Interacting effects of short-term and long-term noise exposure on antipredator behaviour in sand gobies

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In today's marine habitats, anthropogenic noise is widespread in space and time, affecting aquatic animal communities. Short-term exposure to noise is known to affect vital behaviours, such as the ability to evade predators. However, long-term noise pollution may lead to differences in short-term responses between naïve and experienced animals. We investigated the interaction between short-term and long-term sound exposure on the antipredator response of free-ranging sand gobies, *Pomatoschistus minutus*. We tested the effects of short-term boat noise playback on the response to a simulated predator strike in areas across a range of low to high long-term noise disturbance levels. Exposure to boat noise did not affect the startle response, time frozen or response latency of gobies to a predator stimulus. However, individuals exposed to short-term boat noise playback were absent from the experimental area for shorter periods after the predator strike than gobies exposed to the silent control. Moreover, gobies in long-term noisy habitats also stopped avoiding the area after the predator strike under silent control conditions. These changes point to a decreased magnitude in antipredator response, as a function of interacting short- and longer-term levels of disturbance. Thus, prey species alter their antipredator behaviour in ways that can potentially lead to higher mortality for individual prey. This could ultimately have implications at the level of the food web.

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Noise pollution is omnipresent in today's terrestrial and marine habitats and may affect individual species, as well as changing species interactions and animal communities (Barber, Crooks, & Fristrup, 2010; Francis, Ortega, & Cruz, 2009; Kunc, McLaughlin, & Schmidt, 2016; Shannon et al., 2016; Slabbekoorn et al., 2010, 2019). Repeated or continuous exposure to anthropogenic noise may cause long-term changes in animal behaviour, due to processes such as habituation or sensitization (Bejder, Samuels, Whitehead, Finn, & Allen, 2009; Harding et al., 2018). Therefore, studies on noise impact should include the potential effects of habituation and sensitization to long-term sound exposure of non-naïve individuals. Currently, studies only focus on the short-term effects of noise pollution on antipredator behaviour, or on the

changes in direct response to noise after long-term exposure (Harding, Gordon, Eastcott, Simpson, & Radford, 2019; Nedelec et al., 2016; Neo et al., 2016; Radford, Lebre, Lecaillon, Nedelec, & Simpson, 2016; Simpson et al., 2016; Simpson, Purser, & Radford, 2015; Voellmy, Purser, Simpson, & Radford, 2014).

Repeated exposure to particular sounds can either increase or diminish the behavioural response of individuals of a particular population. Behavioural responses may get stronger through sensitization to the disturbance. This is often caused by sudden and loud sounds that induce a startle reflex in animals (Götz & Janik, 2011). Alternatively, the effect of sound on animals that are exposed repeatedly can diminish over time. The diminishing effect of repeated exposure can have three causes. First, animals living in disturbed areas may have become habituated to the noisy conditions (e.g. Nedelec et al., 2016). Second, noncoping individuals may have left the disturbed area, leaving only individuals that are intrinsically more able to cope with the disturbance (Bejder, Samuels, Whitehead, & Gales, 2006). Third, noncoping individuals

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that stay in the area might die sooner than coping individuals, for instance by increased chance of predation (Simpson et al., 2016). A combination of these factors could thus lead to decreased effects of short-term noise exposure for individuals remaining in disturbed areas.

A specific effect of exposure to anthropogenic noise concerns the change in antipredator behaviour of prey. Changes in antipredator behaviour have a high potential to affect survival rates of the prey species, as a decrease in effectiveness of antipredator response could mean death of the organism (e.g. Simpson et al., 2016). Effects of short-term noise exposure on antipredator behaviour have been found across taxa, including fish (McCormick, Allan, Harding, & Simpson, 2018; Simpson et al., 2016, 2015; Voellmy et al., 2014), invertebrates (Chan, Giraldo-Perez, Smith, & Blumstein, 2010; Hubert et al., 2018) and mammals (Kern & Radford, 2016; Morris-Drake, Kern, & Radford, 2016). Most studies showed changes in antipredator response latency, using simulated predators (but see Bruintjes & Radford, 2013 for an exception). One study also included live predation events, showing that prey were indeed more easily caught by a predator under noisy conditions (Simpson et al., 2016). However, the direction of change differed between species: some prey species showed increased response latency under noisy conditions, while others showed a decreased response latency.

Two mechanisms have been proposed to explain these opposite directions of change in response latency of prey under noise exposure. A longer response latency could be explained by distraction by nonrelevant stimuli (the distracted prey hypothesis:

Chan & Blumstein, 2011; Rosa & Koper, 2018), while a shorter response latency could be due to increased vigilance, interpreted as being due to perceived threat by the noise (the risk disturbance hypothesis: Frid & Dill, 2002). Both distraction and vigilance have been reported in experimental studies of predation risk under noise exposure, although for some studies the experimental set-up leaves room for other interpretations (distraction: Chan et al., 2010; McCormick et al., 2018; Morris-Drake et al., 2016; Simpson et al., 2015, 2016; vigilance: Karp & Root, 2009; Kern & Radford, 2016; Shannon et al., 2016; Voellmy et al., 2014). Still, these reported changes were all for animals living in similarly quiet conditions, while the type and magnitude of the effect is likely to be different for individuals in disturbed versus nondisturbed areas (Bejder et al., 2006). To the best of our knowledge, combined effects of short- and long-term sound exposure on antipredator behaviour have never been tested.

To study the effects of short-term and long-term noise on antipredator behaviour, sand gobies, *Pomatoschistus minutus* Pallas, 1770, are a suitable study system. Sand gobies are benthic sit-and-wait predators, which are easy to observe in the field and which have been shown to be sensitive to acoustic disturbance (Blom et al., 2019; de Jong, Amorim, Fonseca, Fox, & Heubel, 2018). They are under high predation pressure by fish and marine mammals (Leopold, 2015; Magnhagen & Forsgren, 1991), so changes in their antipredator behaviour may have large consequences. Goby antipredator behaviour has two stages. When a predator passes, most gobies become less active and burrow themselves in the sand to escape detection (Forsgren & Magnhagen, 2011; Magnhagen,

Figure 1. Experiment locations in the Grevelingen (8) and the Veerse Meer (5) (partially closed river ends in the south of The Netherlands; white square). Locations were selected to include habitats with a gradient in the number of boats passing by per day and the mean ambient sound levels. Harbours near the experimental locations are indicated with a yellow anchor (source: Google Inc.).

1988). If, however, a predator comes too close, gobies will show a startle and flight response to escape a direct attack (Magnhagen & Forsgren, 1991) or bury themselves in the sediment to avoid predation (Ehrenberg & Ejdung, 2008).

Here, we investigated the effects of short-term boat noise on the antipredator behaviour of free-ranging sand gobies inhabiting areas across a range of low to high long-term noise disturbance levels. We addressed the following questions. (1) Is goby behaviour affected by a simulated predator strike? (2) If so, how does playback of boat noise affect a goby's antipredator response (short-term effect)? (3) Is the level of disturbance of the habitat and thereby the level of the experience with noisy conditions related to a goby's antipredator response (long-term effect)? Our results provide insight into how short-term and long-term noise exposure can interact to affect antipredator behaviour.

