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Original Article

Behaviours of Atlantic herring and mackerel in a purse-seine net, observed using multibeam sonar

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To ensure efficient and sustainable purse-seine fisheries, the catch process must be monitored to better understand the reactions of fish to the gear. In this study, we monitored the behaviours of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) schools during purse-seine capture using a multibeam imaging sonar (Simrad MS70, 75–112 kHz) mounted on a research vessel. The fish behaviours differed between species and purse-seine sets. For both species, the acoustic volume backscattering coefficient increased as 0–80% of the seine was hauled aboard, indicating a corresponding increase in fish spatial density. This increase was significantly greater for herring than mackerel. As 0–40% of the seine was hauled aboard the fishing vessel, schools changed their spatial distribution and volume independent of seine hauling, while for some schools, depth and height decreased. The acoustic volume backscattering strength was up to 25 dB higher in the centre of the school than in the edges. The average lateral target strength was estimated for individual fish in the captured herring schools, and the effect of incident angle on the backscattering strength is considered.

Keywords: *Clupea harengus*, multibeam sonar, purse-seining, school behaviour, *Scomber scombrus*.

Introduction

Purse-seining accounts for about 30% of the total world catches (Watson *et al.*, 2006) and includes some of the largest and most valuable fisheries, such as yellowfin tuna (*Thunnus albacores*), skipjack tuna (*Katsuwonus pelamis*), anchoveta (*Engraulis ringens*), Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) (FAO, 2014). There are currently few effective techniques available for monitoring the fish and seine during capture that can provide information about the behaviour and biomass of fish in the net. Such knowledge is essential for improving catch success (Wardle, 1993; Graham *et al.*, 2004; Løkkeberg *et al.*, 2010; Underwood *et al.*, 2015) and reducing discard mortality (Johnsen and Eliasen, 2011; Sarda *et al.*, 2015).

In purse-seine fisheries, sonars are used to detect and assess school characteristics before seine deployment, such as swimming speed, direction and biomass (Misund, 1993; Ben-Yami, 1994). This information is used to identify appropriate targets and, in combination with environmental data, to identify optimal fishing strategies (Ben-Yami, 1994). Once the school is surrounded by the seine, however, the sonar is usually retracted into the hull to avoid damaging it during pursing, i.e. closing the bottom of the seine, and seine hauling. During hauling, the seine volume is gradually reduced and the school is eventually contained adjacent to the side of the vessel prior to being pumped or brailed aboard. Catch monitoring during this stage would provide the fisherman with additional opportunities to evaluate catch biomass and composition. This is particularly important when evaluation of the target school is inaccurate or impractical before seine deployment, and when there may be a need to release unwanted catches to meet loading capacities, quotas restrictions and other fisheries regulations. Information on fish reactions to the purse-seine is also necessary for the development of evidence-based fishing regulations. For example, fisheries regulations in Norway and the European Union forbid the release of dead or dying fish. This regulation is implemented using limits on how late in the fishing process catches can be released from the seine (80–90% seine hauled aboard depending on fishery) (Anon, 2008). This is to ensure that fish densities do not exceed mortal levels (Huse and Vold, 2010; Tenningen *et al.*, 2012). These limits are regarded as precautionary, but scientific studies to support them are lacking.

Refinements to fishing strategies and regulations require the development of better catch monitoring techniques and an understanding of fish responses to capture under different fishing conditions. The purse-seine catch process is difficult to monitor due to the large size and flexibility of the seine (Ben-Yami, 1994). Newly available multibeam sonars with side-looking transducers make it possible to monitor the fishing process. However, the vessel's thrusters and propellers create clouds of air bubbles that often block the sonar beams, and echoes from these bubbles and the seine can be confused with fish echoes. The variation in lateral backscattering strength from fish is highly dependent on the orientation of the fish relative to the acoustic beam (Cutter and Demer, 2007; Holmin *et al.*, 2012), further complicating the interpretation of echoes from the school inside a seine.

In this study, we used a scientific multibeam sonar mounted on a research vessel to image Atlantic herring and mackerel schools and the seine deployed from a fishing vessel conducting normal fishing operations. The primary objective was to describe the dynamics of fish schools during hauling of the purse-seine and to investigate the responses of different species and schools to capture. We first developed methods for extracting school echoes from the surrounding noise (i.e. echoes from the seine, air bubbles created by the vessel machinery and hull and background noise). We then used measures of the acoustic volume backscattering coefficient of the schools to describe the dynamics of the schools during capture, their spatial distribution in relation to the vessel and their collective organization. We discuss the potential for these observation methods in further development of efficient and sustainable purse-seine fisheries.

Methods

Data collection

Two experiments were conducted: during the herring fishing season, March and November 2013 in the northern North Sea and during the mackerel fishing season, October 2014, in the Norwegian Sea. Both experiments were conducted using the Norwegian research vessel 'G.O. Sars'. The purse-seine vessels were MS 'Artus', in 2013, and MS 'Kings Bay', in 2014. MS 'Artus' is 49.8-m long, has a loading capacity of about 500 m^3 and uses a 732-m long by 188-m deep seine. MS 'Kings Bay' is 77.5-m long, has a loading capacity of about 2300 m^3 and uses a 796-m long by 265-m deep seine.

Acoustic data were collected using a calibrated multibeam sonar, Simrad MS70 (Ona *et al.*, 2009). This sonar operates in the frequency range of 75–112 kHz and comprises 500 beams in a 20 (vertical) by 25 (horizontal) grid. The two-way 3-dB beam widths varied from 4.5° to 5.1° (6.4° to 7.2° one-way) vertically and from 2.7° to 4.6° (3.8° to 6.5° one-way) horizontally. Each horizontal fan of beams utilized the same acoustic frequency. The first sidelobe levels in each beam were −25 dB horizontally and −35 dB vertically. The uppermost of the 20 vertical fans was oriented and maintained with active tilt stabilization, parallel to the surface. Combined, these partly overlapping beams form a matrix that covers 60° horizontally and 45° vertically. The sonar thereby provides three-dimensional (3-D) data from each transmission, and 4-D data (3-D plus time) from multiple transmissions. The sonar transducer was mounted on the port side of the vessel's protruding keel, 1.5 m below the ship's keel, at a depth of about 7.5 m. The sonar transmitted 2-ms pulses every 2.5 s, on average, and recorded the enveloped-detected echoes with an along-beam resolution of 38 cm. As the fishing vessel started to haul the seine, GO Sars approached, remaining at a distance of 100–350 m from the vessel, and directed the sonar towards the seine and fishing vessel (Figure 1). The seine and the target school were acoustically monitored throughout the hauling process. To avoid tangling, the seine in the propellers of the research vessel, the seine deployment and pursing operations were not monitored with the sonar. A constant hauling speed was assumed, and the proportion of the seine aboard the fishing vessel at any given time was estimated as the time since hauling started, divided by the time taken to haul the entire seine aboard. Catch weight and average individual fish weight were obtained from the catch landing records.

