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CASE STUDY

AQUACULTURE, FISH and FISHERIES

Increased noise levels cause behavioural and distributional changes in Atlantic cod and saithe in a large public aquarium—A case study

Marica Andersson¹ Ola Svensson^{2,3} Herese Swartz⁴ Jack L. Manera⁵ Michael G. Bertram^{5,6,7} Kertese Swartz⁴ Eva-Lotta Blom⁶

¹Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

²Department of Educational Work, University of Borås, Borås, Sweden

³The Linnaeus Centre for Marine Evolutionary Biology, University of Gothenburg, Gothenburg, Sweden

⁴Universeum, Gothenburg, Sweden

⁵School of Biological Sciences, Monash University, Melbourne, Victoria, Australia

⁶Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

⁷Department of Zoology, Stockholm University, Stockholm, Sweden

Correspondence

Eva-Lotta Blom, Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden. Email: eva.lotta.blom@slu.se,

blom.evalotta@gmail.com

Funding information

Graduate School in Marine Environmental Research at the Gothenburg Centre for Marine Research

Abstract

Investigating the effects of underwater noise on aquatic animals is a research field that is receiving rapidly increasing attention. Despite this, surprisingly few studies have addressed the potential impacts of noise in a marine animal husbandry setting. In this regard, the behaviour of fish in public aquariums can be used as an indicator of well-being, and noise is known to cause behavioural changes. This case study investigates the behaviour of cod (Gadus morhua) and saithe (Pollachius virens) in a large public aquarium when exposed to increased noise levels originating from an aquarium renovation carried out by construction divers. Swimming behaviour, group formation and vertical distribution, along with yawning and scratching frequencies of the fish, were analysed from video recordings made before, during and after the exposure to increased noise levels. The same parameters were also analysed to evaluate potential effects of the presence of divers when not making renovation noise, compared to fish behaviour prior to the renovation. There was a slight change in the depth distribution of both species and a decrease in the number of scratches in cod due to the presence of divers that were not making renovation noise. In the presence of construction noises in the tank, however, both cod and saithe showed a wider array of behavioural changes, including increased swimming speed, changes in depth distribution and increased yawning frequencies. The results from this case study demonstrate that an underwater renovation with increased noise levels impacts fish behaviour and suggests that underwater noise should be considered during the management of aquatic environments, including public aquaria.

KEYWORDS

anthropogenic effects, behavioural ecology, fish

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1 | INTRODUCTION

Anthropogenic noise is known to alter the behaviour of animals from a wide variety of taxa, including birds, invertebrates and mammals (Morley et al., 2014; Richardson & Würsig, 1997; Slabbekoorn & Ripmeester, 2008). For instance, studies on fish have demonstrated behavioural changes in response to noise exposure, including avoidance and diving behaviours, startle and alarm responses, changes in vertical and horizontal displacement, increased swimming speed and changes in food consumption (Fewtrell & McCauley, 2012; Handegard et al., 2003; Mueller-Blenkle et al., 2010; Pearson et al., 1992; Voellmy, 2013). In this regard, behavioural observations are an important tool for evaluating the possible effects of auditory stressors on animals, given that behaviour reflects their health, needs and reactions while remaining an unobtrusive method (Mason & Mench, 1997). As such, behaviour is an established tool for assessing the welfare of captive fish (Martins et al., 2012).

Fish living in captivity, such as in public aquaria and aquaculture facilities, are under constant exposure to background noises originating from various pumps and filter systems (Scheifele et al., 2012). In addition, fish in public aquaria are exposed to unpredictable sudden sounds over a wide variety of intensities and frequencies, for example, from slamming doors, visitors knocking on their aquaria wall, nearby building construction or from maintenance projects inside their aquaria (Neo et al., 2015). These sounds can cause a reduction in their welfare (Sabet et al., 2016) by, for example, causing stress-related behaviours and physiological responses (Anderson et al., 2011) or even changing the hearing threshold of fish (Anderson, 2013). While research on the impacts of anthropogenic noise on marine wildlife is growing, studies on the effects of auditory stressors on fish in public aquariums are poorly represented in the scientific literature (Anderson et al., 2011; Scheifele et al., 2012).

Teleost fish use particle motion and sound pressure to detect acoustic cues in their environment (Nedelec et al., 2016; Wysocki et al., 2009), for example, in communication between individuals, assessing the fitness of potential mates, locating dangers,defending territories and synchronising spawning events (Amorim & Neves, 2008; Amorim et al., 2015; Hawkins & Amorim, 2000). However, these important cues can be masked by anthropogenic noise, which can lead to changes in behaviour and potential flow-on effects such as reduced reproductive success (Blom et al., 2019; Nedelec et al., 2015; Radford et al., 2014; Sierra-Flores et al., 2015). Noise can also disperse large schools of fish, potentially leading to an increased vulnerability to predators and difficulties in the detection and capture of prey as well as deterring fish from ecologically important areas (Slabbekoorn et al., 2010).

