

Behavioral responses of herring (*Clupea harengus*) to 1–2 and 6–7 kHz sonar signals and killer whale feeding sounds

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Military antisubmarine sonars produce intense sounds within the hearing range of most clupeid fish. The behavioral reactions of overwintering herring (*Clupea harengus*) to sonar signals of two different frequency ranges (1–2 and 6–7 kHz), and to playback of killer whale feeding sounds, were tested in controlled exposure experiments in Vestfjorden, Norway, November 2006. The behavior of free ranging herring was monitored by two upward-looking echosounders. A vessel towing an operational naval sonar source approached and passed over one of them in a block design setup. No significant escape reactions, either vertically or horizontally, were detected in response to sonar transmissions. Killer whale feeding sounds induced vertical and horizontal movements of herring. The results indicate that neither transmission of 1–2 kHz nor 6–7 kHz have significant negative influence on herring on the received sound pressure level tested (127–197 and 139–209 dB_{rms} re 1 μ Pa, respectively). Military sonars of such frequencies and source levels may thus be operated in areas of overwintering herring without substantially affecting herring behavior or herring fishery. The avoidance during playback of killer whale sounds demonstrates the nature of an avoidance reaction and the ability of the experimental design to reveal it.

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I. INTRODUCTION

The interest in how human generated sound might affect marine organisms has grown considerably over the past decade (Richardson *et al.*, 1995). The main focus has been on marine mammals, although other aquatic animals such as fish and some invertebrates may also be affected (Hofman, 2004; Popper *et al.*, 2004). Fish have sensitive hearing organs (Ladich and Popper, 2004) and use sound for communication and to perceive their acoustic environment (Fay and Popper, 2000; Popper, 2003). A wide range of anthropogenic sound sources are present in the marine environment, the most intense being vessel traffic, seismic airguns, pile driving, and military sonars (Hofman, 2004; Popper *et al.*, 2004; Hastings and Popper, 2005). One of the earliest studies to demonstrate the possibility of hearing injury in fish was Enger (1981), who showed that sensory cells in the ears of cod (*Gadus morhua*) were damaged when exposed to high-intensity

sounds. Similar effects have also been demonstrated in cichlids (Hastings *et al.*, 1996), snappers (McCauley *et al.*, 2003), and clupeids (Denton and Gray, 1993). Exposure to intense sound may also lead to temporary loss of hearing [temporal threshold shifts (TTSs)] and has been documented for various species of fish in response to seismic shooting (Popper *et al.*, 2005), military sonars (Popper *et al.*, 2007) and simulated white noise (Smith *et al.*, 2004). However, experiments on physical damage and TTS need to be conducted in enclosed environments, with no possibility for the fish to escape from or avoid the sound. Avoidance reactions in the wild have been observed in response to vessel noise (Olsen *et al.*, 1983; Vabø *et al.*, 2002) and seismic shooting (Engås *et al.*, 1996; Engås and Løkkeborg, 2002). Intense sound may also lead to physiological stress (Smith *et al.*, 2004) or prevent fish from hearing biologically relevant sounds (masking) (Popper, 2003).

How anthropogenic sound affects fish will depend on the species, as hearing thresholds among fish are highly variable. Most teleosts are only able to detect frequencies below 500 Hz, called “hearing generalists” (e.g., Chapman and

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Hawkins, 1973; Hawkins and Johnstone, 1978; Mann *et al.*, 1998). Others, the “hearing specialists,” are sensitive to sounds over a wider frequency range (e.g., Popper, 1972; Kenyon *et al.*, 1998). Herring (*Clupea harengus*) is such a hearing specialist and is able to detect frequencies up to at least 4000 Hz (Enger, 1967; Mann *et al.*, 2005) due to a gas filled channel that connects the swimbladder to the otolith organs (Blaxter *et al.*, 1979; Denton and Gray, 1979; Popper *et al.*, 2004).

Norwegian Spring Spawning (NSS) herring is by far the largest herring stock in the northeast Atlantic. It is an important stock both in terms of fisheries and as prey for many other species (Hamre, 1990; Holst *et al.*, 2004; Røttingen and Slotte, 2001). A negative anthropogenic impact would thus potentially have large consequences for the fishery as well as the ecosystem. The annual distribution of NSS herring is divided into three main parts separated by more or less well defined migrations (Holst *et al.*, 2002); spawning along the Norwegian coast in February–March (Johannessen *et al.*, 1995; Røttingen and Slotte, 2001), feeding in the Norwegian Sea in April–September (Holst *et al.*, 2004), and overwintering in October–January (Dragesund *et al.*, 1997). Since the mid-1980s, almost the entire stock has been overwintering in Vestfjorden, Northern Norway (Dragesund *et al.*, 1997). This area has also frequently been used for military antisubmarine warfare exercises, which have involved use of active sonars transmitting at 5–8 kHz. Modern long-range active sonar also covers a frequency band below 2 kHz. Even though signals above 5 kHz would hardly be audible to NSS herring, the lower frequency bands of these sonars are well within their hearing range (Enger, 1967). Behavioral effects of sonars on marine organisms have been suggested (Hofman, 2004), but very few studies have been carried out on their effects on fish. An examination and a quantification of herring behavior in response to military sonars are therefore of high importance to establish environmentally safe sonar operation procedures in areas of high herring density.

Killer whales (*Orcinus orca*) prey on herring during the overwintering period (Similä and Ugarte, 1993; Similä, 1997; Nøttestad, 1998). Feeding killer whales use communication calls which could resemble the sonar signals tested in this study in both frequency and frequency modulation (Stranger, 1995; Van Opzeeland *et al.*, 2005; Miller, 2006). This similarity could potentially cause confusion in herring between sonar pings and killer whale calls and thus induce an antipredator response during sonar exposure.

The objectives of this study were to investigate whether sonar transmission of two different frequency bands; 1–2 kHz (F1) and 6–7 kHz (F2) elicited any behavioral responses in NSS herring. Controlled exposure experiments were conducted on herring in Vestfjorden in November 2006 using a sonar source representative of an operational naval sonar system. In addition, as a control experiment, herring were exposed to playbacks of sounds of herring-feeding killer whales. Herring behavior was monitored by two upward-looking, bottom-mounted echosounders, in an experimental design similar to a vessel avoidance experiment on herring (Ona *et al.*, 2007).