Data processing

All acoustic data were processed in the PROcessing system for advanced MUltibeam Sonar, (PROMUS) (Korneliussen and Heggelund, 2007; Korneliussen *et al.*, 2009), an extension to the LSSS acoustic analysis software (Korneliussen *et al.*, 2016). The sonar data were pre-processed using settings optimized for the detection of dense schools in a noisy environment (Figure 2a). Data were then segmented into three regions: school, seine and vessel and background. The seine and vessel category includes backscatter from the seine, the vessel hull and bubbles created by the vessel's propellers and bow thrusters. Data were segmented by manually selecting a seed voxel, i.e. the smallest sampling unit of the sonar. If the seed voxel passed the detection criteria (Table 1), PROMUS then used the detection criteria to segment the data automatically. Voxels closest in space and time to the accepted seed voxel were added to the already segmented data and the algorithm worked iteratively until no more voxels could be added. Whole schools were segmented several times during seine hauling (Table 2, Figure 2b). When school edges could not be separated from the seine or the vessel echoes, a 20-m^3 sample of the school was segmented by manually selecting the depth, range and fan numbers to be included in the segmentation (Table 2, Figure 2d). The school sample was extracted from close to the middle of the school, but always at least 30 m from the fishing vessel. Purse-seine sets, i.e. the catch process from seine deployment to complete recovery, without catches or fish backscatter, were used for echo segmentation of the seine and vessel (Figure 2c). Each segmentation consisted of 11 sequential pings.

For herring set 1, the volume backscattering strength (S_v; dB re 1 m^{-1}) threshold was varied, −50, −60 and −70 dB, to explore its effect on the segmentation of seine and school echoes and on school volume backscattering coefficient (s_v; m^{-1}) (MacLennan *et al.*, 2002) and school volume (m^3).

Target Strength, incidence angles and internal school s_v

Estimated school volume was averaged over the 11 sequential pings and the mean lateral target strength (*TS*; dB re 1 m^{-1}) of herring was calculated for individual fish via:

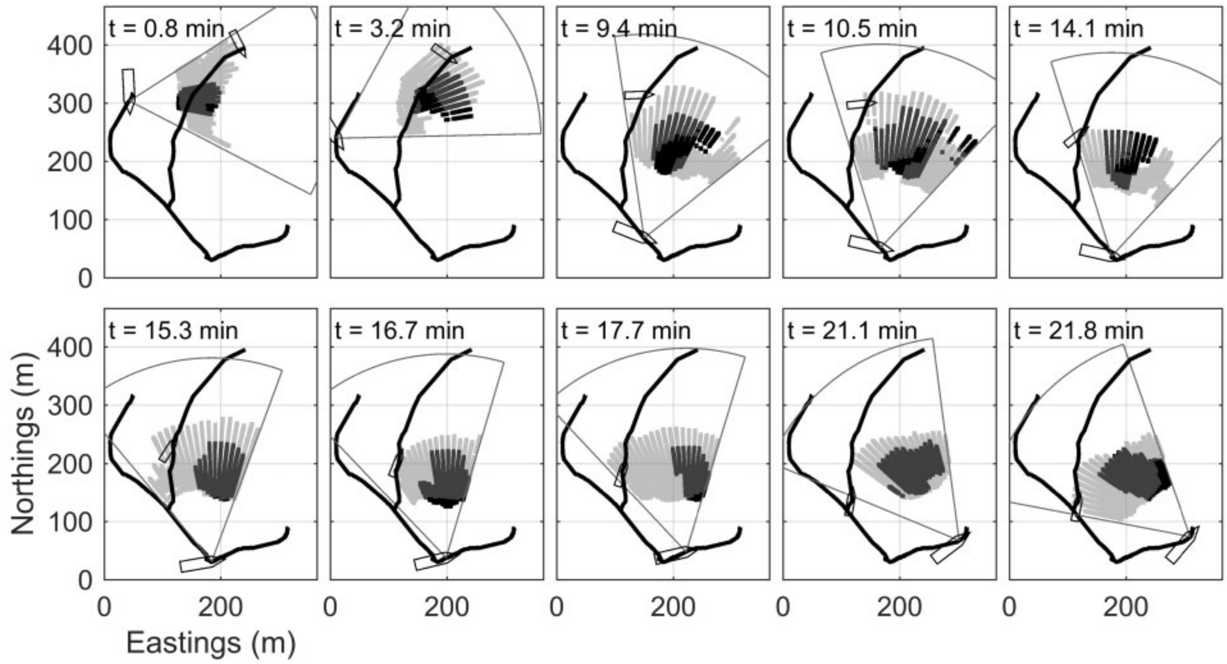

Figure 1. Reconstruction of the monitoring set up and school dynamics in set 1 (0- to-22 min seine hauling), shown in plan-view. Positions and tracks are shown for the fishing vessel (small shape) and the monitoring vessel (large shape). Also shown is the segmented school backscatter (black), seine backscatter (grey) and sonar coverage (sector outlined in grey).

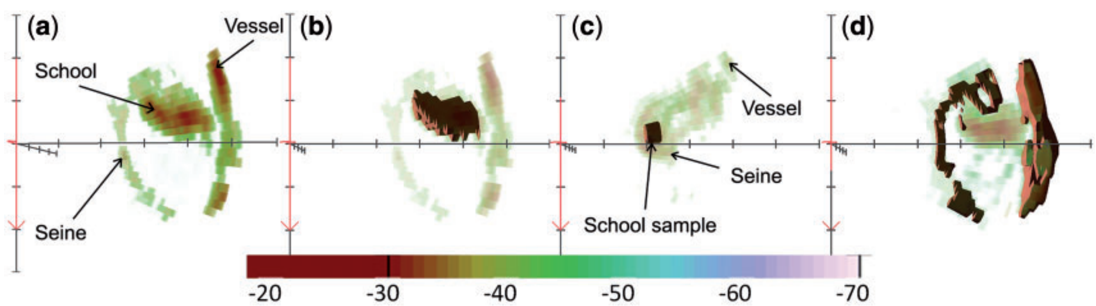

Figure 2. Plan-view visualization of herring school, seine, and vessel created backscatter and data segmentation in PROMUS for set 1, including: (a) pre-processed data; (b) a segmented herring school; (c) a partly segmented school and (d) segmented seine and vessel created backscatter. (a), (b) and (d) illustrate data from the same transmission at 24% haul proportion. (c) is at 45% haul proportion. Segmented data are indicated by the dark overlay. The scale extends from −70 dB to −20 dB. The axes tick marks are every 50 m.

$$TS = 10\log\ ((s_v * W * V)/B),$$

where s_v is the volume backscatter from the school (m^{-1}), W is the average fish weight (kg), V is the school volume (m^3) and B is the catch weight (kg).

The effect of incidence angle on S_v was investigated by first extracting school data by ping (herring sets1, 3, 4, 6 and 8) onto a 3° (horizontal) × 3° (vertical) × 4-m (range) grid. S_v vs. beam direction were examined by plotting S_v within a grid against horizontal and vertical beam direction. The horizontal beam directions ranged from −30° (astern) to +30° (forward). The vertical beam directions ranged from 0° (horizontal) to 45° (downwards).

