

Behavioural responses of wild, spawning Atlantic cod (*Gadus morhua* L.) to seismic airgun exposure

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Seismic airgun surveys to map petroleum deposits in the seabed may impact behaviour of marine animals over large distances. Understanding whether fish spawning behaviour is affected by this anthropogenic noise source is important because reproductive success may be impacted. The fine-scale behavioural responses of Atlantic cod to airgun exposure over an extended period were investigated using an acoustic telemetry positioning system on a spawning ground in Norway. During 2019 to 2021, 135 spawning cod were equipped with telemetry sensor tags and were exposed to airgun shooting during the spawning periods of 2020 and 2021, with varying received sound levels comparable to a full-scale survey at distances of 5 to >40 km. Cod demonstrated only weak responses to the disturbance from repeated 3-h treatment periods over 5-d, swimming on average slightly deeper during seismic exposure compared to silent control periods. This response varied between individuals. Longer-term effects of seismic exposure on swimming depth were not detected. No changes in swimming acceleration, displacement, or area use occurred. These results suggest that relatively distant seismic surveys do not substantially alter cod behaviour during the spawning period at received sound exposure levels varying between 115 and 145 dB re 1 $\mu\text{Pa}^2\text{s}$ over a 5-d period.

Keywords: acoustic telemetry, anthropogenic noise, coastal cod, fish, home range, positioning system, reproduction, seismic surveys, sensor tags, spawning.

Introduction

Seismic exploration, using airguns to acoustically map oil and gas reserves in the seabed, is a major source of anthropogenic noise in the marine environment (Hildebrand, 2009). The low frequency sound from seismic surveys can propagate over long distances and therefore has the potential to disturb marine life on a relatively large spatial scale (Hildebrand, 2009; Duarte *et al.*, 2021). There is a need to understand the impact of such disturbance on marine ecosystems, so that appropriate mitigation and management actions can be taken (Przeslawski *et al.*, 2018; Sivle *et al.*, 2021a).

A growing body of research focuses on the effects of seismic and other anthropogenic noise across a wide variety of marine taxa (Williams *et al.*, 2015; Carroll *et al.*, 2017; Duarte *et al.*, 2021). Recent reviews of this literature indicate, for example, that seismic surveys can cause hearing damage and behavioural responses in marine mammals (Bröker, 2019), and behavioural and physiological responses in some marine invertebrates (Carroll *et al.*, 2017). Teleost fish can also be impacted by this source of anthropogenic noise (Carroll *et al.*, 2017), as they tend to have their best hearing capabilities over a low frequency range that overlaps with sound from seismic surveys (Slabbekoorn *et al.*, 2010; Popper and Hawkins, 2019) and are sensitive to particle motion caused by this type of impulsive sound source (Popper and Hawkins, 2018, 2019).

The impacts of sound from seismic surveys on fish range widely in severity between situations and studies. At close range, exposure to sounds from seismic airguns can cause

temporary hearing damage in fish (McCauley *et al.*, 2003; Popper *et al.*, 2005). In the context of seismic surveys, relatively few individual fish would be expected to be exposed to such high sound levels, whereas many more could potentially be disturbed by lower sound levels at greater distances from the survey (Popper *et al.*, 2005). Anthropogenic sound, including seismic, may mask communication, cause physiological stress, and elicit behavioural responses in exposed animals (Slabbekoorn *et al.*, 2010). Studies on free-ranging fish have mostly reported behavioural responses to airgun sound (Carroll *et al.*, 2017), such as startle responses (Wardle *et al.*, 2001), changes in activity or behavioural states (Løkkeborg *et al.*, 2012; van der Knaap *et al.*, 2021), and changes in distribution either vertically (Slotte *et al.*, 2004) or horizontally (Engås *et al.*, 1996). Other studies report no or minor changes in fish behaviour (Peña *et al.*, 2013) and no change in species assemblages and abundance of fish (Meekan *et al.*, 2021) in response to seismic surveys.

The potential for anthropogenic noise to interfere with successful reproduction of fish is a topic of particular concern (Slabbekoorn *et al.*, 2010; de Jong *et al.*, 2020). Reproduction or spawning is considered a particularly sensitive period in the fish life-cycle, as timing, location, biotic, and abiotic conditions are often critical for successful reproduction (Pörtner and Farrell, 2008; Ciannelli *et al.*, 2015). Vocal fish with highly specific spawning grounds and short spawning periods are predicted to be most sensitive to noise-induced stress and masking during reproduction, though intermittent

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sounds, such as seismic, may be less harmful than continuous sounds (de Jong *et al.*, 2020). Assessing the effects of seismic surveys on successful reproduction is a key step towards determining the overall population consequences of this disturbance (Slabbekoorn *et al.*, 2019).

Atlantic cod (*Gadus morhua* L., hereafter referred to as cod) may be especially vulnerable to sound disturbance during spawning. Cod is a soniferous fish species, with acoustic communication playing an important role in the cod mating system (Hawkins and Picciulin, 2019). During the spawning period, male cod produce low frequency grunts (~50 Hz, Brawn, 1961b, Finstad and Noreide, 2004, Hernandez *et al.*, 2013), which have been associated with aggressive and courtship behaviours (Brawn, 1961a, b; Rowe and Hutchings, 2006). Low frequency noise associated with ship traffic has been found to reduce the effective communication range of spawning cod (Stanley *et al.*, 2017), and low frequency anthropogenic noise can elicit stress responses in cod resulting in reduced egg production and fertilization rates (Sierra-Flores *et al.*, 2015). Additionally, cod tend to demonstrate high site fidelity to spawning areas (Robichaud and Rose, 2001; Skjæraasen *et al.*, 2011; Dean *et al.*, 2014). Therefore, reports that free-ranging cod move away from an area in immediate or delayed response to seismic surveys (Engås *et al.*, 1996; van der Knaap *et al.*, 2021) is further cause for concern. However, in a companion study to the present paper, free-ranging, spawning cod exposed to airgun sound similar to a full-scale seismic survey occurring 5–>40 km away over a period of 5 d did not abandon their spawning site. This was presumably due to high motivation to remain on the spawning grounds despite the prolonged disturbance (McQueen *et al.*, 2022).

Even if cod do not leave the spawning ground, exposure to sound from seismic airguns could provoke behavioural changes that negatively impact spawning success. For example, during a seismic survey feeding cod were found to increase the amount of time they spent inactive, and displayed subtle changes in their distribution without immediately leaving the area (van der Knaap *et al.*, 2021). Subtle behavioural changes have also been reported for cod in net-pen experiments that were exposed to airgun sound (Davidsen *et al.*, 2019; Hubert *et al.*, 2020). Even subtle responses might lead to biologically significant impacts if the duration of the exposure and the response are long enough, and prolonged exposure could cause sensitization. Given that cod exhibit a complex mating system involving a multitude of visual and acoustic behavioural interactions (Brawn, 1961a, b; Hutchings *et al.*, 1999; Rowe and Hutchings, 2004, 2008; Rowe *et al.*, 2008; Meager *et al.*, 2009, 2010, 2018; Skjæraasen *et al.*, 2010; Dean *et al.*, 2014), there appears to be considerable potential for long-duration seismic exposure to impact cod spawning behaviour.

