Noise negatively affects foraging and antipredator behaviour in shore crabs

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Acoustic noise has the potential to cause stress, to distract and to mask important sounds, and thus to affect behaviour. Human activities have added considerable noise to both terrestrial and aquatic habitats, and there is growing evidence that anthropogenic noise affects communication and movement patterns in a variety of species. However, there has been relatively little work considering the effect on behaviours that are fundamental to survival, and thus have direct fitness consequences. We conducted a series of controlled tank-based experiments to consider how playback of ship noise, the most common source of underwater noise, affects foraging and antipredator behaviour in the shore crab, Carcinus maenas. Ship noise playback was more likely than ambient-noise playback to disrupt feeding, although crabs experiencing the two sound treatments did not differ in their likelihood of, or speed at, finding a food source in the first place. While crabs exposed to ship noise playback were just as likely as ambient-noise controls to detect and respond to a simulated predatory attack, they were slower to retreat to shelter. Ship noise playback also resulted in crabs that had been turned on their backs righting themselves faster than those experiencing ambient-noise playback; remaining immobile may reduce the likelihood of further predatory attention. Our findings therefore suggest that anthropogenic noise has the potential to increase the risks of starvation and predation, and showcases that the behaviour of invertebrates, and not just vertebrates, is susceptible to the impact of this pervasive global pollutant.
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To survive and reproduce successfully, animals must minimize the risks of starvation and predation. Events that compromise either the foraging or antipredator behaviour of an individual are therefore likely to have detrimental consequences for its fitness. Stressful events, for example, can lead to changes in the intensity, duration or frequency of particular activities as part of an allostatic response (Broom & Johnson 1993; McEwen & Wingfield 2003; Wingfield 2005). If this response includes a reduction or cessation of normal locomotor activity (see Metcalfe et al. 1987), then the likelihood of successful escape from a predator may be reduced and, if less time is spent foraging, food intake may decline. Food acquisition may also be negatively affected if stress results in unnecessary and costly antipredator responses (Lima & Dill 1990). Moreover, stress might cause a reduction in appetite, mediated by peptides associated with the corticotrophin-releasing factor system (Bernier 2006); animals might be less inclined to search for food when stressed.

Since foraging and antipredator behaviour involve various cognitive processes, including detection, classification and decision making (Shettleworth 2010), events that impair attention could also pose a problem. Effects on attention might arise as part of a stress-related allostatic response (as above), but attention might also be compromised if an animal is distracted (Dukas 2004; Chan & Blumstein 2011). If attention is narrowed, with animals either ignoring stimuli or focusing on a smaller spatial scale (Dukas 2002), then food or predators may be less likely to be detected (Hockey 1970). Distracted animals may also be more likely to respond inappropriately to an imminent threat and run the risk of losing current food items, either because they escape or because they are stolen by others (Dukas 2002). These attention-mediated effects are driven by a limited capacity to attend simultaneously to multiple stimuli (Dukas 2004; Chan & Blumstein 2011).

Many animals are alerted to the presence of predators or prey by auditory cues, such as acts of intraspecific communication or the sounds inadvertently produced as a consequence of movement (Barrera et al. 2011; Siemers & Schaub 2011). Moreover, alarm calls have evolved in a wide range of mammals and birds to warn others of impending danger (Hollén & Radford 2009), while other vocalizations can provide information on the current level of risk (Hollén

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et al. 2008; Bell et al. 2009). Thus, predation and starvation may be more likely if such acoustic information is masked, that is, if the threshold for detection or discrimination of one sound is increased in the presence of another (Brumm & Slabbekoorn 2005). Masking can be complete ('energetic' masking), whereby the signal is not detected at all, or partial ('informational' masking), whereby the signal is detectable by the listener, but the content is hard to understand. Either way, there are likely to be fitness consequences for foragers and potential prey from a reduced ability to detect valuable auditory information (Brumm & Slabbekoorn 2005; Siemers & Schaub 2011; Lowry et al. 2012).

Acoustic noise, especially if it is loud, persistent, unexpected or novel, has the potential to cause stress (Wysocki et al. 2006; Wright et al. 2007), to distract (Hockey 1970; Chan et al. 2010a) and to mask important sounds (Brumm & Slabbekoorn 2005; Siemers & Schaub 2011; Lowry et al. 2012). In recent decades, human activities such as urban development, expansion of transport networks and resource extraction have added considerable noise to both terrestrial and aquatic environments across the globe, and led to major changes in the acoustic landscape (see McDonald et al. 2006; Watts et al. 2007; Barber et al. 2009). Consequently, anthropogenic noise is now recognized as a major pollutant of the 21st century, appearing in national and international legislation (e.g. US National Environment Policy Act and European Commission Marine Strategy Framework Directive). A burgeoning research effort using both natural sound sources and playback experiments has indicated that anthropogenic noise can affect the behaviour of species in a variety of taxonomic groups (reviewed by Tyack 2008; Barber et al. 2009; Slabbekoorn et al. 2010). However, most of that behavioural work has focused on vocal communication or movement patterns (see, e.g. Radford et al. 2012); far less research attention has been paid to foraging and antipredator behaviour, which are of fundamental importance to survival (see Chan et al. 2010a, b; Purser & Radford 2011; Siemers & Schaub 2011; Bracciali et al. 2012 for exceptions).

