Pelagic fish and harbour porpoise at North Sea wind farms: acoustic investigation and science communication

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CHAPTER 2

Response triggering potential of pulse train variants in pelagic fish: a behavioural test using wild-caught herring

RESPONSE TRIGGERING POTENTIAL OF PULSE TRAIN VARIANTS IN PELAGIC FISH: A BEHAVIOURAL TEST USING WILD-CAUGHT HERRING

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Abstract

Anthropogenic sounds increasingly contribute to the underwater soundscape and can have negative consequences for aquatic animals. High-amplitude, impulsive sounds, such as from seismic surveys and pile driving, can be especially harmful to nearby marine mammals and fishes. However, with acoustic deterrent devices, sound may be used as a mitigation measure. These devices play back specific sounds intended to drive animals away from a potentially dangerous site. Previous studies have explored the efficacy of several sound stimuli in guiding marine mammals at sea and fishes in rivers and estuaries. However, there is still little insight into what type of sounds would be most efficient to deter pelagic fishes at sea. In the current study, we played back a set of eight pulse train sound stimuli, varying in amplitude and temporal pattern, to test for response triggering potential in Atlantic herring (*Clupea harengus*) in captive conditions. We expected pulse trains with a fade in amplitude and an accelerating pulse rate to elicit stronger behavioural responses, as this may be perceived as looming and the approach of a potential threat. Groups of four herring clearly responded to the sound exposures by turning. However, other short- and long-term behavioural changes were absent or subtle, and did not reveal significant responsiveness to pulse train variation. Consequently, we found no evidence for specific variants to have potential to improve an acoustic deterrent device for herring. However, our results in captivity with limited effect sizes can also not exclude a horizontal fleeing response in free-ranging conditions. Nevertheless, a follow-up sound exposure study at sea has confirmed limited spatial responsiveness to sound also in free-ranging pelagic fish. Further studies are needed to test whether acoustic features of a looming stimulus can affect response strength in other fish species or in other conditions.

Introduction

Human activities at sea are spreading and the acoustic consequences can have extensive impacts on marine fauna (Slabbekoorn et al., 2010; Kunc et al., 2016; Duarte et al., 2021). This so-called anthropogenic noise can be divided into two general categories: (1) intentional sources, in which sound is used as a monitoring tool, e.g. sonar and seismic surveys, and (2) unintentional sources, in which sound is a by-product, for example during construction work, explosions, and operation of vessels. Behavioural effects of anthropogenic noise may concern many individuals and species (Slabbekoorn et al., 2010). Harbour porpoises (*Phocoena phocoena*) can, for example, be displaced from an area due to construction activities of an offshore windfarm (Benhemma-Le Gall et al., 2021). Seismic surveys can lower the activity level of Atlantic cod (*Gadus morhua*) and disturb their diurnal activity cycles (van der Knaap et al., 2021) and swimming depth (McQueen et al., 2023). In more extreme cases, marine mammals and fishes close to a seismic survey or pile driving location may suffer from hearing damage, injuries, or even die (Ladich, 2008; Popper & Hastings, 2009; Slabbekoorn et al., 2010; Cox et al., 2018). With increasing insight into detrimental effects of noise pollution, noise mitigation measures are becoming more pertinent. For unintentional sound sources, the most evident solution is to reduce the sound intensity as much as possible. Bubble curtains are nowadays used to attenuate pile driving sound to reduce the risk of hearing damage or other negative effects (Hahn & Thomas, 2008; Dähne et al., 2017). For intentional sound sources, reducing the sound intensity could still be an option under certain circumstances or for part of the sound spectrum. Reducing the energy level of irrelevant frequencies in seismic survey sounds could help reduce the adverse effects for specific species (Slabbekoorn et al., 2010). Reduction of sound levels to a non-harmful level, may serve in ecological mitigation, but come with an economic cost. An alternative may therefore be to use so-called acoustic deterrent devices or 'ADDs' prior to threatening loud sound events to deter animals from a dangerous area (Putland & Mensinger, 2019). In their review, Putland & Mensinger (2019), report promising results on fish ADDs, especially in river contexts, yet they also argue that there is potentially a publication bias towards positive results.

Different kinds of ADDs are already used to herd or guide marine or freshwater animals. For example, minke whales (*Balaenoptera acutorostrata*) showed avoidance behaviour to an ADD test, which was actually targeted at seals at fish farms (Boisseau et al., 2021). Playing back sound also reduced the numbers of trapped sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) in the cooling water inlet of a nuclear powerplant in Belgium (Maes et al., 2004). ADDs can also be used to redirect migratory fish to different, more favourable routes (e.g. Sand et al., 2000). The FaunaGuard is an ADD that has been shown to be effective in driving harbour porpoises away (Geelhoed et al., 2017; Voss et al., 2023). ADDs are already in use to prevent fish predation by pinnipeds at fish farms, and harbour porpoises away from the construction site of offshore windfarms before the onset of pile driving (Brandt et al., 2013), although success can be short-term and variable (Götz & Janik, 2013).

Not all sounds of a given amplitude level elicit the same behavioural response. Multiple parameters make up a sound (e.g. frequency and amplitude) and different behavioural responses have been shown in relation to sound stimuli varying in specific parameters (Slabbekoorn et al., 2018). Rapid pulse-trains and broad-band engine-type sounds can elicit a typical stress-indicating behavioural response in fishes in captive studies. For example, in an outdoor pond, broadband sound playback elicited a stronger evasive response from the sound source in silver carp (*Hypophthalmichthys nobilis*) compared to playback of pure tones (Vetter et al., 2017). Pulse trains have been shown to lead to double the behavioural impact compared to continuous sounds in European seabass (*Dicentrarchus labrax*), despite having only one tenth of the sound energy present (Neo et al., 2014).

Pelagic fishes may differ in responsiveness patterns from other species, due to their spatial fluidity and apparent lack of or reduced site fidelity. In Atlantic herring, a vertical diving response was observed to boat enginetype and impulsive sounds in captivity (Doksæter et al., 2012a). Killer whale feeding sounds also induced vertical and horizontal fleeing responses in freeranging herring schools (Doksæter et al., 2012b). In another in situ study, schools of sprat and mackerel (*Scromber scombrus*) were shown to respond to pile-driving-like impulsive sound playback by dispersing and changing depth, respectively (Hawkins et al., 2014). Other sound stimuli have been shown not to elicit a behavioural response, such as naval sonars (Doksæter et al., 2009, 2012a,b) and artificial tones and frequency sweeps (Handegard et al., 2016). Hence, it is not straight forward to elicit a behavioural response with just any sound and studies are needed to explore which sound signals are most efficient to trigger and potentially deter pelagic fishes.

