Sound investigation: effects of noise on marine animals across trophic levels

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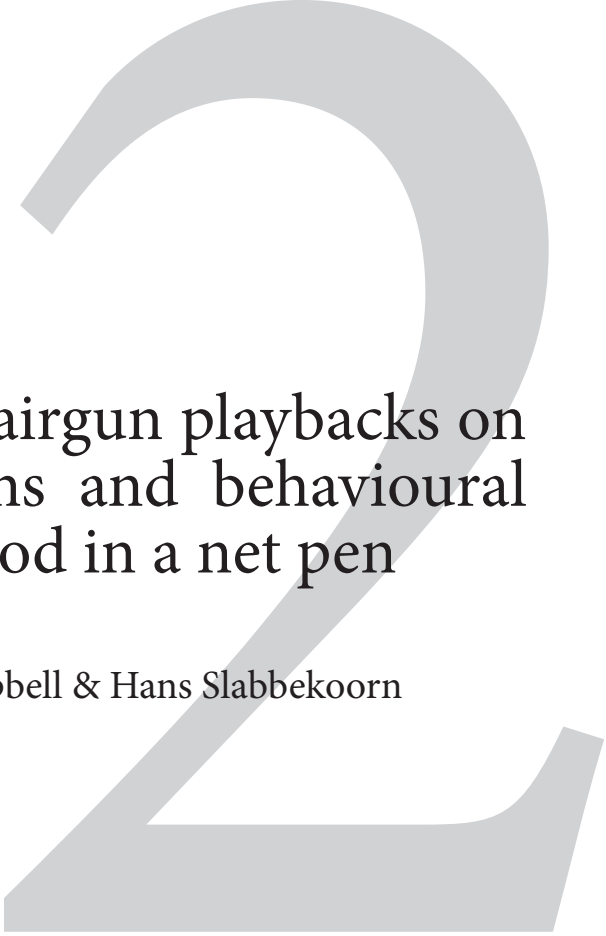
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Effects of seismic airgun playbacks on swimming patterns and behavioural states of Atlantic cod in a net pen

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Abstract

Anthropogenic sound can affect fish behaviour and physiology which may affect their well-being. However, it remains a major challenge to translate such effects to consequences for fitness at an individual and population level. For this, energy budget models have been developed, but suitable data to parametrize these models are lacking. A first step towards such parametrization concerns the objective quantification of behavioural states at high resolution. We experimentally exposed individual Atlantic cod (*Gadus morhua*) in a net pen to the playback of seismic airgun sounds. We demonstrated that individual cod in the net pen did not change their swimming patterns immediately at the onset of the sound exposure. However, several individuals changed their time spent in three different behavioural states during the 1 h exposure. This may be translated to changes in energy expenditure and provide suitable input for energy budget models that allow predictions about fitness and population consequences.

Introduction

Underwater sound pollution can impact fish and other marine life through a range of effects (Carroll et al., 2016; Popper and Hawkins, 2019). A high-amplitude sound source may have a potentially lethal effect through physical injury for nearby fish, while more moderate levels can still have a variety of non-lethal effects for fish over a large range of distances (Halvorsen et al., 2012; Slabbekoorn et al., 2010). Examples of non-lethal effects are acoustic masking, elevated stress levels, and disruption of swimming patterns (Sarà et al., 2007; Slotte et al., 2004; Wysocki et al., 2006). Although non-lethal effects may seem less dramatic, it is likely that more individuals are exposed to moderate sound levels, and therefore, potentially will have a stronger impact at the population level (Boudreau et al., 2018; Lima and Dill, 1989). While many studies have examined the effects of sounds on fish, extrapolating these results to individual fitness or population level effects remains a challenge (Carroll et al., 2016; Williams et al., 2015). Dynamic Energy Budget models (DEB) and the Population Consequence of (Acoustic) Disturbance (PCoD or PCAD) framework provide a tool and framework for this challenge (Leeuwen et al., 2013; Pirotta et al., 2018). Disturbance-induced changes in individual behaviour and physiology have to be translated into changes in vital rates (growth, reproduction and survival). These may subsequently be translated to changes in population dynamics (New et al., 2014; Pirotta et al., 2018). However, comprehensive assessments using these models are rare because of the lack of relevant data (Pirotta et al., 2018; Slabbekoorn et al., 2019).

So far, DEB and PCoD models have not been developed for fish in the context of acoustic disturbance (Hammar et al., 2014; Sivle et al., 2015). However, Soudijn et al. (2020) used a size-structured energy budget model for Atlantic cod to make a sensitivity analysis of potential effects of sound disturbance on population growth. The results indicated that additional energy expenditure and reduced food intake more easily lead to population-level effects than additional direct mortality and direct reproduction failure. In the model, additional energy expenditure and reduced food intake due to acoustic disturbances reduced growth, increased indirect mortality, delayed reproduction, and reduced reproductive output (Soudijn et al., 2020). Using the model, actual population-level effects of sound exposure could be estimated, but quantitative empirical data on behavioural and physiological effects of sound exposure are currently lacking (Pirotta et al., 2018; Slabbekoorn et al., 2019). The results of Soudijn et al. (2020) suggested that it is most relevant to study effect of sound exposures on energy expenditure and food intake.

A variety of studies has investigated behavioural changes of fishes to sound exposures and such non-lethal effects can also be found at larger distances from the sound source. Several studies have shown that sound exposures can affect swimming patterns by eliciting a startle or alarm response (Wardle et al., 2001), avoidance behaviour (Slotte et al., 2004), disrupting schools or groups (Sarà et al., 2007), and by changes in swimming depth (Hubert et al., 2020b). Responsiveness to sound can be lower in fish that live in high disturbance area's (Harding et al., 2018), or fade over sequential sound exposures (Nedelec et al., 2016; Neo et al., 2018), but long-term exposures may still have long-lasting effects (Becker et al., 2013; Payne et al., 2014). Several studies have also shown effects of sound exposure on foraging efficiency, with reduced feeding attempts and increased food handling errors in various captive species (Magnhagen et al., 2017; McLaughlin and Kunc, 2015; Purser and Radford, 2011; Shafiei Sabet et al., 2015; Voellmy et al., 2014) and one study on free ranging damselfish (*Chromis chromis*) (Bracciali et al., 2012). Payne et al. (2014) studied both swimming activity and foraging success in free ranging mulloways (*Argyrosomus japonicus*). Tagged fish in one estuary were less active and inhabited deeper waters during the weekend, and individuals in another estuary had less full stomachs and fewer fish in their diet over the weekend. These differences were likely due to higher boat activity in the weekends (Payne et al., 2014). Studies such as the last one may provide quantitative input for population models and allow parametrization of changes in energy expenditure and intake due to sound exposure.

So-called Hidden Markov Models (HMMs) provide a processing tool with high potential for swimming tracks from acoustic telemetry (Langrock et al., 2012; McClintock and Michelot, 2018). HMMs allow inference of behavioural states throughout the sampling period and they can be fitted to estimate the effect of external stressors on the time spent in the various behavioural states (see e.g. DeRuiter et al., 2017). The resultant time budget changes and step length (swimming speed) distributions can potentially be translated to changes in energy expenditure due to swimming and energy intake due to foraging behaviour, which is suitable input for energy budget calculations in PCoD frameworks (Hubert et al., 2020a; Leeuwen et al., 2013; Williams et al., 2006). HMMs have typically been used for data of relatively low temporal resolution on free ranging animals. For free ranging marine fish, it is especially challenging to track tagged fish at high-enough resolution through acoustic telemetry because of limited detection ranges of tag receivers, problems with relatively short battery life, and tag signal collisions. Furthermore, high resolution data may be necessary to distinguish among critical behavioural states (cf. Nams, 2013; Postlethwaite and Dennis, 2013).

Seismic surveys are a prominent contributor to the underwater soundscape and impact assessments are often part of the permit application (Ainslie et al., 2019; Gisiner, 2016; Sertlek et al., 2019). Marine seismic surveys are performed to explore the geological structure beneath the seafloor, often to search for oil and gas resources (Gisiner, 2016). They are conducted using a vessel towing one or two arrays of airguns and one up to more than ten streamers of hydrophones (Landrø and Amundsen, 2018). The airguns (seismic sources) produce high intensity, low-frequency impulsive sounds at regular intervals (5 – 15 s), potentially for several hours and repeated for several days to weeks and even months (McCauley et al., 2000; Slabbekoorn et al., 2019). Most energy of the sounds produced by airguns falls within the 10 – 300 Hz frequency range (Gisiner, 2016; Sertlek et al., 2019), which is within the hearing range of most – if not all – fish (Popper and Fay, 2011; Radford et al., 2012).

