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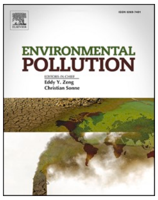

Continuous sound from a marine vibrator causes behavioural responses of free-ranging, spawning Atlantic cod (*Gadus morhua*)☆

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ABSTRACT

Marine vibrators are a new technology being developed for seismic surveys. These devices can transmit continuous instead of impulsive sound and operate over a narrower frequency band and at lower peak pressure than airguns, which is assumed to reduce their environmental impacts. We exposed spawning Atlantic cod (*Gadus morhua*) to sound produced by a prototype, but full-scale, marine vibrator, and monitored behavioural responses of tagged cod using acoustic telemetry. Fish were exposed to 10 × 3 h continuous sound treatments over a 4-day period using a randomised-block design. Sound exposure levels were comparable to airgun exposure experiments conducted previously with the same set-up ranging from ~115 to 145 dB re 1 μPa^{2}s during exposure. Telemetry data were used to assess 1) whether marine vibrator exposure displaced cod from the spawning ground, through estimation of residence and survival probabilities, and 2) fine-scale behavioural responses within the test site, namely swimming depth, activity levels, displacement, and home ranges. Forty-two spawning cod were tagged prior to the exposure, with 22 present during the exposure. All 22 tags were equipped with pressure sensors and ten of these additionally with accelerometers. While no premature departure from the spawning site was observed, cod reacted to the exposure by decreasing their activity levels (by up to 50%, SE = 7%) and increasing their swimming depth (by up to 2.5 m, SE = 1.0 m) within the test site during the exposure period. These behavioural responses varied by sex and time of day. Cod reactions to a marine vibrator may be more pronounced than reactions to airguns, possibly because continuous sound is more disturbing to fish than intermittent sound at the same exposure levels. However, given sample size limitations of the present study, further studies with continuous sound are necessary to fully understand its impact and biological significance.

1. Introduction

Anthropogenic noise in the sea is recognised as a pollutant of marine environments (European Parliament and Council, 2008; Duarte et al., 2021). Sound is produced from a variety of human activities, travels far underwater and can have numerous impacts on marine life (Duarte et al., 2021). Geophysical seismic surveys using airguns are one of the most pervasive sound-producing human activities offshore, conducted to locate oil and gas in the seabed. Airgun arrays used in commercial seismic surveys produce intense, impulsive sounds with a typical zero-to-peak source level of 260 dB (re 1 μPa m) (Gisiner, 2016). The main frequencies produced by airguns are between 10 and 100 Hz, though energy at higher frequencies is also produced (Landrø and Langhammer, 2020). These loud signals can negatively affect marine animals, for example, by causing hearing impairment or behavioural responses in marine mammals, fish and other sensitive marine fauna (Carroll et al., 2017; Bröker, 2019).

Development of alternative sources to conduct geophysical exploration with similar or higher efficiency and quality, and with a lower impact on marine life, has been ongoing since the 1980s (Laws et al., 2019). Marine vibrator (MV) technology is one such alternative with the potential to replace airguns for seismic surveys, and prototype MVs have

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now been developed to a stage where field tests are possible (Laws et al., 2019). MV sources are purported to have a reduced environmental impact due to lower peak sound pressure and the ability to emit only the sound energy that is needed for the seismic imaging (Laws et al., 2019).

In contrast to airguns that emit an impulsive sound at certain intervals, e.g., every 10 s, MVs can transmit continuously. This continuous sound emission is expected to reduce the potential for direct hearing injuries to marine mammals relative to airgun surveys (Matthews et al., 2020; Bøhn et al., 2021), given the sound exposure level criteria for hearing injury for continuous sound (Southall et al., 2019). Lower peak source levels also means that the area of impact is likely to be smaller for an MV than an airgun survey (Matthews et al., 2020). However, continuous sound emission leaves no interval between emitted sound signals for marine animals to dip-listen for relevant sounds or to communicate acoustically. Such continuous sound signals might therefore be more likely to mask important sounds for marine animals (Erbe et al., 2016; Popper and Hawkins, 2019; Southall et al., 2019; von Benda-Beckmann et al., 2021). For example, exposure experiments with sperm whales (*Physeter macrocephalus*) exposed to continuous and pulsed naval sonar indicate that continuous sonar has the same impact on whale behaviour as conventional pulsed sonar for the same sound exposure level (Isojunno et al., 2020), but the potential for masking was higher with the continuous sonar (von Benda-Beckmann et al., 2021). Furthermore, continuous sounds are associated with higher stress-levels in fish, compared to intermittent sounds (de Jong et al., 2020).

MVs emit sound in a narrower frequency band than airguns, with a greatly reduced output at frequencies >150 Hz. This is likely to be highly beneficial for toothed whales (odontocetes), which are most sensitive above this frequency (Southall et al., 2019). However, all the sound energy emitted by an MV lies in the frequency band of particularly sensitive hearing in most fish species, that is, below 200 Hz (Popper and Hawkins, 2019). Fish use sound for a wide variety of functions, including using ambient sound to gather information about their surroundings, to detect prey and predators, and for orientation and navigation (Slabbekoorn et al., 2010; Hawkins and Popper, 2017). Many fish species also produce sound to communicate, attract mates and defend territories (Hawkins, 1986; Hawkins and Picciulin, 2019; Popper and Hawkins, 2019; Popper et al., 2020). Therefore, any disturbance that will affect the ability of fish to detect or produce sounds may impair their fitness. Gadoid fish both hear and produce sound in the frequency range of 50–500 Hz (Hawkins and Picciulin, 2019; Hawkins and Popper, 2020). The most well-studied of these species, Atlantic cod (*Gadus morhua*), is able to detect sound at even lower frequencies (Sand and Karlsen, 2000). Cod produce sound during both adult and juvenile phases, and in particular during spawning, which involves both courtship and male-male agonistic behaviour (Brawn, 1961; Hutchings et al., 1999; Hawkins and Popper, 2020).

In general, the impact of anthropogenic noise on fish includes physical and physiological effects, behavioural disturbance and masking (Slabbekoorn et al., 2010; de Jong et al., 2020). Physical injuries will only occur at short range from a loud sound source, while behavioural responses of fish to sound can occur at much greater distances (Popper and Hawkins, 2019). Behavioural responses to anthropogenic noise include habitat displacement (Engås et al., 1996; Hawkins et al., 2014), which may remove fish from important feeding, breeding or shelter areas. Behavioural changes may also involve a change in activity state (e.g., feeding, travelling) (van der Knaap et al., 2021), thus interrupting fitness-related behaviours.

Behavioural responses of cod to seismic airgun surveys have been investigated by a number of studies, with variable results. Field studies of cod exposed to airguns have shown large-scale movement away from the exposure site (Engås et al., 1996), no avoidance during the exposure followed by some dispersal after the exposure ended (van der Knaap et al., 2021), and no dispersal away from the study area (McQueen et al., 2022). This apparent lack of consistency in responses within the same species highlights the need for contextualizing the sound exposure. In these examples, the fish demonstrating large-scale avoidance were distributed over extensive feeding grounds throughout the Barents Sea (Engås et al., 1996), while the other studies were conducted on fish with high site fidelity to either reef habitat (van der Knaap et al., 2021) or to a spawning ground (McQueen et al., 2022). To compare responses to different sound sources, it is thus crucial to conduct experiments in the same area and time of the year.

Even in situations where cod did not move away from an area during exposure to seismic airguns, they displayed finer-scale changes in behaviour, including changes in swimming depth or activity levels (Davidsen et al., 2019; van der Knaap et al., 2021; McQueen et al., 2023). For cod, the spawning season represents a period when vocalisations and acoustic communication are prevalent, and when fish show high site fidelity. This may make them particularly vulnerable to disturbance from anthropogenic noise, even if they demonstrate a high threshold for abandoning the area.