II. METHODS

Controlled exposure experiments were conducted between 12 and 30 November 2006, onboard the research vessel R/V H. U. Sverdrup II (Kvadsheim *et al.*, 2007).

A. Experimental design

The behavioral response of herring to sonar signals of two different frequency bands were tested: 1–2 kHz (F1) and 6–7 kHz (F2). Herring behavior was monitored acoustically by a system of two upward-looking, bottom-mounted echosounders (Simrad EK 60, Kongsberg Maritime AS, Horten, Norway) placed 400 m apart in a small fjord inside Vestfjorden (Patel, 2007). The echosounders transmitted a narrow beamed 38 kHz signal at a ping frequency of 1 Hz. The northern echosounder (A) was placed at a depth of approximately 400 m, while the southern (B) is at approximately 500 m. The system was connected onshore by an underwater data transmission and power cable. Data were collected in a cabin onshore by a PC running EK60 software, and echograms were continuously steamed to the internet, enabling real-time monitoring onboard the vessel during the experiments. The vessel passed directly above one of the two echosounders (later referred to as “passed echosounder”), while towing the sonar source, transmitting either F1 signals, F2 signals, or no signal (silent control). The echosounder (A or B) having the higher herring density was passed by the vessel in a straight line. Transmission started 1 nmi (nautical mile) from the position of the echosounder, and continued 1 nmi beyond it (referred to as one “passage”). The exact positions of the echosounders are given as their latitude and longitude, and GPS was used to ensure direct passage. During the experiment, the entire ship was darkened in order to prevent any light stimuli from affecting herring behavior. The 38 kHz echosounder of the ship was set in passive mode to avoid interference with the bottom-mounted echosounders. The vessel kept a constant speed (~8 kn) during the run. Killer whale feeding sounds were presented by lowering an underwater speaker (Lubell Labs model LL916, Columbus OH, www.lubell.com) to a depth of 27 m from a small boat, while the vessel made a silent control passage. The sounds played to the herring were monitored by hydrophone to assure that sounds were faithfully played back by the system and that the sounds were not in any way distorted. During passage, the small boat passed within a distance of 5–10 m of the source ship.

The experiment was conducted in a block design. Each block consisted of three passages of the echosounder, with each passage transmitting either F1 signals, F2 signals, or no transmission (silent control) (Table I). When killer whale feeding sounds were played, this stimulus replaced F2 in the block. The order of the different transmission types was randomized to distinguish between presentation order and sonar frequency. One experiment consisted of three blocks, with 1 h between each block. Experiments were conducted at different times of the day in order to separate exposure effects from natural day/night variations associated with diel vertical migration of herring (described in Huse and Korneliussen, 2000). Sound speed profiles through the water column were

TABLE I. Controlled exposure experiments carried out with herring. Experiments 1, 2, 3, and 6 consisted of three blocks each, and herring were exposed to F1 (1–2 kHz) and F2 (6–7 kHz) frequency sonar signals as well as a control run without transmission. Experiments 4 and 5 consisted of one block each, consisting of playback of killer whale feeding sounds (Orca), F1, and a control run. The order of transmission types within each block was randomized.

Experiment	Block	Date	Start time (UTC)	Stop time (UTC)	Transmission order	Echosounder passed
1	1	Nov. 12, 2006	21:05:00	22:16:23	F1-F2-control	A
1	2	Nov. 12, 2006	22:59:29	0:45:04	F2-control-F1	A
1	3	Nov. 13, 2006	1:24:31	3:07:50	control-F2-F1	A
2	1	Nov. 16, 2006	22:40:38	23:54:50	F2-F1-control	B
2	2	Nov. 17, 2006	0:46:31	2:02:04	control-F2-F1	B
2	3	Nov. 17, 2006	2:42:46	3:53:48	F1-control-F2	B
3	1	Nov. 18, 2006	13:21:54	14:34:40	F2-F1-control	A
3	2	Nov. 18, 2006	14:44:05	15:55:48	control-F2-F1	B
3	3	Nov. 18, 2006	16:44:50	17:50:07	F1-F2-control	A
4	1	Nov. 22, 2006	18:21:51	19:32:24	control-Orca-f1	B
5	1	Nov. 25, 2006	18:50:09	19:57:55	F1-control-Orca	B
6	1	Nov. 29, 2006	16:18:15	17:38:19	F1-control-F2	B
6	2	Nov. 29, 2006	18:28:14	17:38:19	F2-control-F1	B
6	3	Nov. 29, 2006	20:32:14	21:43:21	control-F1-F2	B

recorded after each experiment using an STD/CTD (model SD204, SAIV AS, Bergen, Norway). The profiles and sonar source specifications were used as input into an acoustic model (LYBIN, Royal Norwegian Navy and FFI) to estimate received sound pressure levels at the observation point of the echosounders during the experiments (Fig. 1).

B. Sonar source

Sonar signals were transmitted using a multipurpose towed acoustic source (Socrates, TNO-Defence, Security and Safety, The Hague, NL), a military experimental sonar currently used for the sonar research carried out for the Royal