School behaviour during seine hauling

S_v was averaged over 11 pings to mitigate variability due to changes in incidence angle and school volume, depth and height then calculated using the PROMUS software. The volume was estimated by adding the volumes of all voxels where the school was detected, and correcting for edge effects across beams and duration of sound pulses along the beams. The measured school dimension was reduced by one pulse length because the outermost beam where the school was detected partly overlaps with the adjacent beam where the school was not detected.

Distances from the school to the fishing vessel were estimated by first converting the vessel latitude and longitude coordinates to Universal Transverse Mercator (UTM) eastings and northings.

The school bounding box position and rotation relative to the sonar (output from PROMUS) were added to the UTM coordinates of the research vessel, placing the fishing vessel and the school box into the same coordinate system. The distance from the centre of the school to the fishing vessel was then calculated. The distance between the school edges and the fishing vessel was estimated by fitting an ellipsoid to the school bounding box, generating a dense set of points on the surface of the ellipsoid, and then calculating all of the distances between these points and the vessel position. The minimum value was taken to be the closest distance between the school and the vessel.

Table 1. Settings used for acoustic data segmentation.

Setting	Value
Maximum number of pings from seed ping	5
Minimum S_v (dB) for segmentation	−60
Maximum S_v (dB) for segmentation	−10
Inner range (m) for segmentation	20
Outer range (m) for segmentation	350
Minimum depth (m) for segmentation	0
Maximum depth (m) for segmentation	75
Minimum horizontal fan number for segmentation	1
Maximum horizontal fan number for segmentation	20
Minimum vertical fan number for segmentation	1
Maximum vertical fan number for segmentation	25
Width of erode/dilate filter (number of voxels)	5 (5 × 5)
Size of the grid cells used to calculate school size (m)	5 (5 × 5 × 5)
Minimum volume (m^3)	1

The maximum number of pings from seed ping refers to the number of pings before and after the seed ping. Fan numbers are from 1 to 25 on the horizontal plane and from 1 to 20 on the vertical plane. The common pulse duration of 2 ms makes one voxel cover 38 cm along the beams. Across beam a voxel indicates one beam.

For herring set 1, school, seine and vessel backscatter were extracted onto a 3° (horizontal) × 3° (vertical) × 2-m (range) grid. Vessel positions and ensonified volumes were expressed as polygons and combined with the gridded data. A series of plan-view images were then created, each representing one ping during seine hauling.

The behavioural differences of herring vs. mackerel during seining were quantified by comparing s_v at different haul proportions. The behaviours of herring during seining were quantified by changes in school s_v, volume, depth and height, and distance from the fishing vessel. These metrics were compared for multiple herring schools. All segmented school data, including data from partly segmented schools, were used for comparisons of s_v between species, schools and haul proportions, otherwise only fully segmented schools were used.

Statistical analyses

Analyses of covariance (ANCOVA) was used to investigate the effect of segmentation thresholds ($S_v = -50$, -60 and -70 dB) (categorical variable) and hauling proportions (continuous variable) on school s_v and volume. We used a linear mixed-effects model (RCoreTeam, 2015) to examine the effects of acoustic category (species, seine and vessel) and seine hauling on s_v. In the model, we included the purse-seine set nested in the experiment as a random factor to control for potential pseudoreplication, non-independence of the measurements within a set, and for the unbalanced design (varying number of measurements within sets and sets within experiments). The model was corrected for heteroscedasticity using the power variance function. A linear mixed-effects model was also used for testing the effects of seine hauling on school distance from the fishing vessel, depth, vertical extent and volume. The purse-seine set was nested in the experiment as a random factor. Inter-school differences in behaviours during seine hauling were tested with

Table 2. Summary of data segmentation during purse seine capture, including experiment number, set number, date (yyyymmdd) and time (UTC), target species, catch biomass (t) and the number of times the target was segmented (N) and at what stage during hauling (% = percentage of seine hauled at the time of segmentation).

Exp.	Set	Date	Time	Species	Catch	Data segmentation Target	*N*	%
1	1	20130321	1600	Herring	20	Whole school	25	10–41
						Part of the school	17	42–75
						Seine and vessel	16	10–41
	2	20130323	1430	Herring	0	Seine and vessel	7	38–80
	3	20130324	0800	Herring	NA	Whole school	11	1–40
	4	20130325	1000	Herring	20	Whole school	8	17–40
						Part of the school	8	46–82
	5	20130325	1840	Herring	0	Seine and vessel	10	1–39
2	6	20131117	0650	Herring	110	Whole school	7	16–41
						Part of the school	2	43–84
	7	20131117	1440	Herring	52	Part of the school	7	5–79
	8	20131118	0730	Herring	400	Whole school	6	1–17
						Part of the school	3	18–23
3	9	20141023	1530	Mackerel	68	Part of the school	4	21–51
	10	20141024	0510	Mackerel	311	Part of the school	11	24–64
	11	20141029	1145	Mackerel	0	Seine and vessel	14	19–91
	12	20141029	1145	Mackerel	25	Part of the school	3	15–49

Targets are described by *whole school* (the whole school was segmented), *part of the school* (a 20-m^3 sample of the school was segmented), and *seine and vessel* (seine and vessel created backscatter was segmented). A catch of 0 refers to sets where the targeted school escaped before the seine was closed and *NA* refers to a set where seine broke at the end of the haul and catch was lost.

ANCOVA, with haul proportion as the continuous variable and purse-seine set as the categorical variable. The s_v was log-transformed to meet assumptions of normality. Model simplification was used and the underlying assumptions of the final models were not violated. The mean and s.d. of S_v and *TS* were estimated (RCoreTeam, 2015).

Results

Methods for school segmentation

Increasing S_v threshold (−70 to −50 dB) significantly increased the school s_v and decreased the estimated volume, independent of haul proportion (Table 3). For unbiased comparisons, a −60 dB threshold was then used in all of the segmentations.

In five of the six herring sets, the entire school was successfully segmented inside the seine. Schools were segmented between 6 and 25 times, up to a maximum of 41% of the seine hauled (Table 2). In five of the sets, samples of schools were segmented (2–17 times per set and up to a maximum of 82% of the seine hauled) (Table 2). Samples of mackerel schools were segmented, 3–times per set and up to a maximum of 64% seine hauled (Table 2). Seine and vessel created echoes were segmented between 7 and 16 times per empty set (1–91% seine hauled) (Table 2).

The mean S_v of herring was −37.0 ± 4.1 dB and, on average, was 5.7 dB stronger than that from the seine and vessel (−43.3 ± 2.9 dB), and 6.9 dB stronger than mackerel S_v (−42 ± 2.9 dB), hence the mackerel S_v and seine and vessel S_v only differed by about 1 dB. This illustrates the challenges encountered when trying to segment mackerel schools using S_v thresholds. The seine and vessel s_v slightly decreased with increasing haul proportion, whereas school s_v increased with increasing haul proportion ($t_{131} = -4.22$, $p < 0.001$) (Figure 3).

