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

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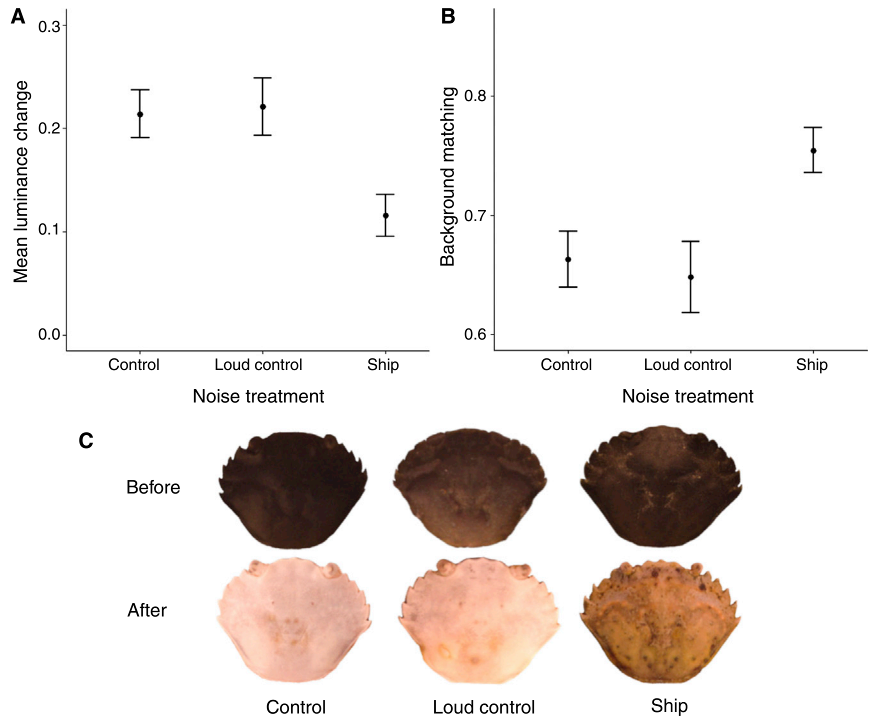

Figure 1. Ship noise reduces luminance change and consequent background matching after eight weeks, but loud control has no effect.
A) Mean change in luminance (avian double cone values) after eight weeks, for each noise treatment with standard error shown. B) Mean level of background matching, measured as the absolute difference in luminance (double cone values) between the crab and background, after eight 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.

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]. Moreover, stress caused by noise pollution may affect physiological processes with no 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 negatively affects defensive responses, with crabs less likely to flee a simulated attack. In contrast, loud natural noises at the same intensity do not affect these 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 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 10–15 dB [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 that can be characterised as ‘stress’ (for example, [2]). Furthermore, studies have focused 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, focusing 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 (that is, a loud control; see Supplemental Information, Figure S1). We used calibrated digital image analyses and modelling of shorebird predator vision 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,C). 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 stress induced by ship noise.

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, 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 the noise treatment to which they had been exposed 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, for example [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 physiological mechanisms of colour change that affect pigment distribution and chromatophore cells [7]. Stress can alter the balance of hormones involved in endocrine-regulated processes such as luminance change and moulting (for example, crustacean hyperglycaemic hormone [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.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure, one Excel file, experimental procedures, supplemental discussion and references, and author contributions, and can be found with this article online at https://doi.org/10.1016/j.cub.2020.01.014.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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