legs extend. Sometimes this action is so rapid and vigorous that the lobster leave the bottom momentarily. Most other body parts remain as they were before scissoring begins. Duration = 1 sec, but observed during almost every agonistic encounter.
Claw boxing	Back- or forehanded striking motion toward opponent – Box hooking/punching One or both claw is armed backwards and quickly punch the opponent's body and/or claw	Punch (Strike 3) / Claw strike (Fight 4)	A lobster attempts to displace an opponent through pushing and pulling using walking legs and pleopod and/or uses claws to push and/or punch claws or body of the opponent / A lobster strikes towards the opponent with one or both of its claws	Claw box (Claw lock 4)	See Atema and Voigt (1995)	Claw boxing (Physical contact claws not used to grasp 3)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw boxing (Physical contact Claws not used to grasp 3)	Vigorous, rapid (jabbing) touching of chelae(s) to opponent's body	Claw boxing (Aggressive 3)	Back- or forehanded striking motion toward opponent	Claw strike	A lobster strikes towards the opponent with one or both of its claws	Jab - boxing (social behaviour)	Poking at other animals' body or claws with own claws	NM	NM	Boxing (Aggressive behaviour)	During continuous pushing, one individual occasionally withdrew a chela and then began pushing or jabbing its opponent. Duration 2-6 sec
Claw grasping	Clamping of claws onto opponent's claw(s) or body	Claw grasp (Fight 4)	A lobster uses its claws to grab and appendage of the opponent	Claw lock (Physical contact 4)	See Atema and Voigt (1995)	Claw locking (Physical contact claws used to grasp 4)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw lock (Physical contact claws used to grasps 4)	Clamping of chelae(s) onto opponent's body, commonly the opponent's chelae(s)	Claw locking (Aggressive 4)	Clamping of claws onto opponent's claw(s) or body	Claw grasp	A lobster uses its claw to grab an appendage of the opponent	NM	NM	NM	NM	NM	NM
Claw locking	"Handshaking" of crusher claws	Claw stretch (Fight 4)	Claws interlocked with opponent, forward stretch of one claw while other claws defends against opponent's outstretched claw	Claw lock (Physical contact 4)	See Atema and Voigt (1995)	Claw locking (Physical contact claws used to grasp 4)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw lock (Physical contact claws used to grasps 4)	Clamping of chelae(s) onto opponent's body, commonly the opponent's chelae(s)	Claw locking (Aggressive 4)	Clamping of claws onto opponent's claw(s) or body	Claw grasp	A lobster uses its claw to grab an appendage of the opponent	Claw lock (social behaviour)	Hand-shake position (crusher locked on crusher) while animals are in a Face Off position	Claw lock (Aggressive)	NM	NM	NM
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Swat (social behaviour)	Swinging of seizer claw of one lobster toward the other – as in a "right hook" usually occurs during a claw lock	NM	NM	NM	NM
Claw ripping	(Rapid) grasp and pull with either claw	Claw rip (Fight 4)	A rapid motion in which a lobster grasps the opponent and pulls at it quickly	Claw rip (Unrestrained 5)	See Atema and Voigt (1995)	Claw ripping (Unrestrained use of claws 5)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw ripping (Unrestrained use of claws 5)	Rapid motion in which lobster grasps a body part of the opponent with its chelae(s) and pulls back quickly with its chelae(s) or jumps away	Claw ripping (Aggressive 5)	(Rapid) grasp and pull with either claw	Claw rip	A rapid motion in which an animal grasps the opponent and pulls at it quickly	Rip (social behaviour)	Quick jerk of body while in claw lock – a very high intensity pull using the whole body	NM	NM	NM	NM
Claw snapping	Rapid opening and closing of (seizer) claw (toward opponent)	NM	NM	Claw snap (Unrestrained 5)	See Atema and Voigt (1995)	Claw snapping (Unrestrained use of claws 5)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Claw snapping (Unrestrained use of claws 5)	Opening and closing chelae(s) quickly, directed towards opponent's body (may or may not actually seize opponent)	Claw snapping (Aggressive 5)	Rapid opening and closing of (seizer) claw (toward opponent)	NM	NM	Snap (social behaviour)	Quick opening and closing of seizer claw, usually without contact (often follows a lunge)	NM	NM	NM	NM

This study		Gherardi et al. 2010		Skog et al. 2007		Breithaupt and Atema 2000		Karavanich and Atema 1998		Atema and Voigt 1995		Huber and Kravitz 1995		Stein et al. 1975		Atema and Engstrom 1971			Scrivener 1971	
<i>Legs</i>																				
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Groom (Non social behaviour)	Rub, scratch or pick at parts of the body with the walking legs	NM	NM	NM	NM
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Rake (Non social behaviour)	Back and forth movement of one or more walking legs across the substrate while the body is still (-.)	NM	NM	NM	NM
