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Effects of a seismic survey on movement of free-ranging Atlantic cod

Highlights

- A full-scale seismic survey affected free-ranging cod behavior in multiple ways
- Cod left the area earlier than expected, 2 days to 2 weeks after the survey
- Cod became less active during the seismic sound exposure, and likely foraged less
- Repeated passage of the survey vessel disrupted the diurnal activity cycle

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In Brief

van der Knaap et al. show that exposure to a seismic survey caused delayed deterrence of free-ranging Atlantic cod. During sound exposure, cod became less active at dusk and dawn, interrupting their diurnal activity cycle. These effects indicate the potential for anthropogenic noise to affect energy budgets and to have population-level consequences.

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Effects of a seismic survey on movement of free-ranging Atlantic cod

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SUMMARY

Geophysical exploration of the seabed is typically done through seismic surveys, using airgun arrays that produce intense, low-frequency-sound pulses[1] that can be heard over hundreds of square kilometers, 24/7.[2,3] Little is known about the effects of these sounds on free-ranging fish behavior.[4–6] Effects reported range from subtle individual change in activity and swimming depth for captive fish[7,8] to potential avoidance[9] and changes in swimming velocity and diurnal activity patterns for free-swimming animals.[10] However, the extent and duration of behavioral responses to seismic surveys remain largely unexplored for most fish species.[4] In this study, we investigated the effect of a full-scale seismic survey on the movement behavior of free-swimming Atlantic cod (*Gadus morhua*). We found that cod did not leave the detection area more than expected during the experimental survey but that they left more quickly from 2 days to 2 weeks after the survey. Furthermore, during the exposure, cod decreased their activity, with time spent being "locally active" (moving small distances, showing high body acceleration) becoming shorter, and time spent being "inactive" (moving small distances, having low body acceleration) becoming longer. Additionally, diurnal activity cycles were disrupted with lower locally active peaks at dusk and dawn, periods when cod are known to actively feed.[11,12] The combined effects of delayed deterrence and activity disruption indicate the potential for seismic surveys to affect energy budgets and to ultimately lead to population-level consequences.[13]

RESULTS AND DISCUSSION

We examined the response behavior of 37 free-ranging Atlantic cod to an experimental seismic survey using fine-scale acoustic telemetry.[14] Cod were caught, equipped with acoustic transmitters, and released at the offshore wind farm Belwind (Figure S1), in the southern North Sea, 50 km offshore, at 20- to 30-m depth. A seismic survey vessel performed a standard survey by towing an array of airguns past the wind farm in continuous loops, with parallel tracks of about 25 km, over a period of 3.5 days, with a closest point of approach to the tagging location of 2.25 km (Figure S1). Fish detection, position, and axillary sensor information, before, during, and after the exposure, were used to answer the following questions. (1) Do cod move out of the study area in response to a seismic survey? (2) Does a seismic survey affect the spatial behavior, overall activity pattern, and diurnal cycles of cod? (3) Is there a relationship between sound-level exposure and cod activity level (e.g., dose response)? We analyzed data on the presence/absence and the detailed, behavioral patterns in spatial use and accelerometer-based activity of cod using hidden Markov models (HMMs),[15–18] and used linear mixed models for the dose-response analysis.

We included daily presence/absence data for all individuals in 2018, with record periods up to 3 months. Additionally, we included reference data from 2 preceding years, 2016 and 2017, both including presence/absence data of 14 different individuals within the same wind farm, with variable record periods (Figure 1A). HMM analysis found no evidence that more cod left during the survey than before or after (Table S1, covariate "seismic"). However, there was a higher probability of fish leaving up to 2 weeks after the end of the sound exposure, indicating a delayed effect on leaving or persistent exposure impact (Figure 1B). Of the exposure covariates tested, the "persistent exposure effect" (comparing during and after exposure to before exposure) had the largest effect (Table S1). The probability that cod remained onsite in 2018 went down significantly from 36%