In this study, we used a series of controlled tank-based experiments to explore how additional noise affected foraging and antipredator behaviour of a common marine crustacean, the shore crab, Carcinus maenas. As our experimental sound to be added, we used playback of ship noise. While underwater anthropogenic noise arises from many sources, including seismic surveys, mining activity, sonar, wind farms and acoustic deterrent devices (Tasker et al. 2010), ship noise is the most common (Vasconcelos et al. 2007) and has alone led to a 10–100-fold increase in low-frequency (20–200 Hz) ambient aquatic noise over the past century (Tyack 2008). To date, the vast majority of studies investigating potential impacts of underwater anthropogenic noise have been conducted on vertebrates (Nowacek et al. 2007; Popper & Hastings 2009; Slabbekoorn et al. 2010). However, crustaceans and other marine invertebrates are capable of hearing (Salmon 1971; Goodall et al. 1990) and use sound for a variety of reasons (e.g. Jeffs et al. 2003; Stanley et al. 2010; Simpson et al. 2011); thus they are likely to be vulnerable to the impact of anthropogenic noise (see Wale et al. 2013).

In two separate foraging experiments, we examined the likelihood and speed with which individuals located a food source and whether their feeding behaviour was disrupted. We predicted that ship noise playback would reduce the likelihood of crabs finding a food item or would result in their taking longer to do so, and that it might lead to an interruption in feeding behaviour. In an additional two experiments, we probed antipredator behaviour. We simulated a predatory attack, and predicted that ship noise playback might make individuals less likely to detect the attack, respond differently or take longer to retreat to shelter. We also investigated the response of crabs to being unrighted (turned on their backs); immobility is a well-documented antipredator behaviour (O'Brien & Dunlap 1975), potentially reducing the likelihood of further

predatory attention, and thus the most appropriate response might be to remain in that position. If ship noise playback impairs decision making, we predicted that crabs would right themselves faster than during playback of ambient noise.

METHODS

Ethical Note

All experiments in this study were approved by the University of Bristol Animal Services Ethical Committee (University Investigation Number: UB/10/034). The research adhered to the legal requirements of the country (U.K.) in which the work was carried out, and all institutional guidelines. Crabs showed no signs of adverse reactions to the test set-ups; all tested individuals appeared to return to normal pretrial behaviour when inspected and fed at the end of each test day. At the end of the experiments, animals were either kept for further study or given to the Bristol Aquarium.

Study Animals and Husbandry

All crabs were collected from Newquay harbour, U.K. (50°25′N 5°5′W), using a seine net, on 9 and 10 February 2012 (first cohort) and on 2 and 3 May 2012 (second cohort). Inside Newquay harbour itself, there is sporadic traffic noise from pleasure craft, fishing and angling boat trips, and speed boats; noise from larger ships further afield is also likely, although those vessels do not enter the harbour itself. Crabs were held for a maximum of 48 h in salt-water tanks at the Blue Reef Aquarium, Newquay before transfer to Bristol Aquarium by courier. During the transfer (265 km; 3.5 h), crabs were out of water, but covered in damp cloths and newspaper, and were maintained at their usual 12–14 °C by the use of surrounding ice packs; this method was adapted from Ingle (1999). Holding tanks (48 × 32 cm and 28 cm high) in Bristol were made of polystyrene, to reduce noise transmission, and received water from one of the Aquarium display tanks, which were plumbed into advanced filtration facilities. Holding tanks were fitted with a subsurface inflow pipe to prevent noise from water falling or collision with the tank floor; the flow was adjusted to allow complete tank flush-through every 30 min and thus ensure the maintenance of high water quality. Sound levels in holding tanks were kept as low as possible and were comparable to those for ambient-noise playback during experiments (holding tank: 116 dB RMS re 1 μPa peaking at 1 kHz; ambient noise recording during playback: 111 dB RMS re 1 μPa peaking at 1.8 kHz; Fig. 1a).