During a seismic survey, the sound exposure level (SEL) is high close to the vessel, and the sound propagates over many kilometres resulting in elevated SEL over a large area (Handegard *et al.*, 2013). It is likely that relatively few fish will experience the highest levels at very short distances from the seismic survey vessel, while many more fish will occur within several kilometres of the survey, where the sound from the airguns is still audible. Understanding the behavioural responses of fish at moderate ranges from a seismic survey is therefore useful for determining large-scale and population-level effects, as more fish will receive lower sound levels that may still induce behavioural reactions at greater distances (Popper and Hawkins, 2019). Such information is also extremely relevant

for management of noise-producing activities at sea, including to determine appropriate buffer zones for protecting important fish spawning grounds (Sivle *et al.*, 2021a). For example, behavioural responses of fish observed at moderate distances from a seismic survey formed the basis of scientific advice in Norway to avoid conducting seismic surveys within 37 km of important cod spawning grounds (Sivle *et al.*, 2021a). However, in the absence of available data from spawning fish, this advice was based on responses of feeding fish to seismic surveys (Engås *et al.*, 1996; Sivle *et al.*, 2021a).

This study therefore uses acoustic telemetry to investigate whether exposure to seismic airgun shooting over an extended period during the spawning season causes fine-scale behavioural changes of cod on a spawning ground, which may impact spawning success. To determine the behavioural responses of cod within a large area around a seismic survey source, spawning cod were exposed to sound levels comparable to a seismic survey operating 5 to >40 km away over a duration of 5 d.

Methods

A controlled exposure experiment was carried out to expose cod at a spawning ground to sound from a small seismic airgun cluster towed from a research vessel. The behaviour of cod at the spawning ground was tracked using acoustic telemetry. The telemetry data were analysed to assess variation in behavioural metrics (swimming depth, acceleration, displacement) and changes in home ranges in response to the experimental exposure to seismic airguns.

The test site was a spawning ground located within a relatively sheltered bay (Bakkasund) in the Austevoll archipelago near Bergen in southwestern Norway (Figure 1). Water depths in the test site range from a few up to 100 m. Cod spawning in this region typically peaks during February and March (Meager *et al.*, 2009).

Seismic exposure survey and sound monitoring

In two controlled exposure experiments during 9–14 February 2020 and 14–19 February 2021, tagged cod at the test site were exposed to sound from seismic airguns. The year 2019 served as a baseline year, when cod were tagged and released at the same time of year as during the exposure years, but no seismic airgun exposure was carried out at the test site.

In the exposure experiments, tagged cod were exposed to three types of treatments: seismic exposure; boat control; and silent control. Each treatment lasted 3 h, and the order of the three treatments was fully randomized within blocks of one of each treatment. During the seismic exposure and boat control, the 55 m source vessel travelled a 4.8 km racetrack with a speed of 3.7 to 5.6 km h⁻¹ (Figure 1). The vessel continued until the end of the 3-h treatment, and then switched to the next treatment. During the silent control treatments, the source vessel stayed in an area acoustically sheltered from the test site by islands (Figure 1), with a straight-line distance from the test site of >5.6 km. The study was designed to mimic a commercial seismic survey with long exposure times, and with the seismic vessel switching between being in relative vicinity (seismic treatments) and being out of audible range (boat control and silent control treatments). Nine blocks were conducted in 2020 and ten blocks were conducted in 2021 over a period of 5 d.

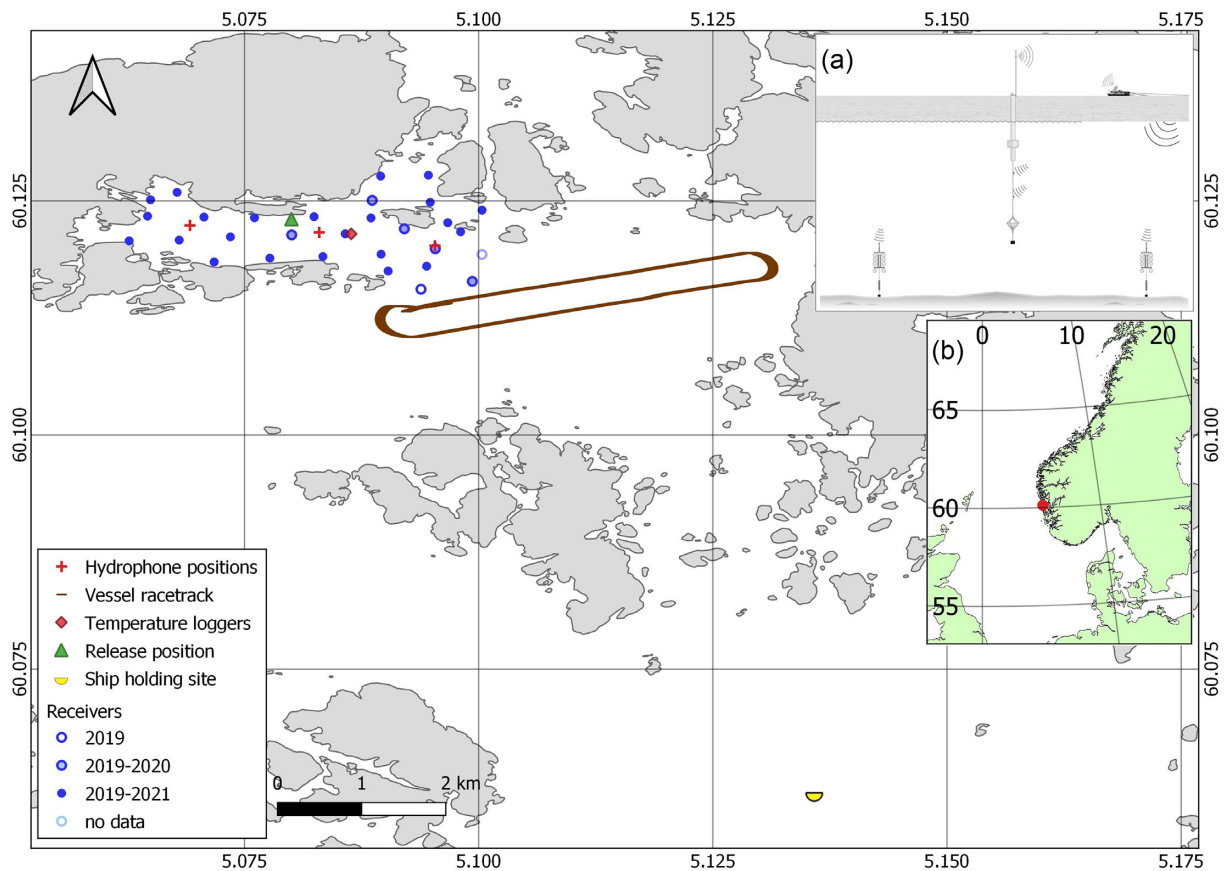


Figure 1. The location of receivers within the test site, and the position where tagged cod were released. Points are shaded by how many spawning seasons of data (denoted by years) they contributed to the study, as some receivers were lost over the course of the experiment. The position of temperature loggers deployed throughout the 3-year study period and the locations of hydrophones deployed during the seismic surveys are also shown. The racetrack travelled by the research vessel during the seismic exposure survey is indicated. The ship holding site represents the area where the ship stayed during silent control treatments. (a) Sketch showing the configuration of hydrophones deployed during the exposure survey, with two hydrophones close to the sea floor in the inner and outer part of the bay and a vertical array in the middle of the test site. (b) Red point indicates location of the study site in relation to the Norwegian coastline.

During seismic exposure treatments, a cluster of two 40 in³ airguns, deployed at 3 m depth, was towed from the source vessel. The airguns fired synchronously every 10 s, operated at a chamber pressure of 110 bar, with an expected nominal broadband peak pressure level of 223 dB re 1 μ Pa-m. The number and size of airguns are smaller than would typically be used in a full-scale seismic survey, thus the sound levels produced resemble a survey occurring at a greater distance from the study site. Further technical details about this survey and the experimental design can be found in a report available online (Sivle *et al.*, 2021b).