In exploring the potential to deter pelagic fishes acoustically, we may learn from other, better studied, taxonomic groups. For example, a sound pattern with deterrent potential could be one that is accelerating (speeding up) and fading in (gaining amplitude), as this could be perceived as looming and indicating the approach of potential danger. Humans have indeed been shown to be more sensitive to accelerating compared to decelerating sound stimuli (Trewhella et al., 2003) and a ramp-up in amplitude has been shown to be more easily and accurately localized compared to ramp-down stimuli (McCarthy & Olsen, 2017). The elevated sensitivity for acoustic features of a looming stimulus has also been reported for rhesus monkeys, (Maier & Ghazanfar, 2007) and mice (Li et al., 2021). In several fish species, elevated sensitivity has been observed in responsiveness patterns to visually looming objects (Walker et al., 2005; Temizer et al., 2015). Synchronous sounds have also been found to add to the responsiveness for a visually looming stimulus in fish (McIntyre & Preuss, 2019; Rodriguez-Pinto et al., 2024). However, it has yet to be determined if looming sound stimuli by themselves also elicit elevated responsiveness in fishes.

Pelagic fish are an ecologically and economically important taxonomic group of marine species. Small pelagic fishes specifically play an important role in the marine ecosystem by transferring nutrients from low to high trophic levels of the food chain (Greenstreet, 1997; Cury et al., 2000; Murphy et al., 2016) and are the target of intensive fishing activities; herring are in the top ten most fished species (FAO, 2022). While most teleost fishes are limited to hearing sounds below 500 Hz (e.g. cod: Chapman & Hawkins, 1973), herring — including Atlantic herring — may detect sound up to 4 kHz or higher (Enger, 1967). Hence, ADD's could be an efficient way to keep them away from e.g. pile driving sites. Herring are also highly sensitive to catching and handling, which make them a challenging species to collect data on in captivity. However, further insights into the effects of acoustic features are needed, and only dedicated studies can yield insights on presumed aversive sound stimuli that can be used in ADD devices.

In the current study, we tested the behavioural response of Atlantic herring to various sound stimuli in an indoor basin, with the intention to improve the efficacy of ADDs. We tested eight different sound stimuli, consisting of broad-band pulses, varying in pattern of amplitude and pulse rate. We investigated their effectiveness of eliciting a behavioural response in wild-caught fish to answer the following research questions: (1) Do herring respond to the playback of sounds compared to baseline behaviour in quiet ambient conditions? (2) Do the fish show different behavioural responses to click trains of varying amplitude and pulse rate? We expected the sound stimuli with an increase in amplitude and an acceleration in pulse rate to have a stronger response triggering potential compared to the other stimuli, as this particular combination of acoustic features could be perceived as a looming stimulus.

Materials and methods

1. Study species and housing

On 16 July 2021, juvenile Atlantic herring were caught in the Westerschelde, an estuary connected to the North Sea in Zeeland (The Netherlands), with a water depth of about 15 m. The fish were caught by professional fishermen with a large net opened in the water column from a fishing boat. When brought on deck, the fish were transferred to two large (500 l) transport tanks, which were provided with aeration. After fishing, the fish were brought back to Stichting Zeeschelp, located in Kamperland (The Netherlands). The fish were divided over two circular stock basins (3 m diameter, 1 m height, filled to about 7000 l volume) with the purpose of lowering the risk of a disease affecting the whole stock. One stock basin was located indoors and one outdoors. Each basin was provided with layer of sand at the bottom of about 2 cm, and continuous flow-through of filtered sea water coming directly from the Jacobahaven, which is a man-made cove in the Oosterschelde located right next to the facility. All basins were aerated and water quality parameters were checked at least once per week. The automatic lighting for the indoor basin matched the diurnal pattern of the outdoor conditions. The fish had an average length of 8.4 cm and weight of 3.7 g, and were fed daily with crushed *Gammarus* sp.

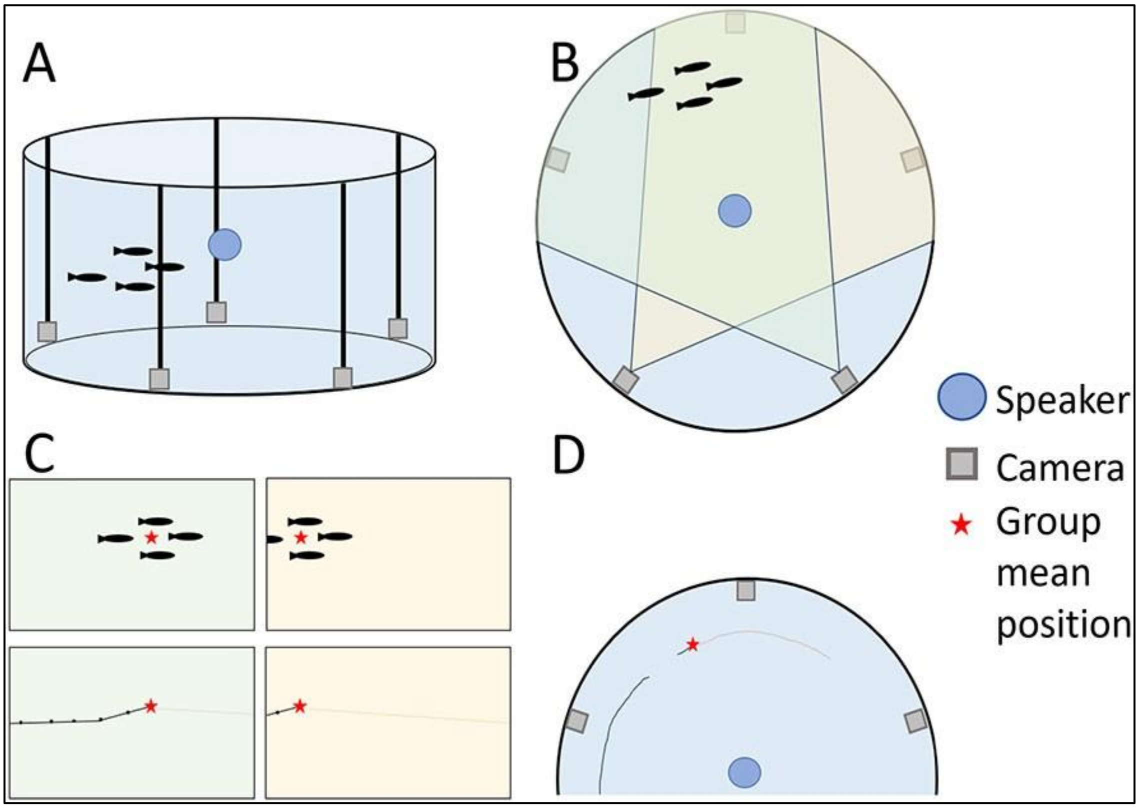

Figure 1. Simplified representation of the experimental basin and fish tracking method. (A) Side view of experimental basin with speaker in the middle, five poles with GoPro cameras evenly distributed along the wall, and a group of four fish. (B) Top view with two overlapping fields of view from two adjacent cameras. (C) On both cameras the group of fish is visible, due to overlap in fields of view, allowing for 3D position calculation. The group mean position was tracked with an automatic tracking software. (D) Top view depicting tracked group mean position.

