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Investigating the impacts of anthropogenic noise on fish behaviour

Ella Waples

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Masters' by Research in the School of Biological Sciences, Faculty of Life Sciences in January 2023.

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Abstract

Anthropogenic disturbance is a growing concern in the natural environment as human presence grows in previously undisturbed areas. Disturbance can lead to environmental stressors such as light, noise and chemical pollutants, increasing temperature and extreme weather events. Anthropogenic disturbance has been shown to cause negative effects for many animal species, from the individual to the ecosystem level. Many animals favour group living, as group behaviour can be beneficial for animals for information sharing and social learning. Individuals within a group can have different personalities and this personality variation may lead to differences in individual responses to anthropogenic stressors, which may lead to implications at the group level. At present, there is a research focus on the effects of anthropogenic noise on marine mammals, birds, and terrestrial animals, however research into the effects of anthropogenic noise on fish physiology and behaviour is beginning to emerge. Different fish species have different hearing mechanisms, with most species having the ability to detect sound through particle motion, therefore incorporating particle motion into sound-based studies will allow a more complete understanding of responses to noise disturbance. Here, I studied the effects of white noise on guppy *(Poecilia reticulata)* behaviour over multiple exposures, using video tracking software to analyse behaviour. In the white noise treatment guppies can be seen to spend more time in the quieter areas of the tank over a week, possibly showing behavioural habituation. This thesis highlights areas that still require further consideration, including the combination of multiple disturbance factors, the effect of multiple exposures to noise, and using appropriate acoustic metrics based on animals' hearing mechanisms. Future research will be important in the implementation of successful mitigation methods in the face of environmental change through anthropogenic disturbance.

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Authors declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: ....*Ella Waples*...................... DATE: ....*06/01/2023*...........

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1.1 Group Behaviour

1.1.1 Group living

Group living is found throughout the animal kingdom, from flocks of birds to shoals of fish. There has been a vast amount of research on what makes group living advantageous as well as the associated costs such as disease and competition (Hughes *et al*., 2002; Rubenstein, 1978). Benefits of group living include the ability for species to share information, which can be used to improve foraging efficiency (Ranta and Kaitala, 1991) and predator avoidance (Beauchamp, 2013) through the confusion and dilution effect (Ioannou *et al*., 2008; Lehtonen and Jaatinen, 2016). Another benefit of group living is social learning, where individuals learn through observation or interaction with others, which has the benefit of being lower risk than individual learning, where individuals learn from past experiences. Being in a group decreases predation risk and allows for more foraging time (Barrett *et al*., 2019). Larger groups have also been shown to respond faster to environmental information as they span a larger area to collect more information in a shorter period of time (Berdahl *et al*., 2013). Group living has also been shown to decrease the stress responses of fish, where recovering in the presence of a group decreased cortisol levels (Culbert *et al.,* 2019). Collective behaviour, where a group coordinates its behaviour, is a key concept within many species' groups, allowing for their survival and achieving the greatest fitness (Artyukhin *et al*., 2015; Jullien and Clobert, 2000). The importance of collective behaviour within fish, and how it is imperative to their survival through antipredator behaviour, movement, foraging and mate choice, has been studied in depth (Brown and Laland, 2003). While group living has many benefits, there are associated risks. These risks include: increased disease transmission (Hughes *et al.,* 2002), increased food competition (Pitcher, 1986), increased conspicuousness of group leaders (Ioannou *et al*., 2019) and within group dominance interactions (Clifton, 1990). Even considering these risks, the costs of group living are often outweighed by the benefits (Bilde *et al.*, 2007; Majolo *et al.,* 2008).

Behaviour varies depending on whether individuals are in groups or alone and can also depend on the environmental context that individuals are from/found. Hansen *et al*., (2021) found that guppies *(Poecillia reticulata)* from high predation areas maintained decision-making speed longer than the low predation fish, but only in groups and not when tested alone (Hansen *et al*., 2021). Fish in groups also had increased decision-making accuracy than those individuals tested alone, thus showing the benefit of being in a group to actively detect the threat of predation. Experienced fish have been shown to share foraging information (Reebs, 2000), allowing groups to increase foraging activity. As environmental stimuli vary so may group behaviour (Sih, 2013), and the extent to which depends on the species and environmental and social context. It is increasingly important to study animals' responses to these changes within a group and an individual context as anthropogenic pressures lead to environmental change.

1.1.2 Personalities within Groups

Animal personalities can be defined as repeatable behavioural variation of an individual across time and contexts. Animal personalities can affect population growth, community dynamics and how species evolve (Wolf and Weissing, 2012). Personality traits that have been reported include aggressiveness (Forkman *et al*., 1995), exploratory behaviour (Kelleher *et al*., 2018), sociability (Gartland *et al*., 2022) and boldness (Laland *et al*., 2011). Different personality traits can lead to the emergence of leaders and followers (Harcourt *et al*., 2009) where leaders may be bolder more exploratory individuals that are the first to gather information (Harcourt *et al*., 2009). Leaders can emerge as a result of a dominant personality (Ákos *et al*., 2014) as well as motivation and experience (Webster, 2017). Leaders have the benefit of first access to food when foraging as a group however they have a higher predatory risk due to their increased boldness and being in the front of the group (Ioannou *et al*., 2019). Personality traits, such as boldness, can also impact how quickly individuals discover shelter and how long they spend within it (Planas-Sitjà *et al*., 2018). A study by Planas-Sitjà *et al*. (2018) showed shyer American cockroaches (*Periplaneta americana*) settled faster and took longer to leave the shelter than bold individuals. This study also showed how cockroach groups adapted to allow for group-variation, where all bold groups showed some of the individuals acting how we expect shier individuals to, a trade-off to favour group aggregation. Individual differences can lead to a change in group alignment and therefore the effectiveness of information transfer, where more proactive individuals have greater alignment (Tang and Fu, 2020). Studying animal personalities will help understand the importance of personality variation, and how this variation might influence the response to environmental change (Roche *et al*., 2016).

When studying personality differences it is important to control for different variables as personality differences can be supressed in certain conditions, such as during foraging (MacGregor *et al.,* 2020). Environmental change can also lead to different responses based on personalities of individuals (Dall *et al*., 2004). Green turtles (*Chelonia mydas)* exposed to snorkeler disturbance showed different responses if they were bold or shy individuals; bolder individuals had greater behavioural plasticity and less consistent responses (Griffin *et al*., 2017). Individuals may also have a different environmental condition they function best at and at environmental extremes certain individuals may be more limited in their behavioural responses (Killen *et al*., 2021). Pollutant exposure can lead to a reduction in behavioural variation, such as guppies exposed to antidepressants reduce variation in inter-individual activity levels (Polverino *et al*., 2021). With increasing environmental changes occurring due to anthropogenic disturbance, understanding how personality variation effects response to disturbance and consequently the effect on group living, will be key to predicting how individuals and groups will respond behaviourally to changing environments.

1.1.3 Private and shared information

Social information is a benefit of group living as individuals can share information which is then used in decision-making (Gil *et al*., 2018), although acquiring social information can occur outside of a group context (Tóth *et al*., 2020). Private information can also be used where individuals acquire information from their own experiences. There are both costs and benefits to private and shared information and many species use a combination of both, depending on the risk and reward of sharing information within a group, particularly when maintaining group cohesion is beneficial for survival (Conradt and Roper, 2005). Individuals using private information may have more accurate, up to date information and have less competition for resources (Swaney *et al*., 2001; Trompf and Brown, 2014). However making decisions alone removes the benefits provided by group living as they have to privately sample the environment which is not energetically efficient, and predator avoidance is more challenging alone (Brown and Laland, 2003). Reebs (2000) demonstrates how golden shiners *(Notemigonus crysoleucas)* share information in a foraging scenario where groups with pre-exposed individuals led the group to food. Sharing information allowed for increase food consumption for the group, benefitting those individuals who may have otherwise taken longer to find food, although if resources were limited this information sharing could lead to a reduced food consumption. Social information can conflict with personal information meaning a decision must be made between the two.

Favouring private over social information can depend on the information individuals have, the size of the group, as well as the costs of leaving the group (Sumpter *et al*., 2008). If guppies consider risk as low, they will rely on personal information regardless of the decisions of their conspecifics (Kendal *et al.,* 2004). Black garden ants (*Lasius niger)* have been shown to use their private information as the social information lacks the detail required on the quality of the food source (Czaczkes *et al*., 2019). Another study found that sociability of individuals can affect behaviour, with a preference to be with the group outweighing being by themselves, which may be advantageous in situations such as foraging (Trompf and Brown, 2014). Larger groups can make faster and more accurate decisions in the context of predator detection and avoidance, through sharing of social information and division of vigilance behaviour (Ward *et al*., 2011). MacGregor *et al.,* (2020) also showed different individual preferences in private and shared information within a group which impacts collective order within the group, with individuals that respond first (using private information) preferring the more disordered group state (MacGregor *et al*., 2020).

Individuals within a group with different personalities have been shown to use private or social information differently (Trompf and Brown, 2014). For example, bold individuals may use social information to avoid competition, and social individuals would rather reduce foraging opportunities to stay in a group, although these personalities are not mutually exclusive. Bolder and more dominant individuals are more likely to be leaders and these personality traits mean that these individuals are more likely to have a consistent influence over group decisions (Strandburg-Peshkin *et al*., 2018). Understanding inter-individual variation, including personalities within a group, may help explain the cohesion of a group and its behaviour.

1.2 Abiotic Stressors

Human disturbance is of growing concern in most natural habitats and can have consequences for animals and their behaviour. Abiotic stressors in an environment can include temperature, light, noise, chemical pollutants, and extreme weather. Abiotic conditions can affect animal behaviour, and responses will vary to changing conditions depending on an individual’s limit of tolerance. Responses can be both behavioural or physiological (Barton, 2002) and there are both population and community level responses, such as the effect on population growth rate and food-web structure (Moe *et al*., 2013). Many studies when evaluating stress response include both behavioural and physiological responses to create a more complete study of the effect of the stressor (Carbonara *et al*., 2020; Malmos *et al*., 2021; Noureldin *et al*., 2021).

Increased temperature caused by anthropogenic induced climate change can have an effect on social interactions as it can affect the energetic cost of these interactions (Fisher *et al*., 2021). It has also been shown to affect species’ visual signals, such as increased intensity of throat colour in male green lizards *(Lacerta viridis),* which is energetically costly (Bajer *et al*., 2012). Fish exposed to warmer waters experience physiological stress which has an energetic cost so they have a reduced capacity to deal with additional stressors (Alfonso *et al.,* 2021), and show increased aggression (Warren *et al*., 2016). Light pollution has been shown to affect animals through sleep disturbance, especially in the mornings (Raap *et al*., 2015) which may have future consequences on fitness. Navigation has also shown to be affected by light pollution, for example sea turtle hatchlings can be lured away from the sea by on-shore lights (Truscott *et al*., 2017) leading to possible survival implications. Light pollution has also been shown to have physiological impacts, such as inhibiting melatonin production at night which drives the biological clock (Brüning *et al*., 2015), possibly impairing the reproduction process (Falcón *et al*., 2010). Noise pollution is a known stressor to animals, from disrupting communication to decreasing the ability for a species to detect predation (Kunc and Schmidt, 2019). Noise can also increase an animals ventilation rate, a physiological response to stress (Nedelec *et al*., 2016). Chemical pollutants have been shown to affect behaviours such as shoaling, which can then reduce foraging efficiency and responsiveness to predators (Mason *et al*., 2021). Physiological responses to chemical pollution include disrupting neural systems and metabolic processes (Saaristo *et al*., 2018). Mortality can be a direct outcome of extreme weather, but it can also affect group living, where after an extreme weather event, resources become limited, increasing within-group competition leading to a reduction in group size

(Schaffner *et al*., 2012). As seen above there are a range of responses, both chemical and physiological to abiotic stressors with many negative consequences.

Abiotic stressors rarely occur individually and instead occur in unison (Fisher *et al*., 2021), often referred to as "multiple stressors" (Orr *et al*., 2020; Wong and Candolin, 2015). To understand potential responses in a natural environment, researchers should test multiple stressors together and separately to account for their potential individual, additive, synergistic and antagonistic effects (Alfonso *et al*., 2021; Jackson *et al*., 2021; Petitjean *et al*., 2019). Additive interactions are when the impact of multiple stressors equals the sum of the individual stressors. Synergistic interactions are when the impact of multiple interactions is greater than the sum of the single effects. Comparatively, antagonistic interactions are where the effects of the stressors are less than the sum of the individual stressors being studied. Studies have been conducted that show impacts of multiple stressors, however the responses are often unpredictable based on the response to the stressors individually (McBryan *et al*., 2013; Townsend *et al*., 2008). For example, a study on porcelain crabs *(Petrolisthes cinctipes)* when combining an increasing temperature and decreasing pH led to an increase in thermal tolerance and decrease in metabolic rate, compared to a small increase in metabolic rate when decreasing pH alone (Paganini *et al*., 2014). Understanding what effects combined stressors have will help develop relevant mitigation measures (Orr *et al*., 2020).

1.2.1 Response to Abiotic Stressors

Groups will respond to changing conditions and disturbances differently depending on the species, combination of disturbance factors, and composition of personalities in the group (Fisher *et al*., 2021). Responses to disturbance are hard to predict where species' life histories and natural histories are so varied (Blumstein, 2016). Altering behaviour, known as behavioural plasticity, is a response to coping with climate change (Beever *et al*., 2017). An example of a species altering their behaviour is physical avoidance where species change environment to avoid to exist without the disturbance. The cost of changing environmental niche can include increased competition and predation risk . Migratory species that move through multiple habitats that could be affected by human disturbance have been shown to consistently avoid disturbance (Végvári *et al*., 2011). The level of disturbance has been observed to be positively correlated with the level of avoidance (Leblond *et al.,* 2013), highlighting the need to quantify the intensity of disturbance when studying species' responses.

Habituation is another response to a stressor where species are repeatedly exposed to a stimuli and over time become desensitised and show a reduced or no response (Blumstein, 2016). Behavioural plasticity also allows species to habituate to environmental disturbance (Geffroy *et al.*, 2015; Vincze *et al.*, 2016). Each change in behaviour may have different costs and benefits on the group as well as on a whole ecosystem level (Snell-Rood, 2013). When human disturbance is in the form of urbanisation of a natural environment, behavioural plasticity is often counted as an advantageous trait, where less adaptable individuals are at a disadvantage (Lowry *et al.,* 2013). With so many factors to be considered when researching anthropogenic disturbance, it is important to study this further, including how the intensity of the disturbance factor may impact a behavioural response. Physiological plasticity is another way in which animals can respond to change, through shifts in neurotransmitters, hormones and their receptors (Milewski *et al*., 2022). Understanding the physiological plasticity of animals may help predict the response to climate change and future species distribution in the changing environments (Evans and Hofmann, 2012; Fuller *et al*., 2010). Behavioural and physiological plasticity can be inter-linked and future studies should look to research the effect of stress on behavioural and physiological plasticity in changing environments (Snell-Rood, 2013).

