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Original Article

Herring perform stronger collective evasive reactions when previously exposed to killer whales calls

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Schooling in fish is understood as a strategy reducing the risk of predation. Yet, it remains unsolved whether schooling fishes can change the structural properties of their collective in order to minimize risk and whether such adjustments promote efficient group-level responsiveness. We conducted a simulated-predator encounter experiment in a sea-cage on a large wild-caught Atlantic herring school (~60 000 individuals). First, we tested whether herring schooling dynamics changed in response to vocalizations of killer whales (feeding calls), a main predator of herring in the wild. We also investigated if herring collective evasive reactions during simulated attacks varied after pre-exposure to killer whale vocalizations. Collective escape reactions (collective diving) were stronger when herring were previously exposed to killer whale vocalizations. However, herring did not modify their schooling dynamics (e.g., school density, school vertical distribution in the water column, fish swimming speed, or correlation strength between individuals, that measures how aligned the fish are as a function of distance) in response to the killer whale feeding calls alone. Overall, our results demonstrate that structural and dynamic changes at the school-level are not necessarily required for the execution of strong collective escape maneuvers, but risk awareness influences collective responsiveness and information transfer among schooling fish.

Key words: acoustics, collective evasive reactions, information transfer, pelagic fish, predation risk, schooling dynamics.

INTRODUCTION

The interaction between prey and their predators is a fundamental process with far-reaching evolutionary and ecological consequences. Avoiding predation is the prevailing functional explanation for why many fishes form schools (Pitcher and Parrish 1993; Rieucau et al. 2015). Schooling is generally understood as an adaptation increasing prey security owing to several antipredator mechanisms including risk dilution (Pitcher and Parrish 1993), improved threat detection (Magurran et al. 1985), predator confusion (Ioannou et al. 2008), and coordinated evasive maneuvers (Pitcher and Wyche 1983; Pitcher and Parrish 1993). Many pelagic fishes aggregate in schools ranging from only few hundred to several millions of individuals. A remarkable property of marine schools, regardless their size, is the ability to perform highly coordinated antipredatory reactions (Nøttestad and Axelsen 1999; Gerlotto et al. 2004; Marras et al. 2012).

Under fluctuating predation risk, making successful avoidance maneuvers requires that schooling fish act on accurate information to correctly assess potential danger. Sharing information about

predation risk is vital for schooling prey, and a school's internal organization (e.g., fish alignment or interfish distances) has been found to play an important role on the efficient propagation of threat-related information among individuals (Herbert-Read et al. 2011; Marras et al. 2012). To date, several mechanisms have been proposed to explain the undamped transmission of information within large schools over very large distances such as waves of agitation (Radakov 1973; Axelsen et al. 2001; Gerlotto et al. 2006) or compressional density waves (Makris et al. 2009). This is supported by in situ observations, during oceanic acoustic surveys, of rapid variations in pelagic school behavior, morphology and internal organization induced by environmental perturbations, anthropogenic disturbances, or predation (Fréon et al. 1992; Misund 1993; Fernö et al. 1998), depicting schooling as a highly plastic process.

Atlantic herring (*Clupea harengus*) is an ecologically and economically important species that forms large schools. Predation risk is known to play an important role in the distribution, temporal levels of activity, or foraging patterns of herring (Fernö et al. 1998). Herring is a key prey for a large spectrum of predator species including fish, sea birds, and marine mammals using different hunting modes. Herring, thus, face the challenge of fine-tuning their antipredator strategies to the prevailing predation risk. In