During the seismic exposure survey, calibrated omnidirectional hydrophones (Naxys Ethernet Hydrophone, model 02345, frequency range: 5 Hz to 300 kHz, sensitivity: -179 dB re V/ μ Pa, gain: 20 dB, sampling frequency 48 kHz, duty cycle: 22 s on, 8 s off) were deployed to capture the ambient sounds and the sounds from the research vessel and seismic airguns. The hydrophones were deployed at four positions within the test site: 8 m above the seafloor (50–65 m depth) at the outer bay and at the inner bay; and at 8 and 37 m depth from a vertical hydrophone array in the centre of the bay (Figure 1).

The hydrophone data were bandpass filtered with a sixth order Butterworth filter (5 Hz–10 kHz) and SEL (ISO, 2017)

were calculated by time integrating the squared pressure over the seismic pulse and applying a $10\log_{10}$ transformation. The pulse was integrated over a 1 s interval around the highest sound pressure value in each 22 s file (see Figure 2 in McQueen *et al.*, 2022). We also calculated SEL over an interval of a similar length prior to each pulse to compare with background noise levels. This approach was also used for the silent and boat control periods.

Acoustic telemetry grid and fish tagging procedure

Thirty acoustic telemetry receivers (VR2Tx, Innovasea, Canada) were deployed in a grid pattern within the test site in October 2018. The grid was designed to allow for simultaneous detection of transmissions on multiple receivers for triangulation of fish positions, confirmed through range testing prior to experiment start (McQueen *et al.*, 2022). The number of receivers retrieved from the test site varied slightly between study years, due to occasional receiver losses, with data retrieved from 29 receivers after the 2019 spawning season, 28 receivers after the 2020 spawning season, and 23 receivers after the 2021 spawning season (Figure 1). A string of ten temperature loggers (HOBO Pendant, Onset Computer, United States) was deployed along a depth profile at a position in the centre of the bay (Figure 1), sampling every 2 h.

Cod were caught within a 2-week period before tagging by local fishers using gillnets or pots within 1 km of the test site. Post-capture, fish were kept in net pens within the area until tagging. Cod were tagged on 29 January 2019, 28 January 2020, and 27 January 2021. Under anaesthesia, cod were measured for weight and length, sexed by ultrasound (Karlsen and Holm, 1994) and egg biopsies were obtained from all females, allowing for further confirmation of sex and spawning readiness through subsequent image analysis (Thorsen and Kjesbu, 2001; McQueen *et al.*, 2022). An acoustic tag was inserted in the body cavity through an incision made on the ventral side of fish, which was then closed by two sutures. Each cod was tagged with one of four types of acoustic transmitter (V13P, V13TP, V13AP, V13TP ADST tags, Innovasea, Canada). These tags transmit unique identity codes (IDs) at 69 kHz and were additionally equipped with combinations of pressure, acceleration, or temperature sensors (Table 1). Transmissions occurred at random intervals, on average every 250 s with a minimum and maximum off time of 200 and 300 s, respectively. Tag life (~290–738 d) far exceeded the expected spawning period. Tags with >1 sensor alternated transmissions between the sensors. Additionally, an external *t*-bar tag (TBA standard anchor *t*-bar tag; Hallprint, Australia) was anchored at the base of the anterior dorsal fin for visual external recognition of tagged fish. Cod were returned to a tank filled with a constant supply of seawater to recover from the tagging procedure, before being transported to the middle of the test site and released (Figure 1).

Permits were given from the Norwegian Directorate of Fisheries to capture fish (permit 19/14024), Norwegian Food Safety Authority for fish tagging and exposure (permit 18034 and 26019), and the Norwegian Petroleum Directorate for permission to conduct seismic shooting (permit 739/2019).

Statistical analysis

The behavioural responses of cod to seismic airgun exposure were examined with linear mixed-effects models for: (1) individual behavioural metrics at two timescales: within the survey (treatment-level analysis) and before-during-after (BDA) the survey; (2) changes in home range characteristics (area change and overlap) for individual fish from before to during the exposure period and corresponding baseline period. All analyses were undertaken in R (v. 4.1.1) (R Core Team, 2021).

Relationship between behavioural metrics and seismic airgun exposure

Data recorded on receivers within the test site during 12.5-d periods encompassing the seismic exposure survey were used for analysis of behavioural metrics. The analysis periods were 05 February 2020 22:50–18 February 2020 06:41 UTC and 10 February 2021 22:43–23 February 2021 11:35 UTC, thus including 4 d before and after each 4.5-d seismic exposure survey.

The behavioural metrics used as response variables in the linear mixed-effects models were swimming depth, acceleration, and displacement. Models were developed separately for each behavioural metric. For analysis of treatment-level responses, behavioural metric data were averaged over 10-min bins. For analysing BDA responses, behavioural metric data were averaged over 1-h bins. Binning data allowed standardization of time-steps and the selected bin widths were a

Table 1. Overview of condition at tagging and number of mature fish tagged per year and by tag type and sex at the test site.

Tag cohort	Sensor type			Sex		Condition at tagging		
	Depth + Acceleration (V13AP)	Depth + Temperature (V13TP)	Depth + Temperature + DST (V13TP-ADST)	Female	Male	Mean length in mm (range)	Mean weight in g (range)	Mean Fulton's K (range)
2019	8	0	0	20	26	655 (480–890)	3 146 (1 282–6 100)	1.1 (0.5–1.5)
2020	32	4	0	33	21	654 (430–900)	3 145 (666–8 950)	1.0 (0.8–1.4)
2021	14	0	21	14	21	595 (390–875)	2 146* (704–>6 000)	1.0 (0.8–1.6)*

* Does not include two individuals > 6000 g that could not be weighed due to the limitations of the scale used in 2021. DST = data storage tag.

Table 2. The number of fish included in analysis, split by response variable, the period selected for analysis (seismic effect), year, and sex.

Seismic effect	Year	Swimming depth			Acceleration			Displacement		
		Female	Male	Sample size	Female	Male	Sample size	Female	Male	Sample size
Treatment-level	2020	17	10	9 498	8	5	4 319	13	10	1 463
	2021	8	6	6 296	5	4	3 891	8	5	3 039
BDA	2020	13	10	6 195	6	4	2 848	12	10	2 657
	2021	8	5	3 706	5	4	2 521	8	4	3 031

The sample size by year for each analysis after binning to 10-min or 1-h intervals is also shown.

compromise between reducing computing time for the larger dataset, while keeping loss of information to a minimum for each analysis. The sample size available varied between analyses, depending on the variables that were included (Table 2).

Swimming depth (distance from surface) data were transmitted from tag pressure sensors, on average every 250 or 500 s, depending on the tag type. However, because not every tag transmission was received, realized intervals were variable within and between fish. For each 10-min interval, the difference between the current and average sea level was subtracted from the swimming depth to correct for tidal variation. Sea level data were downloaded from the Norwegian Mapping Authority, Hydrographic Service (<https://www.kartverket.no/>), for position 60.10°N 5.10°E. The downloaded data provided the water level observed at Bergen, multiplied by a factor of 0.83 and time adjusted by -15 min to estimate the water level at the test site.

Fish acceleration data were transmitted by accelerometer sensors in a subset of the tags (Table 1), on average every 500 s. The accelerometer sensors measured acceleration in three dimensions for 25-s periods and transmitted averaged acceleration information as a vector quantity. Raw acceleration data resembled a gamma distribution and were log-transformed prior to linear mixed-effect model fitting.

