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Condition-dependent responses of fish to motorboats

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Anthropogenic noise is a pollutant of global concern that has been shown to have a wide range of detrimental effects on multiple taxa. However, most noise studies to-date consider only overall population means, ignoring the potential for intraspecific variation in responses. Here, we used field experiments on Australia's Great Barrier Reef to assess condition-dependent responses of blue-green damselfish (*Chromis viridis*) to real motorboats. Despite finding no effect of motorboats on a physiological measure (opercular beat rate; OBR), we found a condition-dependent effect on anti-predator behaviour. In ambient conditions, startle responses to a looming stimulus were equivalent for relatively poor- and good-condition fish, but when motorboats were passing, poorer-condition fish startled at significantly shorter distances to the looming stimulus than better-condition fish. This greater susceptibility to motorboats in poorer-condition fish may be the result of generally more elevated stress levels, as poorer-condition fish had a higher pre-testing OBR than those in better condition. Considering intraspecific variation in responses is important to avoid misrepresenting potential effects of anthropogenic noise and to ensure the best management and mitigation of this pervasive pollutant.

1. Introduction

Anthropogenic noise is a pollutant of global concern, pervading terrestrial and aquatic ecosystems and featuring in environmental legislation worldwide [1–3]. Noise pollution has been shown to have a wide range of detrimental behavioural, physiological, developmental and fitness effects on many different taxa (see [4–6] for recent reviews). To-date, however, most non-human animal studies have considered only whether noise has an impact, making assumptions that conspecifics are ecologically equivalent and, subsequently, using trait means to assess responses [7,8]. Intraspecific variation, stemming from both intrinsic characteristics (e.g. size, sex, body condition) and extrinsic factors (e.g. experience, environmental context) can affect how animals respond to both environmental and anthropogenic stressors [8]. These differences in responses provide the basis on which natural selection acts [9], as well as influencing population dynamics, community structure and ecosystem functioning [10,11]. Failing to address intraspecific variation in responses therefore risks misinterpreting the full impacts of anthropogenic noise, potentially reducing the capacity for mitigation strategies to protect all individuals in a population effectively [7,8].

Body condition can vary greatly between individuals within a population, owing to differences in both intrinsic characteristics (e.g. reproductive state, age) and external factors (e.g. parasitism, food availability, environmental conditions) [12]. Body condition can affect decision-making in animals; for example, malnourished individuals are more likely than those in better condition to display riskier foraging behaviours in the presence of predation threat [13,14]. Further, the condition can affect responses to both natural and anthropogenic stressors [15–17]; for instance, in a study of herbivorous mountain pine beetles (*Dendroctonus ponderosae*), 92% of individuals in 'average' to 'poor' condition died when exposed to host-plant monoterpenes, whereas there was no effect of monoterpene concentration on the survivorship of beetles in 'good' condition [15]. To our knowledge, however, there is only one previous study that has investigated condition-dependent responses to anthropogenic noise [8]: laboratory-based experiments showed that European eels (*Anguilla anguilla*) in poorer body condition exhibited different physiological and behavioural responses to noise playbacks than those in better condition [18]. Condition-dependent responses to noise have never been examined *in situ* using real noise sources.

Here, using experiments exposing fish to real motorboats in field conditions on Australia's Great Barrier Reef, we tested how body condition influences the responses of a common coral reef fish (the blue-green damselfish, *Chromis viridis*) to anthropogenic noise. In coastal marine habitats, recreational motorboats represent a large proportion of marine traffic [19], and their use is forecast to increase considerably over the next few decades, owing to human population growth and development of tourism, fishing and transport [19,20]. While motorboats also generate wake and visual disturbances, the noise component propagates the furthest. In addition, the noise has been indicated as a primary candidate in driving responses to motorboats by studies, including one conducted at the same field site and using the same motorboats as the current work, showing equivalent impacts of real motorboats and loudspeaker playback of motorboat noise [21,22]. Previous research has demonstrated that motorboat noise can affect the behaviour (e.g. orientation, communication, foraging, anti-predator responses) and physiology (e.g. opercular beat rate (OBR), metabolic rate, heart rate) of fishes, with direct consequences for fitness [19,21,23]. Here, we aimed to determine whether intraspecific variation in body condition affects noise impacts, measuring the behavioural and physiological responses of fish in relatively good and poor condition to motorboat noise compared to ambient sound. We predicted that, compared to conspecifics in better condition, poorer-condition fish would be more sensitive to motorboat noise and therefore have an elevated OBR and an impaired anti-predator response to a looming stimulus. The impaired anti-predator response would be characterized by a lower likelihood of startling and a reduced distance to the 'predator' at the time of startle.

