1 School-level structural and dynamic adjustments to risk promote information
2 transfer and collective evasion in herring

3
4 Many large-scale animal groups have the ability to react in a rapid and coordinated manner to
5 environmental perturbations or predators. Information transfer among organisms during such
6 events is thought to confer important antipredatory advantages. However, it remains unknown
7 whether individuals in large aggregations can change the structural properties of their
8 collective in response to higher predation risk, and if so whether such adjustments promote
9 responsiveness and information transfer. We examined the role of risk perception on the
10 schooling dynamics and collective evasions of a large herring school (~ 60 000 fish) during
11 simulated-predator encounters in a sea-cage. Using acoustics we quantified swimming
12 dynamics, collective reactions and the speed of the propagating waves of evasion induced by
13 a mobile predator model. In the higher risk condition, fish swam faster, exhibited stronger
14 circular swimming pattern, and we found an increased correlation strength indicating that the
15 school had a greater ability to collectively respond to a perturbation. When exposed to a
16 simulated threat, collective evasions were stronger and behavioural change (evasion
17 manoeuvres) propagated more quickly within the school under environmental conditions
18 perceived as being more risky. Our results demonstrate that large schools make structural and
19 behavioural adjustments in response to perceived risk in a way that improves collective
20 information transfer, and thus responsiveness, during predator attacks.

21
22
23 *Keywords:* Acoustics, collective evasions, information transfer, large aggregations, predation
24 risk, schooling behaviour.

26 **Introduction**

27 The formation of large animal aggregations is a widespread phenomenon across taxa
28 that spans various ecological contexts. A common property of many such groups, including
29 bird flocks or fish schools, is the ability to react in a rapid, and highly coordinated, manner to
30 environmental factors or predators. Avoiding predation is thought to be the prevailing
31 functional explanation for the formation of many animal groups (Pitcher & Parrish, 1993;
32 Rieucau, Fernö, Ioannou, & Handegard, 2015), and collective responsiveness and information
33 transfer can enhance antipredatory response for many grouping prey species (Couzin, 2009;
34 Handegard et al., 2012; Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015; Treherne &
35 Foster, 1981; Yates et al., 2009). The ability of large animal groups to be responsive to
36 external stimuli raises important questions regarding how information acquired locally can
37 spread rapidly across massive aggregations over great distances (Gerlotto, Bertrand, Bez, &
38 Gutierrez, 2006; Makris et al., 2009; Marras, Batty, & Domenici, 2012; Rosenthal et al.,
39 2015).

40 Laboratory (Rosenthal et al., 2015) and field (Handegard et al., 2012) studies of
41 collective evasion have demonstrated the importance of social transmission, whereby sudden
42 changes in the direction of only a few risk-aware individuals (turning away from a detected
43 threat) can be transmitted as a rapid social contagion through the group (waves of turning).
44 This results in a collective amplification of information and motion away from the potential
45 threat (Couzin, 2007; Couzin, 2009; Radakov, 1973; Rosenthal et al., 2015; Treherne &
46 Foster, 1981). The speed of waves of behavioural responses outpace the speed of approaching
47 predators, and exceed the maximum sustained speed of prey individuals themselves (Godin &
48 Morgan, 1985; Marras et al., 2012; Rosenthal et al., 2015), efficiently alerting the other group
49 members of the potential threats (Treherne & Foster, 1981).

50 In natural environments, grouping prey face the challenge of making decisions, within
51 a collective context, to minimize their predation risk while optimizing other fitness-enhancing
52 activities (Krause & Ruxton, 2002). As well as killing prey, predators can also have profound
53 indirect effects (non-consumptive predator effects) on their prey's distribution, foraging
54 patterns, activity levels or antipredator behaviour (Preisser, Bolnick, & Benard, 2005).
55 However, individual behavioural responses to perceived risk that effect changes at the scale of
56 the aggregation are still not well understood. In particular, little is known about the ability of
57 organisms in large aggregations to alter their collective structure in order to facilitate
58 collective information transfer.

59 Here we explore the role of risk perception on the internal organization and collective
60 evasive reactions of pelagic fish schools (Atlantic herring, *Clupea harengus*). Many fish
61 species aggregate in temporary or long-lasting groups in which individuals cannot interact
62 directly with all shoal members simultaneously. For instance, shoals of Atlantic herring or
63 Peruvian anchovy (*Engraulis ringens*) can reach sizes up to several hundreds of thousands
64 individuals (Blaxter, 1985) and exhibit a wide range of coordinated collective reactions
65 (Pitcher & Parrish, 1993) when confronted by predators (Gerlotto et al., 2004; Marras et al.,
66 2012; Nøttestad & Axelsen, 1999). Oceanic acoustic surveys have revealed natural variation
67 in the distribution, behaviour, morphology and internal organization of pelagic schools,
68 suggesting high degree of plasticity (Fernö et al., 1998; Langård et al., 2014). However it is
69 often not possible to determine why such differences exist. For example, changes in group
70 structure can be driven by changes in individual behaviour (such as the spontaneous
71 alignment among individuals within groups as individual speed increases (Tunstrøm et al.,
72 2013)), but groups can also exhibit different collective structures for the same individual-level
73 behaviours (Couzin, Krause, James, Ruxton, & Franks, 2002; Tunstrøm et al., 2013). Under
74 such conditions of “metastability”, random fluctuations can result in abrupt changes in group

75 structure, as between the milling and polarized (aligned) motions exhibited by golden shiner
76 schools (*Notemigonus crysoleucas*) (Tunstrøm et al., 2013).