2. Experimental setup

A third basin, identical to the stock basins, was used for the experimental setup indoors (Figure 1). An underwater speaker (Lubell UW30; frequency response 100 Hz–10 kHz; Lubell Labs, Whitehall, OH, USA) was hanging from a rod in the middle of the experimental basin at 33 cm depth. The speaker was connected to an amplifier (Kemo M033N; Kemo Electronic, Geestland, Germany) and sound was played back with a portable digital recorder (Tascam DR-07; TEAC Europe, Wiesbaden, Germany). To record the behaviour of the fish, five GoPro cameras (models HERO3, HERO3+, HERO4 and HERO4+; GoPro, San Mateo, CA, USA) were placed evenly divided alongside the basin wall (Figure 1).

3. Sound stimuli and exposure levels

Using Audacity, we created eight different sound stimuli, varying in amplitude and pulse rate (Figure 2). Each sound stimulus consisted of a pulse train of 10.05 s, made with 35 white noise (bandwidth 100–4000 Hz) pulses of 0.02 s each. The upper limit of the white noise bandwidth was around the upper limit of the hearing range of Atlantic herring (Enger, 1967). The lower limit corresponds to the lower end of the frequency response limit of the speaker. We expected the fish to be able to distinguish the sound pulses at this temporal scale since Atlantic herring also produce short burst pulse sounds themselves, by means of bubbles, supposedly serving in social mediation, which would require the ability of perceptual processing (Wahlberg & Westerberg, 2003; Wilson et al., 2003). The amplitude of the sound stimuli was either constant (mean root mean square (RMS) sound pressure level (SPL) 138.7 (SD 4.2) dB re 1 μPa), linearly fading in or linearly fading out (range ± SD 136.6 ± 1.3 to 140.5 ± 0.9 dB re 1 μPa). The pulse rate was either regular (intervals 0.275 s), accelerating (intervals linearly from 0.5 s to 0.05 s) or decelerating (intervals linearly from 0.05 s to 0.5 s).

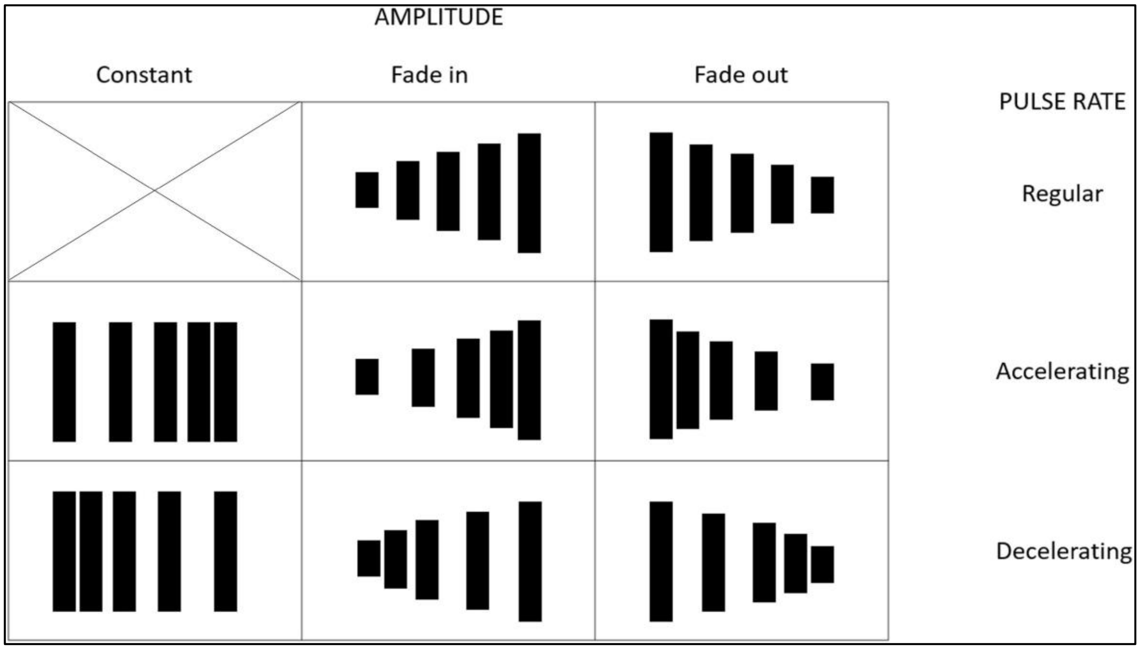

Figure 2. Simplified representation of the eight sound stimuli varying in amplitude and pulse rate: regular fade in, regular fade out, accelerating constant, accelerating fade in, accelerating fade out, decelerating constant, decelerating fade in, decelerating fade out. Pulse trains each consisted of 35 white noise pulses and lasted 10.05s.

To understand how the sound stimuli propagated through the basin, we measured both sound pressure and particle acceleration at various positions in the basin (Figure 3) with the M20 particle velocity sensor (GeoSpectrum Technologies, Dartmouth, NS, Canada). Transect measurements were made every 19 cm from the speaker towards the basin wall, at two depths (33 and 67 cm). To examine the omnidirectionality of the speaker, we also did four circular measurements around the speaker, at 75 cm from the speaker, again also at two depths. The recordings were stored on a laptop at 40 kHz via a current-to-voltage convertor box (GeoSpectrum Technologies) and a differential oscilloscope (PicoScope 3425, Pico Technologies St Neots, UK). We played back and recorded all eight sound stimuli as well as silence. We used a custom-made R package to determine the rms sound pressure levels and sound acceleration levels in the bandwidths 100–1000 Hz and 1000–4000 Hz. Additionally, we determined the power spectral densities (PSD) for each sound treatment and plotted the means across distance and for two depths (Figure 3). In the lower frequencies (100–1000 Hz), sound levels declined with distance from the speaker, with a larger decay in sound pressure levels. At the higher frequencies (1000–4000 Hz), the decay in sound levels is less clear. Sound propagation from the speaker is omnidirectional, as seen by the circular measurements at both depths. Sound spectra were similar for all sound stimuli, and clearly higher than silence (ambient).