2. Methods

This study took place during November–December 2016 at Lizard Island Research Station (LIRS) (14°40′ S, 145°28′ E), Great Barrier Reef, Australia. Experiments were conducted on *C. viridis*, a damselfish that often lives in large shoals (more than 100

individuals), closely associated with live coral habitat [24,25]. In both experiments, fish were exposed to either real motorboats ('motorboat' treatment) or ambient conditions as a control ('ambient' treatment). Five different motorboats were used in each experiment to reduce pseudoreplication; each boat had a 5 m long aluminium hull and a 30 hp Suzuki 2-stroke outboard motor, and motorboats were randomly allocated for use between individual trials. Motorboats were driven continuously 10–200 m from the experimental setup with various steering patterns (see electronic supplementary material for full details of acoustic conditions in each treatment).

On each of nine days, a cohort of *C. viridis* was collected and transported to holding facilities at LIRS (mean ± s.e. number of fish per cohort: 46 ± 1, range: 41–51). All fish in a cohort were measured (mass to the nearest 0.01 g; standard length to the nearest 0.1 cm), and overall body condition was assessed using residual regression analysis, where the position of each individual residual from the mass–length relationship is used as an indicator of relative body condition; this is a commonly used metric for assessing body condition within a population, while controlling for variation in size [26–28]. The subsets of fish with the highest (33%) and lowest (33%) residuals within each cohort (relatively good and poor condition, respectively) were placed into separate aquaria. One day post-capture, fish categorized as being in relatively good or poor condition were taken from holding aquaria and exposed to either the ambient or motorboat treatment in open-water conditions in the field (an independent-measures design). Trials were conducted in counterbalanced blocks to avoid any treatment bias in the time of day or duration that fish were held in the temporary aquaria. Following field trials, fish were transferred into post-experiment holding aquaria.

As a physiological indicator of susceptibility to motorboats, we used OBR as a secondary measure for physiological stress [18,29,30]. For each trial, two fish from each body condition category were randomly selected from their respective holding aquaria and placed into four separate 200 ml transparent rigid plastic chambers, transported out to the study site and placed in water of 1–2 m depth (for full details of holding and transport conditions see the electronic supplementary material). Fish were given a 10 min acclimation period, followed by another 5 min of ambient conditions (pre-testing period) and then a 5 min exposure period consisting of either the ambient or motorboat treatment. This design enabled a change-based analysis that controlled for interindividual differences in pre-testing OBR [31]. Trials were recorded using video cameras (GoPro Hero 3 or 4), with pre-testing and exposure periods separated into different randomly named clips. Videos were analysed in a random order without sound, by a single observer (H.R.H.) who was blind to the treatment and to the trial period. OBR was determined for the duration of each 5 min trial period. The change in OBR over the trial was determined for each fish by subtracting its pre-testing rate from its exposure period rate.