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the Norwegian Sea, killer whale (*Orcinus orca*) is one of the main predators of herring (Nøttestad and Axelsen 1999; Nøttestad et al. 2002a, 2002b). Groups of highly coordinated killer whales hunting and feeding on herring schools generally produce whistles, pulsed calls, echolocation clicks, and tail-slap sounds (van Opzeeland et al. 2005; Simon et al. 2007). The pulsed calls frequently made by killer whales during feeding are known to be in the frequency range 1–10 kHz, with most energy below 5 kHz (Van Parijs et al. 2004; van Opzeeland et al. 2005), being thus audible for herring that have a documented hearing range up to 4 kHz (Enger 1967). Research has revealed that killer whales produced pulsed calls at a higher rate during feeding activities (Simon et al. 2007). It has been demonstrated that Norwegian and Icelandic killer whales use pulsed calls to force herring to herd into tight schools close to the surface (Simon et al. 2006). However, it remains unknown whether herring can make structural and behavioral adjustments at the school-level to minimize the risk of predation from killer whales and whether these changes promote group-level responsiveness when under attack. Answering these questions requires testing schools in social and physical conditions as close as possible to those that fish experience in their natural environments.

An important contemporary challenge is to collect valuable information about large-scale dynamic reactions of marine schools in situ. Acoustics offers a unique opportunity to monitor and quantify behavioral patterns of aquatic organisms (Pitcher et al. 1996; Simmonds and MacLennan 2005; Handegard et al. 2012; Holmin 2013) including fine-scaled prey–predator interactions (Handegard et al. 2012).

The objectives of our study were 1) to establish whether the internal structure and swimming dynamics of a large herring school changed in response to killer whale feeding calls and 2) to investigate whether the collective evasive responses during simulated attacks varied after pre-exposure to feeding calls. To address these aims, we conducted a simulated-predator encounter experiment in a sea-cage. In particular, we 1) examined the changes in schooling dynamics in response to feeding calls and 2) measured the collective escape reactions of herring exposed to a predator model and contrasted the behavior between pre-exposure to playback of feeding calls and no playback. Using a combination of traditional acoustics and high-resolution imaging sonar, we quantified herring schooling behavior and their collective escape maneuver that consists of diving when threatened (Nøttestad and Axelsen 1999).

METHODS

A wild-caught herring school (~14 tones) was held in a standard aquaculture sea-cage (12-m long × 12-m wide × 12-m deep) at the Institute of Marine Research aquaculture facility, Austevoll, Norway. The experiment was carried out between 24 July 2013 and 30 July 2013 (duration day/night: 19h/5h). More details about the housing and the school characteristics can be found in Rieucou, Boswell, et al. (2014).

Killer whale feeding calls were played back using an underwater speaker (Lubell Labs, model LL916, Columbus, OH). The Lubell speaker has a frequency response of ±8 dB from 200 Hz to 20 kHz. Thus, potential sounds below or above this range were not transmitted. The maximum output of the speaker is 180 dB re 1 μPa at 1 m, and killer whale sounds were transmitted at similar source levels than those emitted by wild killer whales, 150–160 dB re 1 μPa at 1 m (Miller 2006; Simon et al. 2007) (Figure 1). The feeding calls were collected in Vestfjorden, Norway, in summer 2013 from wild killer whales feeding on herring. The calls were recorded using a Digital Acoustic Recording Tag (see Johnson and Tyack 2003 for

more details) that was lowered into the water, from a small boat with its engine off, next to a pod of killer whales feeding on herring.

For each playback, a 4-min feeding sequence call was randomly chosen from a bank of available sequences to control for pseudoreplication. The control treatment consisted of turning on the Lubell underwater speaker during 4 min but without playing back any sound.

Predator attacks were simulated by pulling a black-colored predator model built from a plastic bottle (34-cm long × 9-cm wide) at constant speed (~3.40 m/s) across the sea-cage at 2-m depth, similar to Rieucou, Boswell, et al. (2014) and Rieucou, De Robertis, et al. (2014). Previous studies showed that the predator model was efficient at eliciting typical evasive reactions of schooling herring (Rieucou, De Robertis, et al. 2014). The control treatment consisted only of the apparatus used to tow the model (but no model).