Atlantic cod is a popular model species to study the effects of noise pollution, because their hearing is well studied (Chapman and Hawkins, 1973; Sand and Karlsen, 1986) and because it is a commercially important species (Kurlansky, 1999). Catch rates of free ranging cod have been reported to be affected by actual seismic surveys (Engås et al., 1996; Løkkeborg and Soldai, 1993). Several experimental studies examined the effects of sound exposure on captive cod. Tagged cod in a floating pen exhibited increased swimming depth and heart rate during a single, unreplicated, experimental seismic airgun exposure (Davidsen et al., 2019). No startle or strong behavioural responses to exposures of pure tones were observed in a single group of cod in an indoor basis (Kastelein et al., 2008). Another study showed that short-term sound exposure did elicit startle responses in cod larvae, and also that long-term exposure led to initial reduction of growth rate, which disappeared at a later stage (Nedelec et al., 2015). Furthermore, cortisol levels increased during and after playback of sweep tones, and reproductive output of cod in a single treatment tank was lower compared to cod in a single control tank (Sierra-Flores et al., 2015). More studies like these – however, well-replicated – are needed. Especially data on sound impact on individual behaviour and physiology are required to gain insight into the potential effects of sound on cod populations.

In the current study, we examined the effects of sound exposure on cod behaviour in a net pen. We tagged cod with an acoustic tag and experimentally exposed them to playback of airgun sound pulses in a net pen in a cove. We examined the occurrence and magnitude of swimming pattern changes at the onset of the sound pulse series and analysed the time spent in various behavioural states during the exposure by exploiting current advances in processing of telemetry data. Fine-scale, high-resolution data on swimming patterns of captive cod

during sound stimulus playback provide insight into whether and how cod can respond to sound, which may help in interpreting more crude, lower-resolution data on free ranging cod in response to actual seismic survey sound. Our current study may therefore provide input for future experiments and individual energy budget models for the evaluation of sound impact on population dynamics.

Materials and methods

Study subjects

We used 20 wild-caught Atlantic cod (*Gadus morhua*) in this study, with body lengths ranging from 30 to 47 cm. Cod hear sound up to 470 Hz and they are most sensitive in the 60 – 310 Hz range. Below 50 Hz, cod are mostly sensitive to particle motion and above 50 Hz mostly to sound pressure (Chapman and Hawkins, 1973; Sand and Karlsen, 1986). The study subjects were caught by angling at ship wrecks in the Dutch North Sea from a recreational fishing boat during day trips on October 18th and November 15th 2017. During catching, the cod were kept in ~ 500 L transport boxes with continuous air supply and regular refreshment of sea water. After angling, the fish were kept in two cylindrical stock tanks (Ø 3.5 m, depth 1.2 m) at Stichting Zeeschelp, Kamperland, the Netherlands. The stock tanks were continuously refreshed with water from the nearby Oosterschelde marine inlet and the artificial dark-light cycle in the room followed the natural day-night cycle. The fish were fed with defrosted sprat (*Sprattus sprattus*) every other day and were kept in the stock basins for at least a week before being used in the experiment, the fish usually started eating the first or second day after capture.

Experimental arena

The study was conducted in the Jacobahaven, a cove in the Oosterschelde sea inlet of the North Sea, the Netherlands. The cove is about 200 m wide, 300 m long and 2-5 m deep at low and high tide, respectively. The location is relatively sheltered from wind and waves by surrounding dikes and piers and is isolated from external boat traffic, making it a suitable location for sound impact studies. The experiment was conducted using a floating study island (Candock, Canada), consisting of a working platform and an octagonal walkway that supported a net pen (Ø 11.5-12.5 m and a max. depth of 5 m, fig. 1) as arena for the study subjects. The equipment and underwater speaker were supported by the working platform. The study island was bottom-anchored in the centre of the cove with chains and stretchable mooring rope. Detailed sound field measurements in the current experimental setup during previous experiments have revealed a gradual decrease in sound level with increasing distance from the speaker and a ratio of

sound pressure and sound velocity level that is to be expected in the acoustic far field (Hubert et al., 2016).

Tagging and data acquisition

Each fish was tagged with an acoustic transmitter and accelerometer logger (resp. 2 and 6 gram in air). The fish were anaesthetized using 2-phenylethanol (0.6 ml/l seawater) or clove oil (0.05 ml/l). The tags were implanted in the intraperitoneal cavity by making an incision in the abdominal wall, inserting the tag, then suturing the incision. After tagging, the fish was allowed to recover for > 40 hours in a rectangular tank (1.20 m x 1.00 m x 0.65 m) with a continuous inflow of Oosterschelde water. The fish were not fed during this period. The acoustic tag (Model 795-LF, HTI, US) was used to determine the position of the fish. We set the tag to emit 0.5 ms pings of 307 kHz (inaudible to the fish) at a 1 s pulse repetition interval. Pings were recorded by four hydrophones (Model 590-series, HTI, US) that were attached to the outer edge of the octagonal walkway (two at the surface, two close to the bottom, fig. 1) and processed by an acoustic tag receiver (Model 291, HTI, US) which transferred detections to a laptop.

The accelerometer logger (MBLog Mini, Maritime bioLoggers, Canada) measured acceleration along three axes and was used to gain insight into the general activity levels. The logger was set to sample at 100 Hz at 16 bit and stored the data on a micro SD card in the tag. We aimed to time-synchronize the data from the accelerometer to the spatial data of the fish, as the spatial data and the
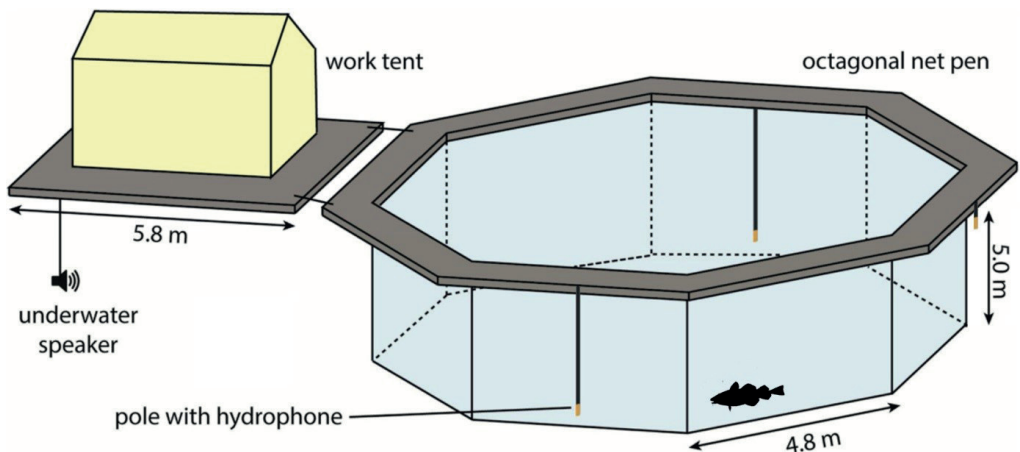

Fig. 1: A schematic overview of the study island (figure adapted from Neo et al., 2016). The square working platform held the telemetry and playback equipment and was connected to the octagonal walkway and net pen with ropes. The four hydrophones recorded the acoustic signals from the tags. The fish represents a single cod test individual, but is not drawn to scale.

sound exposure were linked to the UTC time. For this, we calculated the vector of the dynamic body acceleration (VeDBA) using the accelerometer data and the 2-dimensional swimming speed using the spatial positions. We used the optim function in R to find the strongest correlation between VeDBA and speed while allowing 4 Hz deviation from the set sampling period of the accelerometer and while allowing clock drift by using cross-correlations. Visual observation of the synchronized data streams revealed inconsistencies in the time-synchronisation, possibly due to inconsistent sampling rate of the accelerometer, so we decided to exclude the acceleration time series from further analyses.