TS, incidence angles and internal school s_v

TS for herring in the captured schools varied between −39.6 ± 1.7 and −44.0 ± 1.8 dB, using the average fish weight of 0.35 kg (Figure 4). In all school measurements, S_v was higher in the centre of the school than in the horizontal edges (Figure 5a). S_v reduced with increasing vertical beam angle in sets 1, 6 and 8, the strongest reduction being in sets 6 and 8, which were large schools and covered a wide range of vertical beams (Figure 5b). Within a school, S_v was up to 25 dB higher in the centre of the school than in the edges (Figure 5c).

School dynamic responses to seine hauling

Herring and mackerel responded differently to seine hauling. Although s_v increased with increasing haul proportion for both species, the apparent increase in fish density was significantly stronger for herring ($t_{131} = -2.88$; $p < 0.01$, Figure 3).

For herring set 1, the school remained near the edge of the seine volume (Figure 1). The average distances from the centre and closest edge of the school to the fishing vessel was 80 and 51 m, respectively. These distances fluctuated, but were not significantly correlated to haul proportion (Table 4). No significant correlation was found between school volume and haul proportion (Table 4). Values of s_v and the haul proportion were significantly correlated (Table 4). The depth of the school centre and the height of the school were also significantly correlated with the haul proportion because the fish moved closer to the surface and became vertically compressed as the seine was hauled (Table 4).

Significant interactions were found between haul proportion and purse-seine set for s_v, volume, distance from fishing

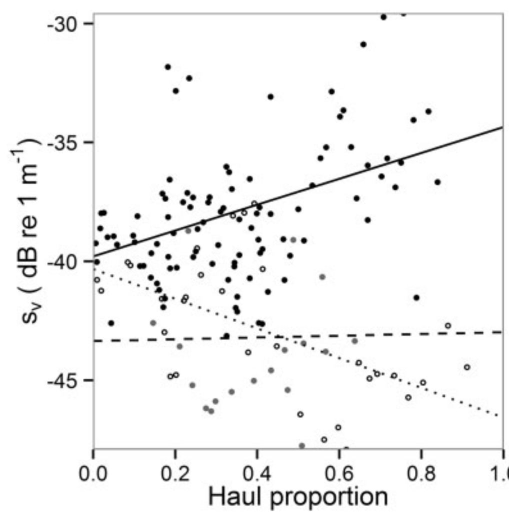

Figure 3. Volume backscattering strength (S_v, dB re 1 m^{-1}) of mackerel (grey filled circles) and herring (black filled circles) schools, and seine and vessel backscatter (open black circles) at different haul proportions. Data from all catches are pooled. Results from the mixed effects model are shown as a solid line for herring ($y = 2.62 \times 10^{-4} x + 1.05 \times 10^{-4}$), a broken line for mackerel ($y = 0.04 \times 10^{-4} x + 0.46 \times 10^{-4}$) and a dotted line for the vessel and seine ($y = -0.71 \times 10^{-4} x + 0.93 \times 10^{-4}$). Values for s_v were converted to S_v (10log(s_v)) in the plot.

Table 3. The mean and s.d. of S_v (dB re m^{-1}) and school volume (m^3) estimated for the herring school in set 1, using three S_v segmentation thresholds.

School characteristic	Mean (s.d.)			ANCOVA model results				
				Res	Threshold		Haul %	
	−50 dB	−60 dB	−70 dB	df	df	*f*-value	df	*f*-value
S_v (dB re m^{-1})	−37.2 (1.4)	−38.4 (1.5)	−39.1 (1.6)	71	2	10.31[a]	1	0.24
Volume ('000 m^3)	85 (21)	117 (26)	139 (32)	71	2	27.14[a]	1	2.61

Also shown are the results from an analysis of covariance of the effects of S_v threshold and haul proportion on school s_v (m^{-1}) and volume. The model results include residual degrees of freedom (Res df), the degrees of freedom (df), and *f*-values for S_v threshold (Threshold) and for haul proportion (Haul %).
[a]Statistical significance, $p < 0.01$.

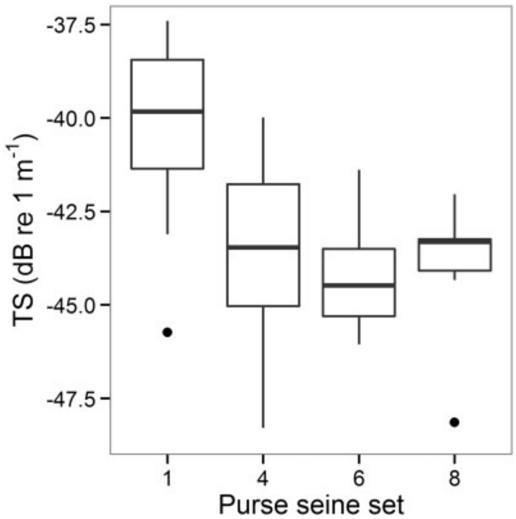

Figure 4. Mean lateral target strength (*TS*, dB re 1 m^{-1}) estimates of individual fish in the captured herring schools. The boxes present the first, second and third quartiles, the vertical lines the range of data, and outliers are plotted as points.

vessel, depth and height, indicating that each school's initial state (intercept) and response to hauling (slope) varied (Table 4). Sets 4 and 8 exhibited the largest decreases in volume and increases in s_v vs. haul proportion (Figures 6 and 7). The school in set 8, resulting in the largest catch of 400 t, was initially positioned farthest away from the vessel (200 m at 0% seine hauled) and moved closer to the vessel as the seine was hauled (80 m at 20% seine hauled). The schools in sets 3 and 4 exhibited the strongest vertical reactions to seine hauling and moved from a depth of 62 to 42 m and from 47 to 37 m, respectively. These schools were deeper at the start of the haul compared with the other schools.

Discussion

In this study, herring schools changed their spatial distributions in the early seining stages (0–40% hauled aboard), indicating actively swimming schools that may have been looking to escape. Previously, in response to a purse-seine, schools have been observed to dive or swim horizontally out of the seine before being fully encircled (Misund, 1993). Here, schools were only observed inside the closed seine, restricting the natural diving response (Pitcher *et al.*, 1996; Nottestad and Axelsen, 1999; Nottestad and Simila, 2001; Wilson and Dill, 2002). Some schools reacted by swimming up and became vertically compressed, a behaviour observed among herring schools when preyed upon by whales (Nottestad and Axelsen, 1999; Nottestad and Simila, 2001).