The experiment consisted of 2 series of 2 experimental conditions (feeding calls or control), and each series consisted of 4 trials of 2 experimental treatments (predator model or fishing line alone) in random order (Figure 2). Each day, we carried out 4 trials of the same experimental condition interspaced by at least 4 h (8:00/12:00/16:00/20:00). A 12-h period separated 2 consecutive experimental days. An experimental trial consisted of the following sequence: 1) monitoring the school density and vertical distribution 1 min before, 2) playing back a feeding call 4-min long sequence or the no sound treatment, 3) a 1-min resting period, and 4) 2 consecutive experimental treatments (predator model or the line alone in random order) (Figure 2). At least 6 min separated 2 exposures within a trial, which was sufficient time to allow herring to return to a normal swimming pattern (Rieucou, De Robertis, et al. 2014).

An upward-looking calibrated 120 kHz EK 60 split-beam echosounder with a 7° beamwidth, pulse length = 0.256 ms, transducer gain = 25.120 dB (Simrad, Kongsberg Maritime AS, Horten, Norway) placed at the bottom of the sea-cage was used to monitor the school vertical distribution and density in response to feeding call playbacks and the collective diving in response to the predator model. Using Echoview 5.2 (SonarData Pty Ltd, Tasmania, Australia), we 1) manually measured the school vertical dimension in echograms and 2) estimated the school density using the volume backscattering coefficient, s_v (per meter), 1 min before and 30 s after each playback. The responses to the predator model were estimated by measuring the vertical extent of the reactions in echograms (Figure 3a).

The school density 1 min before and 30 s after each playback was estimated by the average volume backscattering coefficient, s_v . The school density expressed in fish per m³ within the acoustic beam was estimated by $\frac{s_v}{\sigma_{bs}}$, where σ_{bs} is the backscattering cross-section

of a 31.4-cm mature herring at 6-m depth based on the relationship described for Atlantic herring scattering at 38 kHz by Ona (2003) multiplied by the relative frequency response of herring, that is, $\sigma_{bs,120\text{ kHz}} = \sigma_{bs,38\text{ kHz}} \times 0.50$ (Saunders et al. 2012), to convert the 38 kHz estimates of σ_{bs} to 120 kHz. Previously, Rieucou, De Robertis, et al. (2014) estimated the packing density to be 16.1 fish per m³, corresponding to approximately 60 000 individuals when multiplying by the total volume.

A horizontally looking high-frequency imaging sonar, DIDSON (Dual Frequency Identification Sonar, Sound Metrics, Seattle, WA), operating at 1.8 MHz and recording at 8 frames/s, was deployed on one side of the sea-cage at a 2-m depth. The DIDSON was used in high frequency mode where sound pulses from a 96 beam transducer array form a 28° by 14° field of view, with each beam covering a 0.3° (horizontal) by 14° volume between the −3 dB