Fish positions were calculated from the raw detection data by Innovasea using a hyperbolic positioning method, based on transmission detection times at synchronized receivers (for more details, see Supplementary Material). Calculated positions were averaged over 10-min bins for the treatment-level analysis and 1-h bins for the BDA analysis. Displacement was calculated from these averaged fish positions. The positions were projected to UTM coordinates (zone 32 N) using the R package “rgdal” (Bivand *et al.*, 2021b), and 2D Euclidean distances between consecutive positions of each fish were calculated. Consecutive positions with intervals of >10 min or 1 h were excluded from the treatment-level and BDA analyses, respectively. For the treatment-level analysis, steps which overlapped two different treatments were excluded. Raw displacement data were positively skewed and bounded at zero, and were log-transformed prior to analysis. The 0 m displacement estimates ($n = 3$) were replaced with 0.01 m, well within the positional uncertainty (see Supplementary Material), to allow for log-transformation.

To explore treatment-level behavioural responses to seismic airgun exposure, models were fit using “treatment” (the 3-h treatments conducted within each experimental block) as a fixed effect to represent the seismic effect. Only data recorded during the treatments were included in the treatment-level analysis. Seismic treatment was set as the reference level in the models, to test for differences in behavioural metrics between

seismic and control treatments (*a priori* contrasts). Separate models were fit using “BDA period” [4 d before the seismic survey (B), during the seismic exposure survey (D), 4 d after the survey (A)] as a fixed effect to represent the seismic effect. Data recorded during the entire analysis period were used in the BDA analysis. The “during” period was set as the reference level in tests for differences in behavioural metrics between the BDA periods (*a priori* contrasts). Therefore, a total of six separate models were developed: one at each timescale for each of the three behavioural metrics. Only fish which contributed data for all treatment types or BDA periods were retained in the respective analyses. In cases where a significant difference in behavioural metrics between treatment types or BDA periods was detected, comparisons were conducted *a posteriori* using least-square means [R package “lsmeans” (Lenth, 2018)]. Tukey’s method of *p*-value adjustment was implemented for multiple comparisons.

To account for potential variation in the behavioural metrics not associated with the seismic airgun exposure, additional fixed effects were included in the models, namely sex, year, and a three-level factor indicating day, night, or dusk/dawn to account for diel changes. Timing of sunrise and sunset were assigned using the package “suncalc” in R (Thieurmél and Elmarhraoui, 2019). Day was set to begin 1 h after sunrise and ended 1 h before sunset. Night was set to begin 1 h after sunset and ended 1 h before sunrise. Dawn and dusk were assigned to the intervening 2-h periods [as in Dean *et al.* (2014)].

In addition to including the main effects of the explanatory variables listed above, the following interactions were considered: seismic effect: sex (to assess whether the sexes responded differently to seismic exposure); seismic effect: year (to assess whether the response to seismic varied between study years); and seismic effect: diel phase [to assess whether seismic exposure disrupted diel behavioural patterns, as indicated by van der Knaap *et al.* (2021)]. Given that a previous telemetry study focusing on spawning cod in the same coastal region of Norway found a significant interaction between sex and diel phase in relation to swimming depth (Meager *et al.*, 2009), for the depth models a three-way interaction between sex, diel phase, and seismic effect was also considered. The full suite of fixed effects included in the models of behavioural responses for both timescales are listed in Supplementary Table S2.

Fish ID was included as a random intercept to account for expected inter-individual variation in behaviour and non-independence of observations from the same individual. We also tested whether the inclusion of random slopes improved model fit. A random slope for seismic effect was considered, to account for potential inter-individual variation in the

response to the seismic exposure. For the depth analyses, diel phase was included as an alternative random slope, as clear diel vertical migration patterns were observed in some individuals, and thus depth selection in response to diel phase was expected to vary substantially between individuals.

To account for expected temporal autocorrelation between successive recordings of behavioural indices, a continuous time autoregressive model of order 1 (continuous time AR-1) was fit (Pinheiro and Bates, 2000). The correlation structure was fit to the 10-min or 1-h time steps of the binned behavioural metric data and was nested within fish ID.

The optimum random structures and autocorrelation structure were identified by comparing Akaike's information criteria (AIC) of models including all fixed effects and different combinations of random effects, fit using restricted maximum likelihood (REML) (Zuur *et al.*, 2009). Once the optimum random structures had been determined, the function "dredge" from R package "MuMIn" (Barton, 2020) was used to fit models including the defined optimum random structure and all combinations of fixed effects. Models were fit with maximum likelihood (ML) for selection of fixed effects. The model with the lowest AIC and highest weighting was refit with REML to estimate coefficients. In cases where there was similar support for >1 model ($\Delta\text{AIC} < 2$), the simpler model was used for interpretation of the data (Zuur *et al.*, 2009). Residuals and autocorrelation plots were used to assess model fit. Models were fit using the R package "nlme" (Pinheiro *et al.*, 2021).

Changes in area usage

Changes in home range size and site fidelity in response to seismic exposure were examined using indices of utilization distribution (UD) size change and overlap. Comparable periods during the baseline year were used to assess whether changes in area usage during exposure years were more pronounced than usual. We only included mature fish with at least 30 positions [as in Meager *et al.* (2010)] for both the 4-d period before seismic exposure and during the seismic exposure survey, since small sample sizes underestimate home ranges (Börger *et al.*, 2006).

For each fish, the 95% UD (UD_{95} in m^2) was calculated using the Brownian Bridge kernel method for autocorrelated location data (Horne *et al.*, 2007), using the function "kernelbb" in the R package "adehabitatHR" (Calenge, 2020). This UD_{95} , or home range, is the smallest estimated area where the individual was predicted to have spent 95% of its time during a given period, while accounting for travel between relocations and uncertainty in the recorded positions. A separate UD_{95} was calculated for each fish (a), where $\text{UD}_{95,a,b}$ and $\text{UD}_{95,a,d}$ are defined as home range in the 4 d before (b) and during (d) exposure periods, respectively. The first parameter required for smoothing (sig1) was estimated from the recorded tracks using the ML approach of Horne *et al.* (2007). An estimate of sig1 was calculated for each individual in each period. The median of all sig1 values was used in home range calculation, to facilitate comparisons between individuals and periods. The error associated with the relocations was incorporated into the model by setting the second smoothing parameter (sig2) as the median horizontal positioning error (HPE_m) for that year (i.e. 2.6 m in 2019, 4.6 m in 2020, 4.0 m in 2021, see Supplementary Material and Table S1). Sections of the estimated home ranges that overlapped with land were removed, using a simplified representation of the

Bakkasund coastline (Supplementary Figure S10) and the R package "rgeos" (Bivand *et al.*, 2021a).

To estimate change in size of UD_{95} for each individual from before periods to during exposure periods, we calculated $\Delta\text{UD}_{95,a}$ as:

$$\Delta\text{UD}_{95,a} = \text{UD}_{95,a,d} - \text{UD}_{95,a,b}$$

To investigate the extent of overlap between $\text{UD}_{95,a,b}$ and $\text{UD}_{95,a,d}$ for each individual, a UD overlap index (UDOI) was calculated as:

$$\text{UDOI}_{a,b,d} = 100 \left[\frac{\text{overlap}_{a,b,d}}{\text{UD}_{95,a,b} + \text{UD}_{95,a,d} - \text{overlap}_{a,b,d}} \right],$$

where $\text{overlap}_{a,b,d}$ (in m^2) is the intersection between the $\text{UD}_{95,a,b}$ and $\text{UD}_{95,a,d}$ (Meager *et al.*, 2010; Dean *et al.*, 2012), calculated using the package "raster" in R (Hijmans, 2021). The UDOI ranges between 0 and 100, with 0 indicating no overlap and 100 indicating complete overlap. The UDOI can therefore be considered a measure of the individual's site fidelity over this period, ranging from no change in area usage (UDOI = 100) to a complete change to a new location (UDOI = 0).