Holding tanks contained sand on the floor and two shelters made with inverted plastic flower pots weighted down with a layer of pea gravel secured around the base with Milliput epoxy putty (The Milliput Company, Gwynedd, U.K.). Holding tank lids included a mesh window to allow light to reach the animals; this light did not, however, cover all areas of the tank or reach into shelters and thus animals had a choice of light/dark conditions. Water temperature was kept at 12–14 °C, salinity at 32–35 ppt and water qualities within safe parameters (NO_2^-: <0.3 mg/litre; NO_3^-: 0 mg/litre; NH_3^+: ≤0.25 mg/litre; pH: 7.4–7.9). Crabs were fed every 48 h (except when part of foraging experiments; see below) on a variety of previously frozen meats (cockle, mussel, shrimp, krill, sand eel, mackerel) or dry composite marine pellets (New Era Aquaculture Ltd., Thorne, U.K.), with any excess cleared from the holding tank during tank maintenance no more than 8 h after feeding. Although there was a constant water change within the holding tank (see above), 25% of water was removed by siphon with excess food and waste; this water was replaced by normal tank flow-through. Water changes and the flow-through system ensured
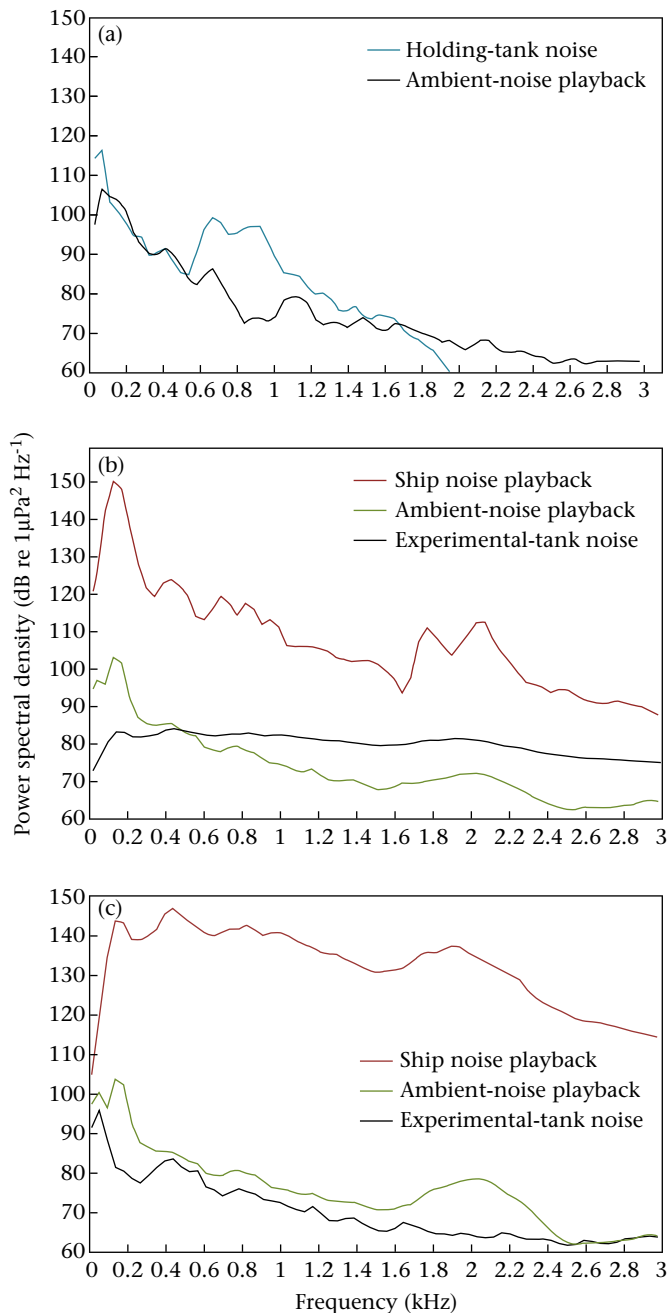
Figure 1. Variation in sound profiles for (a) holding tanks and ambient-noise playbacks, (b) playbacks in the tank used for both foraging experiments and the simulated predatory attack experiment, and (c) playbacks in the tank used for the unrighted crab experiment. Shown are illustrative power spectrographic examples from recordings made in the centre of the relevant tank.

maintenance of constant oxygen levels and the removal of any water that had become 'trapped' in the tank corners.

Noise Treatments

The sounds used as playbacks were from three major U.K. ports (Gravesend, Plymouth, Portsmouth). In each location, recordings were made of both ambient noise and noise generated by a single passing ship at ca. 200 m distance (Gravesend: Rio de la Plata, a 286 m long, 64 730 tonne container ship; Plymouth: Bro Distributor, a 14 m long, 14 500 tonne LPG tanker; Portsmouth:

Commodore Goodwill, a 126 m long, 5215 tonne ferry). Ships were travelling at constant, relatively slow speeds (<10 knots), as enforced by port authorities for vessels entering and leaving estuarine areas. All recordings were made with a calibrated omnidirectional hydrophone (HiTech HTI-96-MIN with inbuilt preamplifier, High Tech Inc., Gulfport, MS, U.S.A.) and an Edirol R09-HR 24-Bit recorder (44.1 kHz sampling rate, Roland Systems Group, Bellingham, WA, U.S.A.). The recording level was calibrated for the R09-HR using pure sine wave signals, measured in line with an oscilloscope, produced by a function generator. Intensity (root mean square, RMS) and power spectral density (units normalized to 1 Hz, Hann evaluation, 50% overlap, FFT size 1024; averaged from 2 min of recording) were calculated for each recording in Avisoft SASLab Pro v4.5.2 (Avisoft Bioacoustics, Berlin, Germany). This analysis found some variation in average noise levels between recordings: ambient tracks between 92 and 106 dB RMS re 1 μPa, and ship noise tracks between 126 and 136 dB RMS re 1 μPa.