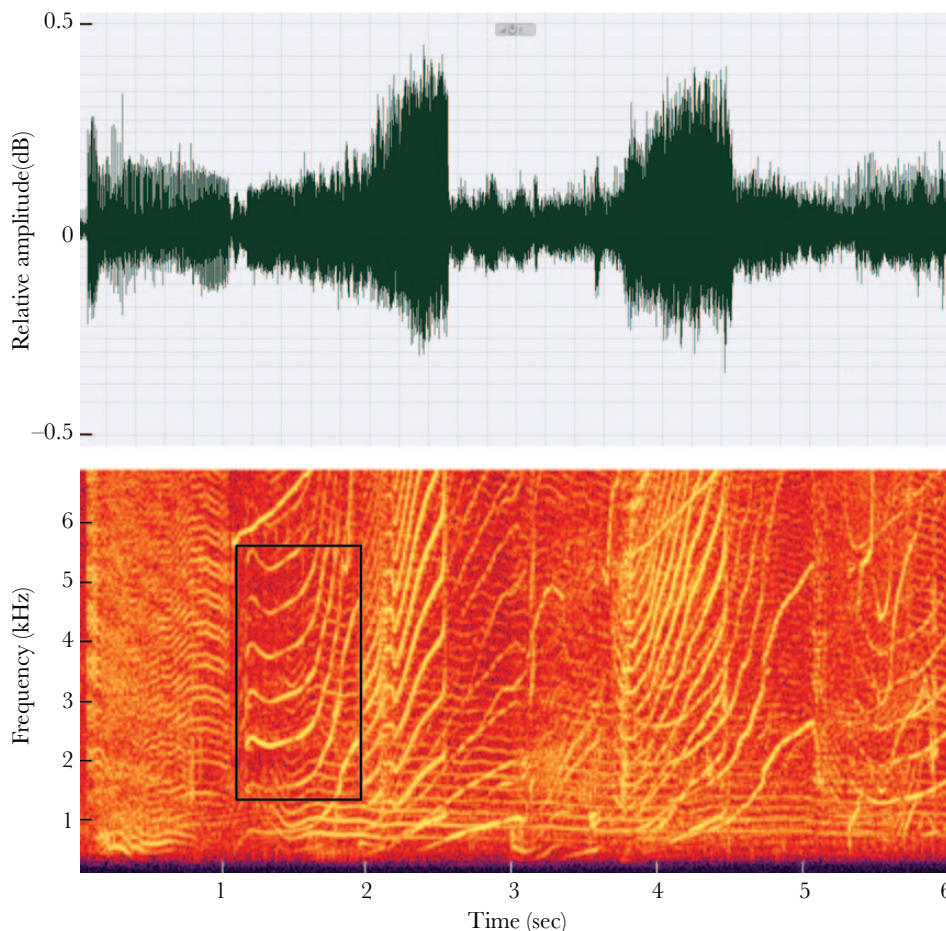


Figure 1
 Example of waveform (upper level) and the corresponding spectrogram (lower level) of a 6-s segment of a killer whale playback. The example shows typical calls, likely from several individual whales. The box shows an example of a typical upsweep call with harmonics.