As new, continuous sound sources are considered for commercial seismic surveys, there is a need for a critical evaluation of their impact on marine life, including fish. Such knowledge is required to inform management decisions, legislation, and regulation of geophysical surveys. A better understanding of the responses of marine life to continuous, low-frequency anthropogenic sound is also relevant given numerous other offshore human activities that produce similar sounds, such as wind turbines and shipping. For a conclusive test of the impacts of such sound sources on animals, field tests with real sound sources are crucial (Popper et al., 2020; Sivle et al., 2021a).

A recent field study investigated the responses of free-ranging, spawning cod to seismic airgun exposure, using an acoustic telemetry array in western Norway (McQueen et al., 2022, 2023). In these experiments, tagged cod on a spawning ground were exposed to seismic airguns during 5-day periods in two spawning seasons, simulating exposure to a distant seismic survey over an extended period. This study found that the tagged cod did not abandon their spawning site in response to the airgun exposure (McQueen et al., 2022), nor did they alter their fine-scale behaviour on the spawning ground, in terms of swimming acceleration, distances travelled and home ranges (McQueen et al., 2023). The only minor behavioural response observed to the treatment was a slight increase in swimming depth during seismic airgun exposures (McQueen et al., 2023).

This established acoustic telemetry array on a known cod spawning ground has provided three years of data on cod behaviour in the region and results from two exposures to seismic airguns. This set-up provides a unique opportunity to test whether responses of free-ranging, spawning cod at the same spawning site respond differently to sounds from a MV during the spawning season. We used the same experimental design, with the same research vessel, at the same time of year, as with the previous airgun studies. Instead of airguns with impulsive, high peak pressure signals, we used a MV with a lower peak pressure source level, but with a continuous signal at similar received accumulated sound pressure levels. The main aim of the present study was to test whether continuous MV signals caused behavioural responses in cod and how these responses might differ from the previously described responses to impulsive airgun signals.

2. Methods

2.1. Marine vibrator and exposure survey

The MV used in this experiment was the MV BASS system developed by Shearwater GeoServices. The BASS has a nominal bandwidth of 3–150 Hz and is designed to be able to emit sound continuously. In commercial applications, several MV units would likely be used together, each operating within a dedicated segment of the nominal bandwidth. Here, a single, prototype BASS MV was used, transmitting a 10 s sweep that was a concatenation of two individual sweeps that would normally be emitted simultaneously by two vibrators (Fig. 1).

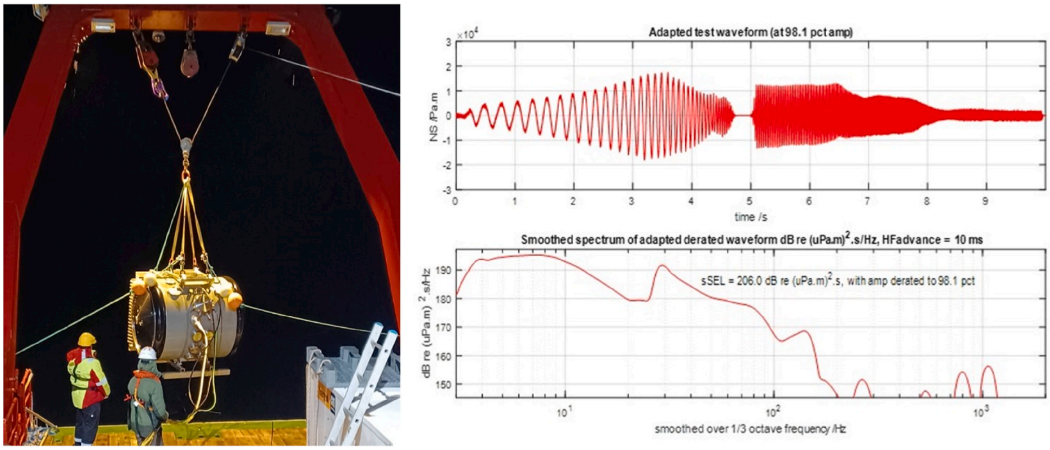

Fig. 1. Left: The BASS MV source used in the MV exposure survey. Right: Notional Source (NS) and spectrum of derated sweep.

During MV exposure treatments, the BASS MV was deployed in the water column from the back of the vessel, at a depth of 5 m.

The prototype BASS MV was not suitable for towing, so for the entire exposure survey the research vessel lay at anchor with the main engines switched off, in a sheltered location at the mouth of a bay containing a cod spawning site (i.e., the test site, Fig. 2). This contrasts to previous airgun experiments, when the vessel travelled around a racetrack near the entrance of the same bay (McQueen et al., 2022, 2023). Since the MV source could not be towed along the racetrack, the MV output signal was programmed to increase and decrease in amplitude to imitate the SEL from the moving airguns, which caused varying amplitude at the receivers with varying distance. It was not possible to match the SEL at all locations within the test site simultaneously because the transmission loss (the attenuation of the sound with distance) is not linear. Calculations were made to find the best possible location and source levels for the MV source to match the SEL from the airgun. The selected vessel anchor location was between the racetrack and the test site, which was a compromise between matching the SEL in the test site to the previous airgun experiments, and practical considerations associated with selecting a suitable and safe position for the vessel to stay with engines off for an extended period. An online report provides additional details about the survey (Sivle et al., 2023).

The MV exposure survey was carried out between 13.02.2022 19:35 and 17.02.2022 18:13 (UTC), using the research vessel H.U. Sverdrup II. The MV exposure survey followed a randomised block design, comparable to the previous airgun experiments (Sivle et al., 2021b; McQueen et al., 2023). We conducted ten blocks of two treatment types: an active sound transmission (MV) treatment and a control treatment. Each block

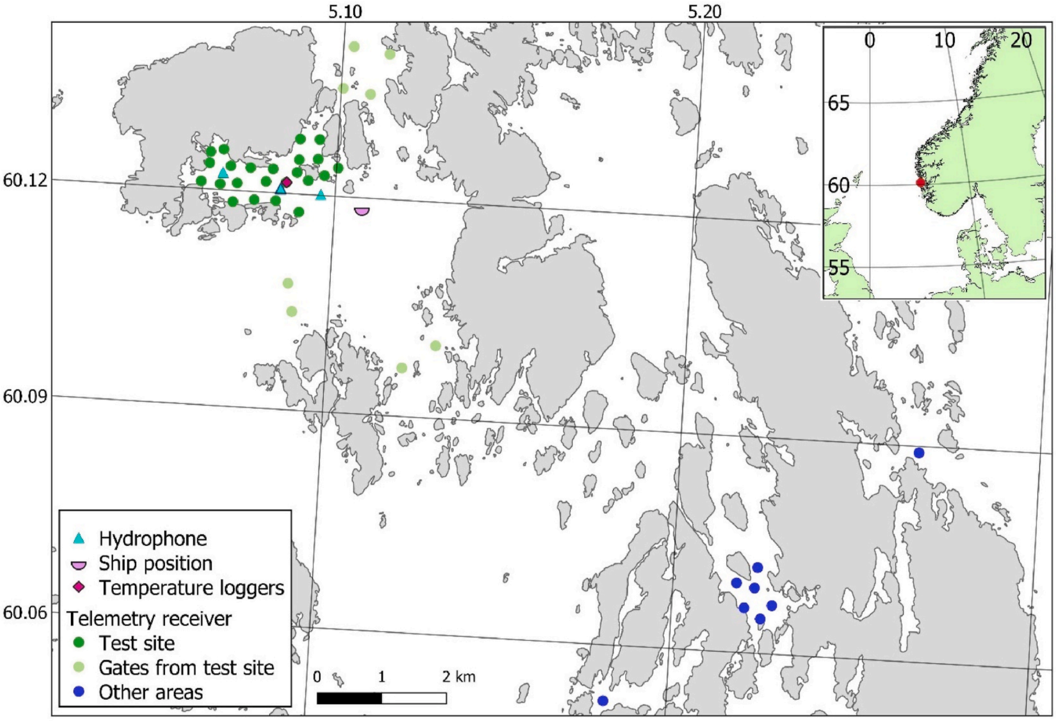

Fig. 2. Map of the locations of telemetry receivers (n = 39) that contributed data to the fish telemetry dataset for the MV exposure survey in 2022. For the location of all receivers that have been placed in this area over the 4 years of the telemetry project, see Fig. 1 in McQueen et al. (2022). The location where the ship was anchored during the MV exposure survey is shown, as are the locations of the hydrophones deployed during the survey. Ten temperature loggers were deployed through the water column at the position shown on the map. The inset map shows the location of the study site (red circle) in relation to the Norwegian coastline. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

contained a 3 h MV exposure treatment and two 3 h control treatments in a random order. The blocks were contiguous, apart from occasional short breaks for equipment maintenance (Sivle et al., 2023). During the MV exposure treatment, the BASS MV produced the previously described sweeps repeatedly and continuously for 3 h. During the 3 h control treatments, the MV was turned off. In the first seven blocks there were two identical control treatments within each block. Again, this was to mimic the exposure design in 2020 and 2021, which included two control treatments in each block (a "boat control" and a "silent control") to distinguish between reactions to vessel sound and airgun sound (McQueen et al., 2023). After the seventh block, there was a 13 h interruption in the exposure schedule, due to damage to the MV source. The second silent control treatment was dropped from the remaining three blocks to achieve the same number of exposure treatments within the same period as during the airgun experiments (see Sivle et al., 2023 for more details).