The anti-predator 'startle' response to a looming stimulus, which mimics the sudden strike of an ambush predator (typical of fishes preying on *C. viridis*), was assessed as a behavioural measure with likely fitness consequences. A startle represents the onset of an escape response to a perceived threat, with poor performance shown to have a direct effect on survival in the wild [21,30,32,33]. The stimulus comprised a 73 cm section of PVC pipe with a black end cap that emerged from a larger pipe when released, appearing as a black disc increasing in size as it approached the fish ([21]; see electronic supplementary material for experimental setup). The stimulus was prevented from hitting the pot containing the focal fish by using a rubber washer at the end of the PVC pipe. An individual fish was transferred into a 500 ml transparent rigid plastic pot that was held in place with a bungee cord on a concrete block positioned on the
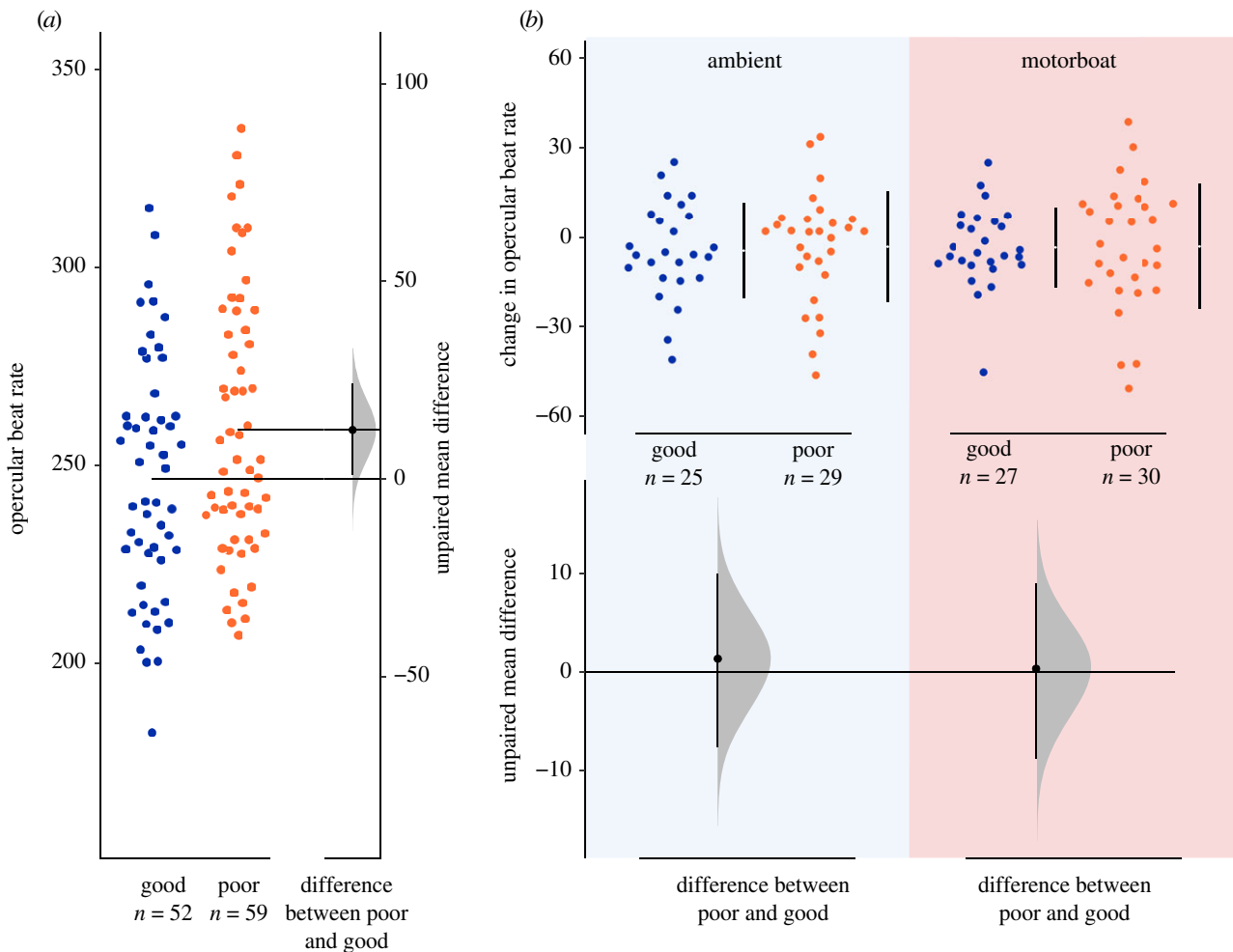
Figure 1. (*a*) Pre-testing OBR (beats per minute) of fish in different relative body condition. (*b*) Change in OBR (beats per minute) (exposure period minus pre-testing period) of fish in different relative body condition when exposed to either the ambient or motorboat treatment. Left-hand section of (*a*) and top section of (*b*): points are the raw data. Standard deviation indicated by the black vertical lines (the central point of which represents the mean) shown in (*b*) only. Right-hand section of (*a*) and bottom section of (*b*): mean difference effect size, with bootstrapped 95% confidence intervals and the resampled distribution of the mean difference, as a comparison between (*a*) body condition and (*b*) body condition per treatment. Estimation plots, mean difference effect sizes and bootstrapped confidence intervals derived from '*DABEST*' R package [34].