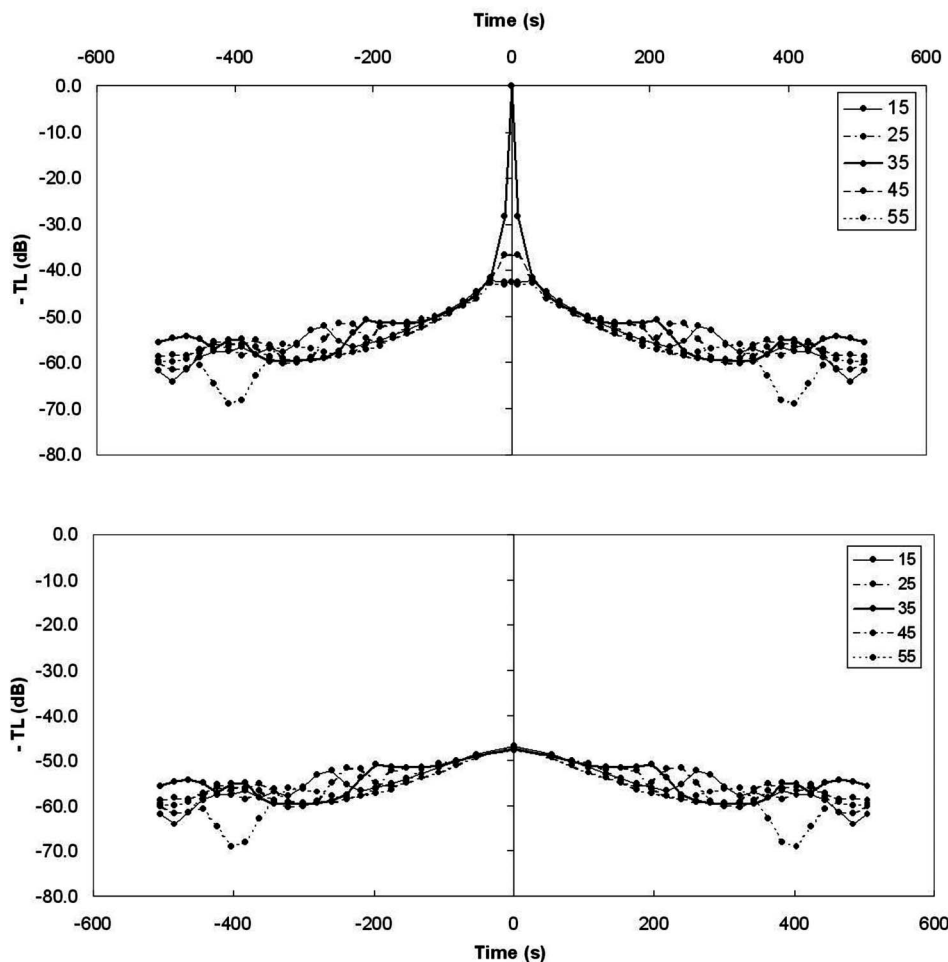


FIG. 1. Typical example of transmission loss (given in figure as TL) from the sonar source to the observation point of the echosounders as a function of time. Transmission started 1 nmi away from the observation point (the echosounder), and the source ship took 10 min (600 s) to pass the echosounder. The herring layer was usually distributed at depths between 10 and 50 m. Data are therefore presented for the individual depths; 15, 25, 35, 45, and 55 m. The source levels were 209 and 197 dB_{rms} (re 1 μPa at 1 m) for F1 and F2 transmissions, respectively, and received levels can be calculated as the difference between source level and TL. Transmission loss were calculated using the acoustic model LYBIN, with input parameters being the measured sound speed profiles and sonar source characteristics. The upper panel shows the received sound pressure levels at the echosounder being passed by the source ship, and the lower panel shows the received levels at the second echosounder, located ~400 m further south.

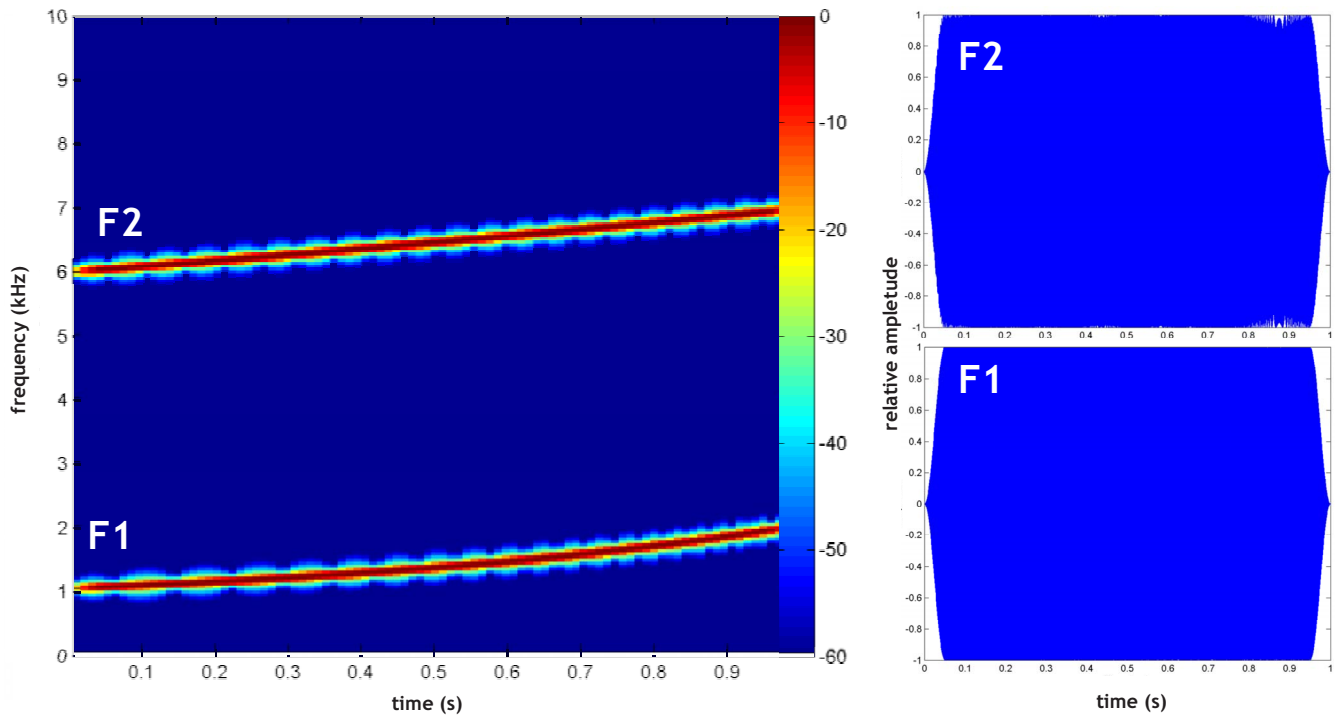


FIG. 2. (Color online) Spectrogram and waveform of the transmitted sonar signals: F1 and F2. The left panel shows the spectrogram for F1 (lower curve) and F2 (upper curve), with frequency as a function of time. The scale on the left indicates intensity (dB). The right panel shows the corresponding waveforms, with relative amplitude as a function of time. The transmitted signals were hyperbolic frequency modulated waveforms from 1 to 2 kHz for F1, 6 to 7 kHz for F2, both with duration of 1 s.