2.2. Sound recordings in the test site

Sound exposure from the MV, as well as ambient sound, was recorded at three distances by hydrophone rigs deployed in the bay (Fig. 2). The sound recording system was adapted from Øvredal and Totland (2012), slightly modified to fit our purpose. In the inner and outer part of the bay, the hydrophone rigs were deployed at the bottom, with the hydrophones placed 8 m above the seafloor at 66 m depth for the inner and 46 m depth for the outer part of the bay. In the centre of the bay, a hydrophone array was deployed, with two hydrophones placed at 8 and 37 m depth. Omnidirectional hydrophones (Naxys 02345 Ethernet Hydrophones) were used, with a frequency range of 5 Hz–300 kHz, and a sensitivity of −179 dB re V/μPa. Sound pressure was recorded at 21 s intervals with 3 s pauses. The hydrophones have an amplifier with an adjustable gain from 0 to 40 dB, and 20 dB gain was used. All hydrophones were calibrated before and after the survey using a Brüel & Kjær 4229 piston calibrator. RBR depth loggers were attached to each hydrophone to record their depths during deployment. The sound pressure recordings were bandpass filtered with a 3rd order Butterworth filter, with lower and upper cut-off at 5 Hz and 10 kHz, respectively. Sound Exposure level (SEL) (ISO, 2017) was estimated both for 1 h periods, once for each treatment, and for 10 s periods with 9 s overlap throughout each 3 h treatment. 1 h was used for comparison with the airgun experiments in 2020 and 2021, as 1 h encompasses one lap of the racetrack by the vessel towing the airguns at 3 knots. The 10 s period was selected to reflect the 10 s duration of the pulses continuously transmitted by the MV source (Fig. 1). This was also comparable to the 10 s interval between the airgun shots for the airgun experiments. The 3 s recording gaps between each 21 s files were filled in using samples from the next recorded sound files, for both the 1 h and the 10 s integration time.

Sound Exposure Levels were calculated by time integrating the squared pressure in the 5–10000 Hz band over the number of samples corresponding to 10 s or 1 h and applying a $10\log_{10}$ transformation. This approach was also used for the silent control periods. The zero to peak sound pressure level (ISO, 2017) was also estimated for 10 s periods with 9 s overlap by selecting the maximum positive or negative peak in each 10 s period.

2.3. Fish telemetry

An acoustic telemetry array has been maintained in Austevoll, western Norway, since October 2018 (McQueen et al., 2022, 2023). The test site consists of a high-density grid of receivers at a known cod spawning site. The bathymetry of the test site is complex, with two deep basins in the outer and inner bay, and shallower shelfs and sills between and around the basins and islands. The maximum depth in the study site is 100 m. Within this dense grid, tag transmissions can be detected on multiple receivers, which allows for fine-scale positioning of fish (Kraft et al., 2023). Additionally, receivers are placed as gates across the exit points from the test site, and at other nearby spawning sites (Fig. 2). The total number of receivers that have been deployed in the study area is 52, but due to occasional receiver losses, the number retrieved after the 2022 spawning season was 39 (Fig. 2).

In 2019–2022, fish were captured within the study site by local fishers using gillnets and pots and were tagged during the last week of January with acoustic transmitter tags. The tag life is up to 766 days, meaning that surviving fish that stay in the area can be detected at the study site up to 2 years after tagging. In 2022, fish tagging was carried out following the same procedures described in detail in McQueen et al. (2022). On 27th January 2022, 50 fish were tagged with acoustic tags and released into the test site. Tags used were equipped with either accelerometer and pressure sensors ($n = 25$, V13AP, Innovasea), or temperature and pressure sensors with data storage capabilities ($n = 25$, V13TP-ADST, Innovasea). Tagged fish were measured to the nearest half centimetre and weighed to the nearest gram (mean (SD) weight and length of fish tagged: 2563 (161) g, 615 (12) mm). They were sexed by observing running milt or eggs. An ovarian sample was taken from females for subsequent image analysis to determine maturity stage. Most tagged fish were classified as "spawning", with 25 spawning males and 17 spawning females tagged. The acoustic tag was inserted through a 3 cm incision into the body cavity, which was closed by two absorbable sutures. Fish were anaesthetised through immersion in a bath of seawater and MS-222 (tricaine methanesulfonate) prior to tagging. Permits to capture and tag fish and conduct experiments with sounds were provided by the Norwegian Directorate of Fisheries (reference 21/16250 and 21/19313) and Norwegian Food Safety Authority (approval number 28733).

Data were downloaded from the telemetry receivers in June each year. The raw detection data were filtered to remove fish assumed to have died (as determined by a lack of movement, Villegas-Ríos et al., 2020), and to remove replicate detections of the same tag transmission. The data recorded within the test site (Fig. 2) were used to estimate fish positions using a hyperbolic positioning method based on detection times at synchronised receivers (analysis provided by Innovasea, see Supplementary material for more details). Only fish classified as spawning ($n = 42$) were included in the statistical analyses.

To investigate potential reactions of the tagged fish to the MV exposure, we investigated fish behaviour at several spatial and temporal scales. We first investigated large-scale movements of fish from the test site by estimating residency and survival probabilities at a weekly scale. This analysis considered all receiver positions across the study area (Fig. 2) and all four years that the acoustic telemetry array has been in place. Secondly, potential changes in behavioural metrics of fish at the test site were studied by comparing swimming acceleration, depth and displacement between the period four days before, during and after the exposure survey. We also compared these behaviours between the control and MV treatments during the exposure survey. Finally, potential changes in site fidelity and home-range size were investigated by comparing changes in home ranges before and during the exposure week, and by comparing relative change in home-range size and overlap to the previous three study years. All analyses were undertaken in R (R Core Team, 2021).

2.4. Modelling of residence probability and survival

Residence and survival probabilities of tagged fish were modelled using the same methods as described in McQueen et al. (2022). This analysis involved treating fish detections on the acoustic telemetry receivers and recapture information for recaptured fish reported from fisheries as capture-mark-recapture histories. Residence probability and survival was then modelled using the hidden Markov implementation of multistate Cormack-Jolly-Seber (MSCJS) models. Survival, emigration and residency of cod at the test site were compared between spawning seasons (first week of February to first week of April) of the baseline (2019), airgun exposure (2020 and 2021) and MV exposure (2022) years.

The states from the capture-mark-recapture histories were: not detected (“0”), detected at the test site (Present; “P”), detected elsewhere (Elsewhere; “E”) and stopped transmitting (Dead; “D”). For this analysis, the test site (P) also included the gate regions, while all other acoustic telemetry receivers were classed as “elsewhere” (E) (Fig. 2). “Dead” fish (D) were individuals that had been reported recaptured by fishers, tags that had reached known shutdown dates, and fish that were presumed dead based on the cessation of movement.