The aim of this case study was to examine whether and how increased noise levels from an in-aquaria renovation carried out by construction divers altered the behaviour of two species of North Sea fish—Atlantic cod (*Gadus morhua*) and saithe (*Pollachius virens*)—in a public aquarium. The study took place over 9 weeks, during which fish were exposed to intermittent noise of low frequencies (<1000 Hz). The behaviour of either species was examined before, during and after the exposure to increased noise levels. We predicted that increased noise

levels from the renovation would have a negative impact on the fish by altering their behaviour in terms of group cohesion, depth distribution and swimming speed, thus indicating a decline in their well-being. Additionally, we predicted that the behavioural effects would remain even after the aquaria renovation was completed.

2 | METHODS

2.1 | Study species

The fish observed in this study were saithe (P. virens, n = 30) and Atlantic cod (G. morhua, n = 25). Both species are free-swimming piscivorous predators (Hansson et al., 1996; Videler & Hess, 1984) that aggregate into spawning schools every year at specific coastal locations for offshore spawning (Bekkevold et al., 2002; Neilson et al., 2003). Atlantic cod tend to shoal closer to the bottom relative to saithe, although they have also been observed in the pelagic zone. Saithe school in the pelagic zone and hunt near the surface (Kullander et al., 2012; Pitcher, 1998). Cod can hear and produce acoustic signals, and experiments have shown that they can detect frequencies between 30 and 470 Hz (Chapman & Hawkins, 1973; Hawkins & Chapman, 1975). Saithe have not, to our knowledge, been assessed for hearing sensitivity, but its congener pollock (P. pollachius) has been shown to detect frequencies between 40 and 470 Hz (Chapman, 1973). Additionally, saithe have a lateral line, which has been proven to have a function in fish hearing (Partridge & Pitcher, 1980) indicating that saithe sound in multimodal ways.

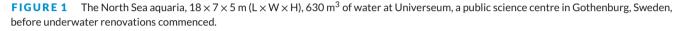
2.2 Study site

This study took place in the North Sea aquaria at Universeum, a public science centre in Gothenburg, Sweden, between 20 August 2018 and 19 October 2018. The aquarium, with dimensions of $18 \times 7 \times 5$ m (L $\times W \times H$), holds approximately 630 m³ of water (Figure 1). To enrich the environment for the fish, the aquarium is equipped with cliffs, plastic kelp, stones, sand and an upside-down boat wreck. The saithe and Atlantic cod observed in this study were wild-caught and had been in the aquarium for a minimum of 2 years. The school of saithe consisted of 30 individuals and the school of cod consisted of 25 individuals. The aquarium had a continuous flow of filtered artificial saltwater. During the study, the temperature in the aquarium was maintained at 12.96–13.06°C, salinity at 29–32 ppt, pH at 7.40–7.80, KH (carbonate hardness) at 7.0–7.7 and dissolved oxygen at 9.46–10.97 mL/L. All water parameters were measured daily.

2.3 Acoustic measurements and sound exposure

During the study, fish were exposed to additional noise that is well within the species' hearing range (<1 kHz) derived from the underwater renovation, which was generated by divers from Aquatic Solutions removing corroding structural steel from the concrete walls in the aquarium. The divers entered the water via stairs at the





renovation site and worked only at a single location in one small area of the aquarium. The stairs were located next to the renovation site and the divers did not move outside of the renovation area. The divers worked between Monday and Friday at intermittent hours between 8:00 AM and 6:00 PM. The tools generating noise were hydraulic saws, pneumatic saws, chisels and hammers. Spectrograms of the harmonic structures are shown in Figure 2. Disturbances occurred in intermittent periods, and the generated noise elevated the energy in the aquarium by an average of \sim 50 dB (Figure 3). The elevated noise exposure during the renovation lasted approximately 6-8 h per day. The renovation work lasted for 21 days in total, with increased noise exposure during 15 of the 21 days (Figure 4). Control recordings were made during 3 days before the renovation at six horizontal locations in the aquarium—see Figure S1 for the locations of hydrophone recordings in the aquarium. Each location was recorded for 10 min at two depths, 2 and 4 m (Figure 3). Sound analysis from the control period showed that the background noise was consistent throughout the aquarium at all locations and depths on all 3 days of recording.

Sounds were recorded using a calibrated hydrophone (HTI-96-MIN with pre-amplifier, High Tech Inc., Gulfport MS; sensitivity: -165 dB re 1 V/ μ Pa, frequency range: 0.02–30 kHz) linked to a digital audio recorder (Song meter SM2+, Wildlife Acoustics, Inc.; sampling frequency: 32 kHz). Sound analyses were performed using Aquatic Acoustic Metrics Interface software (Ren et al., 2012) and Matlab_R2016a (The Mathworks Inc.).