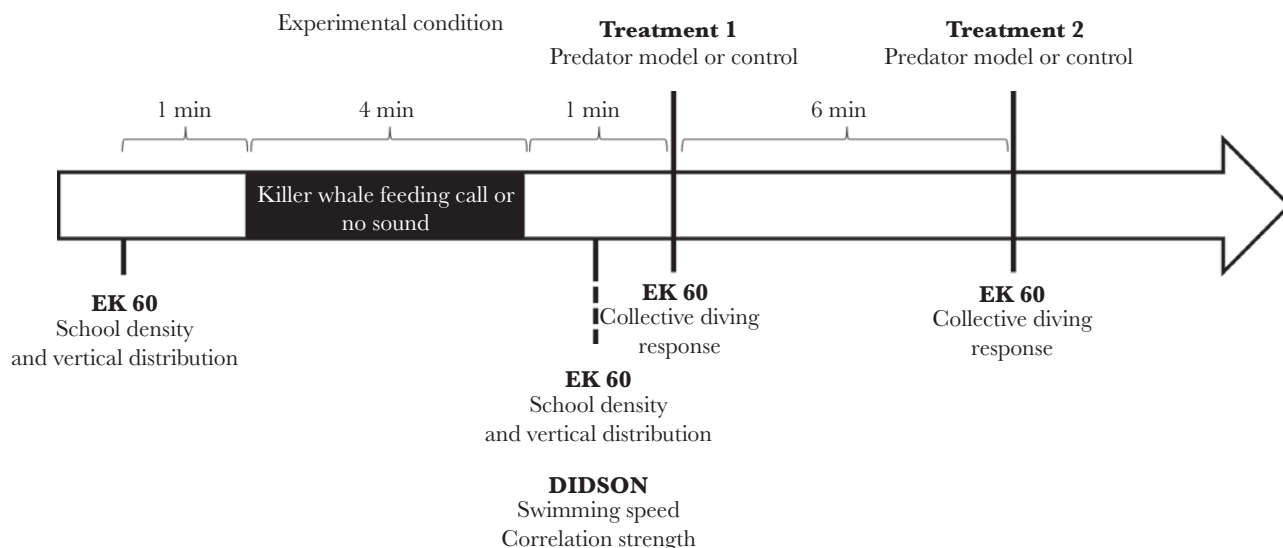


Figure 2
 Description of the sequence of events during an experimental trial. A trial consisted of 1) monitoring the herring school density and vertical distribution 1 min before, 2) playing back a killer whale feeding call 4-min long sequence or the no sound treatment, 3) a 1-min resting period, and 4) 2 consecutive experimental treatments (predator model or the line alone in random order). Also presented in the figure, the sonar type employed (upward-looking EK60 echosounder or the horizontally looking high-frequency imaging DIDSON) and the behavioral metrics measured during each phase of the trial.

points. There are 512 samples along the acoustic axis, and each sample has a resolution of 2 cm along axis. The frame repetition rate was 8 frames/s, and each frame corresponds to an image. The sea-cage wall was just within the field of view at the opposite end. The DIDSON was used to quantify the average school swimming speed and correlation strength in response to the killer whale feeding calls. Particle image velocimetry (PIV; MatPiv v16.1 in MATLAB, Mathworks, MA) was used to estimate the average swimming speed and correlation strength. The correlation strength is a measure of how aligned the fish are as a function of distance.

The noise level in the ultrasonic data is usually higher than video observations, and proper data filtering is required prior to PIV estimation. Simple background subtraction and a time varying gain of $20 \log_{10}$ range were employed to adjust for the spherical spreading loss. The background image was formed by taking the 30th percentile for each pixel intensity along the image sequences, and filtered images were obtained by subtracting the background image and taking the absolute value.

The PIV technique is suitable to detect movements in dense and dynamic groups when individual fish cannot be resolved (Handegard et al. 2012). We used a standard PIV algorithm calculated over a 32×32 window. This resulted in a velocity estimate for each frame

$$\mathbf{v}(m, n) = [v_x(m, n), v_y(m, n)], \quad (1)$$

where each element represents one velocity per 32×32 pixel window, resulting in a matrix with dimensions m by n . The frames where no fish were present were removed by thresholding and replaced with “not a number” (NaN) that were not included in further calculations. The velocity of vectors was further filtered by averaging over 3 consecutive time frames. Apart from the temporal smoothing, the coherence of the PIV measures was improved by means of a local smoothing. A median filter was used to homogenize neighboring PIVs.

To estimate the school state prior to predator model exposure, the average swimming speed, s_k , and average correlation strength, c_k , of the school were quantified. These metrics were calculated based on the PIV values within a time window prior to predator model exposure. The swimming speed s_k was simply the average speed for all PIV vectors within the time window where fish were present, whereas the correlation strength was a measure on how strong the alignment structure was across the school.

To calculate the correlation strength, the PIV values in the matrix where no fish were present and contained NaN were set to zero (the bias that this introduced was corrected for in the normalization below). We, then, subtracted the mean velocity across each time step, that is,

$$\mathbf{u}(m, n) = \mathbf{v}(m, n) - \frac{1}{MN - p} \sum_{m=1}^M \sum_{n=1}^N \mathbf{v}(m, n), \quad (2)$$

where p is the number of NaNs that were replaced by zeros, and m and n are the size of the PIV matrix. For each component of \mathbf{u} , the 2D spatial autocorrelation was calculated using the function `xcorr2` in MATLAB, more specifically

$$c'_x(k, l) = \sum_{m=0}^{M-1} \sum_{n=0}^{N-1} \mathbf{u}_x(m, n) \mathbf{u}_x(m - k, n - l), \quad (3)$$