1.2.2 Anthropogenic Noise

Anthropogenic noise is human generated noise, widely known as a pollutant (Kunc and Schmidt, 2019). Awareness of anthropogenic noise as a threat to the environment is increasing (McGregor *et al*., 2013; Sordello *et al*., 2020) and examples of this include road and shipping traffic (Scobie *et al*., 2014; Tervo *et al*., 2021), construction activities (Powell *et al*., 2006), industrial activities (Copping *et al*., 2020) and recreational noise (Pine *et al*., 2021). Sound is important to many species for communication (Sebeok and Ramsay, 2011), predator avoidance (Keen *et al*., 2020; Morris-Drake *et al*., 2016), territorial defence (Jézéquel *et al*., 2020), foraging (Jensen *et al*., 2011), habitat selection (Simpson *et al*., 2008) and mating (Podos and Cohn-Haft, 2019). Studies have found many consequences of anthropogenic sound disturbance, including increased susceptibility to disease (Masud *et al*., 2020), decreased predator detection (Spiga *et al.*, 2017), change in foraging behaviour (Sweet *et al*., 2022), physiological effects (Romano *et al*., 2004), reduced reproduction success (Nabi *et al*., 2018) and early mortality (Masud *et al.,* 2020).

Masking is one way in which anthropogenic sound can cause disturbance, where an anthropogenic sound covers the original sound used to gather information from the environment or to communicate (Erbe *et al*., 2016). Masking may have negative consequences if species are unable to communicate, for example leading to a decrease in mating success (Schmidt *et al.,* 2014). To counteract for this masking behaviour, a species may change their communication signal, including increasing frequency and reducing variability (Papale *et al*., 2015; Patricelli and Blickley, 2006; Shieh *et al*., 2012). Species may also show avoidance behaviour where they move habitat to avoid the noise pollution and masking effects, to increase their chance of survival (Brehmer *et al*., 2019). Anthropogenic noise can also act a distraction where species have their attention diverted, leading to a slower response to risk (Chan *et al*., 2010). Noise pollution can also be a direct physiological stress to species which can be demonstrated through raising cortisol levels (Romano *et al*., 2004; Sierra-Flores *et al*., 2015) and increased heart rate (Wascher *et al.,* 2022). Depending on the sound source and proximity, sound can cause direct physical damage to hearing mechanisms (McCauley *et al*., 2003).

1.2.3 Anthropogenic noise in aquatic environments

Sound travels further and faster through water due to its higher density, therefore potentially amplifying the effect of anthropogenic pollution (Ladich and Winkler, 2017; Putland *et al*., 2019). Human generated sounds in aquatic environments can vary from continuous sounds which is steady uninterrupted sound, to impulsive sounds which are short durations of noise with a quick onset and decay. Examples of continuous sound include such as shipping and sound from offshore industrial activities including the operation of windfarms and oil platforms and impulsive sounds include sound from construction activities such as pile driving and the construction of windfarms and oil platforms (Prospathopoulos, 2016). Different types of sound have been shown to have differing effects on fish species such as impulsive sound leading to a slower behavioural recovery (Neo *et al*., 2015), and impulsive sound being believed to be of greater harm to mammals leading to auditory damage (Southall *et al*., 2012). Researching relevant sounds and comparing impacts of impulsive and continuous sounds is important to understand a species' response to the different types of sound they could be subjected to, particularly when considering how to mitigate for specific sound pollution sources.

Fish use sound for communication (Maruska *et al.,* 2012), mating behaviour (Amorim *et al.*, 2015), predator and prey detection (Popper *et al*., 2003) and habitat selection (Simpson *et al*., 2008). Therefore if there were changes to the habitat soundscape of the fish, these behaviours could be affected , potentially impacting survival and fitness of the species (Mickle and Higgs, 2018; Radford *et al.*, 2014). The effects of noise have often been recorded in short-term, single exposure studies showing a species' initial response to a noise stimulus. Boat noise has been shown to have a disruptive effect on fish settlement as there is a reduced response to reef sound on a single exposure (Holles *et al*., 2013), nesting behaviour on a single trial (Bruintjes and Radford, 2013; McCloskey *et al*., 2020) and impacting overall survival with one 15 minute exposure (Simpson *et al*., 2016). During pile driving playbacks, fish shoals have shown less cohesive behaviour, a result found from five-minute trials of juvenile seabass shoals *(Dicentrarchus labrax)* (Herbert-Read *et al*., 2017). Ship noise has shown fish to alter their visual displays, increasing the variation in displays during the anthropogenic noise during one 3.5 minute exposure (Kunc *et al*., 2014). These short-term studies show species-specific noise responses to an initial exposure, however due to the nature of anthropogenic noise pollution it is also crucial to study the long-term effects (Radford *et al.*, 2016). Studies have shown reduced responses to repeated sound exposure, for example fish no longer responding to noise with an increased ventilation rate after repeated exposure (Nedelec *et al.*, 2016; Radford *et al.*, 2016). Exploring effects on spawning success, a study on Atlantic cod *(Gadus morhua)* found that long-term noise exposure led to reduced spawning period, but with a similar amount of total eggs produced (Sierra-Flores *et al*., 2015). However, this study used only one experimental and one control group (Sierra-Flores *et al*., 2015). Species may respond differently to long-term effects, and behavioural parameters may show different long-term responses. Because of this, it is important to not only study the initial response to noise recorded in short exposure trials, but also repeatedly test the same groups over time to better understand long-term exposure effects. Studying these long-term effects is particularly important when looking at mitigation of noise pollution, as changing behavioural responses over time may lead to alternative mitigation strategies.

There are a range of behavioural responses found in fish as a result of anthropogenic noise, including effects on feeding, reproduction and predator avoidance (de Jong *et al*., 2020; Simpson *et al*., 2016; Voellmy *et al*., 2014). Behavioural responses can also include avoidance, whereby a fish moves away from an aversive stimulus, or alternatively they might habituate to the sound and not change location in response to the noise (Shafiei Sabet *et al.,* 2015; Ladich, 2019). Fish responses to sound are not limited to behaviour, and individual change may be found in both behavioural and physiological responses (Purser *et al*., 2016). A fish that may show behavioural habituation could be displaying a physiological stress response such as increased ventilation rate (Radford *et al.*, 2016), which could have future implications for survival if this is a long-term effect as it is energetically costly and could affect survival. Developing studies to encompass multiple response types will allow us to develop a more complete picture of the response to sound by fish (Mickle and Higgs, 2018).

When studying the effect of noise, it is important to consider individual level responses. A review by Harding *et al.,* (2019) highlighted how 75% of the studies examined reported significant effects of intraspecific variation in responses to noise. The body condition of fish has been shown to affect its response to noise, where fish in good condition do not show any difference in response to ambient noise or where there is addition of ship noise, compared to those of poor condition who show a decrease in startling to a predator stimulus (rapid bend of the body in order to swim away from the stimulus) in the ship noise condition (Purser *et al*., 2016). Based on current knowledge on how personality can affect behavioural responses, studying the personality-dependent effect of noise on fish may show individual responses (Budaev and Brown, 2011). How personality affects responses to noise has been shown in Great tits *(Parus major;* Naguib *et al*., 2013)*,* but has not been studied specifically in fish. The effects of individual fish behaviour could have a knock-on effect for social groups as group organisation may change (Webster and Ward, 2011). For instance, if groups struggle to communicate, the benefits of shoaling may be lost which may have detrimental impacts on overall fitness of the shoal (Ward *et al*., 2008). Studying noise in the context of individuals and social behaviour is important to predict the potential fitness impacts on populations and communities.

Due to the complexity of aquatic environments, it is often more challenging to carry out sound experiments in the field than the lab, so many sound experiments are conducted within highly controlled laboratory environments (Popper and Hawkins, 2019). The ability to control for other effects allows results to be solely focused on the noise responses, however the artificial environment differs considerably from the natural environment (Slabbekoorn, 2016). Sound may behave differently in experimental tanks due to multiple factors, including tank wall material causing reflection of sound waves and constraints on the depth of the tank water (Campbell *et al.,* 2019). Even once sound has been calibrated in a small tank environment, this can change once fish are added due to the presence of the swim bladder (Rogers *et al*., 2016). Although there are limitations, experiments within aquarium setups provide a good basis of understanding and should be combined with further research in the field to compare the results for each species (Hawkins *et al.,* 2015).

Sound in an underwater environment can be detected through particle motion and sound pressure. Although aquatic mammals use sound pressure to detect sound, most fish and invertebrates use particle motion (Madsen *et al*., 2006; Popper and Fay, 2011; Popper and Hawkins, 2018). Particle motion is the vibration energy as particles move back and forwards, transmitting the oscillatory motion without travelling themselves (Nedelec *et al*., 2016). Fish and invertebrates' bodies vibrate in particle motion, and they detect the difference in vibrations from their body and denser inner ears (otoliths), allowing fish and invertebrates to hear (Radford *et al*., 2012). Sound pressure is the change in pressure as a sound wave passes. Fish that can detect sound using sound pressure are often referred to as hearing specialists, and they have the addition of specialist morphological features (Popper and Fay, 2011). These specialist features can include Weberian ossicles which connect the swim bladder to the inner ear to increase sound detection, where fish with larger swim bladders and increased numbers of ossicles have shown to have an increased hearing ability at high frequencies (Lechner and Ladich, 2008). The addition of specialist features can increase the hearing capacity of species (Putland *et al.,* 2019), and in turn could increase their sensitivity to increased anthropogenic noise.

Sound pressure and particle motion do not have a simple relationship, particularly when close to the sound source, as well as the relationship changing where depth, temperature and salinity are different (Putland *et al.,* 2019). In a study by Campbell *et al*. (2019) they highlight the importance of recording particle motion as well as sound pressure, as especially within smaller tanks as they have a complex relationship that does not match an open water environment. Sound pressure generally decreased closer to the water surface and bottom of the tank, while particle motion recordings were greater at the bottom of the tank as this is a pressure boundary, but this was not found at the surface. A further study directly compared particle motion and sound pressure which demonstrated that particle motion cannot be predicted using hydrophone sound pressure measurements, therefore, laboratory studies should always record particle motion (Jones *et al*., 2019). Particle motion equipment that is small enough to record in smaller tank set ups is enabling the study of behavioural effects in response to particle motion. Until recently, sound pressure has been used as the main approach to record noise in experimental setups due to the accessibility and simplicity of the recording equipment, but the limitations of this have been widely acknowledged (Nedelec *et al*., 2016; Popper and Hawkins, 2018). On the understanding that most fish use particle motion to detect sound, when studying the effects of noise it is important to look at responses to particle motion and not just sound pressure.

Studying group and individual-level behavioural responses to noise while also considering long and short-term effects, personality, particle motion, tank design, and noise source will address some of the gaps in the literature (Harding *et al*., 2019; Nedelec *et al*., 2016; Radford *et al*., 2016). This will provide a wider view on how anthropogenic noise will result in different behavioural changes. Consistency in experimental design, particularly in small tank setups, will allow studies to be more repeatable and comparable (Wale *et al*., 2021).

1.3 Aims of this thesis

In this thesis I aim to examine the effect of anthropogenic disturbance on fish behaviour. In my study I address how impulsive anthropogenic noise pollution can affect guppy behaviour in a tank setup. I consider how the guppies response changes during noise exposure, studying the effect throughout the treatment and during repeated exposures over the course of a week in order to look at a more long-term impact. I use tracking software to study the behaviour of the guppies, focussing on avoidance and habituation behaviour. In the final chapter I summarise my findings and discuss future directions for noise research, as well as suggestions that can be applied to anthropogenic disturbance more generally.

2 Chapter 2: The effect of impulsive white noise on guppy *(Poecilia reticulata)* behaviour.

2.1 Abstract

Noise pollution, and how it may affect the behaviour of different animal species, has been of increasing concern in the underwater environment. Levels of anthropogenic noise have been rising through increasing human construction, shipping, and leisure activities. Fish show a range of behavioural responses to noise pollution including avoidance and tolerance which have been shown to be time dependent, highlighting the importance of long-term studies. Understanding the effects of noise on fish behaviour in highly controlled lab-based studies will allow comparison to species in the wild to best inform mitigation practices. Here we investigated how groups of guppies *(Poecilia reticulata)* respond to impulsive white noise compared to silence, on multiple exposures over a week. Throughout the white noise trials, the guppies moved away from the sound source showing avoidance behaviour, however over the course of the week the guppies increasingly remained in louder areas of the tank, suggesting an increased tolerance to the white noise over time. This long-term tolerance is consistent with the fish habituating to the disturbance. However, the biological importance of this result is questioned as the avoidance behaviour saw guppies move to areas less than 0.5 dB quieter than the loudest areas, and difference between distance from the speaker in white noise and silence trials was less than 2 cm. Future studies should test multiple exposures to sound and where possible test for longer-term impacts, to have a more complete understanding of the ecological impact of anthropogenic noise.

2.2 Introduction

Anthropogenic noise pollution is an increasing problem in the natural environment and the impacts are not yet fully understood. As urbanisation, shipping, tourism, and offshore construction increases within the natural environment, we expect unprecedented growth in this type of pollution (Jerem and Mathews, 2021). Although some level of noise pollution may be unavoidable it is important to assess the implications on wildlife to understand the importance of mitigating and limiting noise pollution (Francis and Barber, 2013; Vakili *et al*., 2020). Studies have shown the negative effect of noise pollution on humans in urban populations who have been exposed to high levels of noise throughout their lives (Araújo Alves *et al*., 2020; Monazzam Esmaielpour *et al*., 2022), so it raises questions on the effect on animals in previously natural environments. Sound travels faster and greater distance in water, with a high variation in how sound behaves in different aquatic environments (Higgs and Radford, 2016), so it is particularly important to consider how noise pollution affects species in aquatic environments where it may be especially harmful. It is important to understand how this increasing anthropogenic disturbance effects aquatic species, to maintain bio-diversity as well as the potential implications on economically important species we rely on for food sources (Hawkins *et al*., 2015).

Noise disturbance can be caused by different anthropogenic sources in an aquatic environment (Studds and Wright, 2007). The type of noise produced can include continuous (Hildebrand, 2009) and impulsive noise (Radford *et al*., 2016), and it varies depending on the noise source. Variation in noise disturbance also results from different sources producing different sound frequencies (Curtis *et al*., 1999; Yusof and Kabir, 2012). Varying noise sources, along with the limitations of a species' hearing frequencies, means noise can affect aquatic species differently depending how they use and interpret noise, whether it is for communication (Putland *et al*., 2017), reproduction (de Jong *et al*., 2020), navigation (Simpson *et al*., 2008), predator avoidance (Popper and Hawkins, 2019), or feeding (Leduc *et al*., 2021). These behaviours are directly linked to fitness and noise can directly affect survival, for example masking the noise of an approaching predator (Popper and Hawkins, 2019), leading to a slower response (Simpson *et al*., 2016). Response to noise may also vary within a group due to individual differences, including animal personality (Harding *et al*., 2019). Understanding the role of personality variation in response to noise will avoid misinterpretations of the results and making inaccurate predictions. It is important to consider all these varying factors when studying the response of animals to noise disturbance.