2.4 | Recording behaviour

Two Sony HDR-CX240E cameras were installed outside the main window of the aquarium to record the behaviour and distribution of cod and saithe (Figure 1). We recorded for 12 days prior to the work (control period), followed by 15 days during the renovation and 6 days during the recovery period after the renovation. Throughout each of these 33 days, the behaviour of fish was recorded for 12 h.

2.5 Behavioural analysis

Behavioural analyses of the two species, cod and saithe, in the aquarium were performed from the video recordings. We scored vertical distribution in the aguarium in terms of time spent within the lower depth zone closest to the bottom, the middle depth zone, the upper depth zone closest to the surface or spread over two or more of these zones. We also measured swimming speed, group formation and the number of scratches and yawns according to the definitions provided in Table 1, following Fewtrell and McCauley (2012). Since the video quality prevented tracking of individual fish, each species was observed and scored together if a behaviour was displayed by 70% or more of the individuals in a school. From each day of video recordings (total of 33 days), we randomly chose 3 min at three different times per day. For every 3 min of video, the group behaviours of the school of cod and saithe were measured and scored as a single value of 1 if the behaviour was present or 0 if it was absent, according to visual observations. If more than one behaviour was observed, the behaviour performed during the majority of the 3-min video was scored. For behaviour, 108 min of video were analysed for the control period, 135 min with noise exposure and 54 min during the recovery period. The number of scratches and vawns observed in the schools during each recording period was counted in the videos. Including the additional analysis of video footage for scratches and yawning behaviour, 162 min of video were analysed for the control period, 189 min with noise exposure and 108 min during the recovery period.

In addition to our main analysis assessing the potential impacts of elevated underwater noise produced by divers on the behaviour of cod and saithe (compared to no divers or divers performing renovation noise in the aquarium), we tested for any potential effects of the divers' presence in the aquarium when not producing renovation noise during the renovation period (n = 36 min, compared to when there were no divers in the aquarium during the control period; n = 108 min) in a smaller dataset using the time frames when divers did not

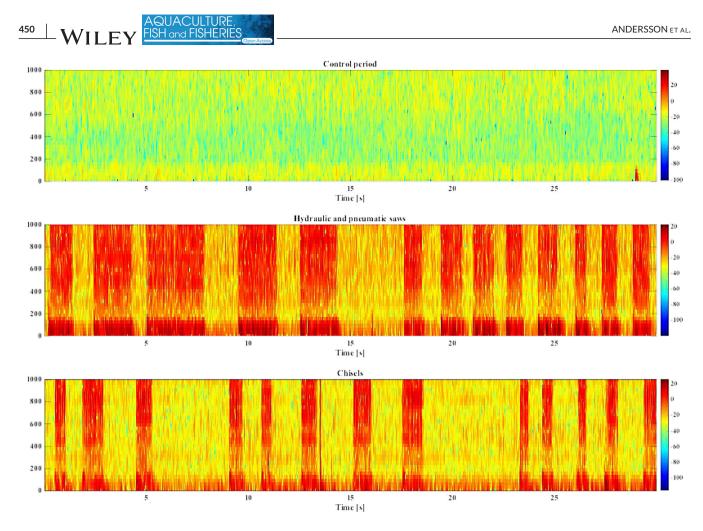


FIGURE 2 Spectrograms of noise output from one recording in the North Sea aquaria of the control period, hydraulic and pneumatic saws and chisels in the renovation period. The harmonic structures are shown for 0–1 kHz, Hamming window (512) with 50% overlap.

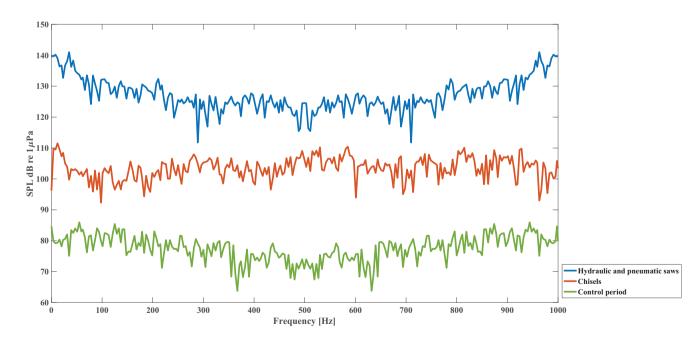


FIGURE 3 Assessment of noise output in the aquarium renovation and control period. Noise and control treatments are shown for 0–1 kHz. Sound pressure level was, on average for all 12 locations, 50 dB higher for noise derived from the renovation, compared to the normal noise levels in this frequency range (50 dB for 0–10 kHz). Noise levels were measured with a hydrophone, placed at six different locations within the tank, at two depths (2 and 4 m). The figure shows average dB from the six locations, at two depths, with a total of 12 sound measurements per treatment.

