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Citation: *The Journal of the Acoustical Society of America* **131**, 1632 (2012); doi: 10.1121/1.3675944

View online: <http://dx.doi.org/10.1121/1.3675944>

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Behavior of captive herring exposed to naval sonar transmissions (1.0–1.6 kHz) throughout a yearly cycle

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(Received 17 February 2010; revised 16 August 2011; accepted 13 December 2011)

Atlantic herring, *Clupea harengus*, is a hearing specialist, and several studies have demonstrated strong responses to man-made noise, for example, from an approaching vessel. To avoid negative impacts from naval sonar operations, a set of studies of reaction patterns of herring to low-frequency (1.0–1.5 kHz) naval sonar signals has been undertaken. This paper presents herring reactions to sonar signals and other stimuli when kept in captivity under detailed acoustic and video monitoring. Throughout the experiment, spanning three seasons of a year, the fish did not react significantly to sonar signals from a passing frigate, at received root-mean-square sound-pressure level (*SPL*) up to 168 dB re 1 μ Pa. In contrast, the fish did exhibit a significant diving reaction when exposed to other sounds, with a much lower *SPL*, e.g., from a two-stroke engine. This shows that the experimental setup is sensitive to herring reactions when occurring. The lack of herring reaction to sonar signals is consistent with earlier *in situ* behavioral studies. The complexity of the behavioral reactions in captivity underline the need for better understanding of the causal relationship between stimuli and reaction patterns of fish. © 2012 Acoustical Society of America. [DOI: 10.1121/1.3675944]

PACS number(s): 43.80.Nd, 43.50.Rq, 43.50.Sr [MCH]

Pages: 1632–1642

I. INTRODUCTION

The effects of anthropogenic sounds on marine animals are increasingly studied, particularly in the past decade (e.g., Nowacek *et al.*, 2007; Popper and Hastings, 2009). Anthropogenic sound sources receiving most attention include ships, seismic air guns, and military sonars (Popper *et al.*, 2004), due to their low-frequency (i.e., long range), high source level, and widespread use. Despite the substantially increased effort, this scientific field remains in its infancy, especially regarding the effects of sound on fish (Popper *et al.*, 2004). Potential negative effects of anthropogenic sounds range from: auditory tissue damage (Enger, 1981; Hastings *et al.*, 1996; McCauley *et al.*, 2003); to temporary hearing loss (Popper *et al.*, 2007); to changes in behavior, such as avoidance of the sound source (e.g., Skalski *et al.*, 1992; Engås *et al.*, 1996; Slotte *et al.*, 2004).

Atlantic herring, *Clupea harengus*, are among the most numerous of the fishes in the North Atlantic. Consequently, they are prey for animals on many trophic levels and are the target of a commercially important fishery (Blaxter, 1985; Hamre, 1990). Herring are sensitive to a wider acoustic bandwidth than most teleost fishes (Chapman and Hawkins, 1973) and can detect frequencies up to 4 kHz (Enger, 1967). However, much remains uncertain about the auditory capabilities of herring and the stimuli and circumstances causing them to react to sounds (Wilson and Dill, 2002; Ona *et al.*, 2007; Sand *et al.*, 2008).

While herring did not react to sounds from a marine mammal deterrent device (Wilson and Dill, 2002), they did respond to various anthropogenic sounds such as seismic shooting (Slotte *et al.*, 2004), and ship noise (Olsen *et al.*, 1983; Misund and Aglen, 1992; Pitcher *et al.*, 1996; Ona *et al.*, 2007). Herring also exhibit seasonally variable avoidance reactions to predator attacks (Fernø *et al.*, 1998; Kvamme *et al.*, 2003), fishing activity (Mohr, 1964, 1971), and approaching vessels (Fernandes *et al.*, 2000; Vabø *et al.*, 2002, Skaret *et al.*, 2006).

Modern, long-range, naval, anti-submarine-warfare sonar systems, hereafter SONAR, typically transmit frequencies ranging from 1 to 10 kHz (Ainslie, 2010). Frequencies in the lower portion of this bandwidth are within the hearing range of herring (Enger *et al.*, 1967), and SONARs are often operated in areas where herring are known to reside. However, wild herring did not exhibit a significant response to SONAR transmissions in the overwintering phase (Doksaeter *et al.*, 2009), but may respond very differently in other phases of their yearly cycle. Here, to explore these possibilities, the behaviors of captive herring are observed during exposure to SONAR and other transmissions, in controlled environments (following Wilson and Dill, 2002; Ona, 2003), during three seasons spanning a year.

II. METHODS

Four experiments were conducted in different seasons during one year (Table I). The experiments involved exposing herring to various stimuli, including a SONAR-transducer towed behind a frigate and simulated SONAR transmissions from a stationary transducer. Continuous sound from an outboard engine and very short duration sounds from a wooden

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TABLE I. Overview of experiments.

Experiment	Date	Exposure type	Experimental location	Number of blocks conducted	Type of runs within block
1	Sept 15–17 2008	Frigate sonar	Sheltered fjord	2	GFM-SFM-CW-CON
1	Sept 15–17 2008	Fence strike	Sheltered fjord	1	FS
2	Jan 20–21 2009	Outboard engine	Aquaculture station	5	EL-EH
2	Jan 20–21 2009	Fence strike	Aquaculture station	1	FS
3	Feb 3–5 2009	Frigate sonar	Sheltered fjord	7	GFM-SFM-CON
3	Feb 3–5 2009	Fence strike	Sheltered fjord	1	FS
4	Sept 29–Oct 01 2009	Simulated frigate sonar	Aquaculture station	7	GFM-SFM-CW-CON
4	Sept 29–Oct 01 2009	Outboard engine	Aquaculture station	4	EL-EH
4	Sept 29–Oct 01 2009	Fence strike	Aquaculture station	1	FS

board striking the net pen fence were included to test whether the captive herring would react, and if our setup were able to detect that reaction.

All experiments used a block design, with each block consisting of runs of similar length of the different exposure types, including control runs, in randomized order. Experiments were conducted at different times of the day, to resolve potential day-night effects. One hour was set initially as separation between the blocks. This was based on previous studies showing herring resumed the initial vertical distribution well within 1 h after exposure to vessel noise (Vabø *et al.*, 2002; Ona *et al.*, 2007).

A. Captive herring

In June 2008, 7.5 t of adult herring (mean length of 30.8 cm, mean weight of 206.4 g) were caught by a commercial purse-seine vessel and transported live to an aquaculture facility operated by the Institute of Marine Research (IMR) in Austevoll, near Bergen, Norway. The fish were kept for approximately 1.5 years in two rectangular-net pens, 12-m long by 12-m wide by 10-m deep (volume = 1440 m³). The herring were fed with standard pellets of small size. The animal collection was permitted by The Royal Norwegian Ministry of Fisheries, and the experiments were permitted by the Norwegian Animal Research Authority. During experiments, approximately four tons of the herring were transferred to a 5-m long by 5-m wide by 20-m deep, movable pen. After end of experiment, the fish were transferred back to the regular pens.

Experiment 2 and 4 were conducted with the experimental net pen positioned at the seaside of the floating pier at the aquaculture station. During experiments 1 and 3 the experimental net pen was towed from the aquaculture station to a close by fjord where the frigate could operate. The pen was then towed at low speed (ca. 0.9–1.9 km/h, depending on the current) by a fishing vessel to minimize any stress on the herring, including scale loss due to increased physical contact with the net walls (Lockwood *et al.*, 1983; James *et al.*, 1986; Misund and Beltestad, 1995). Transit to the site took approximately 10 h, and the herring were allowed to habituate to their new environment for 12 h before the experiments were conducted. The herring were constantly monitored by trained personnel during the transit and habituation period, both visually from the surface and with echosounder and video camera, and after 12 h no signs of behavioral stress were detected, and the

herring were observed feeding. Throughout the experiments, the pen was secured to the fishing vessel. The vessel's bridge housed the equipment for monitoring the experiment and provided communications with the frigate. All engines of the fishing vessel were switched off during experiments. For the experiments at the aquaculture station (experiments 2 and 4) a mobile barrack adjacent to the floating pier and net pen housed the electronics and served as control station.