To investigate whether changes in home ranges were more pronounced during the seismic exposure years compared to the baseline year, $\text{UDOI}_{a,b,d}$ and $\Delta\text{UD}_{95,a}$ were calculated for the exposure periods in 2020 and 2021, and for a comparable period in the baseline year (2019), when no seismic exposure was carried out. For 2019, the $\text{UD}_{95,a,b}$ was calculated from the period 06 February 2019 22:50 to 10 February 2019 22:50, and the $\text{UD}_{95,a,d}$ was calculated from the period 10 February 2019 22:50 to 15 February 2019 06:41. The periods in 2019 were selected to have the same interval since tagging as the periods in 2020. The periods were kept as similar as possible each year to account for seasonal variation.

Linear mixed-effects models were fit to the $\Delta\text{UD}_{95,a}$ and $\text{UDOI}_{a,b,d}$ to test if change in area and degree of site fidelity were related to sex and year. The most complex models for both response variables included sex, year, and an interaction term. The year 2019 was used as the reference level in the model, to compare the results of the baseline year to the results in each exposure year. Rather than grouping 2020 and 2021 to a single "exposure years" level, the years were included as separate levels in the model, to allow detection of potential inter-annual differences in responses. Fish ID was included as a random intercept in all models, as some fish were present in >1 year. Model selection was carried out as described previously through comparison of model AICs.

Results

Sound exposure

In both 2020 and 2021, the seismic signal was clearly stronger than the background noise and the noise made by the source ship without active airguns, even at the furthest distance from the source (Figure 2). The spectral analysis showed that the main energy content of the seismic pulses lay in the frequency range below 100 Hz (see Figure 2c and d, Supplementary Figure S4c and d in McQueen *et al.*, 2022), as is the typical frequency range of conventional seismic airguns (Gisiner, 2016; Landrø and Langhammer, 2020; Prior *et al.*, 2021). However, there was also energy above ambient level at higher

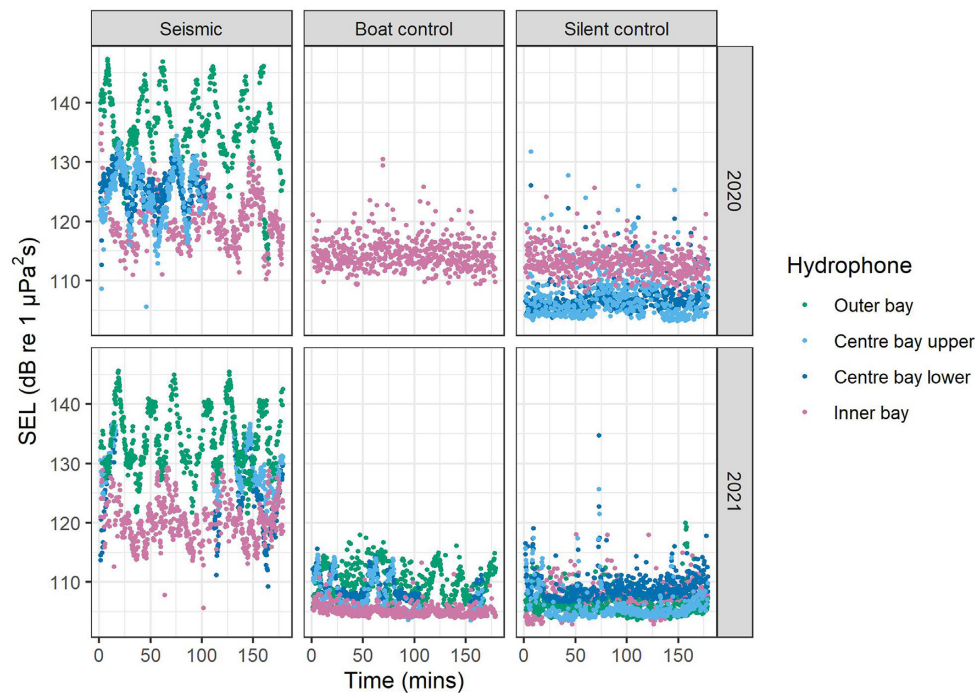


Figure 2. SEL for the three different treatments (seismic, boat control, silent control) for the study years 2020 (upper panels) and 2021 (lower panels). Data were recorded at bottom mounted hydrophone rigs in the outer bay, closest to the source (green points) and inner bay, furthest from the source (pink points), as well as at a hydrophone array in the centre of the bay with two hydrophones: upper at 8 m depth (light blue points) and lower at 37 m depth (dark blue points). For the outer bay, data for control runs (boat control, silent control) were not available for 2020 due to battery failure of the hydrophone. For the centre bay hydrophones, several data gaps were present due to battery limitations of the hydrophones. Recordings of boat control were missing for 2020 for the upper hydrophone and for both years for the lower hydrophone due to battery and hydrophone failure. Plots are constructed using data collected at the different stations during different blocks of both the 2020 and 2021 exposure. X-axis shows time since start of treatment. SEL during seismic treatments varies as the source vessel travelled around the racetrack, peaking when the source vessel reaches the closest point of approach to the test site.

frequencies, and variation between shots (for additional details, see Sivle *et al.*, 2021b; McQueen *et al.*, 2022).

SEL at the different hydrophones varied over time (Figure 2) as the source vessel travelled around the racetrack, resulting in varying distance between the ship and the hydrophones. Different depths along the racetrack and variable shielding from the land also contributed to this observed variation in received sound levels. At the hydrophone in the outer bay, closest to the ship and the sound source, SEL during the seismic treatments varied between 120 and 145 dB re $1 \mu\text{Pa}^2\text{s}$, while at the inner bay hydrophone, at the location furthest from the source, SEL of the seismic signal varied between 115 and 130 dB re $1 \mu\text{Pa}^2\text{s}$ (Figure 2). The levels of the seismic signals were relatively similar between the two years. However, in 2020, due to higher background noise likely caused by stormy weather during the survey period, the signal to noise ratio was lower. Available data from the boat control and seismic control treatments are also shown in Figure 2.

Response of behavioural metrics to seismic airgun exposure

Overall, the only significant relationship between the behavioural metrics and seismic exposure was a treatment-level effect on swimming depth. No relationship between swimming depth and BDA period was detected. No relationships were detected between acceleration or displacement and seismic exposure, at either timescale.

Cod swimming depth data ranged from 0 to 58 m. The simplest models with the lowest AIC for both treatment-level and BDA swimming depth responses to seismic exposure included all main effects (seismic effect, sex, year, diel phase). The selected model for BDA swimming depth responses also included an interaction between BDA period and diel phase (Table 3). The optimum random structure for swimming depth models included the autocorrelation term, fish ID as a random intercept, and diel phase as a random slope (Supplementary Table S2).

The selected treatment-level swimming depth model indicated significant differences in swimming depth between seismic and silent control treatments (*a priori* contrasts, Table 4). To compare the average swimming depths between all treatment type combinations *a posteriori*, least-square means were contrasted between treatments. The only significant contrast was between seismic and silent control treatments (0.39 ± 0.13 m, adjusted $p = 0.01$), with no significant difference apparent between swimming depth during boat control treatments and swimming depth during silent control (0.21 ± 0.13 m, adjusted $p = 0.22$) or seismic treatments (-0.18 ± 0.12 m, adjusted $p = 0.29$). Although the overall effect sizes for differences between treatments were small (0.39 m or less, Table 4), there was considerable variation between individuals (Supplementary Figure S4). Females were shallower than males on average. Both sexes were shallower at night than during the day, with swimming depths at dusk and dawn intermediate. The fixed effect for year indicated

Table 3. The five best models (lowest AIC and highest weight of evidence, w_i) for each behaviour metric and timescale.