77 Changes in group state over time are thought to reflect how aggregated individuals in a
78 group balance the tradeoffs between the benefits and costs of being in a group (Pitcher &
79 Parrish, 1993). For example, overwintering Atlantic herring generally aggregate in highly
80 cohesive and dense schools, and during this period the prime motivation is survival rather
81 than feeding or reproduction (Axelsen, Nøttestad, Fernö, Johannessen, & Misund, 2000).
82 These herring are also well-known to perform a diel vertical migration with a shift from dense
83 schools located close to the sea-bed during the day to avoid visually-mediated predators, to
84 nocturnal diffuse layers at the surface to feed (Blaxter, 1985; Fernö et al., 1998). However, it
85 remains unknown whether individuals in large groups in general, and in large fish schools in
86 particular, respond to higher predation risk by adjusting their behaviour and organising
87 themselves in a way that would favour efficient collective information transfer and evasion.

88 One key challenge is that quantifying such phenomena *in situ* has proven difficult.
89 However in aquatic environments acoustic imaging offers a great opportunity to describe
90 structural and dynamic characteristics of fish shoals under naturalistic conditions (Becker &
91 Suthers, 2014; Handegard et al., 2012; Pitcher, Misund, Fernö, Totland, & Melle, 1996;
92 Simmonds & MacLennan, 2005). For example, in recent years, advances in multi-target
93 computer tracking and post-processing analyses of acoustic video have allowed researchers to
94 quantify the fine-scale motion of aquatic organisms during predator-prey interactions
95 (Handegard et al., 2012).

96 In this study, we tested the hypothesis that individuals in large animal groups adjust
97 their behaviour to improve collective responsiveness in risky situations and to promote
98 efficient information transfer between individuals. First, we tested whether schooling herring
99 respond to situations perceived as more dangerous by swimming faster, closer and in more

aligned manner to other school mates, and with an increased correlation strength (defined as how the behavioural change of one individual affects other individuals in the school as a function of distance), indicating then a greater ability to collectively react in an unison manner. Second, we tested whether such adjustments enhance collective anti-predatory responses when under attack through a more efficient transfer of information between group members. We monitored the collective behavioural patterns of a natural-sized wild-caught herring school (~ 60 000 fish) in a semi-controlled environment (netted sea-cage) using an echosounder and high-resolution imaging sonar. We examined whether swimming dynamics and collective responsiveness of schooling herring are affected by the perception of local risk, which we modified by using two different visual backgrounds, based on the known preference of herring to remain visually cryptic to avoid predation (Blaxter, 1985). In the same experimental sea-cage, we tested the second hypothesis by conducting a simulated-predator encounter experiment where we quantified collective avoidance reactions to a mobile predator model. Using an echosounder and high-resolution imaging sonar, we quantified both collective diving and horizontal avoidance, the so-called “Fountain effect” (Magurran & Pitcher, 1987), whereby fish first split in front of the passing predator and after join again behind it. In addition, we quantified the speed of the collective waves of behavioural responses induced by the predator model using an automated post-processing acoustic video analysis approach.

METHODS

Experimental Setup

In April 2012, 14 tonnes of adult Norwegian Spring Spawning herring were captured by a commercial purse-seine fishery vessel, on the west coast of Norway. After capture, the school was transported using a towing pen to the Institute of Marine Research (IMR)

aquaculture facility at Austevoll, Norway (60°5'20 N 05°15'58 E) located approximately 24 km away from the capture point. The fish were transported at slow speed (less than 1 knot) over 15 h to minimize the risk of injury from the physical contact with the net (Doksæter, Handegard, Godø, Kvadsheim, & Nordlund, 2012; Misund & Beltestad, 1995). At the Austevoll facility, the school was placed in an aquaculture brown-coloured net pen (Egersund Net AS, Egersund, Norway: 12 m long x 12 m wide x 12 m deep, volume = 1728 m³). Fish were fed with small-sized aquaculture pellets in addition to any naturally available food items that flowed into the pen. More details about the housing and the fish characteristics can be found in (Rieucou, De Robertis, Boswell, & Handegard, 2014b). Our experiment was conducted between 16 July and 19 July 2013 (duration day/night: 19 h/5 h) and all tests were conducted directly in the housing net pen on the whole captive school.

To simulate a predator attack, we built a black-coloured predator model created from a plastic bottle (34 cm long x 9 cm wide) covered with water-resistant black vinyl tape. Previous studies showed that such a predator model successfully elicits typical evasive reactions of schooling herring (Rieucou, Boswell, De Robertis, Macaulay, & Handegard, 2014a; Rieucou et al., 2014b). The predator model was highly detectable by schooling herring by *i*) being visually conspicuous (Rieucou et al., 2014a) and *ii*) creating water displacement when in motion underwater (Rieucou et al., 2014a). The model was pulled horizontally across the net pen at 1 m depth via a fishing line. The fishing line was attached to an elastic shock cord extended to constant length, fixed at 20 m from the experimental net pen. By applying tension to the elastic shock cord the model could be rapidly propelled through the net pen (Fig. 1). The speeds of the model were recorded by timing the tow duration, and were found to be consistent between exposures (N = 5, mean $\pm$ SD = 3.4 $\pm$ 0.41 m/s). A control treatment in which the fishing line was pulled through without a model ensured that the noise from the

releasing gear, and the motion of the fishing line itself, was not responsible for causing the fish to exhibit evasive reactions.

Based on fish's preference to remain visually cryptic to avoid predation (Blaxter, 1985), we modified the local housing conditions resulting in different levels of conspicuousness of fish against the visual background. A larger visual contrast between fish and the background is expected to increase the perception of risk by fish. By covering the bottom of the net pen with a white net of the same dimension, we created a higher perceived risk scenario. Thus we had two experimental conditions: a white net (relatively “high risk”) and a brown net (relatively “low risk”). The experiment consisted of 2 series of each experimental condition (16 July: brown net, 17 July: white net, 18 July: brown net, 19 July: white net). Each series consisted of 8 trials of two experimental treatments (predator model and control) presented in random order. Over the 4 consecutive days, fish were exposed to a total of 64 treatments. Based on (Rieucau et al., 2014a), we used a 6 min interval between 2 exposures within an experimental trial to allow the fish to return to a similar schooling dynamic as prior to exposure.