The Hidden Markov model (HMM) implementation of MSCJS models was used (R package “marked” (Laake et al., 2013)), which has parameters for survival (S), detection probability (p) and state transitions (Ψ). Parameterisations of S, p and Ψ were based on standard terms and specific biological predictions on timing of arrival and departure from the spawning ground. Standard terms in the models included constant and time-varied parameters, Markovian and constant Ψ, marked cohorts (all fish tagged on a given day) and the “time since arrival” formulation to test if S or Ψ of each marked cohort varied over time. Sex was included as a grouping variable to allow separate parameters to be estimated for each sex.

We included specific parameters to test for the influence of seismic exposure on survival probabilities and state-transition probabilities, and to compare the effects of the MV exposure to the airgun exposure. These terms were: (1) “seismic week”, where exposure time periods, at weekly intervals, were coded as “1” and other periods as “0”. Hence, the two airgun exposure periods and the MV exposure period were aggregated and compared to other time periods, (2) “MV exposure”, with “1” coding for the comparable baseline period in 2019, “2” for the airgun exposure periods (pooled), and “3” for the MV exposure period. Hence, the “MV exposure” term compared the state transition probabilities between baseline, airgun exposure and MV exposure. (3) “Seismic exposure” was used to compare all four exposure periods, using a comparable period for the baseline year. This was coded as “2” for the airgun exposure in 2020, “3” for the airgun exposure in 2021, “4” for the MV exposure period in 2022 and “1” for a comparable period in 2019.

Other terms designed to test specific predictions included separate intercepts for each spawning period, 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 (nonlinear and linear terms). 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. Instead, we tested different parameter structures one-by-one and retained those that reduced Akaike Information Criterion (AIC) by >2 points. This was first undertaken for each of the three parameters (S, p and Ψ) while 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 55 candidate models. Finally, candidate models were compared using information theoretic criteria, where the Akaike weight (*wi*) represented the weight of evidence in favour of a given model from the set of candidate models, given the data (Burnham & Anderson, 2004). The 95% confidence set included all the models that together accounted for 95 % of *wi*. Residence probability was then calculated in the final model 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.

2.5. Analysis of behavioural metrics

The analysis of behavioural metrics swimming depth, activity levels and displacement followed the same methods as described in full in McQueen et al. (2023). Swimming depth and activity level (log-transformed) were inferred from the tag pressure and acceleration sensors, respectively, with swimming depth corrected for tidal variation. Displacement was calculated as the Euclidian distance between consecutive positions estimated for individual fish, and log-transformed for analysis. Only data recorded within the test site (Fig. 2) were used for these analyses.

Behavioural metric data were analysed at two timescales. We compared 1) behavioural metrics between 3 h treatments within the exposure period (treatment-level analysis) and 2) behaviours before-during-after (BDA) the exposure period. For the shorter-term treatment-level analysis, only data recorded within the treatment blocks were used. Depth, acceleration and position data were averaged over 10-min bins prior to analysis. For the longer-term BDA-level analysis, data recorded during the 4 days before (09.02.2022 19:35 UTC – 13.02.2022 19:35 UTC), during (13.02.2023 19:35 UTC – 17.02.2022 18:13 UTC) and after (17.02.2022 18:13–21.02.2022 18:13 UTC) exposure were used, and data were averaged over 1 h bins. Models were developed separately for each behavioural metric and timescale. Only fish which were detected during all BDA-periods or treatment types were included in analysis. The sample size therefore varied between analyses (Table 1).

Behavioural metric data were analysed using linear mixed effects models (R package “nlme” (Pinheiro et al., 2021),). The explanatory variables included in the starting models were treatment/BDA-period, sex, diel phase, and area of the bay, with 2-way interactions between treatment/BDA-period and each of the other variables. For the depth models, a 3-way interaction between treatment/BDA-period, sex and diel phase was additionally included, as an interaction between sex and diel phase in relation to swimming depth of spawning fish in this region has previously been identified (Meager et al., 2009) (see Supplementary Table S2 for an overview of the most complex models tested). The treatment variable included the levels “MV” and “silent control 1”. Data from the “silent control 2” treatments were not included in this analysis, as this treatment was not included in all experimental blocks, so inclusion of this treatment would have made the analyses unbalanced. The BDA-period variable included the levels “Before” (data recorded in the 4-days before the survey began), “During” (data recorded during the survey) and “After” (data recorded in the 4-days after the survey). Diel phase included the levels “day” (beginning 1 h after sunrise and ending 1 h before sunset), “night” (beginning 1 h after sunset and ending 1 h before sunrise) and “dusk/dawn” (the 2 h intervening periods, as in Dean et al. (2014); McQueen et al. (2023)). Sunrise and sunset were assigned using the R package “suncalc” (Thieurmel and Elmarhraoui, 2019). Diel period was assigned at the level of binning (1 h or 10 min bins), based on the earliest data point within the bin. The area of the bay variable denoted the section of the bay where fish were detected. The “outer bay” was the area closest to the MV source, that is, the receivers to the east of the middle hydrophone (Fig. 2), and the “inner bay” represented all other receivers in the test site.

In cases where a significant difference in behavioural metrics between treatment types or BDA periods was detected, comparisons between all treatment type combinations 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.

Fish ID was included as a random intercept in the models. 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 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.

Table 1

The number of fish included in analysis, split by response variable, the period selected for analysis (seismic effect) and sex. The sample size for each analysis after binning to 10-min or 1 h intervals is also shown.

	Swimming depth			Activity levels			Displacement		
Seismic effect	Female	Male	*sample size*	Female	Male	*sample size*	Female	Male	*sample size*
Treatments	11	11	*5189*	3	7	*2291*	11	10	*1287*
Before-During-After	10	10	*4650*	3	6	*2134*	9	9	*3165*

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 (ΔAIC <2), the simpler model was used for interpretation of the data (Zuur et al., 2009).

2.6. *Analysis of fish home ranges*

Analyses of changes in area usage of individual fish were conducted following the same methods as McQueen et al. (2023). Briefly, changes in home range size and site fidelity in response to seismic exposure were examined using indices of utilisation distribution (UD) size change and overlap. The indices were calculated for the data collected during the MV experiment and compared to the same indices calculated for the baseline year (2019) and the seismic airgun experiment years (2020, 2021), as published in McQueen et al. (2023).

For each fish (a) with at least 30 positions recorded during the 4-days before and during the MV exposure survey (n = 20), a 95% utilisation distribution (UD$_{95}$ in m^2) was calculated for each period. These UD$_{95}$, or home ranges, were calculated using the Brownian Bridge kernel method for autocorrelated location data (Horne et al., 2007), with the function "kernelbb" in the R package "adehabitatHR" (Calenge, 2020). For comparability with previous years, the smoothing parameter value (sig1) as used in the UD$_{95}$ estimation for the years 2019–2021 was applied (0.67). The second smoothing parameter (sig2) was set as the median horizontal positioning error (HPEm) for the 2022 position data (5.1 m, Supplementary material). Sections of the estimated home ranges that overlapped with land were removed, using a simplified representation of the Bakkasund coastline (Supplementary Fig. S12) and the R package "rgeos" (Bivand et al., 2021).

To estimate change in size of UD$_{95}$ for each individual from before (b) periods to during (d) exposure periods, ΔUD$_{95,a}$ was calculated as:

$\Delta UD_{95,a} = UD_{95,a,d} - UD_{95,a,b}$

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

$UDOI_{a,b,d} = 100[overlap_{a,b,d}/(UD_{95,a,b} + UD_{95,a,d}\text{-}overlap_{a,b,d})]$.

where overlap$_{a,b,d}$ (in m^2) is the intersection between the UD$_{95,a,b}$ and UD$_{95,a,d}$ (Meager et al., 2010; Dean et al., 2012), calculated using the R package "raster" (Hijmans, 2021). The UDOI can be considered as 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 MV exposure year compared to the baseline year and the airgun exposure years, linear mixed effects models were fit to the ΔUD$_{95,a}$ and UDOI$_{a,b,d}$. These models were used to test whether change in home range size 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 2022 was used as the reference level in the model, to compare the results of the MV exposure year to the results in the airgun exposure years (2020 and 2021) and the baseline year (2019). Fish ID was included as a random intercept in all models, as some fish were present in more than one year. Model selection was carried out as described previously through comparison of model AICs.