B. Sound exposure

1. Frigate SONAR transmissions

In experiment 1 and 3 herring were exposed to SONAR signals transmitted from a Fridtjof Nansen class multi-purpose frigate of the Royal Norwegian Navy using their combined active/passive towed sonar (CAPTAS mk 2, Thales Underwater Systems) towed at 50 m depth. The transmitted signals were either: (1) 1-s duration, 1.0–1.6-kHz, hyperbolic-frequency-modulated, up-sweep (FM), with 18-s inter-pulse interval; or (2) 4-s duration, 1-kHz, weighted-continuous-wave (CW), with 40-s inter-pulse interval. For either signal, the root-mean-square (rms) sound pressure level of the source (*SL*) was approximately 215 dB re 1 μ Pa at 1 m, typical of SONAR operations in sheltered waters. The maximum *SL* of the SONAR system was not available information.

The SONAR transmissions were introduced either gradually or suddenly. The rms sound pressure level (*SPL*) received by a hydrophone inside the pen gradually increased as the frigate, beginning approximately 1.9 km (one nautical mile) away, approached the pen at 14.8 km/h (8 knots), and reached a maximum *SPL* at the closest point of approach (CPA) equal to 500 m (Fig. 1). The *SPL* gradually decreased as the frigate continued away from the pen to a distance of approximately 1.9 km. During separate runs along the same transect, the transmissions were suddenly introduced at maximum *SPL*, by transmitting the first pulse at CPA, with gradually decreasing RL as the frigate moved away for another 1.9 km. Transects were also run without transmissions (silent controls).

Each block consisted of four separate runs along the transect; gradually introduced FM (GFM), suddenly introduced FM (SFM), gradually and suddenly introduced CW (CW) transmissions, and silent control runs with the transducer in passive mode (CON). In experiment 3, the CW run was removed from the block to obtain more replicates. FM

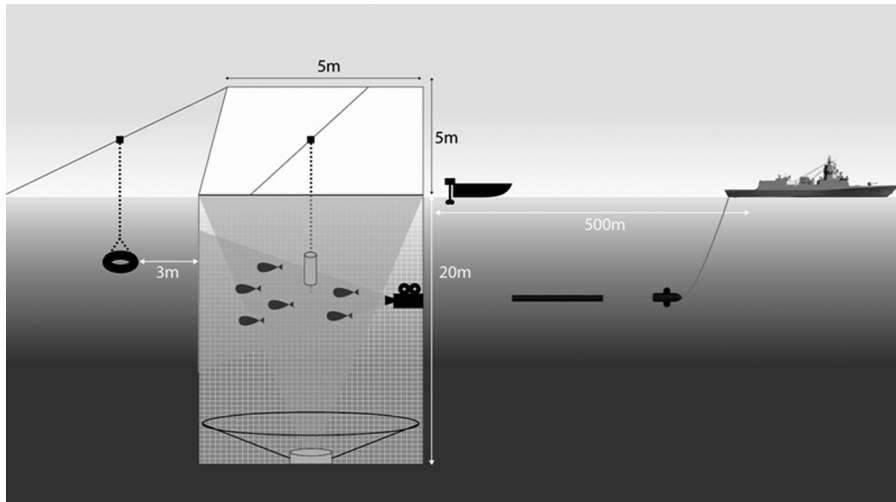


FIG. 1. Experimental setups. The pen is 5 m long by 5 m wide by 20 m deep. The behavior of the herring inside the pen was monitored with a bottom-mounted 200-kHz echosounder transmitting vertically upward and a video camera positioned at 5 m depth, imaging horizontally. The *SPL* values were measured by a hydrophone positioned in the middle of the pen at a depth of 5 m. The stationary source was placed at 5 m depth, 3 m outside the pen. The engine was secured 1 m from the pen.

was chosen since it is expected to be more commonly used than CW in areas typically inhabited by herring. A single CW run was conducted in the end of experiment 3.

2. Simulated-SONAR transmissions

Simulated SONAR transmissions were conducted in experiment 4, to achieve larger maximum-*SPL* values relative to the frigate experiments. The FM and CW waveforms were amplified (L-10, Instruments Inc., USA) and transmitted from a stationary transducer (ITC-2015, International Transducer Corp., USA), positioned 5 m deep and 3 m outside the net pen (Fig. 1). The maximum *SL* was 190 dB re $1 \mu\text{Pa}$ at 1 m at 1.6 kHz, and decreased with frequency.

During experiment 4, the pen was positioned on the seaside of the floating pier at the aquaculture station. Each block consisted of GFM and SFM runs, each 13 min, as well as a CON run, defined as 13 min without transmission. One CW run was also conducted at the end of this experiment.

During GFM runs, the initial *SPL* values approximated those measured when the frigate began its transect. Subsequently, the *SPL* was gradually increased to a maximum level 10 min later, approximately the time required for the frigate to reach the CPA. Then, the *SPL* was gradually decreased for three minutes. During SFM runs, the *SPL* was zero for the first 10 min, then abruptly maximum, and gradually decreased for the last three minutes.

3. Outboard engine sounds and fence strike sound

The primary objective with these exposures was to test whether the herring would react, and if our method were able to detect that behavior. A secondary objective was to compare the properties of the exposure with the sonar exposures.

The outboard engine exposure was conducted in experiments 2 and 4 (Table I) with the pen secured to the seaside of the floating pier at the aquaculture station. The boat with the outboard engine was secured 1 m from the pen (Fig. 1). Continuous, broad-bandwidth sounds were radiated from a two-stroke, 9.9-hp outboard engine (Yamaha) with the propeller disengaged operating at large (EL) and small (ES) number of revolutions. The “exposure” starts with the ignition of the

engine and continues for 30 s at constant RPM. Each block consisted of three EL and three ES runs with 30 s duration, and with 2.5 min between the treatments.

The fence strike exposure was done in all four experiments. A short-duration, low-frequency sound (FS), was generated by striking the fence of the pen with a large wooden stick. This *ad hoc* signal elicited a strong reaction from the herring. An FS run was defined as one pulse, with blocks consisting of 10 runs at 30-s intervals.

C. Behavioral observations

Fish avoidance responses include changes in orientation or swimming direction of individuals, or collective movement, either horizontally or vertically (Pitcher *et al.*, 1996; Nøttestad and Axelsen, 1999), with vertical avoidance, e.g., a diving response, as the most significant (Nøttestad and Axelsen, 1999; Wilson and Dill, 2002). Such a collective vertical avoidance was therefore the most important to investigate. Herring behavior was continuously monitored for such responses, acoustically and optically, before and during each experiment.

1. Acoustical monitoring

Herring behavior was monitored acoustically by a 200-kHz, split-beam echosounder (Simrad EK60), positioned in the bottom of the pen, transmitting vertically upward (Fig. 1). The beam direction and its stability were monitored with a tilt-roll sensor. The echosounder transmitted 1.024-ms pulses every 0.2 s and provided estimates of volume backscatter coefficients (s_v ; m^{-1}), defined as $\Sigma\sigma_{bs}/V$, where V (m^3) is the insonified volume, and σ_{bs} (m^2) is the back-scattering cross-sectional area of each scatterer within V (MacLennan *et al.*, 2002). These data, plotted versus depth and time (echogram), were scrutinized for changes in the vertical distribution of the herring.

Following Doksæter *et al.* (2009), the s_v -weighted-median depth at a given time (μ ; m); indicates the vertical center-of-mass of the herring in the pen. A change in μ , associated with a stimulus (exposure), indicates a potential vertical-avoidance reaction:

$$\delta_E = \mu_{befE} - \mu_{durE}, \quad (1)$$

TABLE II. Video-analysis results.

