



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



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

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The formation of large animal aggregations is a widespread phenomenon across taxa that spans various ecological contexts. A common property of many such groups, including bird flocks or fish schools, is the ability to react in a rapid, and highly coordinated, manner to environmental factors or predators. Avoiding predation is thought to be the prevailing functional explanation for the formation of many animal groups (Pitcher & Parrish, 1993; Rieucou, Fernö, Ioannou, & Handegard, 2015), and collective responsiveness and information transfer can enhance antipredator response for many grouping prey species (Couzin, 2009; Handegard et al., 2012; Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015; Treherne & Foster, 1981; Yates et al., 2009). The ability of large animal groups to be responsive to external stimuli raises important

questions regarding how information acquired locally can spread rapidly across massive aggregations over great distances (Gerlotto, Bertrand, Bez, & Gutierrez, 2006; Makris et al., 2009; Marras, Batty, & Domenici, 2012; Rosenthal et al., 2015).

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

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

In this study we explored the role of risk perception on the internal organization and collective evasive reactions of pelagic fish schools (Atlantic herring, *Clupea harengus*). Many fish species aggregate in temporary or long-lasting groups in which individuals cannot interact directly with all shoal members simultaneously. For instance, shoals of Atlantic herring or Peruvian anchovy, *Engraulis ringens*, can comprise several hundreds of thousands of individuals (Blaxter, 1985) and exhibit a wide range of coordinated collective reactions (Pitcher & Parrish, 1993) when confronted by predators (Gerlotto et al., 2004; Marras et al., 2012; Nøttestad & Axelsen, 1999). Oceanic acoustic surveys have revealed natural variation in the distribution, behaviour, morphology and internal organization of pelagic schools, suggesting a high degree of plasticity (Fernö et al., 1998; Langård et al., 2014). However, it is often not possible to determine why such differences exist. For example, changes in group structure can be driven by changes in individual behaviour (such as the spontaneous alignment among individuals within groups as individual speed increases; Tunstrøm et al., 2013), but groups can also exhibit different collective structures for the same individual level behaviours (Couzin, Krause, James, Ruxton, & Franks, 2002; Tunstrøm et al., 2013). Under such conditions of 'metastability', random fluctuations can result in abrupt changes in group structure, as between the milling and polarized (aligned) motions exhibited by golden shiner, *Notemigonus crysoleucas*, schools (Tunstrøm et al., 2013).

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

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

In this study, we tested the hypothesis that individuals in large animal groups adjust their behaviour to improve collective responsiveness in risky situations and to promote efficient information transfer between individuals. First, we tested whether schooling herring respond to situations perceived as more dangerous by swimming faster, closer and in a 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 a greater ability to react in unison. Second, we tested whether such adjustments enhance collective antipredator 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 (ca. 60 000 fish) in a semicontrolled 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 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 postprocessing acoustic video analysis approach.

METHODS

Experimental Set-up

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 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 × 12 m and 12 m deep, volume = 1728 m³). Fish were fed with small 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 Rieucau, De Robertis, Boswell, and Handegard (2014). Our experiment was conducted between 16 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 predator model created from a plastic bottle (34 cm long × 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 (Rieucau, Boswell, De Robertis, Macaulay, & Handegard, 2014; Rieucau, De Robertis, et al., 2014). The predator model was highly detectable by schooling herring as it was visually conspicuous (Rieucau, Boswell, et al., 2014) and displaced water when in motion (Rieucau, Boswell, et al., 2014). The model was pulled horizontally across the net pen at 1 m depth via a fishing line

which 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 ± 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 two 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 eight 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, Boswell, et al. (2014), we used a 6 min interval between two exposures within an experimental trial to allow the fish to return to a similar schooling dynamic as prior to exposure.

Within an experimental day, two consecutive trials were interspaced by at least 1 h: four trials were conducted in the morning and four 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 to 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 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 when conducting experiments at this scale is the difficulty of capturing, transporting and housing large schools of wild herring. In our study it was impossible to return to the 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 was likely to be very local, and thus the probability of the same fish being exposed to it was 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's vertical distribution and density, an upward-looking calibrated 120 kHz split-beam echosounder with a 7 degree beam-width (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