Experimental design

We conducted 20 trials in which a single cod was exposed to one hour of airgun playback. The 1 h sound treatment was scheduled to start 18 – 22 hours after release in the pen and was followed by 30 min of silence (figure 2a). We scheduled the hour of airgun playback to start 1 hour before or at the peak of high tide to permit the propagation of lower sound frequencies. The shallow water cut-off frequency at 5 m depth was measured to be 150 Hz in the experimental setup. Playback schedules were alternated between 1 hour before and after absolute high tide to control for effects of flow or ebb tide. After the 30 min of silence,
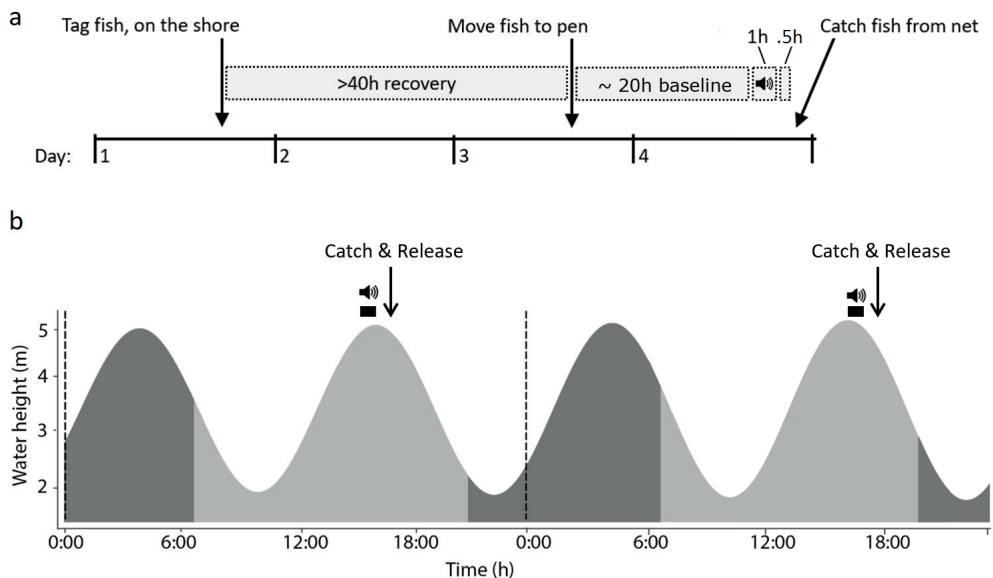

Fig. 2: (a) Timeline of a single trial: the horizontal grey bar represents recovery, baseline, exposure, and post-exposure periods, while the vertical arrows indicate fish tagging, moving, and catching events; (b) Water height levels related to the tidal fluctuation during night (dark) and day (light). Exposures took place just before or after high tide. After the exposure, the experimental fish was caught and a new tagged fish was released in the pen again.

the fish was retrieved from the net pen and replaced with the next experimental individual (figure 2b).

Sound exposure

We exposed the individual fish to one hour of playback of airgun sound pulses at a pulse rate interval (PRI) of 10 s, which is a realistic rate for seismic surveys (Gisiner, 2016; Slabbekoorn et al., 2019). The sound pulses were recordings of a down-scaled airgun (TNO, The Netherlands) with a volume of 10 in^3 and a pressure of 800 kPa (Reichmuth et al., 2016). The recordings were made, using a hydrophone (model 96-Min, HTI), from the study island during high tide (4.5 - 5.0 m water depth) at a distance of 5.8 m with both source and receiver suspended mid-water column. Playback tracks were generated by randomly selected airgun sound pulse recordings spaced by silent intervals (figure 3ab). The tracks were played back with an underwater transducer (LL-1424HP, Lubell Labs, US) from a recorder (DR-07, Tascam, US), via a power amplifier (DIGIT 3K6, SynQ, Belgium) and a transformer (AC1424HP, Lubell Labs). For 9 trials,
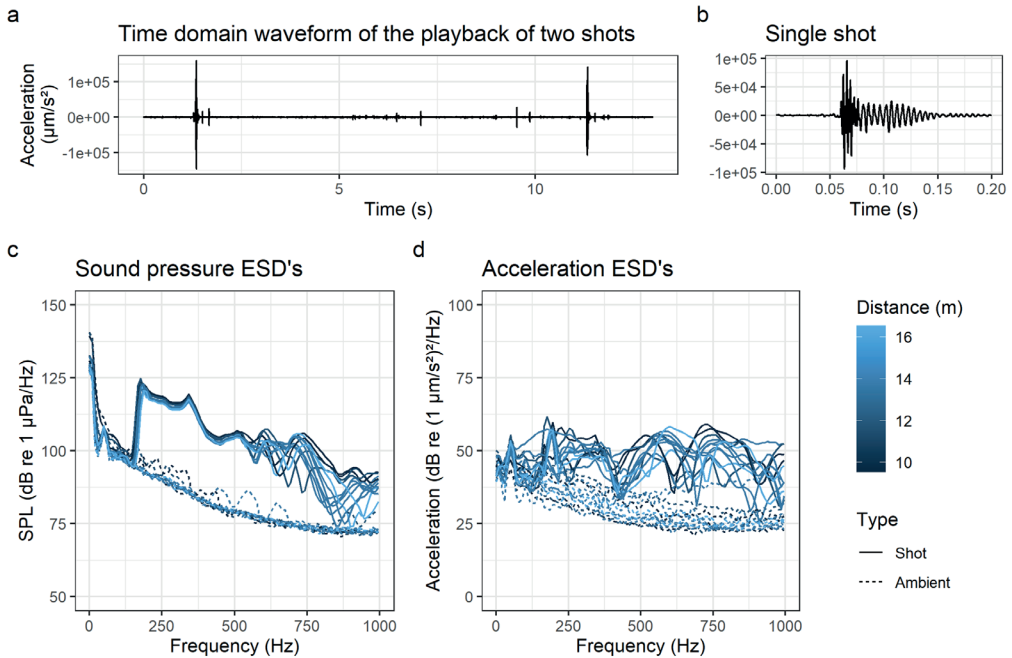

Fig. 3: (a) Sound pressure vs time recording from the net pen of two sequential airgun sound pulses with a 10 s inter-pulse interval and (b) a single sound pulse. (c & d) Energy spectral densities (ESD) of recordings of the playback of airgun sound pulses and the silent (ambient) intervals at various distances from the speaker at 2 m depth, provided in (c) sound pressure level (SPL) and (d) sound particle acceleration. The ESD's were generated using the Hann window type and a window length of 4096 and 50% overlap.

the speaker was suspended mid-water column (~ 2 m deep) at 2 m from the net pen, for 5 trials at 7.8 m from the net pen (~ 2 m deep), and for 6 trials, it was located on the sediment at about 20 m from the net pen (4.5 – 5 m deep). In this way we achieved variation in exposure level and the exposures of all trials were recorded in the pen using a calibrated hydrophone and the three set-ups resulted in mean zero-to-peak sound pressure levels (SPL_{z-p}) of 174, 169, and 152 dB re 1 μPa (100-600 Hz bandpass filter) with the speaker at 2, 7.8, and 20 m from the net pen respectively.

To determine the sound levels and spectra in the net pen, we measured sound pressure and particle velocity in the pen, at 9.7, 11.6, 13.5 and 16.4 m from the speaker, with the speaker at 7.8 m from the net pen. The measurements were done using a M20 particle velocity sensor (GeoSpectrum Technologies, Canada) and logged on a laptop using a differential oscilloscope (PicoScope 3425, Pico Technologies, UK). Recordings were analysed using the manufacturer provided receiver sensitivity data and a 100-600 Hz bandpass filter. The mean zero-to-peak sound pressure level (SPL_{z-p}) of the played back airgun shots at 9.7 m from the speaker was 164 dB re 1 μPa, and the sound particle acceleration (a_{z-p}) was 101 dB re 1 nm/s^2. At 16.4 m, this was 158 dB and 99 dB respectively. The mean SPL of the ambient conditions in the pen was 113 dB re 1 μPa and the mean sound particle acceleration was 61 dB re 1 nm/s^2 (fig. 3cd).

Telemetry positioning

We used YAPS (Yet Another Positioning Solver), a single-state continuous time animal movement model designed to account for positioning error in time of arrival localization, to estimate the positions of the fish (Baktoft et al., 2017). We extended the functionality of YAPS to apply a correlated walk model, implemented as an Ornstein–Uhlenbeck velocity process (Johnson et al., 2008), which should yield more suitable track estimates for highly autocorrelated velocity data. Due to memory limitations during telemetry processing and fitting issues for some trials, we subsampled the telemetry data resulting in pulse repetition intervals of 2 s (n = 17 trials), 3 s (n = 2) or 5 s (n = 1), depending on the detection rates. Across individuals, we obtained on average 91% (range: 45% – 100%) of all expected positions. We used the positions of the fish to determine the swimming speed, turning angle and depth.

Statistics

We applied three models to examine different aspects of changes in swimming behaviour: (1) A randomization test to examine the occurrence of short-term changes from baseline swimming behaviour in response to playback onset, (2) a

non-linear mixed effects model to examine the magnitude and decay of changes from baseline swimming behaviour in response to playback onset, and (3) a three-state discrete-time Hidden Markov Model (HMM) to examine if airgun playback resulted in changes in time spent in various behavioural states.

Randomization Test

Instantaneous changes in swimming behaviour throughout the trials were represented by Mahalanobis distance values, calculated as the mean number of standard deviations of 60 seconds of swimming behaviour (swimming depth, speed and turning angle) from the covariance matrix of the previous 60 seconds. This resulted in time series indicating the magnitude of short-term change in swimming behaviour (fig. 4). To account for potential clock drift, the maximum Mahalanobis distance within 30 seconds before and 30 seconds after the playback onset was taken as the observed response while a null hypothesis was generated by randomly reassigning the 60 second response period to any position in the period before exposure and measuring the maximum Mahalanobis distance within the randomized response period. We then examined whether the observed response exceeded the 95th percentile of 10,000 randomized responses (see Antunes et al., 2014; DeRuiter et al., 2013). This test was applied to each individual.