No.	Response variable	Fixed effects	Random effects	Temporal autocorrelation	df	AIC _i	Δ_i (AIC)	w_i
1	Swimming depth (m), 10-min bins	Y + T + S + DP + T:S	DP ID	10 min ID	17	75 764.1	0	0.18
2		Y + T + S + DP	"	"	15	75 764.8	0.73	0.13
2		Y + T + S + DP + T:S + DP:S	"	"	19	75 765.3	1.26	0.10
4		Y + T + S + DP + T:S + T:Y	"	"	19	75 765.4	1.37	0.09
5		Y + T + S + DP + DP:S	"	"	17	75 765.6	1.57	0.08
6	Swimming depth (m), 1-h bins	Y + BDA + S + DP + BDA:DP + BDA:Y	DP ID	1 h ID	21	54 394	0	0.286
7		Y + BDA + S + DP + BDA:DP	"	"	19	54 394.6	0.6	0.22
8		Y + BDA + S + DP + BDA:DP + BDA:Y + S:DP	"	"	23	54 395.8	1.8	0.12
9		Y + BDA + S + DP + BDA:S + BDA:DP + BDA:Y	"	"	23	54 396	2	0.11
10		Y + BDA + S + DP + BDA:DP + S:DP	"	"	21	54 396.4	2.4	0.09
11	Acceleration ($m s^{-2}$), 10-min bins	Y + DP	1 ID	10 min ID	7	18 332.9	0	0.32
12		Y + T + DP + T:Y	"	"	11	18 333.7	0.8	0.22
13		Y + S + DP	"	"	8	18 334.8	1.9	0.12
14		Y + T + DP	"	"	9	18 335.2	2.3	0.10
15		Y + T + S + DP + T:Y	"	"	12	18 335.6	2.7	0.08
16	Acceleration ($m s^{-2}$), 1-h bins	Y + DP	1 ID	1 h ID	7	9 245.7	0	0.39
17		Y + S + DP	"	"	8	9 247.5	1.8	0.16
18		Y + BDA + DP	"	"	9	9 247.6	1.9	0.15
19		Y + S + BDA + DP + BDA:S	"	"	12	9 248.7	3.0	0.09
20		Y + S + BDA + DP	"	"	10	9 249.3	3.6	0.07
21	Displacement (m), 10-min bins	DP	1 ID	10 min ID	6	14 330.7	0	0.39
22		Y + DP	"	"	7	14 332.2	1.5	0.19
23		S + DP	"	"	7	14 332.7	2	0.15
24		Y + S + DP	"	"	8	14 334.1	3.4	0.07
25		BDA + DP	"	"	8	14 334.2	3.5	0.07
26	Displacement (m), 1-h bins	DP	BDA ID	1 h ID	11	18 217.4	0	0.13
27		S + DP	"	"	12	18 217.9	0.5	0.10
28		Y + DP	"	"	12	18 218	0.6	0.10
29		Y + S + DP	"	"	13	18 218.1	0.7	0.09
30		Y + DP + BDA + BDA:DP + BDA:Y	"	"	20	18 218.9	1.5	0.06

Optimum random-effects structure was selected in a previous step (see Supplementary Table S2). In cases where there was similar support for >1 model ($\Delta AIC < 2$), the simpler model was used for interpretation of the data (selected models are in bold). Y = year; T = treatment; S = sex; DP = diel phase; ID = fish ID.

Table 4. Summary of selected linear mixed-effects models to explain the treatment-level and BDA depth responses of cod.

Response variable	Fixed effect	Estimate	SE	df	t-value	p-value
Swimming depth (m), 10-min bins	Intercept (seismic, 2020, female, day)	19.26	2.13	15 751	9.05	<0.001
	Boat control	-0.18	0.12	15 751	-1.5	0.132
	Silent control	-0.39	0.13	15 751	-2.88	0.004
	2021	9.72	1.7	15 751	5.71	<0.001
	Male	9.91	3.12	36	3.17	0.003
	Dusk/dawn	-0.42	0.22	15 751	-1.97	0.049
	Night	-1.52	0.42	15 751	-3.66	<0.001
Swimming depth (m), 1-h bins	Intercept (during, 2020, female, day)	22.75	1.97	9 858	11.53	<0.001
	After	0.71	0.47	9 858	1.5	0.132
	Before	-0.76	0.52	9 858	-1.47	0.141
	2021	6.57	1.14	9 858	5.76	<0.001
	Male	9.93	2.84	32	3.49	0.0014
	Dusk/dawn	-2.16	0.46	9 858	-4.7	<0.001
	Night	-4.99	1.03	9 858	-4.86	<0.001
	After:dusk/dawn	-0.5	0.32	9 858	-1.54	0.122
	Before:dusk/dawn	0.47	0.33	9 858	1.42	0.156
	After:night	0.03	0.44	9 858	0.08	0.937
	Before:night	-0.07	0.44	9 858	-0.16	0.875

Models also included a random-effects structure, and an autocorrelation structure (see Supplementary Table S2). Models were fit with REML for parameter estimation.

that fish were on average deeper in 2021 than 2020 (Table 4, Figure 3).

The selected BDA swimming depth model predicted that average swimming depth in the 4 d before or after the exposure period did not differ significantly from average swimming depth during the 4.5-d exposure period (Table 4 and Supplementary Figure S5). Similar to the treatment-level analysis, this model indicated that males were deeper than females on average (Table 4 and Supplementary Figure S5). Swimming depth also showed a similar pattern relating to diel phase, with fish of both sexes deepest during the day, shallower at dusk/dawn, and shallowest during the night (Table 4 and Supplementary Figure S5). Although the interaction between diel phase and seismic effect was included in the best fitting models, the parameter estimates indicated that this pattern was not disrupted during the seismic exposure (Table 4 and Supplementary Figure S5). As with the treatment-level model, average swimming depth was found to be deeper in 2021 than 2020 (Table 4).

No treatment-level or BDA effect of seismic exposure was detected in the acceleration or displacement data, with the models with lowest AIC for these behaviour metrics including diel phase (displacement models, Table 3) or diel phase and year (acceleration models, Table 3) as the only fixed effects. Seismic effect and sex were thus not included in the final models for either behavioural metric. The optimum treatment-level acceleration and BDA displacement models included seismic effect as a random slope (Supplementary Table S2), suggesting there may have been some individual variability in relation to seismic exposure. Autocorrelation was detected in all models, and model fit was significantly improved by including fish ID as a random intercept, indicating variation in the behaviour metrics between individuals and correlation of successive records of behaviour metrics (Supplementary Table S2). The year effect in the acceleration models indicated that average acceleration was significantly lower in 2021 than 2020 (Supplementary Table S3 and Figures S6 and S7). Unrelated to seismic exposure, acceleration was higher and displacement greater at night and dusk/dawn than during the day

(Supplementary Tables S3 and S4 and Figures S6 to S9). Displacement per 10 min ranged from 0 to 317 m. Displacement per hour ranged from 0.07 to 934 m. Acceleration records ranged from 0 to 3.5 m s⁻², with the latter being the maximum value the tag could record.

Changes in area usage in relation to seismic exposure

Data from 8, 12, and 7 females and 12, 10, and 5 males in 2019, 2020, and 2021, respectively, were included in home range analysis. Nine fish were present in >1 year. Average time between positions to estimate UD_{95,a,b} ranged between fish from 8 to 173 min with an overall average across all fish of 33 min, and for the UD_{95,a,d} between 6 to 179 min with an overall average across all fish of 35 min. Across all years, the number of positions used to estimate the UD_{95,a,b} ranged from 33 to 695 (mean: 283.7), and the number of positions used to estimate the UD_{95,a,d} ranged from 31 to 978 (mean: 340.6).