There are a range of behavioural responses which can help mitigate the effects of noise including avoidance and habituation. An avoidance response is where a species will avoid a stimulus which will lead to negative consequences, for example avoidance of an anthropogenic noise pollutant may occur through species shifting to different environmental niches (Rogers et al., 2019). The change in environment might affect food, competition, communication and habitat resources (Rogers et al., 2019). Avoiding an aversive sound stimulus may cause a reduced foraging effort, consequently leading to reduced food consumption (Luo *et al*., 2015). Avoidance has been shown by zebrafish as they move away from an active speaker during sound treatments (Shafiei-Sabet *et al*., 2016). Moving to quieter areas can lead to an increased chance of survival for prey (Brehmer *et al*., 2019), as they can detect the predation risk in quieter areas. When individuals do not show an avoidance response, anthropogenic noise has also been shown to reduce the antipredator response (Ferrari *et al*., 2018). Noise pollutants may affect predators and prey differently, and therefore affect the predator-prey interactions (McCormick *et al*., 2018). Predator response to a noise pollutant can include a reduced foraging efficiency, for example the greater mouse-eared bat (*Myotis myotis*) showed increased prey search time with exposure to traffic noise (Siemers and Schaub, 2011). Understanding avoidance response to anthropogenic noise and how it may impact predator-prey interactions is important when looking at ecosystem level effects of anthropogenic noise (Proulx *et al*., 2019).

Alternatively, some species may develop a tolerance to noise over time. Through repeated exposure a species may become desensitised and have less or no response to the stimuli, showing habituation. For example a species responding to noise might not have an avoidance response once they learn the noise is not linked to a direct threat (Nedelec, et al., 2016). Species may also change how they communicate such as altering their calling patterns although it is unknown if fish can directly adapt their calling behaviour in response to anthropogenic noise, such as increases in sound pressure levels and length of calls; this behaviour has been studied in marine mammals, amphibians and birds (Ladich, 2019). Some fish adapt to the increased noise by altering their behaviour when they would usually use audio cues, such as the African cichlid fish who use more visual displays during sound treatments in male-male dominance interactions (Butler and Maruska, 2020). Here the species have learnt to adapt to the sound, not perceiving it as a threat but having to find alternative ways to try and protect their territory which they use for reproduction, food, and shelter. Some research on vocal communication shows that certain species do not appear to have their communication disrupted in the face of anthropogenic noise (Higgs and Humphrey, 2020), so they do not need to adapt. Although adaptation may seem positive it depends on the environment. In some cases it could result in a fitness costs, including increased predation risk as communication signals change, and the associated metabolic costs to change signalling patterns (Read *et al*., 2014). Having sufficient long-term studies to test these effects is also key. It may take time for fish to adapt, and an initial response to a human-generated sound may not be representative of its long-term effects. Nedelec *et al.* (2016) reported increased tolerance of coral reef fish to noise. After two days the hiding rate of the fish decreased, and the ventilation rate did not increase as much after one to two weeks compared to control groups exposed to ambient noise. Other studies also showed signs of increased tolerance shown by ventilation rate reducing from the first noise exposure (Radford *et al*., 2016). Habituation must be considered in long-term studies to determine whether an initial rapid recovery rate leads to habituation (Bruintjes *et al*., 2016). Ensuring that sound studies are conducted over long-term periods will create a fuller picture on the impact of noise on fish species.

Sound can be recorded by both particle motion and sound pressure and fish can respond differently to sound pressure and particle motion (Popper and Hawkins, 2018), therefore it is important to record both in experimental setups when looking for the effects of noise on fish. Particle motion is the process in which particles are moved backwards and forwards in an oscillatory motion, compared to sound pressure which is the difference between the sound pressure at a point and the environment around it (Nedelec *et al.*, 2016). Particle motion and sound pressure only have a relationship under certain conditions (Nedelec *et al.*, 2016), so one cannot be reliably predicted from the other, particularly in shallow tank environments where the sound source is in the near field (within 2 wavelengths of the sound source) (Popper and Fay, 2011). It is particularly important to measure both in tank setups due to the tank walls, as sound waves and particles interact with the walls which may change the effect of the noise (Campbell *et al*., 2019). Particle motion recording techniques have been used in research however the equipment has not been small enough to allow recording in small tank environments, so previous research is often missing this data to provide the full context for how the responses that are recorded are related to the noise. Where possible, recording particle motion will allow a deeper understanding of responses to noise and if there are significant differences between responses to sound pressure and particle motion (Nedelec *et al*., 2016).

Fish hearing is a highly researched topic however there are only a few species with detailed research on their hearing range and mechanisms, as there is large variation between species hearing mechanisms (Wiernicki *et al*., 2020). Hearing generalists and specialists have previously been used to define different species based on their adaptations for hearing, with specialists having more advanced hearing structures including Weberian ossicles (Popper and Fay, 2011), allowing them to detect sound pressure as well as particle motion. Hearing generalists commonly detect sound as particle motion using the otolith organ (Popper and Hawkins, 2018), where it acts as an accelerometer, moving at a relative manner to a receptor. However, it is not known whether hearing generalists, without the specialist hearing functions, can detect sound through pressure. Studies have shown the potential use of the swim bladder for increased hearing frequency range and detection of noise through sound pressure (Popper and Fay, 2011; Wiernicki *et al*., 2020) so fish cannot be so easily categorised into just two groups (Popper *et al*., 2022). Due to the challenge in categorising species into distinct groups based on sound detection, future studies should measure both particle motion and sound pressure when studying the impact of noise (Popper and Hawkins, 2018)

Trinidadian guppies are a sexually dimorphic freshwater fish, commonly used as a model organism due to their short life cycle, ease of breeding and small size, making them a convenient species to maintain in an aquarium environment. Guppies have been used in behavioural studies (Moniruzzaman *et al*., 2018; W. T. Swaney *et al*., 2015), and have shown repeatable individual variation to stressors (Houslay *et al*., 2018). My study focused on the effect of impulsive white noise on guppy behaviour in laboratory conditions. Sounds can be categorised as impulsive or continuous, and impulsive sound was chosen to mimic an anthropogenic noise pollutant such as construction work. White noise was played with a gradient in the tank to study for any avoidance behaviour in response to the impulsive noise. Guppies were chosen as a model organism due to the limited research on their response to sound, where they are otherwise a well-studied organism (Auld *et al*., 2016; Faria *et al*., 2010; Reznick *et al*., 2008; D. Romano *et al*., 2020). White noise was used as an explanatory variable as guppies are a freshwater species so could experience a range of sources of anthropogenic noise disturbance, and white noise encompasses all frequencies of noise across the spectrum of sound. It is also easily generated through sound software.

The initial hypothesis was that guppies would have a freeze or startle response to the impulses of noise compared to their otherwise continuous swimming behaviour; however, this response was not observed during preliminary trials. Two alternative hypotheses were proposed. Firstly, the guppies would develop a tolerance of the noise over time, adapting to the white noise treatment and hence showing reduced avoidance of the louder areas of the tank through the trials and over the week. The second was that guppies would learn the location of the sound source and respond by avoiding the louder areas of the tank across the trials over time.

2.3 Materials and Methods

2.3.1 Ethics Statement

All experimental methods were in accordance with national regulations on animal care and were approved by the University of Bristol Animal Services Ethical Committee (UIN/17/060 and UIN/17/075). Exposure to the noise playback was limited to 15 minutes per trial to minimise stress.

2.3.2 Experimental Animals

Trinidadian guppies were collected from Trinidad in April 2019 from a high-predation site in the Guanapo river. They were exported to the John Krebs field station, University of Oxford, where they were reared for three generations with a specialised breeding plan to maintain genetic diversity. The guppies were moved to the Southwell Street aquarium, University of Bristol, in December 2020. Water temperature was kept at 25˚C ±1, with an average pH of 8.5 (range 7 – 9), and guppies were kept on a 12:12 hr light : dark cycle, with approximately 100 – 150 fish in the 90 L glass tanks.

Female guppies were haphazardly caught 68 - 72 hours prior to their first experimental trial (standard body length range 18 – 33 mm, mean 25.2 mm, measured after the trials using ImageJ, Java1.8.0_172 (Schindelin *et al*., 2012)). Medium to large guppies were selected to allow for accurate tracking and to prevent any potential dominance effects with greater inter-individual size variation (Borg *et al*., 2012). Using larger females also reduced the likelihood of selecting juveniles which have been shown to have different shoaling preferences to adult fish depending on their age (Ledesma and McRobert, 2008). They were held in experimental groups of 8 fish in fry nets (16 x 12.5 x 13.5 cm) suspended within their holding tanks, with number labels for each group randomly allocated. Group size was limited to eight because of the reduced accuracy of the tracking software with larger shoals. Female fish were selected as females have a greater tendency to shoal than males (Richards *et al*., 2010). Experimental fish were fed ZM Granular pellets (© Copyright 2021 ZM Fish Food and Equipment) while kept in the fry nets, rather than their usual varied diet of live and fresh food (including frozen blood worms, cyclops, mysis, brineshrimp and live banana worms) to avoid any confounding effects of food type. To avoid variation in hunger before and during testing, the fish were fed at the end of each day, after all trials for that day had been conducted.

2.3.3 Noise Treatments

Noise treatments were generated in Audacity (Audacity ®, Version 2.4.2). Two 30-minute tracks were created: Track A consisted of 15 minutes impulsive white noise with a 1 second impulse ramped up and down (slowly increasing/decreasing the volume to avoid the speaker 'popping'), at 10 second intervals, followed by 15 minutes silence playback. In Track B, the order of the white noise and silence was switched (i.e. 15 minutes silence followed by 15 minutes impulsive white noise). Using a generated sound for the silence treatment rather than turning the speaker off controlled for any effect of the speaker such as electro interference (Currie *et al*., 2020; Pieniazek *et al*., 2020). A high pass filter was applied to all the tracks to remove sounds below 100 Hz due to the frequency response of the speaker. Three versions of each track were created to control for pseudoreplication and the treatment track was randomised for each group using RStudio (version 1.4.1106; R Studio Team, 2021).

The soundtracks were played on a SanDisk Clip Jam MP3 player through a DNH Aqua-30 under water loudspeaker (frequency response 100 - 10,000 Hz) connected to a Maplin 12 volt battery. The speaker was submerged below the experimental tank facing upwards under the right-hand side of the experimental tank to create a sound gradient (Figure 1) and suspended using elastic on a plastic structure to minimise vibrations through the tank. The speaker was submerged to be more representative of the acoustic exposure fish would usually be exposed to.

Sound recordings were analysed in MATLAB v2013a to calculate power spectral density across the frequency range 100-2000 Hz (Figure 2). To quantify the sound gradient in the arena, hydrophone recordings were taken at 10 cm intervals throughout the tank for the white noise and silence playback using a HiTech HTI-96-MIN hydrophone and Zoom H1n recorder on Level 3 and Level 7, respectively. The recordings were then cropped to 8 second .wav file recordings for each point through Audacity ® (version 2.4.2). These files were analysed with MATLAB v2013a using the paPAM analysis package (Nedelec *et al*., 2016), with a bandpass filter applied between 100 and 2,000 Hz, which covers the hearing sensitivity of fish hearing generalists (Popper and Fay, 2011). The white noise gradient ranged from 140.89 to 129.29 dB and the silence 77.57 to 73.70 dB, within the arena (Figure 3) with the mean sound pressure in the holding tanks at 96 dB. The locations of the hydrophone recordings were extracted from video recorded from above so pixel coordinates could be calculated for each hydrophone recording using ImageJ (Schindelin *et al*., 2012).

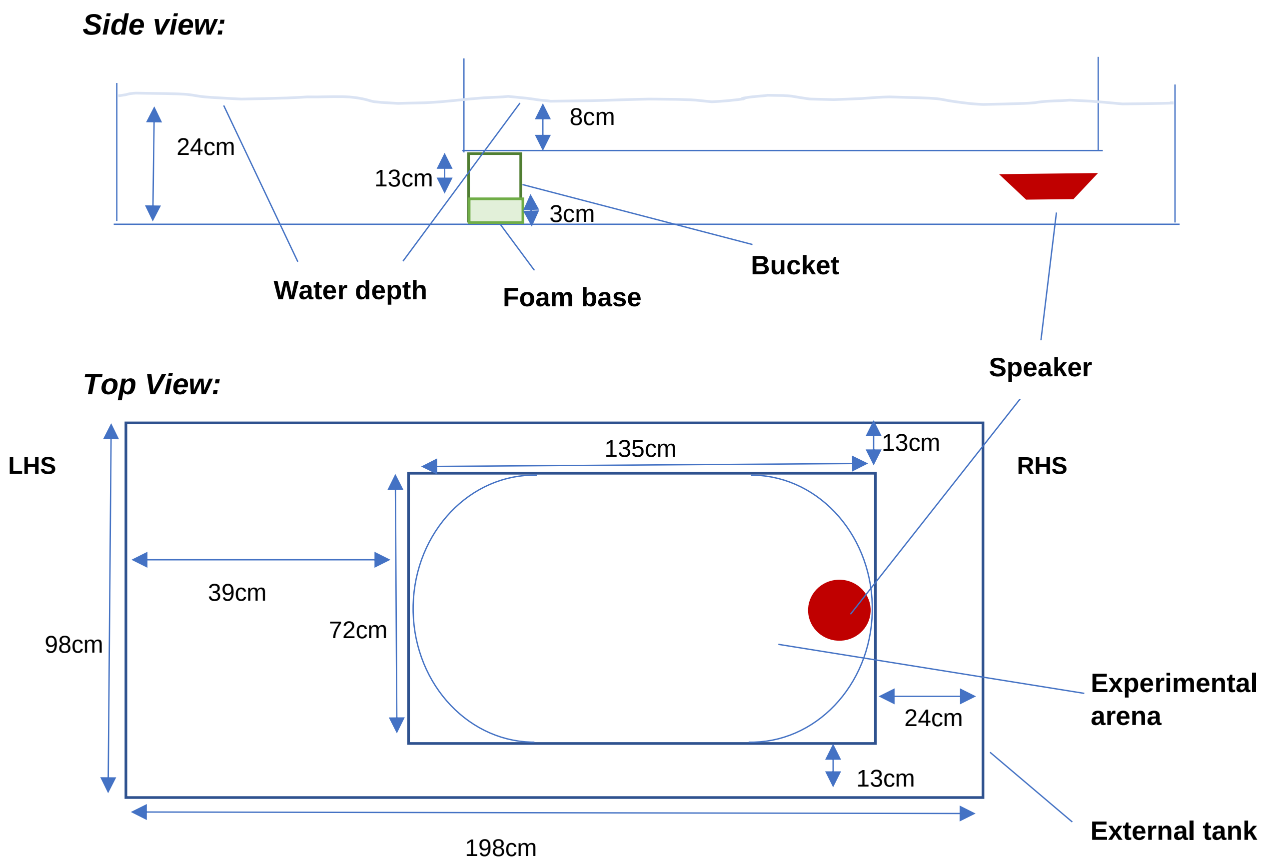

Figure 1: *A diagram of the tank setup (not to scale). Dimensions from the side and top view of the tanks. Speaker diameter 13.7 cm and depth 5.3 cm. Buckets to suspend internal tank on a foam base in green raising the internal tank 16 cm.*