TABLE 1 Definitions of behaviours and distributions of fish used in the analysis of the video recordings, following Fewtrell and McCauley (2012).

Category	Behaviour	Description
School cohesion	Loose groups	Animals in a loose cohesive group, individuals > 2 body lengths apart
	Tight groups	Animals in a tightly cohesive group, individuals < 2 body lengths apart
	No group	Animals swimming individually
Swimming speed	Stationary or slow swimming	Animals either displaying no horizontal or vertical movement, or swimming non-purposefully
	Slow swimming	Animals swimming non-purposefully
	Fast swimming	Animals swimming faster than usual
Vertical position	Lower	Animals situated in lower 1/3 of the aquarium
	Middle	Animals situated in the middle 1/3 of the aquarium
	Upper	Animals situated in the upper 1/3 of the aquarium
	2/3 or more	Animals situated in two or more depth zones
Scratching		Animals scratching themselves against the bottom of the aquarium
Yawning		Animals gaping and then closing their mouth

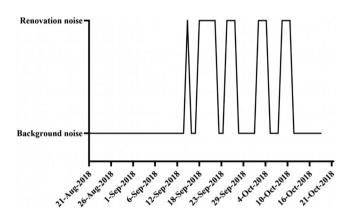


FIGURE 4 The figure shows a timeline of the study in the North Sea aquaria with either background noise or renovation noise in its three phases, the control period, followed by noise exposure and the recovery period.

do any noisy construction work. The fish in the aquarium were habituated to divers being in the aquarium on several occasions each week for activities such as cleaning, feeding and shows for the public. However, to ensure that any potential changes seen in the behaviour of fish during the renovation period were due to elevated underwater noise exposure and not due to the presence of divers in the aquarium who were not producing noise, we performed a supplementary analysis. To do this, we followed exactly the same procedure used for the main behavioural analysis (as previously described in this section and the 'Statistical Analysis' section). More specifically, we analysed all of the same behaviours, and these behaviours were scored in the same way. We randomly selected 3-min sections of videos at three different times per day over 4 days, during which time divers were present in the aquarium but not performing any noisy renovation work. For this supplementary behavioural analysis, 36 min of video were analysed where divers were present in the tank without producing renovation noise. The behaviour of each fish species observed in this context was

then compared to their behaviour when no divers were present in the aquarium during the control period—see Table S1-S6.

2.6 Statistical analysis

In the statistical analyses, the measurements for each 3 min of observations of the two schools were compared between the control period, the renovation period and the recovery period-that is, for each of the two species, all observations included in the tests are on the collective behaviour of the school (the same group of fish). All behaviours and distributions were analysed using chi-squared tests, Fisher's exact tests or generalised linear models (GLMs). Depth distribution, group cohesion and swimming speed were tested with Pearson's chi-squared (tests followed by pairwise Fisher's exact tests with sequential Bonferroni correction (all p < 0.05 are significant after correction). The number of yawns and scratches was analysed using a Poisson distribution (modelbased estimator, link function logit). GLMs are reported with estimated marginal means and 95% confidence intervals. Post hoc tests were used on all GLMs, and all tests are two-tailed. Statistical analyses were performed in SPSS (IMB SPSS Statistics for Windows, version 24.0, IMB Corp.) and R Statistical Software (v. 4.1.2; R Core Team 2021; using the package glmmTMB v. 1.9.3). We are aware that the sequential observations of behaviours of the schools in the aquarium are not necessarily independent of each other. Therefore, these results should be treated with caution. Otherwise, all model assumptions were met.

3 | RESULTS

3.1 | Elevated noise levels had an effect on fish depth distribution

In 35 of the 36 observations before the renovation, the school of cod was observed in the lower aquarium zone (97%) and was spread out

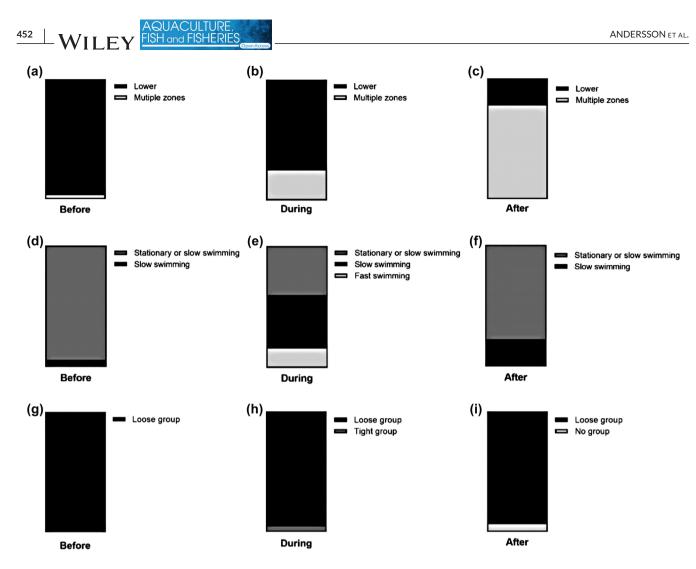


FIGURE 5 Behaviour of the group of cod before, during, and after noise exposure from the underwater renovation. (a–d) show the frequency of distribution across depth zones (a) during the control period, (b) during the renovation period, (c) during the recovery period, (d) frequency of observations of different swimming speeds during the control period. (e–i) show the frequency of observations of (e) different swimming speeds during the recovery period, (g) different group formations during the control period, (h) group formations during the renovation period and (i) of different group formations during the recovery period.