Within an experimental day, 2 consecutive trials were interspaced by at least 1 h and 4 trails were conducted in the morning and 4 trials in the afternoon. After the last trial of a day (at 1700), the white net was either placed in or removed from the net pen according the experimental condition tested the following day (starting at 0900). This 16-h period allowed the fish to recover from the possible disturbance caused by the installation or removal of the white net at the bottom of the net pen.

To investigate the schooling dynamic under naturalistic social conditions, we faced the logistical restrictions as it was not feasible to create smaller subsets to control for pseudoreplication, as is common practice in smaller-scale laboratory experiments. An important limiting factor to conduct experiments at such scale is the difficulty to capture,

transport and house large schools of wild herring. In our study it was impossible to return at sea to capture one or more additional herring schools. However, due to the large number of herring that composed the experimental school and their highly dynamic swimming pattern, it is likely that there was a substantial mixing of individuals and thus different individuals directly encountered the predator model or the fishing line in our trials. In addition, the perception of our simulated predator is likely very local, and thus the probability of the same fish being exposed to it is relatively low. Despite our care, we cannot completely rule out the possible pseudoreplication effect that may have arisen in our study. An important extension to our study would be the development of an experimental framework aiming at testing multiple schools directly in natural conditions and quantifying their collective reactions in different risk-level situations.

Ethical note

The animal collection was approved by The Royal Norwegian Ministry of Fisheries, and the experiment was approved by the Norwegian Animal Research Authority. The Institute of Marine Research is permitted to conduct experiments at the Austevoll aquaculture facility by the Norwegian Biological Resource Committee and the Norwegian Animal Research Committee (Forsøksdyrutvalget).

Imaging and Analysis

To quantify the collective diving responses and to monitor the school vertical distribution and density, an upward-looking calibrated 120 kHz split-beam echosounder with a 7 degree beamwidth (Simrad EK 60, Kongsberg Maritime AS, Horten, Norway) was installed on a gimbal at the bottom of the net pen. Echoview 5.2 (SonarData Pty. Ltd., Tasmania, Australia) was used for post-processing. The school density 1 min before predator

model exposure was estimated by the average area scattering coefficient, s_a ($\text{m}^2 \text{m}^{-2}$). The packing density of the same school has been previously estimated to be 16.1 fish per m^{-3} , corresponding to approximately 60 000 individuals when multiplying by the total volume (Rieucan et al., 2014b). The herring diving responses away from the predator model were estimated by measuring the vertical dimensions of the reaction (void) in echograms similar to Rieucan et al. (2014b) (Fig. 2).

To quantify the dynamic properties of the school prior to and during exposure, a high-frequency imaging sonar, DIDSON (Dual Frequency Identification Sonar, Sound Metrics, Washington, USA), was deployed at 1 m depth transversely looking across the net pen at the same depth as the path of the predator model. The opposite net pen wall was just within the field of view. The DIDSON was used in high frequency mode (1.8 MHz) where sound pulses from a 96 beams transducer array form a 28° by 14° field of view, with each beam covering a 0.3° (horizontal) by 14° volume between the -3dB points. This provides 512 samples along the acoustic axis, with each sample having a resolution of 2 cm along the beam. Acoustic data were acquired 8 times (frames) per s and converted into grey-level images (Fig. 3a). Particle image velocimetry (PIV) was used to estimate the average swimming speed and overall correlation strength in MATLAB (package MatPiv v16.1, Mathworks, Massachusetts, USA; see supplementary material). The correlation strength is a measure of how the behavioural change of one individual affects other individuals in the school. The PIV technique is suitable to detect movements in dense and dynamic groups when individual fish cannot be resolved (Handegard et al., 2012).

Background subtraction and a time varying gain of $20 \log r$ 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.

We used a standard PIV algorithm calculated over a 32 by 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 x 32 pixel window, resulting in a matrix with dimensions m by n . Frames where no fish were present were removed by thresholding. The velocity vectors were further filtered by averaging over 3 consecutive time frames (Fig. 3b). Apart from the temporal smoothing, the coherence of the PIV measures was improved by means of a local smoothing via a median filter.

Estimating the School State Prior to Predator Model Exposure

To estimate the school state prior to predator model exposure, we used three metrics: the average swimming speed s_k , the integrated correlation strength c_k and the average rotational order parameter R_k , where k represents the experimental treatment. The metrics were calculated based on the PIV values in a 30 s interval 5 min prior to exposure (predator model or control). The swimming speed s_k was simply the average speed for all PIV vectors values where fish were present within the time interval. The integrated correlation strength for frame i was defined as

$$c_{ki} = \int_{d=0}^{4m} c(d) \, dd, \quad (2)$$

where $c(d)$ was the correlation strength for frame i measuring how the behavioural change of one individual affects other individuals in the school as a function of distance d (see appendix for details). The c_k is the average c_{ki} over the time interval and is thus a simplified metric for the correlation strength for the school prior to exposure resulting in a single value per

experimental treatment. The upper limit of the integral was set to 4 m since $c(d)$ for $d > 4$ m was fluctuating around zero.

The average rotational order parameter R_k was a measure of the coherence of the overall rotation in a group (see Attanasi et al. (2014)), and is the average of R (see appendix for details) in the interval prior to exposure. In a perfectly coherent rotation, all individuals would have a rotational order close to 1, and in a non-coherent state, the parameter will be close to 0.