The home range analysis provided no indication that cod changed the size of their home ranges more during the seismic exposure years than during the baseline year. Of all models tested for explaining change in size of UD (Δ UD_{95,a}) between before and during exposure periods, the null model had the lowest AIC (Table 5), indicating that neither year [baseline year (2019) compared to exposure years (2020 and 2021)] nor sex improved the model fit. Overall mean \pm SE change in home range was 14288 \pm 17103 m². The mean \pm SE change in home range size per year was 19713 \pm 19775 m² in 2019, -1931 \pm 34975 m² in 2020, and 34979 \pm 29113 m² in 2021.

For site fidelity, characterized as the overlap of an individual cod's home range between the before and during exposure periods (UDO_{I,a,b,d}), there was similar support (Δ AIC < 2) for three models with the lowest AIC: the model with sex as the only fixed effect, the model with sex and year as fixed effects, and the null model (Table 5). The null model can therefore be selected as the simplest model with lowest AIC, indicating that sex and year do not explain the variation in the degree

Table 5. Model selection for linear mixed-effect models fit to $UDOI_{a,b,d}$ and $\Delta UD_{95,a}$ estimates.

No.	Response variable	Fixed effects	Random effects	df	AIC _i	Δ_i (AIC)	w_i
1	$\Delta UD_{95,a}$	none	1 Fish ID	3	1423.6	0	0.60
2		S	“	4	1425.6	2.0	0.22
3		Y	“	5	1426.8	3.2	0.12
4		S + Y	“	6	1428.8	5.2	0.05
5		S + Y + S:Y	“	8	1431.4	7.9	0.01
6	$UDOI_{a,b,d}$	S	1 Fish ID	4	494.8	0	0.43
7		S + Y	“	6	496.3	1.5	0.20
8		none	“	3	496.5	1.8	0.18
9		Y	“	5	496.9	2.2	0.15
10		S + Y + S:Y	“	8	499.1	4.3	0.05

Models were fit with ML for model selection. Differences between model AIC and lowest AIC (Δ_i) and Akaike weights (w_i) are also shown. The simplest models with lowest AIC are emboldened. S = sex; Y = year.

of site fidelity of individual cod. The calculated $UDOI_{a,b,d}$ indicated some overlap of individual home ranges, with the mean \pm SE across all individuals and years 37.3 ± 3.1 . The mean \pm SE $UDOI$ per year was 44.5 ± 4.6 in 2019, 32.8 ± 4.8 in 2020, and 33.6 ± 7.4 in 2021. Additionally, plotting the home ranges onto a map of the test site did not indicate an obvious avoidance of regions close to the vessel racetrack during the exposure periods (Supplementary Figure S10).

Discussion

No pronounced behavioural response was observed in wild, spawning cod exposed to sound from airguns at SEL of 115 to 145 dB re $1 \mu Pa^2s$ over 5 d. The only subtle behavioural response to this exposure was that on average the tagged cod used slightly deeper swimming depths during the seismic treatments than during the silent control treatments. This response varied between individuals. The cod neither changed their swimming activity (acceleration, displacement) during seismic exposure, nor altered their distribution within the bay more during the exposure years than the baseline year.

The SEL at the study site during the seismic treatments (ranging between 115 and 145 dB re $1 \mu Pa^2s$) resembles the predicted SEL at distances of 5 to >40 km from a full-scale seismic array, depending on the propagation conditions (Handegard *et al.*, 2013). It may be argued that SEL at our study site were mostly too low to elicit a strong response from the tagged cod. Previous experiments using captive, hatchery-reared cod (Mueller-Blenke *et al.*, 2010) and wild mackerel and sprat (Hawkins *et al.*, 2014) found that the experimental fish began to react to playback of impulsive sounds at levels towards the upper end of the range of sound levels used in our study. There are difficulties in directly comparing or extrapolating results from these previous experiments to our study system, however. Hawkins *et al.* (2014) studied small pelagic fish, which differ from cod in many ways, including in their hearing abilities (Popper and Hawkins, 2019). Mueller-Blenke *et al.* (2010) used captive, hatchery-reared cod, which may not behave in the same way as wild, free-ranging fish (e.g. Meager *et al.*, 2011). Additionally, these earlier experiments used playback of artificial sound over short periods, whereas we used real airguns over prolonged periods. It is important to acknowledge that seismic surveys occurring at closer proximity to spawning grounds, with higher sound levels than tested in our study, could provoke an increased response from spawning cod. However, it is also important to note that the spatial

and temporal extent of these higher sound levels would be limited compared to sound levels from more distant surveys.

The observed lack of response from swimming behaviours other than swimming depth (acceleration, displacement, area usage) is somewhat unexpected, given that previous studies on free-ranging cod have found that passage of a seismic survey at similar distances can displace cod (Engås *et al.*, 1996), cause behavioural changes consistent with a reduction in feeding activity, and distributional changes consistent with increased roaming (van der Knaap *et al.*, 2021). Net-pen experiments have also indicated that cod altered their horizontal position in response to airgun exposure (Davidsen *et al.*, 2019). The SEL recorded at the test site in our study are in a similar range to these previous experiments that documented behavioural reactions in cod. The SEL at the study site of van der Knaap *et al.* (2021) ranged from around 147 dB re $1 \mu Pa^2s$ at the closest point of approach (2.25 km) of a full-scale seismic array, to around 115 dB re $1 \mu Pa^2s$ at ~20-km distance (see Supplementary Figure S3c in van der Knaap *et al.*, 2021). In Engås *et al.* (1996), SEL was not measured, but reactions were observed in fish up to 33 km from the seismic survey, which overlaps with the range of distances imitated in our study (5–40 km). In Davidsen *et al.* (2019), the distance between the survey vessel and the experimental fish ranged between 0.1 and 6.7 km, and the SEL ranged between 133 and 155 dB re $1 \mu Pa^2s$. Although it cannot be ruled out that some of the variation in responses between studies may be related to specifics of the study design and the sound exposure levels, it seems plausible that other biological factors play an important role.

Situation specific trade-offs likely dictate the level of response of fish to seismic exposure, in an analogous way to animal decision making under predation threat; maximizing fitness through compromising between reducing risk of predation and reducing costs related to lost opportunities for feeding or reproduction (Lima and Dill, 1990; Kavaliers and Choleris, 2001). A strong motivation to stay in the area and continue spawning behaviour, due to the link between spawning and fitness, might explain why we did not observe large behavioural responses. In contrast, previous studies that did report behavioural responses focused on cod in other behavioural states (i.e. feeding; Engås *et al.*, 1996; van der Knaap *et al.*, 2021). Additionally, the fish may have habituated to the disturbance, as the seismic exposure was repeated over several days in our study. However, habituation to or tolerance of a disturbance stimulus does not necessarily indicate a lack of negative impacts (Bejder *et al.*, 2009).