Exposure type	n	Group behavior		Vertical swimming		Number of fish reacting		Overall response	
		Type	Recordings (%)	Type	Recordings (%)	Type	Recordings (%)	Type	Recordings (%)
FM	7	Shoaling ^a	100%	downwards	0%	0	100%	No response ^c	100%
		Schooling ^b	0%	horizontally	100%	<10	0%	Startle ^d	0%
				upwards	0%	>10	0%	Avoidance ^e	0%
						all	0%	Alarm ^f	0%
FMs	8	Shoaling	100%	downwards	0%	0	62.5%	No response	62.5%
		Schooling	0%	horizontally	100%	<10	37.5%	Startle	37.5%
				upwards	0%	>10	0%	Avoidance	0%
						all	0%	Alarm	0%
CW	2	Shoaling	100%	downwards	0%	0	100%	No response	100%
		Schooling	0%	horizontally	100%	<10	0%	Startle	0%
				upwards	0%	>10	0%	Avoidance	0%
						all	0%	Alarm	0%
Con	2	Shoaling	100%	downwards	0%	0	100%	No response	100%
		Schooling	0%	horizontally	100%	<10	0%	Startle	0%
				upwards	0%	>10	0%	Avoidance	0%
						all	0%	Alarm	0%
EH	23	Shoaling	0%	downwards	0%	0	0%	No response	0%
		Schooling	100%	horizontally	0%	<10	0%	Startle	0%
				upwards	100%	>10	0%	Avoidance	26%
						all	100%	Alarm	74%
EL	10	Shoaling	80%	downwards	0%	0	10%	No response	10%
		Schooling	20%	horizontally	50%	<10	0%	Startle	0%
				upwards	50%	>10	50%	Avoidance	90%
						all	40%	Alarm	0%
Trs	5	Shoaling	0%	downwards	0%	0	0%	No response	0%
		Schooling	100%	horizontally	0%	<10	0%	Startle	0%
				upwards	100%	>10	0%	Avoidance	60%
						all	100%	Alarm	40%

^aShoaling—random orientations within the aggregation.

^bSchooling—polarized orientations within the aggregation.

^cNo response—no detected change in behavior.

^dStartle—body flexion and one to two seconds of faster swimming.

^eAvoidance—slow schooling, and diving or horizontal swimming away from source.

^fAlarm—rapid schooling and diving.

where μ_{befE} is the mean μ within a 30-s interval prior to the run (undisturbed condition), μ_{durE} is the mean μ within the first 30 s of the run, and E is the transmission type (i.e., GFM, SFM, CW, CON, EL, ES, or FS).

2. Optical monitoring

Video images were recorded using a light-sensitive camera (Sony DV Cam) mounted in the middle of the pen at depth of 5 m, imaging horizontally (Fig. 1). The camera covers only a relatively minor part of the total pen, and the main objective of the video images was to interpret signals observed in the acoustic observations. The camera was placed at the same depth as the hydrophone, so that the RL given is representative for the herring observed by the camera. Artificial light was not used to avoid its potential effects on herring behavior. Consequently, video was not recorded at night. The video images and hydrophone signals were monitored during

the experiments and recorded synchronously on the video and audio tracks of the camera. The video images were scrutinized for changes in swimming and schooling behavior, following Engås *et al.* (1995), as group pattern, vertical swimming and overall response and an estimate of the number of fish reacting is given (Table II). Group pattern was defined as shoaling (random orientations within the aggregation) or schooling (polarized orientations within the aggregation) (Pitcher, 1983). Vertical swimming was either upwards, downwards or horizontally. Overall response were categorized as no reaction (no detected change in behavior), startle response [body flexion and 1 to 2 s of faster swimming (Blaxter *et al.*, 1981; Kastelein *et al.*, 2008)], avoidance (slow schooling, and diving or horizontal swimming away from the source, or alarm (rapid schooling and diving).

Alarm and avoidance are generally similar, but the alarm indicates a stronger and quicker response. Behavior was scored every 30 s of a run by a trained behavioral

biologist who did not know the stimulus condition. As the video analyses were only used to supplement the acoustic analyses, they were not subject to any statistical analyses.

D. Environmental and biological monitoring

Seawater salinity and temperature were measured versus depth in the vicinity of the pen using a conductivity, temperature, and pressure sensor (CTD; SAIV A/S model SD 204), and an expendable bathythermograph. The latter data were input to an acoustic propagation model (LYBIN) (Hjelmer-vik *et al.*, 2008), to predict the sound propagation conditions between the sonar source and the herring.

A sample of 50 fish was measured for length and weight at capture and at the end of the last experiment. This was used to calculate the fish condition ($100 * \text{weight length}^{-3}$). The general health status of the fish was closely monitored by trained personal during and after the experiments, as well as generally monitored in the time between experiments.

E. Exposure levels

The *SPL* within the pen was recorded with a hydrophone (Bruel & Kjaer type 8106) placed in the middle of the net pen at a depth of approximately 5 m. The pre-amplified hydrophone, powered by a supply (B&K type 5939), has a flat frequency response from 20 Hz to 10 kHz. It was calibrated using a 250-Hz calibration tone with a $SL = 154.25$ dB re $1 \mu\text{Pa}$ (B&K Type 4229 with WA 0658). The signals were recorded on digital audio tape. They were also low-pass filtered and digitized below 8 kHz with a 24-bit analog-to-digital converter system (National Instrument model 9234/USB-9162/LabView, Signal Express V. 8.8), and stored on a computer hard-disk.

Spikes in the sound-pressure data, caused by the echosounder transmissions, were removed using a five-point-median filter. The power spectral density (psd) as a function of time (spectrogram) was calculated by using a 2048-point Hamming window with 50% overlap and a 2048-point fast-Fourier transformation, providing resolutions of 66 Hz and 0.25 s. The *SPL* was calculated versus time by numerically integrating (trapezoidal method) the psd from 10 Hz to 4 kHz within each window.

Data with the largest *SPL* values from each transmission type were analyzed in more detail, without median filtering, and several metrics were calculated. First, the data were amplitude demodulated. *B-duration* is the period when the envelope of the rectified sound pressure is within 10% of its peak value. Next, the data were bandpass filtered (50 to 3500 Hz, Butterworth, Direct-Form II, Second-Order Sections) and the *SPL* and the sound exposure level (*SEL*; dB re $1 \mu\text{Pa}^2 \text{ s}$) were calculated. Metrics for pulsed sounds are based on the period between the rise in the pressure to its peak and then back to the first sign reversal (ANSI, 1986). To obtain comparable measures for all transmission types, the pulse with the maximum peak pressure was used. *Signal-rise time* is the period when the pressure is within 10 to 90% of the peak pressure. *A-duration* is the period from 10% of the peak pressure when increasing to 10% of the peak pressure when decreasing (Fig. 2). *Impulse* (I_{imp}), the pressure

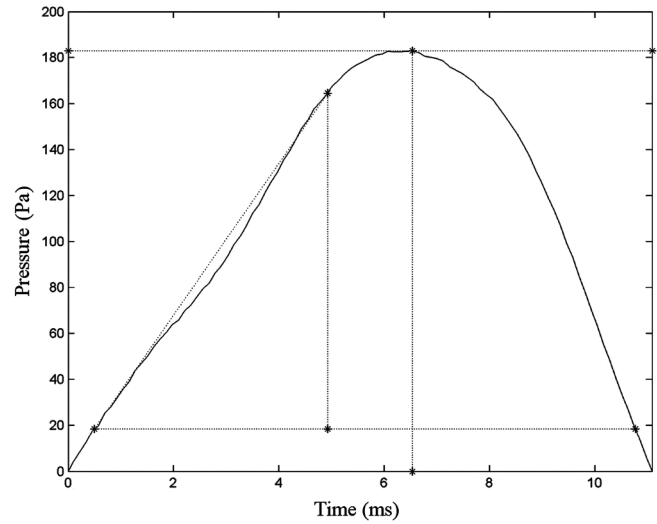


FIG. 2. Fence strike signal. Shown is the rise in pressure from the sign reversal to the peak pressure and then to the first sign reversal following the peak pressure. The *A-duration* is the period between the two asterisks at 10% of the peak pressure. The *signal-rise time* is the period between 10 and 90% of the peak pressure. The signal impulse (I_{imp}) is equal to the area under the curve.

integrated over time, describes the change in momentum and is useful for describing a fast-acting force:

$$I_{imp} = \int_{T_0}^{T_1} p(t) dt, \quad (2)$$

where T_0 is the time of the sign reversal prior to the peak pressure and T_1 is the time of the first sign reversal after the peak pressure (Carey, 2006).