Quantifying the Dynamic Horizontal Avoidance Reactions Towards the Predator Model

To estimate the speed of the behavioural wave ahead of the predator model, we analysed the PIV estimates relative to the position and speed of the predator model (Fig. 3c,d). The predator model position $\mathbf{x}'_i$ was tracked manually from the imaging sonar. The fish velocity component away from the predator model for a given PIV was

$$s'_i(m, n) = \frac{\mathbf{x}_i(m, n) - \mathbf{x}'_i}{|\mathbf{x}_i(m, n) - \mathbf{x}'_i|} \cdot \mathbf{v}_i(m, n), \quad (3)$$

where $\mathbf{v}_i(m, n)$ and $\mathbf{x}_i(m, n)$ are the PIV estimate and PIV cell position, respectively, for time step i after the release of the predator model. The distance between a PIV cell position and the predator model was given by $r = |\mathbf{x}_i(m, n) - \mathbf{x}'_i|$. All the PIVs and corresponding s'_i that were either behind the predator model or did not contain fish targets were discarded in the following analyses. This resulted in a data set with the 3 following variables: the fish velocity component away from the predator model (s'), the time after release of the predator model (t), and the distance from a PIV cell position to the predator model (r).

We fitted the fish velocity component away from the predator, s' , by least squares to a logistic model,

$$s'(r, t) = \Delta s' \frac{e^{-\theta}}{1 + e^{-\theta}} \quad (4)$$

where $\theta = a(r - (r_0 + bt))$, a is the steepness of the transition, r_0 is the distance to the transition at time $t = 0$, $\Delta s'$ is the difference in fish velocity component away from the predator model inside versus outside of the behavioural wave, and b is the increment of the range to the transition per unit time increment, representing the speed of the behavioural wave ahead of the predator. We assumed that s' drops from $\Delta s'$ to zero outside of the behavioural wave (the average s' outside of the behavioural wave was 0.06 ± 0.27 m/s, mean $\pm$ SD). In the estimation, the steepness of the transition was assumed to be $a = 8.79$, which corresponds to a transition range of 0.5 m defined as the range between 10% and 90% of $\Delta s'$. The logistic model fit resulted in estimates of $\Delta s'$, r_0 , and b for each predator model exposure. In this logistic model, the parameter r_0 was considered to be a tuning parameter for the release of the predator model, and was not interpreted as factor of the behaviour of the fish.

To estimate the range of the void of fish around the predator model, r_I , a second logistic model was fitted to the pixel intensities of the sonar images, I , by replacing $s'(r, t)$ by $I(r, t)$, $\Delta s'$ by ΔI , and $(r_0 + bt)$ by r_I in equation (4),

$$I(r, t) = I_0 + \Delta I \frac{e^{-\theta}}{1 + e^{-\theta}} \quad (5)$$

and $\theta = a(r - r_I)$, where ΔI represents the difference in pixel intensities between the background image (I_0) and the school. We excluded time by setting $b = 0$. This logistic model fit resulted in estimates of ΔI and r_I for each predator model exposure.

Statistical Analysis

To determine whether the schooling tendency prior to the model exposure was affected by the experimental condition, we examined the variables measured prior to threat

exposure. One-way ANOVAs were used to test whether school density values 1 min before exposure to the predator model differed between the brown net and white net conditions, to test whether the average swimming speed (s_k), the integrated correlation strength (the area under the correlation curve) (c_k) and the rotational order parameter (R_k) changed between the conditions, and to investigate the effects of the experimental treatments on the strength of herring diving responses (vertical void quantified on echograms) in the brown net and white net conditions. We tested for differences in responses to the predator model between the white net and the brown net conditions by applying a non-parametric Mann-Whitney-Wilcoxon test to the parameter estimates of b , $\Delta s'$, and r_l obtained from the two logistic models (equations 4 and 5).

All analyses were performed in R 3.1.2 (R Development Core Team, USA). The control data (fishing line alone) were not included in the statistical analysis as the control treatment never induced vertical or horizontal avoidance responses in either experimental condition.

RESULTS

School State Prior to Predator Model Exposure

Prior to exposure to the predator model there was no difference in school density between the white and brown net conditions (ANOVA: $F_{1,46} = 0.39$; $P = 0.53$), suggesting that school density, and thus inter-fish distances, remained similar, and constant in both experimental conditions. However, the fish did differ in swim speed, swimming faster in the white net condition (ANOVA: $F_{1,29} = 17.69$; $P < 0.001$; Fig. 4a). The correlation strength proxy between individuals (defined in equation 2) was stronger in the white net condition (Welch two sample t test: $t_{22.09} = -3.85$, $P < 0.001$; Fig. 4b), demonstrating that the integrated correlation strength in the school was higher in the higher risk environments and that the

behavioural changes of fish were more correlated. Furthermore, the local rotational order parameter was greater in the white net condition (ANOVA: $F_{1,29} = 22.45$; $P < 0.0001$; Fig. 4c), suggesting that fish exhibited a stronger circular swimming pattern within the pen in the higher risk condition. No difference was found in swimming speed, correlation strength or rotational order parameter between the two series of the same experimental condition (white net or brown net). This indicates the absence of habituation effect to the two experimental conditions during the study.

Collective Avoidance Reactions Towards the Predator Model

When exposed to the mobile predator model, fish exhibited stronger collective diving responses in the white net condition (ANOVA: $F_{1,21} = 15.45$; $P < 0.0001$; Fig. 4d). No decrease in the strength of the diving reactions to the predator model was observed over the course of the experiment after repeated exposures.

The absolute speed of the behavioural wave ahead of the predator model ($b +$ speed of the predator model) was considerably faster in the high contrast environmental condition (Mann-Whitney-Wilcoxon test: $P < 0.05$, median for the brown net condition: 4.82 m/s; median for the white net condition: 5.83 m/s; Fig. 5). The significance of the test was not affected by the initial values of the model fit in a neighbourhood around the values $\Delta s' = 1$, $r_0 = 1$, $r_I = 1$ and $b = 1$. No difference was found between the treatments for $\Delta s'$ (Mann-Whitney-Wilcoxon test: $P = 0.98$, median for the brown net condition: 2.18 m/s; median for white net condition: 2.28 m/s), or r_I (Mann-Whitney-Wilcoxon test: $P = 0.118$; median for the brown net condition: 0.91 m; median for white net condition: 1.31 m). Although it failed to reach conventional level of statistical significance, it is noteworthy that the median values for $\Delta s'$ and r_I were larger in the white net condition compared to the brown net condition.