METHODS

Study Site

All experiments were conducted April–June 2018 in two salt water lakes, Grevelingen and Veerse Meer, in Zeeland, The Netherlands (Fig. 1). In total, 13 locations were sampled, eight in the Grevelingen and five in the Veerse Meer. Both lakes are in part connected to the North Sea, either directly or via an estuary, and maintain brackish (Veerse Meer) to salt (Grevelingen) conditions. Commercial shipping is rare, but recreational shipping is abundant, especially in summer. Most recreational shipping activity is concentrated around harbours, which leads to a patchy soundscape of quiet and noisy areas. The bottoms of the lakes are typically open areas, mostly covered with sand, with small reef formations on loose rocks and seaweed. Sand gobies are omnipresent in the area and make their nests in the sandy substrate.

Soundscape

At all 13 locations, the soundscape was measured for 22 h during 30 April – 11 May 2019 (24 h was not possible for logistical reasons). Recordings were made using autonomous recorders (Sound Traps, Ocean Instruments, Auckland, New Zealand) at a sample rate of 192 kHz, and temperature was recorded every 10 s. We sampled all locations in the same season, but before the recreational peak. We therefore believe to have assessed fair habitat-dependent noise levels, but differences may actually still be an underestimate of sound conditions later in the year. The recorders were stabilized in the water column using weights and a subsurface float. Water depth at each location was 1.20–2 m. After retrieval, sound recordings were analysed for root-mean-square sound pressure level (SPL_{rms}), during day and night, using PAMGuide (Merchant et al., 2015). For each location, we determined the ambient SPL_{rms} (henceforth called Ambient-SPL) from the soundscape recordings.

Experimental Design

Experiments consisted of exposing free-ranging gobies to a simulated predatory attack (sensu Lorenz & Tinbergen, 1939), in combination with sound playback, according to a nested design. At each location, two treatments were conducted, one silent control (but with the speaker on) and one with boat noise playback. The predator strike consisted of a model predatory fish (constructed from PVC tube, chicken wire and duct tape to have a streamlined front), mounted on an aluminium frame, that – when released – approached the location of the goby. The aluminium frame also supported two cameras (GoPro HERO4, GoPro Inc., San Mateo, CA U.S.A.) to record the behaviour of the gobies (Fig. 2). Only gobies found guarding nests (i.e. stationary location) were targeted to ensure similar experimental start conditions and behavioural context. By itself, nest guarding restricts individual dispersal. Under this condition, gobies exposed to a predation threat may not only incur predation mortality but also lose their reproductive effort. Thus, this behaviour is one that involves a strong trade-off between the risks of mortality against the risk of losing offspring (Maxwell et al., 2018). The frame was placed such that the nest was in the centre of the frame. The playback speaker (Lubell UW30) was placed next to the frame at 1 m distance.

After placement and a 10 min acclimatization period, the playback was started remotely, playing either boat engine sound or the silent control. Five minutes into the 15 min playback, the predator was released remotely by releasing a 5 m rope. Two experiments
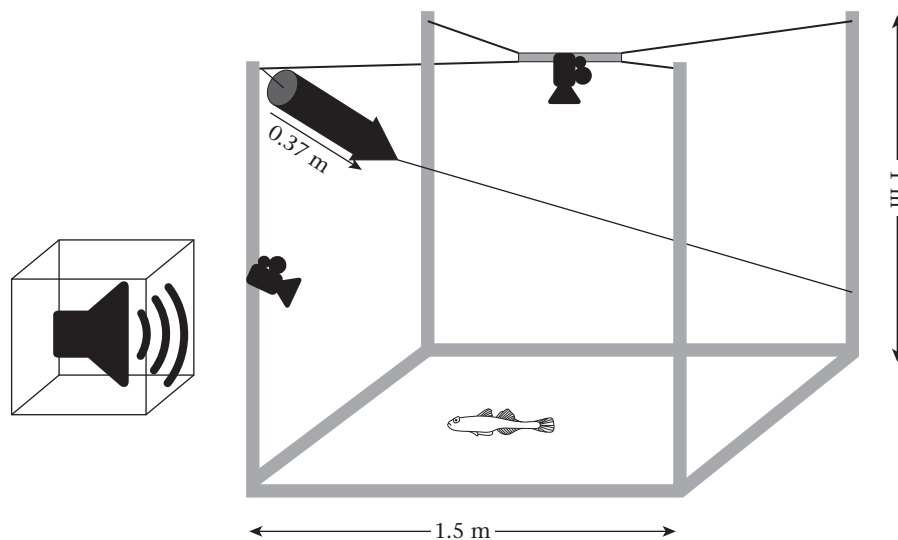

Figure 2. Schematic overview of the experimental set-up. The construction was placed over a goby nest. After a 10 min acclimation period, the speaker played either boat noise or a silent control for 10 min. After the first 5 min of playback, the simulated predator was released by releasing a rope from a distance of 5 m to slide across a fishing line in a simulated predator strike. Cameras recorded the goby's response.

could be conducted simultaneously, one with a silent control and one with boat sound. The two experimental frames were always placed at a distance of 15 m or more apart, because the playback sound did not propagate beyond 10 m (as verified with sound pressure recordings).

Ethical Note

At all times, animals were able to leave the experimental area and thus reduce their exposure to noise. The project was licensed by the Dutch Ministry for Infrastructure and the Environment (Rijkswaterstaat; project number RWSZ 2018-00003561B).

Playback Sounds

All boat engine playback sounds were recorded with an AS1 hydrophone (Aquarian Scientific, Anacortes, WA, U.S.A.) with external amplifier, coupled to a handheld recorder (Tascam DR-100). Sounds were high-pass filtered at 10 Hz to remove static noise from the hydrophone and were cleaned to remove unusually loud sounds, e.g. from water movement. Speaker characteristics led to a high-pass cutoff frequency (i.e. the frequency below which sound does not propagate) of 100 Hz in the field (Fig. 3), which is below the cutoff frequency that occurs naturally because of the shallow waters. Boat sounds were recorded from passing boats at 5–20 m, at several locations in both lakes. Recordings with a section with a clear approach and exit, i.e. with a clear ramp-up and ramp-down of the sound, were selected and copied 5–10 times to produce a 15 min playback stimulus (using Audacity 2.1.1, https://audacityteam.org/). All playback stimuli were normalized to the same dynamic range to standardize playback level. To avoid startle responses at the onset of the playback, a stimulus started with a 10 s fade-in. To avoid pseudoreplication of the stimulus, a different version of the stimulus was used for each location.

Stimulus SPL was measured using an AS1 hydrophone (Aquarian Scientific) with external amplifier, coupled to a handheld recorder (Tascam DR-100). Sound velocity levels (SVL) were measured with an M20 accelerometer (Geospectrum Technologies, Dartmouth, NS, Canada) coupled to an oscilloscope (Picoscope 3000, Pico Technology, Cambridgeshire, U.K.), which was connected to a laptop running a custom-made measuring programme (Campbell, 2019).