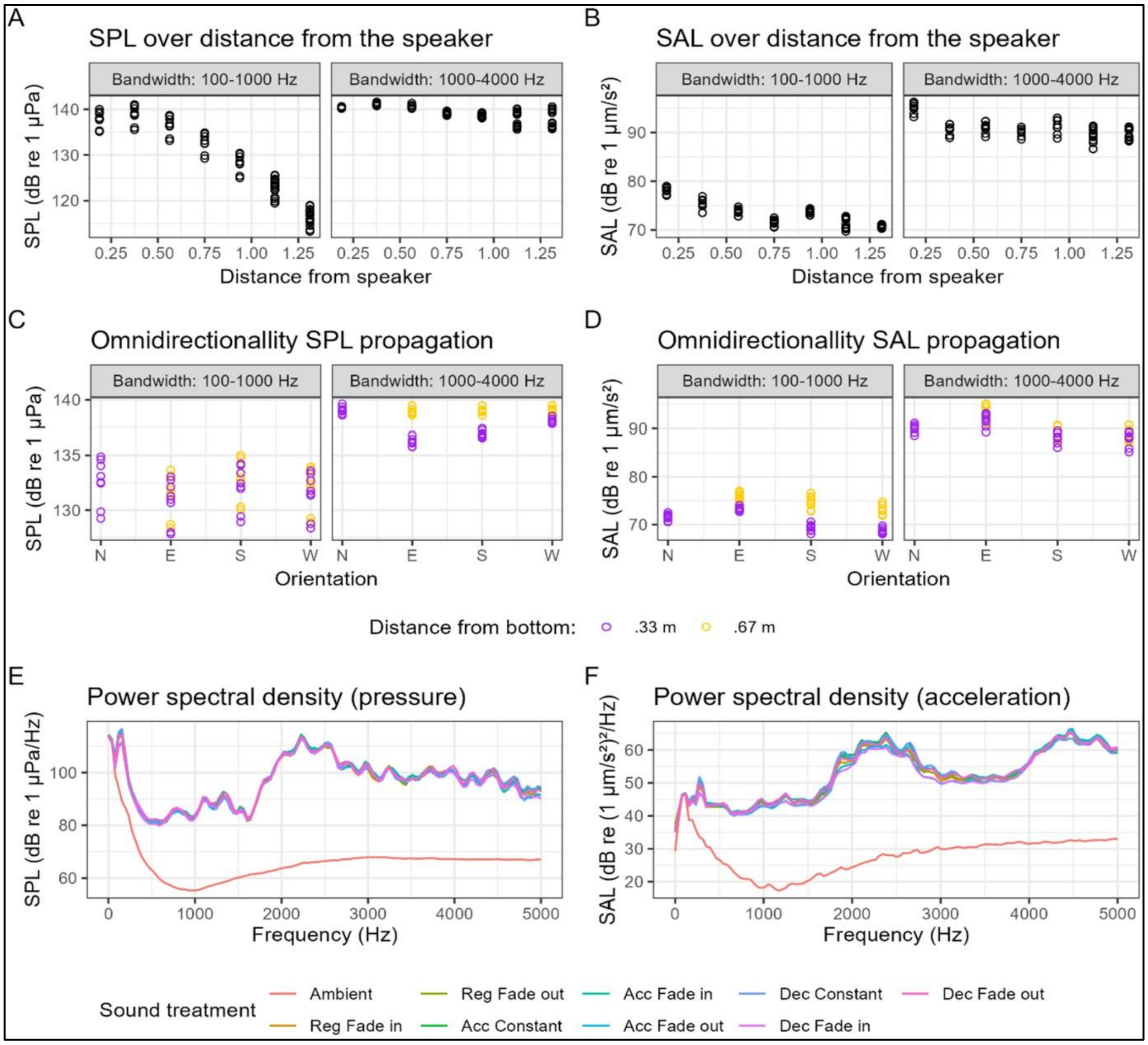

Figure 3. Sound pressure and particle acceleration levels in the experimental basin. (A, B) Sound levels over distance from the speaker in bandwidths 100–1000 Hz and 1000–4000 Hz. (C, D) Sound levels of circular measurements around the speaker, at 75 cm from the speaker, at two depths. (E, F) Means of power spectral densities across distances and depth, for each sound treatment: eight sound stimuli and silence (ambient).

4. Experimental design and exposure protocol

In total, 10 groups of four fish were exposed to the eight different pulse trains, for each group of fish in a randomized order, over the course of two days (Figure 4). We recorded the swimming behaviour of the fish for seven hours on both days. We repeated the playback of each pulse train for a total of 10 exposures per sound stimulus with 1:38 (min:ss) silence intervals in between leading to a total duration of 15 min per sound stimulus treatment. Before the start of the first sound treatment and at the end of the last sound treatment of the day, there was 30 min of silence played back and between each sound stimulus treatment there was 1.4 h silence.