Netherlands Navy. Socrates is equipped with two free-flooded ring transducers, one for each of the frequency bands (F1 and F2), installed in a towed body, and the system was operated from within the vessel's laboratory. The depth of the towed source was approximately 35 m in all experiments. Both the F1 and F2 signals were hyperbolic up-sweeps with signal duration of 1.0 s (Fig. 2). Pulse repetition time was 20 s. These signals are commonly used signals in naval sonar operations. The source levels were 209 dB_{rms} and 197 dB_{rms} (re 1 μ Pa at 1 m) for F1 and F2 signals, respectively. Before transmitting at full power, a ramp-up procedure was performed in order to mitigate potential impacts of sonar transmission on any marine mammals in the area. This procedure consisted of a gradually increasing the source level from 150 to 209 dB_{rms} (re 1 μ Pa at 1 m) for 10 min before F1 transmission, and from 138 to 197 dB_{rms} (re 1 μ Pa at 1 m) for 3 min before F2 transmission. Pulse length was 1.0 s and pulse repetition time 10 s during ramp-up. After ramp-up, full power transmission was initiated with 1 s pulses and 20 s pulse-repetition time.

The killer whale feeding sounds played to the herring were recorded using a digital acoustic recording tag attached to killer whales ("Dtag," Johnson and Tyack, 2003). The sound sequence was extracted from a Dtag recording of a killer whale that had been feeding on herring in the same general area a few days earlier. The Dtag contains a 400 Hz one pole high-pass filter and has a flat frequency response up to 45 kHz. Tag recordings also contained surfacing sounds, which were cut out of the record, and low-frequency flow noise due to the tagged animal movements, which were reduced by high-pass filtering at 800 Hz. The Lubell speaker

has a response ± 8 dB from 600 Hz to 20 kHz. Therefore, the feedings sounds are only representative of actual killer whale feeding sounds over the frequency band of 800 Hz–20 kHz. During feeding, killer whales produce whistles, pulsed calls, and echolocation clicks, as well as intense sounds such as tail-slaps (Van Opzeeland, 2005; Simon *et al.*, 2007a). The feeding sounds played back included calls, echolocation clicks, and tail-slaps (Fig. 3) produced both by the tagged whale and other nearby whales. Because the feeding group in which the whale was tagged consisted of at least 20 animals, most sounds are likely from other whales than the tagged animal. The frequency content of most calls and whistles predominates above 800 Hz, but some low-frequency components of tail-slap sounds were likely removed due to the high-pass filter of the sound sequence. The source levels of the feeding sounds played from the speaker corresponded to previously described source levels of feeding killer whale calls [150–160 dB_{rms} (re 1 μ Pa at 1 m)] (Miller, 2006; Simon *et al.*, 2006).

C. Data analysis

One of the two echosounders was passed during each experiment. Herring at the other echosounder, positioned 400 m away, was thus exposed to a lower received sound pressure level. The passed and nonpassed echosounders were therefore compared with respect to the reactions of herring.

The echosounders recorded the acoustic volume backscatter strength by time and depth at a sampling frequency of 1 Hz over a 100 m range that spanned the main herring layer. Volume backscattering strength is defined as s_v

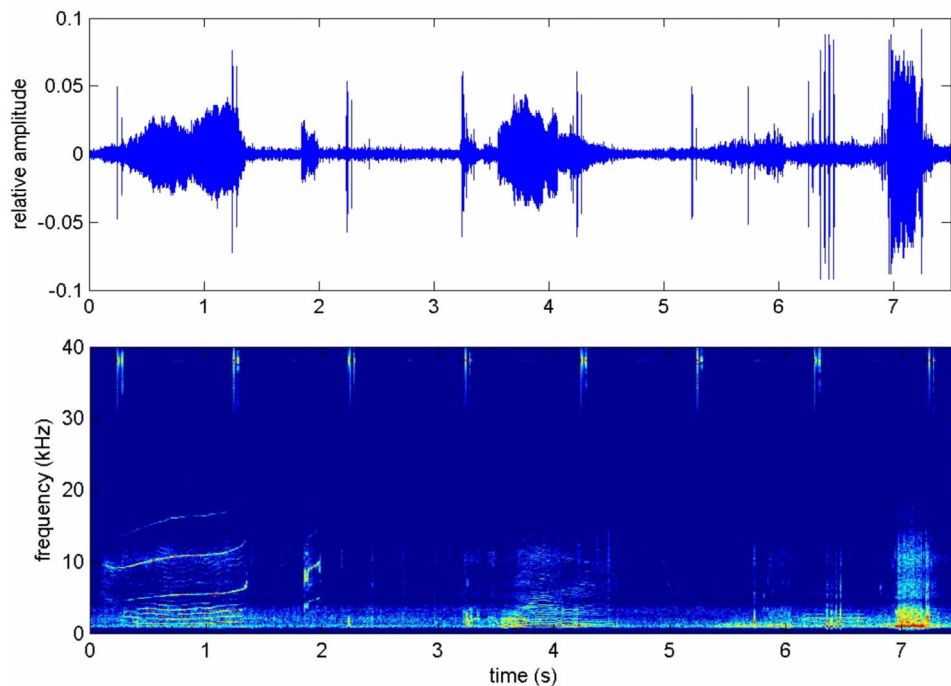


FIG. 3. (Color online) Waveform (top panel) and spectrogram (bottom panel) of a representative segment of the killer whale feeding sounds recorded during playback to herring. Note that the signals from the echosounder used to monitor the behavior of the herring are apparent at 38 kHz. The killer whale sounds include a number of calls, and a tail-slap sound (starting at 7 s). The call around 1 s is a typical example of a call resembling the sonar signals in duration and frequency content (see Fig. 2).