Playback sounds were recorded at 1 and 2 m depth, at ~1 m from the speaker in the centre of the experimental arena. On average, played back boat sounds had an SPL_{rms} of 98–101 dB re 1 μPa and an SVL_{rms} of 83–84 dB re 1 nm/s, at 1–2 m depth, respectively. These levels are similar to boats passing by at 50–200 m (calculated using spherical spreading based on received levels of recorded boats).

Data Analyses

The goby antipredator response could range from (1) freezing, a cryptic response when the predator is passing by, to (2) an active escape response, either (a) a startle without displacement or (b) leaving the site of attack (see Supplementary Video S1 for an example). For each experiment we recorded the time a goby was frozen, whether or not it startled and the time it was away from the visible field of the camera (absent; i.e. left the immediate area of the nest) for 1 min before and 1 min after the predator strike. We conducted 23 experiments with the silent control treatment and 17 experiments with the boat noise treatment. All analyses were done blind to the experimental conditions (i.e. videos were analysed without audio). Behavioural analyses were blind to the start of the predator strike (not visible in the video recording).

Video recordings of the experiments were analysed frame by frame, using Kinovea (version 0.8.15, www.kinovea.org). The time frozen was defined as a period of time in which the goby remained completely still, so excluding times when the goby was showing subtle movements, such as waving of the pectoral fin. Proportion of time frozen was calculated from dividing the time frozen by time in sight of the camera. If the goby left the field of view, it was recorded as having left for the rest of the sampling period, unless a goby coming back into view could be identified as the focal animal (i.e. by returning to its nest). We also measured response latency, another factor that is often found to change due to exposure to anthropogenic noise (Chan et al., 2010; McCormick et al., 2018; Simpson et al., 2015, 2016). This was calculated as the time until the goby showed a change in moving to not moving or vice versa after release of the predator, for example from swimming to frozen or from sitting still to swimming.
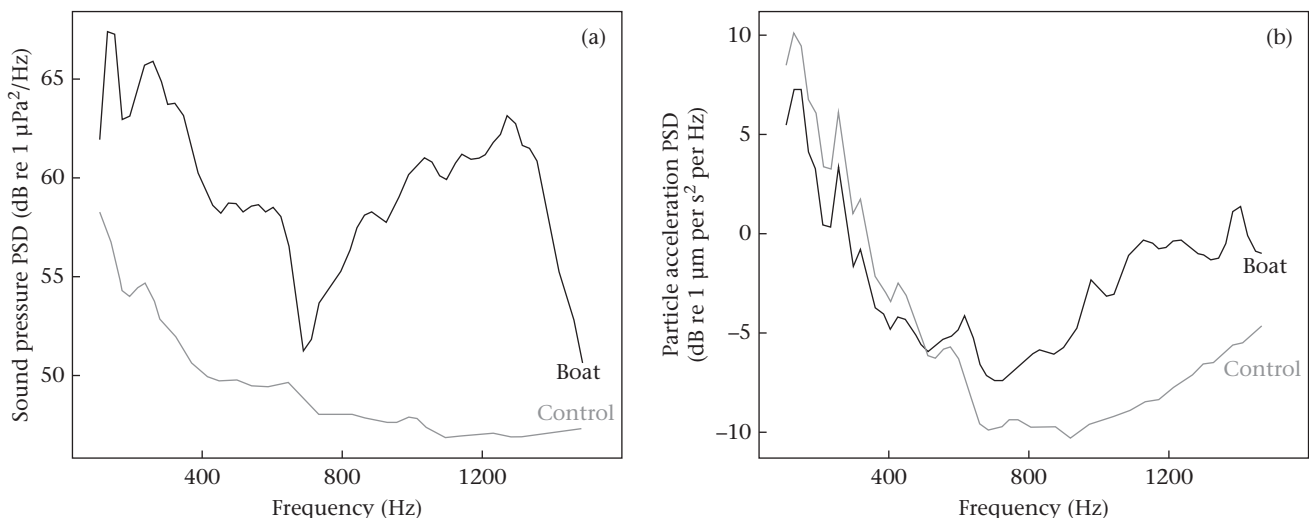

Figure 3. Sound pressure and particle acceleration spectral levels of the stimuli. Average power spectral density (PSD) levels of all silent control (light grey) and boat (dark grey) playback sounds played back in 2 m water depth. PSD levels were measured for (a) sound pressure levels and (b) particle acceleration levels.

Statistical Analysis

To investigate the effect of the sound playback on (1) the proportion of time the individuals were frozen, (2) whether the gobies startled to the predator strike, (3) response latency and (4) the proportion of time the gobies were absent, we performed generalized linear models (GLMs). For measures (1), (3) and (4), we used a beta distribution (link function = logit; Douma & Weedon, 2019). For response latency, this required a zero-one-inflated beta-distributed Monte Carlo Markov chain (MCMC). For the startle response, we used a binomial distribution. Additionally, we performed a zero-inflated beta MCMC on the time gobies were absent before predator release.

Explanatory variables in the full models were treatment type (control or boat noise), Ambient-SPL and the interaction between these two. For the response variable 'proportion of time absent', we also included the time absent before predator release. For the response variable 'response latency', an extra included explanatory variable was whether the goby startled. All control treatments were matched with all boat treatments within the same location to control for location effects. Model assumptions were checked by visual inspection of the predicted versus the fitted residuals.

The response variables 'proportion of time individuals were frozen' and 'proportion of time gobies were absent' were calculated as follows. The proportion of time frozen was calculated as the change in proportion of total time present (which could deviate from the total observation time as gobies left the observation area) in which individuals were frozen before and after predator release. The proportion of time absent was calculated as the change in proportion of the total observation time (60 s) gobies were absent, between the period before predator release and the period after predator release.

$$\text{Change} = \frac{\text{Proportion After} - \text{Proportion Before} + 1}{2}$$

where a value of 0.5 indicates no change in time spent frozen/time absent, a value of 0 indicates the largest decrease in time frozen/time absent from view upon predator release and a value of 1 indicates the largest increase in time spent frozen/time absent after predator release (for the statistical model, a distribution with only positive values was required).

We then investigated the influence of the explanatory variables on the four response variables that we had measured. For the zero-one-inflated MCMC, the influence of the explanatory variables were tested using a likelihood ratio test from the 'lmtest' package (Zeileis & Hothorn, 2002). The other final GLMs were selected using the 'dredge' function from the 'MuMIn' package, which selects the best model based on corrected Akaike information criterion (AICc) scores and circumvents order effects in model selection (Bartoń, 2017). After dredging, variable estimates were calculated by bootstrapping: the data set was resampled from the original data and estimates were calculated 10 000 times. If estimates of the explanatory variables did not cross zero in the 95% confidence interval (CI), explanatory variables were considered to be of significant influence on the response variable. All final models had normally distributed residuals.

RESULTS

Habitat and Experimental Sound Levels

Ambient-SPL ranged from 68 to 96 dB re 1 μPa for the 13 locations (Fig. 4). In many locations (9 out of 13), the Ambient-SPL was slightly to significantly elevated by transient sounds, while long-term ambient sound levels over the day were similar for all locations (Fig. 4). Both lakes had a range of quiet (e.g. Fig. 4a, c) to noisy (e.g. Fig. 4b, d) locations. Boat noise mostly increased sound levels above 200 Hz due to the shallow water depths in all experimental areas (the cutoff frequency at 2 m depth is ~765 Hz). Local wave noise from boats and wind increased sound levels up to 300 Hz, but mostly at frequencies below 200 Hz.