Sand removing	Legs are used to remove sand, which result in back- and - or forward body movements	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
High on legs	Legs stretch which raise the body high off substrate	NM	NM	High on legs (Threat display 2)	See Atema and Voigt (1995)	High on legs (No physical contact threat display 2)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	High on legs (No physical contact threat display 2)	Body is raised above the substrate on fully extended walking legs	High on legs (Aggressive 2)	Body raised high off substrate	Body up	The body is raised high above the substrate on fully extended walking legs	NM	NM	NM	NM	NM	NM	NM
<i>Body (carapace + tail)</i>																				
NM	NM	NM	NM	Separate (Separate 0)	> 1 body length apart, no activity	All behaviours taking place beyond one body length from another animal (Activity A) NM	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Separate (0)	Distance between lobsters greater than one body length	Separating (Neutral 0)	> 1 body length apart	NM	NM	NM	NM	NM	NM	NM	NM	NM
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Exopodite fanning (Neutral 0) NM	Beating of exopodites of maxillipeds NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
Resting	Body not moving	NM	NM	NM	NM	Separate and no activity (No activity 0)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
NM	NM	NM	NM	NM	NM	Turning while facing (No physical contact within one body length 1) NM	See Atema and Voigt (1995) and Karavanich and Atema (1998)	NM	NM	Rapid turning (Neutral 0)	Turning not related to opponent	NM	NM	NM	NM	NM	NM	NM	NM	NM
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Walking	NM	NM	NM	Walk (Non social behaviour)	A series of uninterrupted steps, forward or backward	NM	NM	NM	NM	NM
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Near (social behaviour)	One animal walking close to another unintentionally – i.e. not to “purposefully” initiate and encounter	NM	NM	NM	NM	NM
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	No response (social behaviour)	No reaction to an initiating response of another animal NM	NM	NM	NM	NM	NM
Turning toward	Turning so rostrum points toward opponent	NM	NM	Turn towards (Approach 1)	See Atema and Voigt (1995)	Turning toward (No physical contact within one body length 1)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Turning towards (No physical contact initiation 1)	Lobster is rotating body so that after turn, the lobster is facing the opponent	Turning toward (Aggressive 1)	Turn directed toward oponent	NM	NM	NM	NM	NM	NM	Rapid turning (Aggressive behaviour)	Shown only by aggressive individuals, when their opponent approaches them from the rear. The abdomen appears to be flexed at an angle and the lobster rotates 180° in less than 1 sec. With its chelipeds in the meral spread posture, it is now facing the antagonist. Rare behaviour (also seen when lobster responded to the net).	
Turning away	Turning so rostrum points away from opponent	Retreat (Avoidance 0)	A lobster moves or turns away from an opponent	Turn away (Avoidance - 1)	See Atema and Voigt (1995)	Turning away from opponent (Fleeing -1)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Turning away (Avoidance -1)	Lobster is rotating body so that after turn, the lobster is no longer facing the opponent	Turning away (Submissive 1)	Turning so rostrum points away from opponent	Retreat	An animal moves or turns away from an opponent	NM	NM	NM	NM	NM	NM	NM
Walking away Walking so rostrum points away from opponent		Retreat (Avoidance 0)	A lobster moves or turns away from an opponent	Walk away slowly (Avoidance - 1)	See Atema and Voigt (1995)	Walking away slowly (Fleeing - 1)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Walking away slowly (Avoidance -1)	Walking forward and increasing distance from opponent (speed less than one body length/5 s)	Walking away, slow (Submissive 1)	Slow equals < 1 body length/5sec	Retreat	An animal moves or turns away from an opponent	Flee - running away (social behaviour)	One animal quickly moving forward in an opposite direction from another during an encounter, usually following a Face Off and ending the encounter	Retreat (Defensive)	NM	Walking away (Avoidance behaviour)	Individual moves forward away from its opponent. The abdomen is fully extended with its pleopods stationary and tail fan open. The chelipeds are held 2cm off the bottom, with the palms pointing inward about 30° from the longitudinal body axis. The antennae are usually perpendicular to the body axis, but parallel to the substrate. The method and velocity of locomotion is very similar to following. Duration = few sec to 30 sec, common behaviour pattern but not demonstrated during every agonistic encounter because usually a retreating lobster preferred to face its opponent and back away.	