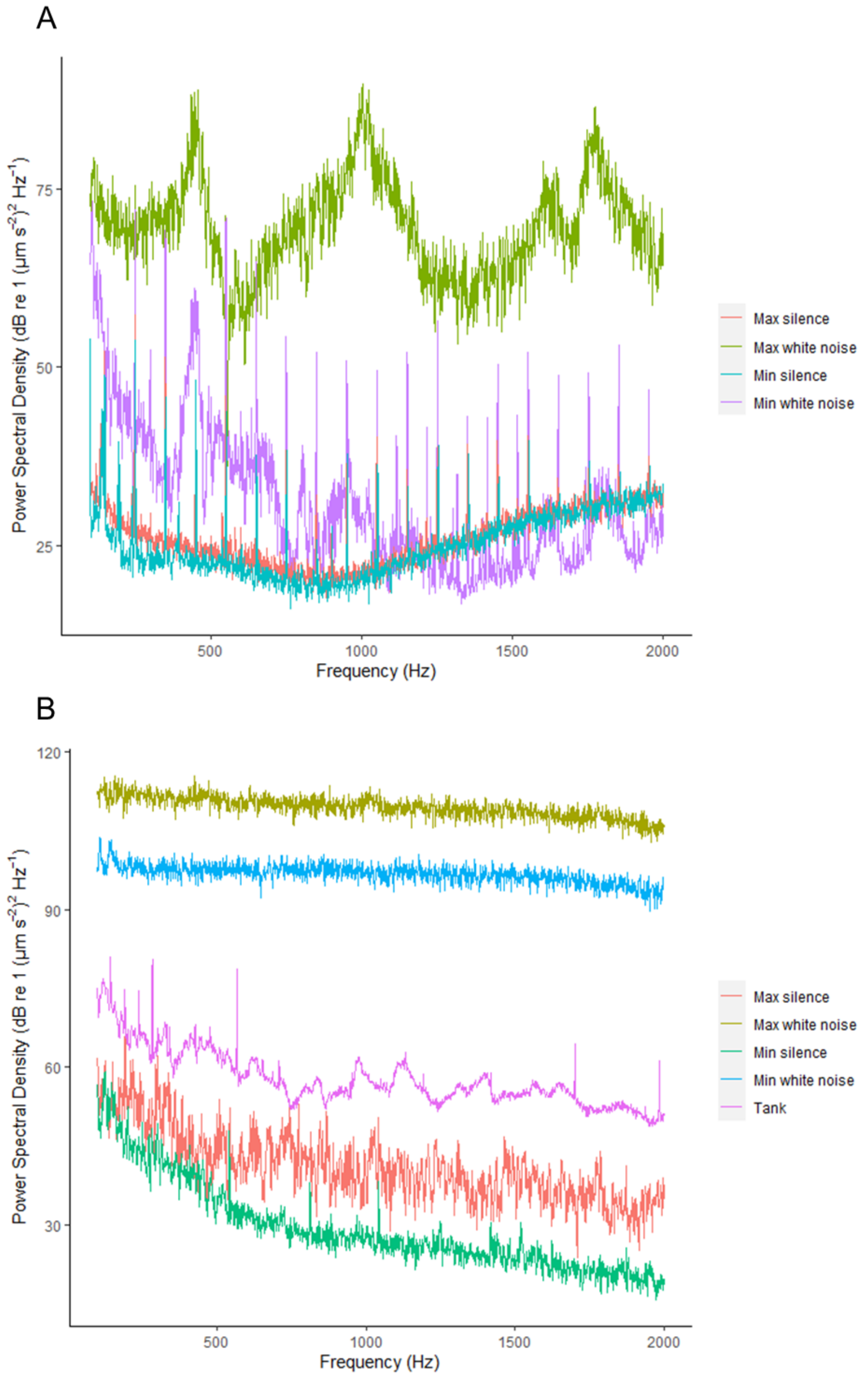

Figure 2: *Spectral content for A) particle motion and B) sound pressure at the maximum and minimum recorded values of white noise and silence in the experimental arena, including the ambient tank noise in the guppies holding tank for sound pressure (labelled Tank). Sound was analysed in MATLAB v2013a using the paPAM analysis packages.*

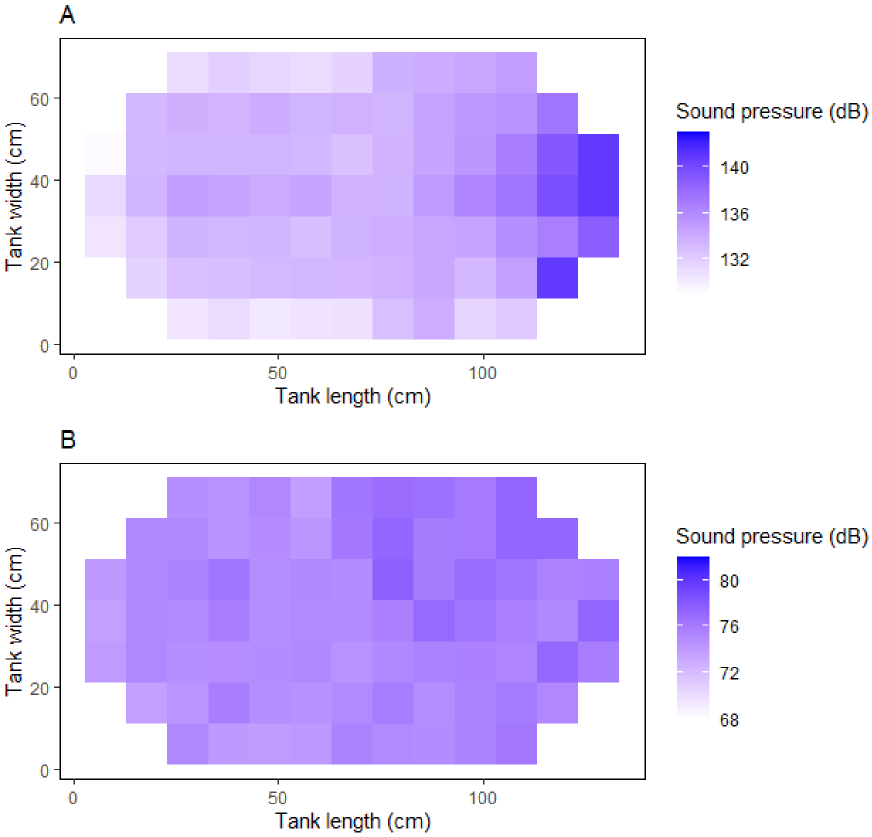

Figure 3: *Heat maps showing recorded sound pressure level (dB) at 10 cm intervals in the experimental arena of the treatment sounds generated in Audacity. A) 10 second hydrophone recordings of a continuous white noise playback. B) 8 second hydrophone recordings of a silence playback. The range of the legends has been standardised to 14 dB for both white noise and silence.*

Accelerometer recordings were taken to measure the particle motion gradient within the tank using a M20-40 Geospectrum Technologies Inc. accelerometer and Zoom H6 recorder, Level 5 for white noise and Level 6 for silence. Recordings were taken at 20 cm intervals where possible, limited by the size of the accelerometer in the small shallow arena, facing towards both the left and right hand side of the tank (Figure 1), for both the silence and white noise treatments. Only the Z-axis was used to record particle motion as the accelerometer had to be horizontal in the shallow arena. The accelerometer recordings were cropped in Audacity ® (version 2.4.2) to 10 seconds for the silence treatment, and a 1 second impulse track and 30 seconds (3 impulses) track for the white noise treatment. Recordings were analysed with MATLAB 2013a using the paPAM analysis package. Mean particle motion over 100-2000 Hz ranged from 69.71 to 32.62 dB re 1 µm s^{-2} in white noise and 25.17 to 26.26 dB re 1 µm s^{-2} in silence (Figure 4). Particle motion can be recorded as acceleration, velocity or displacement with no standard unit agreed. We used the unit for acceleration (dB re 1 µm s^{-2}) because it has been found the most relevant to fish hearing systems (Nedelec *et al*., 2016).

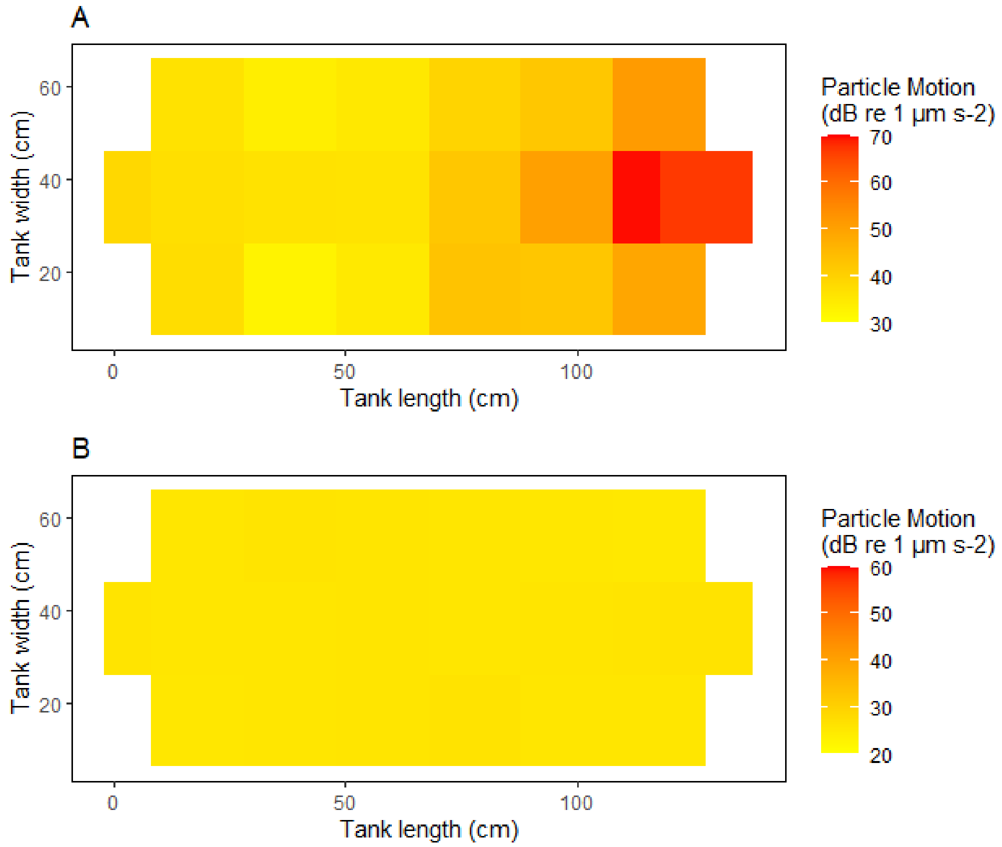

***Figure 4**: Particle motion recordings (dB re 1 μm s^{-2}) at 20cm intervals throughout tank with accelerometer recording horizontally along the tank length. A) recordings from 30 seconds of impulsive white noise. B) recordings from the silence playback.*

2.3.4 Experimental Design

The experimental arena, made from acrylic glass, measured 135 x 72 cm, with a depth of 8cm. The experimental arena was an oval shape to remove the possibility of fish sheltering in corners which is generally their preference, made by blocking the corners with curved white foamed PVC. The experimental tank was positioned within a larger tank of 198 x 98 cm on four buckets, 13 cm tall, one placed in each corner, filled with gravel on 3 cm of foam to minimise vibrations to the experimental arena. As seen in Figure 1, the experimental arena was placed to the right in the external tank, with the speaker under the right-hand side. The external tank was held off the ground on a metal frame to minimise vibrations from the floor and was surrounded with white sheeting to avoid any visual disturbance (Figure 1). Lighting was provided by overhead fluorescent lights with sheeting over the top of the frame to reduce reflections in the tank and to create an even light source from above. A Panasonic 4K HC-VX870 camera was positioned 142 cm above the experimental arena, recording in 4K video (3840 x 2160 pixels) with a frame rate of 29.97 frames per second (fps), connected by Wifi to the Panasonic Image App (version 1.10.19) on a Samsung phone to start the recordings with no disturbance.

The room temperature was set to 26 ˚C. System water was used in the experimental arena, maintained at 25 ± 1 ˚C by the ambient room temperature and a Hepo HP-608 300W Aquarium heater in the external tank. 15-20% water changes were carried out at the start of each week and water quality tests carried out weekly (pH, ammonia, nitrite and nitrate). When the fish were not in the experimental arena, Aquarium Systems Duetto 50 filters were used to maintain the water quality.

Trials were carried out between 24th May 2021 and 29th June 2021. Up to seven groups of eight fish were tested per week, with 22 groups in total. Each group of fish was exposed to a 30 minute treatment once per day on four days, being tested on two consecutive days with a day's break in between. The groups were tested in a random order within each day to control for time of day effects. The sound treatment was alternated for each group on consecutive days between Track A and Track B, with half the groups starting day 1 on Track A and half on Track B to control for the order of the playbacks.

Fish were collected from the fry nets in the holding tanks and transferred into the experimental arena where they were left to acclimate for 15 minutes with the speaker disconnected from the battery. The speaker was then connected, and the playback played through the mp3 player, with the video recording starting at the same time as the sound treatment and being stopped after 30 minutes. After the trial the guppies were returned to their fry nets in the holding tanks.

2.3.5 Video Analysis and Data Processing

Each 30 minute recording from the overhead Panasonic camcorder was saved as multiple video files, so were stitched together using Shotcut (version 21.05.18) maintaining the frame rate of 29.97 and resolution of 3840 x 2160 pixels. Recording from above allows two-dimensional analysis. Previous studies have compared results from two versus three-dimensional analysis for leadership and predator behaviour, and have shown that the results from two dimensional data are representative of those based on three-dimensional data

(Romenskyy *et al*., 2020; Watts *et al*., 2017). Together with the shallow depth of the arena, two-dimensional analysis was considered sufficient.