3. Results

3.1. *Sound exposure*

The MV signal was clearly detectable above background noise (silent control) at all three hydrophone locations (Fig. 3, Supplementary Fig. S4, Supplementary audio files). All the energy of the sound signal was measured to be in the frequency band below 150 Hz, and most of the energy was below 100 Hz (see Sivle et al. (2023) for details). The sound

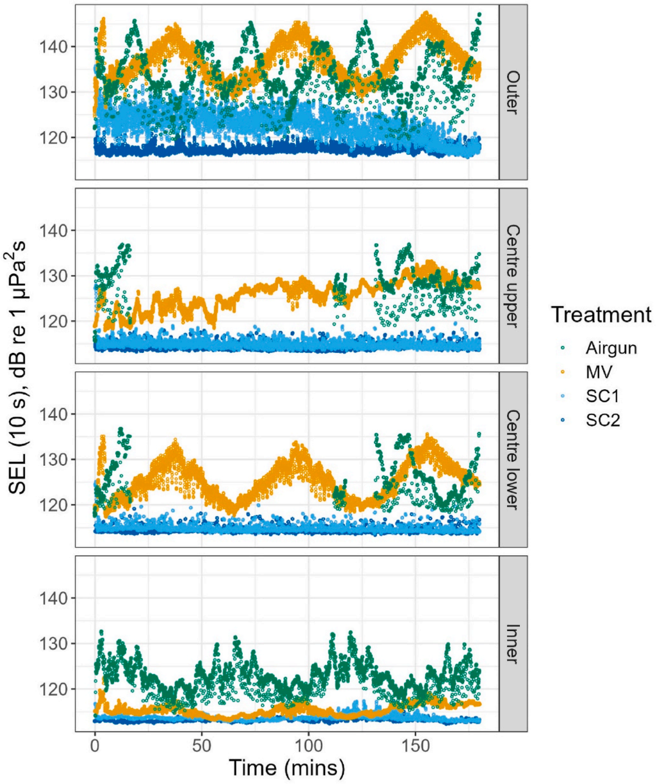

Fig. 3. 10 s sound exposure levels (SEL) with 9 s overlap for marine vibrator (MV) treatments and the 2 silent control treatments (SC1 and SC2). MV, SC1 and SC2 data shown in the figure are from the first experimental block of the MV exposure survey. Position of the inner, outer and centre bay hydrophones are shown in Fig. 2. The centre bay hydrophone array had hydrophones recording at 2 different depths; 8 m ("upper") and 37 m ("lower"). Overlaid in green are SEL values recorded during airgun treatments, recorded during the first block (outer and inner hydrophones) and seventh block (centre hydrophones) of the exposure survey in 2021. Note that battery limitations of the hydrophones used in the centre upper and lower position in 2021 resulted in gaps in the recording. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

exposure level (SEL) integrated over 10 s in the 5–10000 Hz band was between approximately 115 -145 dB re 1 μPa^{2}s (Fig. 3), and the zero to peak sound pressure level was between 115 and 150 dB re 1 μPa (Supplementary Fig. S3).

The current study aimed to expose fish to a similar SEL as during the airgun study: over 10 s, within each exposure treatment period (3 h), and over the entire survey period (30 h in total over 4 days). This objective was achieved for the outer hydrophone and the centre hydrophones, with recordings showing that the MV sound exposure level (SEL) was very similar to the airgun SEL (Table 2, Fig. 3). As expected, the MV SEL was lower than the airgun SEL at the inner hydrophone. Also as expected, the most prominent difference between the MV and the airgun sound signal at all three hydrophones was that the zero to peak sound pressure level of the airguns was much higher (15–20 dB) than that of the MV (Table 2, Supplementary Fig. S3). The background level also varied somewhat within the experimental week (e.g., see the difference between silent control 1 and silent control 2 of the outer hydrophone in Fig. 3). This reflects the natural variation in the background soundscape of the area with occasional recreational, fishing and aquaculture vessels passing, as well as changes in weather.

3.2. Changes in fish behaviour in relation to MV exposure

3.2.1. Residency probability

The best MSCJS model for the test site at Bakkasund had an AIC weight of 73%, indicating strong support for this model amongst the 55 candidate models (Supplementary Table S1). 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) varied between states and non-linearly for the number of weeks since tagging.

The only other candidate model with an AIC weight of over 1% was a very similar model to the top model, the only difference being that a common intercept was included rather than separate intercepts for each state transition. This model had an AIC weight of 26%.

Table 2

Measured sound pressure values for comparison between different blocks of the same exposure, and between the MV and airgun experiments. SEL 1 h is sound exposure level integrated over 1 h for 5–10000 Hz, reported as dB re 1 μPa^{2}s. SEL 10 s (max) is the maximum value of SEL integrated over 10 s for 5–10000 Hz within the 3 h long exposure, reported as dB re 1 μPa^{2}s. Peak (max) is the maximum absolute zero to peak pressure during the 3 h long exposure, reported as dB re μPa. No attempts were made to remove the background noise from the estimates since this is a comparison of the sound the fish experienced (and not the pure sound from the sources). Note that the number of measurements presented varies between hydrophones and experiments due to differences in hydrophone deployment durations.

Hydrophone position within test site	Received Level	MV	Airguns
outer	SEL 1 h	163, 164, 165, 166	165, 163, 163
	SEL 10 s (max)	148, 147, 148, 146	150, 148, 147
	Peak (max)	152, 150, 150, 151	169, 164, 164
inner	SEL 1 h	140, 141	150, 151, 152, 151, 150
	SEL 10 s (max)	119, 121	137, 135, 132, 137, 138
	Peak (max)	126, 129	145, 145, 146, 146, 145
centre upper	SEL 1 h	152, 152, 152	152, 155
	SEL 10 s (max)	133, 131, 134	135, 137
	Peak (max)	137, 136, 139	165, 167
centre lower	SEL 1 h	151, 150, 154	153, 153
	SEL 10 s (max)	136, 134, 136	132, 135
	Peak (max)	139, 135, 140	160, 165

Including seismic exposure effects (with the term “seismic” including both airgun and MV exposure) on S or Ψ did not significantly improve the fit of the final model, indicating that the seismic exposure had no measurable effect on the survival or emigration out of the test site by tagged cod. As shown in Supplementary Table S1, no models that included the seismic week, MV exposure or seismic exposure parameters were included in the 95% AIC confidence set, and the ‘best’ model that included any of these terms was ranked 14 of 55 models (and was outside of the 99.9% confidence interval). This indicates that there was no evidence of an effect of the seismic exposure treatments on the model fit, neither when considering all seismic exposures (airgun and MV) aggregated together (“seismic week” parameter), when comparing the effects of airgun and MV exposures separately (“MV exposure”) or when comparing each exposure separately by year (“seismic exposure”).

Modelled residence probabilities from the selected model demonstrated a marked decline over the spawning period in the baseline (2019), airgun (2020 and 2021) and marine vibrator exposure years (2022) (Fig. 4, Supplementary Fig. S5). This is a similar result to the previous analysis of the 2019–2021 data (McQueen et al., 2022). With the additional data obtained in 2022, the ‘time since arrival’ effect is more significant.

3.2.2. Behavioural metrics

The behavioural metric analysis indicated significant relationships between activity levels of cod and MV exposure, at both the short-term treatment-level and the longer-term BDA-level timescale. There was also a significant relationship between swimming depth and MV exposure at the BDA-level. These responses varied by sex and diel phase. Note the differences in sample sizes between analyses (Table 1). In the following section, pairwise contrasts (±SE) between treatments with $p < 0.05$ are reported, with p-values adjusted for multiple comparisons where necessary. Contrasts from models fit to log-transformed data (activity and displacement analyses) are presented as percentage difference, calculated from back-transformed ratios of relative difference.