Effect of Simulated Predator

Goby behaviour was affected by a simulated predator attack. Although gobies did not change the time they were frozen when the predator was released under the silent control treatment (Table 1), they did startle to the predator (39% of all individuals) and often left their nest site.

Short-term Effect of Boat Noise

There was no significant impact of boat noise playback on the time gobies were frozen. However, there were a number of nonsignificant trends in the freezing data. Gobies tended to increase their time frozen after predator release more under silent playback than under boat noise playback (nonsignificant trend; Fig. 5a, Table 1). Gobies also showed no significant difference in their probability of startling to the predator between silent control and boat noise treatments (Table 1). Of the 23 gobies exposed to the silent control, 9 (39%) startled to the simulated predator, and of the 17 gobies exposed to boat noise, 7 (41%) startled to the simulated predator.

Gobies responded equally fast to the predator release under boat noise treatment and the silent control treatment (Fig. 5b, Table 1). However, the strong variation in individual response latencies observed in short-term silent control conditions disappeared nearly entirely under boat noise playback conditions. Gobies exposed to boat noise playback showed significantly smaller variation in their response latency than those exposed to the silent control (precision value: 95% CI estimate range = [0.5, 2.83]). Gobies that startled showed significantly shorter response latencies (i.e. responded faster) to the predator than gobies that did not startle, both during boat noise and silent control (Table 1; 95% CI estimate range = [-4.05, -1.58]).

Furthermore, gobies responded to the simulated predator by leaving their nest site. During the silent control, gobies spent significantly more time absent from the site after predator release, compared to before release (Fig. 5c, Table 1).

Long-term Effect of Ambient Sound Levels

There was no significant effect of the location-dependent Ambient-SPL on the time gobies were frozen after predator release, but a higher long-term Ambient-SPL in the habitat tended to lead to a decreasing time spent frozen after predator release (nonsignificant trend; Fig. 5d). The presence of a startle response was not affected by long-term noise levels either (Ambient-SPL was therefore excluded from the final model in model selection). Furthermore, Ambient-SPL at the location did not influence response latency for either exposure context (Fig. 5e).

Long-term noise levels in the habitat did affect the time gobies were absent (Fig. 5f). At increasing Ambient-SPL, individuals significantly reduced their time absent from the nest area after release. In contrast, under short-term boat noise playback conditions, there was no change in the time a goby was absent after predator release. This lack of change was caused partly by individuals that did not leave the site after the predator strike but
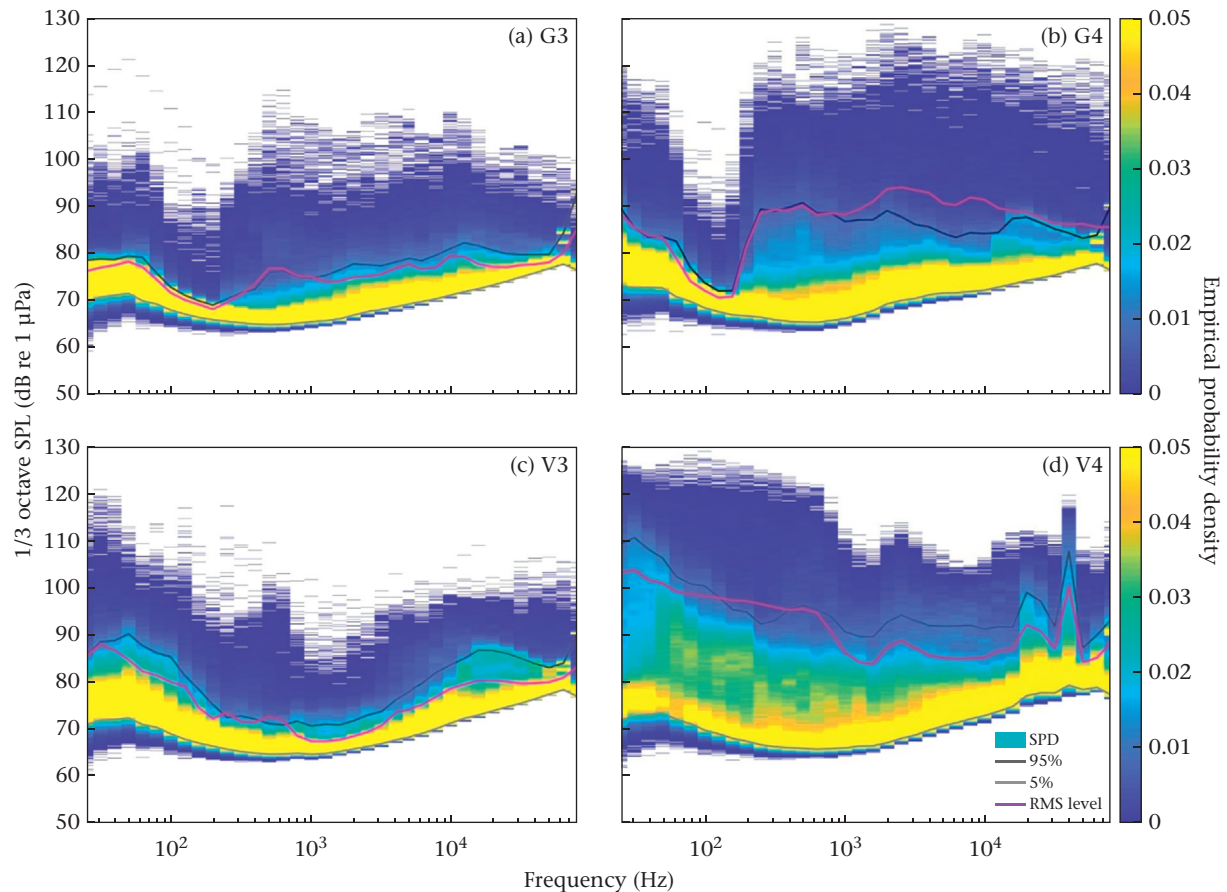
Figure 4. Daytime sound pressure level (SPL) of ambient sound at four of the 13 experimental sites (probability densities of 1/3 octave SPLs). The four panels show (a) a quiet site and (b) a noisy site in the Grevelingen and (c) a quiet site and (d) a noisy site in the Veerse Meer. Colours indicate the probability of a particular sound level occurring, with warmer colours indicating a higher probability. Lines indicate 5% and 95% of all sound levels sampled (light grey and black lines), and SPL$_{rms}$ levels (lilac line). Note the effect of the shallow water cutoff in sound propagation by the dip in sound levels at ~200 Hz (a, b).

appeared even stronger due to individuals that were already absent part of the time before the predator strike.

Absence in the period before the predator strike was significantly more likely to occur during boat noise playback than during the silent control (absence under silent control: 6 individuals; absence under boat noise: 10 individuals; Table 1). Importantly, when controlling for time absent before the predator strike, by including only individuals that did not leave the site, all factors were still significant (Table 2). The lack of change in absence under short-term boat noise playback conditions was not influenced by the longer-term noise levels of the habitat: it was independent of Ambient-SPL (Fig. 5f). At the highest long-term noise levels, the lack of change in absence occurred not only during the short-term boat noise playback, but also during the silent control.