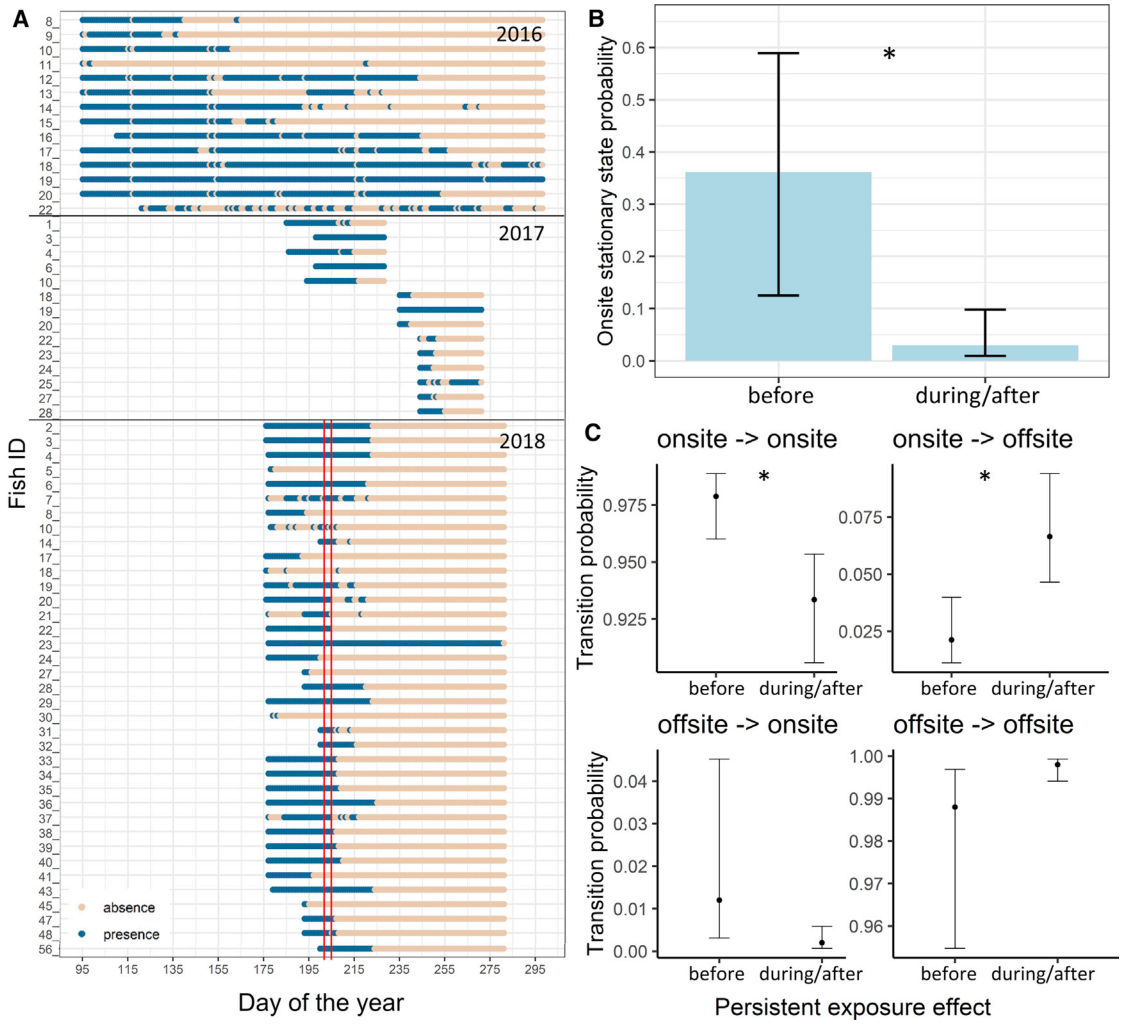

Figure 1. Presence/absence patterns of tagged cod in 2016 (n = 14), 2017 (n = 14), and 2018 (n = 37) at the Belwind wind farm

(A) Horizontal lines represent individual fish presence (blue)/absence (orange) data (note that fish ID does not correspond to the same individual across years), while the tag was active and detection stations were present, per day of the year ("1" indicates January 1). The vertical red lines outline the period during which in 2018 the seismic survey took place (July 21–24).

(B) Model-predicted onsite stationary state probabilities for the seismic survey "persistent exposure effect": before exposure and during/after exposure. An asterisk indicates a significant difference in state probability.

(C) Predicted transition probabilities between states with their 95% confidence intervals (CIs) for the persistent exposure effect variable. An asterisk indicates a significant difference in state probability.

For all probabilities presented in (B) and (C), the values of the other covariates were set to those experienced during the survey period, e.g., year 2018, mean temperature 18.5°C, and the mean of the time in days since release. See also Table S1.

before to 3% during and after the survey (significance was established when there was no overlap between the 95% confidence intervals [CIs]; Figure 1B). During and after the survey, the probability of remaining onsite was significantly lower and the probability that cod switched from onsite to offsite significantly increased (Figure 1C).

Fish distance to the closest turbine gradually increased over the three 4-day periods of analysis, i.e., from "before" to "during" to "after" the seismic exposure in 2018 (Figure 2A), with average distances from a turbine per individual of 21.5 m (SD, 13.6; number of positions, 3,508), 22.6 m (SD, 18.9; positions, 2,950), and 26.7 m (SD, 30.1; positions, 2,587). A linear mixed model demonstrated that after was significantly different from before (estimate, 0.05; post hoc Tukey, $p < 0.001$; Figure 2B) and during (estimate, 0.03; post hoc Tukey, $p = 0.03$; Figure 2B) for the 19 cod included in the analysis. The model covariate current speed (m/s) also had an independent significant effect ($p < 0.001$), with higher current speeds (related to changing tides) correlated with further distances from a turbine (Figure 2B).

Between 27 June and 8 August 2018, 24 cod provided enough position data to derive 313 tracks with between 20 and 735 consecutive half-hour positions per track. HMMs were used to define three behavioral states based on the observed step length between consecutive half-hour fish positions and the mean vector dynamic body acceleration