		Retreat (Avoidance 0)	A lobster moves or turns away from an opponent	Walk away quickly – Run away (Avoidance - 2)	See Atema and Voigt (1995)	Fast walking away (Fleeing -2)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Walking away rapidly (Fleeing - 2)	Walking forward and increasing distance from opponent (speed greater than one body length/5 s)	Walking away, fast (Submissive 2)	Slow equals > 1 body length/5sec	Retreat	An animal moves or turns away from an opponent	Flee - running away (social behaviour)	One animal quickly moving forward in an opposite direction from another during an encounter, usually following a Face Off and ending the encounter	Retreat (Defensive)	NM	Running away (Avoidance behaviour)	Occurs when lobster turns away from its adversary and moves away at a rapid velocity. The cephalothorax is held parallel to the bottom, with the abdomen fully extended and its pleopods rapidly beating. The abdomen is often arched upwards with the expanded tail fan about 5-7cm off the substrate. Enough frictional force may be produced, as the water passes up and over it, to keep the lobster firmly on the bottom; thereby providing better traction. The antennae are held parallel to the bottom and perpendicular to the body axis when running begins. If running is continued for 4 sec or longer, the antennae turn posteriorly so that they become parallel to the body axis. The chelipeds are held quite close together with their palms turned outward slightly. The method of locomotion is similar to that described for rushing. Velocity = 0.5m/s (slower than rushing). Often running away was observed only a few seconds, before sensory contact between the combatants was lost. It occurred frequently when one animal approached the other from the rear. NM	
Walking parallel	Walking parallel to the body axis of the opponent	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
Non observed	Non observed	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Sideways (social behaviour)	Forward and lateral walk simultaneously – crablike movement usually as avoidance	NM	NM	Side-ways (Avoidance behaviour)	The retreating lobster moves sideways away from an opponent, exposing on of its lateral surfaces. The abdomen extends fully, with its pleopods stationary against its ventral surface. The antennae are held in the normal resting posture at angles of 45°, pointing upwards from the tank bottom and away from the body axis. Sideways movement appears similar to normal locomotion among crabs, but is somewhat slower. Observed in half of the agonistic encounters, duration = few sec.	
Walking backward Walking backward so rostrum points toward opponent		NM	NM	NM	NM	Walking backward slowly (Fleeing -1)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Walking backward slowly (Avoidance -1)	Retreating while continuing to face opponent (speed less than one body length/5 s)	Walking backward, slow (Submissive 1)	NM	NM	NM	Retreat - Backing (social behaviour)	A direct consequence of advance or approach – a reverse walk or movement away from another animal (occurs within one body length distance)	Retreat (Defensive)	NM	Backing	Lobster's tail fan is folded and turned partially under the abdomen, with the stationary pleopods, the antennae are parallel with the bottom, and pointing straight ahead or at an angle of 45° from the long axis of the body. The chelae are pointed in the direction of the opponent. In this posture, the lobster is facing its adversary, while avoiding it by backing away. In a few instances the backing lobster was observed holding its chelae in the meral spread posture. Under these conditions the animal was considered to be backing and displaying meral spread. The movements of the walking legs appeared to be very similar to those shown when following, except that the process was reversed. Backing was observed during every encounter and it was the most common avoidance behaviour pattern. Max duration = 3min, velocity = 0.15-0.2m/s NM	