DISCUSSION

Both short-term and long-term noise pollution levels significantly altered the antipredator response of free-ranging sand gobies. Under natural conditions, simulated predator presence invoked an avoidance response in gobies, making them leave the area directly around their nest. The experimental predator attack-induced displacement depended on both short- and long-term noise levels of the habitat. Short-term boat noise induced a reduced avoidance response to the predator: individuals left the immediate surrounding of their nest site for shorter periods. This effect was independent of long-term noise levels in the habitat.

Individuals exposed to high levels of long-term noise, however, also showed suppressed antipredator flight response under silent control conditions. In disturbed sites, where gobies were frequently exposed to high noise levels, incidental short-term noise did not further suppress their response. Hence, short- and long-term noise levels in their habitat interacted to influence goby antipredator response.

Boat Noise-dependent Short-term Effects

Our results provide another example of the impact from boat noise on the response strength towards the visual stimulus of a looming predator (Chan et al., 2010; McCormick et al., 2018; Morris-Drake et al., 2016; Simpson et al., 2015, 2016). However, the observed effects in our study differed from previous observations in the literature. The playback of boat noise induced a shorter period of absence for the gobies, while they also tended to freeze less. This occurred without an apparent delay in detection or processing of the stimulus, as reflected by the lack of a significant effect on response latency. Hence, the hypothesis that the sand gobies are distracted by noise does not hold.

Distraction has been posed as an explanatory mechanism behind alterations in antipredator responses (Chan & Blumstein, 2011). The extra sensory input of the sound could lead to less processing capacity for the risk assessment of the visual predator stimulus. This explanation has been posed in other studies that showed a change in behavioural responses to a nonauditory

Table 1
GLMM model results of the effect of playback type (control or boat noise) on goby behaviour

Response variable	Explanatory variables	Limit estimate			
		2.5%	97.5%	5%	95%
Change in time frozen	Intercept	-5.85	0.75	-5.40	0.35
	Playback type (boat noise)†	-0.28	6.85	0.17	6.38
	SPL	-0.0075	0.067	-0.003	0.06
	Playback type:SPL†	-0.079	0.0019	-0.073	-0.003
	Precision (φ)				
	Intercept*	1.91	3.69	1.96	3.48
	Playback type (boat noise)†	-0.20	2.59	0.049	2.36
Startle	Intercept†	-1.95	7.16×10^{-17}	-1.73	-0.11
	Playback type (boat noise)	-0.42	2.48	-0.16	2.20
Change in time absent	Intercept*	0.65	1.00	0.84	1.00
	Playback type (boat noise)*	4.45×10^{-6}	0.24	1.03×10^{-5}	0.10
	SPL*	0.47	0.50	0.48	0.50
	Playback type:SPL*	0.50	0.53	0.51	0.53
	Precision (φ)				
	Intercept*	0.83	1.87	0.88	1.73
	Playback type (boat noise)†	-0.15	3.03	0.02	2.70
Time absent before pred.	Intercept	-12.28	11.35		
	Playback type (boat noise)	-4.55	23.27		
	SPL	-0.14	0.14		
	Playback type:SPL	-0.27	0.06		
	Probability of 0 (zi)				
	Intercept*	0.16	2.06		
	Playback type (boat noise)*	-2.92	-0.12		
	Precision (φ)				
	Intercept*	0.84	2.87		
Response latency	Intercept	-5.73	5.23		
	Playback type (boat noise)	-7.55	4.43		
	SPL	-0.07	0.05		
	Startle (yes)*	-4.05	-1.58		
	Playback type:SPL	-0.06	0.08		
	Playback type:Startle	-0.15	2.76		
	Probability of 0 or 1 (zoi)				
	Intercept*	-2.03	-0.12		
	Playback type (boat noise)	-2.20	0.99		
	Precision (φ)				
	Intercept	-0.81	0.77		
	Playback type (boat noise)*	0.08	2.30		
	Startle (yes)*	2.25	4.46		

SPL: sound pressure level; zi: zero-inflated; zoi: zero-one-inflated. Models tested the proportion of time a goby was frozen, whether a goby startled, the proportion of time a goby was in sight of the camera and the response latency to the release of the predator. All models included one or more precision variables that described the variance of the posterior distribution of the model. The models for 'time absent before predator release' and 'response latency' separately modelled the probability of observing zero or zero and one. Note that estimate values of the models for time frozen, time in sight and response latency were logit-transformed because of the beta distribution and that estimate values of the model for startle were arcsine-transformed because of the binomial distribution. Estimates should therefore be converted before comparing to the data.
†$P < 0.1$; *$P < 0.05$.

predator stimulus under noisy conditions (Hasan, Crane, Ferrari, & Chivers, 2018; Tidau & Briffa, 2019). However, most experimental studies that have reported a sound-related change in antipredator behaviour due to distraction have also found a larger response latency for distracted animals (Chan et al., 2010; McCormick et al., 2018; Morris-Drake et al., 2016; Simpson et al., 2015, 2016). Whereas the variance in response latency decreased in the present study, gobies did not change their average response latency to the predator; thus, we argue that the individual gobies in our study were not distracted.

However, the addition of the sound stimulus used in this study could have decreased vigilance levels in response to the visual stimulus (Frid & Dill, 2002), possibly in a form of cross-modal habituation (Halfwerk & Slabbekoorn, 2015; Sörqvist, Nöstl, & Halin, 2012). Many species show varying levels of vigilance behaviour, which can be related to cues in their environment associated with variable levels of risk (Laundré, Hernández, & Ripple, 2010; Magrath, Haff, Fallow, & Radford, 2015). The acoustic cue of a boat could be associated with a nonpredatory presence (as people in recreational boats do not tend to fish for gobies and they may guarantee the absence of natural goby predators), leading to a lower risk level of overpassing shadows. Alternatively, it could

be that gobies exposed to boat noise playback were already in a state of heightened vigilance, which would lead to a smaller change in behaviour due to the predator strike. In this case, the individuals exposed to boat noise playback should have already been absent part of the time before predator release. Indeed, gobies that were temporarily absent in the period before predator release, were nearly all exposed to playback of boat noise.