Videos were then tracked with MATLAB 2014a using idTracker (version 2.1; Pérez-Escudero *et al.*, 2014), using the same reference code for each group per week in order to match the identity of each individual in the different videos of that group across the week. The trajectories give x y coordinates for each fish per frame throughout the trial. Frames including missing data removed before analysis. Where frames for one fish were removed due to missing data, the data for the whole group was also removed for that frame. Frames were removed when the fish moved more than 30 pixels per frame (approximately 30cm s^{-1}) because this was likely a result of tracking error as it was too far for a fish to travel in a given frame. The tracking trajectories were smoothed using a Savitzky-Golay filter using R package *Trajr* (McLean and Skowron Volponi, 2018).

To predict the sound exposure through the tank, firstly linear regressions were carried out for hydrophone and accelerometer recordings, using the relationship between the recorded values and the x and y coordinates where they were recorded. The x coordinate data were transformed by third order polynomial and the y coordinate data were transformed by second order polynomial. Then the ‘predict’ function in R was used with this model to fit the sound pressure and particle motion values for each fish coordinate in the experimental arena, in both the white noise and silence treatments (Figure 5 and 6).

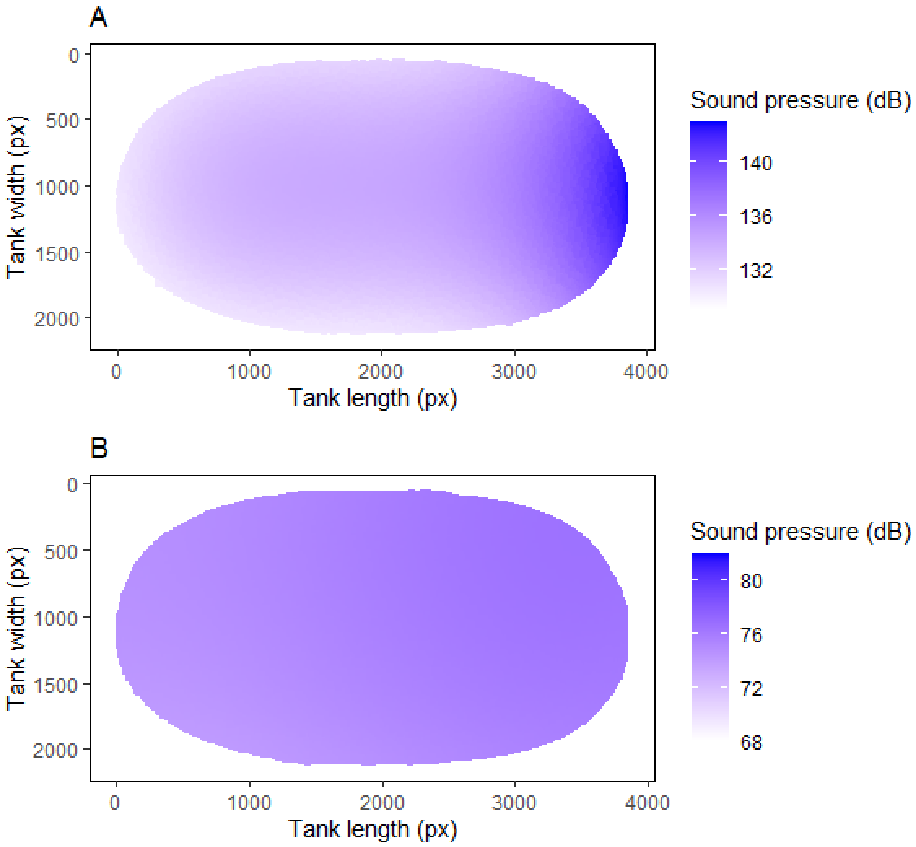

Figure 5: *Heat maps showing the predicted sound pressure (dB) at each coordinate in the tank, using hydrophone recordings analysed with a linear polynomial model. A) white noise treatment, maximum predicted sound 143 dB, minimum 130 dB. B) silence treatment, maximum predicted sound 77 dB, minimum 74. (100 pixels = 5.4 cm)*

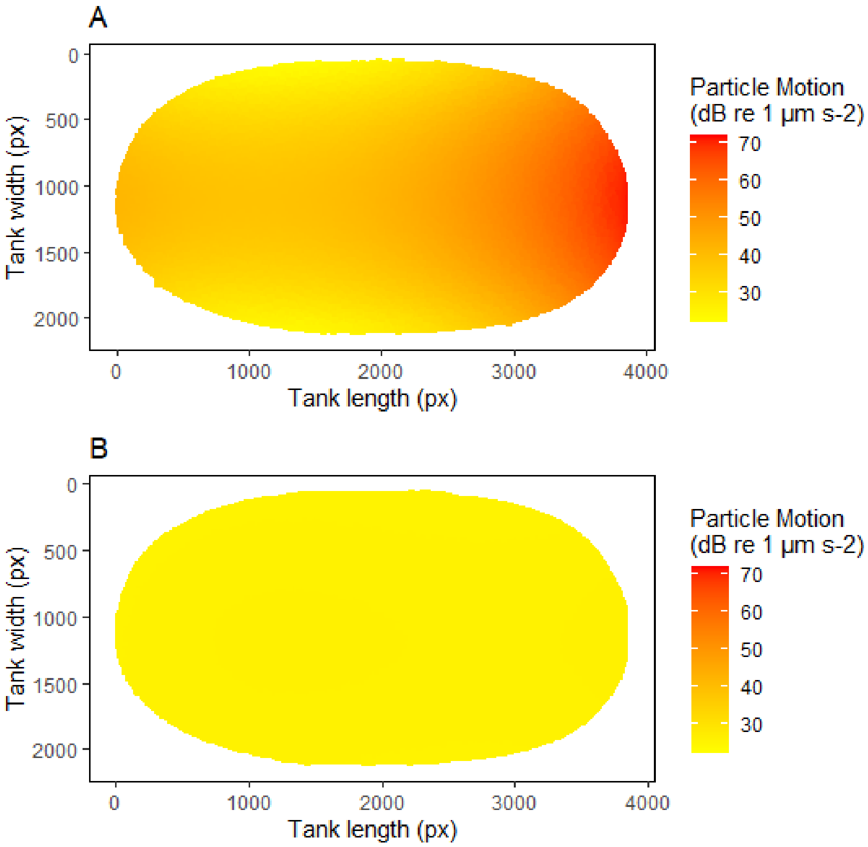

Figure 6: *Heat map showing predicted particle motion exposure (dB re 1 µm s^{-2}) at each coordinate in the tank, using accelerometer recordings analysed with a linear polynomial model. A) white noise treatment maximum particle motion 71.3 dB re 1 µm s^{-2}, minimum 22.9 dB re 1 µm s^{-2}, B) silence treatment maximum particle motion 25.9 dB re 1 µm s^{-2}, minimum 25.2 dB re 1 µm s^{-2}. (100 pixels = 5.4 cm)*

The distance of each fish from the speaker (the loudest hydrophone recording in the tank) was calculated in R after establishing the pixel coordinate for the loudest location in ImageJ. A Spearman's correlation was conducted on particle motion and sound pressure with a correlation coefficient (r_s) of 0.62 indicating a positive association (Figure 7). The final dataset included the distance from the speaker per frame, the predicted sound pressure exposure (referred to from here as sound pressure) and details of each trial including treatment type (white noise or silence), time of day of the trial, day of data collection (1-4) and whether the white noise treatment was first or second in the 30 minute trial. Sound pressure and distance from the speaker data were analysed using an auto-correlation function (ACF) for a random sample of single fish. ACF allows assessment of temporal autocorrelation to determine how many frames apart it took for an individual's data to be temporally uncorrelated, using a 95% confidence interval and based on a null value of zero (no autocorrelation). From the sample, it was established that data points over three seconds (~90 frames) apart were not correlated. Due to the large dataset, 10 second time periods were chosen to calculate the mean of sound pressure, and the distance from the speaker, for each fish per trial. After down sampling, the final white noise dataset had 54,874 data points and the silence dataset had 54,392. These calculated means were then also analysed using an ACF to check for correlation again and the data was no longer correlated (Figure 8). This time-averaged dataset was then used to carry out the statistical analysis.

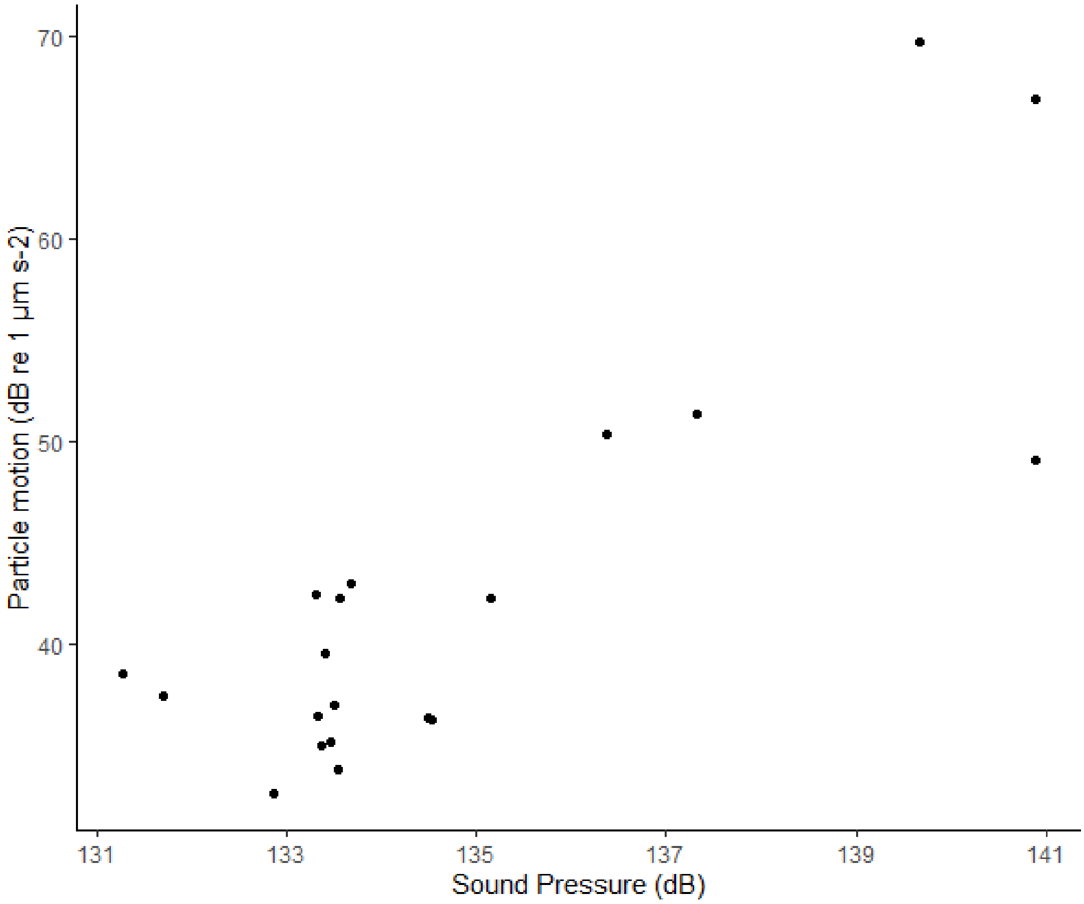

Figure 7: *A plot showing a positive correlation between sound pressure and particle motion of the white noise playback, recorded in the experimental arena at 20 cm intervals.*

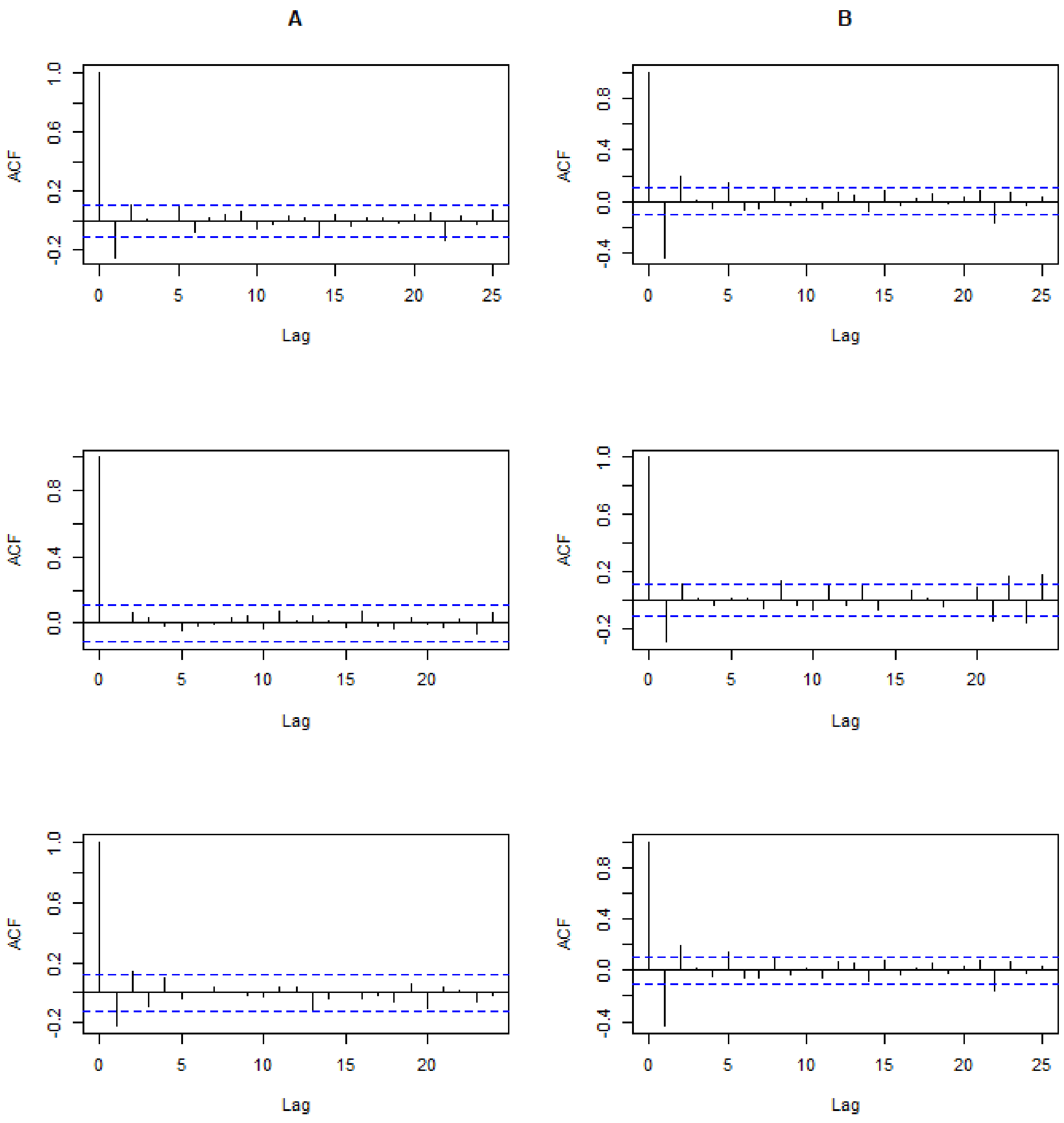

Figure 8: *ACF plots of the data down sampled to every 10 seconds, where 1 lag is 10 seconds. A) predicted sound and B) distance from the speaker, where each row is a different individual fish from a random trial. The dashed blue line shows the 95% confidence interval.*

2.3.6 Statistical Analysis

All analysis was carried out in RStudio (version 1.4.1106; R Studio Team, 2021). To test what level of sound fish were exposed to during the white noise treatments based on their location in the tank, linear mixed models (LMM) and the logit-link function were used (package *glmmTMB;* Brooks *et al.*, 2017) with a Gaussian error distribution. The response variable was sound difference, which was the mean sound pressure at each frame, minus the minimum sound exposure in the tank. Models were run to test the effect of the fixed effects (week, order of the trials throughout the day, day (one to four) of the week, time throughout the trial, and whether white noise was the first or second treatment in the 30 minute trials) on the response variable, sound difference. The response variable was log transformed to meet model assumptions because it was positively skewed. Model assumptions were tested using Q-Q plots for the assumption of normality and dispersion of residuals was verified using the DHARMa residual diagnostics package (Hartig, 2020). Removing each fixed effect individually from a model including all fixed effects and comparing corrected Akaike Information Criterion (AICc) values between models, produced six models to allow for a model comparison approach. The most likely model has the AICc value of 0 and each model within 2 units could be considered a similarly good fit (Harrison *et al*., 2018), and those models within that range that have the least parameters are preferred. When comparing the AICc values between models it can be established which variables have an influence on the response variable. To determine if there were consistent group or individual differences in sound exposure, AICc values were also used to compare the most likely model with and without random intercepts, individual and group, to determine their effect.