		NM	NM	NM	NM	Fast walking backward (Fleeing -2)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Walking backward rapidly (Fleeing -2)	Retreating while continuing to face opponent (speed greater than one body length/5 s)	Walking backward, fast (Submissive 2)	NM	NM	NM	Retreat - Backing (social behaviour)	A direct consequence of advance or approach – a reverse walk or movement away from another animal (occurs within one body length distance)	Retreat (Defensive)	NM	NM	NM	
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Crouching (Submissive 3)	Crouch (in corner), claws extended NM	NM	NM	NM	NM	Submissive posture (Defensive)	NM	NM	NM	NM
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Defensive posture (social behaviour)	Tail tucked under body, body slightly raised, claws open and raised in front of the body, as a shield	NM	NM	NM	NM	NM
Facing	Body not moving and rostrum directed towards opponent	Stand off (Threat 2)	Complete stillness other than antennal movements, less than a body length apart	Face (Approach 1)	See Atema and Voigt (1995)	Facing (No physical contact within one body length 1)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Facing (No physical contact initiation 1)	Lobsters are within one body length and positioned so that both rostrums are facing each other	Facing (Aggressive 1)	Facing each other, within one body length, no touching	NM	NM	Face off (social behaviour)	Head to head confrontation within one body length distance	NM	NM	NM	NM	NM
Walking towards Walking towards so rostrum points toward opponent		Approach (Approach 1)	A lobster advances towards an opponent slowly reducing the distance to less than a body length	Walk towards (Approach 1)	See Atema and Voigt (1995)	Approaching slowly (No physical contact within one body length 1)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Approaching (No physical contact initiation 1)	Walking forward (speed less than one body length/5 s) towards opponent reducing separation to within 1 body length NM	Approaching slow (Aggressive 1)	Walking forward, toward opponent	Approach	A lobster advances towards an opponent slowly (< 1 body length/sec) reducing the distance between the animals to less than 1 body length	Approach - Advance (social behaviour)	Forward movement directed toward another lobster greater than 1 lobster length away - While in a Face Off, one animal move closer to the other	Frontal approach (Aggressive)	NM	Approaching (Aggressive behaviour)	Similar to following, except that in this case the animal moves towards a stationary opponent that is usually showing neither aggressive nor avoidance behaviour. The abdomen is fully extended, the tail fan expanded and the chelae are held as when following. The pleopods appear to be stationary, but the antennae are often almost parallel to the body axis. The lobster moves forward towards the other combatant, but at a lower velocity than when following. Durations 2-6 sec, and was commonly shown with meral spread.	
		Lunge (Approach 1)	Rapid and direct head-first advance towards opponent(s) without hesitation, often with claws outstretched	Run towards (Threat display 2)	See Atema and Voigt (1995)	NM	NM	NM		Approaching fast (Aggressive 1)	NM	Lunge	Similar to approach, but advance towards the opponent is rapid (> 1 body length/sec)	NM	NM	Chasing (Aggressive)	NM	Rushing	One lobster with its chelae in the meral spread posture rush or run towards an opponent. The abdomen is fully extended, with pleopods rapidly beating and tail fan open. During this activity the lobster's body is held about 2 cm off the bottom. At first, the antennae point forward at angles of 45° from the bottom and long body axis, but if rushing continues for more than 2 seconds, they are rapidly turned - as opposed to the usual slow antennae movements - to point backwards at an angle of 20° from the body axis. This movement requires an additional 2 sec and is often not complete before rushing is terminated. Maximum velocity = 0.7m/s. Steps of about 14 cm were taken with the second and third pair of walking legs. This was about twice the distance between foot-steps that the lobsters made when they were following. Rushing was observed at least once during each agonistic behaviour. Duration = 1-6 sec. During long rushes, there was a slight variation, the lobster would extend its chelae straight ahead towards the adversary.	
