



The effect of temporal variation in sound exposure on swimming and foraging behaviour of captive zebrafish



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Anthropogenic noise of variable temporal patterns is increasing in both marine and freshwater systems. Aquatic animals often rely on sounds for communication and orientation, which may therefore become more difficult. Predator–prey interactions may be affected by masking of auditory cues, sound-related disturbance or attentional interference. Here, we investigated the impact on both predator and prey for zebrafish, *Danio rerio*, preying on water fleas, *Daphnia magna*. We experimentally raised ambient sound levels in an aquarium and tested four sound conditions that varied in temporal pattern: continuous, fast and slow regular intermittent and irregular intermittent, which we compared with ambient sound levels with no extra exposure. We found no effects on water flea swimming speed or depth but there was an increasing number of individual zebrafish with an increased number of startle responses, especially to the intermittent sound treatments, which was also reflected in a significant increase in zebrafish swimming speed, but not in any change in zebrafish swimming depth. Discrimination in attacking edible water fleas or inedible duckweed particles was low for the zebrafish and unaffected by sound exposure, but foraging was affected in two ways: intermittent sounds delayed the initial acceleration response and all treatments caused a rise in handling error. These insights confirm that elevated sound levels, and especially intermittent conditions, may affect predator–prey interactions. Our results apply to laboratory conditions but call for outdoor studies that go beyond single-species effects. If acoustic impact of human activities extends to multiple species and their interactions, natural sound conditions may turn out to be important for the stability and dynamics of aquatic ecosystems.

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A variety of human activities introduce anthropogenic noise in different temporal patterns above and below the water surface in marine and freshwater systems (Amoser, Wysocki, & Ladich, 2004; Andrew, Howe, Mercer, & Dzieciuch, 2002; McDonald, Hildebrand, & Wiggins, 2006). Although empirical evidence confirming short-term and especially long-term effects is still scarce, aquatic animals can be negatively affected by anthropogenic noise in many ways (Popper, Fewtrell, Smith, & McCauley, 2003; Popper et al., 2014; Richardson, Greene, Malme, & Thomson, 1995). Masking may, for example, interfere with acoustic communication, soundscape orientation or acoustically guided predator–prey interactions, while anthropogenic noise may also interrupt or modify group movements, migratory activities and courtship or other

reproductive behaviours (for reviews see Hawkins & Popper, 2014; Radford, Kerridge, & Simpson, 2014; Slabbekoorn et al., 2010).

Different taxonomic groups such as marine mammals and fish can be part of the same community, but may be affected by anthropogenic noise in different ways and to a variable extent (Popper et al., 2014; Shafiei Sabet, Neo & Slabbekoorn, 2015; Slabbekoorn et al., 2010; Weilgart, 2007). In air, it has been shown that human-induced changes in ambient noise levels can have direct and indirect effects and can lead to changes in abundance and diversity of animals and plants (Francis, Kleist, Davidson, Ortega, & Cruz, 2012; Francis, Kleist, Ortega, & Cruz, 2012; Francis, Ortega, & Cruz, 2009, 2011a, 2011b). We currently lack such insights for aquatic communities and it is clear that more data are needed that go beyond single-species effects.

Several recent studies in various taxa have revealed an impact of artificial sound levels on predator–prey relationships. For example, Siemers and Schaub (2010) showed that elevated sound levels may negatively affect foraging performance in bats, *Myotis myotis*, by masking auditory cues that are critical for catching invertebrate prey. Quinn, Whittingham, Butler, and Cresswell (2006) also

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reported sound-dependent changes in foraging efficiency in chaffinches, *Fringilla coelebs*, as higher ambient noise levels made them eat less and scan more. In crustaceans, Chan, Giraldo-Perez, Smith, and Blumstein (2010) found that boat sounds distracted hermit crabs, *Coenobita clypeatus*, in such a way that they responded less quickly to a visual stimulus indicating approaching danger. So, it appears that an impact of sound is widespread taxonomically, that acoustic masking or distraction can affect auditory as well as visual perception, and that anthropogenic noise may affect predator as well as prey species.

As far as we know, fish are also likely to be susceptible to the human-induced rise in underwater sound, as they are well known to hear and use sounds for many aspects of their underwater life (Fay, 2009; Ladich, 2004; Slabbekoorn et al., 2010). Like in air, underwater masking effects are determined by the spectral overlap of ambient noise with biologically relevant sounds (Codarin, Wysocki, Ladich, & Picciulin, 2009; Gutscher, Wysocki, & Ladich, 2011; Vasconcelos, Simões, Almada, Fonseca, & Amorim, 2010). Independent of masking, several studies have also reported behavioural changes in response to artificial tones or wideband sounds. For example, Andersson, Dock-Åkerman, Ubral-Hedneberg, Öhman, and Sigray (2007) showed several different behavioural changes in captive roach, *Rutilus rutilus*, and sticklebacks, *Gasterosteus aculeatus*, which were interpreted as species-specific responses to perceived danger of predation risk. Picciulin, Sebastianutto, Codarin, Farina, and Ferrero (2010) revealed a negative impact on the time spent on behaviours that are critical for reproductive success in red-mouthed gobies, *Gobius cruentatus*, in their natural habitat. Sebastianutto, Picciulin, Costantini, and Ferrero (2011) also showed that the typical outcome of acoustically mediated territorial conflicts of this species was undermined under experimentally noisy conditions. Although these studies suggest that predator–prey interactions in fish may also be affected by artificial sound exposure, this phenomenon, which has potential consequences across aquatic food webs, has received relatively little attention.