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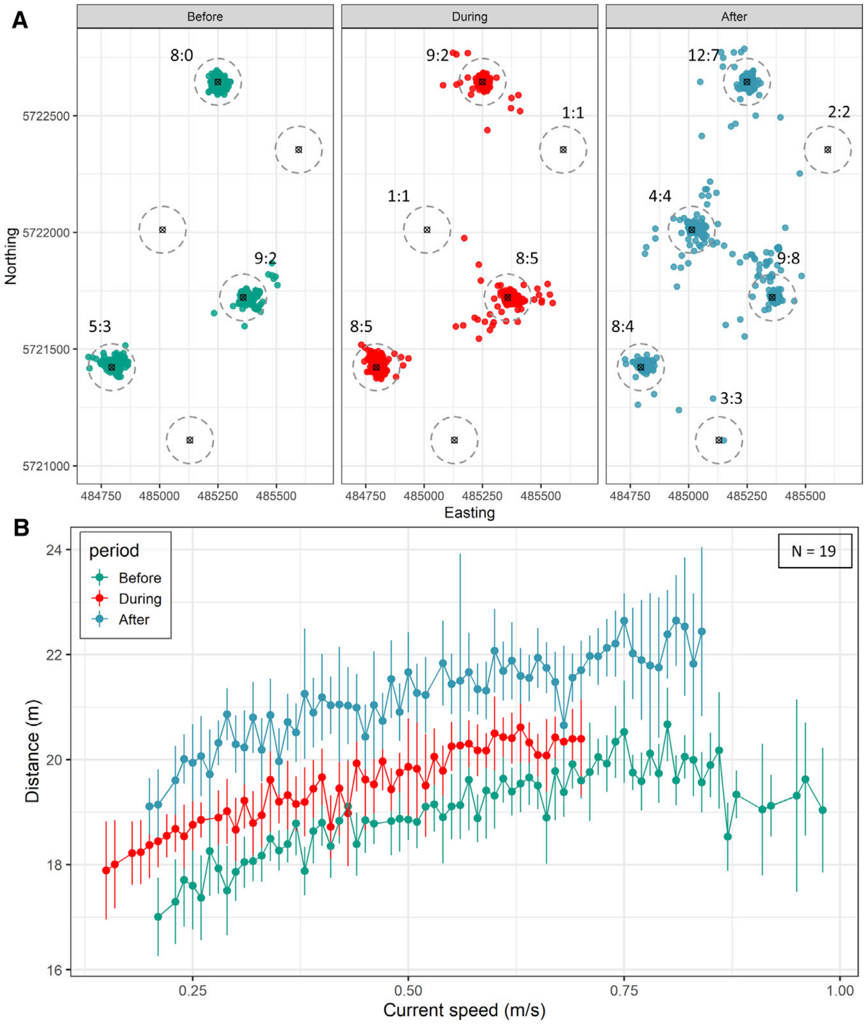

Figure 2. Distance to the closest turbine during the 4 days before (green), during (red), and after (blue) the seismic survey

(A) Spatial distribution of all triangulated cod positions for the 19 fish used in this analysis. Dashed circles outline areas with a radius of 100 m around each wind turbine. Numbers indicate the number of individuals detected around a turbine (left of the colon) and how many of those individuals were detected outside of the 100-m radius (right of the colon), during each period.

(B) Mean and standard deviation of the modeled distance of cod to the nearest turbine, related to current speed (m/s) as predicted by the linear mixed model. Fitted log distance was transformed back to meters. Significant differences in distance were found between the periods during-after ($p = 0.03$) and before-after ($p < 0.001$).

(VeDBA).[19] Behavioral states were then defined as follows: BS1 "inactive" (small step, low VeDBA), BS2 "locally active" (small step, high VeDBA), and BS3 "transit" (large step, low VeDBA) (Figure 3; Table S2). State-transition probabilities were modeled as functions of fish length (cm), current speed (m/s), tidal height (m), hour of day (between 0 and 24), and sea water temperature (°C). We included the covariate seismic on/off (where "on" refers to during the survey period) to model the effect of the survey (Table S3).

Overall, fish spent 47% of the time being inactive, 41% being locally active, and 12% being in transit. Covariates that affected the behavioral states were "seismic exposure" (on/off) and "time since survey start" (0 until start of survey, then increasing with time) (Table S3). The fish were significantly less likely to be locally active and significantly more likely to be inactive (no 95% CI overlap; Figure 4A) during the survey. The hourly HMM state prediction (Figure 4B) furthermore showed a distinct pattern of diurnal activity cycles before and after the seismic survey. Before the sound exposure, the probability of cod being locally active and in transit increased every evening and night (between 19:00 and 5:00), whereas during the day (between 6:00 and 18:00), cod were more likely to be inactive. This diurnal rhythm was disrupted during the seismic exposure, when fish became overall more inactive (Figure 4C).

Finally, we performed an analysis with only the VeDBA, as this was available at a finer timescale than the half-hour position averages, for the 24 fish present during the seismic exposure period. We examined whether there was a dose-response relationship between cod activity and the seismic-survey-related variation in local sound pressure levels (SPLs; within the 100- and 200-Hz-frequency band). Linear modeling showed no effect of SPL on the VeDBA ($p = 0.43$ and $p = 0.78$, for 100- and 200-Hz-frequency bands, respectively). Only temperature had a significant effect on the activity of the cod: they became less active at higher temperatures ($p < 0.001$).

Our results demonstrate that exposure to a seismic survey had an effect on Atlantic cod movement behavior during and after the sound source had passed. In the southern North Sea, cod is a seasonally resident demersal fish.[20,21] However, whereas just 22%–86% of cod left their habitat in the reference data from 2016, 2017, and pre-survey in 2018, all but one individual of the 37 tagged cod had left within 2 weeks after the end of the seismic survey sound exposure. If animals leave their feeding or breeding grounds earlier than usual, or change their migratory behavior and/or routes, in response to an acoustic disturbance, there may be population-level consequences.[5,22] Moreover, if fish stay in an area despite a disturbance, there can still be behavioral and population-level effects. Iafrate et al.,[23] for example, showed that resident reef fish that remained on site during pile-driving sounds were susceptible to behavioral effects during the exposure.