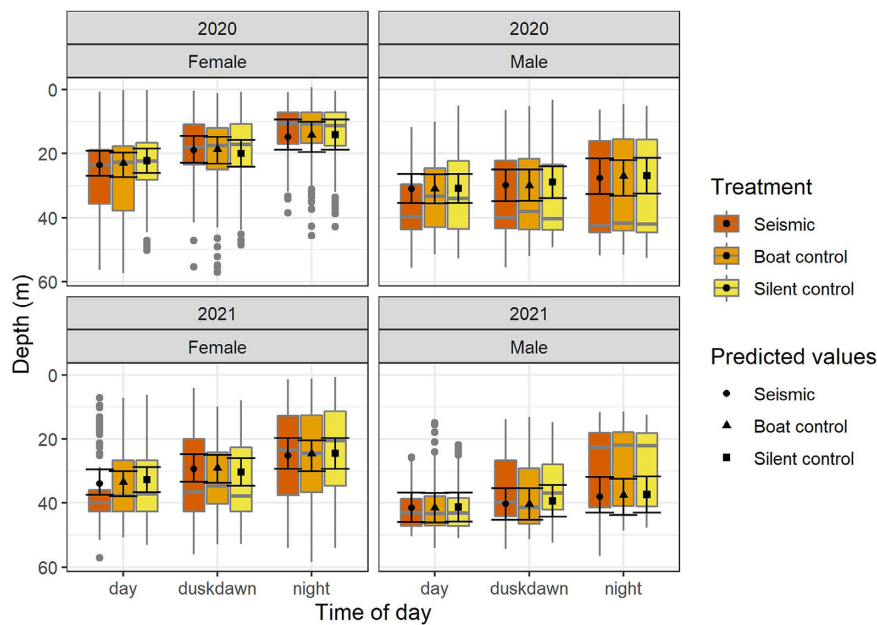


Figure 3. Boxplots showing data used to analyse treatment-level effects of the experimental treatments (seismic, boat control, and silent control) on swimming depth of tagged cod, with data for all individuals combined. For sample sizes per group, see Table 2. Overlaid black points with error bars show the predicted values and 95% CIs from the selected model (model 1 in Table 3, see Table 4 for parameter estimates).

The only behavioural response to seismic exposure observed in this study was a significant increase in swimming depth during seismic treatments relative to silent control periods. An increase in swimming depth in response to exposure to sound from seismic airguns was also observed in other studies. Diving has previously been reported as a response of other fish species to seismic airgun exposure in various experimental settings, including cod and saithe in a net pen (Davidsen *et al.*, 2019), free-ranging whiting (Chapman and Hawkins, 1969), and free-ranging blue whiting, and mesopelagic fish species (Slotte *et al.*, 2004). In general, diving can be considered threat avoidance behaviour, and fish may dive in response to stressful stimuli (Papandroulakis *et al.*, 2014).

Diving has also been reported as a response of various fish species to an approaching vessel (e.g. Handegard and Tjøstheim, 2005; Ona *et al.*, 2007; De Robertis *et al.*, 2008). In the case of Handegard and Tjøstheim (2005), cod reacted to a vessel several hundred metres away, a response that was associated with deployment and use of trawl gear. Although it is not completely understood which specific stimuli from a moving vessel fish react to, it is likely that radiated noise is important (De Robertis and Handegard, 2013). In our study, average swimming depth during the boat control treatments was intermediate between average swimming depth during seismic (deepest swimming depths) and silent control (shallowest swimming depths) treatments, and was not significantly different from either. This may indicate that the vessel itself was partly responsible for the increased swimming depth of cod, though cod seemed to react more strongly to the louder stimulus of the active seismic shooting.

The differences in average swimming depths across all individuals between the experimental treatments were <0.5 m, which is minor compared to the average differences between sexes, years, and diel phases (Figure 3, Table 4). There was, however, substantial individual variation, with much larger differences between treatments observed for some fish (Sup-

plementary Figure S4), indicating that some individuals may be more severely impacted than others. However, the overall small effect sizes suggest that population-level impacts would likewise be minor. None of the overall patterns in depth use, notably those related to sex and diel phases, were disrupted by the seismic treatments (Figure 3). The lack of evidence for a longer-term effect of seismic airgun exposure on swimming depth indicates that any responses were transient. Although it seems unlikely that short-lived diving, within depth ranges that cod traverse during their normal activities, would strongly impact spawning success, any movement in response to seismic airgun exposure may indicate an interruption of natural behaviours. Therefore, studies which can directly measure spawning output are required to test whether swimming depth responses can substantially impact reproduction.

In this study, the behavioural metrics were found to vary with factors other than seismic, providing insights into cod behaviour during the study period. Differences in swimming depth between sexes and diel period, similar to those observed during the limited sample of the spawning period studied here, have already been documented and linked to cod spawning behaviour (Meager *et al.*, 2009). Strong diel variation in acceleration and displacement were also observed. The higher acceleration and longer distances travelled at night and at dusk/dawn suggest increased activity during these periods, when the majority of cod spawning tends to occur (Kjesbu, 1989; Fudge and Rose, 2009; Dean *et al.*, 2014). The lower acceleration during the colder of the two study years (2021, Supplementary Figure S11) was likely caused by a decrease in metabolic scope with decreased temperature (Claireaux *et al.*, 2000), and similar patterns have been observed in both laboratory (Claireaux *et al.*, 1995) and field settings (Freitas *et al.*, 2015). Similarly, the telemetry data revealed clear differences in swimming depth between the two study years, with the cod's use of deeper waters on average during 2021 presumably linked to avoidance of colder surface waters during this

year [Supplementary Figure S11; see also Freitas *et al.* (2021)]. None of these patterns in cod behaviour were disrupted by the seismic exposure. The home range analysis suggested that over the short time periods considered, cod were relatively mobile and distributed throughout the bay, and this also did not change significantly as a response to seismic.

Conclusions and recommendations for future work

In conclusion, we did not find substantial changes in the behaviour of cod in spawning condition at a spawning site when exposed to seismic signals at SEL of 115 to 145 dB re 1 $\mu\text{Pa}^2\text{s}$, corresponding to a relatively distant (5–>40 km) seismic survey over an extended period (5 d). This builds on the results from our companion paper (McQueen *et al.*, 2022), which showed that the same group of spawning cod apparently did not perceive this seismic survey disturbance stimuli as sufficiently high of a risk to warrant leaving the spawning ground and lose spawning opportunities. We did find a small, but significant, increase in swimming depth of cod during seismic exposure. Since depth selection plays an important role in the cod mating system (e.g. Morgan and Trippel, 1996; Windle and Rose, 2006; Meager *et al.*, 2009, 2012; Dean *et al.*, 2014), the impact of such a depth response on spawning success should be examined further.

In this study, we used telemetry data transmitted at a temporal resolution of several minutes and were therefore unable to investigate other potential impacts of the seismic survey on the spawning fish, such as physiological stress responses (e.g. Sierra-Flores *et al.*, 2015; Celi *et al.*, 2016; Amorim *et al.*, 2022), communication masking (e.g. Stanley *et al.*, 2017), distraction (e.g. Chan *et al.*, 2010), and startle responses (e.g. Meager *et al.*, 2011). Further studies are encouraged to assess the risk that such responses to seismic surveys may pose to cod spawning success.

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Supplementary material

Supplementary material is available at the ICESJMS online version of the manuscript.

Conflict of interest

None declared.

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Author contributions

L.D.S., D.N., and K.d.J.: conceptualization; K.M., D.N., J.E.S., and T.N.F.: data curation; K.M., T.N.F., N.O.H., and J.E.S.:

formal analysis; L.D.S. and K.d.J.: funding acquisition; D.N., L.D.S., K.M., J.E.S., E.M.O., Ø.K., P.H.K., T.N.F., N.O.H., and J.J.M.: investigation; L.D.S., J.J.M., P.H.K., K.d.J., D.N., T.N.F., N.O.H., and J.E.S.: methodology; L.D.S. and N.O.H.: project administration; L.D.S.: supervision; K.M. and J.E.S.: visualisation; K.M.: writing—original draft; and all: writing—review and editing.

Data availability

The data underlying this article are available through the Norwegian Marine Data Centre (www.nmdc.no).

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