seabed at 1–2 m depth. Fish were given a 5 min acclimation period, followed by a 2 min exposure period of either the ambient or motorboat treatment. At the end of the exposure period, the looming stimulus was released and the reaction recorded with a video camera (GoPro Hero 3 or 4). Videos were analysed without sound, by a single observer (H.R.H.) who was blind to the treatment. The presence or absence of a startle response (a rapid shift in body position or directional change in swimming trajectory between consecutive frames) was scored [21,30]. In trials with a startle response, the distance from the looming stimulus to the fish at the time of startle was calculated (see electronic supplementary material for full details of methods and statistical analyses).

3. Results

In the pre-testing period, fish in poorer body condition had a significantly higher OBR compared to better-condition conspecifics (Welch two-sample *t*-test: $n_{poor} = 59$, $n_{good} = 52$, $t = -2.07$, d.f. = 108.84, $p = 0.04$; mean difference: 12.4 opercular beats [95% CI = 1.2–24.6]; figure 1*a*). However, the change in OBR from pre-testing to exposure period was not significantly affected by treatment (linear mixed model: $\chi^2 = 0.02$, d.f. = 1, $p = 0.90$), body condition ($\chi^2 = 0.01$, d.f. = 1, $p = 0.93$)

or their interaction ($\chi^2 = 0.34$, d.f. = 1, $p = 0.56$; electronic supplementary material, table S1; figure 1*b*).

The likelihood that fish startled to the looming stimulus was not significantly affected by treatment (general linear model: $\chi^2 = 1.34$, d.f. = 1, $p = 0.25$), body condition ($\chi^2 = 0.70$, d.f. = 1, $p = 0.40$) or their interaction ($\chi^2 = 1.39$, d.f. = 1, $p = 0.24$; electronic supplementary material, table S2). In ambient conditions, fish startled in 22 out of 24 trials and in 16 out of 21 trials for relatively good- and poor-condition fish, respectively; when exposed to motorboats, startle responses were seen in 17 out of 23 and 18 out of 24 trials for relatively good- and poor-condition fish, respectively. However, the distance from the looming stimulus at the onset of the startle response was significantly affected by the interaction between treatment and body condition ($\chi^2 = 4.59$, d.f. = 1, $p = 0.03$; electronic supplementary material, table S3; figure 2). Post-hoc tests revealed that in ambient conditions, there was no significant difference in the distance from the looming stimulus at which fish in either body condition startled (Tukey's pairwise comparison: $p = 1.00$; mean difference: 0.19 cm [95% CI = −2.05–2.89]). However, in the motorboat treatment, fish in poorer condition startled only when the looming stimulus was significantly closer to them than was the case for better-condition conspecifics ($p = 0.003$; mean difference: −3.25 cm [95% CI = −5.62 to −1.28]).
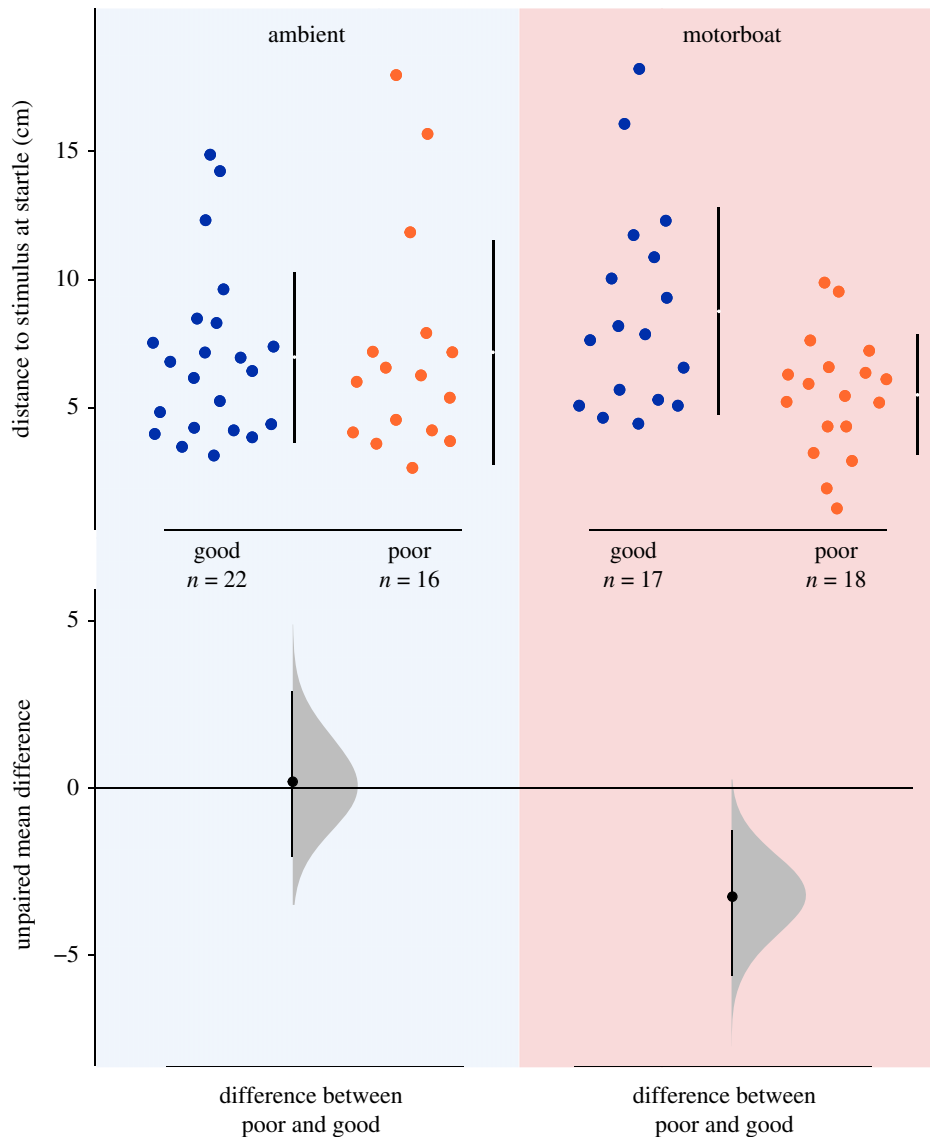
Figure 2. Anti-predator response of fish in different relative body condition to either the ambient or motorboat treatment. Upper section shows raw data points, with the standard deviation indicated by black vertical lines (the central point of which represents the mean). Lower section shows the mean difference effect size, with bootstrapped 95% confidence intervals and the resampled distribution of the mean difference, as a comparison between each body condition for each treatment. Estimation plots, mean difference effect sizes and bootstrapped confidence intervals derived from '*DABEST*' R package [34].

