

Spawning Atlantic cod (*Gadus morhua* L.) exposed to noise from seismic airguns do not abandon their spawning site

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Seismic airgun surveys may disturb and displace fish at large ranges. If such displacement causes fish to abandon spawning grounds, reproductive success could be impacted. To investigate whether airgun sound causes cod (*Gadus morhua* L.) to leave their spawning grounds, acoustic telemetry arrays were deployed on two cod spawning grounds: a test and a reference site. From 2019 to 2021, 136 mature cod from the test site and 45 from the reference site were tagged with acoustic transmitters. Intermittent seismic shooting of two 40 in.³ airguns for 1 week during the spawning periods of 2020–2021 resulted in fluctuating sound exposure levels (SEL) at the test site, comparable to a full-scale industrial survey 5–>40 km away. Residency and survival of tagged cod were analysed with capture–mark–recapture models fitted to the detection and recapture data. Departure rate of the mature cod varied between spawning seasons but was similar between the test and reference sites. Neither survival nor departure significantly differed between seismic exposure and baseline periods. The results indicated that exposure to airguns at received SEL of up to ~145 dB re 1 μ Pa² s, comparable to a seismic survey occurring several kilometres away, did not displace tagged cod from spawning grounds.

Keywords: acoustic telemetry, anthropogenic noise, behavioural response, fish, hidden Markov model, mark–recapture model, seismic surveys, underwater.

Introduction

Anthropogenic noise is recognized as a significant pollutant of the oceans under the European Marine Strategy Framework Directive (MSFD) (European Parliament and Council, 2008). Seismic surveys for oil and gas exploration are an example of deliberate introduction of sound into the marine environment (Duarte *et al.*, 2021). Seismic airguns used in such surveys produce low-frequency sound that can travel large distances, contributing to anthropogenic noise pollution at a relatively large spatial scale (Hildebrand, 2009). Seismic surveys have the potential to disturb a variety of marine taxa (Duarte *et al.*, 2021), including teleost fish, which typically have hearing ranges that overlap with the low-frequency sound produced (Slabbekoorn *et al.*, 2010; Popper and Hawkins, 2019).

Reported effects of seismic airgun exposure on fish range from physical injury at close proximity to an intense sound source (McCauley *et al.*, 2003; Popper *et al.*, 2005) to no apparent behavioural response to a passing seismic survey (Peña *et al.*, 2013; Meehan *et al.*, 2021). Most studies on free-ranging fish have reported some degree of behavioural responses to seismic airgun exposure, including large-scale displacement (Engås *et al.*, 1996), changes in catch composition (Skalski *et al.*, 1992; Engås *et al.*, 1996; Løkkeborg *et al.*, 2012), startle responses (Pearson *et al.*, 1992; Wardle *et al.*, 2001; Hassel *et al.*, 2004), and changes in behavioural state (van der Knaap *et al.*, 2021). In general, the effects of sound exposure on fish are complex. Even within a species, behavioural

responses to external stimuli may vary between ontogenetic stage, season, and internal state of the fish (e.g. Fernö *et al.*, 1998).

Atlantic cod (*Gadus morhua* L., hereafter referred to as cod) is a commercially valuable demersal fish species, with a hearing range between 10 and 650 Hz (Chapman and Hawkins, 1973; Sand and Karlsen, 2000). Most energy from seismic sound is <100 Hz and is therefore audible to cod (Caldwell and Dragoset, 2000; Gisiner, 2016). Cod produce sound during both adult and juvenile phases (Brawn, 1961a, b). Male cod are especially vocal during the reproductive period, when they typically produce grunts at frequencies of around 50 Hz (Brawn, 1961b; Finstad and Noreide, 2004; Hernandez *et al.*, 2013) during agonistic interactions with other males (Brawn, 1961a, b) and during courtship (Rowe and Hutchings, 2006), with the volume and number of grunts being related to mating success (Rowe and Hutchings, 2006, 2008). Other low-frequency vocalizations, such as humming (Rowe and Hutchings, 2006), have also been reported. The overlap of cod hearing and vocalizations with sound from seismic airguns indicates the potential for cod to be disturbed by seismic surveys. The reported link between sound production and reproductive success in captive cod (Rowe and Hutchings, 2006, 2008) suggests that spawning could be a particularly vulnerable stage to disturbance from seismic surveys.

Spawning is generally a sensitive stage in a fish life cycle (Pörtner and Farrell, 2008; Ciannelli *et al.*, 2015), and disturbance during this period could potentially affect the coming

year-class strength. The potential for seismic surveys to disturb fish spawning behaviour and potentially hamper recruitment of important fish stocks has therefore been the basis of scientific advice to limit seismic survey activity close to important spawning sites (Sivle *et al.*, 2021a). Cod spawning may be impacted by anthropogenic noise in a number of ways, including masking of spawning-related vocalizations (Stanley *et al.*, 2017) and decreased fertilization success (Sierra-Flores *et al.*, 2015). Previous studies have shown that cod may move away from an area as an immediate (Engås *et al.*, 1996) or delayed (van der Knaap *et al.*, 2021) response to a passing seismic survey. Given that cod show multiyear fidelity to local spawning sites (Wright *et al.*, 2006; Skjæraasen *et al.*, 2011; Dean *et al.*, 2014; Zemeckis *et al.*, 2014), the potential for cod to abandon spawning sites in response to seismic airgun exposure is of particular concern, as premature departure from a spawning ground could be assumed to result in lost mating opportunities.

Understanding population-level effects of anthropogenic noise on fish is particularly important (Popper and Hawkins, 2019), especially from a management perspective (Williams *et al.*, 2015; Sivle *et al.*, 2021a). In general, only a small number of fish will experience the very high sound levels at close range to a seismic survey, and exposure to such high levels will be short since the seismic source is constantly moving. Of greater importance from a population-level perspective is the response of the larger number of fish at greater distances from the sound source, which are exposed to relatively lower sound levels but over much longer periods. For this reason, behavioural changes have been highlighted as the most important impacts of anthropogenic noise on fish, as behavioural responses are likely to be more widespread than impacts such as physical damage or physiological changes (Popper and Hawkins, 2019). Therefore, in this study we exposed fish to sound exposure levels (SEL) comparable to a seismic survey 5–40 km away over several days. Free-ranging cod have previously been observed to display behavioural responses to seismic surveys within this range (Engås *et al.*, 1996; van der Knaap *et al.*, 2021). Reactions at such ranges have a greater potential to lead to population-level consequences than responses to seismic surveys at closer proximity, as many more fish could be affected.

To assess effects of seismic exposure on cod spawning behaviour, there are clear advantages to monitoring the behaviour of free-ranging fish in their natural environment, rather than in the laboratory or in net pens. Field experiments provide the opportunity to observe natural responses unhindered by the constraints of artificial enclosures. However, it is usually not possible to directly observe fish behaviour in their natural environment, and remote observation techniques must be applied instead. Acoustic telemetry has proven an effective method for gathering valuable data on fine-scale movement, behaviour, and spawning dynamics of free-ranging cod at spawning sites (e.g. Meager *et al.*, 2009, 2010, 2012; Dean *et al.*, 2014; Zemeckis *et al.*, 2014). Tracking fish with acoustic telemetry is also widely used to detect large-scale movements and migrations (Hussey *et al.*, 2015). Acoustic telemetry therefore offers an opportunity to monitor both large-scale movement and small-scale behavioural responses of wild cod to disturbance stimuli (e.g. Dean *et al.*, 2012).