where $-(M - 1) \leq k \leq M - 1$ and $-(N - 1) \leq l \leq N - 1$ and \mathbf{u}_x is the x component of \mathbf{u} . c'_y was similarly calculated by replacing \mathbf{u}_x and \mathbf{u}_y . Note that $\mathbf{u}_x(m, n)$ were set to zero when the indices were outside the original domain for the PIV, for example, when $m - k < 0$, etc. The normalization of the correlations was achieved by dividing the raw correlations by the product of the standard deviation for each $c'_x(k, l)$, that is,

$$\sigma_x(k, l) = \sqrt{\left(\sum_{m=0}^{M-1} \sum_{n=0}^{N-1} u_x^2(m, n) \right) \left(\sum_{m=0}^{M-1} \sum_{n=0}^{N-1} u_x^2(m - k, n - l) \right)} \quad (4)$$

again where $-(M - 1) \leq k \leq M - 1$ and $-(N - 1) \leq l \leq N - 1$. Note that the NaN values that were replaced by zeroes in u_x were added as a zero in the calculation of the standard deviation, which effectively added a zero weight to the PIVs where no fish were present. Replacing the NaNs with zero did therefore not bias the results. The normalized autocorrelations were calculated as

$$c_x(k, l) = \frac{c'_x(k, l)}{\sigma_x(k, l)}, \quad (5)$$

and the corresponding $c_y(k, l)$ were calculated using $c'_y(k, l)$ and $\sigma_y(k, l)$. Because we were not interested in the correlation structure in a particular direction, the combined autocorrelation matrix was defined as

$$c(k, l) = \frac{1}{2} c_x(k, l) + \frac{1}{2} c_y(k, l), \quad (6)$$

where the $1/2$ factor was chosen such that $c(0, 0) = 1$.

The autocorrelation matrix calculates the spatial correlations resolved across the image. However, we were interested in the correlation as a function of distance r . This was resolved by calculating

$$d(k, l) = \sqrt{(k \cdot \Delta x)^2 + (l \cdot \Delta y)^2}, \quad (7)$$

where Δx and Δy is the grid spacing for the PIV velocities in x and y , respectively. For each element in the autocorrelation matrix $c(k, l)$, we had a corresponding distance $d(k, l)$.

The average $c(k, l)$ was calculated across all time steps within the reference window prior to predator model exposure for each unique range $d(k, l)$, that is, for the combinations of (k, l) that gave the exact same distance. This resulted in an estimate of correlation strength as a function of $c(d)$. By definition, $c(0) = 1$ and the correlation falls off at different rates. A simple measure of the overall correlation strength for a treatment was defined as the area under the correlation curve $c(d)$ from $d = 0 - 4$ m, that is,

$$c_k = \int_{r=0}^{4m} c(d) dr, \quad (8)$$

which was used as an explanatory variable for treatment k in our statistical analysis.

Our aim was to explore herring schooling dynamics and collective responses in social conditions that matched natural ones. Logistically, it was not feasible to create smaller subsets of the school to control for pseudoreplication as is common practice in smaller-scale experiments. However, the large number of herring in the school and their highly dynamic swimming pattern likely resulted in substantial mixing of individuals ensuring that different individuals got exposed to the predator model in each trial.

Statistical analyses

We used a series of paired t -tests to determine whether the school vertical distribution in the water column and the school density (s_k) differed 1 min before and 30 s after the feeding calls for both the playback treatment and the control treatment (speaker on but with no feeding call). We used a series of 1-way analyses of variance (Anovas) to test whether the school vertical distribution and density as well as herring average swimming speed (s_k) and average correlation strength (c_k) differed between the feeding call playback and the control treatments.

