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Ship noise inhibits colour change, camouflage, and anti-predator behaviour in shore crabs

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eTOC blurb: Ship noise is a prominent source of underwater sound pollution. Carter *et al.* demonstrate that ship noise has multiple negative effects on animal traits that do not primary rely on acoustics. In shore crabs, colour change to improve camouflage, and predator escape responses are adversely affected by ship noise but not by equally loud ambient noise.

The marine environment is experiencing unprecedented levels of anthropogenic noise. This is known to have adverse effects across a range of taxa, directly affecting sensory systems and behaviours [1]. Stress caused by noise pollution may affect physiological processes that do not have obvious links to the acoustic environment [2]. We show that noise from shipping reduces colour change and consequent camouflage in juvenile shore crabs (*Carcinus maenas*). Furthermore, ship noise causes maladaptive defensive responses, with crabs less likely to flee a simulated attack. In contrast, loud natural noises at the same intensity have none of the same negative effects. Our study shows that anthropogenic noise is likely to be more disruptive than anticipated: in common with other marine invertebrates, shore crabs may perceive sound, but they rely predominantly on other senses. As such, the effects of anthropogenic sound in the marine environment extend beyond interfering with acoustic communication, affecting a variety of behavioural and physiological responses across a wide range of species.

A prominent source of underwater noise pollution is shipping activity, which has increased ambient ocean sound levels by 10-15dB [3]. Recent work has investigated the effects of noise pollution on marine organisms [1]. There is, however, a strong bias toward studies on species and behaviours primarily reliant on acoustic cues. This is despite evidence that exposure to anthropogenic noise has broad systemic impacts which can be characterised as 'stress' [e.g. 2]. Furthermore, studies have focussed primarily on vertebrates, even though many marine invertebrates can detect sound. Marine invertebrates including decapod crustaceans possess a variety of organs for detecting particle motion, including hair-like cells on the body, chordotonal organs on appendages, and statocyst organs in the cephalothorax [4]. Changes in cephalopod behaviour following exposure to anthropogenic noise can be associated with damage to cellular structures [5], demonstrating that negative impacts of noise pollution are not confined to vertebrates.

We use playback experiments to test for effects of noise pollution on juvenile shore crabs, focussing on anti-predator adaptations found across taxa: colour change for camouflage and predator fleeing behaviour. Noise pollution has been shown to increase the time taken for individuals to retreat to a shelter [6], and leads to physiological stress in the form of increased metabolic rates [2]. However, direct comparisons of anthropogenic noise and natural noise of similar amplitude are lacking, and potential effects of noise on non-behavioural anti-predator adaptations have not been investigated. The ability to change colour is widespread in nature, and juvenile shore crabs alter their brightness according to the substrate [7]. Colour change is likely to be especially important for juveniles, which are subject to heightened predation risk. However, colour change likely incurs energetic costs, and may be impaired under stressful conditions [7].

We housed uniform, dark crabs on white backgrounds for eight weeks, a situation in which crabs normally change to a lighter coloration, with minor changes occurring in hours and more noticeable changes occurring over several weeks [5]. We split crabs into three groups, exposing individuals to either noise from shipping, a quiet control ambient noise treatment, or a control noise treatment of the same intensity as the ship noise (i.e. a loud control; see supplementary information, Figure S1). We used calibrated digital image analyses and modelling of shorebird predator vision (supplementary information) to measure changes in crab luminance (perceived lightness). Noise treatment significantly affected luminance change during the eight week exposure period (GLM, $\chi^2_{(2,99)}$=0.048, p=0.001), with individuals exposed to ship noise changing significantly less than those subjected to either ambient or loud control noise (Figure 1A, 1C). Consequently, background matching was affected by ship noise (GLM, $\chi^2_{(2,99)}$=0.364, p=0.001), with individuals in this treatment significantly less camouflaged to predator vision after eight weeks than individuals from the other two treatments (Figure 1B). There was no effect of noise on luminance change when individuals moulted (GLM, $\chi^2_{(2,69)}$=0.032, p=0.409), showing that noise affected colour change within moults. Individuals exposed to ship noise suffered a reduction in growth per moult (GLM, $\chi^2_{(2,69)}$=2.63, p=0.003; control 3.69 mm ± 0.28, loud control 3.83 ± 0.30, ship 2.05 ± 0.26), and a delay in the timing of moulting (Cox proportional hazards, $\chi^2_{(2)}$=6.75, p=0.034; control 29.1 days ± 3.41, loud control 34.6 ± 3.35, ship 38.9 ± 3.41), demonstrating further evidence of ship noise-induced stress.