In this study, we investigate the behaviour of free-ranging cod over three consecutive years at a spawning ground using

acoustic telemetry and a before–after–control–impact (BACI) approach (Smokorowski and Randall, 2017), with one baseline year (before the impact) and two years with seismic airgun exposure: one test site and one reference site. We test the hypothesis that distant seismic airgun exposure over an extended period causes cod to leave their spawning ground. More detailed analyses of fine-scale behaviours of spawning cod within the test site during the seismic airgun exposure experiment are presented in a companion article (K. McQueen *et al.*, under review). Apparent departure of fish from a spawning ground may have a number of explanations such as cessation of spawning, spawning elsewhere, natural mortality, fishing mortality (Zemeckis *et al.*, 2014) and, in the case of telemetry, device failure. Disentangling these causes requires a probabilistic approach because the state of a fish at a given time is not always directly observable. Here, we treat acoustic detections as multistate capture histories and use a hidden Markov implementation of capture–mark–recapture models to test whether seismic exposure causes cod to depart prematurely from a spawning ground, and if so, whether departure rates vary between sexes.

Material and methods

Fish telemetry

In October 2018, 36 acoustic telemetry receivers (VR2Tx, Innovasea, Canada) were deployed in two arrays on two separate spawning grounds within the Austevoll archipelago near Bergen in southwestern Norway. The two arrays acted as one test site (30 receivers) and a smaller reference site (6 receivers) (Figure 1). The test site was Bakkasund, a cod spawning ground in a relatively sheltered bay with depths up to 100 m. The reference site was located in Osen, a small, semi-enclosed bay to which spawning cod show high site fidelity (Skjæraasen *et al.*, 2011). Additionally, single receivers (VR2W or VR2AR, Innovasea, Canada) were placed in the northern, southern, and western exit routes from the test site and on three nearby spawning sites to document the potential use of alternative spawning sites (Figure 1). Receiver range testing confirmed that tags could be detected with a high probability within the test site (see Supplementary Material). Receivers were moored to the seabed using 72 kg weights and were held upright in the water column at 7–10 m from the surface by a trawl float. Each receiver station was marked with a surface-marker buoy. The total number of receivers retrieved and deployed varied between study years, due to occasional receiver losses and extensions to the study area (Figure 1). Ten temperature loggers (HOBO Pendant, Onset Computer, USA) that sampled temperature every 2 h were deployed along the depth profile at each of the two sites (Figure 1).

Cod were captured by local fishermen using gillnets or pots within the study areas. In total, 60, 70, and 51 mature cod were captured and tagged in the years 2019, 2020, and 2021 at both sites (Table 1). Fishing was ongoing for a period of 2 weeks prior to tagging, and captured fish were held in net pens until tagging. Cod were tagged during the last week of January each year, as cod in this region spawn during February and March (Meager *et al.*, 2009).

Fish were placed in a bath of seawater and MS-222 (Tricaine methanesulfonate), at a concentration of 50 mg l⁻¹, to anaesthetize before tagging. Fish were measured to the nearest cm and gram and sexed from observed milt or by ultrasound (Karlsen and Holm, 1994). To further ascertain spawning

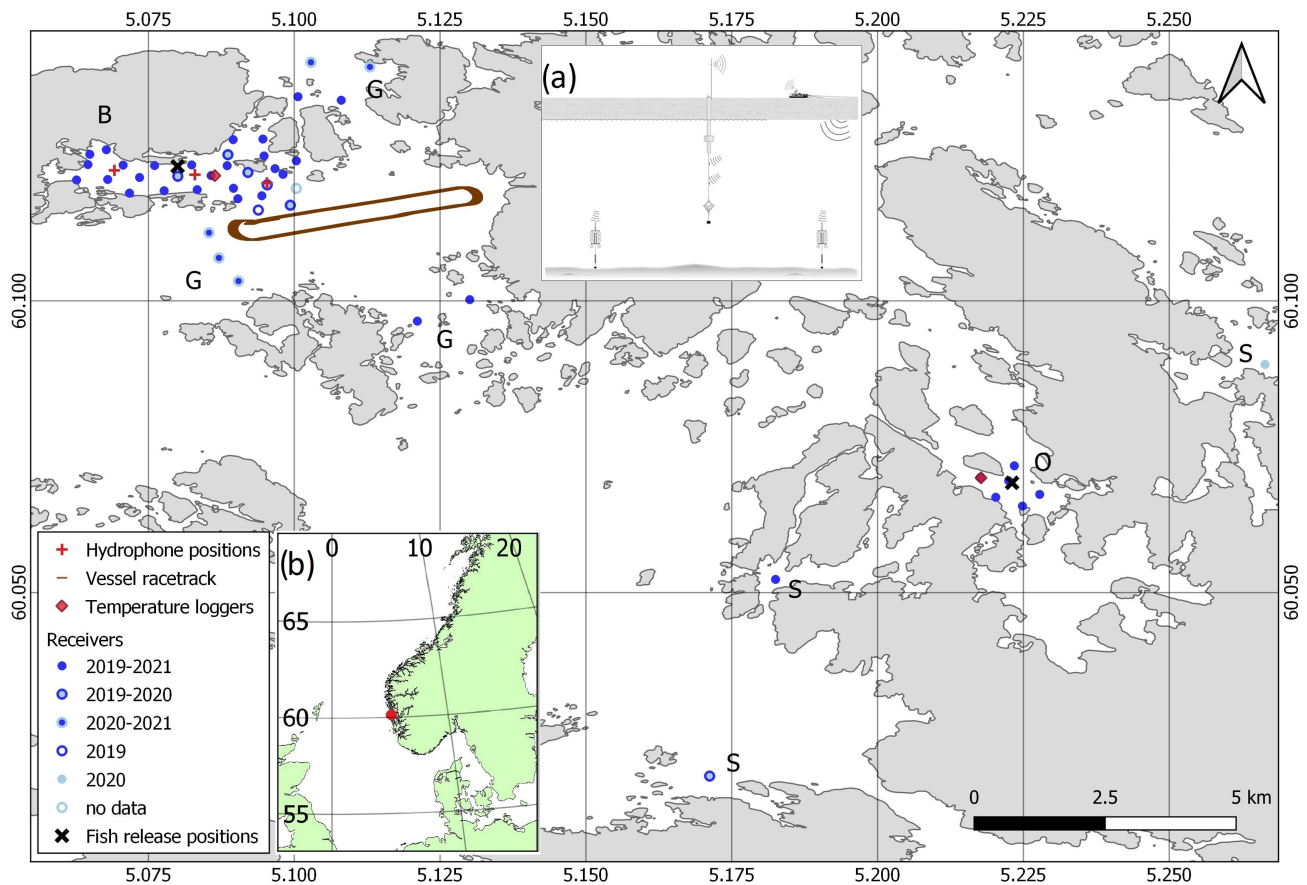


Figure 1. Overview of the telemetry receiver positions and fish release positions. Receivers were placed in the test site at Bakkasund (B); the control site at Osen (O); as gates (G) to control the western, northern, and southern exits from the test site; and at three additional spawning sites in the area (S). The shading of receivers indicates the years for which these receivers contributed data. The locations of the hydrophones and the 4.8 km vessel racetrack for the seismic and boat control treatments are also shown. During silent control periods, the source vessel stayed in a holding area south of the test site that was sheltered from the cod spawning ground by islands. (a) Sketch of the hydrophone placement, with two hydrophones close to the sea floor in the inner and outer parts of Bakkasund and a vertical array in the middle of the test site (B). (b) Location of the Austevoll archipelago in relation to the Norwegian coastline.