Sound samples of 60–140 s, incorporating the highest amplitude of the ship passes (in which amplitude did not vary by more than one quarter in magnitude) and the most stable levels of ambient noise (where there were no events such as boats passing or sounds of objects striking each other under the water) were used to create experimental tracks in Audacity 1.3.13 (http://audacity.sourceforge.net/). Each track included a 30 s fade in, 6.5 min of ambient or ship noise and a 30 s fade out; one sample of ambient or ship noise was looped to create a given playback track. Experimental tracks were played back as WAV files using a similar set-up to Purser & Radford (2011) and Wale et al. (2013): WAV/MP3 Player (Ultradisk DVR2 560 h; frequency range 20–20 000 Hz); amplifier (Kemo Electronic GmbH; 18 W; frequency response: 40–20 000 Hz); potentiometer (set to minimum resistance; Omeg Ltd; 10 K logarithmic); and Aqua 30 underwater speaker (DNH; effective frequency range 80–20 000 Hz). To give consistency between the three exemplars in each treatment, tracks were re-recorded (using the same hydrophone set-up as above) in the centre of the experimental tank and modified (uniform amplification or attenuation); received sound levels for that tank position were therefore 103–108 dB RMS re 1 μPa for ambient noise (chosen to be higher than the noise floor in the experimental tank at low frequencies) and 148–155 dB RMS re 1 μPa for ship noise (Fig. 1b, c). Exact sound levels will differ throughout the tank, but our aim in this study was to consider the potential behavioural impact of additional noise in the environment, not establish the precise links between given sound levels and responses.

The noise playbacks presented a range of frequencies that are likely to fall within the hearing range of shore crabs, inferred from studies on fiddler crabs, *Uca rapax* and *U. pugilator* (Salmon 1971), but the ship noise playbacks peaked at lower frequencies than the ambient-noise playbacks. It is likely that crabs are primarily sensitive to particle motion (Salmon 1971; Goodall et al. 1990), but, for technical reasons, sound levels are given throughout in terms of sound pressure; we do not attempt to establish absolute values for sensitivity, but rather provide an indication of the behaviours that can potentially be affected by the addition of noise to the environment.

General Experimental Design

We chose to conduct our experiments in tanks to control carefully the conditions and contexts of the study animals, and to allow detailed data collection. Care must of course be taken when extrapolating results from tank-based experiments to meaningful implications for free-ranging animals in open water. From a biological perspective, captive animals are usually more constrained than in the wild, although in some of our experiments the

behavioural response measured was localized. Moreover, captive individuals' feeding regimes may not be replicated naturally. From an acoustics perspective, playbacks cannot perfectly replicate natural sound sources and the sound field in a tank is complex (Parvulescu 1964, 1967; Okumura et al. 2002). However, our primary aim was to determine for the first time whether addition of noise can potentially affect various key life history variables in marine invertebrates; future work can then establish the precise effects in natural conditions.

Both foraging experiments and the simulated predatory attack experiment were conducted in a tank (40 × 30 cm and 30 cm high) with walls 4 mm thick; the experiment in which the crab was unrighted took place in a tank (60 × 30 cm and 40 cm high) with walls 6 mm thick. In the former, the playback speaker was placed behind a vertical partition situated 10 cm from one short side; in the latter, the speaker was beneath a platform (Fig. 2). Both experimental tanks were placed on 5 cm thick foam pipe lagging, to minimize sound transfer, and had the sides covered with opaque black paint to half the height, to minimize distraction from visual reflections.
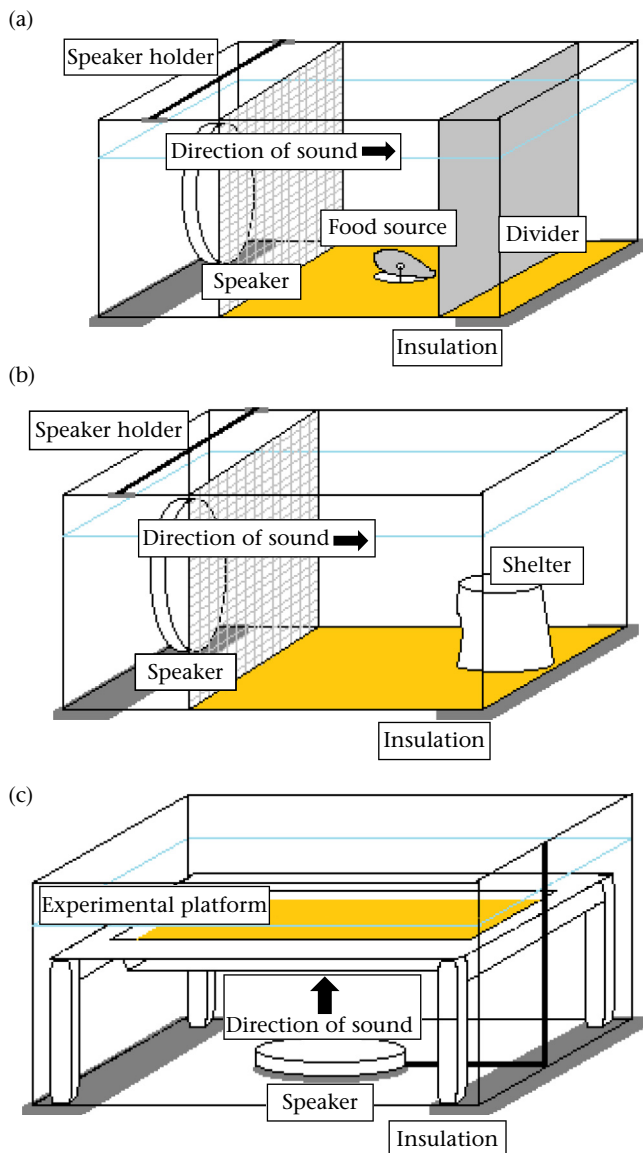