$=\Sigma\sigma_{bs}/V$ (m^{-1}), where V is volume, and σ_{bs} is the backscattering cross sections of individual targets within V (definitions given in MacLennan *et al.*, 2002). Two response variables, depth and s_v , are derived from the data for each passage. One passage is defined as the time interval from when the approaching vessel is 1 nmi away until 1 nmi beyond the bottom-mounted transducer. The depth variable is defined as the s_v weighted median depth throughout the passage, and s_v is defined as the mean volume backscattering s_v over each passing both within the 100 m range. Four different explanatory variables were used to model these response variables: (1) transmission type [F1/F2/control/killer whale playback (orca)], (2) order of the transmission types, (3) experiment, and (4) block number within an experiment. Generalized linear mixed models (GLMMs) (Littell *et al.*, 1996) were fitted to the data. These do not require errors to be independent, and permit a distinction to be made between random and fixed effects, where the errors may be conditional on a set of normally distributed random factors (McCulloch and Searle, 2001). Order and experiment were initially specified as random effects, but due to statistically negligible variance these were fitted as fixed in addition to the initial fixed factors: transmission type and block. In this model, the explanatory variable is linked to the response variable according to

$$g(E[y]) = X\beta + \varepsilon, \quad (1)$$

where y is the response vector (depth or s_v), X is the matrix of the fixed factors, β is the column vector of the fixed effect parameters to be estimated, and ε is the vector of the random errors. The function g is called a link function, a nonlinear function that relates $E[y_i]$ to the linear component $X_i \beta$. For the depth response, a normal-error model with an identity link function was used, while for the s_v response a gamma-error model with a log link function. The GLMMs were fitted in SAS® Version 9.1 using the GLIMMIX procedure

(SAS Institute Inc., 2003). The model estimates β , and probability limits (p -values) of less than 0.05 were used to indicate whether this represented a significant factor in explaining the response. Multiple comparisons (Tukey's) were performed on those factors found to be significant.

III. RESULTS

Six experiments comprising a total of 14 blocks were performed. Four of the experiments consisted of F1-F2-control blocks, with three blocks in each experiment. The last two experiments each consisted of only one block, and the transmission was F1—killer whale playback (orca)—control (Table I).

Depth and s_v values from the passed and the nonpassed echosounder were compared, but neither were significantly different ($p > 0.05$) in any of the experiments or transmission types. During those passages that produced significant avoidance reactions (killer whale playback passages, see Sec. III B), a reaction was detected on both echosounders, indicating that the produced sound was fully detectable for the herring at this range. Data from both echosounders were therefore included in the analysis.

A. Herring reactions to sonar transmission

No obvious difference between the two types of transmission (F1 and F2) and the control could be seen when inspecting the echograms (Fig. 4). However, there was a local effect around the towed body during passage (Fig. 4), regardless of transmission type.

1. Depth response

Experiment was the only significant factor in explaining the average depth response ($p < 0.001$), with Experiment 4 having a herring layer significantly deeper and Experiment 5

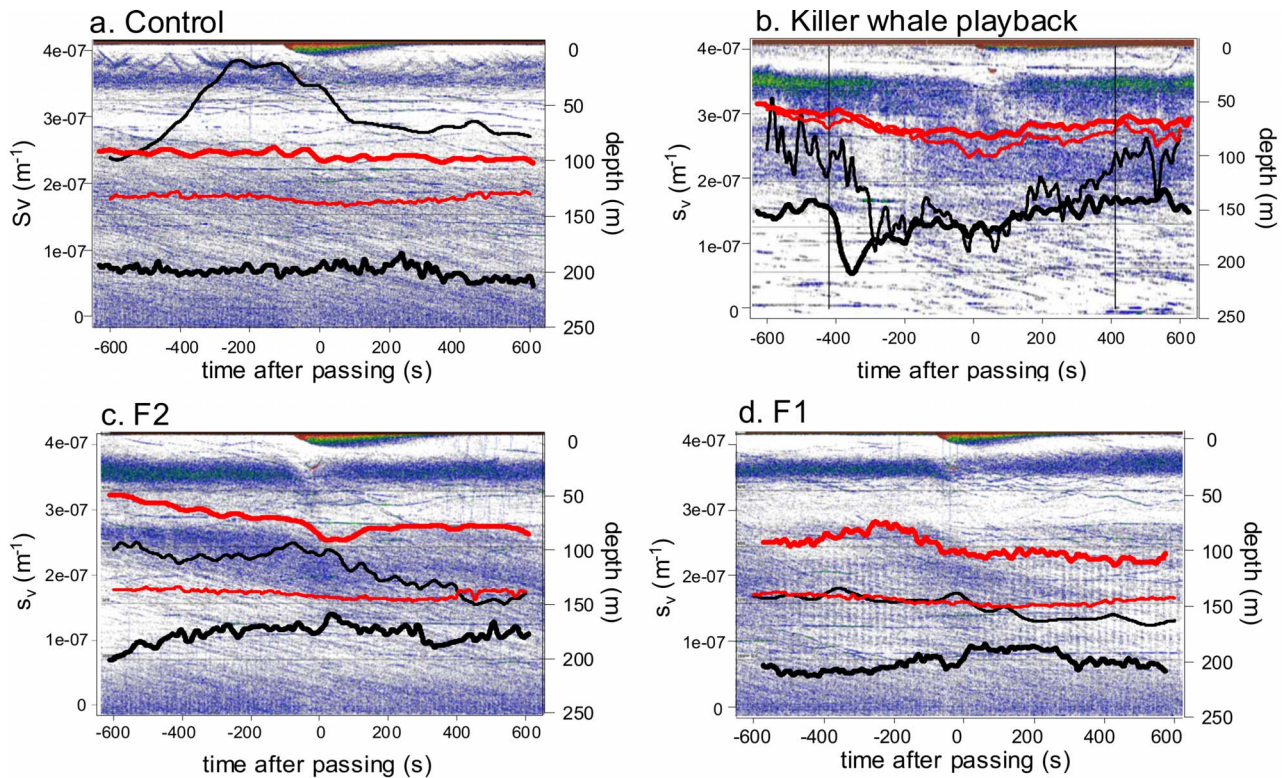


FIG. 4. (Color online) Typical echogram examples. Responses to the sounds were measured as herring density, s_v and herring vertical distribution, $depth$, and are presented as a function of time. Thick lines represent the particular experiment that the echogram is taken from, while thin lines are the average of all passages of this transmission type. The vessel wash from the passing vessel as well as the towed body sonar can be seen as strong distinct echoes around time=0. (a) Control; passage with vessel and sonar source without any transmission. The upper line is s_v experiment, followed by $depth$ experiment, $depth$ average, and s_v average on the bottom. (b) Playback of killer whale feeding sounds. The vertical lines indicate start and stop of playback. The two upper lines indicate $depth$ experiment and $depth$ average, respectively, the lower ones indicate average and experiment, respectively. (c) F2 transmission (6–7 kHz). The upper line is $depth$ experiment, followed by s_v average, $depth$ average, and s_v experiment on the bottom. (d) F1 transmission (1–2 kHz). The upper line is $depth$ experiment, followed by $depth$ average, s_v average, and s_v experiment on the bottom. No clear differences between sonar transmission (F1/F2) and the control can be detected by inspecting the echograms. A small vertical drop in the herring layer is seen at the point in time when the towed body sonar passes, but this reaction is similar for all types of transmission, and hence probably an avoidance to the source rather than the sound. In response to the passage involving playback of killer whale feeding sounds (b), there is a reduction in density that starts before passage of the source, almost immediately after onset of the sound, indicating that this reaction is to the sound. Echograms (a), (c), and (d) are from November 12, 2006, while (b) is from November 22, 2006.