over multiple depth zones during the remaining observation. During the renovation, the school of cod was in the lower aquarium zone during 34 of the 45 observations (76%) and was spread out over multiple depth zones during the remaining observations. During the recovery period, the school of cod was observed in the lower aquarium zone during 4 of the 18 observations (22%) and was spread out across multiple depth zones during the remaining observations ($\chi^2 = 35.00, p < 0.001$). Pairwise Fisher's exact tests showed that the school of cod spent less time in the lower aquarium zone during the renovation, compared to the control period (34/45 vs 35/36, p = 0.001). The cod also spent less time in the lower part of the aquarium during the recovery period, compared to the renovation period (4/18 vs 34/45, p < 0.001) and the control period (4/18 vs 35/36, p < 0.001; Figure 5a-c).

Before the renovation started, the school of saithe was in the upper aquarium zone during all 36 observations. During the renovation, the saithe were observed in the upper part of the aquarium during 16 of the 45 observations (36%), while they were spread across multiple depth zones during the remaining observations. In the recovery period, the saithe were in the upper part of the aquarium during 17 of the 18 observations (94%) and were spread out over multiple depth zones during one observation ($\chi^2 = 47.71$, p < 0.001). Pairwise Fisher's exact tests showed that the school of saithe spent less time in the upper aquarium zone during the renovation, compared to the control period (16/45 vs 36/36, p < 0.001). The school of saithe also spent more time in the upper part of the aquarium during the recovery period, compared to the renovation (17/18 vs 16/45, p < 0.001). There was no difference in the distribution of saithe between the control period and the recovery period (36/36 vs 17/18, p = 0.33; Figure 6a–c).

3.2 | Elevated noise levels had an effect on fish swimming speed

For definitions of fish swimming speed categories, see Table 1. Before the renovation started, the school of cod was observed as being stationary on the bottom of the aquarium or swimming slowly during 34 of the 36 observations (94%), while displaying slow swimming during

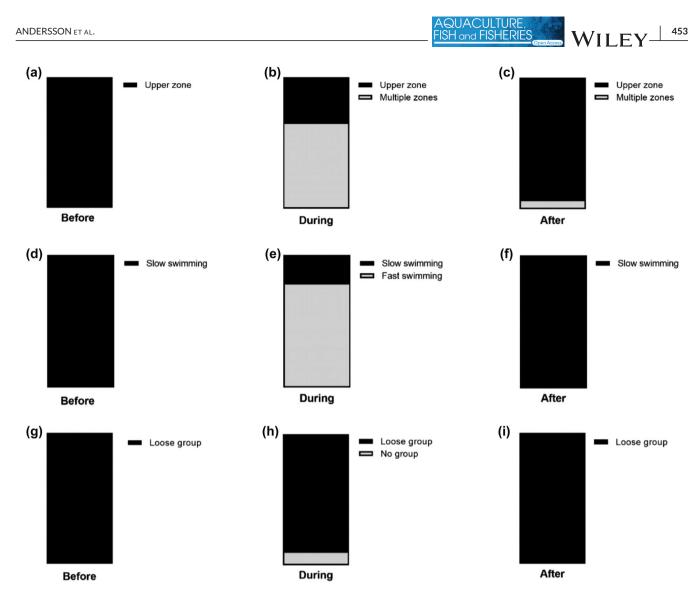


FIGURE 6 Behaviour of the group of saithe before, during and after noise exposure from the underwater renovation. (a–d) show the frequency of distribution across depth zones (a) during the control period, (b) during the renovation period, (c) during the recovery period, (d) frequency of observations of different swimming speeds during the control period. (e–i) show the frequency of observations of (e) different swimming speeds during the renovation period, (g) different group formations during the control period. (h) group formations during the renovation period and (i) of different group formations during the recovery period.

the remaining observations. During the renovation, the school of cod stayed stationary on the bottom or was swimming slowly during 18 of the 45 observations (40%), while displaying slow swimming during 20 (44%) and fast swimming during seven (16%) of the observations. In the recovery period, the school of cod was stationary at the bottom of the aquarium or was swimming slowly during 14 of the 18 observations (78%) and was slowly swimming during the remaining observations ($\chi^2 = 27.90, p < 0.001$). Pairwise Fisher's exact tests showed that the cod increased their swimming speed during the renovation, compared to the control period (18/45 vs 34/36, p < 0.001). During the recovery period, the cod were more frequently swimming slowly or were stationary and/or slow swimming, compared to the renovation period (14/18 vs 18/45, p = 0.011). No difference was seen between the control period and the recovery period (34/36 vs 14/18, $\chi^2 = 1.90, p = 0.09$; Figure 5d–f).