A LMM with a Gaussian error distribution was also used to analyse the distance of an individual from the speaker as a response variable. Distance from the speaker was used based on the indication of a negative association of distance from the speaker and predicted sound in the white noise treatment (Figure 9), with a Spearman's correlation coefficient (r_s) of -0.84. Distance from the speaker was used to compare the results from the white noise treatment to the silence treatment. The fixed and random effects were the same in the models analysing the effects on sound exposure but also included treatment type as a fixed effect. The models were quantified by comparing the AICc values as described above. Again model assumptions were also checked using the DHARMa package in R (Hartig, 2020). To determine if there was an interaction between treatment and time throughout the trial and day of the week, AICc values were also used to compare the most likely model with and without the interaction terms.

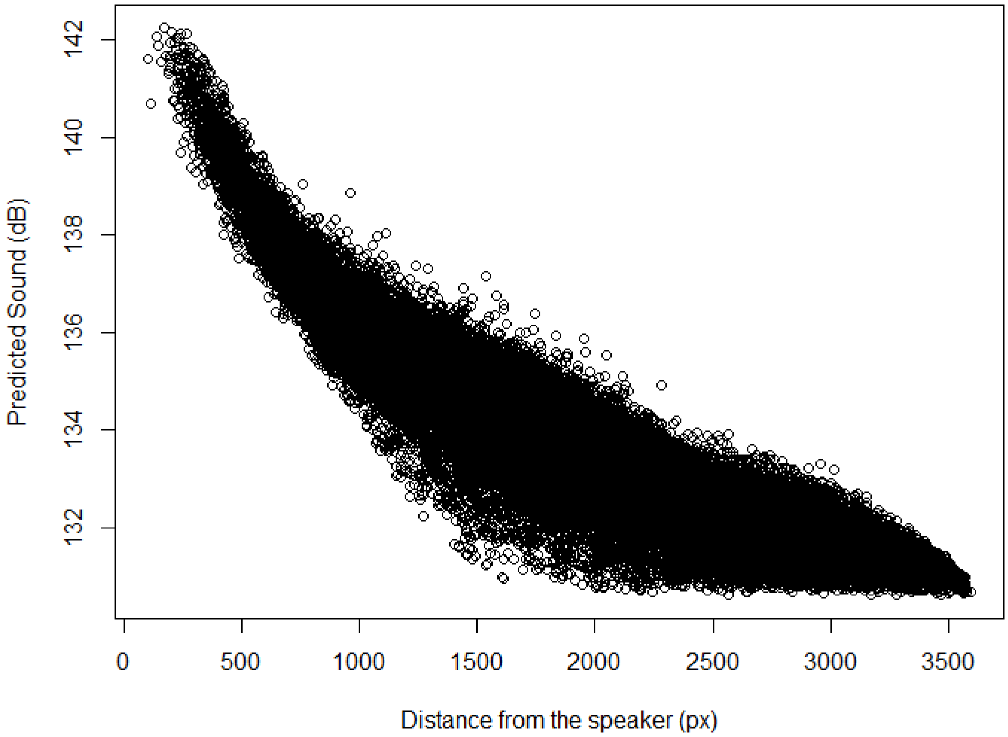

Figure 9: *A plot showing a negative correlation between predicted sound and the distance from the speaker.*

2.4 Results

2.4.1 Noise exposure level during white noise exposure

To determine which fixed effects had an impact on individuals' sound exposure in the white noise treatments of the trials, seven LMMs were compared using the difference in their AICc values (Table 1). Removing the fixed effects of week and time of day reduced the AICc compared to the model with all fixed effects included (the full model; Table 1), suggesting that week or the time of the day do not have an impact on the sound exposure of fish. The time within the trial had an effect on sound exposure (Table 1) as the model with time removed was more than 2 AICc units greater than the full model. Throughout the 15 minute trials, the fish tended to move to quieter areas of the tank, although this is predicted to be by less than 0.5 dB (Figure 10). The full model with day included was more likely than when it was removed (Table 1); over the course of the test days (1 to 4), the fish tended to be exposed to louder sounds within the tank (Figure 11). The order in which the fish were exposed to white noise (first or second 15 minutes in the trial), also influenced the sound pressure (Table 1). When white noise was the first treatment, the fish tended to spend more time in louder areas of the tank, compared to when the white noise treatment followed the silent treatment (Figure 12).

To quantify the effects of the random terms, we ran the most likely model (Table 1) with and without the random terms to test for the impact of group and individual variation, and hence whether these between-subjects differences were consistent. Removing the random terms group and individual separately and together, led to models with an AICc value greater than 2 units more than the most likely model, suggesting both individuals and groups do consistently respond differently to sound exposure (Table 2).

Table 1: *The difference in the corrected Akaike Information Criterion (△AICc) scores for the model with sound pressure as the response variable and random effect of individual nested in group. NA represents the model with all explanatory variables. △AICc shows the difference between the model and the best supported model (△AICc = 0). d.f. is degrees of freedom.*

Explanatory variable removed from the model	△AICc	d.f.
Week	0	8
Time of day	0.5	8
NA (full model)	1.8	9
Day	70.5	8
First or second within a trial	90.9	8
Time throughout trial	102.8	8
Null model (no fixed effects)	256.1	4

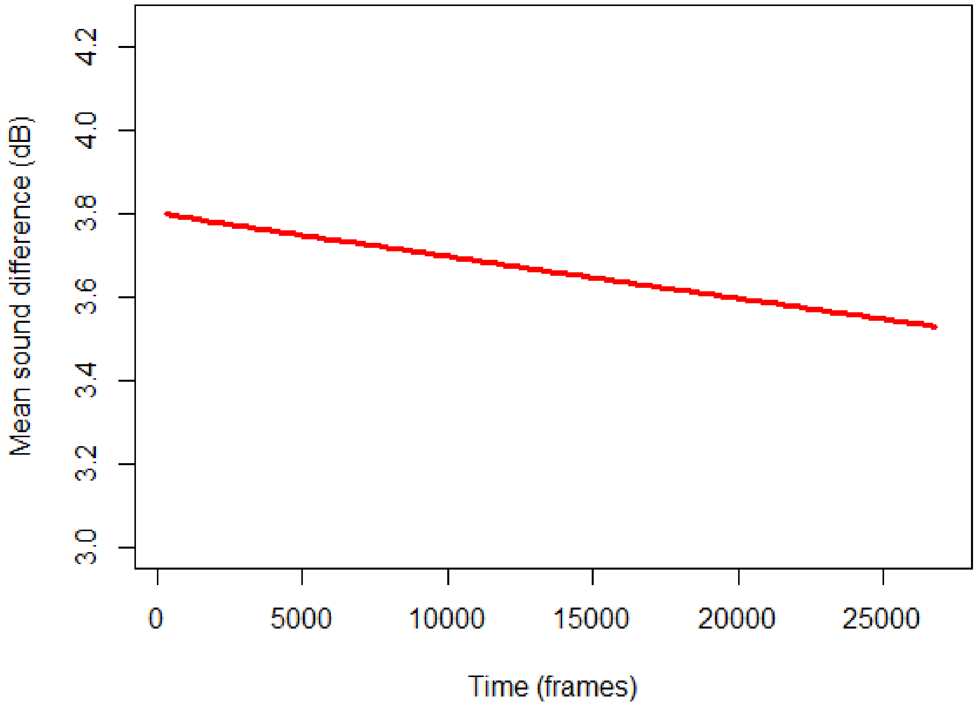

Figure 10: *Fixed effect estimates extracted from the linear mixed model predicting the mean sound difference over time for fish during the white noise treatment. Mean sound difference is the difference between the mean sound pressure at each time frame, minus the quietest predicted sound in the treatment.*

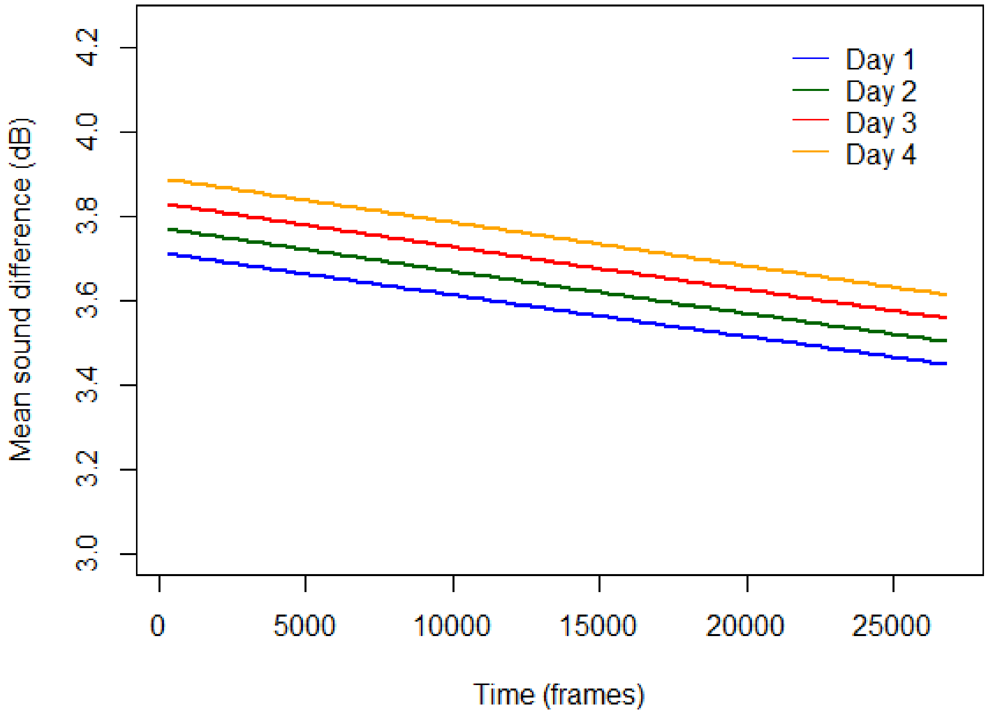

Figure 11: *Fixed effect estimates extracted from the linear mixed model predicting the mean sound difference over time for fish during the white noise treatment. The intercepts for the fixed variable day, are plotted separately.*

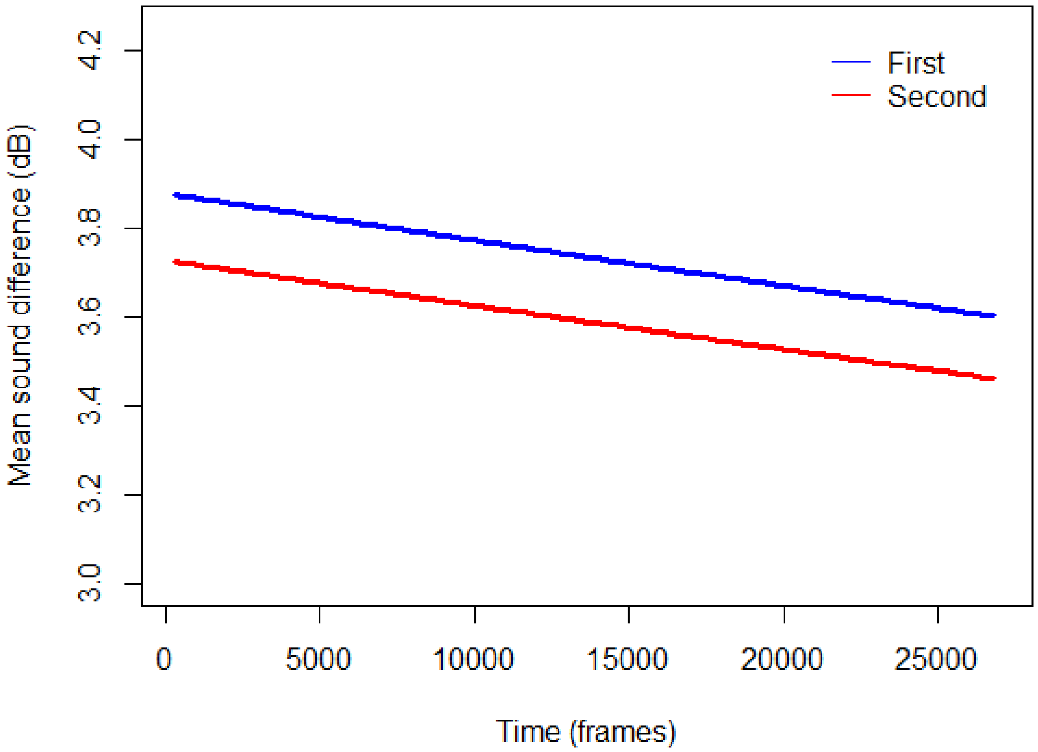

Figure 12: *Fixed effect estimates extracted from the linear mixed model predicting the mean sound difference over time for fish during the white noise treatment. The intercepts for the fixed variables, first or second are plotted as separate lines.*

Table 2: *Comparing the most likely model from table 1 with or without the random effect variables. Each row explains which random variable has been removed. △AICc is the difference in the Akaike Information Criterion and shows the difference between the model and the best supported model. d.f. is degrees of freedom.*

Random effect variable removed from the model	△AICc	d.f.
NA	0	8
Group	35.5	7
Individual	119.6	7
Individual and Group	356.8	6

2.4.2 Distance from the speaker

Eight LMMs were compared using the difference in their AICc values to determine the effect of the white noise treatment versus the silence control treatment on the average distance of the fish from the speaker (Table 3). The fish on average moved further away from the speaker during the 15 minute trials (Figure 13; Table 3). Removing the treatment variable from the full model reduced the model likelihood by >2 AICc units, providing evidence that the treatment affected the fish's distance from the speaker. Fish in the white noise treatment were further away from the speaker (Table 3, Figure 14) by an average of 1. 5 cm compared to the silence treatment. The differences in AICc (Table 3) suggest that week and time of day did not have a strong effect on the distance of the fish from the speaker as the AICc values are less than the full model with all fixed effects included. In the second half of the 30 minute trials, the fish spent more time further from the speaker (Figure 15), supported by removal of order within the trial increasing the AICc by more than 2 units compared to the full model. From day 1 to 4, the fish became closer to the speaker, supported by the AICc values compared to the full model (Table 3).

