

The reaction of a captive herring school to playbacks of a noise-reduced and a conventional research vessel

Nils Olav Handegard, Alex De Robertis, Guillaume Rieucan, Kevin Boswell, and Gavin J. Macaulay

Abstract: Fish avoidance of vessels can bias fisheries-independent surveys. To understand these biases, recordings of underwater radiated vessel noise from a noise-reduced and a conventional research vessel were played back at the same sound pressure levels (SPL) as experienced in situ to Atlantic herring (*Clupea harengus*) in a net pen at two different densities. The noise-reduced vessel recording was also scaled to the same SPL as the conventional vessel to test if characteristics other than SPL affected the reactions. Overall, only weak reactions were observed, but reactions were stronger in the low-density school, in the middle of the pen, and for the scaled silent vessel compared with the conventional vessel. These observations may be attributable to the lack of low frequencies (<50 Hz) in the playbacks, differential motivation for reaction driven by fish density, higher low-frequency noise in the middle of the pen (but lower overall SPL), and characteristics other than SPL. These results call into question the use of SPL as a proxy for fish reaction to vessels as used in standards for construction of research vessels.

Résumé : Les réactions d'évitement de poissons face à des navires peuvent biaiser les inventaires indépendants de pêche. Afin d'évaluer l'étendue de tels biais, une expérience de repasses de séquences de sons a été effectuée sur des bancs de harengs atlantique (*Clupea harengus*), de densités différentes, placés dans des enclos en filet. Les séquences sonores utilisées comprenaient des enregistrements d'un navire conventionnel et d'un navire à niveaux sonores réduits, « navire silencieux », toutes présentées aux mêmes niveaux de pression acoustique (NPA) que ceux auxquels les harengs sont généralement soumis in situ. Le navire à niveaux sonores réduits a également été rehaussé aux mêmes NPA que ceux produits par le navire conventionnel afin de déterminer si des facteurs autres que les NPA peuvent affecter les réactions d'évitement des harengs. En général, seules de faibles réactions aux séquences sonores ont été observées. Cependant, de plus fortes réactions ont été observées pour le banc de faible densité comparées au banc de forte densité, ainsi que de plus fortes réactions lors de repasses de séquences sonores rehaussées du navire silencieux comparées au navire conventionnel. De telles observations peuvent être expliquées soit par l'absence de basses fréquences (<50 Hz) dans les repasses sonores, soit par différents niveaux de motivation à répondre aux repasses en lien avec les différences de densité entre les bancs, soit par l'effet de basses fréquences acoustiques plus élevées au milieu de l'enclos en filet (malgré de plus faibles NPA), ou soit par des facteurs autres que les NPA. Par conséquent, les résultats obtenus lors de notre expérience questionnent la justesse de l'utilisation des NPA comme un indice de réactions de poissons face à des navires; comme il est pratique courante lors de la construction de navires de recherche.

Introduction

It has been documented that fish avoid research vessels, which can cause bias in fisheries-independent acoustic-trawl surveys of fish stock biomass (Mitson 1995; De Robertis and Handegard 2013). These surveys, which are used to support fisheries management, employ calibrated echo sounders in combination with trawl samples to estimate fish abundance (Simmonds and MacLennan 2005). The total uncertainty from these surveys can be decomposed into several factors (Løland et al. 2007). One is vessel avoidance, where fish either are displaced out of the echo sounder beam or change their tilt angle distribution leading to an altered acoustic reflectivity (Nakken and Olsen 1977). Vessel-induced behavioural changes were raised as a potentially large source of bias in fisheries surveys (Olsen et al. 1983) and were later established as a major source of uncertainty in acoustic-trawl surveys (Vabø et al. 2002; Hjellvik et al. 2008). However, the phenomenon varies among species and areas (De Robertis and Handegard 2013), and there is evidence for no avoidance responses in some cases (Fernandes et al. 2000; De Robertis and Handegard 2013).

Fishes have sensitive hearing at the frequencies produced by vessels (Mitson 1995; Slabbekoorn et al. 2010), and it was assumed that underwater radiated vessel noise can initiate avoidance responses (Mitson 1995). Reducing underwater radiated noise was proposed as a remedy to reduce the bias caused by vessel avoidance (Mitson 1995), and many research vessels have subsequently been built according to strict voluntary noise standards adopted by the maritime industry (e.g., the International Council for Exploration of the Sea recommendations (Mitson 1995) and the Det Norske Veritas standard (DNV 2011)). A study performed after one of these new vessels was built concluded that fish do not avoid noise-reduced vessels (Fernandes et al. 2000).

However, more recent studies indicate that these noise standards are not sufficient to mitigate the problem of fish reactions to approaching vessels. When simultaneously comparing the vessel avoidance of herring to the noise-reduced R/V *GO Sars* (GOS) and the conventional R/V *Johan Hjørt* (JH), the vessel avoidance was, contrary to expectations, stronger for the larger but substantially quieter vessel (Ona et al. 2007). A potential explanation for

Received 28 May 2014. Accepted 7 November 2014.

Paper handled by Associate Editor Josef Michael Jech.

N.O. Handegard, G. Rieucan, and G.J. Macaulay. Institute of Marine Research, Bergen, P.O. Box 1870 Nordnes, 5817 Bergen, Norway.

A.D. Robertis. Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA.

K. Boswell. Florida International University, Biscayne Bay Campus, Marine Sciences Building, 3000 NE 151st Street, North Miami, FL 33181, USA.

Corresponding author: Nils Olav Handegard (e-mail: nilsolav@imr.no).

this was put forward by Sand et al. (2008), who hypothesize that the stronger reaction is caused by increased low-frequency particle motion in the near field of the larger and quieter vessel, but this hypothesis has not been tested directly. In addition, there are indications that fish density affects Atlantic herring (*Clupea harengus*) escape responses (Rieucau et al. 2014b). If reactions to vessels are density-dependent, this will introduce density-dependent biases into survey abundance estimates.

The objectives of this paper are as follows: To investigate whether (i) the reactions of Atlantic herring to research vessels can be reproduced by playing back recordings of GOS and JH to captive herring, (ii) the nature of the sound (e.g., the frequency content) affects the reactions, and (iii) the density of fish affects their reactions.

Materials and methods

We addressed the objectives by playing back underwater radiated vessel noise to captive Atlantic spring spawning herring. To address objective (i), we exposed the fish to similar sound pressure levels (SPL) as experienced by the herring during the Ona et al. (2007) experiment for both GOS and JH. However, the playbacks lacked much of the low-frequency components (<50 Hz) produced by the real vessels owing to the limitations of the underwater projector used. To test objective (ii), we scaled the SPL of the noise-reduced vessel playbacks (GOS) to have the same SPL as the playbacks of the conventional vessel (JH). The rationale for this is that if there are differences in how herring react to playbacks of JH and GOS presented at the same SPL, the reaction can be attributed to other characteristics of the sound than SPL, which is the focus of current recommendations for research vessel noise. Finally, we tested objective (iii) by conducting the playback experiments at two different herring shoal densities. The experiment was conducted in a sheltered bay at the Institute of Marine Research's Austevoll research station between 6 and 12 July 2012, under calm weather conditions with light cloud cover with no appreciable surface waves.