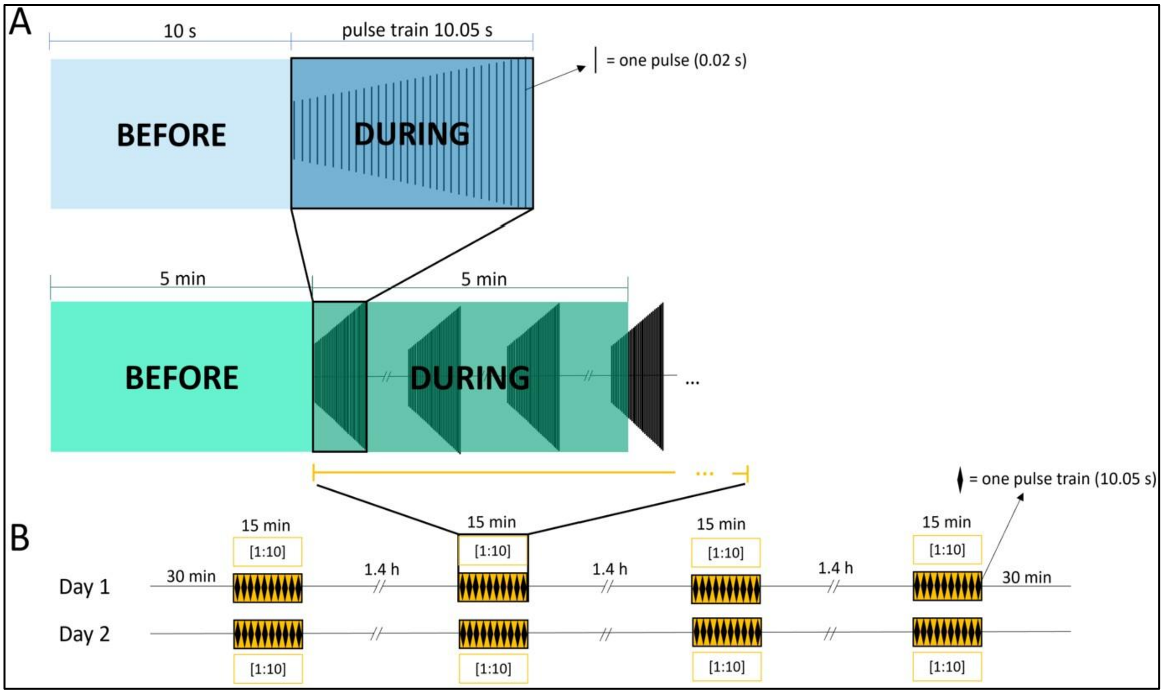

Figure 4. Simplified representation of the sound exposure and method of measuring behavioural change. The dashed lines breaking the timeline indicate that silent periods are longer than depicted here by scale. (A) In this example, one of the sound stimuli is depicted (regular pulse rate and fading in). A short-term response (blue) was measured as the immediate change in behaviour from 10 s before sound onset to 10 s during the pulse train. A long-term response (green) was measured as a change in behaviour from 5 min before a treatment period and 5 min during the treatment period (including just over 3 of the 10 pulse train repetitions in the overall 15 min treatment duration). (B) Two-day exposure with eight different sound stimuli (order was randomised). One diamond indicates one pulse train of a certain stimulus, which was repeated 10 times for a total duration of 15 min for each stimulus. Before the start of the first sound treatment and at the end of the last sound treatment of the day, there was 30 min of silence played back and between each sound stimulus treatment there was 1.4 h silence.

5. Behavioural measurements via 3D tracking

The video footage from the basin was processed with an automatic tracking software (EthoVision XT, Noldus Information Technology, Wageningen, The Netherlands). The software tracked the position of each individual fish of a group. From this, we calculated the mean position of a group. As we had five cameras alongside the wall of the basin, each two consecutive cameras were partially overlapping in field of view (Figure 1). We used these overlaps to calculate the 3D position (x,y,z) in R (Demuynck et al., 2024).

We used the tracked positions of the fish groups to assess their behavioural response, comparing behaviour right before and during playback, and at two different time scales (Figure 4). Short-term behavioural changes were calculated as the change in behaviour from before to during the first pulse train (10 s) of a sound playback period (during–before). Longer term behavioural changes were calculated as the change in behaviour from before to during the first 5 min of a treatment period. During this period, just over three repetitions of the pulse train of a treatment are included, of the total ten repetitions in a 15 min treatment period. We scored behavioural changes in speed, depth, group cohesion, and distance from the speaker. The latter can also be interpreted as thigmotaxis, as in the circular basin, swimming further away from the speaker also means swimming closer to the basin wall. Additionally, we manually scored turning behaviour. A turn was defined as a change in swimming direction. As control, we also scored behaviour for an equal amount of randomly selected silence playback periods for all behaviours. To test the fish's response persistence, we additionally looked at changes in behaviour over the course of the ten repetitions of a sound treatment (lasting 15 min), as well as over the course of the eight sound treatments in two days (Demuynck et al., 2024).

6. Statistics

A total of 10 groups of four fish were exposed to the eight different sound treatments over the course of two days. To answer the first research question on whether herring responds to the sound exposures at all, we used responses to all treatments. For the second question on differential effects of amplitude and pulse rate patterns, we grouped the treatments accordingly, leading to different sample sizes. Due to occasional equipment failure, fish were occasionally out of view of the camera, or a full day of experiments was lost, both leading to additional variation in sample sizes. These sample sizes are specified in each graph (see Results: $n = x$ at the top of each panel of the graphs in Figures 5–7).

Data analysis and statistical tests were conducted using R version 4.3.0 (R Core Team, 2023). A quasibinomial generalised linear model was used to test for an effect of treatment on the proportion of fish showing turning behaviour. ANOVAs were used to test for an effect of treatment on swimming speed, depth, group cohesion and thigmotaxis. The residuals of the ANOVA models did not show any deviations in the diagnostic plots (residuals vs fitted plot and QQ plot), which was taken as an indicator of normal distribution. Follow-up post-hoc tests for explorative, pair-wise comparisons were run with Tukey's HSD correction for multiple testing, using the 'emmeans' package (Lenth, 2023). For all tests, the threshold for significance was assumed at $p = 0.05$.

7. Permits and ethical notes

This experiment was conducted in accordance with the Dutch Experiments on Animals Act and approved by the Dutch Central Commission Animal Experiments (CCD) under no. AVD1060020171085.

Results

1. General response to sound playback

The fish typically swam in circles, relatively close (5–20 cm) to the basin wall. We saw a significantly higher proportion of fish from the group showing turning behaviour during sound playback compared to the quiet control periods (quasibinomial generalised linear model: intercept (control) = −2.41, slope = 3.07, p < 0.001) (Figure 5). From the automatically scored behaviour, the short-term (pulse train 10.05 s) behavioural response to any sound playback was a significant decline in depth (ANOVA: F1,44 = 5.60, p = 0.022) and a non-significant trend for an increase in distance from the speaker (ANOVA: F1,45 = 3.195, p = 0.081) during sound playback compared to silence playback. The other behaviours showed no significant changes during sound playback compared to silence playback: group cohesion (ANOVA: F1,44 = 1.628, p = 0.209) and swimming speed (ANOVA: F1,44 = 0.836, p = 0.365) (Figure 6). On the long term (5 min), none of the behaviours showed any significant changes during sound playback compared to silence: depth (ANOVA: F1,91 = 0.216, p = 0.644), speed (ANOVA: F1,91 = 0.144, p = 0.705), group cohesion (ANOVA: F1,91 = 2.582, p = 0.112) and distance from the speaker (ANOVA: F1,91 = 0.836, p = 0.228). Note that we ran one (turning), four (short-term changes) and four (longterm changes) tests. If we correct for multiple testing, taking clusters of nine (all, including turning), eight (only short- and long-term changes grouped), or four (only short- and long-term changes separate) into account, the turning behaviour remains statistically significant (p ⩾ 0.05 and <0.001), the diving down response became a non-significant trend (p < 0.1) and all other p-values were >0.1.