Table 1. The number of cod (n) tagged at the test site (Bakkasund) and the reference site without seismic exposure (Osen) during 2019–2021, also showing the total body length (TL, mm) and total weight (W, g).

Year	Area	Spawning males			Spawning females			Not spawning	Total tagged
		n	Mean TL (range)	Mean W (range)	n	Mean TL (range)	Mean W (range)		
2019	Reference site	9	512 (440–640)	1 549 (934–3028)	5	560 (450–670)	2 083 (1070–3044)	2	16
	Test site	26	613 (480–890)	2 501 (1282–4500)	20	710 (600–830)	3 984 (2262–6100)	12	58
2020	Reference site	8	534 (470–620)	1 611 (1036–2092)	8	560 (465–720)	1 949 (1222–4006)	1	17
	Test site	21	611 (505–735)	2 492 (1312–4610)	33	683 (430–900)	3 560 (666–8950)	16	70
2021	Reference site	8	537 (490–670)	1 757 (1296–2962)	7	521 (435–565)	1 552 (952–1890)	3	18
	Test site	22	553 (390–725)	1 790 (704–3646)	14	655 (445–725)	2 715* (858–6000)	16	52

Only the spawning fish were included in the statistical analyses.

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

readiness and confirmation of sex, an ovarian sample of about 0.2 ml was taken by inserting a thin plastic tube (Pipelle de Cornier; www.mpmmedicalsupply.com) through the genital pore. The samples were subsequently fixed in 3.6% buffered formaldehyde for at least 2 weeks prior to the analysis of oocyte size using image analysis (Thorsen and Kjesbu, 2001). All collected biopsies were examined in the laboratory to classify each sample into 1 of 4 categories: (1) immature; females showing previtellogenic stages only as the most advanced stage ($n = 7$); (2) early developing; females showing the

cortical alveoli stage as the most advanced stage ($n = 7$); (3) developing; females showing yolk granules ($n = 86$); and (4) spawning; females showing the presence of hydrated oocytes ($n = 1$) (Kjesbu *et al.*, 1996; Skjæråsen *et al.*, 2010). Generally, categories 2–4 are considered likely to spawn in the upcoming spawning period, but category 2 females are likely >1 month from spawning commencement. For the analysis presented here, cod were classified as spawning if egg biopsies were categorized as 3 or 4 (females) or when running milt was observed (males).

An incision was made on the ventral side of each fish so that an acoustic tag could be inserted into the body cavity. The incision was closed with two sutures. The individually coded acoustic tags transmitted at a frequency of 69 kHz at random intervals of 200 s–300 s. Tag life varied from ~198 to 766 d depending on the tag type (V8, V13P, V13TP, V13AP, or V13TP-ADST Innovasea, Canada). Tag weight (2–11.5 g) in relation to fish weight (Table 1) was well below the limits considered to affect the behaviour of fish (Brown *et al.*, 1999). 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 recognition of tagged fish. The external tag displayed a phone number, so that recaptured cod could be reported. Cod were returned to a tank filled with a constant supply of seawater to recover from the tagging procedure, and thereafter transported to the middle of the telemetry array and released (Figure 1).

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

Data were downloaded from the receivers annually after the end of the spawning season (late May/early June). After data were offloaded, each receiver was immediately redeployed in the same position.

The detection data were filtered to remove duplicate detections, suspected false detections, and detections of dead fish (see Supplementary Material). Only data from mature cod that were classified as spawning (Table 1) were included in the analyses presented in this paper.

Seismic exposure survey

Seismic exposure was conducted in two 1-week periods: from 9 to 14 February 2020 and from 14 to 19 February 2021. The surveys used the 55 m research vessel “HU Sverdrup II” with an airgun cluster of two 40 in.³ Texas Instrument Sleeve Guns. The airguns were supplied with two Reveal CompAir 5437 compressors, controlled by a Hot Shot fire control (Real Time Systems). The airguns were fired at 110 bar pressure, with an expected nominal broadband peak pressure level (source level at 1 m distance) of 223 dB re 1 μ Pa m every 10 s. During exposures, the airgun cluster was towed at a depth of 3–4 m and with a speed of 3.7–5.6 km h⁻¹. The GPS position and time of every shot were recorded.

During the seismic exposure survey, the research vessel travelled along a 4.8 km “racetrack” close to the test site (Figure 1). The seismic shooting was carried out in 3 h treatment periods, during which the vessel travelled around the racetrack approximately three times. Active seismic treatments were conducted within blocks containing two 3 h control periods when the vessel either travelled the racetrack without active shooting (boat control) or remained in a sheltered area >5.6 km away from the test site (silent control) (Sivle *et al.*, 2021b). The order of control and seismic treatment periods was randomized within each block. The blocks continued throughout the day and night, with nine blocks completed in 2020 and ten in 2021 (Sivle *et al.*, 2021b). The exposure thus mimicked an authentic seismic survey, with long exposure lines over a period of a week, with the seismic vessel interchanging between being in relative vicinity (active seismic treatments) and being out of audible range (controls).

Sound monitoring during seismic survey

Omnidirectional hydrophones (Naxys Ethernet Hydrophone, model 02345, frequency range: 5 Hz–300 kHz, sensitivity: –179 dB re V/ μ Pa, gain: 20 dB) were used to record sound pressure during the entire period of the exposure week to capture the ambient sounds and the sounds from the research vessel and seismic airguns. Recordings were conducted at three positions: 8 m above the seafloor (50–65 m depth) at the entrance of the bay and at the inner part of the bay; and at 8 and 37 m depth from a vertical hydrophone array in the centre of the bay (Figure 1).

The sound pressure was sampled over 22 s periods with 8 s pauses at a 48 kHz sampling frequency. Before and after deployment, the hydrophones were calibrated using a Brüel and Kjær 4229 piston calibrator. RGB depth loggers were attached to each hydrophone.

The data were bandpass filtered with a 6th order Butterworth filter, with lower and upper cut-offs of 5 Hz–10 kHz, respectively. The sound pressure recordings from the hydrophones were used to calculate SEL (ISO, 2017) by time-integrating the squared pressure over the seismic pulse and applying a 10log₁₀ transformation. In practice, we integrated the pulse over a 1 s interval around the highest sound pressure value in each 22 s file (Figure 2). We also calculated the SEL over a similar-length interval prior to the pulse to be able to compare the background noise levels to the SEL over the pulse. This approach was also used for the silent and boat control periods.

Modelling of residence probability and survival

Multistate Cormack Jolly Seber models (MSCJS) were used to analyse the detection and recapture histories of tagged fish. The test site at Bakkasund and the reference site at Osen were modelled separately. Briefly, this probabilistic approach was used to model the likely state of tagged fish (i.e. present at the release site, present elsewhere, or dead) that were in practice only observable when fish were detected by an acoustic receiver or reported dead by a fisher. For this analysis, fish were considered present at the test site if they were detected within the main array (B in Figure 1) or at the gate areas in the wider Bakkasund area (G sites in Figure 1). Acoustic detection logs were supplemented with information on fisheries recaptures of tagged cod to create capture histories for each week that coded for the following states: (1) not detected (“0”), (2) detected at the release site (Present; “P”), (3) detected elsewhere (Elsewhere; “E”), and (4) stopped transmitting (Dead; “D”). This latter state included tagged fish that were recaptured and reported dead by fishers, fish that were presumed dead (see Supplementary Material), and tags that had reached known shutdown dates. Transitions were fixed such that fish were removed from the model once state “D” was reached; that is, once a fish was caught or the battery stopped transmitting, it could not be detected again.