significantly shallower than the rest [Table II, Fig. 5(a)]. No significant effects were found for the following factors:

TABLE II. Significant Tukey comparisons of the four factors included in the statistical model (experiment, block, transmission type, and order of transmissions), three factors had significant effect in explaining the average horizontal (S_v) and vertical (depth) response of herring; experiment (significant for depth and S_v), block, and transmission (significant for S_v).

Factor	Significant differences, s_v -response	Significant differences, depth-response
Experiment	Exp. 1-Exp. 3 Exp. 2-Exp. 3 Exp. 2-Exp. 4 Exp. 3-Exp. 4 Exp. 3-Exp. 5 Exp. 4-Exp. 2 Exp. 4-Exp. 5	Exp. 1-Exp. 4 Exp. 2-Exp. 4 Exp. 3-Exp. 4 Exp. 5-Exp. 4
Block	Block 1-Block 3 Block 2-Block 3	
Transmission	Control-Orca F2-Orca	

transmission type ($p=0.247$), block ($p=0.268$), or order of transmission types within a block ($p=0.840$).

2. Density response

Significant factors in explaining the average s_v response were experiment ($p<0.001$) and block ($p=0.0003$). *Post hoc* (Tukey) comparisons showed which of the different experiments and blocks that differed (Table II). Experiment 3 had a significantly higher s_v , and Experiment 4 had significantly lower s_v than the rest [Fig. 5(a)]. Within the experiments, block 3 had a significantly lower s_v than the first two ($p=0.0003$) [Fig. 5(b)]. There was neither significant effect of the order of the transmission types ($p=0.914$) [Fig. 5(d)] nor between the three types of transmission (F1-F2 control) ($p=0.529$) [Fig. 5(c)]; hence the sonar signals (F1 and F2) did not cause any reaction different from that of a passage without any transmission (control).

B. Herring reactions to playback of killer whale feeding sounds

The sonar transmission passages, F1 and F2, were not significantly different from the control passages of no trans-

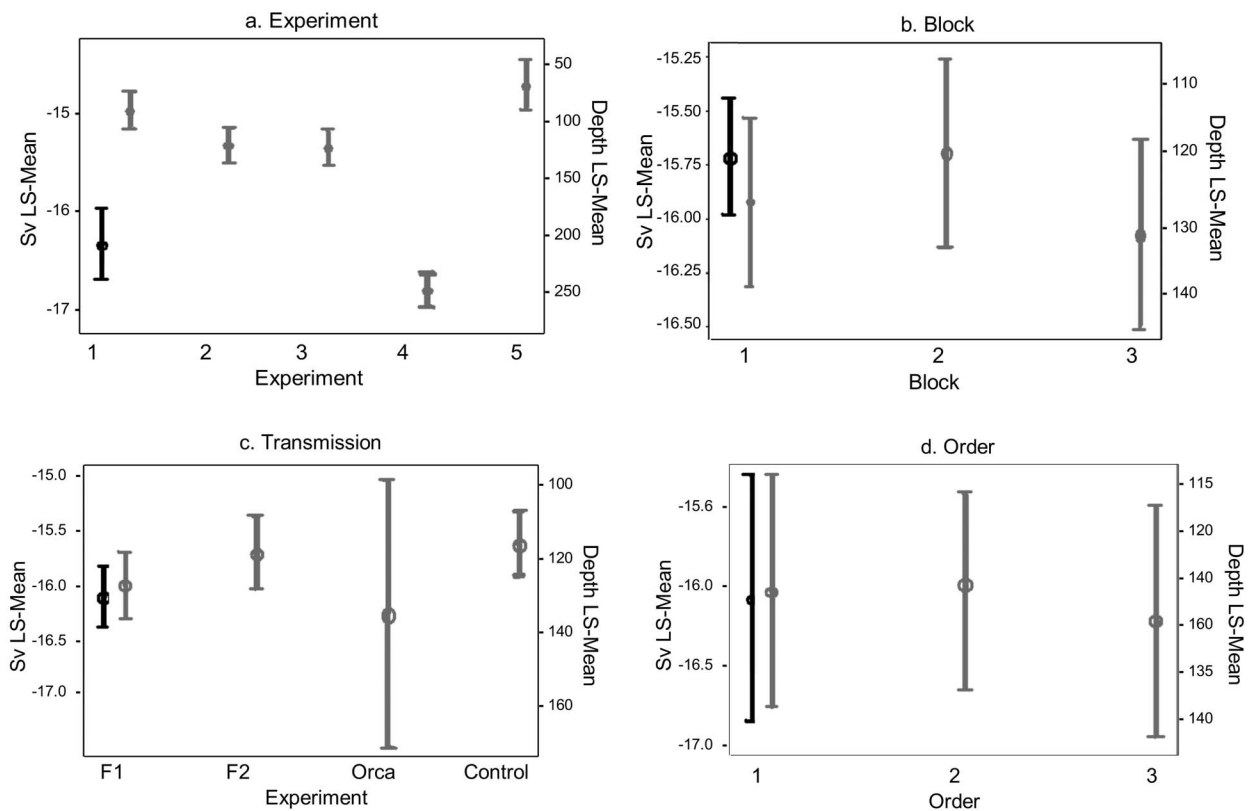


FIG. 5. Estimates and 95% confidence bounds for the predicted average density response, s_v (left bars in black), and vertical response, $depth$ (right bars in gray), for the following factors: (a) experiment, (b) block within experiment, (c) transmission type, and (d) order of the types of transmission. (a) There were significant differences between the experiments. Experiment 4 produced significantly lower values than the other days regarding both s_v and depth. Experiment 3 had significantly higher s_v than the other days. (b) Block 3 had a significantly lower s_v than blocks 1 and 2 within an experiment, but no significant differences were found with respect to depth. (c) There were no significant differences between the two sonar transmission types (F1 and F2) and the control either for s_v or depth. Playback of killer whale feeding sounds (Orca), however, had significantly lower s_v values than F2 and control. (d) There was no significant effect of the order of the types of transmission, nor for s_v nor depth.