The selected linear mixed effects model fit to the activity data (recorded as acceleration in m s $^{-2}$) for the treatment-level analysis included treatment, diel phase, and an interaction between treatment

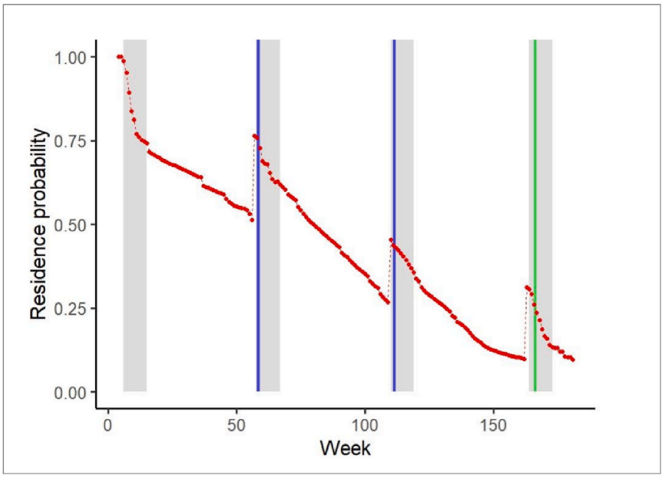

Fig. 4. Mean residence probabilities (±95 % confidence intervals) at the test site for each weekly interval from February 2019 (Week 5: 29.01.2019 to 04.02.2019) to May 2022. Residence probabilities were calculated from the final MSCJS by taking the average of all individuals and represent the probability that released fish are present at the test site. The grey areas are the assumed spawning periods, the blue vertical bars are airgun exposure survey periods, and the green bar is the MV exposure survey period. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and diel phase(Table 3, Supplementary Table S3). For the BDA-level analysis, the selected model included BDA-period, sex, diel phase, and interactions between sex and BDA-period, and diel phase and BDA-period (Table 3, Supplementary Table S3). The treatment-level analysis indicated that activity levels were lower during the MV exposure treatments than during the silent control treatments, but only at dusk/dawn (−36 ± 9 %, $p = 0.001$) (Supplementary Fig. S6, Table 4). The BDA-level analysis indicated that females were less active during the exposure period than before and after, at day (during-before: -48 ± 7 %, $p < 0.001$; during-after: -50 ± 7 %, $p < 0.001$) and night (during-before: -41 ± 7 %, $p < 0.001$; during-after: -27 ± 9 %, $p = 0.03$). At dusk/dawn, females were less active during the exposure period than before (−39 ± 8 %, $p < 0.001$). For males, the pattern was not as consistent. A significant difference in male activity levels between BDA-periods was only detected during the day. Males were more active at daytime after the exposure survey, compared to before and during the survey (during-after: -39 ± 7 %, $p < 0.001$; after-before: 54 ± 19 %, $p = 0.001$) (Fig. 5a, Table 4). Overall, males and females were more active during dusk/dawn and night than during the day (Fig. 5, Supplementary Fig. S6, Table 4).

For the swimming depth data, the selected linear mixed effects models included diel phase (treatment-level analysis), and BDA-phase, sex, diel phase, and interactions between all fixed effects (BDA-level analysis) (Table 3, Supplementary Table S3). There was no detectable difference in swimming depths between treatments, but there was a significant difference between survey periods (i.e., the ‘before-during-after’ effect). The selected BDA-level model indicated significant differences in swimming depths between BDA-periods at dusk/dawn and night for males and females. Females had deeper swimming depths during than before the exposure survey (dusk/dawn: 2.5 ± 1.0 m, $p = 0.03$; night: 2.4 ± 0.9 m, $p = 0.02$), with no difference between swimming depths during and after the survey, or between before and after the survey. Males had deeper swimming depths after the exposure survey than before (dusk/dawn: 3.4 ± 1.1 m, $p = 0.008$; night: 3.5 ± 1.0 m, $p = 0.003$), with the swimming depths during the survey intermediate (Fig. 5). Overall, there was no significant difference in average swimming depths between males and females (Table 4). In general, swimming depths were shallower at dusk/dawn than during the day, and shallowest at night (Table 4, Fig. 5, Supplementary Fig. S7).

For the displacement data (distances travelled between consecutive detections), the best fitting models at both timescales included sex and diel phase as the only fixed effects (Table 3, Supplementary Table S3). Therefore, there was no indication that the MV exposure affected displacement behaviours of fish. Overall, males had greater displacement values than females, and displacement was greater at dusk/dawn and night than during the day (Supplementary Table S4, Supplementary Fig. S8&S9).

3.2.3. Home ranges

The home range analyses provided no indication that cod area usage within the bay changed during the MV exposure, compared to previous years with airgun exposure or no exposure. The null models for change in home range size ($\Delta UD_{95,a}$) and degree of site fidelity ($UDOI_{a,b,d}$) were selected (Table 3, Supplementary Table S3), indicating that neither sex nor year (baseline year, airgun years, MV years) affected these home range characteristics (Supplementary Figs. S10 and S11). Plotting the home ranges onto a map of the test site did not indicate any obvious avoidance of the area close to the source vessel during the survey (Supplementary Fig. S12).

4. Discussion

The aim of this study was to investigate the responses of free-ranging, spawning cod to an experimental exposure from a MV, and to compare the findings to previously published results from experimental airgun exposures at the same site. The experimental design allows comparison of behavioural responses to continuous and impulsive sound with similar cumulative sound exposure levels, produced by these two types of seismic survey sources. We found that the MV did not cause spawning cod to leave their spawning site prematurely. However, cod reduced activity levels and increased swimming depth during the exposure period. These findings differ from the results of the airgun experiments, where the only response detected was a shorter-term increase in swimming depth during airgun exposures (McQueen et al., 2023).

We found no evidence to suggest that spawning cod abandoned their spawning site in response to exposure to the MV, mirroring the finding that spawning cod did not leave the site when exposed to seismic airguns at comparable sound exposure levels (McQueen et al., 2022). As discussed in McQueen et al. (2022), it is possible that due to strong site affinity, cod are unlikely to be displaced from their spawning grounds by exposure to anthropogenic noise at the levels tested in these studies, which by design mimicked prolonged exposure to distant seismic surveys. However, the ‘time since tagging’ effect was more pronounced than in the previous analysis (McQueen et al., 2022), which is likely to be partly because of the increased statistical power associated with the additional year of data, but could also reflect the post-tagging departure of fish to other spawning areas. We did not find any changes in home range characteristics or displacement values of cod in relation to MV exposure, also corresponding to the results from the airgun experiments (McQueen et al., 2023), indicating that horizontal movements of cod within the bay were not affected.

Although cod were not displaced from the spawning ground by the MV exposure, they did display some fine-scale behavioural changes. We detected significant reductions in activity levels, both when comparing activity between exposure treatments and control periods, and between 4-day periods before, during and after the exposure survey. Such a response was not observed for spawning cod exposed to airguns (McQueen et al., 2023). However, this finding does have similarities to van der Knaap et al. (2021), who reported that free-ranging, foraging cod switched from an active to an inactive state during exposure to a

Table 3

The best models (lowest AIC and highest weight of evidence, w_i) for each behaviour metric and timescale, and for models fit to $UDOI_{a,\ b,\ d}$ and $\Delta UD_{95,\ a}$ estimates. Optimum random structure was selected in a previous step (see Supplementary Table S2). In cases where there was similar support for more than one model ($\Delta AIC<2$), the simpler model was used for interpretation of the data. Δ_I is the difference in AIC between the selected model and the model with the lowest AIC. See Supplementary Table S3 for additional model selection details for each response variable. Y=Year; S=Sex; DP = Diel phase; T = Treatment; BDA=Before-during-after; ID= Fish ID, B = area of the bay.