DISCUSSION

Our results demonstrate that behavioural change by individuals in large prey schools in response to changing environmental conditions can substantially alter collective response to a perceived threat. In a relatively high contrast environment, where fish are known to feel more threatened, they swam faster, exhibited stronger circular swimming pattern (suggesting therefore a greater alignment of motion with neighbours), and we found a stronger correlation strength (more correlated behavioural responses) indicating that the school had a greater ability to collectively respond to a perturbation. This is consistent with experimental results on coordinated schools under laboratory conditions where an increase in swimming speed results in increased alignment among individuals (Katz, Tunström, Ioannou, Huepe, & Couzin, 2011; Tunström et al., 2013). In addition, herring performed stronger collective evasive responses, both vertically (diving) and horizontally (Fountain effect), when they were in the high contrast environment. The vertical extent and the horizontal speed at which information about the approaching predator model propagated were greater in the white net condition than in the brown net condition indicating that information about a threat spreads faster among faster, more well aligned, and likely more risk-aware, fish. It has been previously found that individuals in large Peruvian anchovy schools to be more homogenously distributed and more aligned with each other after the passage of a first wave of agitation in response to attacks from sea lions (*Arctocephalus australis* and *Otaria byronia*) (Gerlotto et al., 2006).

The speed of collective waves ahead of the predator model (4.82 m/s; and 5.83 m/s for the brown net and white net conditions respectively) matched previous estimations of the speed of collective behavioural responses in captive herring swimming in small schools, 50 fish, (6.7 m/s) (Marras et al., 2012) and the speed of “waves of agitation” in massive wild anchovy schools when exposed to predation (7.45 m/s) (Gerlotto et al., 2006). Thus our

results demonstrate that individuals in large fish schools can make behavioural, and consequently structural, adjustments that modulate information transfer and collective responsiveness during predator attacks. By adopting a spatial organization that favours the speed and range of propagation of information about threat-related cues among school members, schooling fish likely reduce their risk of capture.

Previous research has shown that correlation length (the spatial scale over which individuals can socially transmit velocity information among group members (Cavagna et al., 2010)) in wild schooling prey fish is much greater than the typical inter-fish distance (Handegard et al., 2012). As a result individuals can become rapidly, and distantly, informed regarding the location of a predator by responding to the velocity of neighbours. It has been found that some predators can use strategies that reduce the prey groups' cohesion and disrupt collective information transfer. For example, predatory sea trouts (*Cynoscion nebulosus*) employ a group-hunting attack strategy that increases the likelihood that prey shoals (juvenile Gulf menhaden, *Brevoortia patronus*) will split, and this results in a decrease in prey distance to predators (and thus likely an increase in risk) (Handegard et al., 2012).

Inter-individual distances among grouping organisms may be an important factor in explaining how information can propagate efficiently and rapidly via social interactions. For instance, in captive schools of herring, stronger collective reactions are observed in denser schools with, thus, shorter inter-fish distances (Rieucau et al., 2014b). Research also revealed that the rapid propagating compressional waves characteristic of the formation of vast free-ranging herring shoals do not occur until the shoals first reach a critical density ($\sim 0.2 \text{ fish/m}^{-3}$) (Makris et al., 2009). These compressional waves can be one order of magnitude faster than herring swimming speed and can span over kilometres (Makris et al., 2009). In our study, however, herring did not react to an increasing level of conspicuousness by forming denser

aggregations. It is possible that confinement in the experimental sea-cage may have restricted the density change compared to an open system.

Schooling fish can gain information about threats using cues gathered from different sensory modalities (Brown, 2003; Kim et al., 2009), and it would be interesting in future studies to explore how large marine schools evaluate the level of and respond to predation risk from different types of predator cues such as acoustical (e.g., vocalizations of marine predators), chemical or hydraulic cues, sensed by the mechanoreceptors located in the lateral line system.

Our results strengthen the idea that large marine fish schools can display a high degree of behavioural and structural plasticity at the face of biotic (e.g., consumptive and non-consumptive predator effects) (Langård et al., 2014) or abiotic factors (e.g., thermocline, pycnocline or light level) (Fernö et al., 1998; Mackinson, 1999). We foresee context-dependent response by marine schools as valuable source of information to develop non-intrusive assessment tools to evaluate how commercially-important pelagic fishes perceive anthropogenic disturbances in various situations. This, for example, will provide managers with tools that can be used to either ameliorate housing conditions and practices in fish farms, regulate slipping procedures (i.e., the deliberate release of unwanted catches from purse seines during fishing operations) or spatial planning and design of marine renewable energy devices (e.g., tidal turbines), based on the observed structural and dynamic variations in schooling tendency of marine fishes. Overall, understanding the plasticity of collective behaviour can provide important information to shed light on the evolutionary and ecological processes that underlie the formation and maintenance of marine schools and structure trophic interactions.