In line with these results,[23] we found several behavioral changes during and after the seismic survey period that can be attributed to acoustic disturbance. Cod gradually, but

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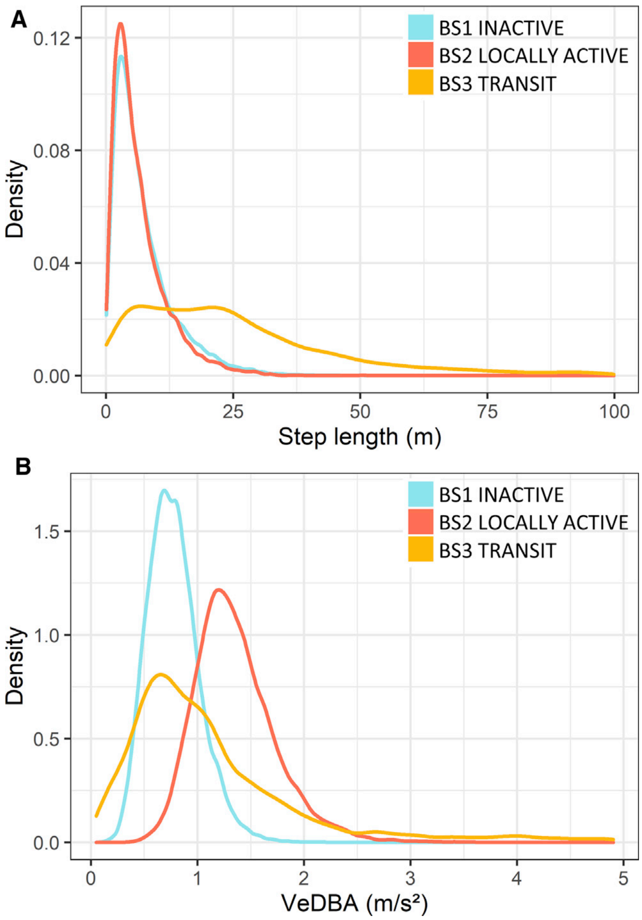

Figure 3. Distribution and classification of two data streams used for the behavioral hidden Markov model (HMM)

Step length in meters between positions (A) and mean vector of the dynamic body acceleration (VeDBA) in m/s^2 (B), over the three behavioral states: BS1 "inactive" (blue), BS2 "locally active" (red), and BS3 "transit" (yellow). See also Table S2.

significantly, increased their distance to the nearest wind turbine after the sound exposure period compared to before and during exposure. At the same time, more individuals were observed at more than one wind turbine, indicating that the larger distances from a turbine may be associated with increased roaming behavior and turbine switching.[12] This could be an indication of deviant movement behavior eventually leading up to departure from the detection area.

Importantly, the movement analysis revealed an impact of the seismic sound exposure on the behavior of cod: during the survey, cod spent a significantly larger portion of their time being inactive. Moreover, the clear daily activity cycle they exhibited in reference periods, being locally active for most of the time during dusk and dawn, was disrupted during the seismic sound exposure. Based on stomach analysis, Reubens et al.[11] demonstrated that cod at wind turbines feed mostly at dusk and dawn. Indeed, in the present study, the behavioral state locally active was associated with high VeDBA values, which are considered to be a good proxy for movement activity,[19,24–26] suggesting that feeding behavior is very likely included in this behavioral state.[26]

Overall, our results demonstrate that cod became less active during the entire sound exposure period, which may have important repercussions for their foraging time and food intake. Previous reported responses of cod to acoustic stressors in captive studies were at a scale of minutes to hours.[7,8,27] Here, we observed disruption of activities and daily rhythm over a much longer period, throughout the 3.5-day survey period, and a possible delayed deterrence effect up to 2 weeks after the exposure.

The results from the current study are an important step forward in providing quantitative field data on individual fish for population-level effect studies of seismic surveys.[4,13,28] Behavioral changes may affect the energy an individual spends on growth and reproduction, if they lead to changes in metabolic maintenance rates or food intake rates. Such changes have been shown to be more influential at the population level in the long term than direct changes in reproductive output or mortality.[13] In the current study, we found potential changes in both: cod activity levels, as well as the diurnal rhythm of behavioral states that likely include feeding. We now need additional information to quantify energy expenditure per behavioral state, and how food intake is affected by the change in diurnal rhythm, to adequately model population-level effects.[13,15,29,30]

The delayed deterrence and persistent effect in leaving the area may also have consequences for energy expenditure and food intake, as the cod might spend more time swimming and less time feeding at their preferred foraging grounds. To quantify how leaving affected the energy balance, more information is still needed on where the animals went and what feeding conditions they experienced at those places. The tagged cod may have moved toward the coast, as they are expected to do later in the season,[20,31] or even just to another similar nearby site at a turbine or shipwreck.[12] Such information cannot be deduced from our current dataset and will require the use of tags that can track fish over larger distances.[14] These tags are, however, inevitably larger than conventional acoustic tags, and they need to be recovered or have to transmit their data to a satellite, both of which are still important bottlenecks for data acquisition.[14,32]

The vessel track, going back and forth past the wind farm, was designed to optimally mimic an actual survey (apart from the absence of towed streamers with hydrophones) and to establish sound-level-related behavioral changes (e.g., create a dose response). However, the analysis of VeDBA data at high time resolution revealed no indication of a sound-level-dependent dose response of cod activity. This lack of a significant result in the short-term analyses, in combination with the significant results in the longer-term analyses (delayed effect of more fish leaving after the survey and increased inactivity during the survey), may reflect the pace of response patterns for this type of marine fish. Cod may not have responded instantaneously to the airgun sounds, but they may have changed their behavior more gradually over a longer time period. We believe that this should be an important alert, for any noise impact study, to be aware of species-specific timing of behavioral response patterns.