mission. The passages involving playback of killer whale feeding sound did, however, produce significantly lower s_v than the control passages ($p=0.016$), indicating a reduced density in herring when exposed to the killer whale sounds. Killer whale playback passages also had clearly lower s_v than those of the F1 and F2 passages, but this was significant only for F2 ($p=0.046$ for F2, $p=0.067$ for F1). Visual inspection of the echograms involving killer whale passages clearly shows a reduction in herring density (s_v) almost immediately after the start of playback [Fig. 4(b)]. The average depth associated with the killer whale playback passages was notably lower than during other transmission types [Fig. 5(c)]. However, this difference was not significant ($p=0.335$). The estimate for killer whale playbacks had far lower precision both for s_v and depth, a natural consequence of having only two experiments of this type, compared to 12 for the other transmission types.

IV. DISCUSSION

This study has documented how overwintering NSS herring react to typical military sonar signals in the frequency band of 1–7 kHz, and has important implications for establishing guidelines for a safe operation of military sonars in areas densely populated by herring.

A. Experimental methods

The present results demonstrate that overwintering herring do not avoid sonar sounds at the tested received levels by neither horizontal nor vertical escape reactions. The reliability of these findings is strengthened by the immediate reduction in density and vertical movement seen during passages involving playback of killer whale feeding sounds. These passages demonstrate the nature of herring avoidance reactions, as well as the capability of the experimental setup to detect and describe such reactions.

We used experimental setups similar to those employed by Vabø *et al.* (2001) and Ona *et al.* (2007) for studying herring reactions to vessel noise. In the present study, it was essential to know the avoidance effects caused by the vessel and the towed sonar source, in order to separate behavioral reactions caused by an emitted signal from that caused by the vessel. Our results shows an intermittent drop in the herring layer at the time the vessel with the towed sonar passed the echosounder (visible effect in echograms in Fig. 4 at around time=0). This reaction lasted less than a few minutes and resembles the response characterized as vessel avoidance by Ona *et al.* (2007). This avoidance was the same for all types of passages, including the silent controls with no sonar transmission. This reaction is therefore likely to be caused by

avoidance to the passing vessel. It might also be an avoidance of the wire towing the sonar, as has been previously described by Handegard and Tjøstheim (2005), or possibly an avoidance of the towed body itself. The observed reaction also occurred within the same time interval as the measured vessel avoidance (within 2 min before vessel passage) (Ona *et al.*, 2007). With the source levels tested, sonar sound was well within the detection range of herring from the onset of transmission (approximately 10 min before vessel passage) (Fig. 1). The reaction to killer whale playback showed an avoidance reaction starting at about the time of sound onset, and a similar reaction should thus be expected for a potential sonar reaction. The statistical analysis was conducted on s_v and depth values averaged over the entire period of full power transmission, totally approximately 20 min. The vessel effect was detected only by the passed echosounder, but there was no significant difference in average s_v and depth between the two echosounders, indicating no confounding effect on the statistical analyses. The experimental setup was therefore considered adequate to separate a reaction to the sonar from that caused by a vessel/wire reaction.

B. Herring reactions to sonar transmission and killer whale playback

There was no significant reduction of herring density (s_v) or vertical position (depth) of the herring layers during runs involving sonar transmission (F1 or F2) compared to the control runs without any transmission. The daytime experiment (Experiment 3) produced significant differences in herring distribution [Table II, Fig. 5(a)], attributable to the observed typical diel variation (Huse and Korneliussen, 2000). Such variations, however, were taken into account in the models. There was also a significant reduction in herring density in the last block of each experiment [Fig. 5(b)]. The results presented here suggest that this is more likely to have been caused by diel variation or an adaptive response to the vessel and towed body than exposure to sonar.

The playback of killer whale feeding sounds induced an immediate dispersal response and downward movement of the herring, clearly visible in the echograms [Fig. 4(b)]. Both the average s_v and depth values were noticeably lower than during the control passages [Fig. 5(c)], although the effect was only significant for s_v , and the power relatively weak. However, the experimental effort was unbalanced with respect to the playback of killer whale sounds, with only approximately 1/6 of the effort used on measuring responses compared to the other types of transmission. It is compelling to speculate in that a study with equal effort put into the killer whale playbacks as to the other transmission types might provide a strong statistical case for differences. More studies of killer whale playback experiments of similar setup should therefore be performed.

In this study, source levels during full power transmission were 197 and 209 dB_{rms} re 1 μ Pa at 1 m for F1 and F2, respectively. With a maximum transmission loss of -70 dB (see Fig. 1), herring were exposed to a minimum received sound pressure level of 127 dB_{rms} (F1) and 139 dB_{rms} (F2) re 1 μ Pa. Received level increased as the source ship moved

closer to the observation point at the echosounder, as a function of distance/time (Fig. 1). At night, when most of the experiments were carried out, high-density layers of herring were located between 10 and 50 m, and the source was towed at 35 m. At the closest point of drive-by, some herring were thus within a few meters range of the source, and received sound pressure levels will thus approximately equal the source levels (197 and 209 dB_{rms} re 1 μ Pa at 1 m for F1 and F2, respectively). The precise source level of operational military sonars within the different nations navies are often regarded classified information, but are likely to exceed the level used in the present experiment. We can thus not exclude the possibility of an effect when received levels exceed those tested here. However, the volume of water exposed to such levels is relatively small, and the fish biomass exposed to levels above 209 dB_{rms} re 1 μ Pa would be too small to have any effect on the population level (Kvadsheim and Sevaldsen, 2005).

Herring in the area are primarily caught by purse seine vessels, with herring catchability being strongly dependent on the diel migration toward the surface at night (described by Huse and Koreliussen, 2000). The present results show that naval sonar does not affect this behavior and is therefore not expected to have any negative influence on the fishing fleet's ability to catch herring. It is also unlikely that the specific conditions in the test location including background noise levels, the presence of shipping or other factors, would decrease the sensitivity of the fish.