Interacting Short- and Long-term Effects

Combining the effects of short-term noise playback with existing long-term noise conditions showed that long-term exposure to noise changed the baseline response of gobies to a simulated predator. Gobies living in long-term noisy sites and exposed to the silent control treatment tended to freeze for shorter periods when exposed to the simulated predator and did not increase their time absent from the site. Furthermore, while gobies living in quiet sites that were exposed to boat noise temporarily left their nests even before the predator strike, gobies in noisy sites tended to do so less. The latter, however, was not significant with the current sample size. After the predator strike, there was no change in time absent for gobies exposed to boat noise playback, regardless of the
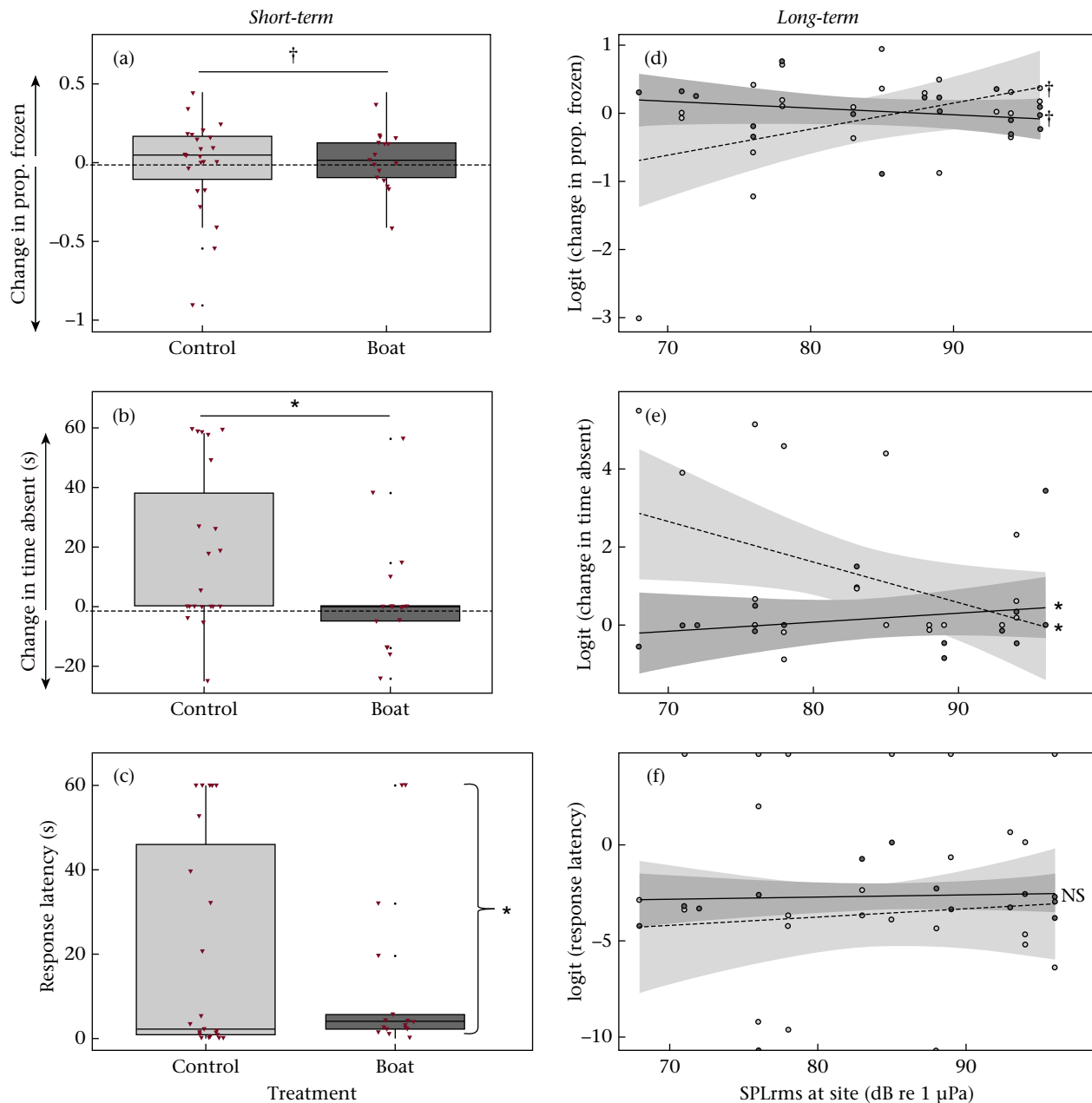
Figure 5. Goby response to short- and long-term noise conditions. Effect of silent control (light grey, $N = 23$) and short-term boat noise exposure (dark grey, $N = 17$) playback on (a, d) the change in the time gobies were frozen before and after predator release, (b, e) the change in time gobies were absent before and after predator release and (c, f) the response latency to the simulated predator. Dashed lines show correlations between long-term ambient noise levels and goby response parameters during the silent control (dashed line, light grey circles) and during boat noise (solid line, dark grey circles). $\dagger P < 0.1$; $*P < 0.05$. Note that the average response latency did not change significantly between silent control and boat noise playback, whereas the variance changed significantly.

noisiness of the site. Hence, when exposed to boat noise, gobies in noisy sites likely stayed put after predator release, while gobies in quiet sites kept leaving the site, as they had done before release.

The increased time absent before predator release suggests that boat noise playback induced a heightened vigilance state in sand gobies, but that this effect diminished with site noisiness. Hence, gobies that were frequently exposed to boat noise may have had higher tolerance levels than gobies from quiet sites. Animals exposed to long-term disturbance often have increased tolerance to short-term disturbance (Bejder et al., 2009). For example, free-ranging cichlids from sites with relatively high acoustic disturbance did not significantly increase their oxygen consumption

levels when exposed to short-term playback of boat noise, while their conspecifics from lower-disturbance sites did (Harding et al., 2018).

The varying levels of vigilance induced by the boat noise playback put the lack of behavioural change upon predator release into perspective. Even thgcqough gobies from all sites seemed to respond similarly when exposed to a predator strike under boat noise playback, the pre-existing differences in time absent suggest that gobies in quiet sites had an increased vigilance state that was not further elevated by the predator strike. In contrast, the gobies in noisy sites may have had a diminished vigilance state that led to a reduced response to the predator strike, regardless of the type of

Table 2
GLMM model result for change in time absent, including only individuals that were present 100% of the observation time before predator release

	Estimate	SE	Z	P
Intercept*	8.72	2.39	3.65	<0.001
Playback type (boat noise)*	-12.13	3.78	-3.21	<0.01
SPL*	-0.09	0.028	-3.32	<0.001
Playback type:SPL*	0.14	0.044	3.12	<0.01
Precision (φ)				
Intercept*	1.38	0.33	4.16	<0.0001
Playback type (boat noise)	0.35	0.60	0.59	0.6

For gobies that were present 100% of the observed time before predator release, the time they were absent after predator release was influenced by playback type and sound pressure level (SPL). The model separately modelled the probability of observing zero or zero and one. Note that estimate values of the model were logit-transformed because of the beta distribution. Estimates should therefore be converted before comparing to the data.
*$P < 0.05$.

sound exposure. A similar result was found for juvenile Ambon damselfish, *Pomacentrus amboinensis*, that were trained on predator cues in noisy conditions (Ferrari et al., 2018). When released into the field as adults, they showed increased mortality compared to fish that had been trained in quiet conditions, suggesting that noise can reduce learning ability. Perhaps the long-term exposure of the gobies in our study led to a similar reduced learning ability for predator risk.

