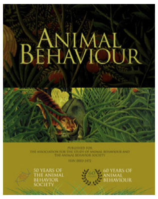
Animal Behaviour 86 (2013) 111–118

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Noise negatively affects foraging and antipredator behaviour in shore crabs

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ARTICLE INFO

Article history:
Received 25 January 2013
Initial acceptance 6 March 2013
Final acceptance 8 April 2013
Available online 10 June 2013
MS. number: 13-00078R

Keywords:
anthropogenic noise
Carcinus maenas
distraction
environmental change
invertebrate behaviour
pollution
predation risk
shore crab
starvation risk
stress

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.

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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0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.05.001

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