References

412 Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Melillo, S., Parisi, L., et al. (2014).
 413 Collective behaviour without collective order in wild swarms of midges. *PLoS*
 414 *Comput Biol*, 10(7), e1003697. doi: 10.1371/journal.pcbi.1003697
 415 Axelsen, B. E., Nøttestad, L., Fernö, A., Johannessen, A., & Misund, O. A. (2000). 'Await' in
 416 the pelagic: dynamic trade-off between reproduction and survival within a herring
 417 school splitting vertically during spawning. *Marine Ecology Progress Series*, 205,
 418 259-269. doi: 10.3354/meps205259
 419 Becker, A., & Suthers, I. M. (2014). Predator driven diel variation in abundance and
 420 behaviour of fish in deep and shallow habitats of an estuary. *Estuarine, Coastal and*
 421 *Shelf Science*, 144(0), 82-88. doi: 10.1016/j.ecss.2014.04.012
 422 Blaxter, J. H. S. (1985). The herring: A successful species? *Canadian Journal of Fisheries*
 423 *and Aquatic Sciences*, 42(S1), 21-30. doi: 10.1139/f85-259
 424 Brown, G. E. (2003). Learning about danger: chemical alarm cues and local risk assessment
 425 in prey fishes. *Fish and Fisheries*, 4(3), 227-234. doi: 10.1046/j.1467-
 426 2979.2003.00132.x
 427 Cavagna, A., Cimorelli, A., Giardina, I., Parisi, G., Santagati, R., Stefanini, F., et al. (2010).
 428 Scale-free correlations in starling flocks. *Proceedings of the National Academy of*
 429 *Sciences*, 107(26), 11865-11870. doi: 10.1073/pnas.1005766107
 430 Couzin, I. (2007). Collective minds. [10.1038/445715a]. *Nature*, 445(7129), 715-715.
 431 Couzin, I. D. (2009). Collective cognition in animal groups. *Trends in Cognitive Sciences*,
 432 13(1), 36-43. doi: 10.1016/j.tics.2008.10.002
 433 Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective
 434 memory and spatial sorting in animal groups. *Journal of Theoretical Biology*, 218(1),
 435 1-11. doi: 10.1006/jtbi.2002.3065

436 Doksæter, L., Handegard, N. O., Godø, O. R., Kvadsheim, P. H., & Nordlund, N. (2012).
 437 Behavior of captive herring exposed to naval sonar transmissions (1.0--1.6 kHz)
 438 throughout a yearly cycle. *The Journal of the Acoustical Society of America*, 131(2),
 439 1632-1642.

440 Fernö, A., Pitcher, T. J., Melle, W., Nøttestad, L., Mackinson, S., Hollingworth, C., et al.
 441 (1998). The challenge of the herring in the Norwegian sea: Making optimal collective
 442 spatial decisions. *Sarsia*, 83(2), 149-167. doi: 10.1080/00364827.1998.10413679

443 Gerlotto, F., Bertrand, S., Bez, N., & Gutierrez, M. (2006). Waves of agitation inside anchovy
 444 schools observed with multibeam sonar: a way to transmit information in response to
 445 predation. *ICES Journal of Marine Science: Journal du Conseil*, 63(8), 1405-1417.
 446 doi: 10.1016/j.icesjms.2006.04.023

447 Gerlotto, F., Castillo, J., Saavedra, A., Barbieri, M. A., Espejo, M., & Cotel, P. (2004). Three-
 448 dimensional structure and avoidance behaviour of anchovy and common sardine
 449 schools in central southern Chile. *ICES Journal of Marine Science: Journal du*
 450 *Conseil*, 61(7), 1120-1126. doi: 10.1016/j.icesjms.2004.07.017

451 Godin, J.-G., & Morgan, M. J. (1985). Predator avoidance and school size in a cyprinodontid
 452 fish, the banded killifish (*Fundulus diaphanus* Lesueur). *Behavioral Ecology and*
 453 *Sociobiology*, 16(2), 105-110. doi: 10.1007/BF00295142

454 Handegard, N. O., Boswell, K. M., Ioannou, C. C., Leblanc, S. P., Tjøstheim, D. B., &
 455 Couzin, I. D. (2012). The dynamics of coordinated group hunting and collective
 456 information transfer among schooling prey. *Current Biology*, 22(13), 1213-1217. doi:
 457 10.1016/j.cub.2012.04.050

458 Katz, Y., Tunström, K., Ioannou, C. C., Huepe, C., & Couzin, I. D. (2011). Inferring the
 459 structure and dynamics of interactions in schooling fish. *Proceedings of the National*
 460 *Academy of Sciences*, 108(46), 18720-18725. doi: 10.1073/pnas.1107583108

- Kim, J. W., Brown, G. E., Dolinsek, I. J., Brodeur, N. N., Leduc, A. O. H. C., & Grant, J. W. A. (2009). Combined effects of chemical and visual information in eliciting antipredator behaviour in juvenile Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, 74(6), 1280-1290. doi: 10.1111/j.1095-8649.2009.02199.x
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. USA Oxford University Press.
- Langård, L., Fatnes, O., Johannessen, A., Skaret, G., Axelsen, B., Nøttestad, L., et al. (2014). State-dependent spatial and intra-school dynamics in pre-spawning herring *Clupea harengus* in a semi-enclosed ecosystem. *Marine Ecology Progress Series*, 501, 251-263. doi: 10.3354/meps10718
- Mackinson, S. (1999). Variation in structure and distribution of pre-spawning Pacific herring shoals in two regions of British Columbia. *Journal of Fish Biology*, 55(5), 972-989. doi: 10.1111/j.1095-8649.1999.tb00733.x
- Magurran, A. E., & Pitcher, T. J. (1987). Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 229(1257), 439-465. doi: 10.1098/rspb.1987.0004
- Makris, N. C., Ratilal, P., Jagannathan, S., Gong, Z., Andrews, M., Bertsatos, I., et al. (2009). Critical population density triggers rapid formation of vast oceanic fish shoals. *Science*, 323(5922), 1734-1737. doi: 10.1126/science.1169441
- Marras, S., Batty, R. S., & Domenici, P. (2012). Information transfer and antipredator maneuvers in schooling herring. *Adaptive Behavior*, 20(1), 44-56. doi: 10.1177/1059712311426799
- Misund, O. A., & Beltestad, A. K. (1995). Survival of herring after simulated net bursts and conventional storage in net pens. *Fisheries Research*, 22(3-4), 293-297. doi: 10.1016/0165-7836(94)00326-R

486 Nøttestad, L., & Axelsen, B. E. (1999). Herring schooling manoeuvres in response to killer
 487 whale attacks. *Canadian Journal of Zoology*, 77(10), 1540-1546. doi: 10.1139/z99-
 488 124

489 Pitcher, T. J., Misund, O. A., Fernö, A., Totland, B., & Melle, V. (1996). Adaptive behaviour
 490 of herring schools in the Norwegian Sea as revealed by high-resolution sonar. *ICES*
 491 *Journal of Marine Science: Journal du Conseil*, 53(2), 449-452. doi:
 492 10.1006/jmsc.1996.0063

493 Pitcher, T. J., & Parrish, J. K. (1993). The functions of shoaling behaviour. In T. J. Pitcher
 494 (Ed.), *The behaviour of teleost fishes* (2nd ed., pp. 363–439). London: Chapman and
 495 Hall.