F. Statistical analysis

Differences in fish behavior between the sonar exposure runs (GFM, SFM, and CW) and the positive control runs (EL, ES, and FS) were statistically evaluated and compared to control runs (CON) based on the acoustic data. The null hypothesis (H_0) is that the change in median depth from the undisturbed to the stimulus situation (δ_E) does not differ between the control runs and those with SONAR/engine/fence strike exposure:

$$H_0 : \delta_{CON} = \delta_{GFM} = \delta_{SFM} = \delta_{CW} = \delta_{EL} = \delta_{ES} = \delta_{FS}. \quad (3)$$

The alternative hypothesis (H_1) is that δ_E differs significantly between the control runs and those with one or more of the exposures types:

$$H_1 : \delta_{CON} \neq \delta_{GFM} \text{ or } \delta_{CON} \neq \delta_{SFM} \text{ or } \delta_{CON} \neq \delta_{CW} \text{ or } \delta_{CON} \neq \delta_{EL} \text{ or } \delta_{CON} \neq \delta_{ES} \text{ or } \delta_{CON} \neq \delta_{FS}. \quad (4)$$

This approach was also used to test for significant differences between: the sonar transmission types and the positive control; and between season (summer, winter, and autumn) for each exposure type.

The δ_E data were fit using the linear regression method. The best-fit data were compared by analysis of variance (ANOVA), and significant differences identified by a Tukey test. The functions used for the linear-regression, ANOVA, and Tukey-test were *lm*, *aov* and *TukeyHSD*, respectively (R Development Core Team, 2008).

III. RESULTS

Four experiments were conducted within the course of a year, representing summer, winter, and autumn (Table I). The experiments included a total of 29 replicate blocks comprising: 14 GFM, 14 SFM, 4 CW, 8 CON, 26 EL, 25 ES, and 9 FS runs. The transmissions in two of the CW runs were introduced gradually, and two were introduced suddenly. Due to the low number of replicates, all of the CW runs were combined.

A. Acoustical observations

Visual inspections of the echograms indicated that group behaviors did not change appreciably during the GFM, SFM, CW, or CON runs, while most of the EL, ES, and FS runs exhibited strong vertical avoidance (see Figs. 3 and 4). In contrast, during the first SFM run, the fish swam upwards. However, there was no significant differences between the CON, GFM, SFM, and CW runs ($p = 0.08$, $n = 44$). Therefore, H_0 was not rejected, indicating that the vertical-swimming behavior of captive herring does not change significantly when exposed to SONAR.

There was a significant difference between the CON, ES, EL, and FS runs ($p = 0.004$, $n = 71$). The CON runs were significantly different from the EL and FS runs, but were not significantly different from ES runs. Therefore, H_1 is accepted, indicating that the vertical-swimming behavior

of captive herring does change significantly when exposed to engine and the fence-strike sounds.

There was a significant difference between the GFM, SFM, and CW runs and the EL, ES, and FS runs ($p = 2.27 \times 10^{-7}$, $n = 99$). Also, the GFM, SFM, and CW runs were significantly different from the EL runs; and the CW and SFM runs differed significantly from the ES and FS runs.

There were no significant differences between the runs during the three seasons (GFM: $p = 0.95$, $n = 16$; SFM: $p = 0.101$, $n = 16$; EL: $p = 0.059$, $n = 25$; and ES: $p = 0.439$, $n = 24$; Fig. 5). There were too few replicates to test the CW and FS runs.

B. Optical observations

1. SONAR (GFM, SF, and CW) exposure and control (CON)

During all GFM, CW, and CON runs, the herring exhibited normal shoaling and horizontal swimming, and no visually detectable responses (Table II, Fig. 3). For the eight SFM runs, however, three exhibited startle responses to the stationary source. In these cases, fewer than 10 fish responded to the first two to three sonar transmissions and then the fish exhibited no response. This confirms results from the acoustic observation that no large scale vertical avoidance was induced by the SONAR.

2. Engine (EL and ES) and fence strike (FS) exposure

For the EL runs, 74% exhibited a startle response and 26% showed an avoidance response. Response was generally stronger in the first run in a block, indicating habituation. For the ES runs, 90% exhibited avoidance response and 10% showed no response. In a few cases of avoidance response,



FIG. 3. (Color online) Video images of fish behavior. (Top) In a typical GFM run, the herring shoal and swim horizontally both before and during the exposure. (Bottom) In a typical FS run the herring shoal before exposure and exhibit an alarm response, all diving, during exposure.