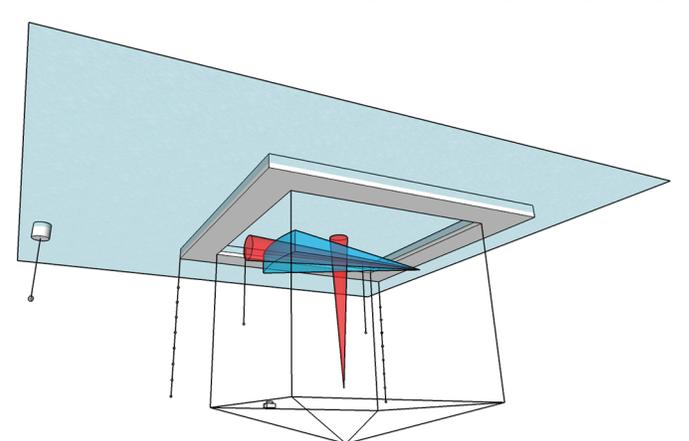
Captive herring

In April 2012, 15 000 kg of adult herring were caught by a commercial purse-seine vessel. The fish were captured in two hauls, in Bårsundet (8000 kg) and Soredvågen (7000 kg), both in Tysnes, Hordaland, Norway. The herring belong to the Norwegian Spring Spawning stock, similar to that of the Ona et al. (2007) experiment. The herring were held for 3 months prior to the experiments, which were conducted in a 12 m × 12 m × 12 m net pen (Fig. 1). The total length and mass of the herring (mean ± standard deviation) at the time of the experiments was 31.4 ± 2.2 cm and 219 ± 50 g, respectively. The fish were schooling and swimming in a circular pattern within the pen (Rieucau et al. 2014b). A more detailed description of the capture process, school size, and fish housing facilities is available elsewhere (Rieucau et al. 2014a). After spawning in the spring, wild *C. harengus* generally form small and dense schools that migrate towards foraging grounds over the summer period (Nøttestad et al. 1996), compared with the winter period during which herring aggregate in massive shoals that can reach sizes up to several million individuals (Misund 1993).

Vessel noise playbacks and the sound pressure levels within the pen

Vessel noise was played back to the captive herring using a Hegel HD2 High End USB Music streamer device, which was modified to produce waveforms down to 5 Hz. This was connected to a Cerwin-Vega CXA-10 power amplifier driving an underwater transducer. The transducer (similar to that used by Engås et al. 1995) was based on a moving coil acting against an electromagnet that drives a membrane of 0.3 m in diameter. A tone sweep was played back to the amplifier-transducer combination, and the combined system operated most effectively above 50 Hz. The electromagnet

in the transducer was driven with a SMPS switch mode DC power supply providing up to 230 V at 6 A. The maximum continuous power rating was 0.5 kW for the moving coil and 1.5 kW for the electromagnet. The nominal maximum source level at 300 Hz was 200 dB re 1 µPa at 1 m, which was sufficient to reproduce the SPL experienced by the herring in the Ona et al. (2007) experiments.



in the transducer was driven with a SMPS switch mode DC power supply providing up to 230 V at 6 A. The maximum continuous power rating was 0.5 kW for the moving coil and 1.5 kW for the electromagnet. The nominal maximum source level at 300 Hz was 200 dB re 1 µPa at 1 m, which was sufficient to reproduce the SPL experienced by the herring in the Ona et al. (2007) experiments.

To ensure that we generated the correct SPLs within the pen, we monitored the SPL using a pair of calibrated Brüel & Kjær (B&K) type 8106 hydrophones mounted at 5 m depth in adjacent corners inside the net pen (Fig. 1). The hydrophones were factory-calibrated across their full frequency range in 2012, prior to the experiment, and the calibrations were verified on site using a B&K Type 4229 hydrophone calibrator with a B&K WA0658 coupler. We also measured the vertical distribution of sound energy within the pen via two vertical eight-hydrophone arrays located at two adjacent corners <1 m outside the net pen (Fig. 1). The shallowest hydrophone in each array was 2 m below the sea surface, with subsequent hydrophones at 1 m intervals. The 16 channels of vertical hydrophone array data were low-pass-filtered with a cutoff at 4 kHz using a BenchMaster 21M Kemo 255G filter, amplified with an OctaMic II pre-amplifier, and then digitized at 10 kHz with a National Instruments PC-based data acquisition system. The signals from the two B&K hydrophones were pre-amplified with a B&K Nexus conditioning amplifier and digitized by the National Instruments acquisition system. The hydrophones in each array were calibrated by the manufacturer to have the same relative response over the frequency range of interest, and we obtained an absolute calibration by placing a B&K hydrophone adjacent to one of the array hydrophones and then adjusting the array calibration factor to produce the same SPL as measured by the B&K hydrophone when exposed to test tones that covered the frequency range of interest.

The digitized hydrophone data were imported to Matlab (Mathworks, Inc., Natick, Massachusetts, USA) for further analysis. A low pass finite impulse response filter (firpmord, Fpass = 1 kHz, Fstop = 1.1 kHz) was applied before presenting the data, and 50 Hz power line interference on the array hydrophones was removed using an infinite impulse response notch filter (49–51 Hz). The pressure data were separated into 0.1 s bins, and the root mean square (RMS) pressure was calculated within each 0.1 s window. The SPL was calculated by applying 20log₁₀ to the RMS pressures. The

power spectral density over the 6 s window of maximum exposure was estimated via Welch's method (pwelch).

The radiated noise produced by GOS and JH was recorded during the [Ona et al. \(2007\)](#) experiment (their figure 2). To facilitate playback and to fit the playbacks to the design of the experiment, the noise recordings were windowed with a 3 s linear increase in sound pressure, kept at the original level through "vessel passing" for 30 s, followed by a 2 s linear reduction in sound pressure. The maximum SPL was reached 22 s into the modified recording, and the total treatment lasted 35 s. Both the recording and the playback differ from the real signal in that the recording only records the pressure component of the vessel noise, and the playback, played back at a different distance, alters the relationship between particle motion and pressure component of the sound. However, current guidelines for vessel noise are only based on the pressure component, which is similar in magnitude in the [Ona et al. \(2007\)](#) in situ experiment and our vessel noise playbacks.

Assuming spherical spreading, the source levels (at 1 m range) for the two vessels were 171.7 and 158.3 dB re 1 μ Pa for JH and GOS, respectively ([Ona et al. 2007](#)). The top of the herring layer in the experiment by [Ona et al. \(2007\)](#) was at 30 m. Ideally, we would project similar levels in the pen as those experienced by the herring in that experiment. Again assuming spherical spreading, we estimate a transmission loss of 29.54 dB. The desired levels inside the pen were thus 171.7 - 29.54 = 142.16 dB re 1 μ Pa for JH and 158.3 - 29.54 = 128.76 dB re 1 μ Pa for GOS. In addition, we scaled the GOS recording to give the same SPL as JH, that is GOSup = 142.16 dB. The source used to project the playbacks puts little energy in the water at frequencies less than 50 Hz, and herring hearing sensitivity has a uniformly low threshold up to 1200 Hz and drops off dramatically at higher frequencies ([Enger 1967](#)). To confirm that we were generating the desired playback levels, we measured the SPL of playbacks and then adjusted the playbacks to match the desired SPL (see section on Sound levels in the pen in the Results).

A conductivity, temperature, depth (CTD) probe (SAIV A/S STD/CTD, model SD204) was used to estimate sound speed ([Chen and Millero 1977](#)) as a function of depth in and around the net pen for 12 of the 15 sound exposure experiments (refer to [Fig. 4e](#)). The water temperature at 2 and 10 m depth was 15.2 \pm 0.6 $^{\circ}$ C (mean \pm standard deviation) and 14.0 \pm 0.3 $^{\circ}$ C, while the salinity was 28.8 \pm 4.4 ppt and 29.2 \pm 4.9 ppt, respectively. The CTD was deployed and allowed to equilibrate for 3 min near the surface, then lowered to at least 40 m depth.

Observations of fish behaviour in the net pen

We used a combination of optical and acoustic techniques to observe and quantify fish behaviour in the net pen: vertically and horizontally aligned echo sounder transducers, an upward-looking camera, and a horizontal-looking imaging sonar (Dual Frequency Identification Sonar, Sound Metrics, Washington, USA; [Fig. 1](#)). All four sensors were used in a qualitative assessment of the herring reactions. The vertical echo sounder provided data for quantitative observations of the behavioural response. This approach is similar to that of earlier studies ([Doksaeter et al. 2012](#); [Rieucou et al. 2014a](#)) that evaluated the behavioural response of schooling herring exposed to low-frequency military sonars and simulated predator attacks, respectively.