496 Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of
 497 intimidation and consumption in predator-prey interactions. *Ecology*, 86(2), 501-509.
 498 doi: 10.1890/04-0719

499 Radakov, D. V. (1973). *Schooling in the ecology of fish*. New York: Wiley.

500 Rieucau, G., Boswell, K. M., De Robertis, A., Macaulay, G. J., & Handegard, N. O. (2014a).
 501 Experimental evidence of threat-sensitive collective avoidance responses in a large
 502 wild-caught herring school. *PLoS ONE*, 9(1), e86726. doi:
 503 10.1371/journal.pone.0086726

504 Rieucau, G., De Robertis, A., Boswell, K. M., & Handegard, N. O. (2014b). School density
 505 affects the strength of collective antipredatory responses in wild-caught herring
 506 (*Clupea harengus*): A simulated predator encounter experiment. *Journal of Fish*
 507 *Biology*, 85, 1650-1664.

508 Rieucau, G., Fernö, A., Ioannou, C. C., & Handegard, N. O. (2015). Towards of a firmer
 509 explanation of large shoal formation, maintenance and collective reactions in marine

510 fish. *Reviews in Fish Biology and Fisheries*, 25, 25-37. doi: 10.1007/s11160-014-
511 9367-5

512 Rosenthal, S. B., Twomey, C. R., Hartnett, A. T., Wu, H. S., & Couzin, I. D. (2015).
513 Revealing the hidden networks of interaction in mobile animal groups allows
514 prediction of complex behavioral contagion. *Proceedings of the National Academy of*
515 *Sciences*, 112(15), 4690-4695. doi: 10.1073/pnas.1420068112

516 Simmonds, J., & MacLennan, D. N. (2005). *Fisheries Acoustics: Theory and Practice* (2nd
517 edition ed.). Oxford: Blackwell Science.

518 Treherne, J. E., & Foster, W. A. (1981). Group transmission of predator avoidance behaviour
519 in a marine insect: The trafilgar effect. *Animal Behaviour*, 29(3), 911-917. doi:
520 10.1016/s0003-3472(81)80028-0

521 Tunström, K., Katz, Y., Ioannou, C. C., Huepe, C., Lutz, M. J., & Couzin, I. D. (2013).
522 Collective states, multistability and transitional behavior in schooling fish. *PLoS*
523 *Computational Biology*, 9 e1002915.

524 Yates, C. A., Erban, R., Escudero, C., Couzin, I. D., Buhl, J., Kevrekidis, I. G., et al. (2009).
525 Inherent noise can facilitate coherence in collective swarm motion. *Proceedings of the*
526 *National Academy of Sciences*, 106(14), 5464-5469. doi: 10.1073/pnas.0811195106
527
528
529
530
531
532
533
534

535 **Appendix**

536 The correlations strength $c(d)$ were calculated as follow. First, the PIV values were set to zero
 537 where no fish were present or where the PIV contained “not a number” (NaN). As this causes
 538 bias in the correlations, it was corrected for in the normalization below. First, the mean
 539 velocity across each time step was subtracted, i.e.,

$$\mathbf{u}(m, n) = \mathbf{v}(m, n) - \frac{1}{MN - p} \sum_{m=1}^M \sum_{n=1}^N \mathbf{v}(m, n), \quad (\text{A1})$$

540 where p is the number of NaN's that were replaced by zeros, and M and N are the sizes of the
 541 PIV matrix. For each component of $\mathbf{u}$, the 2 dimensional spatial autocorrelation was
 542 calculated using *xcorr2* in MATLAB (the Mathworks, Natick, Massachusetts, U.S.A.),

$$c'_x(k, l) = \sum_{m=0}^{M-1} \sum_{n=0}^{N-1} u_x(m, n) u_x(m - k, n - l), \quad (\text{A2})$$

543 where $-(M - 1) \leq k \leq M - 1$, $-(N - 1) \leq l \leq N - 1$ and u_x is the x component of $\mathbf{u}$. By
 544 replacing u_x by u_y , the correlation on y direction, c'_y , was similarly calculated. The $u_x(m, n)$
 545 were set to zero outside the original domain for the PIV (e.g., when $m - k < 0$, etc). The
 546 correlations were normalised using the standard deviation defined as

$$\sigma_x(k, l) = \sqrt{\left(\sum_{m=0}^{M-1} \sum_{n=0}^{N-1} u_x^2(m, n) \right) \left(\sum_{m=0}^{M-1} \sum_{n=0}^{N-1} u_x^2(m - k, n - l) \right)}, \quad (\text{A3})$$

547 in the x direction, again where $-(M - 1) \leq k \leq M - 1$ and $-(N - 1) \leq l \leq N - 1$.
 548 Replacing the NaN values by zeroes in the calculation u_x does not cause bias since it also
 549 adds a zero in the calculation of the standard deviation, resulting in zero weight to the PIVs
 550 where no fish were present. The normalized autocorrelations were then calculated as

$$c_x(k, l) = \frac{c'_x(k, l)}{\sigma_x(k, l)}, \quad (\text{A4})$$

551 and similarly for $c_y(k, l)$. The combined autocorrelation matrix, regardless of direction, was
 552 defined as

$$c(k, l) = \frac{1}{2} c_x(k, l) + \frac{1}{2} c_y(k, l), \quad (\text{A5})$$

553 where the $\frac{1}{2}$ factor was chosen such that $c(0,0) = 1$.