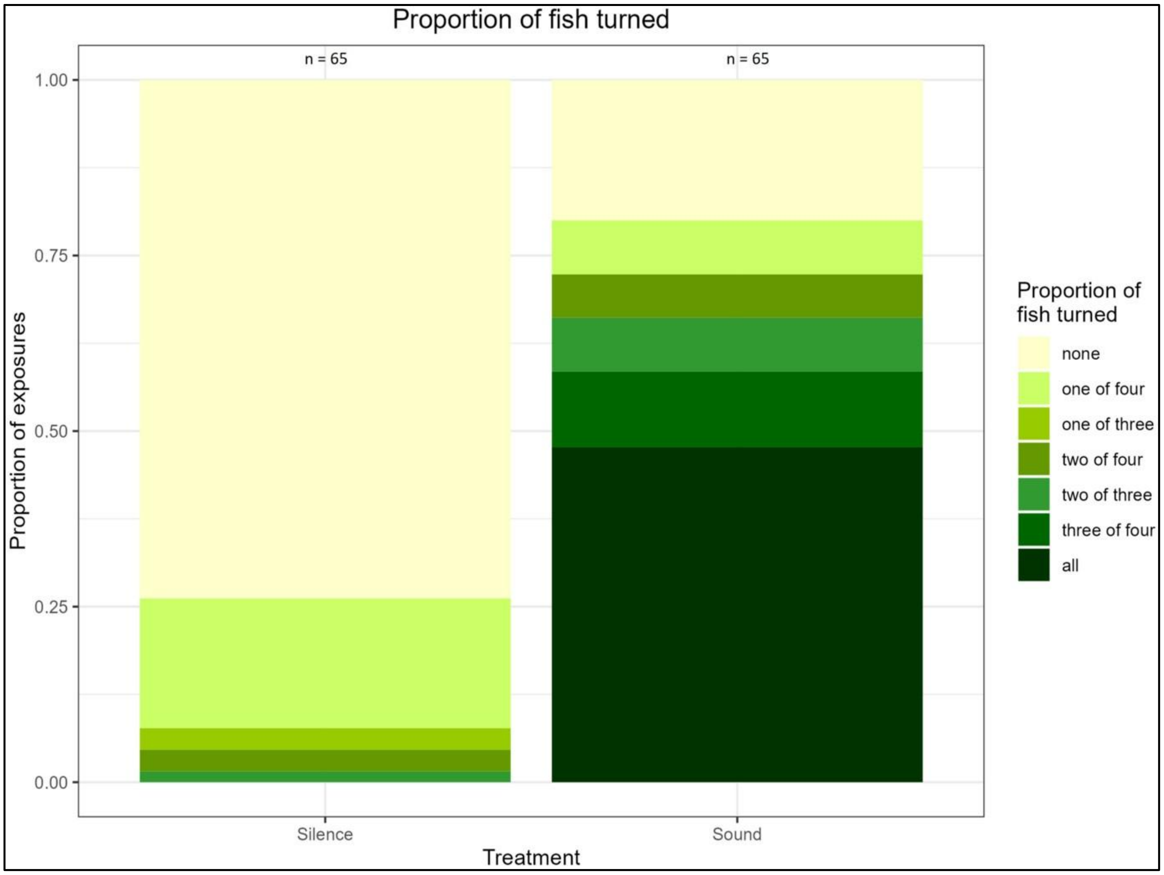

Figure 5. Proportion of fish of a group showing turning behaviour, during sound and silence playback. A turn was defined as a change in swimming direction. The difference between sound and silence in proportion of fish showing turning behaviour was statistically significant.

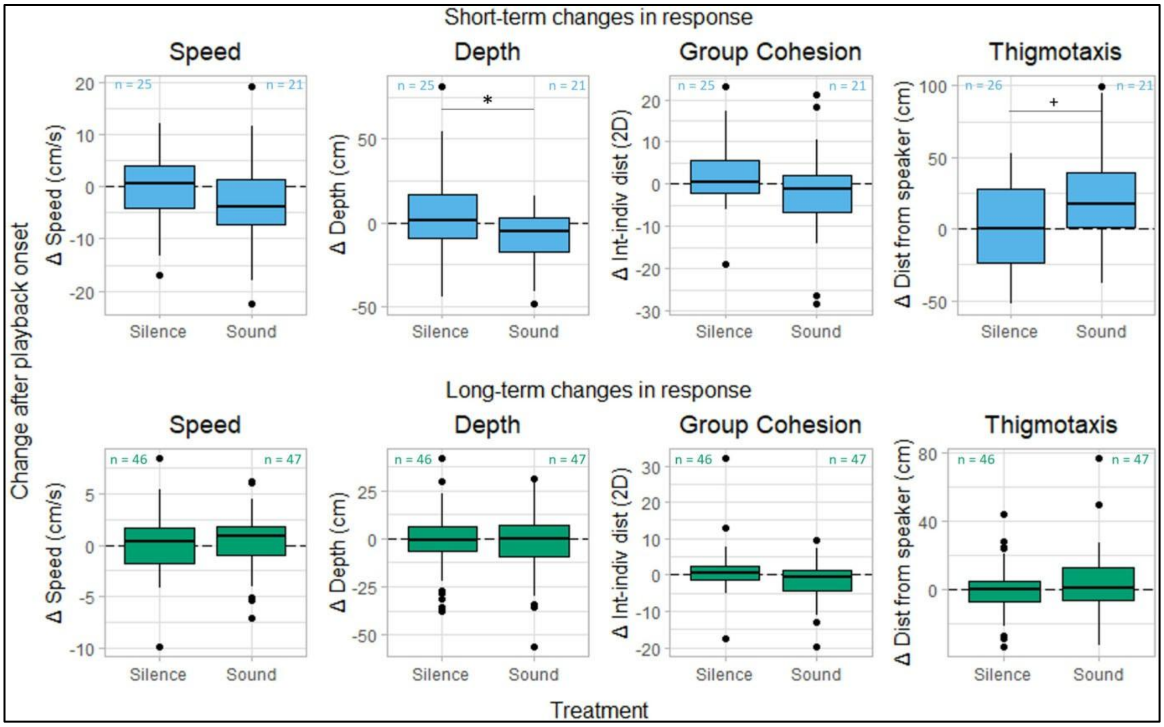

Figure 6. Short- and long-term changes in speed, depth, group cohesion and thigmotaxis (or distance from speaker), calculated by the subtraction of behaviour before from during playback. A positive value indicates an increase, while a negative value indicates a decrease in the behaviour. During the sound exposures, at a short timescale, the fish appeared to swim downwards (indicated by *), while there also was a tendency for an increase in distance from the speaker during sound playback (indicated by +). These effect sizes were not significant after correction for multiple testing.