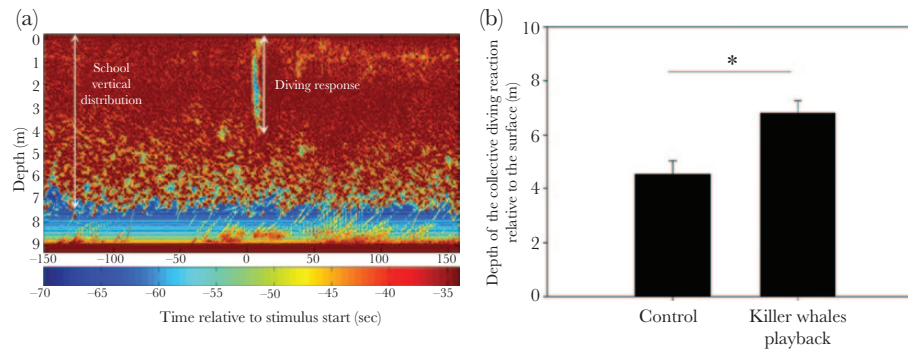


Figure 3

(a) Echogram illustrating the collective diving response during exposure to the predator model. (b) Maximum depth of the collective responses (mean \pm standard error) to the predator model in the control and killer whale feeding call playback conditions.

We tested whether the maximal depth of the collective diving responses toward the predator model differed between the killer whale feeding call treatment and the control (no feeding call) using a 1-way Anova.

All statistical tests were performed in Statistica 11 (StatSoft Inc.; www.statsoft.com). The control data (fishing line alone) were not included in the statistical analysis, as the treatment never elicited evasive responses. Only trials for which the predator model crossed the school were analyzed.

RESULTS

No significant difference in the school vertical distribution were found 1 min before and 30s after the feeding calls for the playback treatment (paired t -test: $n = 6$, $t = 2.08$, degrees of freedom [df] = 5, $P = 0.09$) or 1 min before and 30s after turning on the underwater speaker on for the control treatment (paired t -test: $n = 5$, $t = 0.21$, df = 4, $P = 0.84$). We did not find a significant difference in school density (s_v) before and after the killer whale feeding call playbacks for the 2 treatments (paired t -tests: playback: $n = 6$, $t = 1.84$, df = 5, $P = 0.12$; control: $n = 5$, $t = -1.37$, df = 4, $P = 0.24$). Neither the vertical distribution (1-way Anova: $F_{1,9} = 0.04$; $P = 0.85$), density (1-way Anova: $F_{1,9} = 0.20$; $P = 0.66$), average swimming speed (1-way Anova: $F_{1,9} = 0.01$; $P = 0.97$), or correlation strength (1-way Anova: $F_{1,9} = 0.05$; $P = 0.82$) differed between the feeding call playback and the control treatments (Table 1). This suggests that playbacks of killer whale feeding calls alone did not induce any significant changes in school structure and dynamics (objective 1).

The school performed stronger diving responses toward the predator model when previously exposed to feeding calls compared to without any prior sound stimulus (objective 2) (1-way Anova: $F_{1,9} = 11.32$; $P < 0.008$) (Figure 3b).

Table 1

Response variables for the change in school structure in response to killer whale feeding call playbacks

	Control ($n = 5$)		Killer whales playback ($n = 6$)		$F_{1,9}$	P value
	Mean	Standard error	Mean	Standard error		
School vertical distribution (m)	9.46	0.49	9.58	0.451	0.04	0.85
School density (dB re 1/m)	-25.91	0.63	-25.53	0.58	0.20	0.66
Swimming speed (pixels/s)	11.76	1.76	11.84	1.611	0.01	0.97
Correlation strength (area under the curve)	0.23	0.05	0.23	0.05	0.05	0.82

DISCUSSION

Herring did not modify their school structure in response to the killer whale feeding call playbacks alone, but the school performed stronger collective escape reactions when the fish were previously exposed to predator vocalizations. Despite the absence of acute behavioral and structural adjustments in response to the killer whale playbacks, herring displayed greater collective reactions in situations that were probably perceived as more risky. Our results indicate that risk awareness influences group-level responsiveness and how efficiently predator-related information propagates within a large fish school.