The school of saithe was swimming slowly during all the 36 observations made during the period before the renovation commenced. During the renovation, the school of saithe displayed slow swimming during 10 of the 45 observations (22%) and fast swimming during the remaining observations. In the recovery period, the school of saithe was observed to swim slowly during all 18 observations ($\chi^2 = 64.97$, p < 0.001). Pairwise Fisher's exact tests showed that saithe were more frequently swimming fast during the renovation period, compared to the control period (10/45 vs 36/36, p < 0.001). Further, saithe were more frequently displaying slow swimming behaviour during the recovery period, compared to the renovation period (18/18 vs 10/45, p < 0.001). No change in swimming speed was found between the control period and the renovation period (36/36 vs 18/18, p = 1) (Figure 6d–f).

3.3 | Elevated noise levels had no effect on group formation

For definitions of group formation categories, see Table 1. In the period before the renovation, the school of cod was observed in a loose group structure during all 36 observations. During the renovation, they were observed in a loose group structure during 43 of the 45 observations (96%), while in a tight group structure during the remaining observations. During the recovery period, the school of cod was in a loose group formation during 17 of the 18 observations (94%) and was in no group formation during the remaining observations ($\chi^2 = 1.82$, p = 0.40; Figure 5g-i).

In the period before the renovation, the school of saithe was observed in a loose group structure during all 36 observations. During the renovation period, they were observed in a loose group structure during 41 of the 45 observations (91%) and with no group formation during the remaining observations. During the recovery period, the school of saithe was seen in a loose group formation during all 18 observations ($\chi^2 = 5.00$, p = 0.082; Figure 6g–i).

3.4 | Elevated noise levels had an effect on the number of yawns

There was a difference in the number of yawns within the school of cod between the observation periods (GLM, Wald $\chi^2 = 27.559$, df = 2, p < 0.001). Post hoc tests (least significant difference, LSD) showed an increase in the number of yawns during the renovation, compared to the control period (p < 0.001). The number of yawns decreased again between the renovation and the recovery period (p = 0.001). No difference was found between the control period and the recovery period (p = 0.419; control period 1.22, 0.91–1.64; renovation period 2.84, 2.39–3.38; recovery period 1.61, 1.25–2.08; estimated marginal mean, 95% Wald confidence interval; Figure 7a).

There was a difference in the number of yawns within the school of saithe between the observation periods (GLM, Wald $\chi^2 = 10.675$, df = 2, p = 0.005). Post hoc tests (LSD) showed an increase in the number of yawns by the saithe during the renovation period, compared to the control period (p = 0.009). The number of yawns decreased again between the renovation period and the recovery period (p = 0.013). No difference was found between the control period and the recovery period (p = 0.999; control period 0.89, 0.63–1.26; renovation period 1.62, 1.29–2.04; recovery period 0.92, 0.65–1.29; estimated marginal mean, 95% Wald confidence interval; Figure 7b).

3.5 | Elevated noise levels had ambiguous effects on the number of scratches

There was a difference in the number of scratches within the school of cod between the observation periods (GLM, Wald $\chi^2 = 52.301$, df = 2, p < 0.001). Post hoc tests (LSD) for cod showed that the number of scratches decreased during the renovation, compared to the

control period (p < 0.001). There was also a decrease in the number of scratches between the control period and the recovery period (p < 0.001). No difference was found between the renovation period and the recovery period (p = 0.967; control period 5.00, 4.32–5.79; renovation period 2.13, 1.75–2.61; recovery period 2.00, 1.59–2.52; estimated marginal mean, 95% Wald confidence interval; Figure 7c).

There was a difference in the number of scratches within the school of saithe between the observation periods (GLM, Wald $\chi^2 = 16.120$, df = 2, p < 0.001). Post hoc tests (LSD) for saithe showed a decrease in the number of scratches during the recovery period, compared to the control period (p = 0.001) and a decrease from the renovation period to the recovery period (p = 0.026). No difference was found between the control period and the renovation period (p = 0.412; control period 1.06, 0.77–1.45; renovation period 0.76, 0.54–1.06; recovery period 0.33, 0.19–0.59; estimated marginal mean, 95% Wald confidence interval; Figure 7d).