Recently, a study experimentally explored the impact of artificial noise on predator–prey interactions in sticklebacks catching water fleas, *Daphnia magna*. Purser and Radford (2011) were able to show that sound playback, compared to more quiet conditions, increased the number of errors in food particle discrimination and food handling. Voellmy et al. (2014) showed that different species may respond differently to playback of additional ship sounds as European minnows, *Phoxinus phoxinus*, differed from sticklebacks in becoming less active and more social. These experimental data clearly show an acoustic impact on a seemingly visual task with a direct impact on fish foraging efficiency. As masking is unlikely to be important, the performance decline may be due to attentional shifts (Dukas & Dukas, 2002; Mendl, 1999) as found in the studies on birds and hermit crabs mentioned above (Chan et al., 2010; Quinn et al., 2006). In the experimental studies on fish (Purser & Radford, 2011; Voellmy et al., 2014), it was assumed but not investigated that the effect of sound on foraging efficiency was caused by an impact on the predator and not on the prey and the relevance of temporal variation in sound characteristics (cf. Neo et al., 2015; Neo et al., 2014) remained unexplored.

Zebrafish, *Danio rerio*, are a very suitable model system to assess behavioural changes in response to environmental conditions in general (e.g. Cachat et al., 2010; Egan et al., 2009; Gaikwad et al., 2011; Gerlai, Lee, & Blaser, 2006) and to tackle questions of the impact of sound on predator–prey interactions in particular. Neo et al. (2015) exposed adult zebrafish to different sound patterns and showed initial startle responses, relatively brief anxiety-related response behaviours, but no longer-lasting effects or spatial avoidance. They reported sound exposure-related changes in swimming speed and group coherence, while fish moved upwards

in response to moderate sound levels (112 dB re 1 μ Pa) and downwards (for brief periods) in response to higher sound levels (120–140 dB re 1 μ Pa). We have no insight yet into whether and how foraging behaviour in this species is affected by exposure to sound (cf. Purser & Radford, 2011; Voellmy et al., 2014), but zebrafish readily feed on live prey and provide a perfect model system to assess the impact of temporal variation in sound exposure on foraging efficiency.

Water fleas, *Daphnia* spp., are small crustaceans and important food items for many fish species in freshwater systems (e.g. Ebert, 2005; Gulati, 1990). They show predictable spatial behaviour by avoiding darker water areas and preferring open space (negative scototaxis and negative thigmotaxis), which probably reduces exposure to predators that may hide in the dark and in vegetation (e.g. Dodson, Tollrian, & Lampert, 1997; Van Gool & Ringelberg, 1995). Although sensory systems for aquatic invertebrates may vary, both short-term effects of sound on response behaviour to approaching predators (Chan et al., 2010) and long-term effects of sound on growth and reproduction (Lagardère, 1982) have been reported, for example in crustaceans. Furthermore, at a larval stage, marine crustaceans have been reported to respond phonotactically to reef sounds (e.g. Radford, Jeffs, & Montgomery, 2007; Stanley, Radford, & Jeffs, 2011). Also, larvae of aquatic invertebrates, of similar size as water fleas, have been shown to either increase or decrease their swimming activity in response to natural and anthropogenic exposure to sound (Stocks, Broad, Radford, Minchinton & Davis, 2012). Therefore, we believe it is important to check whether anthropogenic noise has any effect on water flea behaviour that may have consequences for predation risk (cf. Morley, Jones, & Radford, 2014).

In the current study, we tested the impact of temporal variation in artificial noise exposure, mimicking temporal and spectral patterns of artificial sounds that exist in natural environments, on (1) behaviour of water fleas (*D. magna*), (2) behaviour of zebrafish and (3) zebra fish preying on water fleas. We measured startle responses, swimming speed and spatial distribution in water fleas and zebrafish. Sound treatments varied in being continuous or intermittent and the latter category in being fast or slow and in having regular or irregular intervals. We aimed to answer the following questions. Does exposure to artificial noise reduce foraging efficiency of zebrafish hunting for water fleas and is this impact attributable to a behavioural impact on prey, predator or both? Furthermore, does variation in temporal patterns matter? We expected water flea swimming behaviour to change with the onset of sound exposure and foraging efficiency of zebrafish to be negatively affected by sound exposure through an impact on foraging performance, discrimination and handling (cf. Purser & Radford, 2011; Voellmy et al., 2014). We also expected less impact from continuous sound than from intermittent sound and less impact from regular than from irregular sound exposure.

METHODS

Animal Maintenance and Housing

Zebrafish (adult, 4–6 months old and of the wild-type, short-fin variety) were obtained from a local pet supplier in Leiden (Selecta Aquarium Speciaalzaak, who obtains stock from Europet Bernina International BV; Gemert-Bakel, The Netherlands). The fish were housed in a long stock tank (200 × 40 cm and 50 cm high) connected to a water circulation system before being transferred individually and sequentially to the experimental set-up. The fish stock was kept at 24 ± 1 °C on a 14:10 h light:dark cycle (light switched on from 0600 to 2000 hours) and was fed on dry food twice a day (DuplaRin M, Gelsdorf, Germany). After the experiment,

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