The current dataset provides an extensive case study, but drawing conclusions on causal relationships should be done with caution, as our study is a single event and results could potentially be influenced by other confounding factors. Examples of such factors could be the unobserved arrival of a

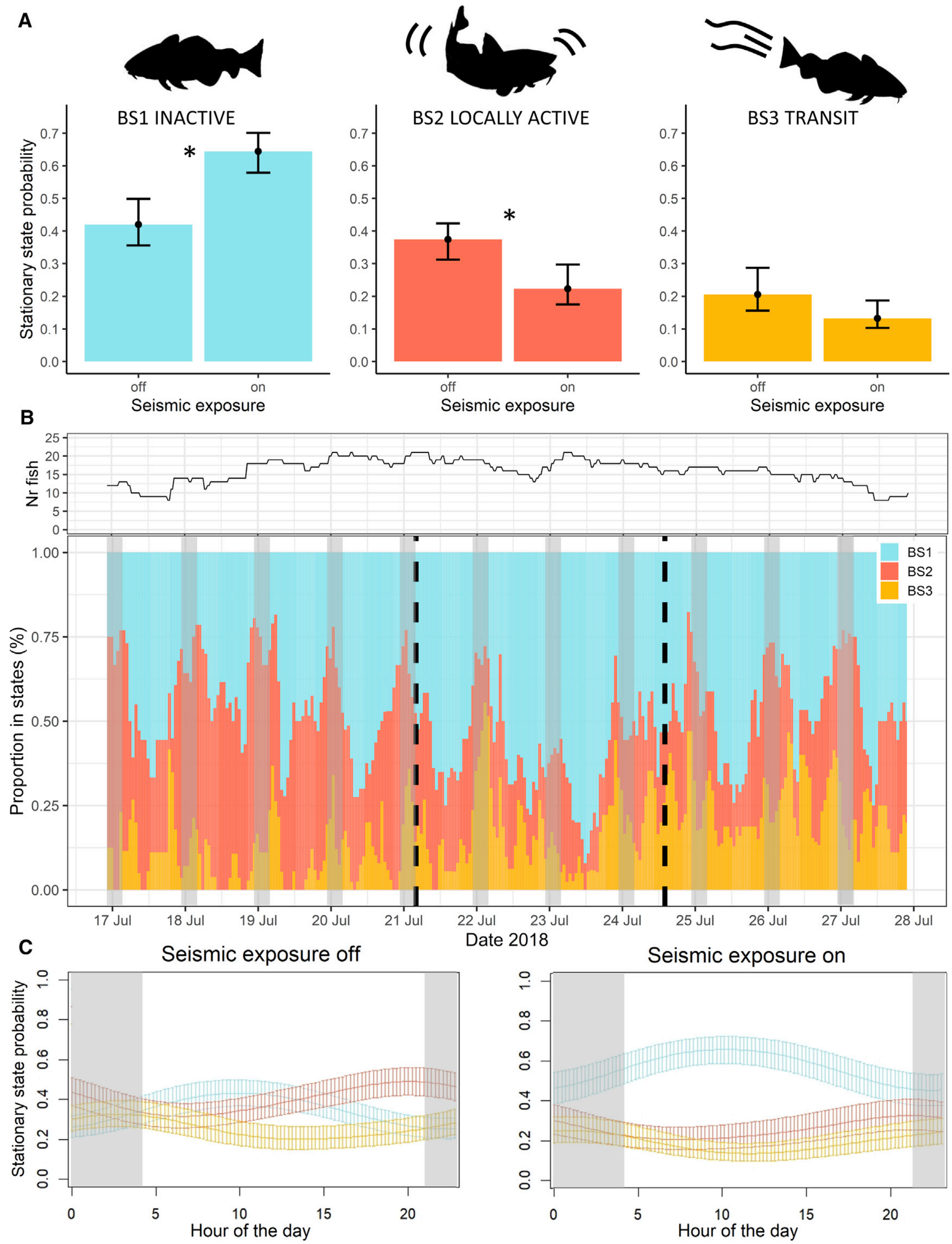

Figure 4. HMM output for the behavioral states of cod: BS1 in blue: inactive; BS2 in red: locally active; and BS3 in yellow: transit

(A) The stationary state probability for the 24 fish in each of the three behavioral states between seismic exposure off and seismic exposure on. Vertical lines represent the 95% CIs; an asterisk indicates a significant difference (no 95% CI overlap) between exposure off and on in state probability.

(B) Derived proportion of the time cod spent in the three behavioral states between July 17 and 28; the number of animals present during that time is plotted (top). Night is shaded, and start and end of the experimental seismic survey are indicated with vertical dashed lines (i.e., on July 21 and 24).