The Hidden Markov Model (HMM) implementation of MSCJS models was used (“marked” package of R, Laake *et al.*, 2013), which has parameters for survival (*S*), detection probability (*p*), and state transitions (Ψ). The parameterizations of *S*, *p*, and Ψ were based on standard terms and specific biological predictions on the timing of arrival and departure from the spawning ground. Standard terms in the models included constant and time-varying parameters, Markovian and constant Ψ , marked cohorts, and the “time

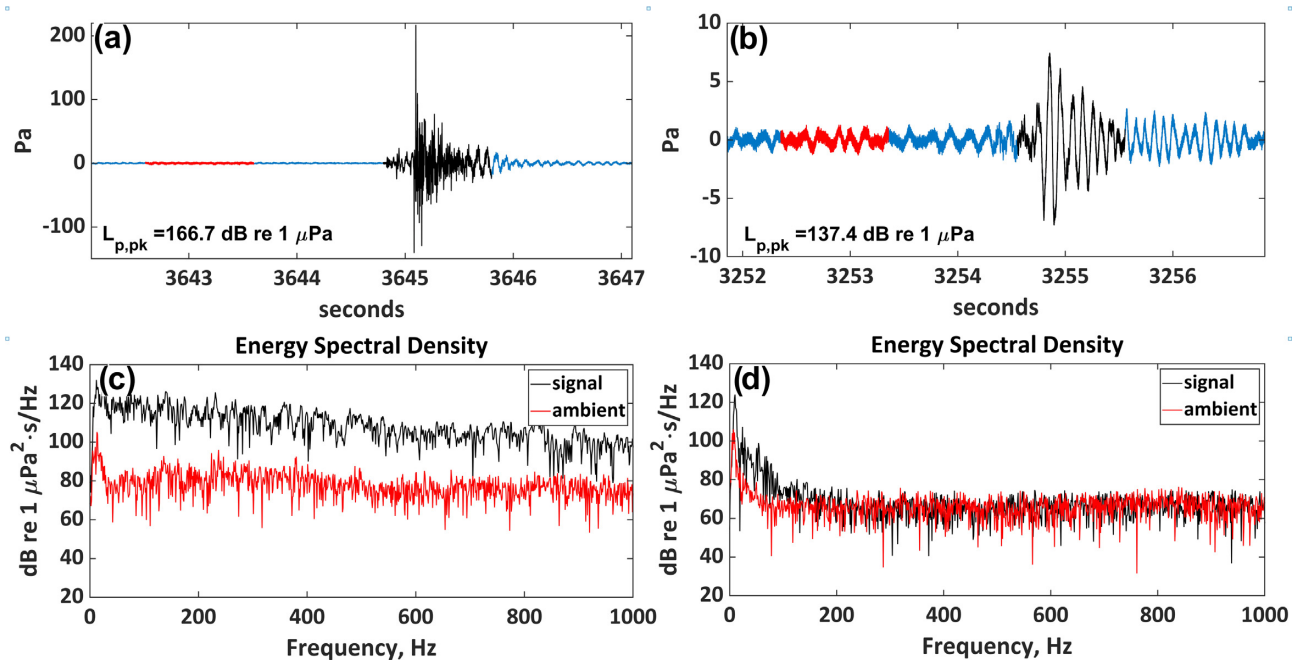


Figure 2. (a) and (b) example waveforms of the seismic signal, recorded at the outer and inner bay hydrophones, respectively, as the source vessel was at the closest point of approach to the test site. The black curves are the 1 second intervals used to time-integrate the squared pressure and apply the $10\log_{10}$ transform to obtain SEL for each pulse, respectively. $L_{p,pk}$ is the zero-to-peak sound pressure level (ISO, 2017). For comparison, the SEL for a similar length interval prior to the pulse were calculated (red curves). Note the different y-axis ranges in panels (a) and (b). (c) and (d) energy spectral densities of the signal pulses shown in (a) and (b), respectively, for the 1 s interval over the seismic pulse (black curves) and the 1 s interval prior to the pulse (red curves). The red curve includes ambient noise and noise from the vessel. Examples of waveforms recorded as the source vessel was at the furthest point of approach are given in Supplementary Figure S4.

since arrival” formulation to test if S or Ψ of each marked cohort varied over time. Sex was used as a grouping variable. We included specific parameters to test for the influence of seismic exposure on survival probabilities and state transition probabilities. This included “seismic exposure”, which compared state transitions and survival during the seismic exposure period of 2020 and 2021 with the same period (February) in 2019 to control for seasonal differences in fish emigration and survival. We also compared survival and state transitions between seismic exposure and other time periods by coding weeks with seismic exposure as “1” and other periods as “0”.

Other terms designed to test specific predictions included separate intercepts for each spawning period (for the purposes of this analysis, a spawning period was defined as from the first week of February to the first week of April), intercepts for spawning and non-spawning periods, linear and nonlinear functions of days since the onset of spawning, and functions that allowed parameters to vary over the study period (non-linear and linear terms). The mean temperature at 10 m depth was also included as a covariate.

The complexity of the multistate models and the processing time for each model meant that it was not feasible to fit all combinations of the parameter specifications that were considered. Instead, we tested different parameter structures one-by-one and retained those that reduced the Akaike Information Criterion (AIC) by >2 points. This was undertaken for each of the three parameters (S , p , and Ψ); the other two parameters were set to be time-invariant. We then constructed a model using the parameter specifications with the lowest AIC values. In the next step, we tested whether biologically relevant interactions further reduced AIC by >2 points. This

procedure resulted in 39 candidate models for the test site and 40 candidate models for the reference site. Finally, candidate models were compared at each site using information-theoretic criteria, where the Akaike weight (w_i) represented the weight of evidence in favour of a given model from the set of candidate models, given the data (Burnham and Anderson, 2004). The 95% confidence intervals set included all the models that together accounted for 95% of w_i . The residence probability was calculated for each time interval as the mean probability of fish being in the “P” state after first decoding the HMM into the most likely sequence of states for each individual.

Results

Sound exposure

In both 2020 and 2021, the seismic signal at the test site was clearly stronger than the background noise and the noise made by the source ship without the airgun, even at the furthest distance from the source (Figures 2 and 3). The spectral analysis showed that the main energy content of the seismic pulses lay in the frequency range <100 Hz (Figure 2c and d, Supplementary Figure S4c and d), as is the typical frequency range of conventional seismic airguns (Gisiner, 2016; Landrø and Langhammer, 2020). However, there was also energy above ambient level at higher frequencies and variation between shots (Figure 2c and d, Supplementary Figure S4c and d) (Sivle *et al.*, 2021b).