Non-linear Mixed Model

A mixed model was applied to examine the magnitude and decay of the response to playback onset over all trials. Here, Mahalanobis distance values were calculated with respect to the entire trial and deviations from baseline behaviour in response to the playback onset were assumed to decay exponentially. We only used the swimming speed and turning angle of the fish for this and not swimming depth because the tidal variation limited the maximum depth of the fish. This did not yield a bias for the previous analysis because that earlier analysis focussed on short-term behavioural changes when compared to short baselines. The inclusion of depth in the current analysis would possibly yield a problematic bias when the entire trial would be used as baseline (covariance matrix). The swimming speed and turning angle were converted into normal distributions by fitting, respectively, gamma and wrapped Cauchy distributions to the data streams before using them in Mahalanobis distance calculation. The model was formulated as (I) where the subscripts a, b, and c indicate design matrices and coefficients for the baseline, response magnitude, and response decay, respectively, and t is the time since exposure onset. φ is the latent auto-regressive (AR(1)) process where ρ indicates the strength of the process and ψ is the Gaussian distributed error term. The individual ID was treated as a random intercept effect applied to the baseline conditions (a). The model was implemented

using a maximum likelihood framework in R with TMB (Kristensen et al., 2016) and hypothesis testing was carried out using a parametric bootstrap.

$$\log(\mu) = X_a\beta_a + I(t) \cdot X_b\beta_b e^{X_c\beta_c \cdot (-t)} + \varphi$$

$$I(t) := \begin{cases} 1 & \text{if } t \geq 0, \\ 0 & \text{if } t < 0. \end{cases} \qquad\qquad \text{(I)}$$

$$\varphi_t = \rho \cdot \varphi_{t-1} + \psi_t$$

$$\psi \sim \text{Gaussian}(0, \sigma^2)$$

Hidden Markov Model

HMMs for animal movement were used to examine if the sound exposure altered the time spent in various behavioural states. The R package MomenuHMM (McClintock and Michelot, 2018) was used to fit HMMs to the horizontal step length and turning angle of the fish. We fitted HMM null models with 1, 2 and 3 states to all individual fish and compared the AIC scores to determine the number of behavioural states that were best supported by the models. We do not report the fit of models with more than 3 states because the AIC tended to favour models with (much) higher number of states, whereas this is biologically less interpretable (cf. Pohle et al., 2017). Combinations of 'Tide height', 'Sun elevation', and 'Treatment period' (Before, During & After) were applied as state transition probability covariates during selection of the best fitting model. Comparison of AIC scores, broadly across all individuals, indicated that the inclusion of all covariates resulted in the best fitting models (Appendix 1, table 3).

When running the models, the resulting state transition probability p-values for the covariate 'Treatment period' appeared to over-attribute natural variation in swimming behaviour, commonly observed in the baseline period, to the effect of During and After in 'Treatment period'. This is likely due to the During and After period being too short, relative to the long baseline, to average out biases resulting from natural fluctuations in swimming behaviour, especially those related to tide (which we synchronized with the starting times of the exposure periods to guarantee sufficient water levels to allow propagation of relatively low frequencies). As a result, state transition coefficient p-values for 'Treatment period' were not used for hypothesis testing.

Instead, HMMs were used to simulate null hypothesis distributions for time spent in each behavioural state. Per each individual, the fitted HMMs were used

to simulate 10,000 realizations of the expected behavioural state during each trial in the absence of the sound exposure while preserving the remaining observed covariate values ('Tide height' and 'Sun elevation'). For each hour, the observed proportion of time in each behavioural state was compared to the null hypothesis distribution. If the deviation of the observed data from the null hypothesis was larger during or after the treatment period, we interpreted this as an effect of the sound treatment.

Results

All fish showed variable swimming patterns in time, but typically used the whole space available, horizontally and vertically. We found no strong overall pattern of
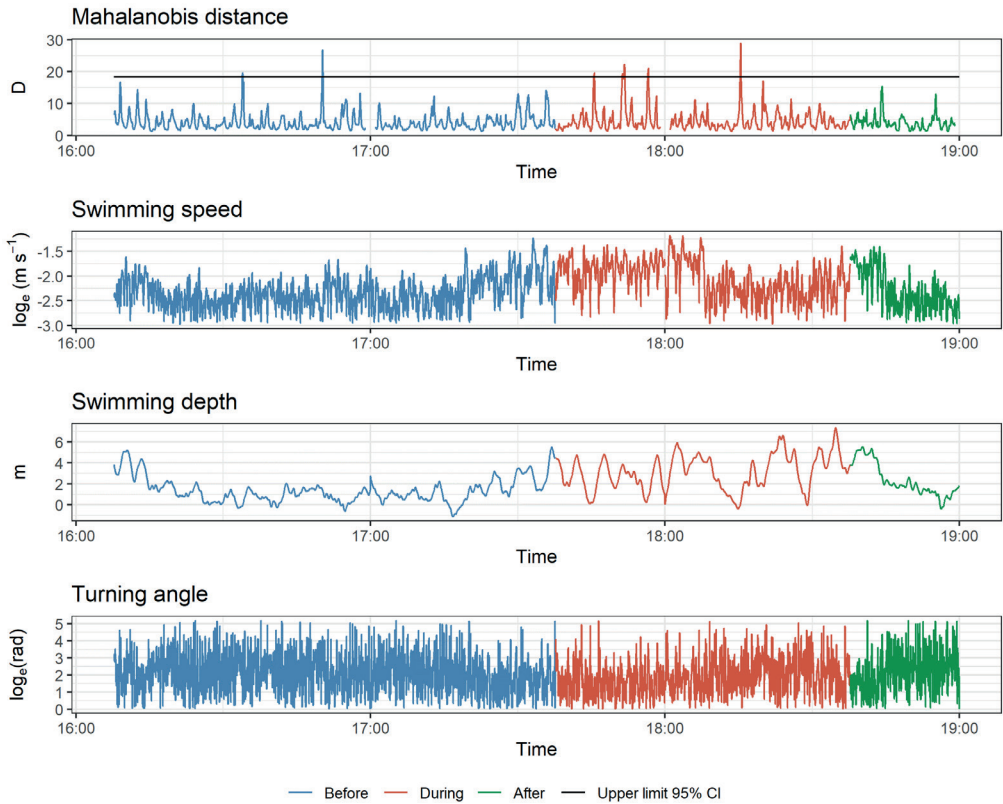

Fig. 4: Top panel shows the Mahalanobis distance over the course of 3 h of a single fish, with the median and upper limit of the 95th percentile of the Mahalanobis distances during the Before period, resp. pink and red line. The Mahalanobis distance at the start of the sound exposure does not exceed the 95th percentile, so the current fish did not immediately respond to the sound treatment. The panels below depict the swimming speed ($\log_e$(m s^{-1})), swimming depth (m, distance from the bottom of the grid) and turning angle ($\log_e$(radians)) that were used to construct the Mahalanobis distance (D).

change during the exposure, compared to the baseline period. The randomization test showed that only one individual exhibited a response magnitude that exceeded the 95th percentile of randomized responses (Appendix 1, table 1). This result is within the expected type 1 error rate for this test, thus there is no evidence for an immediate behavioural response at the onset of the sound exposure.

The results from the individual analyses were also reflected by our tests for significant changes at group level. With respect to the non-linear mixed effects model, no significant response was observed at the onset of the sound exposure (figure 5). In addition, there was no consistent significant change in swimming behaviour during the entire treatment period (Appendix 1, figure 1).