Volume backscatter increased for some schools, indicating that the fish volumetric density increased with haul proportion. An increase in school density enhances transfer of predator cues between individuals, promoting collective responsiveness and efficient evasive reactions (Marras *et al.*, 2012; Rieucau *et al.*, 2014). During purse-seining, it is important to ensure fish do not exceed their natural densities in case there is a need to release unwanted catches (Tenningen et al., 2015). Catch regulation through releasing parts of the catches can result in high mortalities, which generally increases as the fish become more crowded. This is particularly true for mackerel, where entire schools have died during release (Lockwood *et al.*, 1983; Huse and Vold, 2010). Herring not only is more resilient than mackerel, but also has high mortality rates (up to 50%) when released after crowding (Tenningen *et al.*, 2012). For the fish to survive, it is important that fish releases occur before they reach high crowding densities. However, current uncertainties over lateral *TS* (−32 to −44 dB) (Pedersen *et al.*, 2009) preclude the development of actionable metrics of crowding density.

The behaviours evoked by seining differ between species. The increase in s_v (and volumetric density) with haul proportion was significantly higher for herring than for mackerel. Fish schools react to sound produced by vessel propellers and machinery (Olsen, 1971; Mitson and Knudsen, 2003), displacement of water by the vessel (Sand *et al.*, 2008), and view of the seine (Misund, 1993; Hosseini and Ehsani, 2014). Biological differences between species may result in different swimming behaviours and reactions to capture. For example, herring and mackerel have different swimming endurances (He, 1993), and mackerel are less sensitive to vessel sound (Hawkins, 1986; Misund, 1993). However, these differences may be difficult to discern in the sonar data because backscatter from mackerel has less contrast to that from the seine, compared with herring. Consequently, the methods in this study should be improved to better extract scattering from mackerel and other weakly scattering fish schools, during purse-seining. The relative frequency response, commonly used for acoustic species identification (Korneliussen and Ona, 2003; Korneliussen, 2010), may differ between mackerel and the seine (skipper P-CR, pers. comm.) and if so could facilitate such extraction.

School responses to capture differ between purse-seine sets. Large schools have less space available inside the seine, restricting their movements and forcing them into higher fish densities. Schools farther away from the seine and deeper are forced closer to the vessel and shallower as the seine is hauled. Fish reactions to capture by purse-seine are influenced by the fishes' ability to detect the gear and its inherent avoidance behaviour (De Robertis and Handegard, 2013; Rieucau *et al.*, 2014). For example, schools are generally easier to capture at night when ambient light is low, when it is difficult for the fish to visually detect the fishing net (Misund, 1993; Olla *et al.*, 2000). Therefore, crowding and other fish behaviors may vary between catches due to variations in fishing conditions and discard regulations may need to consider dynamic fishing conditions.

Backscatter from fish is strongly dependent on the incidence angle of the acoustic beam at the sonar frequencies used in this work, being strongest when approximately perpendicular to the sagittal axis (Cutter and Demer, 2007; Nishimori *et al.*, 2009; Tang *et al.*, 2009; Holmin *et al.*, 2012). The incidence angle is a combination of the distribution of fish orientation and the beam steering angles. Unless the fish orientation distribution is fully random each beam will observe a different incidence angle distribution. Therefore, changes in estimated school volume and S_v may more strongly reflect changes in fish orientation relative to the acoustic beam rather than changes in actual school volume or density.

The 3-D backscatter directivity characteristics of herring could be used to acoustically sense the behaviour and orientation of the fish. However, due to the variable position of the sonar relative to the school, it was difficult to do this in our study. Regardless, our data show a peak in S_v in the centre of the schools, which

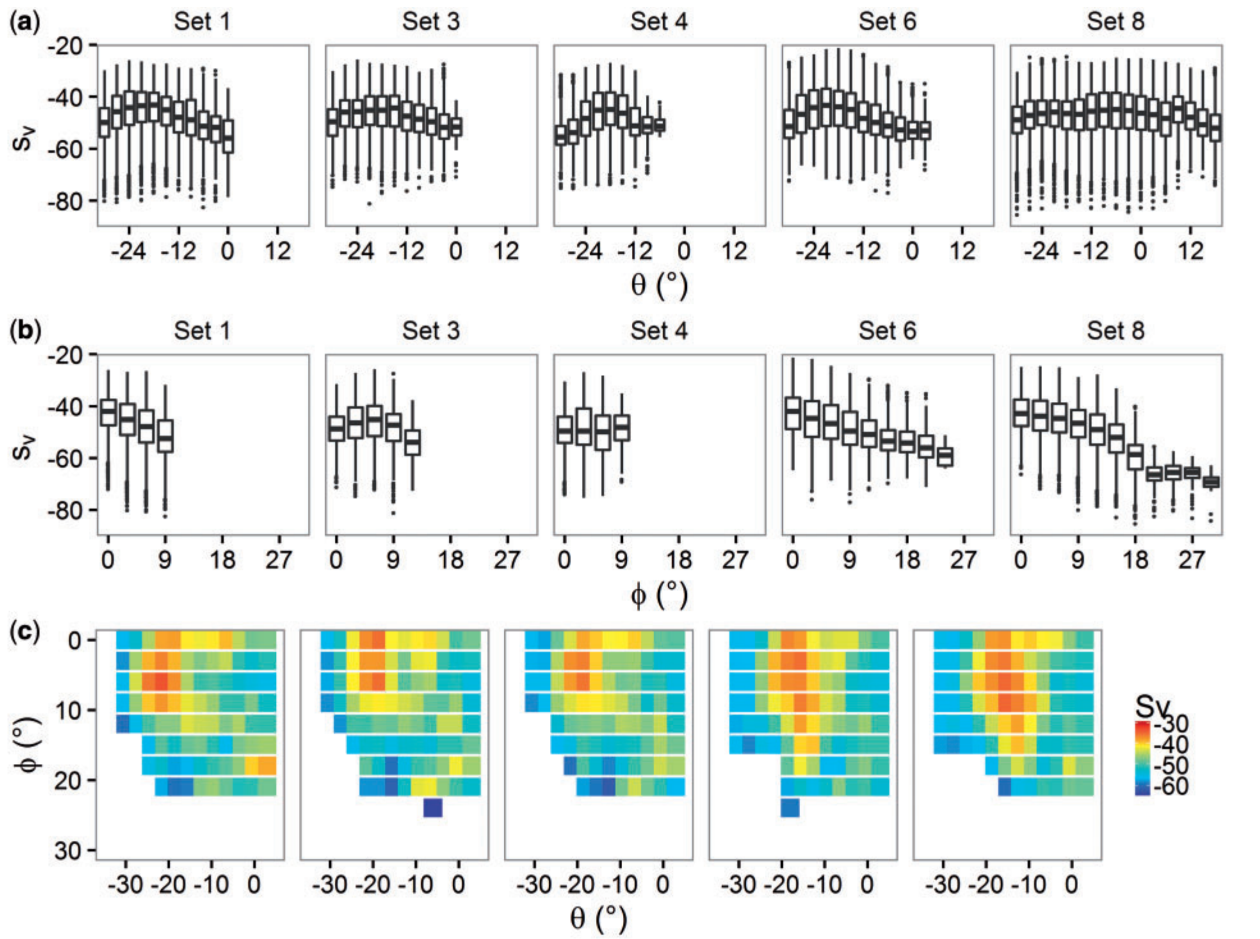

Figure 5. The variation in school S_v with effect of horizontal (θ) and vertical (Φ) beam steering angles [(a) and (b), respectively]. The values contributing to the boxplots were extracted from a $3^\circ \times 3^\circ \times 4$-m grid within the school. The boxes present the first, second and third quartiles, the vertical lines present the range of data, and outliers are plotted as points. Panel (c); range-averaged S_v from five sequential pings in set 6. The vertical axis indicates the sonar beam angle below horizontal. The horizontal axis indicates the sonar beam angle relative to athwartship (positive values are forward).