Echo sounder observations

A split-beam echo sounder was used to observe the vertical and horizontal distribution of herring in the pen. A Simrad EK 60 general purpose transceiver was connected to a multiplexer that allowed two transducers to be operated sequentially. Two Simrad 120 kHz 7CD transducers were connected to the multiplexer, one looking horizontally at 1.3 m depth on the side of the pen and one on a gimbal near the bottom of the pen and oriented vertically (at approximately 9 m depth). The pulse repetition rate was 4.3 Hz

and the pulse duration was set at 256 μ s and later reduced to 128 μ s (we unsuccessfully tried to improve single target detections). Collection range was from transducer face to 15 and 11 m for the horizontal and vertical transducer, respectively. Both echo sounder channels were calibrated on the last day of the experiment using the standard sphere method ([Foote et al. 1987](#)) at both pulse lengths used.

The vertically aligned echo sounder provided quantitative information about the volume backscattering coefficient (s_v), which is proportional to fish density ([Maclennan et al. 2002](#)), and the mean vertical distribution as a function of time before and during exposure ([Fig. 2](#)). The mean s_v in the depth interval between 0.3 and 8.5 m at the time of the playback was compared with mean s_v prior to initiation of the playback, using the vessel avoidance coefficient (VA) of [Vabø et al. \(2002\)](#), which is the ratio of backscattering coefficients observed during vessel passage and prior to exposure, defined as

$$VA = A_{\text{pass}}/A_{\text{ref}}$$

where A_{pass} and A_{ref} are mean s_v from the time interval (-152 to -88) s and (-3 to 3) s, respectively, relative to maximum sound level, which corresponds to 21 s into the playback (cf., [Fig. 3](#)). The time intervals were chosen to be consistent with previous work on vessel avoidance ([Vabø et al. 2002](#); [De Robertis and Wilson 2011](#); [De Robertis and Handegard 2013](#)).

Herring often dive when disturbed ([Vabø et al. 2002](#); [Ona et al. 2007](#); [Doksaeter et al. 2012](#)), and to examine any changes in mean depth of the herring backscatter in response to the playbacks, we defined the depth difference dd as the difference in s_v -weighted mean depth prior to the vessel playback and the time interval surrounding the maximum level of vessel noise playback

$$dd = d_{\text{ref}} - d_{\text{pass}}$$

where d_{ref} and d_{pass} are the s_v -weighted mean depth ([De Robertis and Wilson 2011](#)) calculated over the same depth and time intervals as the VA ratios. Since depth is a positive value for greater depth, a negative dd corresponds to a deeper depth distribution of acoustic backscatter.

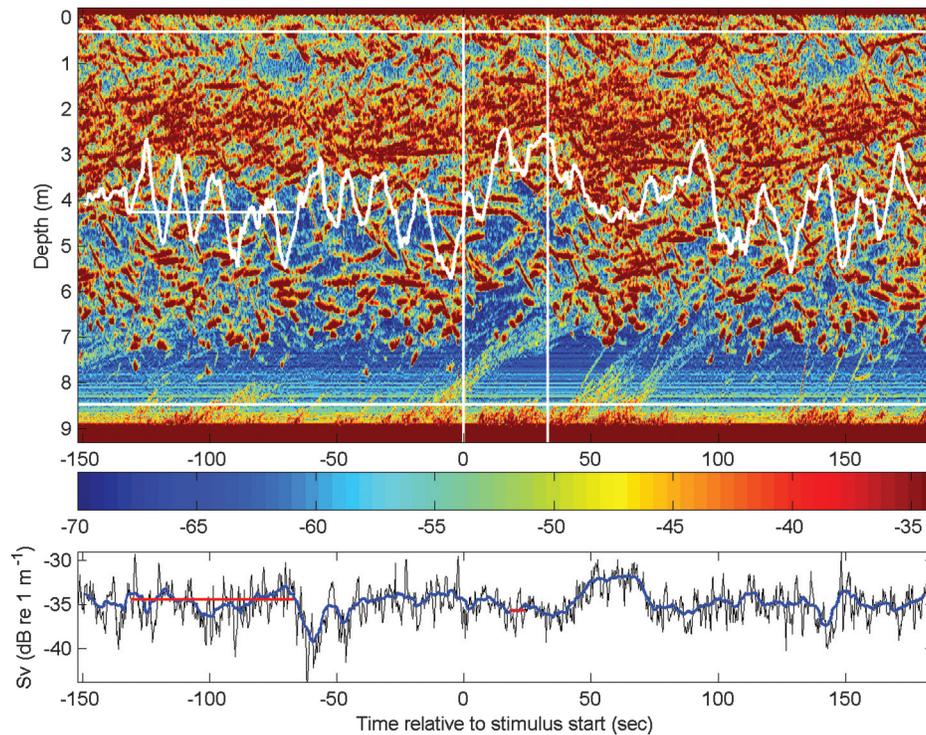
Imaging sonar and HD camera

A horizontally aligned DIDSON imaging sonar was mounted at 1.5 m depth and ensonified a horizontal slice across the pen ([Fig. 1](#)). The sonar was operated in high-frequency mode (1.8 MHz) with an observation range of 1.3–10.3 m. Focal range was calculated to be 6.9 m, and the pulse repetition rate was 7 Hz. A high-resolution night view colour camera (Sony 500TVL HQ 560TVL) was placed 3 m away from the pen wall, close to the bottom pointing upwards. The imaging sonar and camera observations were used to qualitatively assess the behavioural change in response to the playbacks.

Qualitative scoring method

To ground truth the quantitative observations and to ensure that potentially subtle changes in behavior not detected by our quantitative analysis were identified, we prepared the observations from the four different sensors as graphs and video clips and presented them to a blind scoring team (i.e., the scoring team was unaware of the treatment although shoal size was detectable from the images). The results are qualitative and the absolute levels of the reactions will be subjective, but any *difference* in responses between vessel types should be detectable. The echo sounder data was presented in a similar fashion to [Fig. 2](#), and the camera and Didson video clips were organized such that they started 5 s prior to the 25 s exposure. Five analysts, without knowledge of the experimental design, scored each video and image from 0 to 5,

Fig. 2. Time series of herring backscatter from the vertical echo sounder during a playback of GOS scaled-up vessel noise. The playback starts at time = 0 and the data prior to this time represent the distribution prior to exposure to vessel noise playback. (Upper panel) An echogram (i.e., colour time series display of $\log_{10}(s_v)$) from the vertically aligned echo sounder. The horizontal white lines across the panel denote the depth range from which the response parameters were calculated; the vertical white lines denote the playback interval; the white curve is the s_v -weighted mean depth; and the short horizontal lines between -131 and -67 s and between 18 and 24 s denote the time interval and value for defining the depth distribution prior to and during maximum exposure used to define dd (depth difference). (Lower panel) The mean volume backscattering strength (S_v ; i.e., $10\log_{10}(s_v)$) as a function of time relative to stimulus start. The blue line is a 31-point running mean, and the horizontal red lines define the undisturbed and the disturbed state used to define VA (vessel avoidance). The example is taken from block 14 (cf., online supplementary data set, Table S1¹).



where 5 represented a strong behavioural response and 0 no response. The mean response over the scorers (5) and observation types (4) was calculated for each treatment, resulting in a response variable similar to VA and dd.

Experimental design

The playbacks were presented to the fish in a randomized block design as part of a larger experiment in which a nested block of four different treatments (synthetic sounds (Handegard et al., in press), predator models (Rieucan et al. 2014a), orca playback (in preparation), and vessel noise (this paper)) were presented in random order to the herring. The randomized block design (i.e., randomly arranging the order of these treatment types) was used to control for a potential effect of the order of the different experimental treatments within a block. We performed one to three blocks per day (cf., online supplementary data set, Table S1¹ for the vessel noise treatments) during daylight. Within each block, the sub-blocks of a given treatment type (i.e., tones, predator models, vessel playbacks) were presented in random order, and each treatment was separated by 20 min. Each individual trial within a sub-block of a given treatment was separated by 3 min from the other treatments in the sub-block (i.e., the JH, GOS, and GOS up-scaled in the case of the vessel playbacks), and the trials were presented in random order.