Using the HMMs, we identified support for three behavioural states in all fish based on AIC (Appendix 1, table 2): 1) high swimming speed and low turning angle (which we labelled 'transit'); 2) moderate speed and moderate turning angle ('locally active'); and 3) low speed and high turning angle ('inactive') (figure 6). Note that we tried to select relatively neutral labels, to not infer more interpretation than we can base on the kinetic description. When comparing the time spent in the behavioural states and mean step lengths from the observed data with the time spent in the states from the simulated data, there is a trend for larger deviations from the simulated baseline behaviour in the period during and after sound exposure (figure 7). Several individuals tended to spend
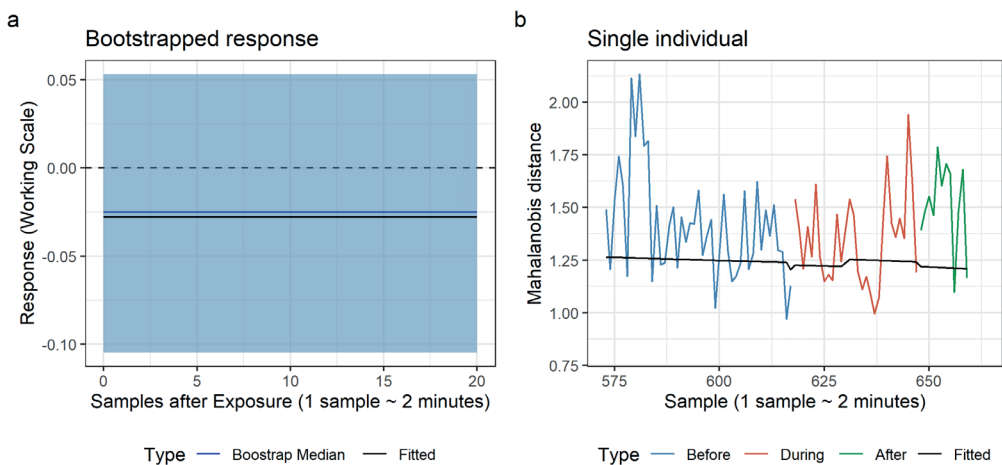

Fig. 5: (a) Bootstrapped response to exposure on the working scale ($\log(\mu)$, see formula I) of the model. The shaded area indicates the bootstrapped 95th percentile interval of the response. The response magnitude does not significantly differ from 0, indicating no immediate response to exposure onset. (b) Observed and fitted data of a single fish, the last 3 h of the trial.

relatively more time in the transit state and less time in locally active and inactive during and after the playback, which is supported by the higher step lengths. Due to experimental design limitations, we could not test the significance of these trends.
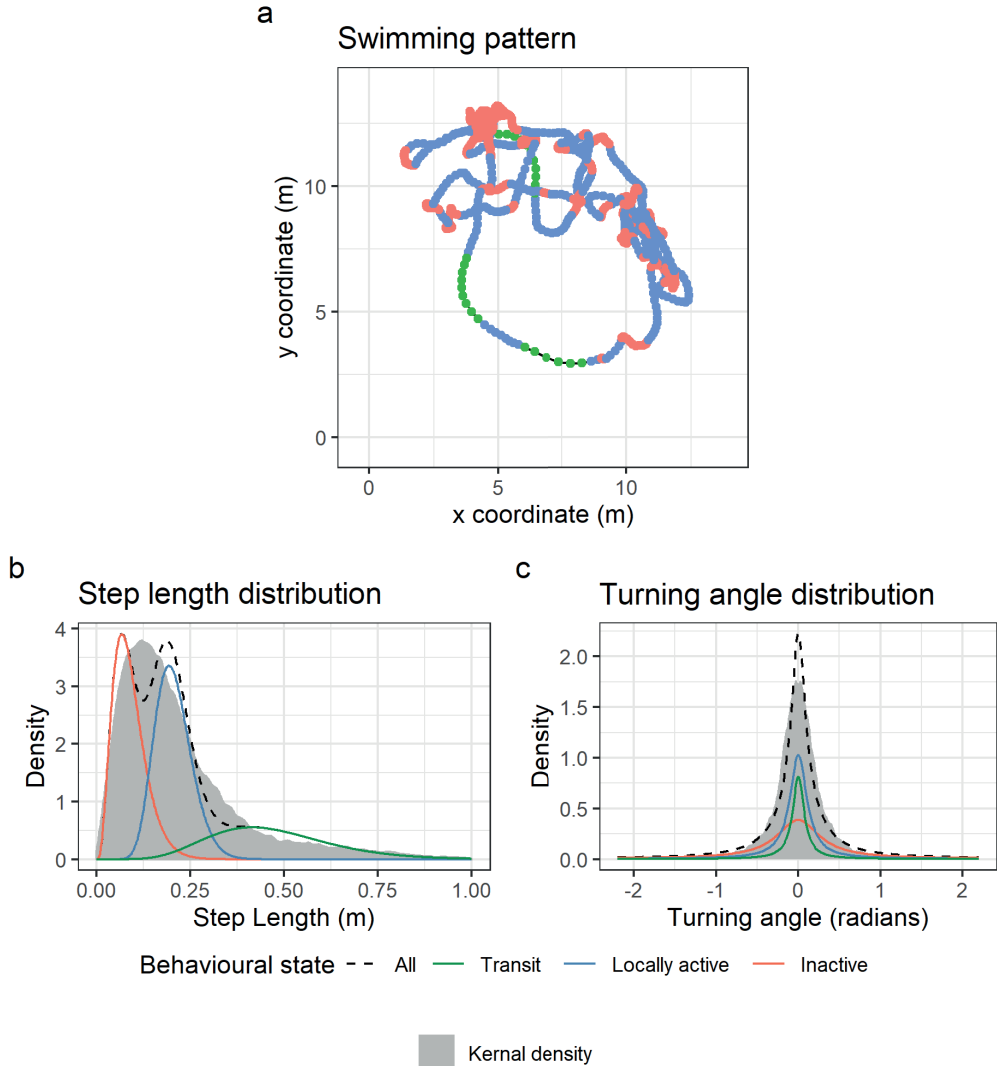

Fig. 6: (a) Top view swimming patterns (26 min) of a single individual with the behavioural state indicated by colour. (b & c) The step length (swimming speed) and turning angle distribution for each behavioural state of the same individual for the entire trial. The lines show the fitted distributions while the grey shaded area shows the kernel density plot of the observed distribution.
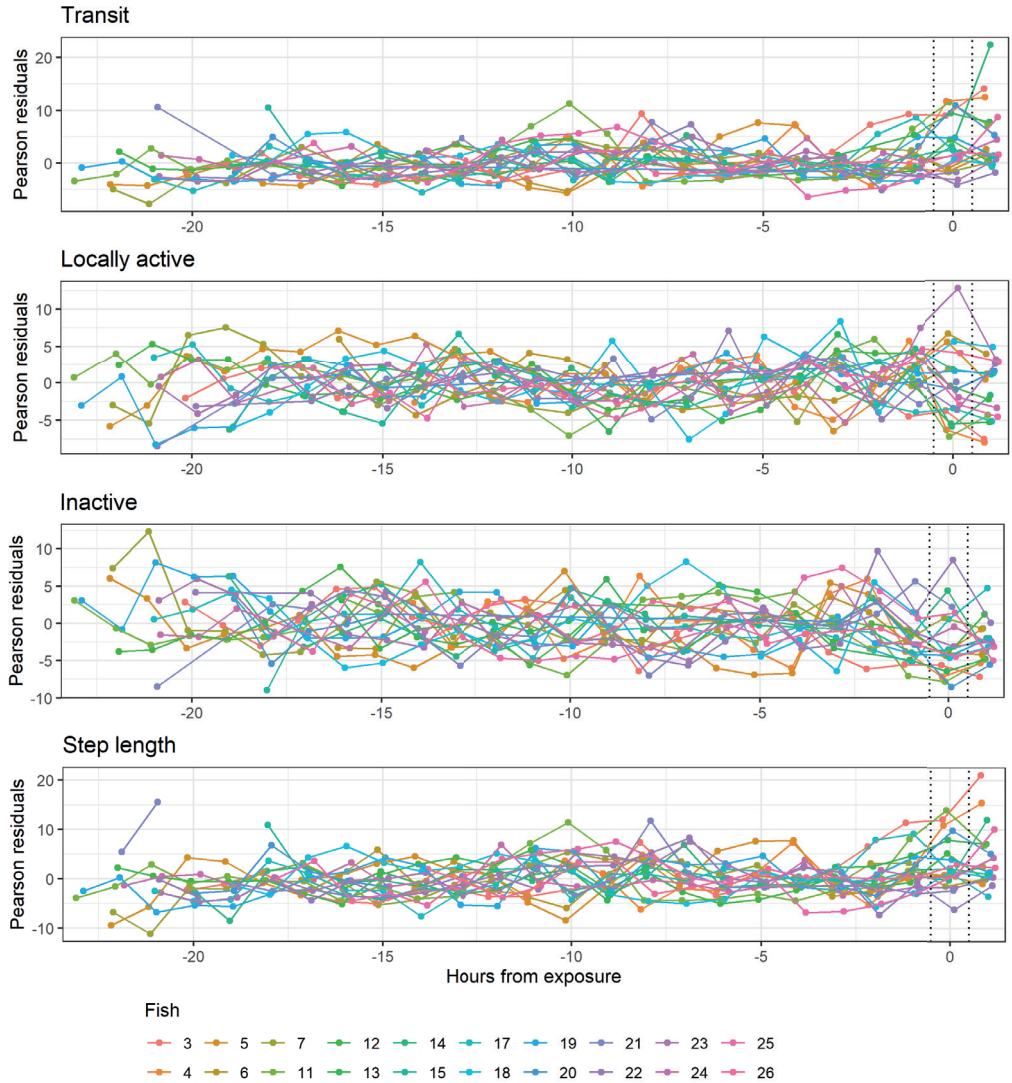
Fig. 7: For each of the three behavioural states and the step length distribution; the amount of standard deviations (Pearson residuals) of the observed time spent and step length from the mean time spent and step length of the simulated data (for absolute data, see Appendix I, figure 2). The vertical dashed lines indicate the hour of sound exposure. The colours indicate the different individuals, hourly datapoints are lacking if the individual had less than 25% of the expected positions that hour.