Very few studies have examined how military sonars may affect fish. Jørgensen *et al.* (2005) investigated the effect of 1.5–6.5 kHz sonar signals on juvenile fish of different developmental stages and species, including herring. No tissue damage was found and postexposure development was normal, but juvenile herring showed strong behavioral reactions when exposed to sonar signals close to the assumed resonance frequency of the swimbladder. When exposed to levels above 180–190 dB_{rms} re 1 μ Pa, significant mortality was observed in juvenile herring (Jørgensen *et al.*, 2005), but Kvadsheim and Sevaldsen (2005) showed that this mortality would constitute less than 1% of the daily mortality of juvenile herring. Compared to natural mortality, even large scale military exercises would thus not significantly impact stocks of juvenile herring significantly at a population level. Thus, apparently herring is particularly sensitive to acoustic stimuli when they are exposed to sound corresponding to the resonance frequency band of the swimbladder. This resonance frequency band will depend somewhat on the species morphology but is mainly determined by the size of the fish and the depth (Løvik and Hovem, 1979). Adult herring at 10–50 m depth, which is the depth of the herring layer in most of the present experiments, is expected to have a resonance frequency between 1.0 and 2.5 kHz (Løvik and Hovem, 1979), corresponding to F1. Thus, this study has shown that even when exposed to sonar signals corresponding to swimbladder resonance, adult herring does not appear to react significant to such signals. However, the signal type used was frequency modulated sweeps, which will barely touch on the resonance frequency band for a very short moment. Long duration continuous wave signals may have a

different effect. Popper *et al.* (2007) studied the effect of very low-frequency sonar signals (below 1 kHz) and found a minor auditory temporary threshold shift, but no mortality, nor damage on tissue or sensory cells in the rainbow trout (*Oncorhynchus mykiss*). The present results are supported by those of Popper *et al.* (2007) that fish do not avoid a military sonar transmitting within their hearing range. Slotte *et al.* (2004) studied the behavioral effects of seismic shooting on herring and found no short term effects. A long-term decrease in biomass following a period of seismic shooting was observed, but they pointed out that this might just as well have been caused by feeding migration or natural fluctuations.

The reaction to the killer whale feeding sounds did cause an avoidance reaction by the herring, suggesting the intriguing possibility that fish were able to distinguish the killer whale feeding sounds from the sonar sounds. Reactions by clupeid fish to sounds of odontocete predators are also documented in previous studies (Mann *et al.*, 1998; Wilson and Dill, 2002).

Killer whales are the main predator on overwintering herring in Vestfjorden (Similä and Ugarte, 1993; Similä, 1997; Nøttestad, 1998), and such avoidance reactions as observed here are often seen in response to attacks (Nøttestad, 1998; Nøttestad and Axelsen, 1999), with hearing assumed to be an important cue inducing predator avoidance (Similä and Ugarte, 1993). Predation pressure by killer whales during overwintering is severe (Nøttestad and Axelsen, 1999), and awareness and vigilance are important to be able to escape from a predator. On the other hand, herring do not feed during overwintering, and energy minimization is thus of great importance (Slotte, 1999). Overwintering herring should thus be in a state of high sensitivity to predator calls, but escape reactions, with high energetic costs, should be avoided when unnecessary. Being able to discriminate predator sounds from other similar sounds will offer a great advantage and maximize energy conservation by limiting reactions to real threats. It is, however, not known which sound component in the recording used during the killer whale playback that triggered the escape reactions. In addition to the F1 signals, which are of high similarity in frequency and frequency modulation characteristics as some killer whale feeding calls (Miller, 2006; VanParijs *et al.*, 2004; Moore *et al.*, 1988), the sounds played back also included tail slaps and echolocation clicks. However, the majority of the energy in the echolocation clicks (Simon *et al.* 2007b) is above the hearing capability of herring (Enger, 1967; Mann *et al.*, 2005). Tail slaps (Simon *et al.*, 2005) on the other hand will be highly audible to herring, but potential sounds of frequencies lower than 800 Hz will be cut off due to the high-pass filter of the speaker. Hence, the sounds that the herring reacted to were mainly in a similar frequency range as the sonar signals. In addition to frequency and waveform, fish may be able to evaluate the repetition rate of a sound signal representing an odontocete predator (Astrup and Møhl, 1998). Which characteristic of the sound is played back cannot be determined in this study. Some of the difference in the reaction to the killer whale sounds playbacks may have been due to differences in how they were presented. The killer

whale sounds were played back from a speaker located within the herring layer from the start of the playback, while the sonar source was gradually approaching the herring. However, the present results show that the experimental setup used in this study were adequate to reveal a potential escape reaction, thus acting as a negative control for the lack of response to the sonar signals.

Even though the present results demonstrate that overwintering herring show a lack of avoidance when exposed to sonar signals above 1 kHz, herring are known to change their behavior according to their functional, physiological, and motivational states (feeding, spawning, overwintering, and migrating) in terms of catchability (Mohr, 1964; Mohr, 1971) schooling dynamics, swimming speed, and reactions to different stimuli (Nøttestad *et al.*, 1999). Reactions to vessel noise also differed from being strong during the overwintering period (Vabø *et al.*, 2001) to relatively weak during prespawning (Skaret *et al.*, 2006). This may indicate that herring in different stages of their life history phase perhaps also may react differently to a military sonar. Such differences in reactions are controlled by trade-offs between predation risk, spawning success, and feeding, all of which differ between functional states (Nøttestad *et al.*, 1999). This demonstrates the need for more studies of how herring in different life history stages may react to military sonars. Nøttestad *et al.* (1999) found the most pronounced difference in behavior between herring in the nonfeeding state and during feeding after spawning was terminated. The present study concerned nonfeeding, overwintering herring, and a future study should thus focus on postspawned, feeding herring.

V. CONCLUSIONS

The results presented in this study leads to the conclusion that the operation of sonar systems at the tested frequencies and source levels (above 1 kHz and 209 dB_{rms} re 1 μ Pa at 1 m) will not have any large scale detrimental effects on overwintering herring populations or on the commercial herring fishery. Thus, such sonar systems may be safely operated in areas of overwintering herring, such as in Vestfjorden. More studies of similar character should be performed, involving both sonar transmission and killer whale playback, on herring during parts of their yearly cycle, such as, e.g., during the feeding or spawning period in order to allow the results to be more widely generalized.

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