Table 4. Mean and range of distance of school from the vessel (measured from school centre and from the closest edge), school depth, height, S_v and volume.

	Mean (range)	Species-level		School-level						
				Res	Hauling		Set		Interaction	
		df	*t*-value	df	df	*f*-value	df	*f*-value	df	*f*-value
Distance centre (m)	84 (37–220)	51	−0.8	47	1	17.9^a	4	27.3^b	4	10.9^b
Distance edge (m)	51 (14–150)	51	−0.8	47	1	7.5^a	4	10.7^b	4	6.9^b
Depth (m)	37 (22–63)	51	4.7^a	47	1	211.4^b	4	142.6^b	4	3.6^c
Height (m)	31 (15–55)	51	−3.4^a	47	1	43.7^b	4	41.3^b	4	3.0^c
S_v (dB re m^{-1})	−37 (−43 to −30)	131	6.1^b	85	1	40.8^b	5	8.8^b	5	7.4^b
Volume ('000 m^3)	79 (9–61)	51	−1.1	47	1	45.7^b	4	42.5^b	4	4.1^a

Mixed effects models (lme) were used to investigate the effects of seine hauling on school characteristics at species level. Model results include the degrees of freedom (df) and t-value. ANCOVA models (lm) were used to investigate the effects of seine hauling and purse seine set on school characteristics at school level. Results include residual degrees of freedom (Res df), degrees of freedom (df), and f-value for the effects of haul proportion, set and the interaction between haul proportion and set.

Statistical significance, $^b p < 0.001$, $^a p < 0.01$ and $^c p < 0.05$.

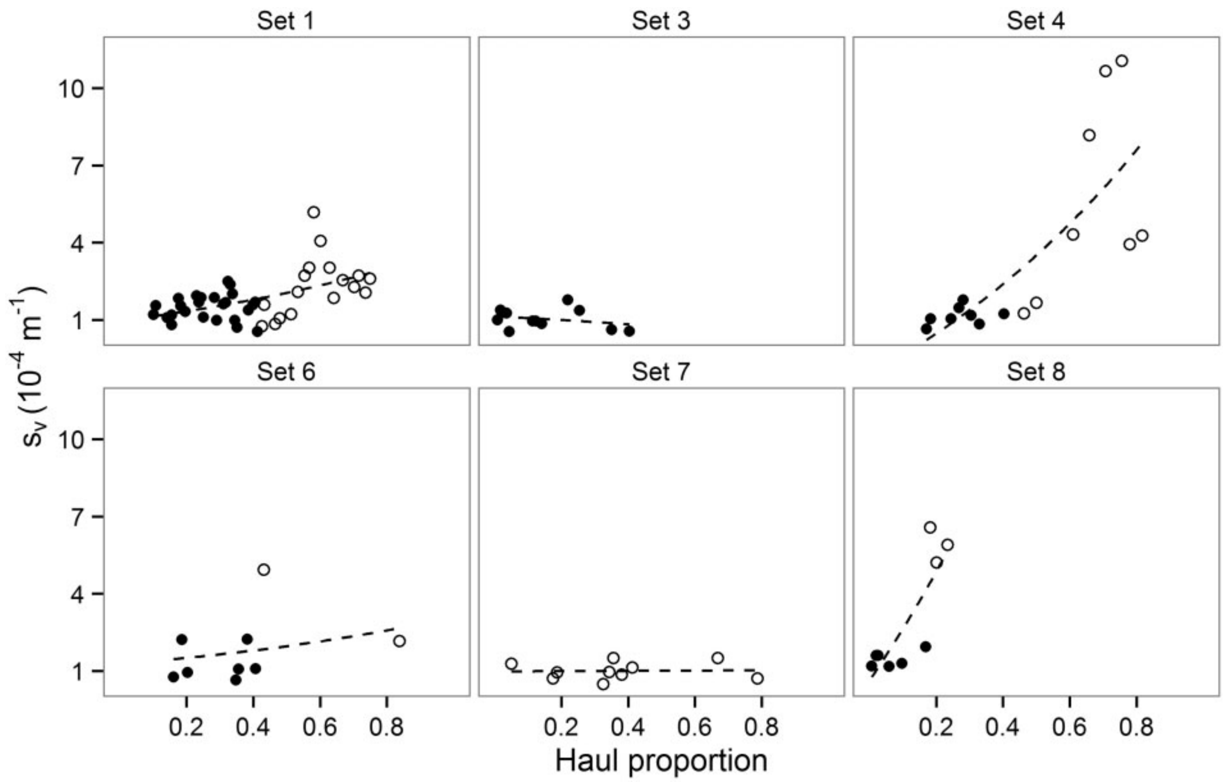

Figure 6. Volume backscattering coefficient (s_v, m^{-1}) of segmented herring schools (filled circles) and partly segmented herring schools (open circles) vs. haul proportion. Results from the ANCOVA are shown with broken lines.