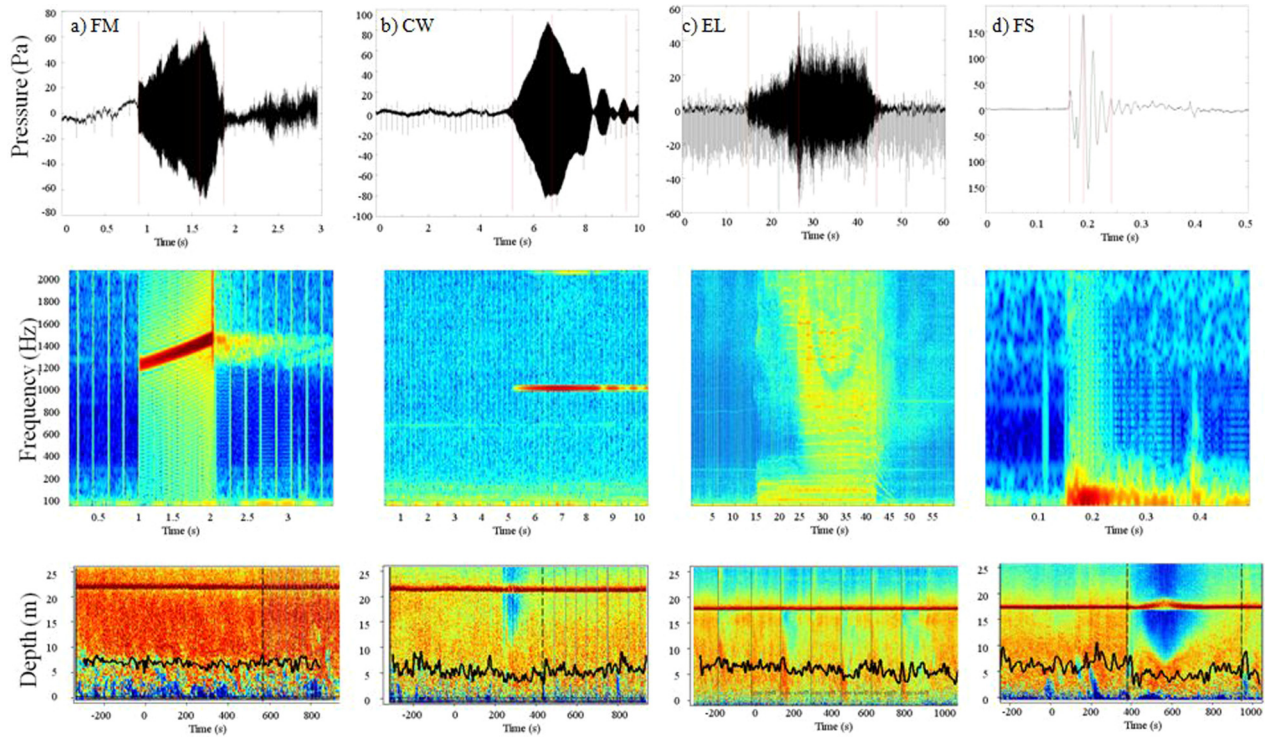


FIG. 4. (Color online) Signal waveforms, spectrograms, and echograms. The columns correspond to (a) FM, (b) CW, (c) engine, and (d) fence strike runs. The waveforms exemplify the signal sound pressure (Pa). The middle vertical line indicates the peak pressure. The other two vertical lines indicate the period, B -duration, when the envelope of the rectified pressure is 10% of the peak pressure. The spectrograms illustrate the noise spectral density ($\text{dB re } 1\mu\text{Pa}^2 \text{ Hz}^{-1}$) versus time. The example echograms show the volume backscattering strength ($\text{dB re } 1 \text{ m}^{-1}$) versus depth and time. The stippled vertical lines in the GFM and CON runs indicate the CPA. The filled vertical lines indicate the time of a sonar pulse, the start of the engine, or a fence strike. The curves indicate the backscattering-weighted-median depth.

the schools did not dive, but moved horizontally away from the sound source.

For the FS runs, 60% exhibited an alarm response and 40% showed an avoidance response, supporting the results from the acoustic analysis. An alarm response at the first pulse was followed by the weaker avoidance response to subsequent pulses within a run, again indicating habituation.

Video results from engine and fence strike sound confirm the results from the acoustic analyses with a significant different reaction to these sounds compared to the control/SONAR exposures.

C. Exposure levels

Each of the sound signals was characterized (Table III). The GFM and SFM signals had the largest SPL (168 dB re $1\mu\text{Pa}$), SEL (168 dB re $1\mu\text{Pa}^2\text{s}$), and $peak\ pressure$. The FS signal had the largest I_{imp} . Background noise varied somewhat between seasons and experiments, from 115 to 120 dB

re $1\mu\text{Pa}$ in experiment 4 (October) to 125 dB re $1\mu\text{Pa}$ in experiment 3 (February).

D. Environmental and biological conditions

1. Fish condition

At the start of the study fish condition was 0.69 and at the end of the last experiment 0.70, indicating that the fish did not grow during the period. A high mortality rate was reported immediately after arrival at the aquaculture station, but stabilized after a few days, remaining stable throughout the captive period, and did not increase during or close after experiments. The general health status of the fish were reported to be good throughout the captive period of 1.5 years.

2. Seawater temperature

The seawater temperature within the 20-m deep pen varied substantially between seasons. During experiment 1

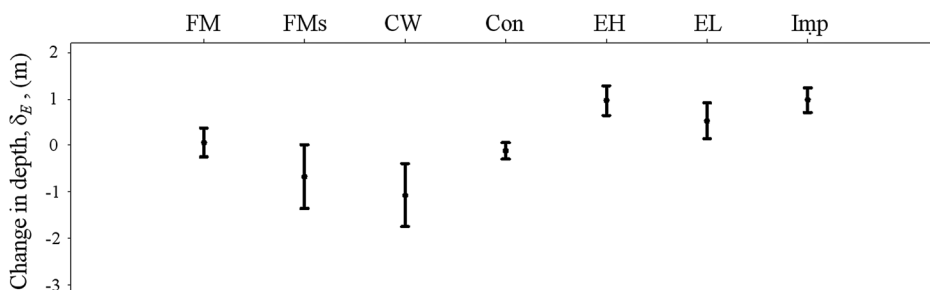


FIG. 5. Change in depth versus exposure type. A positive δ_E indicates that the fish dove; a negative δ_E indicates ascent.

TABLE III. Metrics for the various transmission types. Some metrics are not applicable (n/a) for the broad bandwidth signal from the outboard engine.

Unit	Received level (RL) dB re 1 μ Pa [rms]	Sound exposure level (SEL ^a) dB re (1 μ Pa ² s)	B-Duration ^a s	Peak pressure ^b Pa	A-Duration ^b ms	Signal rise time ^b ms	Impulse ^b μ Pa s
FM	168	168	0.9483	947	0.270	0.153	166 000
CW	150	156	4.34	94.9	0.458	0.161	28 000
MB	137	152	29.2				
FS	156	145	0.08	183	10.3	4.4	1 216 600

^aAverages for the duration of the exposure.

^bMeasured between the sign reversals occurring before and after the peak pressure.

(summer), the temperature was greater than 15 °C. During experiments 2 and 3 (winter) it was between 5 °C and 7 °C. During experiment 4 (autumn), it was approximately 10 °C close to the surface, increasing to about 10 m depth, and was approximately 15 °C from 10 to 20 m depth.

3. Propagation conditions

During the SONAR runs, the transmissions propagated from the source at 50 m depth towards the pen spanning 0 to 20 m depth. During experiment 1 (summer), the temperature was warm at the surface and decreased with depth, resulting in a sound speed minimum at 120 m. These conditions caused the SONAR transmissions to be refracted down towards a sound channel below the depth of the net pen. In contrast, during experiment 3 (winter), the temperature was cold at the surface and increased with depth, resulting in a sound speed maximum at 100 m. These conditions caused the SONAR transmissions to be refracted upwards, towards the pen. These differences resulted in higher *SPL* values during experiment 3 (162 dB re 1 μ Pa) compared to experiment 1 (158 dB re 1 μ Pa).

IV. DISCUSSION

The present study has documented that herring in a net pen do not react by any significant vertical avoidance responses when exposed to sonar signals transmitted from an operational source on board a frigate naval ship in the frequency range 1.0–1.6 kHz and received sound pressure levels up to 168 dB re 1 μ Pa, and that this lack of response is consistent throughout all phases of the yearly cycle.

A. Experimental methods

Studies of the behavioral responses of captive animals to stimuli may be useful to estimate the levels which trigger responses (McCauley *et al.*, 2003, Popper *et al.*, 2005, 2007). Studying animals in captivity allows the experimental conditions to be controlled and standardized. Notwithstanding the advantages of studying captive animals, their behavioral responses may not be representative of those from *in situ* animals. For example, anthropogenic sounds may cause *in situ* fish to flee (e.g., Engås *et al.*, 1996; Engås and Løkkeborg, 2002), while captive fish, without that option, must respond differently or not at all (Popper and Hastings, 2009).

In nature, avoidance reactions by herring may include either horizontal movement or diving by the school (Nøttestad and Axelsen, 1999), with diving as most common response

(Pitcher *et al.*, 1996; Simila, 1997; Nøttestad and Axelsen, 1999). This form of avoidance reaction, i.e., schooling and diving, is confirmed by these experiments in the cases of the engine and fence-strike stimuli (Figs. 3 and 4). The results also indicate that the pen dimensions were sufficient to allow typical vertical avoidance reactions and that the captive fish were capable of responding.

Herring typically exhibit a strong diel vertical-migratory behavior (DVM; Huse and Ona, 1996), which may modulate their response to sound exposure. Therefore, experiments were conducted during various times of day. Comparing the vertical distribution of the fish on the echograms does not indicate such vertical difference, probably due to the pen not being deep enough for the typical vertical migration that may be up to several hundred meters (Huse and Korneliusen, 2000).

No significant differences were observed between the control and the SONAR exposure. This negative result may have type II error, i.e., acceptance of the H_0 when it should be rejected, if the experiment or analysis was incapable of detecting a reaction. However, the optically and acoustically observed responses in the EL, ES, and FS runs, and the significant differences between the engine and SONAR exposures, demonstrated that the experimental design and analysis methods did allow detections of avoidance reactions when they occurred.