Discussion

In the current study, we experimentally exposed individual Atlantic cod in a net pen to the playback of seismic airgun sound pulses and examined changes in

swimming patterns of the fish. Our results demonstrate that only one individual altered its swimming pattern significantly at the onset of the sound and that altogether individual cod did not change their swimming patterns, neither immediately at the onset nor over the whole period of the sound exposure. However, several individuals seemed to change their distribution of time spent in three behavioural states during the 1 h exposure, compared to the baseline. The time spent in behavioural states may be translated to energy expenditure and in future experiments possibly also integrated with food intake, and thereby be used as input for Population Consequences of (Acoustic) Disturbance (PCoD or PCAD) models.

Short-term vs. long-term behavioural response

We did not find an immediate change in swimming patterns upon the start of the sound exposure, neither when using a short time window right before the sound exposure as baseline (Randomization test; individual analysis), nor with the entire trial as baseline (Non-linear mixed model; group analysis). In accordance with the current results, two other studies showed that a single group of captive cod did not exhibit an immediate short-term response to pure tones (cod of 42-46 cm, Kastelein et al., 2008) or to seismic airgun exposure (cod of 38-73 cm, Davidsen et al., 2019). Despite the lack of immediate, short-term behavioural responses in cod, several studies are indicative of more long-term behavioural changes in cod during sound exposures (Davidsen et al., 2019; Engås et al., 1996; Løkkeborg and Soldai, 1993).

We estimated the time spent in various behavioural states for all individuals using HMMs for animal movement. Several individuals seemed to have changed their time spent in various behavioural states due to the sound exposure; several spent more time transiting and less time being locally active or inactive. A change in time budget expenditure does not necessarily imply a sudden change at the onset of the sound, but can also mean staying in a particular state for longer or switching back to a state more quickly. It has been shown in zebrafish (*Danio rerio*), for example, that an immediate response does not necessarily correlate with a prolonged response (Shafiei Sabet et al., 2016). Nevertheless, most behavioural response studies on the effects of sound focus on immediate changes at the onset of the sound exposure, whereas long-term changes in activity patterns may be more relevant for exploring consequences at population level (Hubert et al., 2020a).

Individual energy budget

The various behavioural states and accompanying swimming speed distributions

may be indicative of different levels of energy expenditure and food intake (Lundquist et al., 2012; Williams et al., 2006), which in turn can be linked to growth, survival and reproductive output using PCoD/PCAD models (Pirotta et al., 2018; Soudijn et al., 2020). We labelled the states in the current study as 'transit', 'locally active' and 'inactive', representing respectively swimming patterns of high speed and low turning angle, moderate speed and moderate turning angle, and low speed and high turning angle. Swim tunnel experiments have shown that fish swimming at higher speed use more oxygen, which can be used as a proxy for energy use (Tudorache et al., 2008). For fish in swim tunnels that have been tagged with accelerometers, the vector of the dynamic body acceleration (VeDBA) could also be linked to oxygen use (Metcalfe et al., 2016; Wright et al., 2014). Such swim tunnel experiments with cod are necessary to translate our swimming speed data to energy use. It should be mentioned that additional energy expenditure due to potentially elevated stress levels is not covered by the current approach and requires additional experiments (Rabasa and Dickson, 2016; Sierra-Flores et al., 2015). The importance of the quantification of energy expenditure and intake in all behavioural states to quantify the impact of anthropogenic disturbance has been addressed in several marine mammal studies (Christiansen et al., 2010; Lundquist et al., 2012). Williams et al. (2006) actually quantified the consequence of boat traffic on killer wales (*Orcinus orca*) and estimated that the change in activity budget led to an increase in energy expenditure of 3-4% and a decrease in energy intake of 18% (based on reduced foraging time).

Foraging behaviour could serve as a proxy for energy intake. 18 out of 20 fish in the current experiment had food in their stomachs at the end of their trials, indicating that the majority of the fish exhibited foraging behaviour in the net pen. A basin experiment on Atlantic cod described foraging behaviour as relatively slow swimming close to the bottom and turning frequently (Hubert et al., 2020a), which was in line with reported behaviour of free ranging Atlantic cod (Rose, 2019). This reported foraging behaviour appears to resemble the swimming patterns from the locally active- and inactive-state most, so it may be that these states also included foraging behaviour. However, in the current study we cannot discriminate between foraging behaviour and other locally active and inactive behaviour. Such insight requires additional data from accelerometers and/or gyroscopes, validated by experiments with parallel video-tracking (Kawabata et al., 2014). Explicit confirmation of associations between foraging behaviour and behavioural states, enriched with accelerometer/gyroscope data, would likely yield critical entry data for PCoD/PCAD models. The actual energy intake for free ranging cod would also require data on success rate of foraging in the wild and about nutritional value of their prey items. Such data may come

from video experiments with captive fish (e.g. Shafiei Sabet et al., 2015) and stomach content data from free ranging fish (e.g. Payne et al., 2014).

Experimental design with respect to HMMs

We did not provide state transition probability p-values for the covariate 'Treatment period', whereas this is typically provided from analyses using HMMs (e.g. DeRuiter et al., 2017). In the current analysis, the state transition probabilities appeared to over-attribute natural variation in swimming behaviour to the effect of During and After in 'Treatment period', likely due to the During and After periods being relatively short (resp. 1 and 0.5 h) compared to the Before period (~ 20 h). So, for future experiments it should be considered to use longer and/or multiple exposures to reduce biases resulting from natural fluctuations in swimming behaviour. Despite the lack of reliable state transition probability p-values, we gained insight into the effect of the sound exposure by using the HMMs to simulate null hypothesis distributions for time spent in each behavioural state and to compare this to the observed time spent. However, we should be cautious while interpreting these results. For several individuals, the deviation of the observed from the simulated time spent in particular behavioural states during the sound exposure, seemed already initiated in the hour before the exposure. This may be due to the timing of the sound exposures, always ending or starting at absolute high tide to allow relatively low frequencies to propagate in the shallow cove. We aimed to prevent a bias from the tide by making sure that the baseline was long enough to contain one other high tide besides the high tide of the exposure (tidal period is ~ 12:25 hh:mm, baseline period was ~ 20 h) and by using the tide as covariate in the analysis. However, it may be that the behaviour in the first and second high tide was different (for some individuals) because of an interaction with acclimation to the pen over time. Such a bias can be avoided by longer trials and by exposing fish throughout the tidal period at a deeper test site.

Captive vs. free ranging fish

In studies on captive fish, the experimental control and data resolution is potentially relatively high (Slabbekoorn, 2016). This also enabled us to explore novel methods of data processing and analyses and may aid in the interpretation of lower resolution data of free ranging fish. It should be clear that it was not the goal of the current study to determine absolute response levels of cod to seismic surveys, because of the limited validity of behavioural responses and limited acoustic realism of the scaled sound exposure. The behaviour of the wild-caught individuals in the current study is likely not directly comparable to free ranging individuals (cf. Wright et al., 2007), for example, because they were not able to

swim away from the sound source. The location of the net pen was also relatively shallow, whereas cod typically live in deeper water, and only migrate closer to shore for spawning (Reubens et al., 2013; Righton et al., 2010). Furthermore, the acoustic stimulus differed from actual seismic survey sound at sea because the speaker did not produce low-frequency sound, was not moving, and both the soundscape and propagation in shallow water differ from deeper water, where cod are more likely to be exposed to seismic surveys.

Ultimately, data on the effects of sound on fish should be collected in the field with free ranging animals and actual anthropogenic sound sources (Popper and Hawkins, 2019). However, fish are difficult to observe in the field, they typically do not surface such as marine mammals and most are too small to carry the same sophisticated loggers as marine mammals. Free ranging fish can be observed with baited camera's, echosounders/Didsons, telemetry, and by diving researchers, but through all methods it is challenging to track individuals over an extended period of time (Bruce et al., 2018), to collect high resolution data, and to not affect fish behaviour by the observation method (Bracciali et al., 2012). Since both indoor and outdoor studies provide us with opportunities and limitations, it is good to be aware of them and to use a complementary approach to gain insight into the effects of sound on fish (Slabbekoorn, 2016).

Conclusions

In the current study, Atlantic cod seemed unresponsive to sound as they did not change their swimming patterns immediately at the onset of the sound exposure. However, several individuals changed their time spent in several behavioural states during the 1 h sound exposure. Several individuals spent more time transiting and less time being locally active or inactive, this may be indicative of changes in energy budgets and may ultimately affect their health and vital rates (growth, survival, and reproduction). Such data are suitable input for PCoD/PCAD models, but further validation of behavioural states and their link to energy budgets and health is needed. Nevertheless, we think that the current approach of data collection and processing is promising and could be applied in future studies on captive and free ranging fish. In future captive studies, video data combined with spatial data may increase insight into food intake and thereby aid in biological interpretation and the translation to bio-energetics of behavioural states.