The random terms (individual and group) were included and removed from the most likely model (Table 4). Removing the random terms led to AICc values greater than 2 compared to the most likely model, suggesting there are consistent differences between individuals and group responses to sound as measured by their distance from the speaker.

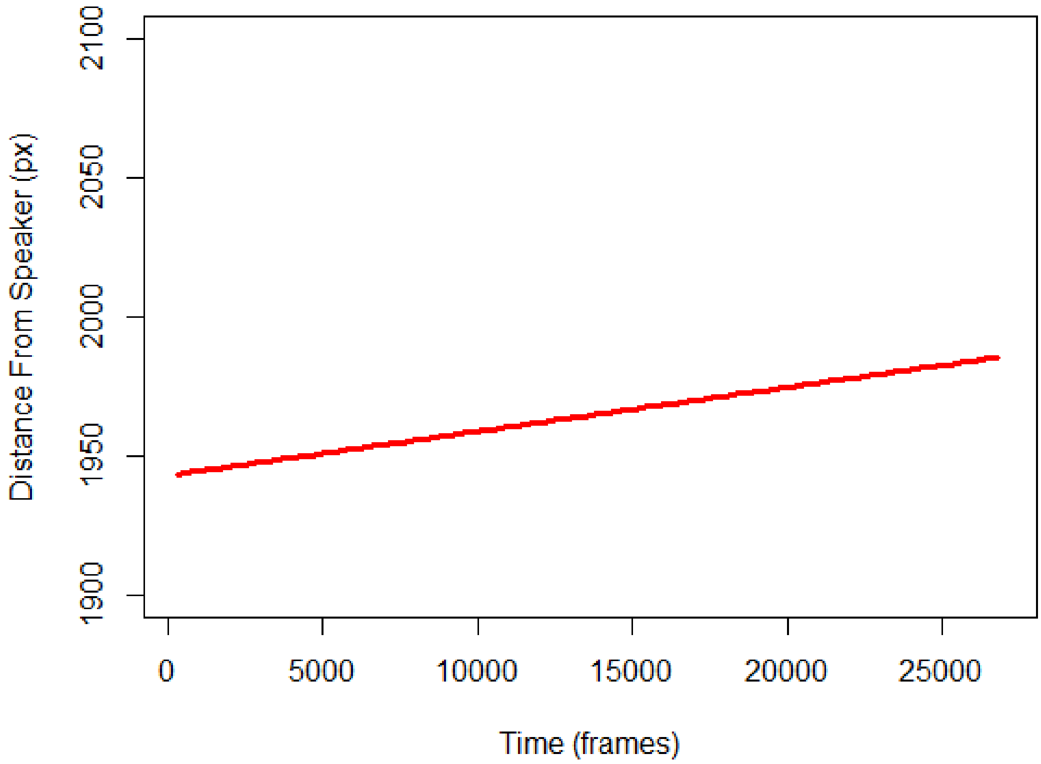

Figure 13: *Fixed effect estimates extracted from the linear mixed model predicting the distance from the speaker over time for fish during both treatments. (100 pixels = 5.4 cm)*

Table 3: *The difference in the corrected Akaike Information Criterion (△AICc) scores for the model with distance from the speaker as the response variable and the random effect of individual nested in group. NA represents the model with all explanatory variables. △AICc shows the difference between the model and the best supported model (△AICc = 0). d.f. is degrees of freedom.*

Explanatory variable removed from the model	△AICc	d.f.
Time of day	0	9
Week	1	9
NA (full model)	1.4	10
White noise or silence treatment	4.6	9
Time during the trial	28.4	9
First or second within a trial	32	9
Day	83.1	9
Null model (no fixed effects)	145.4	4

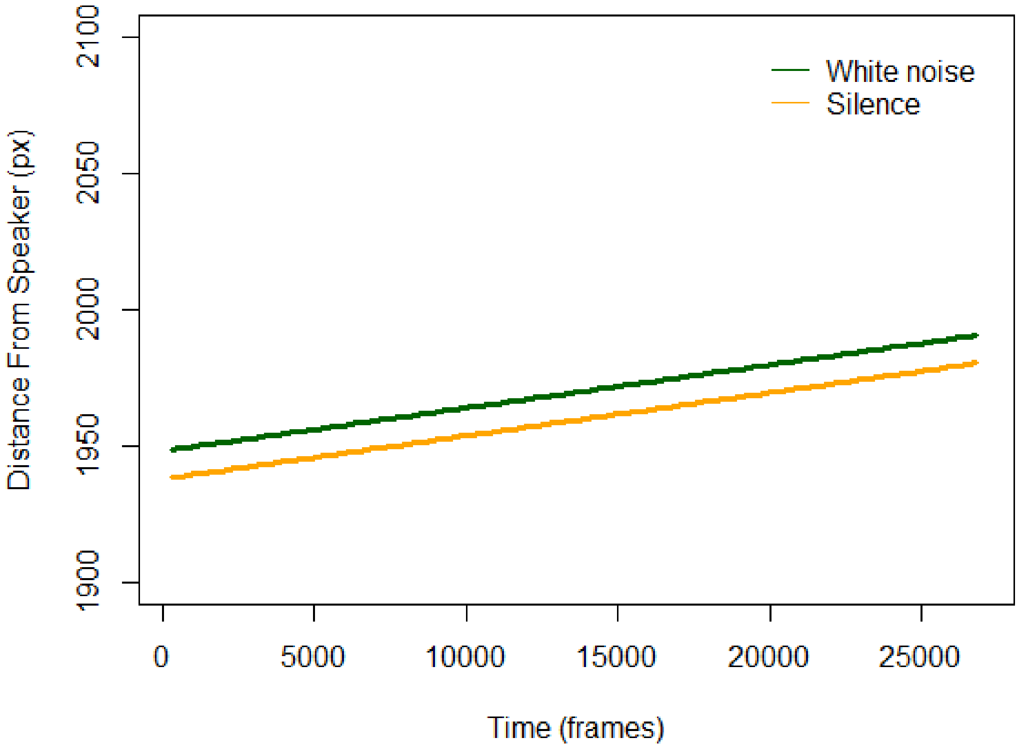

Figure 14: *Fixed effect estimates extracted from the linear mixed model predicting the mean distance from the speaker over time for fish during the white noise and silence treatments. The intercepts for the fixed variable treatment type, white noise and silence, are plotted separately. (100 pixels = 5.4 cm)*

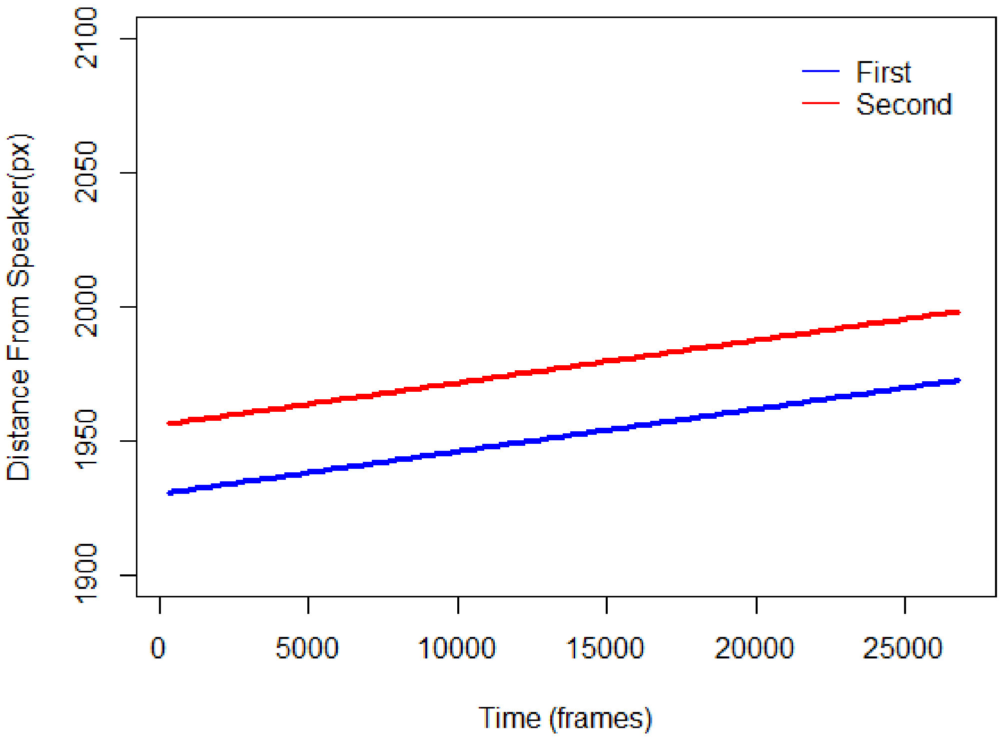

Figure 15: *Fixed effect estimates extracted from the linear mixed model predicting the distance from the speaker over time for fish during both treatments. The intercepts for the fixed variable looking at first or second treatment in the trial, are plotted separately. (100 pixels = 5.4 cm)*

Table 4: *Comparing the most likely model from Table 3 with or without random effect variables. Each row explains which random variable has been removed. ΔAICc is the corrected Akaike Information Criterion and shows the difference between the model and the best supported model. d.f. is degrees of freedom.*

Random effect variable removed from the model	**ΔAICc**	**d.f.**
NA	0	9
Individual	45.8	8
Group	50.2	8
Individual and Group	253.2	7

The interaction effects of treatment type and time throughout the trial, and treatment type and day of the week were included and compared to the most likely model (Table 5). The model with both interaction terms led to AICc values greater than 2 compared to the most likely model and the simplest model had no interaction terms, suggesting that there are no consistent differences between distance from the speaker in the white noise and silence treatments.

Table 5: *Comparing the most likely model from Table 3 (NA) with interactive effects. Each row explains which interactive effects have been added. △AICc is the corrected Akaike Information Criterion and shows the difference between the model and the best supported model. d.f. is degrees of freedom.*

Interaction effect added to the model	**△AICc**	**d.f.**
NA	0	8
White noise or silence treatment * Time during trial	1	9
White noise or silence treatment * Day	1.5	9
White noise or silence treatment * Time during trial + White noise or silence treatment * Day	2.5	10

2.5 Discussion

During the white noise treatment, the guppies tended to move to quieter areas of the tank, suggesting avoidance of an aversive stimulus. Despite some indication of avoidance behaviour, the sound difference as fish moved from louder to quieter areas of the tank was less than 0.5 dB (Figure 10). Since the difference between the mean sound the fish were exposed to and the quietest sound in the tank was not less than 3 dB, this indicates that fish did not appear to move to the quietest areas of the tank. Avoidance behaviour to loud noise is expected as fish try to escape disturbance and potential harm, highlighted by the use of acoustic deterrents to manage fish populations (Putland and Mensinger, 2019). However, in practice the success of the deterrents is not guaranteed (Deleau *et al*., 2020; Jesus *et al*., 2019). A study on zebrafish showed the fish respond to elevated sound with a startle response and decreased time spent near the active speaker however during the sound treatment the zebrafish did not show a significant preference to the quiet escape chamber (Shafiei-Sabet *et al.,* 2016). It was unclear whether the sound gradient was distinct enough for the zebrafish to be able to seek out the quieter areas. This should be considered when analysing the results for the guppies' response to the noise treatment; are the guppies able to detect a 0.5 dB sound difference and thus are they actively moving to the quieter area of the tank?

At the end of the week guppies still avoided the loudest areas of the tank but with a reduced response than in the first trial (Figure 11). This suggests that although fish are still avoiding the impulsive noise, they may have become more tolerant over the four trials, possibly habituating to the white noise. This may occur as the guppies habituate and learn the noise is not related to a direct threat. Neo *et al.,* (2018) showed inter-trial habituation in a similar study involving seabass, as seabass, which typically change their depth as a stress response, performed less bottom diving in response to repeated noise exposures. It has also been shown that fish that live in habitats with more motorboat disturbance showed no effect to a motorboat playback, compared to an increased oxygen consumption for fish from a low disturbance site (Harding *et al*., 2018). Avoidance and habituation is also species dependent; species that have complex hearing structures will show permanent behavioural changes if these structures become permanently damaged from chronic exposure, so habituation cannot occur (Mickle *et al*., 2019).

The biological importance of the guppies tending to spend more time in the quieter areas of the tank during the white noise treatment is questioned due to the sound difference of less than 0.5 dB from the start to the end of the trial. The predicted gradient in the tank in the white noise treatment was 13 dB (Figure 5), however the guppies were still occupying areas greater than 3 dB louder than the quietest area (Figure 10). It has been shown that a 6 dB reduction (i.e. quieter) is equivalent of doubling the distance from a sound source (Banner, 1971). A difference of 0.5 dB is then only increasing the distance from the speaker by < 10%. More research needs to be conducted on the specific hearing sensitivity of guppies to know whether they can detect this 0.5 dB sound difference, and therefore to determine whether it was an active decision to move into the quieter tank areas. Generally, details on hearing capabilities of most fish species are not known (Popper and Fay, 2011), so filling this knowledge gap will also allow improved future predictions of responses to noise as well as making comparisons between species. Whilst studies often focus on one level of sound exposure compared to a control (de Jong *et al*., 2018; Pieniazek *et al*., 2020), Campbell *et al.* (2019) used a similar sound gradient to the present study, to analyse swimming speed and freezing response. To improve this and future studies, a larger sound gradient could be established in the white noise treatment, exposing the guppies to considerably quieter areas more similar to the guppies holding tank (96 dB), as the quietest predicted area in the white noise tank was 130 dB.