2. Sound treatment effects

At the short timescale (pulse train 10.05 s), there was a non-significant trend for a pulse rate effect on the change in speed (ANOVA: $F_{2,20} = 2.626$, $p = 0.097$). There was a non-significant trend for a larger speed reduction during regular sounds compared to during accelerating sounds (posthoc: $t(20) = 2.277$, $p = 0.083$) (Figure 7). For all of the other behavioural changes (depth, group cohesion, thigmotaxis) at short timescale, differences between sound treatments were not significant (ANOVAs and post-hoc tests: all $p > 0.1$) (Figure 7). Also for turning behaviour, no significant difference was found between the sound treatments (ANOVAs and post-hoc tests: all $p > 0.1$). At the longer-term timescale, we found no differences between sound treatments for any of the behaviours (speed, depth, group cohesion, thigmotaxis; ANOVAs and post-hoc tests: all $p > 0.1$). We tested for an interaction effect between the sound stimuli variables, to see if certain combinations of amplitude and pulse rate patterns would elicit a stronger response in the fish. We found no interaction effects of the grouped stimuli (grouped by amplitude: constant, fade in, fade out; and grouped by pulse rate: regular, accelerating, decelerating) for any of the behaviours both at short- and long-term (ANOVAs: all $p > 0.1$).

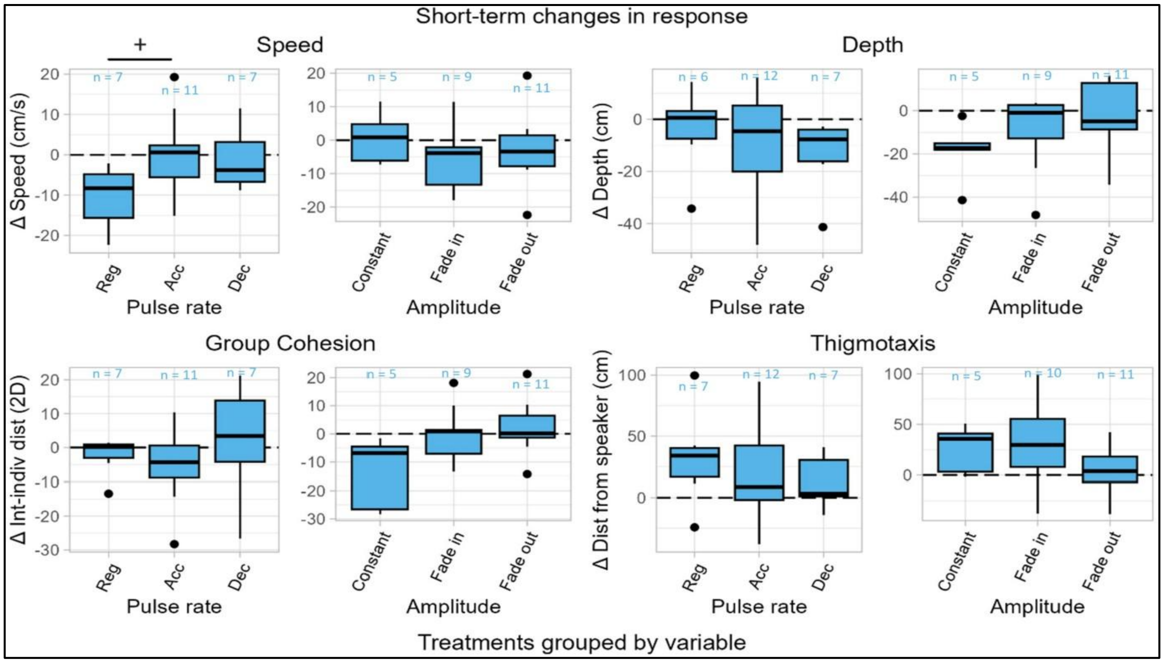

Figure 7. Sound stimuli effects on short-term changes in speed, depth, group cohesion and thigmotaxis (distance from speaker). The sound stimuli are grouped on the x-axis by variable: pulse rate and amplitude. A non-significant difference (indicated by +) was observed between regular and accelerating sound stimuli on speed.

Discussion

In the current study, we exposed groups of wild-caught herring to different sound treatments and used cameras to examine their behavioural response strength. We found the following answers to our research questions: (1) The herring responded to sound playbacks and we found the most distinct and significant effect in turning behaviour. Other behavioural changes were subtle and non-significant after correction for multiple testing. We believe it is still worthwhile to mention that the explorative testing suggested that the fish swam slightly deeper after the onset of sound exposure events compared to just before, while there were no such patterns in the other short- or long-term measures: speed, group cohesion or thigmotaxis (proximity to wall and distance from speaker). (2) We did not find significant differences in response levels related to stimulus variation and hence could not confirm the perceptual impact of a fade-in amplitude and an accelerating pulse rate as a looming stimulus for a fish species.

1. Meaning of turning responses

The wild-caught herring responded to our sound exposure stimuli through a clear change in their regular swimming pattern of consistent rounds, rarely far away from the circular basin wall. At a short time-scale (10 s), the clearest response to sound was found in turning behaviour. For almost half of the time of sound exposure, turning behaviour was displayed by all fish of a group. Turning may be associated with schooling behaviour, or less tightly coordinated shoaling. For example, an indoor study with golden shiners (*Notemigonus crysoleucas*) showed that the direction of turning of a focal fish in a small shoal (two or three fish) was mostly related to the position of its nearest neighbours (Katz et al., 2011). If fish turn more towards their nearby neighbours, turning may lead to a more cohesive group, and may be an adaptive response to a threat. In the wild, changes in the school structure of a school of herring have been associated with the approach of other schools, potential predators and a research vessel (Pitcher et al., 1996). A possible mechanistic explanation for some of these conditions and our results could be that noisy conditions undermine the sensing of nearby swimming fish by the lateral line system, which could thereby trigger a masking-induced turning response to check school mates. In our results however, turning was not restricted to the individuals in the two front positions and there was no significant change in group cohesion observed during sound exposure.

Despite a lack of a connection between the turning response to school cohesion, we believe that turning could still indicate a general state of vigilance or anxiety in the fish. Turning may affect individual and school movement predictability to a predator and group cohesion may yield protection especially to those fish that are not at the edge, which may be the rewarding target of turning individuals in larger schools (Pitcher et al., 1996; Doksæter et al., 2009; Katz et al., 2011). It should also be noted that in our study the schools of fish were much smaller than what is common for Atlantic herring in natural conditions, yet even the small group of fish still showed clear schooling behaviour. Fast turns, as observed in our small schools of herring, can also be seen as part of a 'startle reaction' as a sudden response to a potential threat. Starle reactions typically involve both turning and an increased swimming speed and can result in the fish school swimming away from the sound source, unlike in our study but as reported in another sound playback study testing multiple North sea fish species (including Atlantic herring) in captivity (Kastelein et al., 2008).