Ethical statement

This experiment was conducted in accordance with the Dutch Experiments

on Animals Act and approved by the Dutch Central Commission Animal Experiments (CCD) under no. AVD1060020171085.

Supplementary information

Supplementary information associated with this article is available from the publication DOI:10.1016/j.marpolbul.2020.111680.

Data accessibility

All data used for the analyses reported in this article is available from the Zenodo Repository, DOI:10.5281/zenodo.4013336.

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References

Ainslie, M. A., Heaney, K. D. and Macgillivray, A. O. (2019). Guest Editorial Special Issue on Verification and Validation of Air Gun Source Signature and Sound Propagation Models. IEEE J. Ocean. Eng. 44, 551–559.

Antunes, R., Kvadsheim, P. H., Lam, F. P. A., Tyack, P. L., Thomas, L., Wensveen, P. J. and Miller, P. J. O. (2014). High thresholds for avoidance of sonar by free-ranging long-finned pilot whales (*Globicephala melas*). Mar. Pollut. Bull. 83, 165–180.

Baktoft, H., Gjelland, K. Ø., Økland, F. and Thygesen, U. H. (2017). Positioning of aquatic animals based on time-of-arrival and random walk models using YAPS (Yet Another Positioning Solver). Sci. Rep. 7, 1–10.

Becker, A., Whitfield, A. K., Cowley, P. D., Järnegren, J. and Næsje, T. F. (2013). Does boat traffic cause displacement of fish in estuaries? Mar. Pollut. Bull. 75, 168–73.

Boudreau, M. L., Scrosati, R. A. and Wong, M. C. (2018). Predator (*Carcinus maenas*) nonconsumptive limitation of prey (*Nucella lapillus*) feeding depends on prey density and predator cue type. J. Ethol. 36, 259–264.

Bracciali, C., Campobello, D., Giacoma, C. and Sarà, G. (2012). Effects of nautical traffic and noise on foraging patterns of mediterranean Damselfish (*Chromis chromis*).

PLoS One 7,.

Bruce, B., Bradford, R., Foster, S., Lee, K., Lansdell, M., Cooper, S. and Przeslawski, R. (2018). Quantifying fish behaviour and commercial catch rates in relation to a marine seismic survey. Mar. Environ. Res. 140, 18–30.

Carroll, A. G., Przeslawski, R., Duncan, A., Gunning, M. and Bruce, B. (2016). A critical review of the potential impacts of marine seismic surveys on fish & invertebrates. Mar. Pollut. Bull. 114, 9–24.

Chapman, C. J. and Hawkins, A. D. (1973). A field study of hearing in the cod, *Gadus morhua* L. J. Comp. Physiol. 85, 147–167.

Christiansen, F., Lusseau, D., Stensland, E. and Berggren, P. (2010). Effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. Endagered Species Res. 11, 91–99.

Davidsen, J. G., Dong, H., Linné, M., Andersson, M. H., Piper, A., Prystay, T. S., Hvam, E. B., Thorstad, E. B., Whoriskey, F., Cooke, S. J., et al. (2019). Effects of sound exposure from a seismic airgun on heart rate, acceleration and depth use in free-swimming Atlantic cod and saithe. Conserv. Physiol. 7, 1–19.

DeRuiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, W. M. X., Sadykova, D., Falcone, E. A., Friedlaender, A. S., Joseph, J. E., Moretti, D., Schorr, G. S., et al. (2013). First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. Biol. Lett. 9, 0–4.

DeRuiter, S. L., Langrock, R., Skirbutas, T., Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S. and Southall, B. L. (2017). A multivariate mixed hidden Markov model for blue whale behaviour and responses to sound exposure. Ann. Appl. Stat. 11, 362–392.

Engås, A., Løkkeborg, S., Ona, E. and Soldal, A. V. (1996). Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). Can. J. Fish. Aquat. Sci. 53, 2238–2249.

Gisiner, R. C. (2016). Sound and Marine Seismic Surveys. Acoust. Today 12, 10–18.

Halvorsen, M. B., Casper, B. M., Matthews, F., Carlson, T. J. and Popper, A. N. (2012). Effects of exposure to pile-driving sounds on the lake sturgeon, Nile tilapia and hogchoker. Proc. R. Soc. B Biol. Sci. 279, 4705–14.

Hammar, L., Wikström, A. and Molander, S. (2014). Assessing ecological risks of offshore wind power on Kattegat cod. Renew. Energy 66, 414–424.

Harding, H. R., Gordon, T. A. C., Hsuan, R. E., Mackaness, A. C. E., Radford, A. N. and Simpson, S. D. (2018). Fish in habitats with higher motorboat disturbance show reduced sensitivity to motorboat noise. Biol. Lett. 14, 20180441.

Hubert, J., Neo, Y. Y., Campbell, J. A. and Slabbekoorn, H. (2016). Particle motion and pressure soundscape in outdoor vs indoor set-up. In Proceedings of Meetings on Acoustics, p. 070007.

Hubert, J., Wille, D. A. and Slabbekoorn, H. (2020a). Exploring effects of sound on the time budget of fishes: An experimental approach with captive cod. In Proceedings of Meetings on Acoustics, p. 010012.

Hubert, J., Neo, Y. Y., Winter, H. V. and Slabbekoorn, H. (2020b). The role of ambient sound levels, signal-to-noise ratio, and stimulus pulse rate on behavioural disturbance

of seabass in a net pen. Behav. Processes 170, 103992.

Johnson, D. S., London, J. M., Lea, M. A. and Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. Ecology 89, 1208–1215.

Kastelein, R. A., Heul, S. Van Der, Verboom, W. C., Jennings, N., Veen, J. Van Der and de Haan, D. (2008). Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz. Mar. Environ. Res. 65, 369–77.

Kawabata, Y., Noda, T., Nakashima, Y., Nanami, A., Sato, T., Takebe, T., Mitamura, H., Arai, N., Yamaguchi, T. and Soyano, K. (2014). Use of a gyroscope/accelerometer data logger to identify alternative feeding behaviours in fish. J. Exp. Biol. 217, 3204–3208.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H. and Bell, B. M. (2016). TMB: Automatic Differentiation and Laplace Approximation. J. Stat. Softw. 70,.

Kurlansky, M. (1999). Cod: A Biography Of The Fish That Changed The World. Toronto: A.A. Knopf Canada.

Landrø, M. and Amundsen, L. (2018). Introduction to Exploration Geophysics with Recent Advances. Bivrost.

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D. and Morales, J. M. (2012). Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology 93, 2336–2342.

Leeuwen, A. Van, Huss, M., Gårdmark, A., Casini, M., Vitale, F., Hjelm, J., Persson, L. and Roos, A. M. De (2013). Predators with Multiple Ontogenetic Niche Shifts Have Limited Potential for Population Growth and Top-Down. Am. Nat. 182, 53–66.

Lima, S. L. and Dill, L. M. (1989). Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Løkkeborg, S. and Soldai, A. V. (1993). The influence of seismic exploration with airguns on cod (*Gadus morhua*) behaviour and catch rates. ICES mar. Sci. Symp 196, 62–67.

Lundquist, D., Gemmell, N. J. and Würsig, B. (2012). Behavioural Responses of Dusky Dolphin Groups (*Lagenorhynchus obscurus*) to Tour Vessels off Kaikoura, New Zealand. PLoS One 7, e41969.

Magnhagen, C., Johansson, K. and Sigray, P. (2017). Effects of motorboat noise on foraging behaviour in Eurasian perch and roach: a field experiment. Mar. Ecol. Prog. Ser. 564, 115–125.

McCauley, R. D., Fewtrell, J., Duncan, A. J., Jenner, C., Jenner, M., Penrose, J. D., Prince, R. I. T., Adhitya, A., Murdoch, J. and McCabe, K. (2000). Marine Seismic Surveys – A Study of Enviromental Implications. APPEA J. 40, 692–708.

McClintock, B. T. and Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. Methods Ecol. Evol. 9, 1518–1530.

McLaughlin, K. E. and Kunc, H. P. (2015). Changes in the acoustic environment alter the foraging and sheltering behaviour of the cichlid *Amititlania nigrofasciata*. Behav. Processes 116, 75–79.

Metcalfe, J. D., Wright, S., Tudorache, C. and Wilson, R. P. (2016). Recent advances in telemetry for estimating the energy metabolism of wild fishes. J. Fish Biol. 88, 284–297.

Nams, V. O. (2013). Sampling Animal Movement Paths Causes Turn Autocorrelation.

Acta Biotheor. 61, 269–284.