B. Herring reactions

Herring did not exhibit significant responses to the SONAR signals with *SL* values equal to 215 dB and 190 dB re 1 μ Pa at 1 m for the towed sonar source and the stationary source, respectively. The CPA of the frigate was 500 m and the stationary source was 3 m from the fish. The corresponding maximum received *SPL* values were equal to 162 and 168 dB re 1 μ Pa, thus well above the background noise. Higher source level will increase the received level, and reactions to such increased RL cannot be excluded. However, the SFM signals from the nearby stationary source (sudden-onset and high-intensity signal) did cause startle responses in a few fishes. In contrast, the engine sound caused a much more significant response.

The results of this study are mainly consistent with those of some earlier studies. Doksæter *et al.* (2009) examined the effects of 1 to 6 kHz SONAR signals on *in situ* herring and found no significant response. On the other hand, Jørgensen *et al.* (2005) exposed juvenile herring to SONAR signals of 1.5–6.5 kHz and observed a strong response. They also

observed fish mortality when the received *SPL* values exceeded 180–190 dB re $1\mu\text{ Pa}$, with the threshold of mortality apparently depending on the overlap between the frequency of the transmitted signal and the expected swimbladder resonance frequency of the exposed fish. Thus, the strong reactions and mortality may have resulted from *SPL* values much higher than those tested here at swimbladder resonance frequencies, or a possible enhanced sensitivity of juvenile fish relative to adult fish, or both.

Resonance frequency depends on the size and depth of the fish (Løvik and Hovem, 1979). The average length of $\sim 29\text{ cm}$ suggests a swimbladder with a resonance frequency of approximately 1 kHz at 13 m depth, increasing with depth to about 1.6 kHz at 18 m (Løvik and Hovem, 1979). While the SONAR signals span this range entirely, they only include the resonance frequency momentarily and may not include enough cycles to cause the swimbladder to resonate long enough to cause problems. The CW signals, however, may excite resonance in some fish at some depths.

Herring reactions tend to vary seasonally (Mohr, 1964, 1971; Vabø *et al.*, 2002; Kvamme *et al.*, 2003; Skaret *et al.*, 2006). They are generally more sensitive to stimuli, such as sounds from predators, during winter (November to February), and least sensitive in spring and summer after spawning has ended (Nøttestad *et al.*, 1996; Fernø *et al.*, 1998; Kvamme *et al.*, 2003). In this study, the SONAR transmissions did not cause behavioral responses in the herring during the experiments in autumn, winter, or summer. The engine noise and impulse sounds produced a vertical avoidance response, with both sound types producing a somewhat stronger response during the winter experiments. Low sample size of the impulse sound did not allow for a statistical comparison by season. Significant seasonal difference was not produced by the engine noise either, but a trend towards stronger response in winter was observed ($p=0.056$). The fish in this study were captive, fed year-round, and could not migrate. Despite captivity, the fish did feed more actively during spring and summer compared to winter, suggesting they retained at least some of their normal seasonal behavior (Holst *et al.*, 2004).

Anthropogenic sound may trigger an anti-predator response (Walther, 1969; Frid and Dill, 2002), involving costs in terms of spent energy and lost opportunities for feeding or mating. Therefore, the decision to react to a sound depends on the cost of avoidance and the probability of being attacked (Lima, 1998; Lima and Dill, 1990). An ability to discriminate sound cues associated with a predator attack from other sounds would limit the costs of avoidance responses to only real threats (Wilson and Dill, 2002). Such cues may include frequency bandwidth and modulation, *SPL*, *peak pressure*, *signal rise time*, and *repetition rate* (Hildebrand, 2009). Particular cues that are involved in triggering sound responses are not fully understood, (e.g., Ona *et al.*, 2007; Sand *et al.*, 2008), but frequency content (e.g., Enger *et al.*, 1993; Wilson and Dill, 2002) and *SPL* (e.g., Mitson, 1995; Engås *et al.*, 1995; Jørgensen *et al.*, 2005) are most often used to explain the observed reactions.

In this study, strong diving responses were induced by the very short duration, low-frequency, fence-strike sound

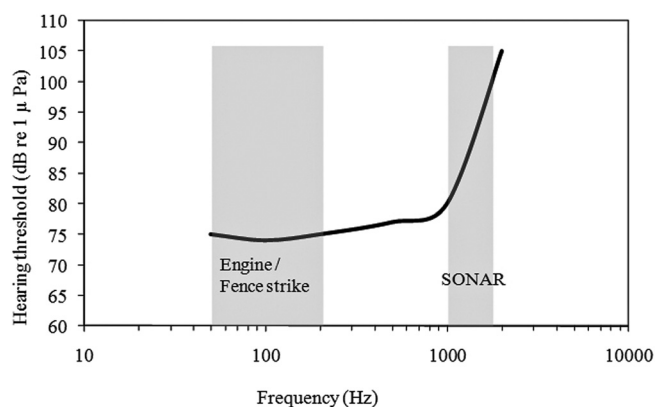


FIG. 6. Audiogram for herring (*Clupea harengus*), reconstructed from Enger (1967). Bandwidth of engine noise/fence strike and SONAR are indicated.

and by the continuous, broad-band engine sound. Despite having the largest *SPL*, *SEL*, and peak pressures (Table III), the sonar transmission caused no response. Compensating for the frequency-dependent hearing sensitivity of herring (Enger, 1967; Blaxter *et al.*, 1981), e.g., subtracting 5–25 dB re $1\mu\text{ Pa}$ from the sonar *SPL* (Fig. 6), the perceived *SPL* for the sonar signals is still higher than for the engine noise, indicating perceived *SPL* to not predict behavioral response in herring, in agreement with earlier studies on fish (Wahlberg and Westberg, 2005) and marine mammals (Madsen *et al.*, 2006).

Engås *et al.* (1995) showed that herring reacted to authentic vessel sounds but not to synthesized, smoothed, vessel sounds with the same *SPL* values and frequency content. This suggests that these two sound features may be incomplete indicators of a reaction. In contrast to *SPL*, *SEL*, and *peak pressure*, the I_{imp} was much higher for the fence strike sound than for the SONAR signal (Table III). Perhaps the large gradient in energy flux characterizing the fence strike is more predictive of an avoidance response. This hypothesis is supported by earlier findings where herring were shown to react more to sound irregularities than to sounds gradually increased to high levels (Schwartz and Greer, 1984). The fence strike sound involves a rapid change in momentum and the elicited avoidance reaction may be related to the kinetic part of the sound signal. Sound pressure is sensed by oscillations of the swimbladder being transferred to the inner ear (Sand and Hawkins, 1973), while the otolith organ reacts to particle displacement (Chapman and Sand, 1974). At higher frequencies, swimbladder oscillations exceed the particle motion from the sound, and pressure is the dominant stimuli (Sand and Hawkins, 1973; Denton *et al.*, 1979). At low frequencies, particularly below 20 Hz and in the near field of the sound source, particle motion is the dominant stimuli (Sand and Hawkins, 1973). Strong avoidance reactions to such sounds in the 0 to 20 Hz range have been observed for a wide range of juvenile and adult species such as salmon (*Salmo salar*) (Enger *et al.*, 1993; Sand *et al.*, 2001), gadoids (Handegard and Tjøstheim, 2005), and cyprinids (Sonny *et al.*, 2006). Sand *et al.* (2008) suggested that near field particle acceleration associated with the moving hull of a ship is the major stimulus causing herring to exhibit avoidance response.