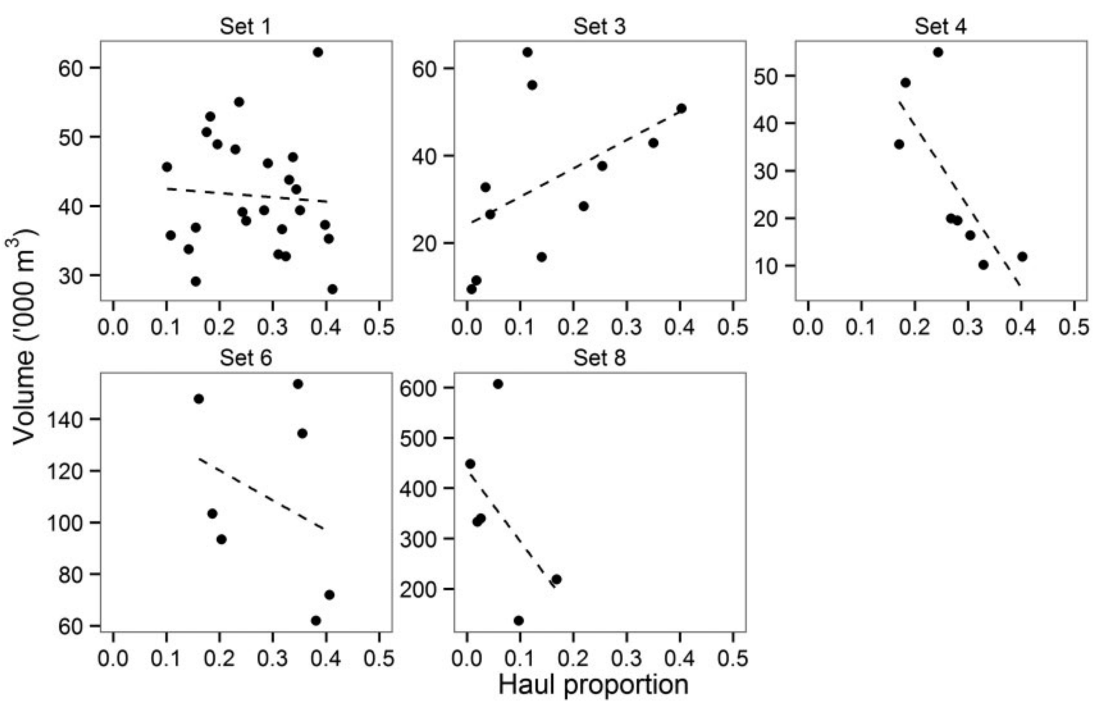

Figure 7. Estimated school volume vs. haul proportion. Results from the ANCOVA are shown with broken lines.

indicates that fish orientation was not fully random. Herring are likely to pack more densely in a seine and take on a more coordinated swimming behavior (Misund, 1993; Ben-Yami, 1994). Assuming that the fish orientation was polarized to some degree, the drop off in S_v towards the edges of the schools suggests that the fish are milling with their aspect changing from side-on in the centre to end-on at the edges of the school. Modeled estimates of the 3-D-averaged *TS* show that the change in *TS* of a single fish, from side-on to end-on orientation can be up to 30 dB (Tang *et al*., 2015), which is close to the 25-dB change we found in our schools. A decline in *TS* with increasing declination was also predicted (Tang *et al*., 2009), being about 10 dB less than what we observed in the schools. Alternatively, the S_v of the polarized school can reduce as a result of increasingly non-broadside incidence angles towards the outer beams. Our data do not show any effect on S_v by the horizontal beam steering angle, but the difference in S_v varied up to 15 dB over the 30° range of the vertical beam steering angles. The effects of beam steering angle on S_v were likely masked by the stronger effects of fish orientation. A peak in S_v in the centre of the school may also result from higher packing density in the centre of the school or multipath reverberation.

A future challenge is to accurately estimate school density and biomass inside the seine using sonar. Acoustic biomass estimates require accurate estimates of *TS*, which depends on species, size, acoustic frequency, fish orientation relative to the acoustic beam and depth (Foote, 1987; Ona, 2003; Cutter and Demer, 2007; Pedersen *et al*., 2009). Orientation is the strongest variable influence on the backscattering strength at the frequencies used by the MS70 (Cutter and Demer, 2007; Nishimori *et al*., 2009; Holmin *et al*., 2012). Consequently, additional information about fish swimming behaviour is required to accurately estimate fish school abundance using sonar (Nishimori *et al*., 2009; Holmin *et al*., 2012). The lateral *TS* of *in situ* herring varies between −32 and −44 dB, measured horizontally at depths ranging from 50 to 350 m (Pedersen *et al*., 2009), while model estimates place it between −36 and −42 dB (Nishimori *et al*., 2009). These estimates are up to 5 dB lower and less frequency dependent than *in situ* dorsal estimates (Foote, 1987; Ona, 2003). Our indirect mean lateral *TS* estimates varied between −37 and −48 dB, ~5 dB lower than the lateral-aspect *TS* of *in situ* fish. The uncertainty of our *TS* estimates comes from uncertainties in the estimates of school volume, s_v and from averaging over an unknown distribution of incidence angles. Catch and average individual weight were accurately measured at the fish landing site. The uncertainties involved in these lateral *TS* estimates preclude drawing firm conclusions from this difference, but characteristics of herring behaviour while in a seine could contribute to the difference. The coordinated behavior will give more variable s_v (Holmin *et al*., 2012) over relatively short time periods. Increased packing density may lead to bias in s_v as a result of acoustic extinction (negative bias) or multi-scattering (positive bias) (Stanton, 1983; Zhao and Ona, 2003), as can air bubbles between the sonar transducer and fish (Loland *et al*., 2007).

This study gives some insight into the behavior of schools captured by purse-seine and identifies challenges and future potential for purse-seine catch monitoring. Monitoring of the school and seine during seine deployment and pursing allows the skipper to adjust fishing strategies according to school and gear behaviour, thereby increasing catch success. We were not able to monitor these fishing stages, but with fishing vessel mounted multibeam sonars with side-looking transducers, this can be done and the methods developed and tested in our study can be useful for improving purse seine catch efficiency. In future, a study on internal school S_v at fine spatial and temporal resolution using a fixed sonar position will provide a better understanding of the school behaviour and swimming orientation during capture. Together with accurate lateral *TS*, school biomass and density can then be measured more accurately.

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References

Anon 2008. Act of 6 June 2008 no. 37 relating to the management of wild living marine resources ("The marine resources act"). Norwegian Ministry of Trade, Industry and Fisheries.

Ben-Yami, M. 1994. Purse seining manual, Fishing News Books, Oxford. 416 pp.

Cutter, G. R., and Demer, D. A. 2007. Accounting for scattering directivity and fish behaviour in multibeam-echosounder surveys. ICES Journal of Marine Science, 64: 1664–1674.

De Robertis, A., and Handegard, N. O. 2013. Fish avoidance of research vessels and the efficacy of noise-reduced vessels: a review. ICES Journal of Marine Science, 70: 34–45.

FAO. 2014. The State of World Fisheries and Aquaculture. Food and Agriculture Organization of the United Nations, Rome. 243. pp.

Foote, K. G. 1987. Fish target strengths for use in echo integrator surveys. Journal of the Acoustical Society of America, 82: 981–987.

Graham, N., Jones, E. G., and Reid, D. G. 2004. Review of technological advances for the study of fish behaviour in relation to demersal fishing trawls. ICES Journal of Marine Science, 61: 1036–1043.

Hawkins, A. D. 1986. Underwater sound and fish behaviour. *In* The Behaviour of Teleost Fishes, 1st edn, pp. 114–151. Ed. by T. Pitcher. Croom Helm, Sydney.

He, P. 1993. Swimming speeds of marine fish in relation to fishing gears. ICES Marine Science Symposia, 196: 183–189.

Holmin, A. J., Handegard, N. O., Korneliussen, R. J., and Tjostheim, D. 2012. Simulations of multi-beam sonar echos from schooling individual fish in a quiet environment. Journal of the Acoustical Society of America, 132: 3720–3734.

Hosseini, S. A., and Ehsani, J. 2014. An investigation of reactive behavior of yellowfin tuna schools to the purse seining process. Iranian Journal of Fisheries Sciences, 13: 330–340.

Huse, I., and Vold, A. 2010. Mortality of mackerel (*Scomber scombrus* L.) after pursing and slipping from a purse seine. Fisheries Research, 106: 54–59.

Johnsen, J. P., and Eliasen, S. 2011. Solving complex fisheries management problems What the EU can learn from the Nordic experiences of reduction of discards. Marine Policy, 35: 130–139.

Korneliussen, R. J. 2010. The acoustic identification of Atlantic mackerel. ICES Journal of Marine Science, 67: 1749–1758.

Korneliussen, R., and Heggelund, Y. 2007. Processing 4-D acoustic data from the Worlds most advanced multi-beam fisheries sonar.

Proceedings of the 30th Scandinavian Symposium on Physical Acoustics, Geilo.

Korneliussen, R. J., Heggelund, Y., Eliassen, I. K., Oye, O. K., Knutsen, T., and Dalen, J. 2009. Combining multibeam-sonar and multifrequency-echosounder data: examples of the analysis and imaging of large euphausiid schools. ICES Journal of Marine Science, 66: 991–997.

Korneliussen, R. J., and Ona, E. 2003. Synthetic echograms generated from the relative frequency response. ICES Journal of Marine Science, 60: 636–640.

Korneliussen, R. J., Heggelund, Y., Macaulay, G. J., Patel, D., Johnsen, E., and Eliassen, I. K. 2016. Acoustic identification of marine species using a feature library. Methods in Oceanography, in press.

Lockwood, S. J., Pawson, M. G., and Eaton, D. R. 1983. The effects of crowding on mackerel (Scomber scombrus L) - physical condition and mortality. Fisheries Research, 2: 129–147.

Loland, A., Aldrin, M., Ona, E., Hjellvik, V., and Holst, J. C. 2007. Estimating and decomposing total uncertainty for survey-based abundance estimates of Norwegian spring-spawning herring. ICES Journal of Marine Science, 64: 1302–1312.

Løkkeborg, S., Fernö, A., and Humborstad, O. B. 2010. Fish behavior in relation to longlines. *In* Behavior of Marine Fishes. Ed. by P. He. pp. 105–141. Wiley-Blackwell, Iowa. 329 pp.

MacLennan, D. N., Fernandes, P. G., and Dalen, J. 2002. A consistent approach to definitions and symbols in fisheries acoustics. ICES Journal of Marine Science, 59: 365–369.

Marras, S., Batty, R. S., and Domenici, P. 2012. Information transfer and antipredator maneuvers in schooling herring. Adaptive Behavior, 20: 44–56.

Misund, O. A. 1993. Avoidance-behaviour of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) in purse seine capture situations. Fisheries Research, 16: 179–194.

Mitson, R. B., and Knudsen, H. P. 2003. Causes and effects of underwater noise on fish abundance estimation. Aquatic Living Resources, 16: 255–263.

Nishimori, Y., Iida, K., Furusawa, M., Tang, Y., Tokuyama, K., Nagai, S., and Nishiyama, Y. 2009. The development and evaluation of a three-dimensional, echo-integration method for estimating fish-school abundance. ICES Journal of Marine Science, 66: 1037–1042.

Nottestad, L., and Axelsen, B. E. 1999. Herring Schooling Manoeuvres in Response to Killer Whale Attacks. Canadian Journal of Zoology, 77: 1540–1546.

Nottestad, L., and Simila, T. 2001. Killer whales attacking schooling fish: why force herring from deep water to the surface?. Marine Mammal Science, 17: 343–352.

Olsen, K. 1971. Influence of vessel noise on the behaviour of herring. *In* Modern Fishing Gear of the World, p. 537. Ed. by H. Kristjonsson. Fishing News Books, London.

Olla, B. L., Davis, M. W., and Rose, C. 2000. Differences in orientation and swimming of walleye pollock *Theragra chalcogramma* in a trawl net under light and dark conditions: concordance between field and laboratory observations. Fisheries Research, 44: 261–266.

Ona, E. 2003. An expanded target-strength relationship for herring. ICES Journal of Marine Science, 60: 493–499.

Ona, E., Mazauric, V., and Andersen, L. N. 2009. Calibration methods for two scientific multibeam systems. ICES Journal of Marine Science, 66: 1326–1334.

Pedersen, G., Handegard, N. O., and Ona, E. 2009. Lateral-aspect, target-strength measurements of in situ herring (*Clupea harengus*). ICES Journal of Marine Science, 66: 1191–1196.

Pitcher, T. J., Misund, O. A., Ferno, A., Totland, B., and Melle, V. 1996. Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high-resolution sonar. ICES Journal of Marine Science, 53: 449–452.

RCoreTeam 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Rieucau, G., De Robertis, A., Boswell, K. M., and Handegard, N. O. 2014. School density affects the strength of collective avoidance responses in wild-caught Atlantic herring *Clupea harengus*: a simulated predator encounter experiment. Journal of Fish Biology, 85: 1650–1664.

Sand, O., Karlsen, H. E., and Knudsen, F. R. 2008. Comment on “Silent research vessels are not quiet” J. Acoust. Soc. Am. 121, EL145-EL1501 (L). Journal of the Acoustical Society of America, 123: 1831–1833.

Sarda, F., Coll, M., Heymans, J. J., and Stergiou, K. I. 2015. Overlooked impacts and challenges of the new European discard ban. Fish and Fisheries, 16: 175–180.

Stanton, T. K. 1983. Multiple-scattering with applications to fish-echo processing. Journal of the Acoustical Society of America, 73: 1164–1169.

Tang, Y., Nishimori, Y., and Furusawa, M. 2009. The average three-dimensional target strength of fish by spheroid model for sonar surveys. ICES Journal of Marine Science, 66: 1176–1183.

Tenningen, M., Pena, H., and Macaulay, G. J. 2015. Estimates of net volume available for fish shoals during commercial mackerel (*Scomber scombrus*) purse seining. Fisheries Research, 161: 244–251.

Tenningen, M., Vold, A., and Olsen, R. E. 2012. The response of herring to high crowding densities in purse-seines: survival and stress reaction. ICES Journal of Marine Science, 69: 1523–1531.

Underwood, M. J., Winger, P. D., Ferno, A., and Engas, A. 2015. Behavior-dependent selectivity of yellowtail flounder (*Limanda ferruginea*) in the mouth of a commercial bottom trawl. Fishery Bulletin, 113: 430–441.

Wardle, C. S. 1993. Fish behaviour and fishing gear. *In* The Behaviour of Teleost Fishes, 2nd edn, pp. 609–643. Ed. by T. Pitcher. Chapman & Hall, London.

Watson, R., Revenga, C., and Kura, Y. 2006. Fishing gear associated with global marine catches - I. Database Development. Fisheries Research, 79: 97–102.

Wilson, B., and Dill, L. M. 2002. Pacific herring respond to simulated odontocete echolocation sounds. Canadian Journal of Fisheries and Aquatic Sciences, 59: 542–553.

Zhao, X. Y., and Ona, E. 2003. Estimation and compensation models for the shadowing effect in dense fish aggregations. ICES Journal of Marine Science, 60: 155–163.

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