SEL recorded at the different hydrophones fluctuated over time due to the varying distance from the source vessel as it travelled around the racetrack (Figure 3). Changes in depth

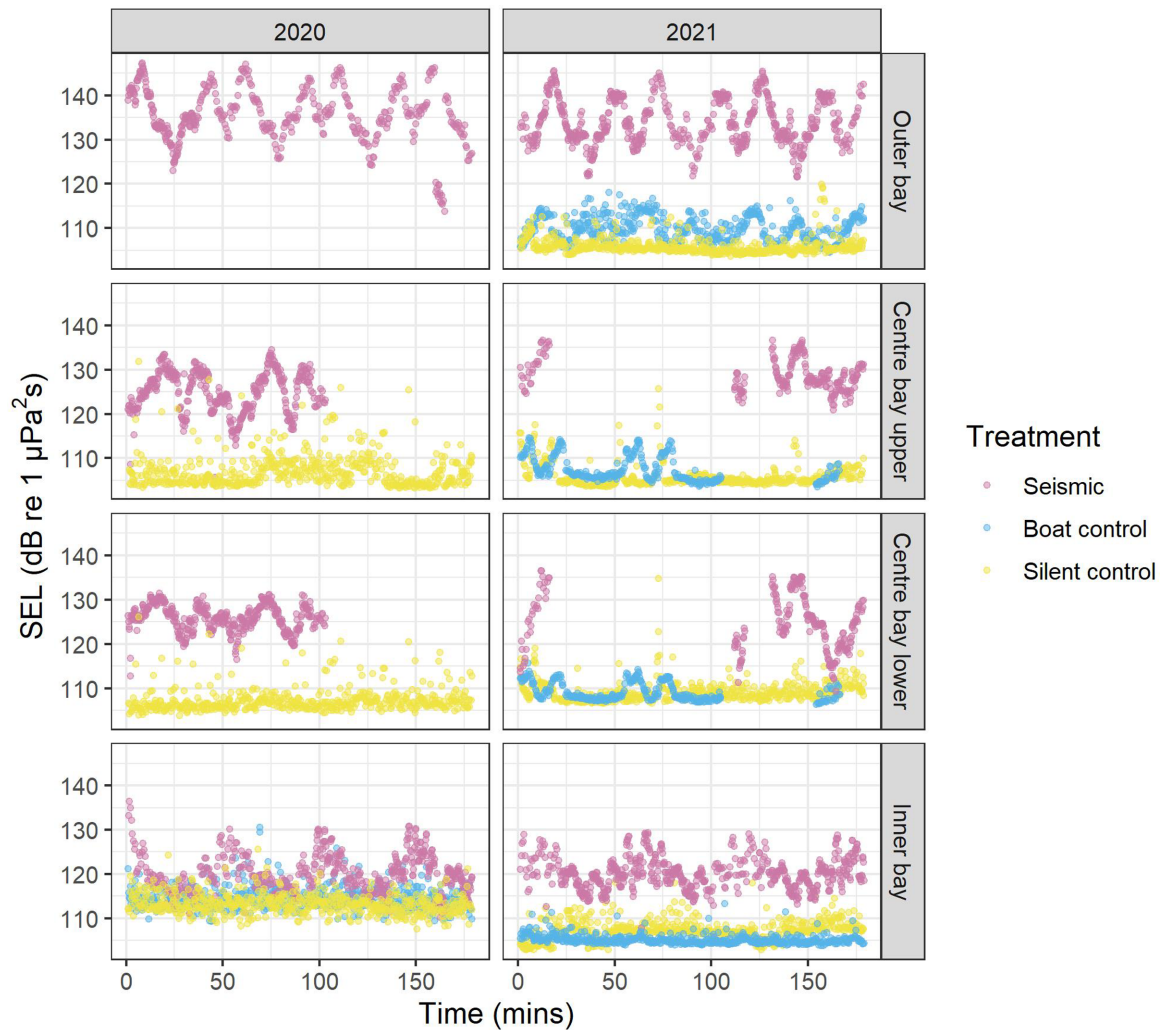


Figure 3. SEL recorded by hydrophones placed in the inner, central upper, central lower, and outer part of the bay (rows, see Figure 1 for hydrophone positions) as a function of time since the start of the seismic exposure. SEL varied as the source vessel travelled around the racetrack, peaking when the source vessel reaches the closest point of approach to the test site. The recording time of the centre hydrophones was limited by battery power, resulting in an incomplete dataset. The lack of data recorded at the outer hydrophone during control periods in 2020 and during boat control periods in the centre hydrophones in 2020 was due to device failures. Plots are constructed using the data collected at the different hydrophones during different blocks of both the 2020 and 2021 exposure surveys.

along the racetrack and variable shielding from land also contributed to the observed variation in received sound levels. At the hydrophone in the outer part of the bay, closest to the ship and the sound source, the SEL integrated over the seismic pulse 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 sound source, the SEL varied between 115 and 130 dB re $1\mu\text{Pa}^2\text{ s}$. Fish located in the outer part of the bay were hence exposed to higher sound levels than those in the inner part of the bay. In the centre of the bay, the sound varied between around 120 and 135 dB re $1\mu\text{Pa}^2\text{ s}$ (Figure 3).

The SEL were higher in the upper than the lower part of the water column. The background noise between seismic shots was also higher at the upper hydrophone (Sivle *et al.*, 2021b), probably due to sound from surface waves. The levels of the seismic signals were relatively similar between the two years. However, due to intense wind and rain in 2020, the background noise level during the controls and between shots was higher in 2020. This caused a lower signal-to-noise ratio (SNR) in 2020 compared to 2021.

Movement patterns of tagged cod

The tagged mature cod displayed differing movement patterns during the study period. Over the three study years, 60 of the 136 mature cod tagged at the test site (Bakkasund) were detected in the Bakkasund region regularly or occasionally both during and outside the spawning period, while 56 left the area during or shortly after the spawning period (Supplementary Figure S5). Additionally, across all years, 18 cod left immediately after tagging, before the start of the spawning season. Two tags were not detected at all within the test site. Overall, the presence of cod within the array gradually declined throughout the spawning period of each year, during both the baseline (2019) and seismic exposure years (2020, 2021), and at the test and reference sites (Figure 4).

Some cod were detected at the test site during multiple spawning seasons: 13 and 2 cod tagged in 2019 were also present during the 2020 and 2021 spawning seasons, respectively, and nine cod from the 2020 tagging cohort were also present during the 2021 spawning season (Supplementary Figure S5).