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particular predator,[33] or increasing water temperatures reaching above certain thresholds for the local cod stock.[34,35] Rising water temperatures due to global warming are known to affect welfare of local populations and to drive changes in species distributions in the North Sea[36], and fish are thereby likely dealing with an accumulation of multiple anthropogenic stressors. Therefore we do believe that replication would be valuable,[4,7] especially to shed light on effects of the interplay of multiple stressors on single species as well as on species interactions and the local ecosystem.[33,37] Furthermore, cod vocalizations can be interrupted and masked during the sound exposure,[38] which could be an additional response measure and impact factor, respectively, and should be investigated in future studies.

Understanding how anthropogenic stressors such as noise pollution affect fish populations is important if we want to achieve a "good environmental status" (GES)[39] of our seas, a goal set for all member states in the marine strategy framework directive by the European Union.[39] The North Atlantic is heavily impacted by human activities and the soundscape is dominated by noise from shipping and seismic surveys[1]. Seismic explorations of the seabed are still needed for future offshore developments, related to oil and gas, or for renewable energy sources, such as offshore wind farms and CO_2 deposition.[40,41] The results of our empirical study on Atlantic cod, in combination with the theoretical exploration of likely causes of population-level effects,[13] suggest that exposure to seismic survey sounds could affect the GES of the North Sea through an impact on the cod population. We therefore believe that replication of the current study, in the same or at other places and with the same or other species, is warranted, but that we also need to follow up with additional information on movement-related oxygen use,[42] behavioral-state-related feeding rates,[28] and prey nutritional values[13]. The insights from our study underline the applied relevance of further investigations into the impact of seismic airgun sounds, and also stress the general validity of conservation concerns about anthropogenic noise pollution in the marine environment.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2021.01.050.

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AUTHOR CONTRIBUTIONS

I.v.d.K., J.R., H.V.W., and H.S. were involved in the concept development and experimental design of the study; I.v.d.K., J.R., H.V.W., J.H., and H.S. collected the data; I.v.d.K. performed the analysis with input from L.T., M.A., J.H., and B.M.; I.v.d.K. led the manuscript writing, and all authors edited the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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(C) Stationary state probability with 95% CI for the covariate "hour of the day," acquired through the HMM when seismic exposure is off (left) and seismic exposure is on (right). Night is shaded (time zone Coordinated Universal Time; UTC). For all probabilities presented, the values of the other covariates were set to their mean during the sound exposure period: e.g., fish length 39 cm, current speed 0.46 m/s, time since start 1.7 (days), temperature 18.7°C, and (for A only) hour 12:00.
See also Figure S2 and Table S3.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Cod acoustic telemetry detection data including sensor information	European Tracking Network	https://lifewatch.be/etn/
Data analysis and code	This paper	https://doi.org/10.14284/438
Software and algorithms		
RStudio	R Code Team	https://www.r-project.org/
momentuHMM: R package for analysis of telemetry data	McClintock and Michelot[18]	https://cran.r-project.org/web/packages/momentuHMM/index.html
nlme package	CRAN	https://cran.r-project.org/web/packages/nlme/index.html
MuMIn package	CRAN	https://cran.r-project.org/web/packages/MuMIn/index.html
multcomp package	CRAN	https://cran.r-project.org/web/packages/multcomp/index.html

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Inge van der Knaap (iej.vanderknaap@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

The datasets and code generated during this study are available at the Marine Data Archive: https://doi.org/10.14284/438 and the raw detection datasets can be requested through the European Tracking Network: https://www.lifewatch.be/etn/

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study site and telemetry setup

This study took place in the Belgian and Dutch part of the North Sea between 27 June and 1 October 2018. Fish were tracked in the Belgian offshore Belwind/Nobelwind wind farm (51.670°N 2.802°E; Figure S1A), situated on the Bligh Bank, approximately 50 km offshore from the coastal harbor of Zeebrugge. The water depth at the wind park area varied between 15 – 37 m, including tidal fluctuations (and at our study site this was 3 m); currents in the wind farm predominantly run from northeast to southwest[43].

Acoustic telemetry was used to record presence and track movement of Atlantic cod at the study site. We deployed a total of 21 VR2AR receivers (Innovasea) from 1 June until 9 October around six wind turbines (Figure S1B). A circle (r = 150 m) of six receivers was deployed around three of these turbines (i.e., B8, C9 and C10) in a positioning array, intended for fine-scale positioning of the acoustically tagged fish. Around the other three turbines (i.e., C8, B9 and B10), lone standing receivers served to detect presence/absence of the tagged fish (Figure S1B). The receivers were moored using customised anchoring with the receiver placed on top of a 1.5 m tall stainless steel tripod (weighing 80 kg)[44].

Fish tagging

A total of 51 Atlantic cod (total length between 32.0-56.0 cm, with an average of 39.3 cm) were caught, tagged, and released within 2 m from one of the 6 experimental turbines. Catching and tagging of free-ranging animals was ethically approved under certificate number EC2017-080, in line with official guidelines for animal welfare in Flanders (Belgium). We tagged and released individual fish on six different days prior to the experimental seismic survey: 25-28 June 2018, 12 and 19 July 2018 (Figure 1A), using the same procedures as van der Knaap et al.[45] to surgically insert a V13AP (Innovasea) tag in the abdominal cavity of the fish. The tags were set to transmit at random intervals between 50-100 s, at which point they transmitted a signal lasting ~5 s at 69 kHz. The V13AP tags included an accelerometer and pressure sensor, allowing collection of information on body acceleration and depth. The tags alternatingly recorded and transmitted the information from each sensor. The accelerometer sensor measured acceleration in three directions and provided cumulative means over 37 s in the three dimensional vector dynamic body acceleration (VeDBA),

$$VeDBA = \sum_{i=1}^{T} \frac{\sqrt[2]{x_i^2 + y_i^2 + z_i^2}}{T}$$

where x, y, and z are the acceleration values recorded from each axis at sample i over the sample period T.