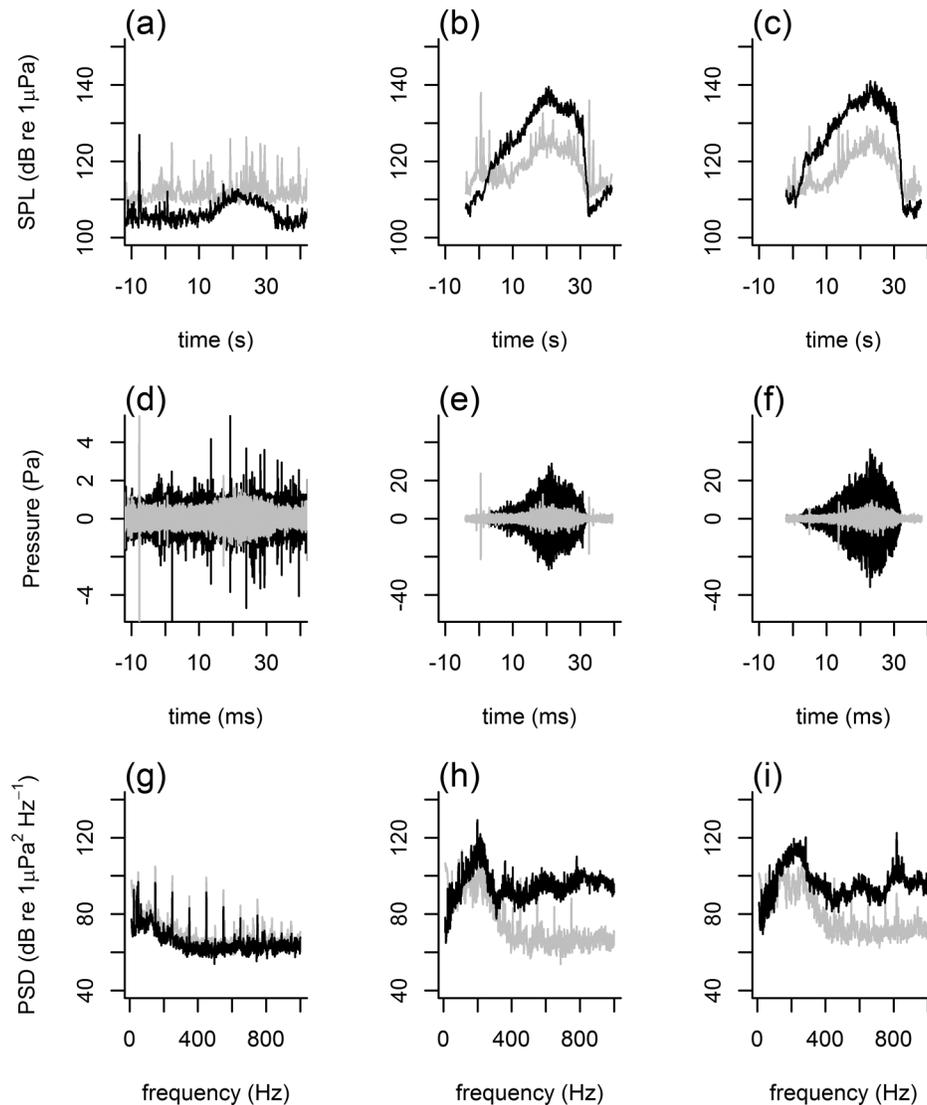
A total of 45 vessel noise playbacks were conducted over 15 blocks. In three vessel noise trials, no data was recorded because of tech-

nical problems with the recording equipment (cf., supplementary data set, Table S1¹). Owing to logistical challenges associated with transferring fish between net pens, the shoal size was not randomized, and initially six blocks with a small shoal size were carried out, followed by nine blocks with a large shoal size. The approximate density of fish in the pen was verified using the echo sounder. The volume backscattering coefficient from the large shoal was approximately 10 times higher than that of the low-density shoal, corresponding to a density of 1.5 and 16.1 herring·m⁻³ in the small and large shoals, respectively (Rieucan et al. 2014b). Based on observations of Holmin (2013), the estimated packing density observed from the large shoal reflects the social condition that wild Atlantic herring experienced during periods where the principal motivation is survival rather than feeding (summer) or reproduction (spring). Conversely, the estimated packing density of the small herring shoal corresponds to wild school densities observed during feeding periods (summer).

This experimental design allowed the use of two-way ANOVAs to examine the effect on the explanatory variables (VA, dd, and the qualitative scores) of vessel noise type (three levels: GOS, GOSup, and JH) and shoal size (two levels: L (large) and S (small)), as well as interaction terms and the block effect. Tukey's post hoc tests were used to identify differences among vessel types and school densities. The homoscedasticity (homogeneity of variance) assumed in the ANOVA was tested using Bartlett's test.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0257>.

Fig. 3. Noise measurements from the reference hydrophone in the corner closest to the source (black lines) and at the other side of the pen (gray lines) from block 4. The sound pressure levels (SPL; panels a, b, c), sound pressure (panels d, e, f), and power spectral density (PSD; panels g, h, i) at the time corresponding to the maximum noise level are shown for the GOS (a, d, g), GOSup (b, e, h), and JH (c, f, i), respectively.



Results

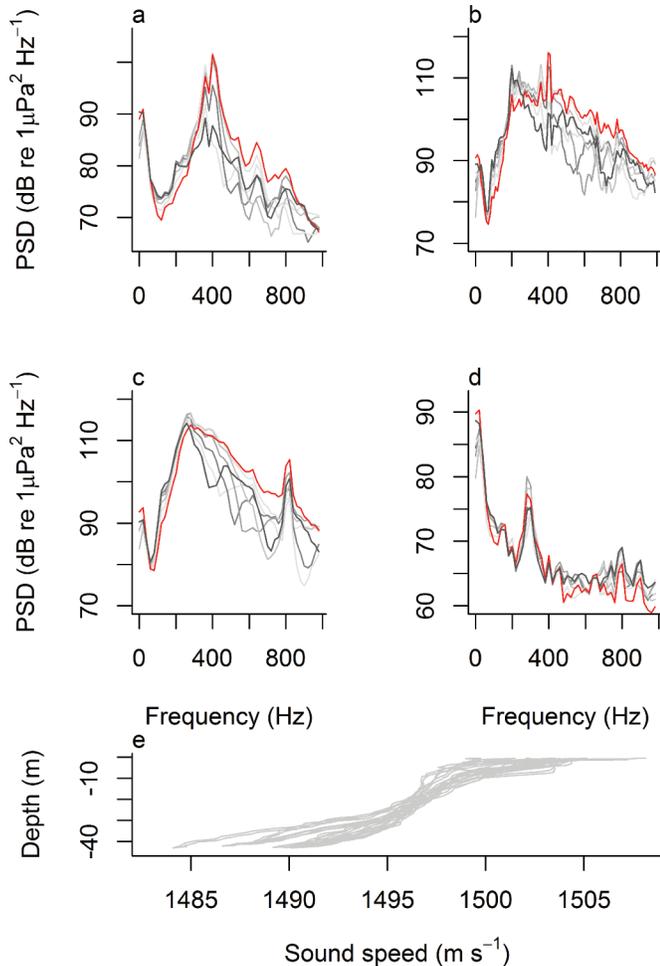
Sound levels in the pen

The objective of the experiment was to play back ship noise to the herring at the same SPLs as those experienced in the field experiments. The maximum SPLs within the net pen was 114.6, 137.9, and 138.8 dB re 1 μ Pa for GOS, GOSup, and JH, respectively (Fig. 3). The maximum SPL was defined as the 90th percentile of the SPL recorded by the B&K reference hydrophone closest to the source, within a 6 s window centred on the time of maximum SPL. The GOS sound levels were lower than the target (by 14.2 dB), while the GOSup and JH sound levels were less than, but close to, the target level (by 4.3 and 3.4 dB, respectively). The low GOS level resulted from a miscalculation, and the others were close to the maximum level that could be projected by equipment. The target SPLs were initially chosen to correspond to the expected SPL experienced 30 m below the vessel (i.e., at the depth of the shallowest herring in the Ona et al. 2007 experiment), and using the same assumptions used to set the target levels, the actual playback levels corresponded to distances of about 150, 49, and 44 m for GOS, GOSup, and JH, respectively. The fish layer observed in the Ona et al. (2007) experiment extended 30 to 75 m, and the herring

began to dive in response to GOS and JH at a range of \sim 600 m (Ona et al. 2007, their figure 1). Under the same simple assumptions, this corresponds to an SPL of \sim 102.7 and 116.1 dB re 1 μ Pa, respectively (i.e., the herring in the in situ case were reacting at much lower SPL than the levels of the experimental playbacks). Furthermore, the levels for GOSup and JH are similar, which allows testing of the hypothesis that reactions to these playbacks at similar SPL will be equivalent.