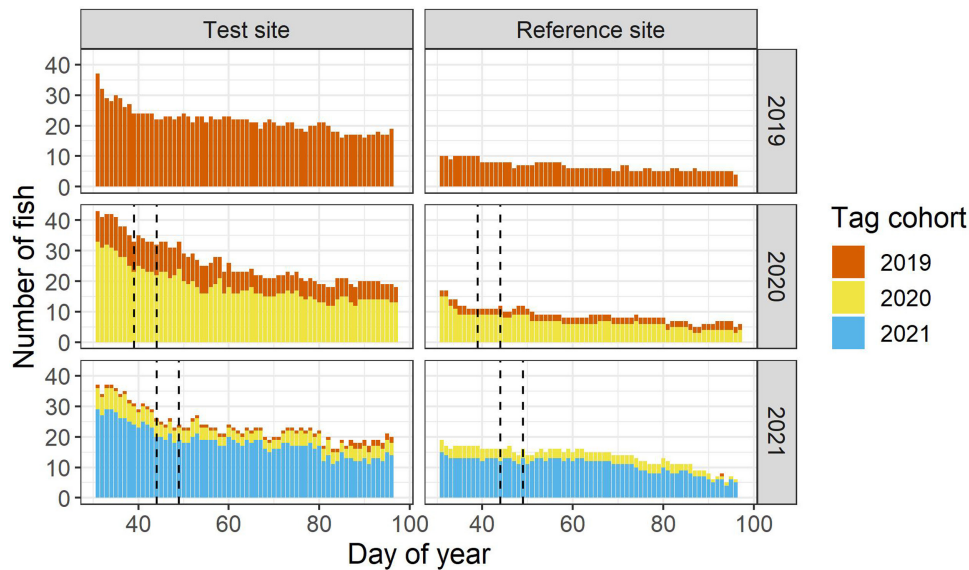


Figure 4. Number of fish detected each day during the spawning season (here defined as 1 February–7 April) at each spawning ground: the test site at Bakkasund (including the array and the outer Bakkasund area) and the control site at Osen, during each spawning season. The vertical dashed lines are the seismic exposure periods. Only fish tagged in the respective spawning grounds are included. Fish with known fates during a spawning period (i.e. died or battery ceased) were excluded from this figure.

At the reference site, the movement patterns of tagged cod were likewise mixed. Of the 45 mature cod tagged at the reference site over the three study years, 25 were detected regularly or occasionally throughout the year at the control site, 16 left during or shortly after the spawning period, and three left immediately after tagging, before the spawning period (one returned occasionally during the year). Two tags were not detected at all within the reference site. Similar to the test site, the presence of cod at the reference site gradually declined throughout the spawning period each year (Figure 4). Four cod from the 2019 tagging cohort were also present during the 2020 spawning period, with three also detected in the 2021 spawning period. Four cod from the 2020 tagging cohort were also detected in the 2021 spawning season (Supplementary Figure S5).

Residency and survival probabilities

The best MSCJS model for the test site had an AIC weight of 99%, indicating that there was little support for the other 38 candidate models (Table 2). This final model included a survival parameter (S) that varied between marked cohorts and a capture probability (p) that varied over time. State transition probability (Ψ) also varied over time and between spawning seasons, sexes, and states. Including seismic exposure effects on S or Ψ did not improve the fit of the final model, indicating that the seismic exposure had no measurable effect on survival or emigration out of the area by tagged cod at the test site.

The final model predicted that residence probabilities at the test site declined at a faster rate during the spawning season in 2020 than in other years (Figure 5). Examination of the Ψ estimates indicated that this was because of higher fishing recaptures in the spawning season of 2020 than in other years. This was true for both males and females, but male recaptures were especially high in 2020 (Supplementary Figure S7). Throughout the year, 19 fishing recaptures were reported in 2020 compared to 11 in 2019 and four in 2021 (Supplementary Figure S6). Female emigration from the test site was also higher

in 2020 than during other years (Supplementary Figure S7). Both emigration and fishing recaptures were elevated prior to the seismic exposure and continued afterwards. Weekly survival estimates for the 2020 (0.967, 95% CI: 0.956–0.975) and 2021 (0.949, 95% CI: 0.921–0.968) marked cohorts were also lower than the cohort marked in 2019 (0.986, 95% CI: 0.981–0.990).

At the reference site of Osen, the best model included separate Ψ slopes (Table 3) for each spawning period. The best model had a much lower AIC than competing models, with an Akaike weight of 0.999. This model was equivalent to model 1 for the test site (Table 2) but without separate state transitions for males and females.

The trend in residence probabilities of tagged fish over time at the reference site was markedly similar to the test site for each of the three spawning seasons (Figure 5). As at the test site, emigration rates were the highest during the spawning season of 2020 (Supplementary Figure S6). Also similar to the test site, survival at the reference site varied between cohorts and capture probability varied over time, with the highest survival in the 2019 cohort (0.989, 95% CI: 0.981–0.994) compared to 2020 (0.980, 0.965, to 0.989) and 2021 (0.953, 0.901, to 0.979). Reported fisheries recaptures from the fish released at the reference site were low, at two in 2019, two in 2020, and four in 2021 (Supplementary Figure S6). In contrast to the test site, differences between sexes were not included in the best model.

Discussion

The hypothesis of this study was that exposure to sound produced by seismic airguns at a moderate distance over an extended period would displace cod from spawning grounds. However, we found no evidence that exposure to seismic airgun shooting at received levels up to ~ 145 dB re $1 \mu\text{Pa}^2\text{s}$ SEL, comparable to a full-scale industrial airgun survey at a distance of ~ 5 – 40 km (Handegard *et al.*, 2013), caused

Table 2. Multistate CMR models for the fish released at the test site (Bakkasund).

Model rank	Survival	State transition (Ψ)	Description of state transition formulae	Detection probability	ΔAIC	w_i
1	S_c	$\Psi_{Ts1X}^{P-E} \neq \Psi_{Ts1X}^{E-P} \neq \Psi_{Ts1X}^{P-S} \neq \Psi_{Ts1X}^{E-D}$	Linear trend over time for each sex, spawning season, and transition.	p_t	0	0.99
2	S_c	$\Psi_{s(T)}^{P-E} \neq \Psi_{s(T)}^{E-P} \neq \Psi_{s(T)}^{P-D} \neq \Psi_{s(T)}^{E-D}$	Nonlinear trend over time that varies between transitions.	p_t	12.8	.002
3	S_c	$\Psi_{Ts1}^{P-E} \neq \Psi_{Ts1}^{E-P} \neq \Psi_{Ts1}^{P-D} \neq \Psi_{Ts1}^{E-D}$	Linear trend over time for each spawning season and transition.	p_t	15	<0.001
4	S_c	$\Psi_{s2}^{P-E} \neq \Psi_{s2}^{E-P} \neq \Psi_{s2}^{P-D} \neq \Psi_{s2}^{E-D}$	Varies between spawning season and outside spawning season and between transitions.	P_t	2.15.7	<0.001
5	S_c	$\Psi_{s(dsp)}^{P-E} \neq \Psi_{s(dsp)}^{E-P} \neq \Psi_{s(dsp)}^{P-D} \neq \Psi_{s(dsp)}^{E-D}$	Nonlinear trend of days since onset of spawning for each spawning season and transition.	P_t	16	<0.001

The model in bold had the most support (highest AIC weight of evidence, w_1) when comparing 39 candidate models (the top five shown in the table) and was used for interpretation of the data. The subscript “X” represents sex (male and female), “t” denotes a parameter that was allowed to vary between capture occasions (weekly intervals), “s” denotes a linear trend over time (weekly intervals), “s(T)” denotes a nonlinear spline over time; “c” represents fish tagged in a given year (tagging cohort); “s1” denotes the spawning year (0 = outside of spawning, 1 = 1 February–7 April 2019, 2 = 1 February–7 April 2020; 3 = 1 February–7 April 2021); “s2” denotes the spawning season (1 = 1 February–7 April within any year, 0 = other times) and “dsp” days after onset of spawning season (days since 1 February). Parameters to test for the effect of seismic exposure on survival and state transitions included “sw”, which was coded as a “1” for weeks with seismic exposure and “0” for other times, and “se”, which was included to compare seismic exposure during 2020 (coded as “2”) and 2021 (coded as “3”) with the same period in 2019, where there was no exposure (February 2019, coded as “1”). States: “P” is present at the release site, “E” emigrated, the “D” tag stopped transmitting, or the fish is dead (tag recovered or stationary in the array).

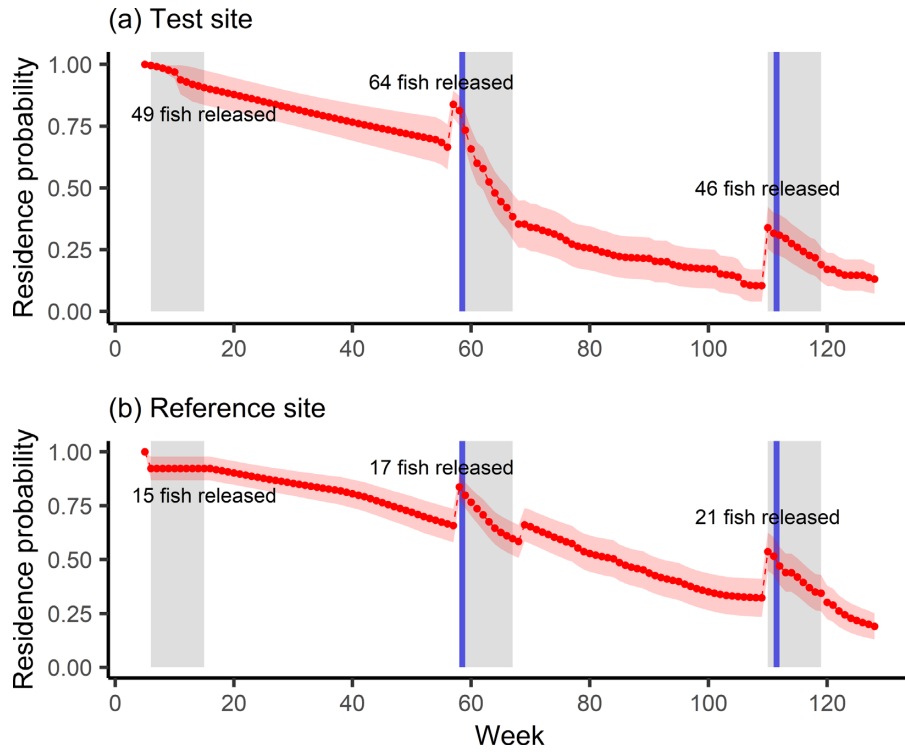


Figure 5. Mean residence probabilities (\pm 95% CI) at the test site (a) and the reference site (b) for each weekly interval from February 2019 (Week 5: 29/01/19–4/02/19) to June 2021 (Week 128: 8/06/21–14/06/21). Residence probabilities were calculated from the final MSCJS by taking the average of all individuals and representing the probability that released fish are present at Bakkasund or Osen. The grey areas are spawning periods, and the blue vertical bars are seismic exposure periods.

premature departure of cod from the spawning ground. Even though the departure rate of cod from the spawning grounds was variable between three spawning seasons, it was very similar between the reference and test sites for each year, suggesting emigration from the spawning sites was linked to factors other than seismic exposure. This interpretation was further supported by specific tests for the effect of seismic exposure on cod survival and emigration rates. Although there was a

rapid decrease in residency during the spawning period of the first exposure year, the emigration and fishery recaptures began prior to the seismic exposure period. It therefore seems unlikely that the departures were caused by seismic exposure.

The lack of large-scale, horizontal movements of cod exposed to sounds produced by seismic airguns was somewhat unexpected given the findings of some previous studies. Seismic shooting has previously been reported to result in a

Table 3. The best 5 of 39 multistate CMR models (highest AIC weight of evidence, w_i) for the fish released at the reference site (Osen).

Model rank	Survival	State transition (Ψ)	Description of state transition formulae	Detection probability	Δ AIC	w_i
1	S_c	$\Psi_{T_{S1}}^{P-E} \neq \Psi_{T_{S1}}^{E-P} \neq \Psi_{T_{S1}}^{P-D} \neq \Psi_{T_{S1}}^{E-D}$	Linear trend over time that varies between spawning seasons and transitions.	p_t	0	0.99
2	S_c	$\Psi_{T_{S1X}}^{P-E} \neq \Psi_{T_{S1X}}^{E-P} \neq \Psi_{T_{S1X}}^{P-D} \neq \Psi_{T_{S1X}}^{E-D}$	Linear trend over time that varies between sexes, spawning seasons, and transitions.	p_t	16	<0.001
3	S	$\Psi_{T_a}^{P-E} \neq \Psi_{T_a}^{E-P} \neq \Psi_{T_a}^{P-D} \neq \Psi_{T_a}^{E-D} + \Psi_{T_a}^{P-E} = \Psi_{T_a}^{E-P} = \Psi_{T_a}^{P-D} = \Psi_{T_a}^{E-D}$	Varies between transitions, with a separate parameter for days since tagging.	p_t	29.1	<0.001
4	S	$\Psi_X^{P-E} \neq \Psi_X^{E-P} \neq \Psi_X^{P-D} \neq \Psi_X^{E-D} + \Psi_{T_a}^{P-E} = \Psi_{T_a}^{E-P} = \Psi_{T_a}^{P-D} = \Psi_{T_a}^{E-D}$	Varies between transitions and sexes, with a separate parameter for days since tagging.	p_t	32.1	<0.001
5	S_c	$\Psi_{sc}^{P-E} \neq \Psi_{sc}^{E-P} \neq \Psi_{sc}^{P-D} \neq \Psi_{sc}^{E-D} + \Psi_{T_a}^{P-E} \neq \Psi_{T_a}^{E-P} \neq \Psi_{T_a}^{P-D} \neq \Psi_{T_a}^{E-D}$	Varies between transitions and seismic exposure periods. Effect of days since tagging varies between transitions.	p_t	33.9	<0.001

The model in bold had the best support and was used for the interpretation of the data. The parameters used are explained in the caption to Table 2, with the exception of “Ta”, which represents the number of days since tagging.

considerable decline in catch rates of cod at long distances (~33 km) from the source (Engås *et al.*, 1996). A decline in catch rates and densities of cod and other gadoids persisted for 5 d after the seismic survey ended and was attributed to avoidance of the airgun sound (Engås *et al.*, 1996). Cod have also displayed avoidance behaviour of a trawling vessel (Handegard and Tjøstheim, 2005), another noisy low-frequency stimulus.

A possible explanation for the lack of a detectable response to sound produced by seismic airguns in the present study is that the tagged cod had a strong affinity to the site, as previous studies indicate that this is a factor that may influence how fish react to seismic exposure. For example, resident fish associated with a rocky reef did not leave their habitat during exposure to airgun shooting (Wardle *et al.*, 2001). A telemetry study on a tropical demersal fish species (*Lutjanus sebae*), assumed to be a site attached with small home ranges, found no evidence that tagged fish showed long-term displacement during or immediately after a seismic survey (Meekan *et al.*, 2021). Strong, multiyear site fidelity to spawning sites has been previously demonstrated for Norwegian coastal cod at the reference site in this study (Skjæraasen *et al.*, 2011), and in the current study we found that many of the tagged cod remained in the test and reference sites year-round (Supplementary Figure S5). The high site fidelity of cod to these areas may therefore partially explain the lack of displacement observed in our experiments. The earlier study that found strong, immediate displacement reactions of cod to seismic sound was conducted in the open ocean on migrating and feeding cod (Engås *et al.*, 1996), which may have been less associated with specific sites. A deviation from this pattern can be found in a study in the Dutch part of the North Sea, where cod show strong site fidelity and high residency to feeding grounds within wind farms (Reubens *et al.*, 2013; van der Knaap *et al.*, 2021). Despite this strong site fidelity, wind turbine-associated cod appeared to leave the area during the 2 weeks after a seismic survey ended, although they did not show an immediate evasive or avoidance response to a full-scale seismic source (van der Knaap *et al.*, 2021). In this situation, the lack of a control and a very moderate response to a single exposure, with

displacement occurring after the end of exposure, raise the potential for alternative explanations than avoidance of noise from the seismic survey.