Fish react more to low-frequency sounds at low *SPL* values than they do to high-frequency sounds at high *SPL* values (e.g., Schwartz and Greer, 1984; Sand *et al.*, 2008; Popper and Hastings, 2009). Most of the energy in the engine and fence strike sounds was below 200 Hz (Fig. 4), while all the energy in the SONAR signal was above 1 kHz (Fig. 4). Also, the pen was in the acoustic near field of the engine and fence-strike sound sources, which could have created a particle motion stimulus that would have been stronger than the measured sound pressure level implies (Sand *et al.*, 2008). The strong reactions to the fence strike and engine noise are therefore most likely explained by the low-frequency, sudden-onset and near field components of the sounds. The complexity in reactions shown in this study does however emphasize the need for a better understanding of the causal relationship between acoustic stimuli and reaction patterns of fish, and is an important task for future studies.

In conclusion, this study has documented that herring in a net pen do not react by any significant avoidance responses when exposed to naval sonar signals in the frequency range 1.0–1.6 kHz and received sound pressure levels up to 168 dB re 1 μ Pa, and that this lack of response is consistent throughout all phases of the yearly cycle.

ACKNOWLEDGMENTS

The Frigate Service of the Royal Norwegian Navy is greatly acknowledged for contributing dedicated-time on a frigate. Special thanks to the Commanding Officers and Underwater Warfare Officers of HNoMS Roald Amundsen and HNoMS Fridtjof Nansen who executed the experiment in a collaborative and very professional manner. Commander Harald Tholo and his team of the Royal Norwegian Navy Material Command are acknowledged for supplying the equipment and instructions necessary to simulate SONAR signals. The personnel at Austevoll aquaculture station, especially Gunnar Didriksen, are thanked for their help and for taking excellent care of the fish. Atle Totland at IMR is thanked for his perpetually good mood and helpful participation in the experiments. Karl Thomas Hjelmervik and Lars Kleivane, both at FFI, are thanked for their valuable advice regarding suitable placements of the net pen based on an analysis of acoustic propagation, and for participating in the frigate experiments, respectively. The crew of the fishing vessel “MS Liaskjæren” is thanked for their skillful assistance, and towing of the net pen. David Demer is greatly acknowledged for his careful reading and correcting of the manuscript. This study was financed by the Norwegian Research Council and the Norwegian Ministry of Defense.

Ainslie, M. A., (2010). *Principles of Sonar Performance Modeling* (Springer-Praxis, Chichester).
 ANSI (1986). S12.7-1986, *American National Standard: Methods for Measurements of Impulse Noise* (Acoustical Society of America, New York).
 Blaxter, J. H. S. (1985). “The herring—A successful species,” *Can. J. Fish. Aquat. Sci.* **42**, 21–30.
 Blaxter, J. H. S., Gray, J. A. B., and Denton, E. J. (1981). “Sound and startle response in herring shoals,” *J. Mar. Biol. Assoc. U.K.* **61**, 851–869.
 Carey, W. (2006). “Sound sources and levels in the ocean,” *IEEE J. Ocean Eng.* **31**, 61–75.

Chapman, C. J., and Hawkins, A. D. (1973). “Field study of hearing in cod, *Gadus morhua* L.,” *J. Comp. Phys.* **85**, 147–167.
 Chapman, C. J., and Sand, O. (1974). “Field studies of hearing in two species of flatfish *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae),” *Comp. Biochem. Phys. A* **47**, 371–385.
 Denton, E. J., Gray, J. A. B., and Blaxter, J. H. S. (1979). “The mechanics of the clupeid acoustico-lateralis system: Frequency responses,” *J. Mar. Biol. Assoc. U.K.* **59**, 27–47.
 Doksaeter, L., Kvadsheim, P. H., Godø, O. R., Handegard, N. O., Donovan, C., Lam, F. P., and Miller, P. J. O. (2009). “Behavioral response of herring (*Clupea harengus*) to 1–2 and 6–7 kHz sonar signals and killer whale calls,” *J. Acoust. Soc. Am.* **125**, 554–564.
 Enger, P. S. (1967). “Hearing in herring,” *Comp. Biochem. Phys.* **22**, 527–538.
 Enger, P. S. (1981). “Frequency discrimination in teleosts—Central or peripheral?” in *Hearing and Sound Communication in Fishes*, edited by W. A. Tavolga, A. N. Popper, and R. R. Fay (Springer Verlag, New York), pp. 243–255.
 Enger, P. S., Karlsen, H. E., Knudsen, F. R., and Sand, O. (1993). “Detection and reaction of fish to infrasound,” *ICES Mar. Sci. Symp.* **196**, 108–112.
 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.
 Engås, A., and Løkkeborg, S. (2002). “Effects of seismic shooting and vessel-generated noise on fish behaviour and catch rates,” *Bioacoustics* **12**, 313–315.
 Engås, A., Løkkeborg, S., Ona, E., and Soldal, A. V. (1996). “Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*),” *Can. J. Fish. Aquat. Sci.* **53**, 2238–2249.
 Fernandes, P., Brierley, A., Simmonds, E., Millard, N., McPhail, S., Armstrong, F., Stevenson, P., and Squires, M. (2000). “Fish do not avoid survey vessels,” *Nature* **404**, 35–36.
 Fernø, A., Pitcher, T. J., Melle, W., Nøttestad, L., Mackinson, S., Hollingworth, C., and Misund, O. A. (1998). “The challenge of the herring: Making optimal collective spatial decisions,” *SARSIA* **82**, 149–167.
 Frid, A., and Dill, L. (2002). “Human-caused disturbance stimuli as a form of predation risk,” *Conserv. Ecol.* **6**, 11.
 Hamre, J. (1990). “Life history and exploration of the Norwegian spring-spawning herring,” in *Biology and Fisheries of the Norwegian Spring Spawning Herring and Blue Whiting in the Northeast Atlantic*, edited by T. Monstad (Institute of Marine Research, Bergen, Norway), pp. 5–39.
 Handegard, N. O., and Tjøstheim, D. (2005). “When fish meet a trawling vessel: Examining the behaviour of gadoids using a free-floating buoy and acoustic split-beam tracking,” *Can. J. Fish. Aquat. Sci.* **62**, 2409–2422.
 Hastings, M. C., Popper, A. N., Finneran, J. J., and Lanford, P. J. (1996). “Effects of low-frequency underwater sound on hair cells of the inner ear and lateral line of the teleost fish *Astronotus ocellatus*,” *J. Acoust. Soc. Am.* **99**, 1759–1762.
 Hildebrand, J. A. (2009). “Anthropogenic and natural sources of ambient noise in the ocean,” *Mar. Ecol. Prog. Ser.* **395**, 5–20.
 Hjelmervik, K. T., Dombestein, E., Mjølness, S., Sæstad, T. S., and Wegge, J. (2008). “The acoustic raytrace model Lybin: Description and applications,” in *Underwater Defence Technology Conference UDT 2008*.
 Holst, J. C., Røttingen, I., and Melle, W. (2004). “The Herring,” in *The Norwegian Sea Ecosystem*, edited by H. R. Skjoldal (Tapir Academic Press, Trondheim, Norway), pp. 203–226.
 Huse, I., and Ona, E. (1996). “Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring,” *ICES J. Mar. Sci.* **53**, 863–873.
 Huse, I., and Korneliussen, R. (2000). “Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus* L.),” *ICES J. Mar. Sci.* **57**, 903–910.
 James, A. G., Hutchings, L., Brownell, C. L., and Horstman, D. A. (1986). “Methods of capture and transfer to the laboratory of wild pelagic fish,” *S. Afr. J. Mar. Sci.* **6**, 17–21.
 Jørgensen, R., Olsen, K. K., Falk-Petersen, I. B., and Kanapthippilai, P. (2005). “Investigation of potential effects of low frequency sonar signals on survival, development and behaviour of fish larvae and juveniles,” Report, Norwegian College of Fishery Science, NO, http://triton.nfh.uit.no/dok/lydrapport_m_vedlegg_28_04-05.pdf (Last viewed June 24, 2010).
 Kastelein, R. A., van der Heul, S., Verboom, W. C., Jennings, N., van der Veen, J., and de Haan, D. (2008). “Startle response of captive North Sea