METHOD DETAILS

Experimental seismic survey

The seismic survey was conducted at the study site from 21-24 July 2018 (by the MV Geo Caribbean, contracted through CGG, Norway). The airgun-array consisted of 36 airguns (G-Gun II Sercel) with a total volume of 2950 in^3 (48.3 L), which fire every 10 s during operation. This airgun configuration and firing sequence are standard for a real seismic survey, and the track lines and firing procedures were also realistic for an actual survey. Unlike in an actual survey, streamers and hydrophones were absent. The vessel track consisted of 11 passes alongside the wind farm, crossing the Dutch-Belgian border (Figure S1A). The exposure started approximately 30 km North of the wind farm with a gun test and ramp-up (lasting 40 min), passed by the wind farm 11 times with a closest point of approach of 2.25 km, and ended approximately 25 km North-East from the wind farm (Figure S1A), while maintaining an average speed of 2.2 m/s. During the entire survey period, the airguns fired 2352 times.

Sound measurements and processing

Sound measurements were collected using a moored hydrophone (AMAR G3), at 22 m depth, attached to a 60 kg mooring anchor, and positioned in the middle of the receiver area (Figure S1B). The recording period lasted from 13 July to 3 September 2018, covering sufficient time before, during and after the seismic survey sound exposure experiment. The AMAR was equipped with a hydrophone (M36) and three orthogonally oriented, low-sensitivity particle motion sensors (microelectromechanical systems, MEMS), both sampling at a rate of 32 kHz. Recordings were converted to sound pressure level (SPL) and sound particle acceleration level (PAL) respectively in decidecade (ddec) bands (ref: ADEON soundscape spec[46]) with center frequencies ranging from 10 Hz to 16 kHz. Our acoustic terminology follows ISO 18405.

Ambient sound pressure level (SPL, re 1 μPa^2) fluctuates with time and at our site the median SPL (60 s temporal observation window (TOW[46]) was 116 dB (inter-quartile range (IQR) 5 dB) in the 40 - 400 Hz ddec bands (band filter selected to match cod hearing) for all ambient recordings (Table S4). During the exposure period, the median SPL rose by 7 dB to 123 dB (IQR 14 dB). At the closest point of approach (at 2.25 km), SPL averaged over 60 s was 147.2 dB re in the 40 - 400 Hz ddec bands (see Figure S3A and Table S4 for a more in-depth description of the ambient levels).

The self-noise particle acceleration level (PAL, re 1 $(\mu m/s^2)^2$ had a median value of 70 dB (60 s TOW) with IQR 0.4 dB in the 40 - 400 Hz ddec bands (Figure S3B; Table S5). PAL reached above self-noise levels when the vessel came within 6 km from the study site, the median value increased to 79 dB, with IQR 5 dB when the vessel was within 2.5 km of the study site. At the closest point of approach (at 2.25 km) PAL was 90.0 dB (see Figure S3B and Table S5, for further detailed particle motion description).

Single pulse sound exposure level (SELss) was calculated for the 40-400 Hz and 10 Hz-16 kHz ddec bands, from the 60 s sound exposure divided by the number of actual airgun shots (between 5-7 shots) within that time period (Figures S3C and S3D). The cumulative sound exposure level (SELcum, re 1 $\mu Pa^2 s$) over the 3.5 day survey period at the receiver position was 186.3 dB in the 40 - 400 Hz band.

QUANTIFICATION AND STATISTICAL ANALYSIS

Fish position triangulation and filtering

After recovery of equipment, corrections for receiver clock drift of the receivers during the deployment period were done by applying a linear time correction over the entire sampling period (VUE, Innovasea). We subsequently transformed the detection data into 2-dimensional locations through time difference of arrival (TDOA) positioning[47], using a web interface hosted by Innovasea (i.e., 'VPS lab'). The Innovasea's TDOA algorithm applies weighted averaging of positions from subsets of receivers for a given tag transmission to reduce overall positioning error, although the exact error terms used for weighting and position error estimates are not provided to the end user. The position was only determined when the tag signal was detected by at least three receiver stations.

Positions were filtered based on an associated horizontal positioning error (HPE) of below 8.9 which removed 2% of the positions[45]; HPE is a unit-less error metric used in Innovasea systems. This cut-off removed positions outside of the positioning arrays that had a clear linear direction bias known to be associated with large positioning error. Furthermore, we removed tags from the dataset if: tagged fish left the detection area within 24 h after tagging, if tags failed to emit any signal (fish 11 and 55), or if tags provided static positions indicative of tag loss or fish mortality (fish 6, 38 and 47).

Data analysis

We used two discrete-time hidden Markov models (HMMs) to determine fish presence/absence and behavioral states from the telemetry data. HMMs are suited for multivariate datasets with temporal autocorrelation, such as the current dataset, and return the probabilities of an animal being in each of a set of mutually exclusive behavioral states (17, 26). HMMs were applied in R (version 4.0.0) using the 'momentuHMM' package (version 1.5.1).