Factors such as life history and internal state or motivation may also influence fish reactions to disturbance stimuli. For example, herring (*Clupea harengus*) reactions tend to vary seasonally, with spring-spawning herring being more sensitive to sound stimuli during their pre-spawning stage in winter and least sensitive in spring and summer during spawning and feeding (Vabø *et al.*, 2002; Skaret *et al.*, 2005, 2006; Peña *et al.*, 2013). They thus display risk-averse behaviours in the pre-spawning phase, when surviving until spawning is prioritized, and display riskier behaviours during periods when spawning and feeding are prioritized (Skaret *et al.*, 2006). The lack of reactions observed in spawning cod may be due to their prioritization of spawning over avoidance of the potential threat signalled by the seismic exposure. Cod have previously been shown capable of assessing the threat posed by predator signals and responding accordingly, especially when there is uncertainty about the level of risk (Meager *et al.*, 2011, 2018). Cod are batch spawners, and an earlier study at this spawning area reported likely spawning intervals of 3–4 d (Meager *et al.*, 2010). If female cod react by swimming away from spawning habitat and partners, they may lose the opportunity for successful fertilization of one or more egg clutches. Similarly, males that leave the spawning ground may lose access to spawning females or their place in the lekking arena (Meager *et al.*, 2010). There are therefore strong incentives for spawning cod to remain at the spawning site, despite the potential threat signalled by the sounds from the airguns.

This interpretation is in line with predation risk theory, whereby animals will not switch habitat in response to a disturbance stimulus if the cost of fleeing outweighs the risk of staying and if alternative habitats are far away or of low quality (Frid and Dill, 2002). There are several other cod spawning sites near Bakkasund (Figure 1), and the lack of habitat switching from the tagged cod suggests that the disturbance was not strong enough to induce spawning site dispersal. Studies demonstrating dispersal of cod from spawning sites in response to deployment of fishing gear (Morgan *et al.*, 1997;

Dean *et al.*, 2012) indicate that cod can be induced to leave the spawning ground if the perceived risk is high enough.

When comparing the responses of fish to seismic airgun exposure between studies, it is also relevant to consider the SEL received by the fish. In this study, we used a downscaled airgun cluster with much lower source levels than a real seismic survey. The highest SEL were recorded at the test site when the seismic vessel passed closest to the bay, with the measured SEL within the bay reaching ~ 145 dB re $1 \mu\text{Pa}^2 \text{ s}$. These highest levels correspond to a distance of ~ 5 – 40 km from a full-scale seismic survey, depending on local propagation conditions (Handegard *et al.*, 2013).

The range of SEL measured in this study is similar to those measured at the study site of van der Knaap *et al.* (2021) at a wind farm in the North Sea, with the SEL at their study site ~ 147 dB re $1 \mu\text{Pa}^2 \text{ s}$ at the closest point of approach (2.25 km) of a full-scale seismic array (see Supplementary Figure S3c in van der Knaap *et al.*, 2021). The duration of sound exposure was longer and more continuous, without silent periods, in van der Knaap *et al.* (2021). These slightly higher and more continuous SELs also did not induce any strong, immediate avoidance behaviour from feeding cod resident at the wind farm (van der Knaap *et al.*, 2021). In the study of Engås *et al.* (1996), where substantial avoidance was observed at distances up to 33 km from the seismic vessel towing a full-scale array, sound levels were unfortunately not measured. Some of the fish in the study of Engås *et al.* (1996) were much closer to the source than 5 km and hence likely experienced higher SEL than the cod at our study site. However, an avoidance response of cod was observed even at the furthest distance studied (33 km from the source; Engås *et al.*, 1996), where the SEL was likely within the range measured in our study. We postulate that SEL is not the only reason for the differences in reactions observed between these studies and that behavioural state and motivation also play an important role. Furthermore, received sound levels may not be the best predictor of fish reactions to such disturbance stimuli, as fish may respond to other factors such as visual cues, water displacement from the passing ship, and particle acceleration, further complicated by variation in responses related to fish physiological state and predation risk, as discussed previously (De Robertis and Handegard, 2013). Nonetheless, it is possible that with a larger airgun array and higher SEL, a more pronounced response from spawning cod may have been elicited.

Although not linked to the seismic exposure, we detected considerable variation in emigration rates between years, but with very similar patterns at the reference and test sites. This suggests that some other external/environmental factor, common to both sites, was influencing the annual emigration rates. No association between temperature and emigration was found, and thus the drivers of this variation remain unknown. Together with the observation that the decline in residency began before seismic exposure and continued afterwards, these findings highlight the importance of collecting data from reference and test sites before, during, and after exposure and over several years when testing for an effect of seismic sound or another disturbance on residency of fish at a spawning site to, avoid mistakenly ascribing declining residency to seismic airgun exposure.

In conclusion, free-ranging spawning cod did not abandon their spawning grounds in response to seismic airgun shooting at SEL up to 145 dB re $1 \mu\text{Pa}^2 \text{ s}$. Our results indicate that

adult cod, presumably engaged in spawning activities and with a strong habitat affinity, are unlikely to abandon their habitat during exposure to seismic airguns at these received levels. Even if cod do not leave the spawning grounds, changes in behaviour, masking of communications, or increased physiological stress may nonetheless impact spawning success. A companion paper that used the same telemetry data to analyse fine-scale behaviour of the spawning cod at the test site found only subtle changes in cod behaviour related to the seismic airgun exposure (K. McQueen *et al.*, under review). There were indications that cod swimming depth increased in response to seismic exposure, but no changes in other metrics of swimming activity or area usage were observed (K. McQueen *et al.*, under review). These companion studies suggest that spawning cod behaviour is not strongly affected by seismic airgun exposure at these received levels. However, unobserved impacts on spawning success cannot yet be ruled out, for example, as has recently been reported for breeding Lusitanian toadfish (*Halobatrachus didactylus*) exposed to boat noise (Amorim *et al.*, 2022). Seismic surveys occurring at closer proximity, producing higher received sound levels, may also provoke an increased behavioural response from the spawning cod.

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Supplementary material

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

Author contributions

Conceptualization: LDS and DN; data curation: KM, DN, JES, and TNF; formal analysis: JJM, TNF, NOH, and JES; funding acquisition: LDS; investigation: DN, LDS, KM, JES, EMO, ØK, PHK, TNF, NOH, and JJM; methodology: LDS, JJM, PHK, DN, TNF, NOH, and JES; project administration: LDS and NOH; supervision: LDS; visualization: KM, JJM, TNF, and JES; writing—original draft: KM and LDS; writing—review and editing: all.

Conflict of interest

The authors have no conflicts of interest to declare.

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Data availability statement

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

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