NM		NM	NM	Follow (Approach 1)	See Atema and Voigt (1995)	Following slowly (No physical contact within one body length 1)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Following (No physical contact initiation 1)	Walking towards opponent while opponent is walking away	Following slow (Aggressive 1)	Walking toward opponent while opponent moves away	NM	NM	Follow (social behaviour)	Slow movement of one animal after another which has moved away	NM	NM	Following (Aggressive behaviour)	When one lobster is following another, the abdomen is fully extended, with the tail fan fully opened. The chelipeds are held about 3cm off the bottom, with the long axes of the palms pointed towards each other distally. The pleopods are stationary as during meral spread, but the antennae are often perpendicular to the body axis. In this posture, the lobster simply follows its opponent. During this behaviour, steps of approximately 7cm are taken with the second and third pair of walking legs. The first and fourth pair of walking legs appear to be actively moved only half this distance. Maximum duration = 3min, and a lobster follow at about 0.15m per second. NM	
		Chase (Strike 3)	Rapid pursuit of retreating opponent	NM	NM	Fast following (No physical contact within one body length 1)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Following (No physical contact initiation 1)	Walking towards opponent while opponent is walking away	Following fast (Aggressive 1)	NM	NM	NM	Chase (social behaviour)	Quick movement of lobster in pursuit of another, during an interaction	Chasing (Aggressive)	NM	NM		

This study		Gherardi et al. 2010		Skog et al. 2007		Breithaupt and Atema 2000		Karavanich and Atema 1998		Atema and Voigt 1995		Huber and Kravitz 1995		Stein et al. 1975		Atema and Engstrom 1971		Scrivener 1971	
<i>Tail</i>																			
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Tail under (Neutral 0)	Abdomen flexed under cephalothorax	NM	NM	NM	NM	NM	NM	NM	NM
NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	Pleopod beating (Neutral 0)	Fanning movement of pleopod appendages	NM	NM	NM	NM	NM	NM	NM	NM
Tail flipping Fast, backward escape (with claws and legs extended)		Tail-flip escape (Avoidance 0)	A contraction of the abdomen which propels the lobster backward for a rapid escape	Tail flip away (Avoidance - 2)	See Atema and Voigt (1995)	Tail flipping (Fleeing -2)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Jumping away (Fleeing -2)	Rapid flexion of abdomen causing lobster to quickly propel itself backwards, away from opponent (tail flip)	Tail flipping (Submissive 3)	Fast, backward escape (with claws and legs extended)	Tailflip	An escape response during which a rapid contraction of the abdomen propels a lobster backward	Tail flip - abdomen flex (social behaviour)	Rapid flexing of the abdomen under the body so as to propel the animal backwards – an escape movement)	NM	NM	Abdomen flexing (Avoidance behaviour)	Vigorously pushes its body upwards and backwards with the four pairs of walking legs. This raises the individual off the bottom and propels it backwards through the water. As it leaves the bottom, the lobster brings its antennae, chelae and walking legs together anteriorly, to point straight ahead (parallel to the body axis). The legs are now close to the ventral surface of the cephalothorax. This posture produces a streamline body form which is less resistant to backward movement through the water. The open tail fan is rapidly brought down under the body by contraction of the ventral abdominal muscles (the abdomen is now folded in upon itself). This propels the lobster backwards approximately 1m. As it sinks to the bottom, the individual moves the walking legs back to their normal position (perpendicular to the axis). The abdomen may flexed several times, before the animal returns to the bottom. This is accomplished by folding the tail fan, while the abdomen is being extended; then expanding it, before the abdomen is flexed again. Usually the animal is carried far enough for its adversary to lose sensory contact. When a lobster is approached from the rear it often propels itself completely over the top or the opponent. Occurred in every agonistic encounter, duration = few sec, velocity = 0.9/sec.
		NM	NM	Jump away (Avoidance - 2)	See Atema and Voigt (1995)	Jumping (Fleeing -2)	See Atema and Voigt (1995) and Karavanich and Atema (1998)	Jumping away (Fleeing -2)	Rapid flexion of abdomen causing lobster to quickly propel itself backwards, away from opponent (tail flip)	Jumping (Submissive 2)	Quick, upward-directed tail flip	NM	NM	NM	NM	NM	NM	Jumping (Avoidance behaviour)	Flexes the abdomen vigorously in a manner similar to that described for abdomen flexing but claws are held in the normal medial spread posture and the walking legs remain perpendicular to the body axis. The animal flexes its abdomen only once and is propelled backwards about 60 cm before returning to the bottom. Max duration = few sec, half of the encounters. Jumping appeared to be a reflex variation of abdomen flexing. The animals did not lose sensory contact when one of them had performed the behaviour pattern, because immediately afterwards they continued their agonistic behaviour.
		Tail-flip (Fight 4)	Contraction of the abdomen to propel animal backwards in an attempt to rip off opponent's appendage	Aggressive tailflip (unrestrained 5)	See Atema and Voigt (1995)	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM