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## **Beyond a Simple Effect: Variable and Changing Responses to Anthropogenic Noise**

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## Abstract

A growing number of experimental studies have demonstrated that exposure to anthropogenic noise can affect the behavior and physiology of a variety of aquatic organisms. However, work in other fields suggests that responses are likely to differ between species, individuals, and situations, and across time. We suggest that issues such as interspecific and intra-population variation, context-dependency, repeated exposure and prior experience, and recovery and compensation need to be considered if we are to gain a full understanding of the impacts of this global pollutant.

## 1 Introduction

Human activities such as urban development, the construction and exploitation of natural resources, and transportation have increased around the globe in the last century, changing the acoustic environment both on land and underwater (Jasny, 1999; McDonald et al., 2006; Watts et al., 2007; Barber et al., 2009). In addition to the unprecedented modification of the natural soundscape, the nature of the sound generated by human activities is often very different from that arising from natural sources; anthropogenic noises may differ from abiotic or biotic sounds in such acoustic characteristics as constancy, rise time, duty cycle and impulsiveness (Hildebrand, 2009; Popper & Hastings, 2009). Consequently, anthropogenic noise presents a very real, and often novel, challenge to animals, and is now recognised as a pollutant of international concern (e.g. inclusion in the US National Environment Policy Act and the European Commission Marine Strategy Framework Directive, and as a permanent item on the agenda of the International Maritime Organisation's Marine Environmental Protection Committee).

In recent years, anthropogenic noise has been demonstrated to affect a variety of taxonomic groups across a range of scales, from the physiology and behavior of individuals to changes at the population and community level (see Tyack, 2008; Barber et al., 2009; Popper & Hastings, 2009; Slabbekoorn et al., 2010; Kight & Swaddle, 2011 for reviews). Experimental studies on aquatic

organisms have indicated that mammals, fishes, and invertebrates are all vulnerable. For instance, noise causes alterations in the vocal signaling, movement patterns, foraging behavior, and hearing thresholds of marine mammals (e.g. Bejder et al., 2006; Mooney et al., 2009; di Iorio & Clark, 2010; Tyack et al., 2011). In fishes, movement, settlement, foraging, social interactions, and anti-predator behavior are all influenced by anthropogenic noise (e.g. Purser & Radford, 2011; Bruintjes & Radford, 2013; Holles et al., 2013; chapter by Everley, Radford, & Simpson; chapter by Simpson, Radford, Holles, Ferrari, Chivers, McCormick, & Meekan), which has also been shown to cause stress, temporary threshold shifts, and injury (e.g. Smith et al., 2004; Wysocki et al. 2006; Halvorsen et al., 2012). Marine invertebrates, which use sound for a variety of reasons (e.g. Simpson et al., 2011; Vermeij et al., 2011), are also impacted as anthropogenic noise has both physiological and behavioral consequences (e.g. Wale et al., 2013a, b).

## 2 Beyond a simple effect

Understandably for an emerging research field (the majority of studies have been published in the last three years; reviewed in Radford et al., 2012; Morley et al., in review), the main question considered in experimental studies to date has been the straightforward, yet important: ‘Does anthropogenic noise have an impact?’ We argue that attention also needs to focus on additional questions relating to variable and changing responses to noise, and we outline some examples below.

### 2.1 Interspecific differences

It is likely that there will be stable interspecific differences in susceptibility and responses to elevated noise levels depending on variation in, for example, hearing ability (Fay et al., 2008) and mechanisms of physiological stress response (Hofer & East, 1998). Direct comparisons of species in response to the same noise source in the same contexts are rare. However, Halvorsen et al. (2012) recently showed variation in the level of injury caused to different fish species by exposure to the same pile-driving stimulus. Voellmy (2013) has also demonstrated that the foraging and anti-predator behavior of three-spined sticklebacks (*Gasterosteus aculeatus*) and European minnows (*Phoxinus phoxinus*) is affected differently by the same noise playbacks. In sympatry, and particularly if there is

overlap in ecological niches, such differences may affect the relative success of each species under scenarios of disturbance, and so potentially affect community composition and structure. These effects could arise through alterations in the interactions between, for example, competitors, predators and prey, and plants and pollinators (see Francis et al., 2009, 2012).

## 2.2 Intra-population variation

It is clear from other research fields that factors such as sex, dominance status, age, size and condition may all influence how members of the same population are affected by a given stimulus, including environmental change arising from human activities (Kiffney & Clements, 1996; Huntingford et al., 2006; Xu et al., 2010). While empirical work on the impacts of anthropogenic noise has tended to focus on the overall response of cohorts of individuals, studies are beginning to consider potential intra-population differences in response. For instance, Wale et al. (2013a) found that heavier shore crabs (*Carcinus maenas*) consume a disproportionately larger amount of oxygen than smaller individuals when exposed to playback of ship noise. Brintjes & Radford (2013) discovered that dominant male and female individuals of the cooperatively breeding cichlid fish species *Neolamprologus pulcher* exhibit different behavioral responses to the same playback of boat noise. More recently, Purser et al. (in prep.) have shown that European eels (*Anguilla anguilla*) in poorer body condition (relative weight) suffer more detrimental physiological and behavioral consequences than individuals in better condition. Consistent inter-individual differences in response could have impacts on population dynamics and for harvests of commercially important species.

## 2.3 Context-dependent responses

The response of an animal can be dependent on its current situation (e.g. Bell et al., 2009, 2010), with increasing evidence that context can influence the harmful effects of human activities on animal welfare (see Huntingford et al., 2006 and references therein). Recent work by Brintjes & Radford (2013) showcases that the impact of anthropogenic noise can be context-dependent: playback of boat noise resulted in a reduction in anti-predator defense by *Neolamprologus pulcher* group members if no eggs were present in a nest, but not if eggs were present. Moreover, social interactions

between dominants and subordinates were affected differently by the same noise playbacks depending on whether group members were engaged in defense behavior or nest digging. The implication is that responses to anthropogenic noise are not fixed, but rather show some element of flexibility, which may or may not be under the control of the individual.

#### 2.4 Repeated exposure and prior experience

Responses to pollutants may change across time (Piola & Johnson, 2009; Whitehead et al., 2010) as a result of such processes as habituation, tolerance and sensitization (Bejder et al., 2009). Although noise-related experiments have, from an understandable logistical perspective, often involved a single presentation of the relevant stimulus, organisms in most natural situations are likely to experience chronic or repeated noise exposure. Exploring how responses can change and are dependent on prior experience is thus important (Simpson et al., 2010; chapter by Voellmy, Purser, Simpson, & Radford). Wale et al. (2013a) showed that while shore crabs repeatedly exposed to ambient-noise playback increase their oxygen consumption (perhaps due to handling stress), those individuals repeatedly exposed to playback of ship noise do not exhibit a similar change. It is possible that they already show a maximum response on first exposure to ship-noise playback, but they might also be habituating or becoming tolerant over time. Voellmy (2013) has also recently demonstrated, by manipulating holding-tank noise conditions, that prior acoustic experience can influence responses of fish to experimental playbacks, while Holles et al. (in prep.) have found that repeated exposure to boat-noise playback can affect subsequent behavioral and physiological responses in the early life-stages of both fish and marine invertebrates.

#### 2.5 Recovery and compensation

Many anthropogenic noise events are transient in nature (Hildebrand, 2009; Popper & Hastings, 2009), and short-term impacts of noise may not necessarily translate into long-term consequences (see Bejder et al., 2006). While it is clear that behavior and physiology can be detrimentally impacted during the period of elevated noise (see Section 1), effects on survival and reproductive success will be dependent on whether, and how quickly, the affected individuals recover

to baseline performance levels and if they can compensate. Brintjes et al. (in prep.) have recently found that the detrimental effects of ship-noise playback on European eel anti-predator behaviour and respiratory rate are not sustained when the noise ceases. Species will differ in their ability to recover and compensate (Voellmy, 2013), and compensation itself may carry a variety of inherent costs (see Purser & Radford, 2011). Thus, studies are needed which look at longer timeframes and consider post-exposure periods as well as when the noise itself is apparent.

### 3 Conclusions

The human population is projected to increase by 2.3 billion between 2011 and 2050 (United Nations 2011) and thus noise pollution is not just a pressing issue, but one of ever-increasing concern. It is now well established that anthropogenic noise does indeed impact a wide range of animals. As the research field moves forward, we advocate the exploration of a wider range of questions, such that we can understand more fully the range of effects of this global pollutant and thus optimize strategies to mitigate impacts to both aquatic and terrestrial ecosystems.

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