An unexpected result is that the greater collective evasive reactions displayed by herring after being exposed to killer whale feeding calls were not preceded by observable behavioral and structural school-level changes. It has been previously shown that a school's configuration and internal organization (high levels of alignment between fish, reduced interfish distances) are important features for the efficient information transfer among school members (Gerlotto et al. 2006; Marras et al. 2012; Rieucou, De Robertis, et al. 2014), a process thought to be essential for evading predators. However, we found that changes in school structure are not necessarily required for stronger collective escape maneuvers after immediate pre-exposure to killer whale calls. It is possible that herring fine-tune their schooling tendency to the nature of predation risk in a treat-sensitive manner as suggested by Rieucou, Boswell, et al. (2014), but without changing their school structure and dynamics. A common hunting strategy employed by killer whales is to herd herring in dense aggregations to increase catch success (Nøttestad and Axelsen 1999). It would be interesting in future studies to test whether, by not displaying their typical antipredator strategy that consists of schooling more tightly when threatened, risk-aware herring might avoid falling into a deadly trap that favors the hunting tactics of killer whales.

It is also possible that seasonal motivation state affects herring collective responsiveness. For instance, a previous field study has demonstrated that wild overwintering herring perform vertical escapes when exposed to playbacks of killer whale feeding calls (Doksæter et al. 2009), whereas schooling herring tested in a semicontrolled system, but this time during the summer feeding period, were less responsive to killer whale playbacks (Sivle et al. 2012). An animal escape decision is a trade-off between evasion costs and capture risk. Overwintering herring generally become risk averse and more responsive as the spawning season approaches when the prime motivation is survival. After spawning (corresponding to our study period), herring motivation shifts toward feeding. Then, synchronized antipredator responses may be traded-off against feeding to accumulate energy reserves (Nøttestad et al. 1996; Axelsen et al. 2000).

Previous research has shown that birds and humans are able to evaluate the distance to a sound source (Naguib and Wiley 2001). A recent study by DeRuiter et al. (2013) demonstrates that marine mammals have also this ability by observing behavioral reactions to a close sound source and a lack response to a distant sound source of equivalent received level. It is possible, then, that fish may also use cues, such as the sound reverberation, to determine the distance to a sound source. However, because of the relative proximity of the sound source to the herring school (10 m) in our study, it is unlikely that distance assessment to the sound source by herring exposed to our playbacks can explain the absence of behavioral reaction to the killer whale feeding calls.

Another plausible explanation is that far-field acoustic cues about predators are not sufficient alone to trigger structural modifications at the school level. In aquatic systems, prey can detect the presence, location, and the nature of a threat from cues collected through diverse sensory channels acting independently or in an additive manner (Kim et al. 2009). By combining inputs from multiple sensory cues from a potential threat, an animal can improve its assessment of local risk leading to efficient antipredatory responses, that is, the “sensory complement” hypothesis (Ferrari et al. 2008; Rieucan, Boswell, et al. 2014). It remains to be seen if this is the case for schooling herring preyed on by social marine mammals.

Our study raises new questions relevant to understanding the mechanisms that underlie collective reactions and information transfer in large marine schools. One or several mechanisms, other than those leading to observable changes in school structure, might intervene during school-level reactions. Generally, such structural changes include increased swimming speed and correlation strength or reduced interfish distances (Herbert-Read et al. 2011). Physiological changes in herring (plasma cortisol, lactate, or blood ions) have been reported in response to intense stress such as extreme crowding during purse seine fisheries (Tenningen et al. 2012), with demonstrated drastic effects on fish schooling behavior and overall responsiveness. Future research could measure immediate physiological stress responses to killer whale calls and relate this to the collective avoidance reactions. This will help ascertaining the mechanisms at work during risk assessment and coordinated collective escapes in fish schools. In particular, as they allow testing schools in social and physical conditions close to natural ones, mesocosm studies could help shed light on the ecological and evolutionary processes driving the arms race for survival between schooling prey and their predators.

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