The vertical distribution of sound recorded by the vertical hydrophone array showed that the SPL in the net pen tended to decrease with depth and with increasing distance from the source. The SPL at the shallowest hydrophone was between 2 and 6 dB higher than at the deepest hydrophone depending on the playback type. The hydrophone array indicates that there was higher SPL in the upper part of the pen compared with that in the middle and lower parts, which is not consistent with a direct application of range-dependent acoustical spreading (if this were the case, the hydrophones at the same depth as the sound source, 5 m, should have the highest SPL). Furthermore, the vertical distribution of sound was frequency-dependent; although the overall SPL (50 Hz to 2 kHz) was higher in the upper water column, the SPL at lower

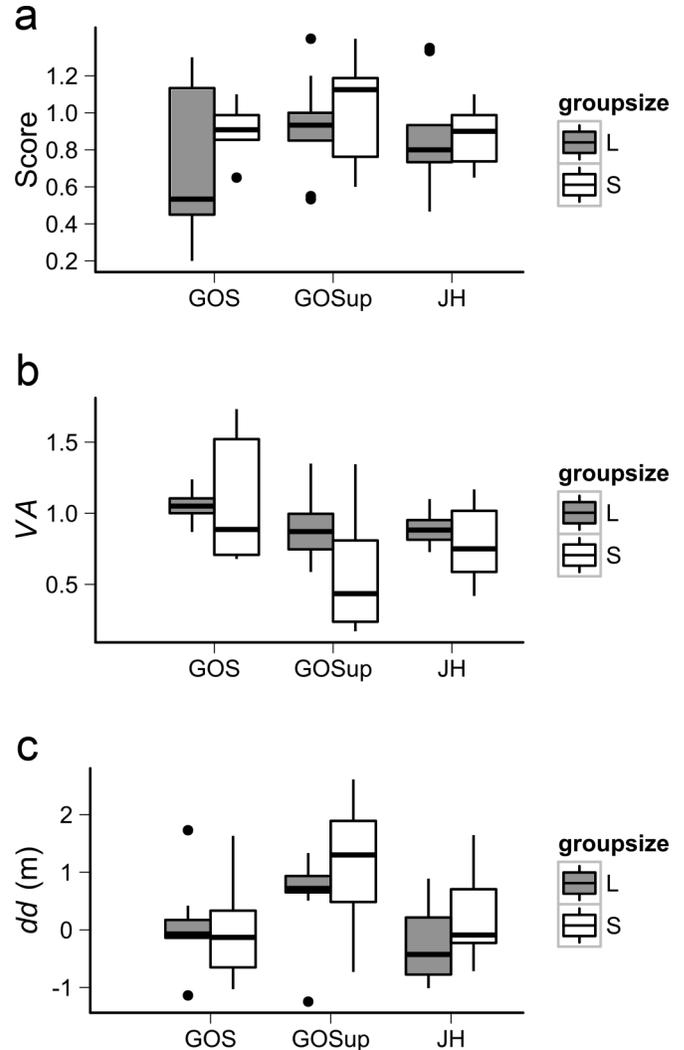
Fig. 4. (a–c) Variation in power spectral density (PSD) with depth for the three playback types measured by the vertical hydrophone arrays for GOS (a), GOSup (b), and JH (c) for the vertical hydrophone arrays near the source (cf., Fig. 1). The recording is taken from block 4. (d) The background noise level recorded prior to the exposure. The different curves in each plot represent each element in the vertical array, where the red and black lines are the curves for 2 and 9 m, respectively, and the increasing darker shades in between are the hydrophones in 1 m depth increments (darker lines with increasing depth). (e) The vertical distribution of sound speed throughout the experiment where each line represents one conductivity, temperature, depth (CTD) cast.



frequencies (50 to ~300 Hz) was higher close the bottom of the pen (Fig. 4).

Background noise in the pen was measured during periods when no playbacks were occurring. The GOS playback peaked at about 16 dB above the background noise level recorded by the distant array, while the upscaled GOS and JH playbacks were about 40 dB higher than the background levels. The background SPL had a slight depth dependence (Fig. 4d), but the depth dependence during playbacks was much larger (Figs. 4a–4c), ruling out the effect of any depth-related calibration issues. Background noise SPL decreased with increasing frequency, with unexplained peaks at about 300, 800, and 850 Hz (Fig. 4d). Background noise was consistent in the periods before and after the blocks, with a mean background SPL of 114 dB re 1 μPa and a standard deviation between blocks of 2.6 dB (calculated in log domain between blocks). The sound speed estimates were similar and consistent for all of the exposure blocks, and hence the sound propagation

Fig. 5. Boxplots representing (a) the score from the qualitative scoring team, (b) the vessel avoidance (VA) in terms of reduction in backscatter, and (c) the change in s_v -weighted vertical distribution (dd) in response to the different stimuli. The boxes represent the quartiles, the horizontal line is the median, and the whiskers extend from the boxes to 1.5 times the interquartile range. Values outside this range are shown as dots.



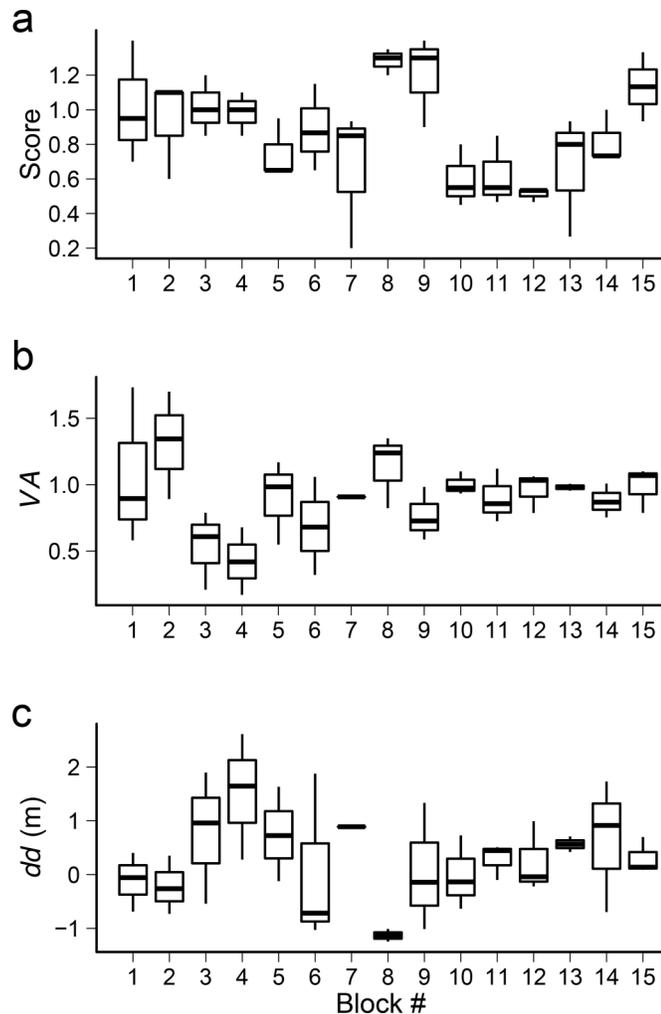
conditions were similar among blocks (Fig. 4e). The measured SPL was correspondingly similar and consistent among blocks.

Observations of fish behaviour

The results from the blind qualitative scoring team showed that in general, the responses to the playbacks were weak (Fig. 5a). The mean score assigned by each panelist across the different observation systems was 0.87 ± 0.04 (mean \pm standard error). This response was weaker than expected from previous observations of dramatic herring reactions to the vessels (Vabø et al. 2002; Ona et al. 2007), as the potential scores ranged from 0 to 5, where 5 represented the dramatic coordinated escape response exhibited by startled herring (e.g., as observed by Doksaeter et al. 2012 for exposures to impulsive sound). When comparing the different treatments (Fig. 5a), the scoring panel did not reveal any significant differences among the treatments for vessel type ($F_{[2,26]} = 2.0$, $p = 0.16$), shoal size ($F_{[2,26]} = 1.9$, $p = 0.17$), or the interaction term ($F_{[2,26]} = 0.191$, $p = 0.83$). However, there was a significant effect of block number ($F_{[13,26]} = 3.1$, $p = 0.0063$), but no clear trend of

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by FISKERIDIREKTORATET on 02/02/15
For personal use only.

Fig. 6. Boxplots representing (a) the score from the qualitative scoring team, (b) the vessel avoidance (VA) in terms of reduction in backscatter, and (c) the change in s_v -weighted vertical distribution (dd) in response to the different blocks. The boxes represent the quartiles, the horizontal line is the median, and the whiskers extend from the boxes to 1.5 times the interquartile range. Blocks 1–6 and 7–15 are the low- and high-density cases, respectively.



decreased reactions with time that would be consistent with a habituation effect (Fig. 6). The ANOVA assumption of homogeneity of variance was met (Bartlett's test of homogeneity of variances, $K^2 = 1.546$, $df = 2$, $p = 0.4616$).

The mean change in VA during exposure across all treatments was 0.9, and the $\log(VA)$ was significantly different from 0 (two-sided t test, $p < 0.01$), indicating a weak overall effect. The median for the different treatments ranged from 0.4 to 1.1 (Fig. 5b). Using the two-way ANOVA, we detected a significant main effect of both the vessel type ($F_{[2,23]} = 7.8$, $p = 0.002$) and shoal density ($F_{[1,23]} = 9.8$, $p = 0.004$) on $\log(VA)$. A weaker but significant interaction between $\log(VA)$ and both vessel type and shoal density was observed ($F_{[2,23]} = 4.12$, $p = 0.03$), and a block effect was detected ($F_{[13,23]} = 2.9$, $p = 0.011$). A stronger negative effect on $\log(VA)$ was found when herring were exposed to GOSup compared with GOS (Tukey's post hoc test, $GOS-GOSup = 0.46$, $p = 0.001$). A nonsignificant difference was found between JH and GOSup ($JH-GOSup = 0.22$, $p = 0.14$) and between GOS and JH ($GOS-JH = 0.23$, $p = 0.14$). By ordering the effects, one can infer that GOSup had the strongest negative effect on the $\log(VA)$ parameter, followed by JH and then GOS. The reaction (in terms of $\log(VA)$) of the low-density shoal

was significantly stronger than the response of the high-density herring school (Tukey's post hoc test, $L-S = 0.3$, $p = 0.004$). The ANOVA assumption of homogeneity of the variances for the $\log(VA)$ was violated (Bartlett's test of homogeneity of variances, $K^2 = 12.5$, $df = 2$, $p < 0.01$), as the observed variance of $\log(VA)$ for the low-density shoal was approximately twice that of the high-density shoal. The general effect of heterogeneity on the ANOVA test used here is that statistical power is reduced, which increases the probability of type II errors (i.e., failure to reject the false null hypothesis).

We found a mean change in mean vertical position of 0.30 m across the different treatments, with a positive response indicating an upward shift (i.e., a *surfacing* response) in vertical distribution of herring backscatter. There was an overall positive trend (close to, but not significant, at 5% levels) across all treatments (two-sided t test, $p = 0.068$), and the median change in vertical distribution between the different treatments ranged from -0.3 to 1.3 m (Fig. 5c). A significant main effect of vessel type was observed ($F_{[2,23]} = 5.11$, $p = 0.014$). A significantly stronger upward shift in distribution was found for GOSup compared with JH ($GOSup-JH = 0.86$ m, Tukey's post hoc test: $p = 0.020$) and GOSup compared with GOS ($GOSup-GOS = 0.77$ m, $p = 0.04$). No significant difference was detected between GOS and JH ($GOS-JH = 0.09$ m, $p = 0.94$). By ordering the effects, one can infer that GOSup playbacks resulted in a stronger upward shift in herring backscatter than playbacks of JH or GOS. Shoal density did not significantly affect the change in vertical position ($F_{[1,23]} = 1.8$, $p = 0.20$), and neither did the interaction between vessel type and shoal density ($F_{[2,23]} = 0.85$, $p = 0.44$) or the block ($F_{[13,23]} = 1.8$, $p = 0.12$). The ANOVA assumption of homogeneity of variance was met (Bartlett's test, $p = 0.70$).

Discussion

In general, the responses of the penned herring to our playbacks were weaker than anticipated, given the responses exhibited by herring reacting to vessels observed in situ (Vabø et al. 2002; Ona et al. 2007). Crowding in the pen may have altered the avoidance response reactions, but earlier studies on Norwegian Spring Spawning herring held in pens produced dramatic responses to other types of sounds (Doksaeter et al. 2012), in particular those with impulse-like characteristics and broadband noise (which included lower frequency components than in the current work). In addition, the herring used in this study were much more reactive to predator models (Rieucan et al. 2014a) than the vessel playbacks, which indicates that the fish were capable of more dramatic reactions and that the vessel playbacks were not highly disturbing to the herring. It is therefore likely that lower-frequency components are important in eliciting the observed reactions (Schwarz and Greer 1984; Sand et al. 2008).

Although the overall reaction to the playbacks was weak, the results show that GOSup induces the strongest reaction followed by JH and then GOS. Because of a miscalculation, the GOS recording was played back at a relatively lower level compared with GOSup and JH. However, the GOS level was still higher compared with what herring experienced at the start of the reaction in the Ona et al. (2007) experiment, and this should not affect our conclusions. Note that for VA the reactions to GOSup and JH were not significantly different, but the strength of the test was weakened because of a lack of homoscedasticity, and the observed trends support the inference that playbacks of GOSup at the same levels as JH are more disturbing than playbacks of JH. The frequency spectrum of the JH and GOS playbacks appear only slightly different (Fig. 3), but it is clear from previous work where herring respond to killer whale (*Orcinus orca*) playbacks and not sonar upsweeps with very similar frequency characteristics that behavioural reactions to sounds with similar frequency content can be very different (Doksaeter et al. 2009). Sound is an important sensory mechanism for fish (Slabbekoorn et al. 2010), and it is likely

that fish are able to make nuanced interpretations of underwater sounds and that subtle changes in sounds can elicit different behavioural responses. This is well known in terrestrial ecology; for example, vocal performance in birds may be used by conspecifics to assess the competitive potential of the signaller, and methods to assess their complex vocalization patterns are still being developed (e.g., Geberzahn and Aubin 2014). Our results suggest that fishes make subtle distinctions when interpreting acoustic cues, perhaps related to the interplay between the particle movement and pressure components of the sound (Sand et al. 2008). In future studies, emphasis should be placed on identifying the characteristics of sound eliciting behavioural reactions in fishes, which will require the development of new methodology to quantify the characteristics of the sound and the behavioural response of fishes.

When disturbed, schooling herring typically perform a coordinated diving response (Vabø et al. 2002; Ona et al. 2007; Doksaeter et al. 2012). However, in this study, the reactions were weaker and the depth distribution of herring backscatter became shallower during the simulated vessel passage. Without the vertical hydrophone array measurements, the upward shift in herring acoustic backscatter combined with an assumption of spherical spreading could have mistakenly been attributed to fish moving out of areas of high SPL. However, since the measurements reveal that overall SPL is decreasing with depth, an upward movement of fish would have led the fish into areas of higher SPL. After the quantitative analysis of the responses, we revisited the observations to try to determine, post hoc, if we could explain these results. In blocks 3 and 4, there seems to be a void created at 5 m depth and some indications of diving, but this is not evident at shallower depths. A similar pattern is seen in block 14 (see Fig. 2). These are the blocks with the strongest “surfacing” response (Fig. 6) and could support an explanation of the quantitative results. If the fish at 5 m depth and below start diving, the acoustic reflectivity of these fish will drop substantially because of the change in orientation (Nakken and Olsen 1977). Since the upper layer seemed unaffected, this will cause the s_v -weighted vertical distribution to shift upwards. If the reactions of shallower fish are lower than those of deeper fish, an overall reduction in VA (i.e., a stronger decrease in water column backscatter during playback) will be associated with an increase in dd (a shift in backscatter vertical distribution towards the surface). This is indeed what is observed; there is a clear negative relationship between VA and dd (correlation coefficient -0.57 , Pearson’s product-moment correlation, $p < 0.001$). Thus, the apparent diving response is likely to be due to a depth-dependent change in the acoustic backscatter from individual herring caused by a depth-dependent change in orientation.

The apparent diving response in the lower part of the school offers an explanation of the observed “surfacing” response, but does not explain why the upper layer seems unaffected. This cannot be explained by SPL, since the vertical hydrophone array shows that the SPL is higher in the upper layer. However, when filtering the hydrophone data by frequency, this relationship reverses, indicating that there is relatively more energy below 200 Hz at deeper depths than shallower depths (Fig. 4). This is consistent with the hypothesis that the lower frequencies, which are at higher levels at depth, are the stimulus responsible for the stronger response. This inference is corroborated by the stronger reaction of these herring to playbacks of lower-frequency tones than high-frequency tones (Handegard et al. in press).

The lower-density herring shoal exhibited significantly stronger reactions to the vessel noise playbacks compared with the high-density shoal. The difference in the strength of the observed responses to the vessel noise between the low- and high-density shoals can potentially be interpreted as a differential assessment of predation risk. Shoaling is commonly presented as an adaptive strategy that enhances fish safety through the action of several antipredatory mechanisms, which include a numerical dilution of

risk (Pitcher and Parrish 1993), collective predator detection (Magurran et al. 1985), a confusion effect (Landeau and Terborgh 1986; Ioannou et al. 2008), or coordinated escape maneuvers (Pitcher and Parrish 1993). The safety of prey is expected to increase with aggregation size; fish in larger shoals may enjoy reduced predation risk compared with fish in smaller shoals (Pitcher and Parrish 1993; Krause and Ruxton 2002). In our study, herring in the low-density shoal may have been more risk-averse and less likely to delay escape reactions owing to a weaker “safety in numbers” mechanism.

The internal characteristics of fish aggregations such as density or size may influence the extent to which herring shoals respond to vessels. Therefore, the effect of shoal size or density and fish physiological state may be important factors that mediate how fish react to vessel noise in natural conditions (De Robertis and Handegard 2013), with the potential consequence of introducing density-dependent effects in acoustic survey estimates. It is also worth noting that several field experiments of vessel avoidance (e.g., Vabø et al. 2002; Ona et al. 2007) have been conducted when herring are tightly aggregated (because it is easier to perform the experiments then), and this may have biased the overall picture (De Robertis and Handegard 2013). If we are to better understand the potential shoal density-dependent effects in survey estimates, future empirical work should be directed towards how characteristics of fish aggregations influence the behavioural responses of pelagic fish to external stimuli such as approaching research vessels in situ.

Repetitive presentation of stimuli with the same characteristics at short intervals of time can lead to habituation, with a decrease of responsiveness as shown in zebrafish (*Brachydanio rerio*) (Eaton et al. 1977). However, habituation can be minimized by increasing the interstimuli time intervals (Eaton et al. 1977). It is well-recognized that randomizing the presentation order of stimuli can prevent habituation in experimental subjects (Schleidt et al. 1983). Owing to the randomized design, the characteristics of a given stimulus were unpredictable for the herring. In the larger experiment that included synthetic sounds (Handegard et al., in press), predator models (Rieucou et al. 2014a), orca calls, and vessel noise (the study described here), this may have contributed to reduce the risk for habituation and sequence effects, as suggested by Schleidt et al. (1983). There was a significant block effect in the responses, but no clear reduction in the strength of behavioural responses over time (Fig. 6), suggesting that habituation was not the main factor affecting the observed responses. Furthermore, the time intervals between two consecutive exposures were sufficient to allow the fish to regain the same swimming pattern and distribution as prior to exposure (see Rieucou et al. 2014b).

In conclusion, the behavioural reactions of herring exposed to playbacks of vessel recordings were weaker than expected. Although the experiment replicated the sound field produced by research vessels at frequencies greater than 50 Hz, very little of the energy produced by a vessel at lower frequencies was transmitted into the pen. This lack of a strong low-frequency component may explain the relatively weak reactions observed during the playbacks. This is consistent with the stronger reaction of the deeper fish, which were exposed to overall higher low-frequency SPLs than the shallower fish. Our findings support the previous suggestion that low frequencies play a key role in eliciting fish avoidance reactions (Schwarz and Greer 1984; Sand et al. 2008). In future studies, we need to measure lower-frequency perturbations (e.g., those caused by the vessel slowly rocking in the waves) if we are to understand the phenomenon of vessel avoidance. Particle motion sensors (Sigray and Andersson 2011) may provide a tool for this. There is also clear evidence that the reactions to vessels depend on the nature of the sound and fish density and that blindly relying on SPL as an indicator for the potential for fish avoidance reactions of approaching vessels will be misleading.

Acknowledgements

This work was financed by the Norwegian Research Council (grant 204229/F20). We are grateful to the following people: Endre Grimsbø, Lise Doksaeter Sivle, and Lars Stien for their technical help during the experiments and data analysis; Kirsti Børve Eriksen, Felicia Juanita Keulder-Stenevik, Herdis Langøy Mørk, Georg Skaret, and Anne-Britt Skar Tysselev for participating in the qualitative scoring team; and Jens Hovem and NTNU (Norwegian University of Science and Technology) for providing their vertical hydrophone array and Tim Cato Netland, Bo Peng, and Alexios Korakas for assistance in its use. The animal collection was approved by The Royal Norwegian Ministry of Fisheries, and the experiment was approved by the Norwegian Animal Research Authority. The Institute of Marine Research is permitted to conduct experiments at the Austevoll aquaculture facility by the Norwegian Biological Resource Committee and the Norwegian Animal Research Committee (Forsøksdyrutvalget). The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of their home institutions. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