Comparing distance from the speaker in white noise and silence treatments suggests that the guppies are further away from the speaker during the white noise treatment (Figure 14), implying an avoidance to the sound. However, the biological importance of this is questioned due to the difference in distance from the speaker between white noise and silence being less than 1.5 cm which is minimal proportionate to the tank size (Figure 1). Similarly, when looking at the interaction effects there doesn't seem to be any interaction of treatment with time in trial or day (Table 5). This implies that the change over time and day is also seen in the silence part of the trials, suggesting that something other than white noise is causing the avoidance. Due to the avoidance throughout the trial changing less than 2 cm for both white noise and silence, a suggestion is that this could be caused by the random swimming movements of the guppies who may still experiencing stress from the transfer from their holding tank, which masks the response to the noise. A longer acclimation period would allow more time to recover from the disturbance of being transferred from their fry nets in to the holding tanks which may have caused an increased stress response (Ramsay *et al*., 2009). Acclimation periods are species specific and can be up to two hours to show consistent behaviour (Makaras *et al*., 2021). The 10-minute acclimatisation period in the present study was set based on acclimation times in previous studies on guppies (Burns, 2008; O'Neill *et al*., 2018) and in order to test multiple groups on one day. Increasing acclimation periods in guppies from 2 - 5 minutes has shown increased reliability in emergence behaviour (Burns, 2008), but another study has shown 2 hours of acclimation shows the highest consistency of behaviour (O'Neill *et al*., 2018).

Further study could research a range of acclimation periods to find optimum acclimation for guppies for a specific behaviour, to ensure accurate responses to the treatments are recorded.

When the guppies were exposed to the silence treatment before the white noise treatment, they had a greater tendency to move to quieter areas in the tank during the white noise treatment (Figure 12). This could be due to the silence period extending the acclimation time, allowing the fish longer to acclimatise to the experimental tank, allowing them to find the quieter areas of the tank. However, when comparing the effect of treatment order on the distance from the speaker in both the white noise and silence treatments, in the second half of the trial guppies appear to be further from the speaker in both treatments (Figure 15), suggesting the species may acclimate to the experimental environment throughout either treatment. Increasing acclimation time may increase the consistency of behavioural responses to treatment types (O'Neill *et al*., 2018).

We found that individuals and groups responded differently to the noise stimulus. This is expected due to personality variation which can affect an individual's response to disturbance (Bruintjes and Radford, 2013; Harding *et al*., 2019; Naguib *et al*., 2013). Bruintjes and Radford (2013) showed how anthropogenic boat noise affected dominant individuals, as they became more aggressive to their subordinates, however the subordinates did not increase their submissive behaviour during the boat noise. Changes in an individual's behaviour within a group may affect the group's social dynamics (Webster and Ward, 2011). In Webster and Ward's study, groups also responded differently to noise. Groups of differing condition and individual size have shown to be affected differently by noise (Casper *et al*., 2013; Purser *et al*., 2016). Groups were randomly selected in our study to counteract for group bias but in future studies, analysis of individuals within a group could be conducted to control for condition or size within a group. Intra-population variation is important to consider as it will have effects on mitigation measures and populations as a whole.

Tracking of the guppies was carried out using idTracker (version 2.1; Pérez-Escudero *et al.*, 2014). Due to the small size of the fish and the large experimental arena, the accuracy of tracking individual guppies across the trials cannot be guaranteed. The large tank size was used in order to establish a sound gradient, however improving the acoustic insulation/setup could allow a smaller tank to be used without compromising the sound gradient, in order to increase tracking accuracy. Alternatively, to improve future studies, using higher resolution tracking software that can guarantee the accuracy of identifying individuals consistently across trials, would allow for a more detailed comparison of individual-level behaviour across each day. Accurately establishing whether individuals learnt or habituated to the sound at different rates may show whether fish with different personality traits, responded differently to a noise stimulus, allowing for a deeper understanding of inter-individual variation. Previous studies have also looked at habituation over trials, or acclimatisation based on past exposure, but do not identify individuals across the trials (Harding *et al*., 2018; Neo *et al*., 2018). The seabass used in Neo's study (2018) were individually tagged so research on individual responses is possible especially with larger species, with the future focus looking for long-term behavioural patterns across trials rather than just within a single trial.

Experimental fish used in laboratory experiments are often bred from many generations of laboratory reared fish. To maintain laboratory environments there are water treatment systems, air conditioning and continuous human disturbance, with the sound pressure in the guppies' holding tank in this study being 96 dB. This means that the fish may have been adapted to this level of anthropogenic disturbance and may therefore respond differently to noise stimuli than a wild population. Although the guppies used in this study were only third generation laboratory reared, it is possible that this is sufficient time for the individuals to become accustomed to the background sounds, following the trend from this 4-day study. This limitation provides many challenges to overcome because if wild populations were used in laboratory studies the change in environments may also lead unrepresentative effects of the noise stimuli. Alternatively, we could consider conducting the same study in a controlled natural environment, controlling for as many variables as possible, including the area in which fish can move in order to be able to record their behaviour. The sound would propagate more naturally however background sounds could not be controlled for, although these would likely be the sounds fish were already adapted to. Comparing behavioural responses in laboratory and field based studies of the same species may allow the best understanding of noise responses (Pieniazek *et al.,* 2020).

Equipment to record particle motion is still being developed for small tanks, and the equipment used in my study could not record on all its axes. This means the equipment cannot be used to record at the same spatial intervals as the hydrophone due to its physical size so predicted values may not be as accurate. As the technology develops and recording equipment designed for shallow water becomes more accessible, working out the relationship between particle motion and sound pressure will become more accurate in near field small tank setups.

This study suggests that the relationship between particle motion and sound pressure is positively correlated (Figure 7), so just the sound pressure was used as this set of data had a higher sample rate across the dimensions of the tank. Being able to study the effects of both sound pressure and particle motion on the effect of fish behaviour with high accuracy as equipment develops, will allow the impacts to be fully explored (Nedelec *et al*., 2016). The importance of comparing both sound pressure and particle motion in noise based studies is widely acknowledged in current scientific literature (Popper and Hawkins, 2018).

Understanding responses to anthropogenic noise is key to establishing the effect of noise as a pollutant and possible detrimental effects it may have on a species and the ecosystem. Avoidance or habituation to noise are different responses to stressors, with differing outcomes for these behaviours. Avoidance of noise for groups of fish has yet to be fully researched (Proulx *et al.,* 2019). Habituation to anthropogenic disturbance can be beneficial for maintaining a consistent source of resources (Blumstein, 2016), at the potential cost of continuing physiological stress (Ditchkoff *et al*., 2006), and reduced predatory avoidance (Geffroy *et al*., 2015). The full effects of noise exposure on fish, particularly long-term, are still unknown (Neo *et al*., 2018).

It was found that guppies habituate to an anthropogenic noise stimulus over testing across multiple days, while also showing avoidance behaviour during a 15-minute trial. The extent of these effects requires further research to establish the biological significance of avoidance to anthropogenic noise disturbance. As equipment develops, it will be more achievable to look specifically at particle motion with biologically relevant results, as not all fish hear through sound pressure. Comparing fish responses in laboratory and natural habitats will help establish a more complete picture on the effect of anthropogenic noise on fish. Similarly, focusing on long-term effects will also build on current knowledge and will help inform if mitigation of anthropogenic noise pollution can be achieved and how to approach this.

3 Chapter 3: General Discussion

3.1 Overview

Anthropogenic noise is a type of pollutant with growing concern, as humans exploit more natural environments. Anthropogenic noise may have implications on animal behaviour but the extent to which is context dependent. Research on noise in aquatic environments is growing, with focus moving from primarily marine mammals to include fish and aquatic invertebrates too (Hawkins and Popper, 2017). The type and duration of the noise will impact the level of disturbance, and whether the disturbance effect is maintained or if habituation is demonstrated by animals. Understanding the long-term impacts of anthropogenic noise will be important in the future, to effectively design mitigation measures and to understand when and where it will be of important to apply them. While researching, it is important to consider the species hearing mechanism to correctly understand what they can hear and are responding to. Based on fish's hearing mechanisms, studying the response to particle motion as well as sound pressure is important since many fish species detect sound through particle motion (Nedelec *et al.*, 2016).

3.2 Summary of Study

In our study guppies can be seen to demonstrate avoidance behaviour to a sound stimulus over one trial, but over the longer-term (a week) guppies appear to show habituation to the sound. This is in agreement with studies investigating long-term effects of where fish habituate to noise (Harding *et al*., 2018; Neo *et al*., 2018), however many studies still use single exposure when investigating the effect of sound (Bruintjes and Radford, 2013; Holles *et al*., 2013; McCloskey *et al*., 2020; Simpson *et al*., 2016). The biological significance of our result is questioned due to the small sound difference the guppies experience when moving to only slightly quieter areas of the tank, as well as the small difference in distance from the speaker between white the noise and silence treatments. Ensuring there was a significant sound gradient across the tank would allow greater confidence in the results that the guppies are avoiding the sound by choosing quieter areas and it is not due to preference of a specific area of the tank.

While both particle motion and sound pressure were recorded in this study, only sound pressure was used to study response variables. Particle motion and sound pressure were shown to be positively correlated and the sound pressure recordings were more representative of the tank due to the ability to record more frequently throughout the tank, which is why it was chosen as the response variable. The development of particle motion equipment suitable for small tanks will allow more accurate measurements of particle motion. This will improve the understanding of the relationship between particle motion and sound pressure and allow further study of the response variables to particle motion. From our understanding of fish biology, particle motion should be used as the independent variable as it is the main hearing mechanism of fish (Nedelec *et al.*, 2016; Popper and Hawkins, 2018).

3.3 Future Directions

In this study, responses were recorded on a long-term basis rather than just a single exposure, but recordings were still limited to a week. Researching time frames of habituation for study species would be important, as it is challenging to generally categorise long and short-term responses into time frames. Comparing previous studies of habituation to different abiotic factors may allow for a more informed prediction on how organisms will respond to disturbance through behavioural plasticity (Snell-Rood, 2013). Ensuring that future studies always include information on multiple exposures will help develop our understanding of the potential for habituation (Radford, *et al.*, 2016), especially as anthropogenic disturbance is often ongoing.

From this study and previous work it can be seen that repeated exposure to noise can increase tolerance (Nedelec *et al*., 2016). Studies on model organisms in laboratory experiments, or in the field, often use fish who have previous exposure to noise disturbance, and therefore may have already shown some evidence of habituation. Testing individuals which haven't been previously exposed to noise disturbance outside their natural habitat will allow an accurate initial response to be recorded and therefore will be able to show a complete time frame of habituation. This will provide more relevant information when establishing mitigation solutions to habitats that haven't previously been disturbed by anthropogenic noise that humans are developing in, such as when establishing new sites for offshore windfarms and the associated construction noise when erecting these (Thompson *et al*., 2013).

When analysing behavioural responses in our study, we saw habituation over time, however this does not account for physiological responses. Physiological responses to noise include increased ventilation rates and cortisol levels (Cox *et al*., 2018; Nedelec *et al*., 2016). Increasing levels of the stress hormone cortisol, can affect growth (Weil *et al.,* 2001), reproduction (Consten *et al.,* 2001) and survival (Pickering and Pottinger, 1989). Although a species may have shown behavioural habituation, noise exposure may still have negative impacts due to physiological stress. Species may show physiological habituation. For example, Nile tilapia *(Oreochromis niloticus)* were used in a long-term study over 120 days where initial opercular ventilation rate increased with noise exposure, but then showed a decline back to the original levels (Kusku, 2020). Understanding the interaction between physiological and behavioural responses and potential habituation of both or either response, will allow a more complete picture to be formed on the stress response to anthropogenic noise (Mickle and Higgs, 2018), and this can be applied to anthropogenic disturbance more generally.

The guppy is a well-studied model organism however limited research has been conducted on its hearing capabilities and how it responds to anthropogenic sound disturbance. The guppy's habitat is typically in pools in freshwater streams. Due to populations being geographically isolated guppies can experience different selection pressures for example, high and low predation sites (Grether *et al.*, 2001). These differences have led to different behavioural responses of each group (Templeton and Shriner, 2004). Although limited research has been conducted on guppies response to sound, De Waele *et al.,* (2022) showed that guppies use different cues to establish pools in which to jump into, speculating that guppies used visual and sound cues to jump safely into a deep pool. The visual and sound cues were tree cover over the river and sound of the ripples respectively (de Waele *et al.,* 2022). With some evidence that guppies use sound as a cue, understanding the impact of anthropogenic noise on their behaviour will help establish if mitigation methods for anthropogenic sound in their natural environments is required. Exploring the impact of anthropogenic sound on guppies from different predation sites would also give an insight as to whether guppies respond differently based on their selection pressures and this will help establish the impacts of multiple stressors (Orr *et al.,* 2020). Knowing that research on anthropogenic sound is underrepresented in freshwater systems highlights another reason to continue developing sound studies on the guppy both in the lab and field (Jerem and Mathews, 2021).

Anthropogenic disturbance does not usually occur as a single stressor, therefore there is a need to study the impact of multiple stressors (Orr *et al*., 2020). Anthropogenic disturbance, other than noise pollution, can include chemical contamination of environments, habitat alteration, invasion, warming, and acidification (Murphy and Romanuk, 2012). Understanding the interlinked effect of multiple stressors is key to developing knowledge on biodiversity conservation and management of ecosystems. Combining stressors may have additive, synergistic or antagonistic effects, and interactions can be complex and unpredictable (Crain *et al.*, 2008; Jackson *et al.*, 2016). Additive and synergistic interactions may have greater negative responses than single stressors alone, so predicting which stressors may have these interactions is particularly important when considering how to mitigate the impact of these stressors. Although antagonistic effects may suggest a reduced impact of the stressors, overall impacts may still be negative (Jackson *et al*., 2016). When the interaction is antagonistic it is important to consider how to reduce or moderate both stressors simultaneously or more damage may be caused (C. J. Brown *et al.*, 2013). Antagonistic effects have been shown to be more common in freshwater environments compared to marine environments (Jackson *et al*., 2016), possibly due to the environmental variability in freshwater ecosystems. When studying multiple stressors it is important to consider that multiple stressors may not occur in identical time frames, and will therefore have different effects from individuals, due to what stage in their life cycle they are, to whole ecosystems (Orr *et al.*, 2020; Jackson *et al.*, 2021). In future studies, particularly when wanting to understand how to implement mitigation responses to anthropogenic disturbance, incorporating multiple stressors in studies will allow a more complete understanding of the impact of anthropogenic disturbance (Orr *et al*., 2020).

3.4 Conclusions

The result of my study suggests potential short-term avoidance and long-term habituation to anthropogenic noise which supports current work focussing on long-term sound exposure and habituation (Radford *et al.,* 2016). Ensuring studies include multiple exposures will help develop our understanding of animal habituation to disturbance. It is important to consider how animals will be exposed to anthropogenic sound when conducting future research in this area, including how fish detect the sound, through particle motion or sound pressure, based on their hearing mechanisms. Similarly, anthropogenic disturbance rarely comes as an isolated stressor (Orr *et al.,* 2020) and considering multiple stressors interacting with sound disturbance and factoring these into experimental design is important. This will allow a more complete understanding of the impacts of anthropogenic noise for species in their natural habitat, particularly when implementing mitigation measures.

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