554 To quantify the correlation as a function of distance r instead of k and l , we calculated

$$d(k, l) = \sqrt{(k \cdot \Delta x)^2 + (l \cdot \Delta y)^2}, \quad (\text{A6})$$

555 where Δx and Δy are the grid spacing for the PIV velocities in x and y , respectively. The
 556 average $c(k, l)$ was calculated for each unique distance $d(k, l)$, i.e., for the combinations of
 557 (k, l) that gave the exact same distance. The result was an estimate of correlation strength $c(d)$
 558 as a function of distance.

559 The calculation of the rotational order parameter was calculated based on Attanasi et
 560 al. (2014) (their equation 8). Since our observation system was two dimensional and did not
 561 cover the whole school, we chose the centre of the pen $\mathbf{x}_0$ as the reference for the calculation,
 562 and used the sonar plane as the projection plane for the calculations. The simplified 2D
 563 equation for calculating the rotational order for each time step is then
 564

$$R = \frac{1}{MN - p} \left| \sum_{m,n} \frac{\mathbf{x}(m, n) \times \mathbf{v}(m, n)}{|\mathbf{x}(m, n) \times \mathbf{v}(m, n)|} \cdot \mathbf{e}_z \right|, \quad (\text{A7})$$

565 where $\mathbf{x}(m, n) = [m \cdot \Delta x \quad n \cdot \Delta y \quad 0]^T - \mathbf{x}_0$, $\mathbf{e}_z$ is the unity vector normal to the horizontal
 566 sonar plane, and $\mathbf{v}(m, n)$ is the PIV vector with a zero padded for the vertical dimension
 567 (along $\mathbf{e}_z$).

568

569

570

Figure legends

Figure 1. Fig. 1. (a) Schematic representation of the experimental net pen. Predator encounters were simulated using a bottle-shaped black predator model. An upward-looking 120 kHz split-beam echosounder (Simrad EK 60) was placed at the bottom of the experimental pen to monitor collective diving reactions and a DIDSON (Dual Frequency Identification Sonar, Sound Metrics, Washington, USA) horizontally oriented toward the predator model's path was used to monitor fish horizontal avoidance responses. (b) An underwater picture showing the white net placed at the bottom of the net pen during the white-net condition. Also shown in picture (b) the 120 kHz EK 60.

Figure 2. Example of an echogram obtained from the upward-looking 120 kHz EK 60 echosounder used to quantify the school density prior to predator model exposure and the collective diving response during simulated attacks. The colour scale shows the values of the volume backscattering strength, S_v , expressed in dB re 1 m^{-1} .

Figure 3. (a) Acoustic frame from the high-frequency imaging sonar (DIDSON) transversely looking across the net pen before exposure to the predator model. (b) Estimation of the swimming speed of herring within the school prior to predator model exposure using a particle image velocimetry (PIV) algorithm. The PIVs (arrows) correspond to the 32×32 pixel window discretization of the acoustic data with an input resolution of 674×400 pixels (height $\times$ width). The colour code shows the estimated speed in pixels/s for each PIV. (c) and (d) Illustration of the quantification procedure of the collective horizontal avoidance reaction towards the predator model. PIV estimates were analysed relative to the position of the predator model, which was manually tracked. The speed of the behavioural wave ahead of the predator model (grey area) was extracted at times t_i and t_{i+} , panel (c) and (d) respectively.

The fish velocity component away from the predator model (s') gives the speed of each PIV.

The distances from each PIV to the predator model for t_i and $t_{i'}$ are given by r_i and $r_{i'}$

respectively.

Figure 4. (a) Herring swimming speed in the brown net and white net conditions. Coloured triangles indicate the means $\pm$ SE and opened dots show trails. (b) Correlation strength between individual fish (mean $\pm$ SE) prior to predator model exposure in the two experimental conditions. Also presented in panel b, the change in correlation strength as a function of the distance between individuals for each trail in the brown net (red lines) and white net (blue lines) conditions. (c) Local rotational order parameter (mean $\pm$ SE) in the two experimental conditions before exposure to the predator model exposure. (d) Maximum depth of the diving collective responses (mean $\pm$ SE) to the predator model in the brown net and white net conditions.

Figure 5. Average velocity component away from the predator model, s' , in range and time bins of width 0.5 m and 0.25 s, respectively, plotted against distance on the x axis and time on the y axis. An increase in saturation of blue colour indicates an increase in velocity component, s' , and the fitted line $s(r, t) = 0.5$ of the logistic model, representing the estimated behavioural wave front, is plotted in black in each frame. Also presented a box plot, with interquartile range (IQR), whiskers (lower quartile + 1.5 x IQR, upper quartile + 1.5 x IQR) and median, showing the speed of the behavioural wave ahead of the predator model in the brown net and white net conditions.

Figure 1.

639 **Figure 2.**

640

641

642

643

644

645

646

647

648

649

650

651

652

Figure 3.

656 **Figure 4.**

670 **Figure 5.**

671

672

Acknowledgments

We are grateful to E. Grimsbø, L. Doksæter, L. Stien, G. Macaulay and the fish keepers at the Austevoll aquaculture facility for their technical help during the experiment. We thank A. Fernö for his useful comments while we were developing the original idea of this paper. This work was financed by the Norwegian Research Council (204229/F20). J.C.C. was partially supported by a grant from Iceland, Liechtenstein and Norway through the EEA Financial Mechanism operated by Universidad Complutense de Madrid. I.D.C. was supported by NSF (PHY-0848755, IOS-1355061, EAGER-1251585), ONR (N00014-09-1-1074, N00014-14-1-0635), ARO (W911NG-11-1-0385, W911NF-14-1-0431), and Human Frontier Science Program (RGP0065/2012).