Figure 2. Tank set-ups for (a) both foraging experiments, (b) the simulated predatory attack experiment, and (c) the unrighted crab experiment.

All crabs used in experiments weighed between 40 and 60 g, and were randomly allocated to one of the two sound treatments (ambient or ship noise). Experiments used an independent-samples design to avoid any potential carryover effects. Separate groups of crabs were used for each experiment, to remove any compounding effects from repetitive handling stress and/or exposure to sound (see Wale et al. 2013). Two cohorts of animals were tested within each experiment, the first occurring 1−3 months before the second; experiments in each cohort were conducted at the same time of day to remove any bias caused by the circadian rhythm of the crabs (see Bojsen & Witthøfft 1998). Each animal was randomly assigned one of the three playback tracks in each treatment. Thirty-six animals were tested in each experiment in counterbalanced blocks of six (ambient and ship noise from each of three harbours).

Foraging Experiments

Prior to both foraging experiments, crabs were food deprived for 96 h. After placement in the holding area of the experimental tank (Fig. 2a), crabs in both experiments were given 30 s to acclimatize. The food source in both cases was a mussel, *Mytilus edulis*, which had been drilled through and attached to a stainless steel washer on the tank floor (as per Jensen et al. 2002). In the food search experiment, the playback track was first started and the divider between the holding area and the experimental area then removed. Each crab was given a maximum of 7.5 min (equivalent to a single ship pass in the playback tracks) to find the food source, after which individuals were noted as having been successful or not. For those that were successful, the time taken to locate the food source was recorded.

In the feeding-disruption experiment, the divider was first removed and the crab allowed to find the food source without any playback of noise. Once the food was found and the animal had begun eating, the playback track was started and any reaction recorded in real time by the observer. Feeding was considered disrupted if the animal ceased eating, indicated by a cessation in maxilliped movement (normally ca. 5 beats/s; cessation scored if at least 5 s with no beats), complete freezing of the animal or movement away from the food. After 1 min of noise, a lack of any such response was recorded as no apparent distraction.

Antipredator Experiments

The simulated predator attack experiment began when an animal was taken from the pre-experimental holding tank and placed into the shelter provided in the experimental tank (Fig. 2b). The shelter was identical to that in the holding tanks (see above). The playback was started when the crab first ventured out of the shelter. After the 30 s fade in on the playback track, a wooden dowel was plunged by hand into the water and straight out again (only the dowel touched the water), directly in front of the crab; this was used to simulate the action of a bird attempting to catch the crab. The initial reaction of the crab to the predator stimulus was recorded as either running (movement away from the stimulus) or freezing (cessation of all movement). After the dowel was removed, the time taken for the crab to return to the shelter was recorded. Crabs were classified as returning to shelter either when they entered it or stopped in the gap between it and the back of the experimental tank.

To examine the righting behaviour of crabs when unrighted (placed on their back), the playback track was started and after 15 s an animal was placed inverted on the sand tray in the experimental tank (Fig. 2c). The crab was then pinned in this position using a 3 cm diameter stainless steel washer, mounted on a brass rod at 20°

with Milliput (see O'Brien & Dunlap 1975). The crab was held in this position for 15 s, since pinning for 30 s or longer can trigger an immobility response (O'Brien & Dunlap 1975). The restraint was then removed and the time until the crab had completely turned over and its second pereiopod touched the sand was recorded.