3.6 Divers per se had slight effects on behaviours

The school of cod was observed in the lower zone of the aquarium during 35 out of 36 observations (97%) made during the control period and in two or more depth zones during the remaining observations. When divers were present but not making noise, the cod were observed in the middle zone during one out of 12 observations (8%), in the lower zone during six out of 12 observations (50%) and in two or more zones during the remaining observations (p < 0.001). The school of saithe was observed in the upper part of the aquarium during all control observations. When divers were present but not making noise, they were observed in the upper part of the tank during nine out of 12 observations (75%), in the middle part during one out of 12 observations (8%) and in two or more depth zones in remaining observations (p = 0.013). When no divers were present, cod were in a loose group formation in all observations, and similarly during 11 out 12 observations (92%) when divers were present but not making noise, and otherwise observed in no group formation (p = 0.25). Saithe were only observed in a loose group formation both with divers absent and with divers present but not making noise (p = 1). The cod school was observed as swimming slowly or stationary at the bottom during 34 out of 36 observations (94%) and swimming slowly during the remaining observations when no divers were present. With divers present but not making noise, they were observed as swimming slowly or stationary at the bottom during 10 out of 12 observations (83%) or otherwise swimming slowly (p = 0.257). Saithe were only observed to swim slowly both with divers absent and with divers present but not making noise (p = 1).

Furthermore, yawns of both species (cod: Wald $\chi^2 = 0.618$, df = 1, p = 0.432; saithe: Wald $\chi^2 = 0.315$, df = 1, p = 0.575) and scratches of saithe (saithe: Wald $\chi^2 = 0.00$, df = 1, p = 0.999) were not impacted by the presence of divers that were not producing noise in the aquarium. Conversely, cod performed fewer scratches when divers not making renovation noise were present in the aquarium relative to no divers being present in the aquarium (Wald $\chi^2 = 31.808$, df = 1, p < 0.001). More specifically, we saw a decrease of approximately four scratches

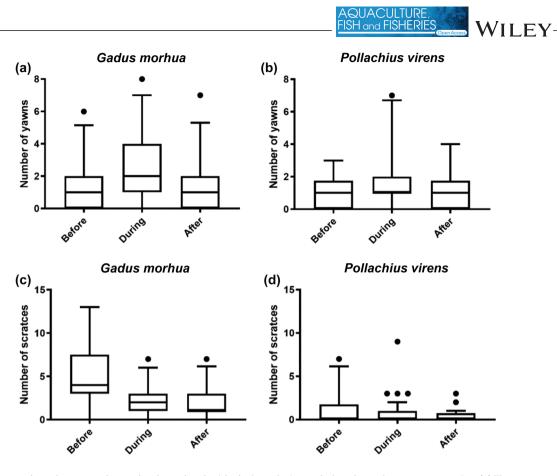


FIGURE 7 The number of yawns and scratches by cod and saithe before, during and after the underwater renovation. (a) The average number of yawns performed by the saithe, (c) the average number of scratches performed by the cod and (d) the average number of scratches performed by the saithe. Whiskers show the 95th to the 5th percentiles with outliers.

on average during the period when divers were in the tank not making renovation noise relative to when there were no divers in the aquarium (no diver period 5.00, 4.32–5.79; divers present with no renovation noise period 0.67, 0.33–1.33; estimated marginal mean, 95% Wald confidence interval).

4 DISCUSSION

In this case study, we found changes in the behaviour of a school of cod and a school of saithe in a public aquarium during exposure to an underwater renovation producing construction noise. Both species displayed changes in vertical distribution, swimming speed and group formation during the noise exposure from the renovation. The school of cod was always close to the bottom of the aguarium during the control period. However, when the noise increased during the renovation period, the school increased its vertical distribution and was observed to occupy multiple depth zones more frequently. The school of saithe stayed in the upper zone of the aquarium during the control period, although during the renovation when the noise levels increased, the school moved closer to the bottom. Shifts in vertical distribution have been observed in response to a variety of auditory stressors in both captive and wild fish and are considered an attempt to avoid or escape the noise source (Engås et al., 1996; Handegard et al., 2003; Pearson et al., 1992).

The schools of both species were predominantly observed in loose group structures throughout the noise exposure. There were occasions where groups were seen to shift in terms of their structure during the noise exposure, such as tight group structures for the school of cod and no group formation for the school of saithe. These behaviours were, however, only seen in less than 10% of the observations.

In response to noise, cod and especially saithe also increased their swimming speed, and when the noise levels returned to the aquarium's background level, both cod and saithe immediately resumed slow swimming behaviour and/or being stationary at the bottom. None of the changes in swimming speed were observed when divers were present but not making noise, suggesting that it was caused by the construction noise. The findings align with previous studies that have reported increased swimming speed in response to underwater noise (Fewtrell & McCauley, 2012; Handegard et al., 2003; Kastelein et al., 2008). Combined with the observed shifts in vertical distribution, we therefore suggest that periods of increased noise levels in public aquaria or aquaculture facilities should be minimised to avoid altered behaviour in fish.