To assess whether the seismic survey sound exposure had an effect on the presence of cod in the area, we combined the newly collected data of 2018 with detection data of Atlantic cod tagged in the same wind farm ('Belwind') in 2016 and 2017. Data from fish that were detected for less than 24 h after tagging and stationary tags (i.e., fish dying or losing the tag) were again removed from the analysis. We only used data from individuals from 2016 and 2017 that were within the size range of the individuals from 2018 (32 −58 cm, total length), resulting in a total of 14, 14 and 37 fish for 2016, 2017, and 2018, respectively. Next, the presence or absence of individuals was defined for each day during the entire study period: from the moment of tagging until receiver recovery. Fish were considered present if they were detected for more than 1 h per day (Figure 1A). We applied a non-spatial hidden Markov model (HMM) to examine if the experimental seismic survey increased the probability that individuals would leave the study area during the survey period or whether there was a decaying or persistent effect, starting from the survey onset and including part or the whole period after the survey. Daily observations of presence/absence (Bernoulli distribution) per individual (65 fish in total) were fitted to the states 'on-site' and 'off-site'. Covariates included in the model were: year, decay after tagging (exponential decay over time since a fish was tagged), and temperature (°C). To model the effect of the survey, the covariates seismic on/off (where on just refers to during the survey period), decay survey (value of 1 during the survey followed by an exponential decay after the end of the survey), and seismic persistent (where on refers to both during and after the survey period) were examined (Table S1). The fitted model included all presence/absence data per individual as a single track[48].

Fish positions from four days before until four days after the survey period (17 to 28 July 2018) were selected to examine the effect of the seismic survey sounds on the distance of the fish to the turbines. The four day period was selecteded to balance the data between the three different periods: before, during and after. The fish that were tagged two days before the survey, and fish that left the area before the end of the survey period, were excluded from this analysis (yielding a sample size of n = 19 for this analysis). Positions were projected to UTM (zone 31) and averaged over half-hour bins per individual. The distance to the closest turbine was calculated as the Euclidean distance in meters. The minimum distance between two turbines was 450 m, and consequently, if a position was calculated to be further than 225 m from a turbine at the center of a receiver array, it was excluded from the analysis. Distance measurements were positively skewed; therefore, a log-transformation was applied to normalize the distribution. We applied a Linear Mixed Model, which accounted for temporal autocorrelation (AR(1), R package 'nlme' version 3.1), and in which fish ID was a random variable and the fixed effect covariates were: the survey period (before, during and after), hour of the day (cosinor of hour), current speed (m/s), temperature (°C), and tidal change between consecutive points (m). Model selection was done based on AIC comparison using model dredging ('MuMIn' version 1.43). The best model (lowest AIC) was: log(distance) ~period + current speed + tidal + (1|fish). To examine whether distance of fish to the turbine differed between periods, a host-hoc test was preformed (Tukey HSD 'multcomp' version 1.4).

We applied spatially explicit HMMs to examine if the seismic survey had an effect on the movement behavior of the study animals. For this analysis, individuals were included that were present for a sufficient amount of time, before, during and after the exposure period, resulting in a sample size of 24 fish. The number of animals present varied over time between 8 and 21, because some fish were temporarily not detected or left the detection area. As raw detection data from the receivers frequently included missed detections and low accuracy on the calculated positions, time-difference-of-arrival locations were averaged over 30-minute bins. Individual movement paths were only retained if they had at least twenty subsequent positions. Observed data streams consisted of step length (Euclidean distance between two subsequent positions) and the associated mean VeDBA transmitted by the tag's acceleration sensor, per 30 minute time period. As no robust, numerical selection criteria for choosing the number of states for HMMs exist[49,50], we based the number of states on the expected number of biologically meaningful behavioral types that could be distinguished in the data (c.f. Hubert et al.[7], resulting in: 'Inactive' (Behavioral State 1, BS1), 'Locally active' (BS2), and 'Transit' (BS3) (Figure 3; Table S2). Individual variation was accounted for in the model by including fish length as a covariate. State transition probabilities were modeled as functions of: fish length (cm), current speed (m/s), tidal height (m), hour of day (as $\cos(2\pi t/24\ h)$ and $\sin(2\pi t/24\ h)$, where t is the time of the observation between 0 and 24 h) and sea water temperature (°C). To model the effect of the survey, the covariates: seismic on/off (only "on" during survey period), time since start survey (value of 0 until the start of the survey after which it increased with time) decay survey (value of 1 during the survey followed by an exponential decay after the end of the survey) and seismic persistent (on during and after the survey period) were examined (Table S3). Model selection was based on AICs (Table S3).

Potential short-term response patterns to noise exposure levels were examined based on all VeDBA measurements, transmitted by the tags of the 24 fish present during the seismic survey period. The VeDBA data were available as mean acceleration data measured over periods of 37 s and accumulated for all three directions, at a mean resolution of 18.8 ± 14.0 (SD) minutes. We applied a Linear Mixed Model, which accounted for temporal autocorrelation (AR(1), R package 'nlme' version 3.1), and in which the fixed effect covariates were: sound pressure level (SPL of the 100 or 250 Hz frequency band), current speed (m/s), temperature (°C), and tidal change (m). Model selection was done based on AIC comparison, using model dredging ('MuMIn' version 1.43). The best model (lowest AIC) did not include SPL and was: VeDBA $\sim$temperature.