Data Analysis

Statistical analyses were conducted in R version 2.14.2 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). Data fitted the assumptions of normality and homoscedasticity for parametric testing. In some cases, two-sample t tests were adjusted accordingly for unequal variances, resulting in altered degrees of freedom. Owing to external events or unusual behaviour, data from six individuals across the four experiments were not available for analysis; final sample sizes were therefore 35 for the food search experiment, 36 for the feeding-disruption experiment, 34 for the simulated predatory attack experiment, and 33 for the experiment in which the crab was unrighted. We conducted more than one test on each experimental data set. However, since application of sequential Bonferroni corrections (Rice 1989) does not qualitatively alter any of our findings, and since there is considerable debate about whether such corrections should actually be made for multiple testing using the same data set (see Nakagawa 2004), we present the uncorrected statistical output in the Results.

RESULTS

Foraging Experiments

The two cohorts of crabs used for each of the foraging experiments did not differ significantly in their likelihood of finding the food source (chi-square test: $\chi_1^2 = 0.01$, $P = 0.927$), their search times (two-sample t test: $t_{33} = 0.21$, $P = 0.837$) or their likelihood of being disrupted from feeding (chi-square test: $\chi_1^2 = 0.11$, $P = 0.739$); cohorts were therefore combined for an assessment of the effect of ship noise playback. The ability of crabs to find the food item was not impaired by the playback of ship noise compared to ambient noise: crabs in the two sound treatments did not differ significantly in either their likelihood of locating the food in the available time (chi-square test: $\chi_1^2 = 2.90$, $P = 0.089$; Fig. 3a) or in the time taken to find the food source (two-sample t test, only individuals that found the food: $t_{25} = 0.75$, $P = 0.458$; Fig. 3b).

Sound treatment did, however, have a significant effect on the behaviour of feeding crabs (chi-square test: $\chi_1^2 = 16.05$, $P < 0.001$). Individuals exposed to ship noise playback were more likely to suspend feeding than were those experiencing ambient-noise playback (Fig. 3c).

Antipredator Experiments

All tested individuals in both sound treatments responded to the simulated predatory attack by freezing or running; no individuals failed to detect the attack. The two cohorts of crabs used did not differ significantly in the type of initial reaction (chi-square test: $\chi_1^2 = 2.03$, $P = 0.154$) or in their time to find shelter (two-sample t test: $t_{32} = 0.46$, $P = 0.650$); samples were therefore combined for an assessment of the effect of ship noise playback. There was no significant difference in the initial reaction to the predator stimulus depending on whether ambient or ship noise was playing (chi-square test: $\chi_1^2 = 0.15$, $P = 0.699$; Fig. 4a). However, crabs exposed to ship noise playback took significantly longer to return to shelter than those experiencing ambient-noise playback (two-sample t test: $t_{19} = 3.95$, $P = 0.001$; Fig. 4b). This was true of both those
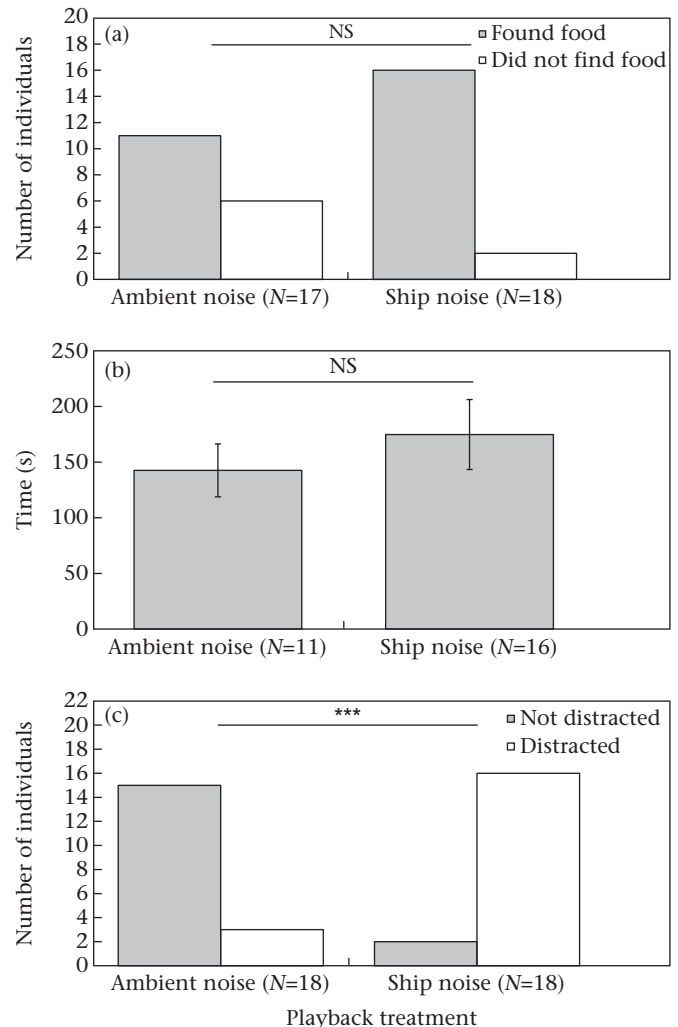