4. Discussion

When exposed to motorboats, *C. viridis* in poorer body condition startled to a looming stimulus when it was closer to them than was the case for conspecifics in better condition, despite there being no significant effect on a physiological metric for fish in either body condition. The reduced performance of poorer-condition fish matches results of a previous laboratory-based noise playback study on European eels [18], but using real motorboats in open-water conditions for acoustic validity. Previous research has shown equivalent behavioural responses to real motorboats and loudspeaker playback [21,22]; as such, we strongly believe that the responses observed here are driven, at least to a large extent, by the noise component of motorboat disturbance.

Our experiments go beyond simply documenting that anthropogenic noise has an effect, by considering intraspecific variation in responses. Documenting such variation is necessary for a more complete understanding of this global pollutant [8]. Individuals that perform better or are less susceptible to detrimental impacts of noise will define the evolutionary

potential of the population, which has implications for population resilience in an increasingly noisy world [8]. Further, if intraspecific response variation is ignored, mitigation strategies may be ineffective at protecting the more susceptible cohorts. For instance, the body condition of individual fish can vary both spatially and temporally; exposure to anthropogenic noise in periods of poor condition (for example, spawning periods [12,35]) may prove more detrimental than at other times. Therefore, additional noise regulations (e.g. speed limits, mandatory passing distances, regulations on engine type) could be introduced at these times to minimize the potential harm when individuals are most susceptible [36].

The reduction in anti-predator performance of poorer-condition individuals may be driven by underlying physiological effects. Pre-testing OBR was significantly higher in fish with poorer body condition than those in better condition, which could indicate chronic stress in the former. Elevated stress can affect cognitive functioning (e.g. by causing lapses in attention [37]) and reduce the available energy to respond appropriately to additional challenges, e.g. avoiding predators [38–41]. Both mechanisms might explain the reduced

anti-predator performance in poorer-condition fish under stressful conditions observed in this study. Reduced anti-predator performance would likely translate into reduced fitness in the wild; previous work has demonstrated that noise-affected prey fish suffer higher predation rates than those in ambient sound conditions [21].

The lack of a noise impact on OBR in this study is unexpected. Previous studies have found OBR to be affected by anthropogenic noise in several fish species [30,42,43], and the significant anti-predator behavioural response shows that *C. viridis* is affected by motorboats in some regards. In principle, transport stress may have caused a ceiling effect, where fish were maximally stressed and so were unable to respond to the passing motorboats. However, this is unlikely given the spread of the raw data around the mean (figure 1*b*), with some fish displaying changes of 39–51 opercular beats from pre-testing levels. The apparent lack of an effect on OBR might indicate that fish were coping with increasing metabolic demand by alternative physiological mechanisms and/or that the physiological metric used was not sensitive enough to detect treatment-based effects in *C. viridis*. Adoption of alternative physiological metrics may have revealed plausible mechanisms of how individuals were coping with the additional stressor [44].

Our experiments add to the small but increasing body of work investigating intraspecific variation in responses to anthropogenic noise [8]. However, identifying the existence of intraspecific variation in responses is only the first step. Further work should seek to identify how condition-dependent susceptibility to noise translates to population-level consequences through potentially increased mortality of poorer-condition fish. The effect size between conspecifics in relatively good and poor condition exposed to motorboats was 3.25 cm; this represents 69% of the average body length of fish collected for the experiment. A change in startle distance of this magnitude might represent the difference between life and death when attempting to evade an ambush predator; natural selection can act on such margins over multiple generations. Assessing population responses in the wild will help our understanding of the full ecological impacts of the individual differences observed in this study. Intraspecific variation influences population dynamics, community structure and ecosystem functioning [10,45]; failing to consider intraspecific variation therefore risks over- or under-estimation of impacts and compromises our ability to determine the full implications of this pervasive pollutant [8]. Mitigation strategies and management decisions surrounding anthropogenic noise must encompass intraspecific variation to ensure that all individuals in a population are protected.

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