In terrestrial settings, animals living in areas that are more frequently disturbed by humans often show diminished antipredator behaviour (Lowry, Lill, & Wong, 2013). This is hypothesized to have two possible causes: (1) habituation to nonthreatening stimuli that leads to overall reduced responses to disturbance; (2) reduced exposure to predators that avoid disturbed sites (Geffroy, Samia, Bessa, & Blumstein, 2015). Perhaps our noisy sites contained fewer predators, as (especially larger, marine mammal) predators often avoid acoustic disturbance when the site is not vital for their survival (Carstensen, Henriksen, & Teilmann, 2006; Kok et al., 2018). However, the relatively short distances between the sites make this less likely. If actual predation levels were not diminished, gobies in long-term noisy conditions would suffer an increased risk of predation at these sites.

Conclusions

Both short-term and long-term disturbance by boat noise affected the antipredator behaviour of free-ranging sand gobies in this study. This signifies that not only pristine (in terms of acoustic pollution) areas might be affected by noise disturbance and requires conservation effort. Decreasing the noise disturbance in areas with more long-term acoustic pollution should also be considered, since our results show that long-term disturbance can lead to behavioural changes beyond the direct period of noise exposure (i.e. in ambient conditions). Since both the behaviour of the predator and the prey affects the outcome of the interaction (DiRienzo, Pruitt, & Hedrick, 2013), a change in behaviour in one or both likely changes predator–prey dynamics, although too little is known to predict the consequences at the population level (Kunc et al., 2016; Slabbekoorn et al., 2019). Studies thus need to focus on combined short-term and long-term effects of noise on animals, preferably at the community level.

Author Contributions

H.S. conceived of the study; A.K., F.V. and H.S. designed the study; K.T. and J.L. designed the equipment for the data collection; A.K. and D.vH. collected the data; A.K. analysed the data and drafted the manuscript; D.vH., K.T., J.L., F.V. and H.S. critically revised the manuscript.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2020.12.001.

References

Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution, 25*(3), 180–189. https://doi.org/10.1016/j.tree.2009.08.002

Bartoń, K. (2017). *MuMIn: Multi-model inference (R package version 1.43.15)*. https://CRAN.R-project.org/package=MuMIn.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series, 395*, 177–185. https://doi.org/10.3354/meps07979

Bejder, L., Samuels, A., Whitehead, H., & Gales, N. (2006). Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Animal Behaviour, 72*(5), 1149–1158. https://doi.org/10.1016/j.anbehav.2006.04.003

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., et al. (2006). Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology, 20*(6), 1791–1798. https://doi.org/10.1111/j.1523-1739.2006.00540.x

Blom, E., Kvarnemo, C., Andersson, M. H., Svensson, O., Dekhla, I., Schöld, S., et al. (2019). Continuous but not intermittent noise has a negative impact on mating success in a marine fish with paternal care. *Scientific Reports, 9*, Article 5494. https://doi.org/10.1038/s41598-019-41786-x

Bruintjes, R., & Radford, A. N. (2013). Context-dependent impacts of anthropogenic noise on individual and social behaviour in a cooperatively breeding fish. *Animal Behaviour, 85*(6), 1343–1349. https://doi.org/10.1016/j.anbehav.2013.03.025

Campbell, J. (2019). *Picoscope3000Logger (Version 1.1.1)*. Retrieved from: https://gitlab.com/RTbecard/Picoscope3000Logger.

Carstensen, J., Henriksen, O. D., & Teilmann, J. (2006). Impacts of offshore wind farm construction on harbour porpoises: Acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Marine Ecology Progress Series, 321*, 295–308. https://doi.org/10.3354/meps321295

Chan, A. A. Y.-H., & Blumstein, D. T. (2011). Attention, noise, and implications for wildlife conservation and management. *Applied Animal Behaviour Science, 131*(1–2), 1–7. https://doi.org/10.1016/j.applanim.2011.01.007

Chan, A. A. Y.-H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic noise affects risk assessment and attention: The distracted prey hypothesis. *Biology Letters, 6*(4), 458–461. https://doi.org/10.1098/rsbl.2009.1081

DiRienzo, N., Pruitt, J. N., & Hedrick, A. V. (2013). The combined behavioural tendencies of predator and prey mediate the outcome of their interaction. *Animal Behaviour, 86*(2), 317–322. https://doi.org/10.1016/j.anbehav.2013.05.020

Douma, J. C., & Weedon, J. T. (2019). Analyzing continuous proportions in ecology and evolution: A practical introduction to beta and dirichlet regression. *Methods in Ecology and Evolution, 10*(9), 1412–1430. https://doi.org/10.1111/2041-210X.13234

Ehrenberg, S. Z., & Ejdung, G. (2008). Daily activity pattern of the sand goby, Pomatoschistus minutus (Pisces), at low light intensity. *Hydrobiologia, 603*(1), 129–137. https://doi.org/10.1007/s10750-007-9253-4

Ferrari, M. C. O., McCormick, M. I., Meekan, M. G., Simpson, S. D., Nedelec, S. L., & Chivers, D. P. (2018). School is out on noisy reefs: The effect of boat noise on predator learning and survival of juvenile coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences, 285*(1871), Article 20180033. https://doi.org/10.1098/rspb.2018.0033

Forsgren, E., & Magnhagen, C. (2011). Conflicting demands in sand gobies: Predators influence reproductive behaviour. *Behaviour, 126*(1/2), 125–135. https://doi.org/10.1163/156853993X00371

Francis, C. D., Ortega, C. P., & Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Current Biology, 19*(16), 1415–1419. https://doi.org/10.1016/j.cub.2009.06.052

Frid, A., & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology, 6*(1), 11. http://www.consecol.org/vol6/iss1/art11/

Geffroy, B., Samia, D. S. M., Bessa, E., & Blumstein, D. T. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution, 30*(12), 755–765. https://doi.org/10.1016/j.tree.2015.09.010

Götz, T., & Janik, V. M. (2011). Repeated elicitation of the acoustic startle reflex leads to sensitisation in subsequent avoidance behaviour and induces fear conditioning. *BMC Neuroscience, 12*, Article 30. https://doi.org/10.1186/1471-2202-12-30

Halfwerk, W., & Slabbekoorn, H. (2015). Pollution going multimodal: The complex impact of the human-altered sensory environment on animal perception and performance. *Biology Letters, 11*(4), Article 20141051. https://doi.org/10.1098/rsbl.2014.1051

Harding, H. R., Gordon, T. A. C., Eastcott, E., Simpson, S. D., & Radford, A. N. (2019). Causes and consequences of intraspecific variation in animal responses to anthropogenic noise. *Behavioral Ecology, 30*(6), Article 20180441. https://doi.org/10.1093/beheco/arz114

Harding, H. R., Gordon, T. A. C., Hsuan, R. E., Mackaness, A. C. E., Radford, A. N., & Simpson, S. D. (2018). Fish in habitats with higher motorboat disturbance show reduced sensitivity to motorboat noise. *Biology Letters, 14*(10). https://doi.org/10.1098/rsbl.2018.0441

Hasan, M. R., Crane, A. L., Ferrari, M. C. O., & Chivers, D. P. (2018). A cross-modal effect of noise: The disappearance of the alarm reaction of a freshwater fish. *Animal Cognition, 21*(3), 419–424. https://doi.org/10.1007/s10071-018-1179-x