Figure 3. Results of the foraging experiments. (a) Number of crabs that did or did not find a food source, (b) mean $\pm$ SE time taken to find the food source, and (c) number of crabs that were or were not disrupted from their feeding during playback of ambient or ship noise. Sample sizes are provided in parentheses. ***$P < 0.001$.

individuals that initially reacted by freezing ($t_6 = 2.97$, $P = 0.030$) and those that ran in response to the simulated predatory attack ($t_{15} = 4.12$, $P = 0.001$).

In the experiment in which crabs were unrighted, there was no significant difference between the two cohorts in the time that individuals took to right themselves (two-sample t test: $t_{31} = 0.23$, $P = 0.817$); samples were therefore combined to assess the effect of ship noise playback. Crabs experiencing ship noise playback turned over significantly faster than those played back ambient noise ($t_{17} = 5.97$, $P < 0.001$; Fig. 4c).

DISCUSSION

Single exposure to the playback of noise from an individual ship resulted in a variety of behavioural changes in shore crabs: their feeding was disrupted, they were slower to return to shelter following a simulated predatory attack, and they righted themselves faster when inverted. Previous work has shown that anthropogenic noise, including that from ships, can affect the behaviour of marine mammals (e.g. Parks et al. 2007; Castellote et al. 2012). Of more direct relevance, given the shared ability to detect particle motion, is the recent work demonstrating that such
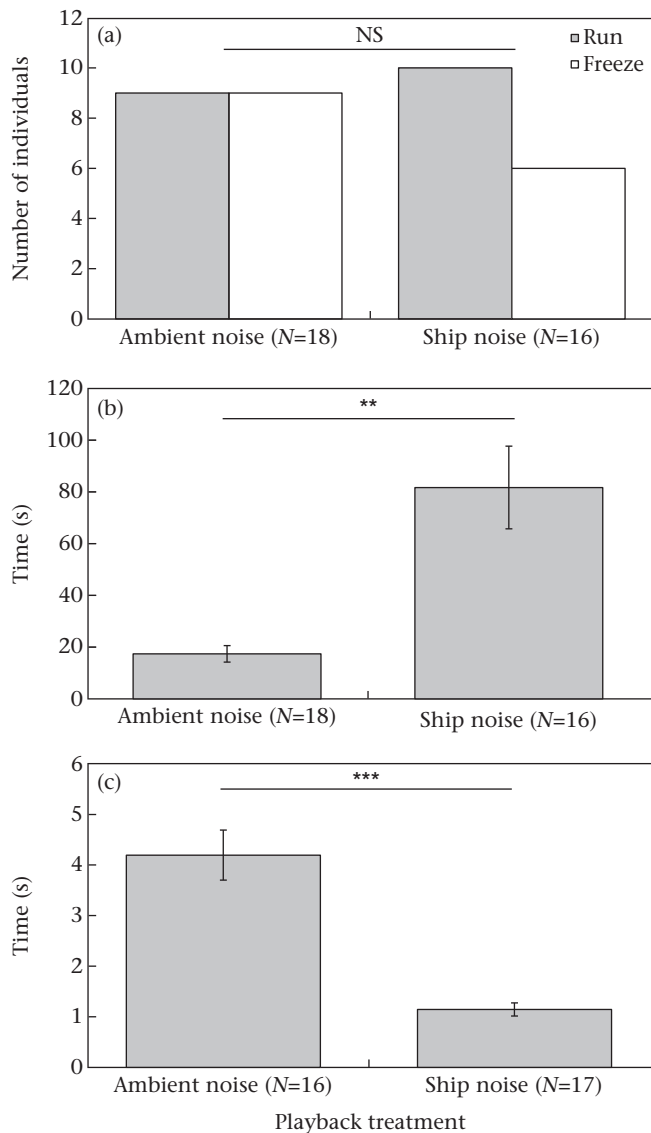
Figure 4. Results of the antipredator experiments. (a) Number of crabs that ran or froze as an initial response to a simulated predatory attack, (b) mean ± SE time taken to return to a shelter in the immediate aftermath of the simulated attack, and (c) mean ± SE time taken to right themselves from an inverted position during playback of ambient or ship noise. Sample sizes are provided in parentheses. **$P < 0.01$; ***$P < 0.001$.

noise could also affect fish behaviour (e.g. Purser & Radford 2011; Bracciali et al. 2012; Bruintjes & Radford 2013). However, our findings represent the first indication that marine decapods can be affected behaviourally by underwater anthropogenic noise (see Wale et al. 2013 for a physiological response); studies have shown this is also true of terrestrial decapods, with evidence for increased distraction and decreased antipredator responses when exposed to playback of anthropogenic noise (Chan et al. 2010a, b; Stahlman et al. 2011). Future work needs to ascertain whether the demonstrated responses occur in natural conditions, and the scale of likely impact in response to real sources of anthropogenic noise.