Response variable	Fixed effects	Random effects	Temporal autocorrelation	df	AIC_i	Δ_i	wi
Swimming depth (m), 10-min bins	DP	1 | ID	10 min | ID	6	27186.0	1.48	0.08
Swimming depth (m), 1 h bins	BDA + S + DP + BDA:S + BDA:DP + S:DP + BDA:S:DP	DP | ID	1 h | ID	26	26986.1	0.00	0.46
Acceleration ($m\ s^{-2}$), 10-min bins	DP + T + T:DP	1 | ID	10 min | ID	9	5299.2	1.66	0.09
Acceleration ($m\ s^{-2}$), 1 h bins	BDA + S + DP + BDA:S + BDA:DP	1 | ID	1 h | ID	15	3427.5	0.00	0.67
Displacement (m), 10-min bins	S + DP	1 | ID	10 min | ID	7	4262.5	0.16	0.16
Displacement (m), 1 h bins	S + DP	BDA | ID	1 h | ID	12	9663.3	0.00	0.56
$\Delta UD_{95,\ a}$	None	1 | ID	none	3	1955.2	0	0.51
$UDOI_{a,\ b,\ d}$	None	1 | ID	none	3	672.8	0.17	0.34

Table 4
Summary of selected linear mixed effects models to explain the treatment-level and BDA-level acceleration and swimming depth responses of cod. Models also included a random structure, and an autocorrelation structure (see Table 3). Parameter estimates of are on the log-scale for acceleration models, and linear scale for swimming depth models. Models were fit with REML.

Response variable	Fixed effect	Estimate	SE	df	t-value	p-value
Acceleration (m s^{-2} log-transformed), 10-min bins	Intercept (MV, day)	−1.14	0.16	2276	−7.24	<0.001
	Dusk/dawn	0.25	0.12	2276	2.02	0.04
	Night	0.53	0.10	2276	5.30	<0.001
	Silent control 1	0.02	0.10	2276	0.25	0.81
	Dusk/dawn: Silent control 1	0.42	0.16	2276	2.65	0.01
	Night: Silent control 1	0.09	0.13	2276	0.74	0.46
Acceleration (log-transformed), 1 h bins	Intercept (during, female, day)	−1.19	0.21	2115	−5.56	<0.001
	After	0.69	0.14	2115	4.89	<0.001
	Before	0.66	0.14	2115	4.76	<0.001
	Male	0.45	0.25	7	1.78	0.12
	Dusk/dawn	0.45	0.07	2115	6.28	<0.001
	Night	0.54	0.09	2115	6.38	<0.001
	After: male	−0.20	0.15	2115	−1.38	0.17
	Before: male	−0.60	0.14	2115	−4.18	<0.001
	After: dusk/dawn	−0.42	0.10	2115	−4.11	<0.001
	Before: dusk/dawn	−0.17	0.10	2115	−1.62	0.11
	After: night	−0.38	0.12	2115	−3.12	0.002
	Before: night	−0.13	0.12	2115	−1.11	0.27
Swimming depth (m), 10-min bins	Intercept (day)	26.75	1.36	5165	19.71	<0.001
	Dusk/dawn	−1.11	0.35	5165	−3.15	0.002
	Night	−2.63	0.51	5165	−5.13	<0.001
Swimming depth (m), 1 h bins	Intercept (during, female, day)	29.11	1.75	4614	16.59	<0.001
	After	−2.50	1.16	4614	−2.16	0.03
	Before	−2.27	1.11	4614	−2.04	0.04
	Male	−1.47	2.51	18	−0.59	0.57
	Dusk/dawn	−2.52	0.87	4614	−2.89	0.004
	Night	−7.31	2.04	4614	−3.58	<0.001
	After: male	2.63	1.67	4614	1.58	0.12
	Before: male	4.19	1.67	4614	2.51	0.01
	After: dusk/dawn	0.68	0.78	4614	0.87	0.39
	Before: dusk/dawn	−0.26	0.74	4614	−0.35	0.73
	After: night	1.57	1.04	4614	1.51	0.13
	Before: night	−0.09	0.99	4614	−0.09	0.93
	Male: dusk/dawn	−0.52	1.26	4614	−0.41	0.68
	Male: night	0.82	2.91	4614	0.28	0.78
	After: male: dusk/dawn	1.02	1.13	4614	0.90	0.37
	Before: male: dusk/dawn	−3.25	1.14	4614	−2.86	0.004
	After: male: night	−0.35	1.51	4614	−0.23	0.82
	Before: male: night	−3.97	1.51	4614	−2.63	0.01

seismic airgun survey. The fact that a reduction in activity levels in response to exposure to airguns was not observed in spawning cod (McQueen et al., 2023), but has been observed for foraging cod (van der Knaap et al., 2021), may indicate that both behavioural state and type of sound exposure affect the type of behavioural response observed.

Van der Knaap et al. (2021) reported a particular reduction in activity at dusk/dawn, as also detected in the treatment-level analysis in this study. The reduction in activity levels at dusk/dawn may be explained by higher baseline activity levels during this period, allowing greater scope for a reduction in activity to be detected. Cod have been described to freeze in response to predator signals/perceived danger (e.g., Meager et al., 2011), and it has been suggested that this behaviour is displayed when predator risk is uncertain (Meager et al., 2018). The reduction in activity levels could also reflect a decrease in spawning activity, due to fish waiting for quieter periods to resume spawning (de Jong et al., 2020), as discussed in more detail below. In our study, the longer-term activity level response was particularly pronounced for females, while for males, the patterns were not as consistent.

An important caveat when interpreting the results relating to activity levels is the low number of individual fish included in analysis. Twenty-five fish were equipped with accelerometers at the beginning of the study. However, only three females and six (BDA-level analysis) to seven (treatment-level analysis) males ultimately contributed activity data to the analysis. This was due to some fish leaving the area or being fished before or during the exposure survey, or being excluded from analysis due to not being in spawning condition. For the female fish, a reduction in activity levels during the survey was visible for each of the three fish (Supplementary Fig. S13). However, a larger sample size would give greater confidence that the behaviour of these individuals is representative of the population.

In general, it is both a major advantage and an unavoidable disadvantage of conducting exposure experiments on free-ranging animals that the animals are free to leave the study area at any time. The advantage is that this allows the possibility to observe natural behaviours including avoidance reactions or dispersal away from an area. Such behavioural reactions are highly relevant for understanding the impacts of anthropogenic noise on fish (Popper and Hawkins, 2019), and are difficult to investigate using fish confined to net pens or tanks (Hawkins et al., 2020, Slabbekoorn, 2016). However, conducting experiments using free-ranging, tagged fish in marine environments means that the number of animals present in the study site cannot be controlled following tagging and release. The possibility that animals leave the area before the exposure period, resulting in lower sample sizes than expected, is therefore always a risk in such studies (see e.g., Bruce et al., 2018). Increasing the number of individuals tagged is not necessarily a solution, because commonly used acoustic telemetry set-ups have an upper limit on how many transmitting tags can be present within a system, beyond which there is high chance of signal collisions and reduction in signal detections (Simpfendorfer et al., 2008). Repeating the experimental exposure over multiple years, can be a means to increase sample size (as in McQueen et al., 2023).

Cod also increased their swimming depth during the MV exposure period. For females, this was observed as a significant increase in swimming depth during the survey period. Female swimming depths in the days after the survey were intermediate between the depths before and during the survey, indicating a gradual return to baseline (before-survey) swimming depths. For males, there was a trend towards deeper