Camouflage is a primary defence in avoiding predation, but once discovered, animals must rely on additional defences. We examined the response of individuals to a simulated predator attack to determine the impact of ship noise on escape behaviour. Under normal circumstances, shore crabs flee from predators. Previous work found that ship noise increased the time taken for adults to retreat during a simulated attack but did not affect the likelihood of individuals responding [6]. However, here we found that juveniles were less likely to respond to a simulated predator, and when responding were slower to retreat when exposed to ship noise than to the other treatments (Figure S2) (GLM, $\chi^2_{(2,278)}$=31.09, p<0.0001; and GLM, $\chi^2_{(2,339)}$=43.9, p<0.0001 respectively). This was consistent for all individuals, regardless of which noise treatment they had been exposed to for the previous eight weeks.

Negative responses to noise are only displayed in individuals exposed to loud anthropogenic noise from shipping, but not in those exposed to loud natural ambient sounds. This distinction indicates that some aspect of ship noise makes it more stressful than its amplitude alone would predict. Many of the already documented effects of noise *per se* (particularly those related to stress rather than masking [e.g. 2]) may be specific to anthropogenic noise, rather than simply additional environmental noise. Why anthropogenic noise has such effects requires further study to determine whether it relates to its frequency distribution or temporal structure. The effects on luminance change, moulting, and growth that we observed may be the outcome of reduced energy availability associated with stress, impacting on physiological mechanisms of colour change affecting pigment distribution and chromatophore cells [7]. Stress can alter the balance of hormones involved in endocrine-regulated processes such as luminance change and moulting (e.g. CHH [8]), as well as the pattern of investment in behaviours [9]. Stress can also impair cognitive function and diminish decision-making and awareness, which may account for the disrupted antipredator response [6].

Further research is needed to determine the specific mechanism(s) underpinning the responses demonstrated.

A reduction in camouflage under exposure to ship noise will likely lead to an increase in detection by predators and consequent predation risk. This amplifies the need for rapid anti-predator behaviours. However, in the presence of ship noise, crabs were slower to retreat and often entirely failed to respond to simulated predators. This reveals multiplicative negative impacts of noise on predation risk. Human impacts are widely affecting the efficacy of anti-predator coloration, including camouflage on a global scale [10]. Our findings suggest that other marine species for which there is little evidence for a primary importance of acoustic communication may also be affected by marine noise pollution.

Author contributions: All authors conceived and designed the study and experiments. EEC undertook the experiments and analyses, with contributions from MS and TT. All authors wrote the paper.

Acknowledgements: We thank Steve Simpson, Andy Radford and Matthew Wale for sharing their underwater sound recordings and three anonymous referees for valuable comments.

Declaration of interests: The authors declare no competing interests.

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Figure 1: Ship noise reduces luminance change and consequent background matching after eight weeks, but loud control has no effect. A) Mean change in luminance (avian double cone values) after eight weeks, for each noise treatment with standard error shown. B) Mean level of background matching, measured as the absolute difference in luminance (double cone values) between the crab and background, after 8 weeks, for each noise treatment, with standard error shown. Lower values indicate better matching and consequently a greater level of camouflage. Control n=30; Loud Control n=36; Ship n=32. C) Representative examples of an individual from each noise treatment whose level of change reflected the average for that group, at the start and end of the experiment. Each of these individuals moulted during the experiment. Photographs were all enhanced in brightness equally for presentation purposes only.

Data S1. Original data from the experiments. The sheet 'Luminance' includes change in luminance of individual crabs over the duration ('day') of experiment, size of crabs, whether they moulted during the experiment, and level of background matching, by treatment ('noise'). Sheet 'Moult' contains data for the time for each crab to moult, and changes in size and luminance under each treatment. Sheet three ('Predator Response') contains the data for the behavioural response trials, including whether crabs responded to a simulated predator attack, the time to respond, previous noise exposure during the colour change experiment, and current noise treatment during the trial ('Track').