2. Swimming depth

Another response pattern in our results was statistically less robust, but is in line with our interpretation of turning being an indication of moderate disturbance. Fish swam deeper in the basin during sound playback compared to the baseline control periods of ambient quiet, also at the short timescale. Swimming down is a commonly observed behavioural response to a disturbance in captive fish, both in indoor as well as outdoor studies (Sarà et al., 2007; Handegard et al., 2010; Hawkins et al., 2014; Hubert et al., 2020). Diving responses have also been reported for free-swimming herring schools in previous studies: for example in response to killer whale feeding sounds (L. Doksæter et al., 2009, 2012), in response to killer whale attacks (Nøttestad & Axelsen, 1999), and in response to approaching predators and vessels (Pitcher et al., 1996; Ona et al., 2007). Hence, although the depth shift was only modest in our experiment, diving seems to be a clear disturbance response, with potential to assess variation in response strength related to stimulus variation (Neo et al., 2018). Further, the basin in our study had a limited depth range, hence potentially limiting the effect size of the dive response.

3. Lack of looming stimulus effect

Although we found a clear and abundant turning response and the suggestion of a moderate downshift in swimming depth, we did not find any significant variation linked to the different sound features across treatments. We expected the sound stimulus with a combination of an amplitude fade in and accelerating pulse rate to elicit the strongest response in fish, in a similar way as looming stimuli trigger stronger responses in humans (Trewhella et al., 2003), monkeys (Maier and Ghazanfar, 2007) and mice (Li et al., 2021). One hypothesis of why a looming stimulus would be important for these terrestrial mammals is because it may be related to hearing footsteps coming closer and running faster in case of an approaching predator on land (see e.g. Elliott et al., 1977; Stankowich & Coss, 2007). In water, fish are also known to be affected by proximity or speed of an approaching predator (Walker et al., 2005), but data on the underlying mechanism so far only involve visually looming stimuli without sound (Gallagher & Northmore, 2006; Temizer et al., 2015) or with synchronous sounds having a potentially synergistic effect (McIntyre & Preuss, 2019; Rodriguez-Pinto et al., 2024).

The lack of a response to the acoustic features of a looming stimulus may be due to a modest effect size overall, or a limited sample size for the amount of different stimuli tested. We also acknowledge that we still explored only limited variety in the specific temporal pattern of accelerating and fading in pulse trains. However, it could be true that fish in general are not sensitive to acoustic features that trigger at least several terrestrial mammal species, and there may be an ecological explanation. A threatening predator running on land towards prey could be associated with fading in and accelerating sounds, which is unlikely to occur in water. Predators like harbour porpoise use pulse trains for foraging, with accelerating pulse rates during the so called "buzz", but these vocalisations are outside of the hearing range of most prey species. The lack of a functional reality in water may be the reason that we did not find a looming effect related to fade in amplitude and accelerating pulse rate. Species-specific interpretation of the same environmental stimuli is referred to as the Umwelt concept of von Uexküll (Bueno-Guerra, 2018; Von Uexküll, 2013), and may well explain divergent responses to the acoustic features of a looming stimulus between terrestrial and aquatic taxa.

4. Application of sound as deterrent

The restricted space of the captive conditions and the short-term nature of the behavioural response do not allow for strong statements about application potential in the field for acoustic deterrent devices (ADDs). The lack of strong spatial shifts, vertically and especially horizontally, in captivity should therefore not be directly extrapolated to free-ranging conditions. Furthermore, the increased turning behaviour as immediate response could indicate potential for a deterrent effects in the field, yet the reaction may work out differently in a large school at sea and fleeing responses remain to be tested in the field. In previous research, horizontal avoidance has been observed in Atlantic herring in the field in response to killer whale feeding sounds, on top of a vertical diving response (L. Doksæter et al., 2009). Diving down may be the most common response to disturbances in free-ranging herring schools, yet they also seem to be capable of horizontal avoidance. We therefore believe it is worthwhile to test acoustic responsiveness at sea, and to explore the potential for acoustic deterrents for pelagic fishes. However, in a follow up field study at sea, using very similar sound stimuli, we found no spatial shifts in free-ranging pelagic fish (Hubert et al., 2024), which is in line with the absence of changes in speed and depth in the longer-term measurements of the current study in captivity.

In general, extrapolation from indoor studies on captive animals to outdoor conditions for free-ranging animals should typically not be about absolute thresholds or absolute response levels, and has to be done with great care anyway (Slabbekoorn, 2016; Hubert et al., 2020;). However, in our case we have done both. In the present indoor basin study we took advantage of the amount of detail in which we could observe the behaviour of the captive herring and the amount of control for the exposure conditions and sample sizes. We followed up with an outdoor exposure study at sea with free swimming fishes (Hubert et al., 2024). We tested responsiveness of free-ranging pelagic fishes via bottom-mounted echosounders to similar pulse train variants in the Belgian part of the North Sea. However, in this study the amount of control was naturally lower, e.g. we could not control what fish species was exposed. Interestingly, also in that study we did not find any significant spatial shifts; fish did not dive down and did not flee horizontally away from the area of elevated sound exposure (Hubert et al., 2024). The sound levels of the current study with captive herring were higher than in the field study at sea. In combination, these studies suggest that ADDs may not have the same deterrent potential for fish as for marine mammals, although other sound stimuli could still be tested for the potential to trigger a stronger response in fish. Furthermore, it is possible that louder sounds at sea, or the presence of different fish species, may yield more responses, but this should be investigated before we can exclude any value for ADDs and acoustic herding of fishes.

Conclusions

Our results showed clear responsiveness to sound in wild-caught Atlantic herring in captive conditions, mainly in turning behaviour. Turning behaviour may reflect a moderate level of alertness and anxiety and may serve in schooling dynamics of larger aggregations of free-ranging fish at sea. Our follow-up study at sea did not reveal strong reactions either, and a lack of any spatial responsiveness. The potential for sound to be used in ADDs for acoustic herding of pelagic fishes seems therefore not so high, based on the current results and the follow-up test at sea. The overall subtle behavioural changes did not reveal any impact of pulse train variation nor a looming stimulus effect from fade-in amplitude or accelerating pulse rate. The perceptual salience of these specific features may be restricted to terrestrial animals, where the stepping sounds of an approaching predator may get louder and faster. However, our negative results could be due to a modest effect size, and we therefore suggest further studies. We also argue we need more insight from fish movement patterns at more and louder sound exposure conditions at sea, and data on more species is necessary for any taxonomic extrapolations.

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