Nedelec, S. L., Simpson, S. D., Morley, E. L., Nedelec, B. and Radford, A. N. (2015). Impacts of regular and random noise on the behaviour, growth and development of larval Atlantic cod (*Gadus morhua*). Proc. R. Soc. B Biol. Sci. 282, 1–7.

Nedelec, S. L., Mills, S. C., Lecchini, D., Nedelec, B., Simpson, S. D. and Radford, A. N. (2016). Repeated exposure to noise increases tolerance in a coral reef fish. Environ. Pollut. 216, 428–436.

Neo, Y. Y., Hubert, J., Bolle, L., Winter, H. V., Ten Cate, C. and Slabbekoorn, H. (2016). Sound exposure changes European seabass behaviour in a large outdoor floating pen: Effects of temporal structure and a ramp-up procedure. Environ. Pollut. 214, 26–34.

Neo, Y. Y., Hubert, J., Bolle, L. J., Winter, H. V. and Slabbekoorn, H. (2018). European seabass respond more strongly to noise exposure at night and habituate over repeated trials of sound exposure. Environ. Pollut. 239, 367–374.

New, L. F., Clark, J. S., Costa, D. P., Fleishman, E., Hindell, M. A., Klanjšček, T., Lusseau, D., Kraus, S., McMahon, C. R., Robinson, P. W., et al. (2014). Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. Mar. Ecol. Prog. Ser. 496, 99–108.

Payne, N. L., van der Meulen, D. E., Suthers, I. M., Gray, C. A. and Taylor, M. D. (2014). Foraging intensity of wild mulloway *Argyrosomus japonicus* decreases with increasing anthropogenic disturbance. Mar. Biol. 162, 539–546.

Pirotta, E., Booth, C. G., Costa, D. P., Fleishman, E., Kraus, S. D., Lusseau, D., Moretti, D., New, L. F., Schick, R. S., Schwarz, L. K., et al. (2018). Understanding the population consequences of disturbance. Ecol. Evol. 8, 9934–9946.

Pohle, J., Langrock, R., van Beest, F. M. and Schmidt, N. M. (2017). Selecting the Number of States in Hidden Markov Models: Pragmatic Solutions Illustrated Using Animal Movement. J. Agric. Biol. Environ. Stat. 22, 270–293.

Popper, A. N. and Fay, R. R. (2011). Rethinking sound detection by fishes. Hear. Res. 273, 25–36.

Popper, A. N. and Hawkins, A. D. (2019). An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. J. fish 94, 692–713.

Postlethwaite, C. M. and Dennis, T. E. (2013). Effects of Temporal Resolution on an Inferential Model of Animal Movement. PLoS One 8, 1–11.

Purser, J. and Radford, A. N. (2011). Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). PLoS One 6, e17478.

Rabasa, C. and Dickson, S. L. (2016). Impact of stress on metabolism and energy balance. Curr. Opin. Behav. Sci. 9, 71–77.

Radford, C. A., Montgomery, J. C., Caiger, P. and Higgs, D. M. (2012). Pressure and particle motion detection thresholds in fish: a re-examination of salient auditory cues in teleosts. J. Exp. Biol. 215, 3429–35.

Reichmuth, C., Ghoul, A., Sills, J. M., Rouse, A. and Southall, B. L. (2016). Low-frequency temporary threshold shift not observed in spotted or ringed seals exposed to single air gun impulses. J. Acoust. Soc. Am. 140, 2646–2658.

Reubens, J. T., Braeckman, U., Vanaverbeke, J., Van Colen, C., Degraer, S. and Vincx, M. (2013). Aggregation at windmill artificial reefs: CPUE of Atlantic cod (*Gadus morhua*) and pouting (*Trisopterus luscus*) at different habitats in the Belgian part of the North Sea. Fish. Res. 139, 28–34.

Righton, D. a., Andersen, K. H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., Michalsen, K., Hinrichsen, H. H., Bendall, V., Neuenfeldt, S., et al. (2010). Thermal niche of Atlantic cod *Gadus morhua*: Limits, tolerance and optima. Mar. Ecol. Prog. Ser. 420, 1–13.

Rose, G. A. (2019). Atlantic Cod: Bio-Ecology of the Fish. John Wiley and Sons Ltd.

Sand, O. and Karlsen, H. E. (1986). Detection of infrasound by the Atlantic cod. J. Exp. Biol. 125, 197–204.

Sarà, G., Dean, J. M., Amato, D. D., Buscaino, G., Oliveri, A., Genovese, S., Ferro, S., Buffa, G., Martire, M. Lo and Mazzola, S. (2007). Effect of boat noise on the behaviour of bluefin tuna *Thunnus thynnus* in the Mediterranean Sea. Mar. Ecol. Prog. Ser. 331, 243–253.

Sertlek, H. Ö., Slabbekoorn, H., ten Cate, C. and Ainslie, M. A. (2019). Source specific sound mapping: Spatial, temporal and spectral distribution of sound in the Dutch North Sea. Environ. Pollut. 247, 1143–1157.

Shafiei Sabet, S., Neo, Y. Y. and Slabbekoorn, H. (2015). The effect of temporal variation in sound exposure on swimming and foraging behaviour of captive zebrafish. Anim. Behav. 107, 49–60.

Shafiei Sabet, S., Wesdorp, K., Campbell, J., Snelderwaard, P. and Slabbekoorn, H. (2016). Behavioural responses to sound exposure in captivity by two fish species with different hearing ability. Anim. Behav. 116, 1–11.

Sierra-Flores, R., Atack, T., Migaud, H. and Davie, A. (2015). Stress response to anthropogenic noise in Atlantic cod *Gadus morhua* L. Aquac. Eng. 67, 67–76.

Sivle, L. D., Kvadsheim, P. H. and Ainslie, M. A. (2015). Potential for population-level disturbance by active sonar in herring. ICES J. Mar. Sci. 72, 558–567.

Slabbekoorn, H. (2016). Aiming for Progress in Understanding Underwater Noise Impact on Fish: Complementary Need for Indoor and Outdoor Studies. In The Effects of Noise on Aquatic Life II (ed. Popper, N. A.) and Hawkins, A.), pp. 1057–1065. New York, NY: Springer New York.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C. and Popper, A. N. (2010). A noisy spring: The impact of globally rising underwater sound levels on fish. Trends Ecol. Evol. 25, 419–427.

Slabbekoorn, H., Dalen, J., de Haan, D., Winter, H. V., Radford, C., Ainslie, M. A., Heaney, K. D., van Kooten, T., Thomas, L. and Harwood, J. (2019). Population-level consequences of seismic surveys on fishes: An interdisciplinary challenge. Fish Fish. 20, 653–685.

Slotte, A., Hansen, K., Dalen, J. and Ona, E. (2004). Acoustic mapping of pelagic fish distribution and abundance in relation to a seismic shooting area off the Norwegian west coast. Fish. Res. 67, 143–150.

Soudijn, F. H., van Kooten, T., Slabbekoorn, H. and de Roos, A. M. (2020). Population-level effects of acoustic disturbance in Atlantic cod: a size-structured analysis based on energy budgets. Proc. R. Soc. B Biol. Sci. 287, 20200490.

Tudorache, C., Viaene, P., Blust, R., Vereecken, H. and De Boeck, G. (2008). A comparison of swimming capacity and energy use in seven European freshwater fish species. Ecol. Freshw. Fish 17, 284–291.

Voellmy, I. K., Purser, J., Flynn, D., Kennedy, P., Simpson, S. D. and Radford, A. N. (2014). Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms. Anim. Behav. 89, 191–198.

Wardle, C., Carter, T., Urquhart, G., Johnstone, A. D., Ziolkowski, A., Hampson, G. and Mackie, D. (2001). Effects of seismic air guns on marine fish. Cont. Shelf Res. 21, 1005–1027.

Williams, R., Lusseau, D. and Hammond, P. S. (2006). Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biol. Conserv. 133, 301–311.

Williams, R., Wright, A. J., Ashe, E., Blight, L. K., Bruintjes, R., Canessa, R., Clark, C. W., Cullis-Suzuki, S., Dakin, D. T., Erbe, C., et al. (2015). Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management. Ocean Coast. Manag. 115, 17–24.

Wright, A. J., Soto, N. A., Baldwin, A. L., Bateson, M., Beale, C. M., Clark, C., Deak, T., Edwards, E. F., Fernández, A., Godinho, A., et al. (2007). Anthropogenic Noise as a Stressor in Animals: A Multidisciplinary Perspective. Int. J. Comp. Psychol. 20, 250–273.

Wright, S., Metcalfe, J., Hetherington, S. and Wilson, R. (2014). Estimating activity-specific energy expenditure in a teleost fish, using accelerometer loggers. Mar. Ecol. Prog. Ser. 496, 19–32.

Wysocki, L. E., Dittami, J. P. and Ladich, F. (2006). Ship noise and cortisol secretion in European freshwater fishes. Biol. Conserv. 128, 501–508.