- fish species to underwater tones between 0.1 and 64 kHz," *Mar. Environ. Res.* **65**, 369–377.
- Kvamme, C., Nøttestad, L., Fernø, A., Misund, O. A., Dommasnes, A., Axelsen, B. E., Dalpadado, P., and Melle, W. (2003). "Migration patterns in Norwegian spring spawning herring: Why young herring swim away from the wintering area in late summer," *Mar. Ecol. Prog. Ser.* **247**, 197–210.
- Lima, S. L. (1998). "Stress and decision making under the risk of predation: recent developments from behavioural, reproductive, and ecological perspectives," in *Advances in the Study of Behaviour*, edited by P. Slater, P. A. M. Iler and M. Manfred (Academic Press, New York), Vol. 27, pp. 215–290.
- Lima, S. L., and Dill, L. M. (1990). "Behavioural decisions made under the risk of predation," *Can. J. Zool.* **68**, 619–640.
- Lockwood, S. J., Pawson, M. G., and Eaton, D. R. (1983). "The effects of crowding on mackerel (*Scomber scombrus* L.)—Physical condition and mortality," *Fish. Res.* **2**, 129–147.
- Løvik, A., and Hovem, J. M. (1979). "An experimental investigation of swimbladder resonance in fishes," *J. Acoust. Soc. Am.* **66**, 850–854.
- 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.
- Madsen, P., Wahlberg, M., Tougaard, J., Lucke, K., and Tyack, P. (2006). "Wind turbine underwater noise and marine mammals: Implications of current knowledge and data needs," *Mar. Ecol. Prog. Ser.* **309**, 279–295.
- McCauley, R. D., Fewtrell, J., and Popper, A. N. (2003). "High intensity anthropogenic sound damage fish ears," *J. Acoust. Soc. Am.* **113**, 638–642.
- Misund, O. A., and Aglen, A. (1992). "Swimming behavior of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling," *ICES J. Mar. Sci.* **49**, 325–334.
- Misund, O. A., and Beltestad, A. K. (1995). "Survival of herring after simulated net bursts and conventional storage in net pens," *Fish. Res.* **22**, 293–297.
- Mitson, R. B. (1995). "Underwater noise of research vessels: Review and recommendations," ICES Cooperative Research Report No. 209, 61 pp. (ICES, Copenhagen).
- Mohr, H. (1964). "Reaction of herring to fishing gear revealed by echosounder," in *Modern Fishing Gear of the World*, edited by G. von Brandt (Fishing News Books, London), Vol. 2, pp. 253–257.
- Mohr, H. (1971). "Behaviour patterns of different herring stocks in relation to ship and midwater trawl," in *Modern Fishing Gear of the World*, edited by H. Kristjónsson (Fishing News Books, London), Vol. 3, pp. 368–371.
- Nowacek, D. P., Thorne, L. H., Johnstone, D. W., and Tyack, P. (2007). "Responses of cetaceans to noise," *Mamm. Rev.* **37**(2), 81–115.
- Nøttestad, L., Aksland, M., Beltestad, A., Fernø, 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**, 277–284.
- Nøttestad, L., and Axelsen, B. E. (1999). "Herring school manoeuvres in response to killer whale attacks," *Can. J. Zool.* **77**, 1540–1547.
- 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 Fisheries Report* (FAO, Rome).
- Ona, E. (2003). "An expanded target-strength relationship for herring," *ICES J. Mar. Sci.* **60**, 493–499.
- Ona, E., Godø, O. R., Handegard, N. O., Hjellevik, V., Patel, R., and Pedersen, G. (2007). "Silent vessels are not quiet," *J. Acoust. Soc. Am.* **121**, 145–150.
- Pitcher, T. J. (1983). "Heuristic definition of fish shoaling behaviour," *Anim. Behav.* **31**, 611–613.
- Pitcher, T. J., Misund, O. A., Fernø, A., Totland, B., and Melle, V. (1996). "Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high-resolution sonar," *ICES J. Mar. Sci.* **53**, 449–452.
- Popper, A. N., Fewtrell, J., Smith, M. E., and McCauley, R. D. (2004). "Anthropogenic sound: Effects on the behaviour and physiology of fishes," *Mar. Technol. Soc. J.* **37**, 35–40.
- Popper, A. N., Smith, M. E., Cott, P. A., Hanna, B. W., MacGillivray, A. O., Austin, M. E., and Mann, D. A. (2005). "Effects of exposure to seismic airgun use on hearing of three fish species," *J. Acoust. Soc. Am.* **117**, 3958–3971.
- Popper, A. N., Halvorsen, M. B., Kane, A., Miller, D. L., Smith, M. E., Song, J., Stein, P., and Wyscocki, L. E. (2007). "The effects of high-intensity, low-frequency active sonar on rainbow trout," *J. Acoust. Soc. Am.* **122**, 623–635.
- Popper, A. N., and Hastings, M. C. (2009). "The effects of anthropogenic sound on fishes," *J. Fish Biol.* **75**, 455–489.
- R Development Core Team (2008). "R: A language and environment for statistical computing," R Foundation for Statistical Computing, Vienna.
- Sand, O., and Hawkins, A. D. (1973). "Acoustic properties of the cod swimbladder," *J. Exp. Biol.* **58**, 797–820.
- Sand, O., Enger, P. S., Karlsen, H. E., and Kundsén, F. R. (2001). "Detection of infrasound in fish and behavioural response to intense infrasound in juvenile salmonids and European silver eels: A minireview," *Am. Fish. Soc. Symp.* **26**, 183–193.
- Sand, O., Karlsen, H. E., and Knudsen, F. R. (2008). "Comment on 'Silent research vessels are not quiet'" *J. Acoust. Soc. Am.* **123**, 1831–1833.
- Schwartz, A., and Greer, G. L. (1984). "Responses of Pacific herring *Clupea harengus palassi*, to some underwater sounds," *Can. J. Fish. Aquat. Sci.* **41**, 1183–1192.
- Similä, T. (1997). "Sonar observations of killer whales (*Orcinus orca*) feeding on herring schools," *Aquat. Mamm.* **23**, 119–126.
- Skalski, J. R., Pearson, W. H., and Malme, C. I. (1992). "Effects of sounds from a geophysical survey device on catch-per-unit-effort in a hook-and-line fishery for rockfish (*Sebastes* spp.)," *Can. J. Fish. Aquat. Sci.* **49**, 1357–1365.
- Skaret, G., Slotte, A., Handegard, N. O., Axelsen, B. E., and Jørgensen, R. (2006). "Pre-spawning herring in a protected area showed only moderate reaction to a surveying vessel," *Fish. Res.* **78**, 359–367.
- Slotte, A., Hansen, K., Dalen, J., and Ona, E. (2004). "Acoustic mapping of pelagic fish distribution and abundance in relation to a seismic shooting area off the Norwegian west coast," *Fish. Res.* **67**, 143–150.
- Sonny, D., Knudsen, F. R., Enger, P. S., Kvenstuen, T., and Sand, O. (2006). "Reactions of cyprinids to infrasound in a lake and at the cooling water inlet of a nuclear power plant," *J. Fish Biol.* **69**, 735–748.
- Vabø, R., Olsen, K., and Huse, I. (2002). "The effect of vessel avoidance of wintering Norwegian spring spawning herring," *Fish. Res.* **58**, 59–77.
- Wahlberg, M., and Weserberg, H. (2005). "Hearing in fish and their reactions to sounds from offshore wind farms," *Mar. Ecol. Prog. Ser.* **288**, 295–309.
- Walther, F. R. (1969). "Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884)," *Behaviour* **34**, 184–221.
- Wilson, B., and Dill, L. M. (2002). "Pacific herring respond to simulated odontocete echolocation sounds," *Can. J. Fish. Aquat. Sci.* **59**, 542–553.