Hubert, J., Campbell, J., van der Beek, J. G., den Haan, M. F., Verhave, R., Verkade, L. S., et al. (2018). Effects of broadband sound exposure on the interaction between foraging crab and shrimp: A field study. *Environmental Pollution, 243*, 1923–1929. https://doi.org/10.1016/j.envpol.2018.09.076

de Jong, K., Amorim, M. C. P., Fonseca, P. J., Fox, C. J., & Heubel, K. U. (2018). Noise can affect acoustic communication and subsequent spawning success in fish. *Environmental Pollution, 237*, 814–823. https://doi.org/10.1016/j.envpol.2017.11.003

Karp, D. S., & Root, T. L. (2009). Sound the stressor: How hoatzins (Opisthocomus hoazin) react to ecotourist conversation. *Biodiversity & Conservation, 18*(14), 3733–3742. https://doi.org/10.1007/s10531-009-9675-6

Kern, J. M., & Radford, A. N. (2016). Anthropogenic noise disrupts use of vocal information about predation risk. *Environmental Pollution, 218*, 988–995. https://doi.org/10.1016/j.envpol.2016.08.049

Kok, A. C. M., Engelberts, J. P., Kastelein, R. A., Helder-Hoek, L., Van de Voorde, S., Visser, F., et al. (2018). Spatial avoidance to experimental increase of intermittent and continuous sound in two captive harbour porpoises. *Environmental Pollution, 233*, 1024–1036. https://doi.org/10.1016/j.envpol.2017.10.001

Kunc, H. P., McLaughlin, K. E., & Schmidt, R. (2016). Aquatic noise pollution: Implications for individuals, populations, and ecosystems. *Proceedings of the Royal Society B: Biological Sciences, 283*(1836), Article 20160839. https://doi.org/10.1098/rspb.2016.0839

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *Open Ecology Journal, 3*(3), 1–7. https://doi.org/10.2174/1874213001003030001

Leopold, M. F. (2015). *Eat and be eaten: Porpoise diet studies*. Ph.D. thesis. Wageningen, The Netherlands: Wageningen University.

Lorenz, K., & Tinbergen, N. (1939). Taxis und Instinkthandlung in der Eirrolbewegung der Graugans. 1. *Zeitschrift für Tierpsychologie, 2*(1–3), 1–29.

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews, 88*(3), 537–549. https://doi.org/10.1111/brv.12012

Magnhagen, C. (1988). Changes in foraging as a response to predation risk in two gobiid fish species, *Pomatoschistus minutus* and *Gobius niger*. *Marine Ecology Progress Series, 49*, 21–26. https://doi.org/10.3354/meps049021

Magnhagen, C., & Forsgren, E. (1991). Behavioural responses to different types of predators by sand goby *Pomatoschistus minutus*: An experimental study. *Marine Ecology Progress Series, 70*, 11–16.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews, 90*(2), 560–586. https://doi.org/10.1111/brv.12122

Maxwell, R. J., Zolderdo, A. J., de Bruijn, R., Brownscombe, J. W., Staaterman, E., Gallagher, A. J., et al. (2018). Does motor noise from recreational boats alter parental care behaviour of a nesting freshwater fish? *Aquatic Conservation: Marine and Freshwater Ecosystems, 28*(4), 969–978. https://doi.org/10.1002/aqc.2915

McCormick, M. I., Allan, B. J. M., Harding, H. R., & Simpson, S. D. (2018). Boat noise impacts risk assessment in a coral reef fish but effects depend on engine type. *Scientific Reports, 8*, Article 3847. https://doi.org/10.1038/s41598-018-22104-3

Merchant, N. D., Fristrup, K. M., Johnson, M. P., Tyack, P. L., Witt, M. J., Blondel, P., et al. (2015). Measuring acoustic habitats. *Methods in Ecology and Evolution, 6*(3), 257–265. https://doi.org/10.1111/2041-210X.12330

Morris-Drake, A., Kern, J. M., & Radford, A. N. (2016). Cross-modal impacts of anthropogenic noise on information use. *Current Biology, 26*(20), R911–R912. https://doi.org/10.1016/j.cub.2016.08.064

Nedelec, S. L., Mills, S. C., Lecchini, D., Nedelec, B., Simpson, S. D., & Radford, A. N. (2016). Repeated exposure to noise increases tolerance in a coral reef fish. *Environmental Pollution, 216*, 428–436. https://doi.org/10.1016/j.envpol.2016.05.058

Neo, Y. Y., Hubert, J., Bolle, L., Winter, H. V., ten Cate, C., & Slabbekoorn, H. (2016). Sound exposure changes European seabass behaviour in a large outdoor floating pen: Effects of temporal structure and a ramp-up procedure. *Environmental Pollution, 214*, 26–34. https://doi.org/10.1016/j.envpol.2016.03.075

Radford, A. N., Lebre, L., Lecaillon, G., Nedelec, S. L., & Simpson, S. D. (2016). Repeated exposure reduces the response to impulsive noise in European seabass. *Global Change Biology, 22*(10), 3349–3360. https://doi.org/10.1111/gcb.13352

Rosa, P., & Koper, N. (2018). Integrating multiple disciplines to understand effects of anthropogenic noise on animal communication. *Ecosphere, 9*(2), Article e02127. https://doi.org/10.1002/ecs2.2127

Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., et al. (2016). A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews of the Cambridge Philosophical Society, 91*(4), 982–1005. https://doi.org/10.1111/brv.12207

Simpson, S. D., Purser, J., & Radford, A. N. (2015). Anthropogenic noise compromises antipredator behaviour in European eels. *Global Change Biology, 21*(2), 586–593. https://doi.org/10.1111/gcb.12685

Simpson, S. D., Radford, A. N., Nedelec, S. L., Ferrari, M. C. O., Chivers, D. P., McCormick, M. I., et al. (2016). Anthropogenic noise increases fish mortality by predation. *Nature Communications, 7*, Article 10544. https://doi.org/10.1038/ncomms10544

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., & Popper, A. N. (2010). A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution, 25*(7), 419–427. https://doi.org/10.1016/j.tree.2010.04.005

Slabbekoorn, H., Dalen, J., de Haan, D., Winter, H. V., Radford, C. A., Ainslie, M. A., et al. (2019). Population-level consequences of seismic surveys on fishes: An interdisciplinary challenge. *Fish and Fisheries, 20*(4), 653–685. https://doi.org/10.1111/faf.12391

Sörqvist, P., Nöstl, A., & Halin, N. (2012). Working memory capacity modulates habituation rate: Evidence from a cross-modal auditory distraction paradigm. *Psychonomic Bulletin & Review, 19*(2), 245–250. https://doi.org/10.3758/s13423-011-0203-9

Tidau, S., & Briffa, M. (2019). Distracted decision makers: Ship noise and predation risk change shell choice in hermit crabs. *Behavioral Ecology, 30*(4), 1157–1167. https://doi.org/10.1093/beheco/arz064

Voellmy, I. K., Purser, J., Simpson, S. D., & Radford, A. N. (2014). Increased noise levels have different impacts on the anti-predator behaviour of two sympatric fish species. *PLoS One, 9*(7), Article e102946. https://doi.org/10.1371/journal.pone.0102946

Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression relationships. *R News, 2*(3), 7–10. https://CRAN.R-project.org/doc/Rnews/.