Interestingly, we found that both cod and saithe yawned more when exposed to elevated noise levels, compared to the control and recovery periods. This change was also only observed during periods of construction noise and not by the presence of divers not making noise. Yawning is a behaviour that occurs in all groups of vertebrates, although the functional role can vary (Gallup, 2011). Across

455

various animal groups, vawning has been associated with stretching, increases in respiration (although yawning in fish is a different behaviour than increased ventilation rate) and filling social roles such as communicating tiredness, hunger or boredom (Daquin et al., 2001). As the mechanical motion of yawning demands strong contractions of muscles, and various fish species have been observed to change their yawning frequency both during increased excitement and when interacting with conspecifics, it has been hypothesised that yawning activates the body and enables the fish to better respond (Rasa, 1971). Supporting this hypothesis, yellowtail damselfish (Microspathodon chrysurus) shown models of a conspecific and a novel object increased their yawning rate (Rasa, 1971). Therefore, the observed increase in yawning frequencies during noise exposure within the renovation period may have been due to an increase in excitement or vigilance caused by the noise per se. Alternatively, this increase in yawning behaviour may have been caused by an increase in con- or heterospecific interactions caused by changes in vertical distributions and swimming behaviours.

As opposed to the yawning behaviour, the changes in scratching behaviour were less clear. The cod displayed a decrease in scratching behaviour during the construction work, both with divers working in silence and when making construction noises, and the frequency remained low during the recovery period. The saithe scratched themselves less during the recovery period, but there was no difference between the control period, compared to the quiet or noisy periods of the renovation. Scratching behaviour in fish is often associated with irritation, parasitic infestations or other discomforting factors. For example, fish infected by external parasites often scratch themselves against aquarium walls and other objects (Roy & Panigrahi, 2010; Saha & Bandyopadhyay, 2015). However, the fish in the aquarium at Universeum are frequently examined by a veterinarian, and it is unlikely that a parasite load caused the behaviour and would differ between the observation periods.

Due to our experimental design, we cannot determine if the behavioural changes observed were caused by the renovation noise only or by the presence of divers producing this renovation noise. In order to explore the effects of the divers' presence in the aquaria, we compared behaviours of the control period with videos when divers were present but not producing noise. We found that the presence of divers not making noise caused a slight change in fish behaviour in terms of the depth distribution of both saithe and cod and a reduction in the scratching frequency of the cod. The group structure, swimming speed, yawning frequency and scratching behaviour of saithe, however, remained the same. Once the divers started producing noise, a wider array of behavioural changes were seen, including increased swimming speed, changes in depth distribution and increased yawning frequencies. Taken together, these observations suggest that the noise from the construction work had a major effect on fish behaviour, which should be considered in husbandry practices and the management of captive fish.

5 CONCLUSION

Our results demonstrate that several weeks of underwater renovation generating construction noise changed the behaviour and distribution of schools of Atlantic cod and saithe in a large public aquarium. We observed changes in depth distribution and swimming speed as well as in yawning and scratching frequencies. Additionally, the presence of divers that were working without making renovation noise had a slight effect on fish behaviour in terms of depth distribution and the scratching frequency of cod. This case study contributes important insights into the impacts of anthropogenic noise on fish residing in public aquaria. It also highlights the need for careful consideration and management of noise levels within these environments to minimise potential negative effects on the well-being and behaviour of fish. Understanding how fish modulate their behaviour in response to noise exposure can contribute to our knowledge of their adaptive capabilities and provide valuable insights for the management of aquatic environments, including public aquaria, where noise disturbances may occur.

AUTHOR CONTRIBUTIONS

Marica Andersson: Formal analysis; investigation; methodology; visualisation; writing-original draft; writing-review and editing. Ola Svensson: Formal analysis; writing-original draft; writing-review and editing. Terese Swartz: Supervision. Jack Manera: Formal analysis; writing-original draft; writing-review and editing. Michael Bertram: Formal analysis; validation; writing-original draft; writing-review and editing. Eva-Lotta Blom: Investigation; methodology; project administration; resources; supervision; writing-original draft; writing-review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data is available at DRYAD (https://doi.org/10.5061/dryad. kkwh70s9d).

ETHICS STATEMENT

This was a 'natural experiment' during a maintenance project of the North Sea public aquarium at the Universeum public science centre. All observations of fish behaviour were made from the hall where the public watch the aquarium. Universeum did not report any mortality during or in the immediate period after the renovation.

ORCID

Marica Andersson [®] https://orcid.org/0009-0005-7520-2453 Ola Svensson [®] https://orcid.org/0000-0003-3752-3131 Jack L. Manera [®] https://orcid.org/0009-0003-7947-6473 Michael G. Bertram [®] https://orcid.org/0000-0001-5320-8444 Eva-Lotta Blom [®] https://orcid.org/0000-0002-8839-4141

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457

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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