Animals disturbed while foraging, especially if they move away from the food source, run the risk of losing the item, either because the prey escapes or because it is stolen; food acquisition is highly competitive in decapod crustaceans (Smallegange et al. 2009). Lost food would increase the amount of foraging time required to satisfy energetic needs, at the cost to other essential behaviours

(Abrahams & Dill 1989) and potentially an increased predation risk; animals often have to trade off vigilance with time spent foraging (Lima & Dill 1990). Moreover, selection of more items to ensure the same food intake increases the likelihood of foraging errors, such as the consumption of toxic or harmful food, especially since performance mistakes may be more likely in noisy conditions (see Purser & Radford 2011). If individuals persistently or frequently had to increase their foraging effort or compensation is not possible, then there would be likely consequences for growth, reproductive success and survival; individuals might also be at a competitive disadvantage (Pintor & Sih 2008), although that depends on the relative impact of noise on different species.

Noise also appears to have a negative impact on important antipredator behaviours in the shore crab. Retreating into a shelter, where the prey becomes inaccessible, is a well-known defence mechanism (Guerra-Bobo & Brough 2010; Rossong et al. 2011), and extra time spent in exposed conditions before reaching safety increases the chances of predation. Of course, the vulnerability to predation depends on how predators are affected by noise, since not all species are affected similarly (see Francis et al. 2011). Crabs placed on their backs and exposed to ship noise playback also righted themselves faster than those experiencing ambient noise. From a functional perspective, a faster righting could be perceived as beneficial, with the crabs able to escape predation quicker, spending shorter periods of time on their back with their weak undersides exposed. However, because remaining motionless may reduce the likelihood of further predatory attack (O'Brien & Dunlap 1975), ceasing this behaviour sooner could further increase the predation likelihood, with ultimate consequence for survival.

It is possible that animals might habituate to continuous exposure to the same noise, or become more tolerant of it (Smith et al. 2004; Bejder et al. 2009). If so, the potential impacts discussed above would be lessened over time. However, variable or unpredictable exposure or the occurrence of novel noise might prevent this (for example, various fish species produced increased cortisol in response to variable boat noise but not to continuous Gaussian noise; Wysocki et al. 2006) and could even lead to a sensitized response to such disturbances. The processes of habituation and sensitization to noise exposure are only just beginning to be explored (Masini et al. 2008; Wale et al. 2013) and the implications are far from simple (Bejder et al. 2009), so further research is certainly warranted.

Our study did not explicitly explore whether stress, distraction, masking or a combination of these underpins the demonstrated behavioural responses to noise playback. Masking is perhaps unlikely as an explanation for our results, because there were no obvious acoustic cues or signals available, certainly in the two foraging experiments (which utilized pinned mussels) or the experiment when the crab was unrighted. Previous work has suggested that exposure to noise can reduce attention to a primary task, such as foraging or the detection of predators (Chan et al. 2010a; Purser & Radford 2011), because attention capacity is limited (Mendl 1999; Dukas 2002). However, crabs in our experiments did not take longer to find a food item and were no less likely to respond to the simulated predator attack during ship noise playback, which does not lend any support to the distraction hypothesis (see Chan et al. 2010a; Chan & Blumstein 2011). It is possible that our set-up was too simple to allow any such effects to be determined: for instance, the limited confines of the tank may have made finding the food item rather too easy. Future work needs to test explicitly between potential underlying mechanisms for noise-induced differences in behavioural responses (see Chan et al. 2010a; Siemers & Schaub 2011).

In general, studies of anthropogenic noise both on land and underwater have tended to focus on vertebrates (Tyack 2008; Barber et al. 2009; Slabbekoorn et al. 2010; Radford et al. 2012). The

paucity of attention on invertebrates is not commensurate with their abundance and diversity (they make up 60% of marine species, for example), their importance ecologically (as essential components of food webs) and economically (especially in light of changing fisheries), or their value in terms of new natural products (Cesar et al. 2003; Ausubel et al. 2010; Leal et al. 2012). Care is clearly needed when interpreting our results from tank-based playback experiments (chosen to ensure tight control of potential confounding factors) in a real-world context. Tank playbacks cannot replicate natural sound fields perfectly (Parvulescu 1964, 1967; Okumura et al. 2002) and crustaceans probably detect sounds using particle motion (Goodall et al. 1990). However, given the paucity of studies examining the impact of anthropogenic noise on foraging and antipredator behaviour in any taxa, even preliminary indications in this regard are potentially valuable. Moreover, our study highlights both that invertebrates are likely to be susceptible to the impacts of anthropogenic noise and that they provide a tractable option for detailed investigations into the impacts of this pervasive global pollutant.

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