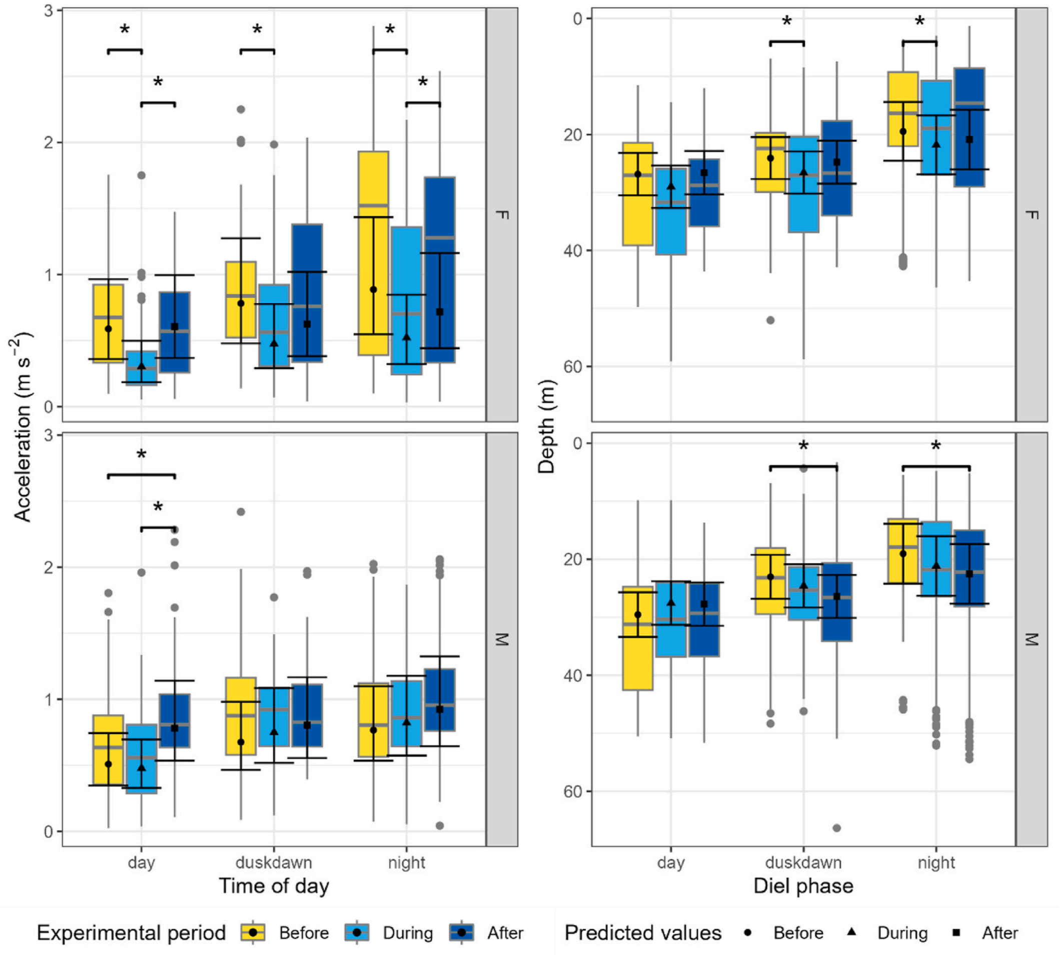

Fig. 5. Boxplots showing data used to analyse before-during-after effects of marine vibrator exposure on activity levels (left column) and swimming depth (right column) of tagged cod. For sample sizes per group, see Table 1. The median behavioural metric values are represented by the thick grey line, the interquartile range between the 1st and the 3rd quartile by the box, 1.5 x the interquartile range by the whiskers and outliers by single grey points. Overlaid black points with error bars show the least-squares means and associated Tukey's 95% confidence intervals (back-transformed from logarithmic to linear scale for activity level data) from the selected models. Significance asterisks and bars show significant contrasts, after Tukey's p-value adjustment. Panels show results for females (F) and males (M) separately.

swimming depths across the entire analysis period, as the swimming depths after the survey were significantly deeper than the swimming depths before, and the swimming depths during the survey were intermediate. A similar, gradual, long-term trend towards deeper swimming depths was observed during the airgun experiments (see Table 4 and Supplementary Fig. S5 in McQueen et al., 2023). In theory, swimming to deeper depths, particularly when combined with reduced activity levels, may reduce the frequency of spawning related encounters between males and females, even if the depths that fish swim to are within their normal range. In this study we did not detect a difference in swimming depths between treatments, which would have been expected if there was a short-term effect of the MV on cod swimming depth. Since the MV exposure experiment was only conducted during one year, we cannot rule out that the observed long-term increase in swimming depth could have been related to factors other than the exposure. Nevertheless, increasing swimming depth in response to the MV exposure would be a plausible explanation, as vertical avoidance in response to anthropogenic noise disturbance is well-documented for fish. Such a response has been observed in response to impulsive sounds such as seismic airguns (e.g., Slotte et al., 2004; Davidsen et al., 2019; McQueen et al., 2023) and more continuous sound stimuli such as an approaching vessel (Handegard and Tjøstheim, 2005; Ona et al., 2007; De Robertis et al., 2008). We found no swimming depth response during the day. Cod tend to stay closer to the seafloor during the day in the spawning period (Meager et al., 2009), so the possibility to increase swimming depths during the day may therefore have been limited.

Overall, our data give an indication that cod behaviour was disrupted to a greater degree by the MV than the airguns, as more changes in behaviour were detected during the MV exposure than the airgun exposures. Given that SEL were similar between the experiments, we conclude that the continuous nature of the sound produced by the MV, compared to the pulsed sound produced by the airguns, is responsible for the increased reaction from the fish. This follows de Jong et al. (2020), who concluded from a meta-analysis that continuous sounds are more likely to impact stress responses of fish than intermittent sounds, though the mechanisms causing increased stress responses are unclear. Continuous sounds are also more likely to mask acoustic communications than intermittent sounds (Erbe et al., 2016; Popper and Hawkins, 2019; Southall et al., 2019; von Benda-Beckmann et al., 2021; de Jong et al., 2020). For species such as cod, which use acoustic communication extensively during courtship and mating, masking of vocalisations may lead to decreased spawning activity due to reductions in courtship activity or altered behaviour (de Jong et al., 2020). For example, painted goby (*Pomatoschistus pictus*) females were less likely to spawn with an available male while exposed to continuous noise (de Jong et al., 2018). Similarly, Lusitanian toadfish (*Halobatrachus didactylus*) exposed to continuous boat noise decreased activity levels and vocal activity associated with mating, which led to reduced reproductive success (Amorim et al., 2022). Fish that use acoustic communication during mating may wait for quieter periods to continue acoustic courtship and/or spawning behaviour (de Jong et al., 2020). Such a response to continuous noise may explain the reductions in activity observed in this study, which were not observed in response to the intermittent sounds from the airgun experiment.

There were also differences in the frequency spectrum between the airgun and MV signals. Both the MV and airguns produced signals with most energy below 100 Hz. The main difference between the signals was that the airguns also produced energy at high frequencies (see Fig. 2 in McQueen et al., 2022). Cod hear best at low frequencies (<160 Hz) (Chapman and Hawkins, 1973), therefore it is mainly the lower frequency components of the signals that we expect to have an effect on cod behaviour.

5. Conclusions

MVs are still under development, and, to our knowledge, have not yet been used in commercial seismic surveys. The potential impacts of anthropogenic sound produced by MV on behaviour of fish should be considered by managers and policy makers, before the technology is brought into commercial use. Despite possible advantages of MV surveys in comparison to traditional airgun surveys for some marine mammal species (Matthews et al., 2020), the potential for fish to be disturbed by the continuous sound produced should not be overlooked. Although the sample size is somewhat limited, our study provides a first indication that this type of continuous, low frequency sound may be more disturbing to fish than the impulsive sound produced by airguns, when SEL are similar. However, responses to both the air gun and the MV signals were subtle and the biological significance of such responses will depend on the duration of the exposure. Due to the lower source levels expected for MV surveys, a smaller proportion of the population may be exposed to such SEL than for seismic airgun surveys. The trade-off between potentially higher impact at smaller scales and lower impacts at larger scales should be carefully considered in mitigation measures. The output of MVs is highly configurable, allowing great flexibility in the frequency and levels produced. Future studies should investigate whether changes to the signal produced during MV surveys could reduce the impact on key marine species. For example, leaving gaps between sound emissions for allowing fish to communicate and listen to biologically relevant sounds could reduce the impact of MV exposure on fish.

CRediT authorship contribution statement

Kate McQueen: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Lise Doksæter Sivle:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Tonje Nesse Forland:** Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing. **Justin J. Meager:** Formal analysis, Methodology, Visualization, Writing – review & editing. **Jon Egil Skjæraasen:** Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. **Esben Moland Olsen:** Investigation, Writing – review & editing. **Ørjan Karlsen:** Investigation, Writing – review & editing. **Petter H. Kvadsheim:** Investigation, Methodology, Writing – review & editing. **Karen de Jong:** Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

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

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Appendix A. Supplementary data

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