References

- Chen, C.-T., and Millero, F.J. 1977. Speed of sound in seawater at high pressures. *J. Acoust. Soc. Am.* **62**: 1129–1135. doi:10.1121/1.381646.
- De Robertis, A., and Handegard, N.O. 2013. Fish avoidance of research vessels and the efficacy of noise-reduced vessels: a review. *ICES J. Mar. Sci.* **70**: 34–45. doi:10.1093/icesjms/fss155.
- De Robertis, A., and Wilson, C.D. 2011. Silent ships do not always encounter more fish (revisited): comparison of acoustic backscatter from walleye pollock recorded by a noise-reduced and a conventional research vessel in the eastern Bering Sea. *ICES J. Mar. Sci. J. Cons.* **68**: 2229–2239. doi:10.1093/icesjms/fsr146.
- DNV. 2011. Rules for classification of ships, part 6 chapter 24, SILENT Class Notation. Det Norske Veritas AS.
- Doksaeter, L., Godø, O.R., Handegard, N.O., Kvasdheim, P.H., Lam, F.-P.A., Donovan, C., and Miller, P.J.O. 2009. Behavioral responses of herring (*Clupea harengus*) to 1–2 and 6–7 kHz sonar signals and killer whale feeding sounds. *J. Acoust. Soc. Am.* **125**: 554–564. doi:10.1121/1.3021301. PMID:19173441.
- Doksaeter, L., Handegard, N.O., Godø, O.R., Kvasdheim, P.H., and Nordlund, N. 2012. Behavior of captive herring exposed to naval sonar transmissions (1.0–1.6 kHz) throughout a yearly cycle. *J. Acoust. Soc. Am.* **131**: 1632–1642. doi:10.1121/1.3675944. PMID:22352533.
- Eaton, R.C., Bombardieri, R.A., and Meyer, D.L. 1977. The Mauthner-initiated startle response in teleost fish. *J. Exp. Biol.* **66**: 65–81. PMID:870603.
- Engås, A., Misund, O.A., Soldal, A.V., Horvei, B., and Solstad, A. 1995. Reactions of penned herring and cod to playback of original, frequency-filtered and time-smoothed vessel sound. *Fish. Res.* **22**: 243–254. doi:10.1016/0165-7836(94)00317-P.
- Enger, P.S. 1967. Hearing in herring. *Comp. Biochem. Physiol.* **22**: 527–538. doi:10.1016/0010-406X(67)90615-9. PMID:6075148.
- Fernandes, P.G., Brierley, A.S., Simmonds, E.J., Millard, N.W., McPhail, S.D., Armstrong, F., Stevenson, P., and Squires, M. 2000. Fish do not avoid survey vessels. *Nature*, **407**: 152. doi:10.1038/35025149.
- Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., and Simmonds, E.J. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES CRR No. 144.
- Geberzahn, N., and Aubin, T. 2014. Assessing vocal performance in complex birdsong: a novel approach. *BMC Biol.* **12**: 58. doi:10.1186/s12915-014-0058-4. PMID:25096363.
- Handegard, N.O., Boswell, K.M., De Robertis, A., Macaulay, G.J., Rieucou, G., and Sivle, L.D. (In press.) Investigating the effect of tones and frequency sweeps on the collective behavior of penned herring (*Clupea harengus*). In *Effects of noise on aquatic life II*. Springer.
- Hjellvik, V., Handegard, N.O., and Ona, E. 2008. Correcting for vessel avoidance in acoustic-abundance estimates for herring. *ICES J. Mar. Sci.* **65**: 1036–1045. doi:10.1093/icesjms/fsn082.
- Holmin, A.J. 2013. Analysis of multi-beam sonar echos of herring schools by means of simulation [online]. The University of Bergen. Available from <https://bora.uib.no/handle/1956/6967> [accessed 23 October 2014].
- Ioannou, C.C., Tosh, C.R., Neville, L., and Krause, J. 2008. The confusion effect — from neural networks to reduced predation risk. *Behav. Ecol.* **19**: 126–130. doi:10.1093/beheco/arm109.
- Krause, J., and Ruxton, G.D. 2002. *Living in groups*. Oxford University Press, Oxford.
- Landeau, L., and Terborgh, J. 1986. Oddity and the “confusion effect” in predation. *Anim. Behav.* **34**: 1372–1380. doi:10.1016/S0003-3472(86)80208-1.
- Løland, A., Aldrin, M., Ona, E., Hjellvik, V., and Holst, J.C. 2007. Estimating and decomposing total uncertainty for survey-based abundance estimates of Norwegian spring-spawning herring. *ICES J. Mar. Sci.* **64**: 1302–1312. doi:10.1093/icesjms/fsm116.
- MacLennan, D.N., Fernandes, P.G., and Dalen, J. 2002. A consistent approach to definitions and symbols in fisheries acoustics. *ICES J. Mar. Sci.* **59**: 365–369. doi:10.1006/jmsc.2001.1158.
- Magurran, A.E., Oulton, W.J., and Pitcher, T.J. 1985. Vigilant behaviour and shoal size in minnows. *Z. Tierpsychol.* **67**: 167–178. doi:10.1111/j.1439-0310.1985.tb01386.x.
- Misund, O.A. 1993. Dynamics of moving masses: variability in packing density, shape, and size among herring, sprat, and saithe schools. *ICES J. Mar. Sci.* **50**: 145–160. doi:10.1006/jmsc.1993.1016.
- Mitson, R.B. 1995. Underwater noise of research vessels, review and recommendations. International Council for Exploration of the Sea.
- Nakken, O., and Olsen, K. 1977. Target strength measurements of fish. *Rapp. Process Verbaux Reun. Cons. Int. Explor. Mer.* **170**: 52–69.
- Nøttestad, L., Askland, M., Beltestad, A., Fernö, A., Johannessen, A., and Misund, O.A. 1996. Schooling dynamics of norwegian spring spawning herring (*Clupea harengus* L.) in a coastal spawning area. *Sarsia*, **80**(4): 277–284. doi:10.1080/00364827.1996.10413601.
- Olsen, K., Angell, J., Pettersen, F., and Løvik, A. 1983. Observed fish reactions to a surveying vessel with special reference to herring, cod, capelin and polar cod. *FAO Fish. Rep.* **300**: 131–138.
- Ona, E., Godø, O.R., Handegard, N.O., Hjellvik, V., Patel, R., and Pedersen, G. 2007. Silent research vessels are not quiet. *J. Acoust. Soc. Am.* **121**: EL145–EL150. doi:10.1121/1.2710741. PMID:17471759.
- Pitcher, T.J., and Parrish, J.K. 1993. Functions of shoaling behaviour in teleosts. In *Behaviour of teleost fishes*. Edited by T. Pitcher. Chapman & Hall, New York. pp. 363–439.
- Rieucou, G., Boswell, K.M., De Robertis, A., Macaulay, G.J., and Handegard, N.O. 2014a. Experimental evidence of threat-sensitive collective avoidance responses in a large wild-caught herring school. *PLoS ONE*, **9**: e86726. doi:10.1371/journal.pone.0086726.
- Rieucou, G., De Robertis, A., Boswell, K.M., and Handegard, N.O. 2014b. School density affects the strength of collective avoidance responses in wild-caught Atlantic herring *Clupea harengus*: a simulated predator encounter experiment. *J. Fish Biol.* **85**: 1650–1664. doi:10.1111/jfb.12520. PMID:25243659.
- Sand, O., Karlsen, H.E., and Knudsen, F.R. 2008. Comment on “Silent research vessels are not quiet” [*J. Acoust. Soc. Am.* **121**, EL145–EL150]. *J. Acoust. Soc. Am.* **123**: 1831–1833. doi:10.1121/1.2839134.
- Schleidt, W.M., Shalter, M.D., and Carawan, T.C. 1983. The effect of spatial context on habituation to a predator model. *Z. Tierpsychol.* **61**: 67–70. doi:10.1111/j.1439-0310.1983.tb01326.x.
- Schwarz, A.L., and Greer, G.L. 1984. Responses of Pacific herring, *Clupea harengus pallasi*, to some underwater sounds. *Can. J. Fish. Aquat. Sci.* **41**(8): 1183–1192. doi:10.1139/f84-140.
- Sigray, P., and Andersson, M.H. 2011. Particle motion measured at an operational wind turbine in relation to hearing sensitivity in fish. *J. Acoust. Soc. Am.* **130**: 200–207. doi:10.1121/1.3596464. PMID:21786890.
- Simmonds, J., and MacLennan, D. 2005. *Fisheries acoustics*. In *Theory and practice*. 2nd ed. Blackwell Science, Oxford.
- 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. doi:10.1016/j.tree.2010.04.005. PMID:20483503.
- Vabø, R., Olsen, K., and Huse, I. 2002. The effect of vessel avoidance of wintering Norwegian spring spawning herring. *Fish. Res.* **58**: 59–77. doi:10.1016/S0165-7836(01)00360-5.