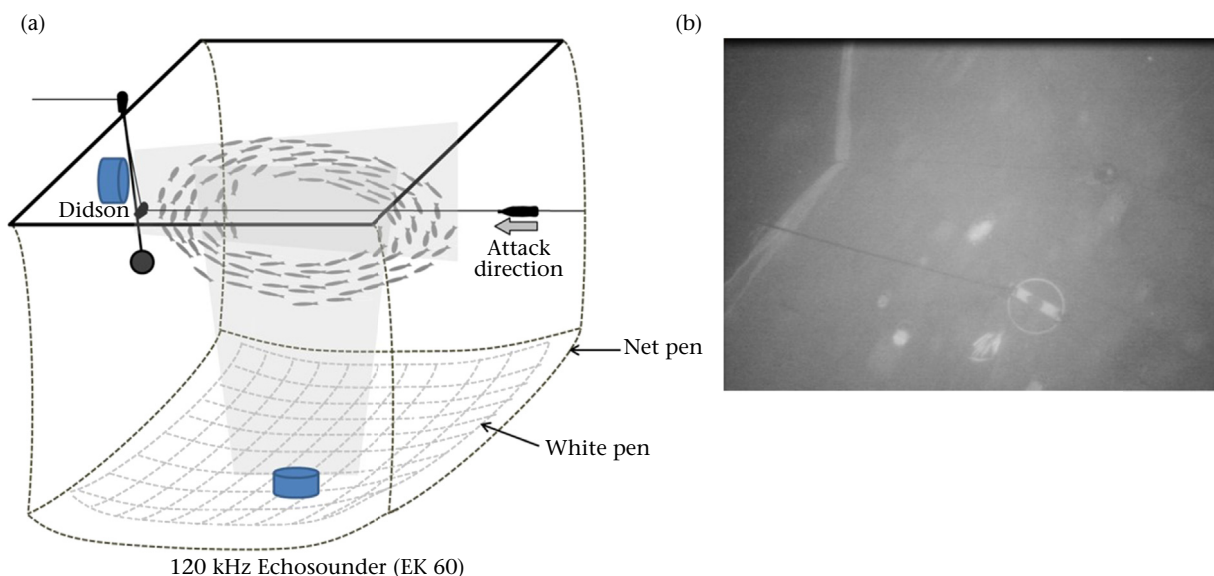


Figure 1. (a) Schematic representation of the experimental net pen. Predator encounters were simulated using a bottle-shaped black predator model. An upward-looking 120 kHz split-beam echosounder (Simrad EK 60) was placed at the bottom of the experimental pen to monitor collective diving reactions and a DIDSON (dual frequency identification sonar, Sound Metrics, Washington, U.S.A.) horizontally oriented towards 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 (b) is the 120 kHz EK 60.

exposure was estimated by the average area scattering coefficient, s_a (m^2/m^2). The packing density of the same school has been previously estimated to be $16.1 \text{ fish}/\text{m}^3$, corresponding to approximately 60 000 individuals when multiplying by the total volume (Rieucan, De Robertis, et al., 2014). 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, De Robertis, et al. (2014; 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, U.S.A.), 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-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 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, Natick, MA, U.S.A.; see Appendix). 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 for detecting 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 32×32 pixel window, resulting in a matrix with dimensions m by n . Frames in which no fish were present were removed by thresholding. The velocity vectors were further filtered by averaging over three 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 $d > 4 \text{ m}$ fluctuated 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 noncoherent state, the parameter will be close to 0.

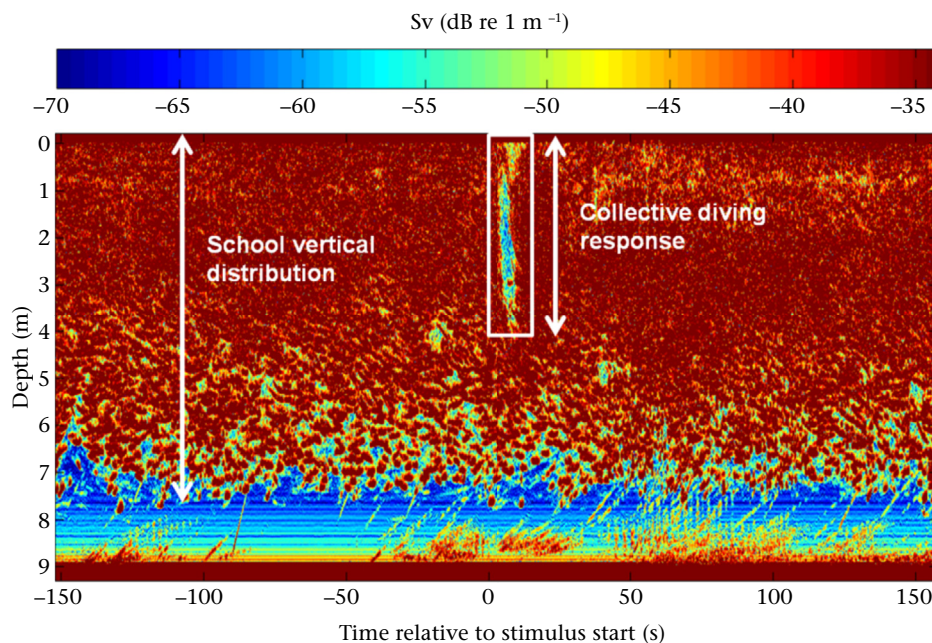


Figure 2. Example of an echogram obtained from the upward-looking 120 kHz EK 60 echosounder used to quantify the school density prior to predator model exposure and the collective diving response during simulated attacks. The colour scale shows the values of the volume backscattering strength, S_v ,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

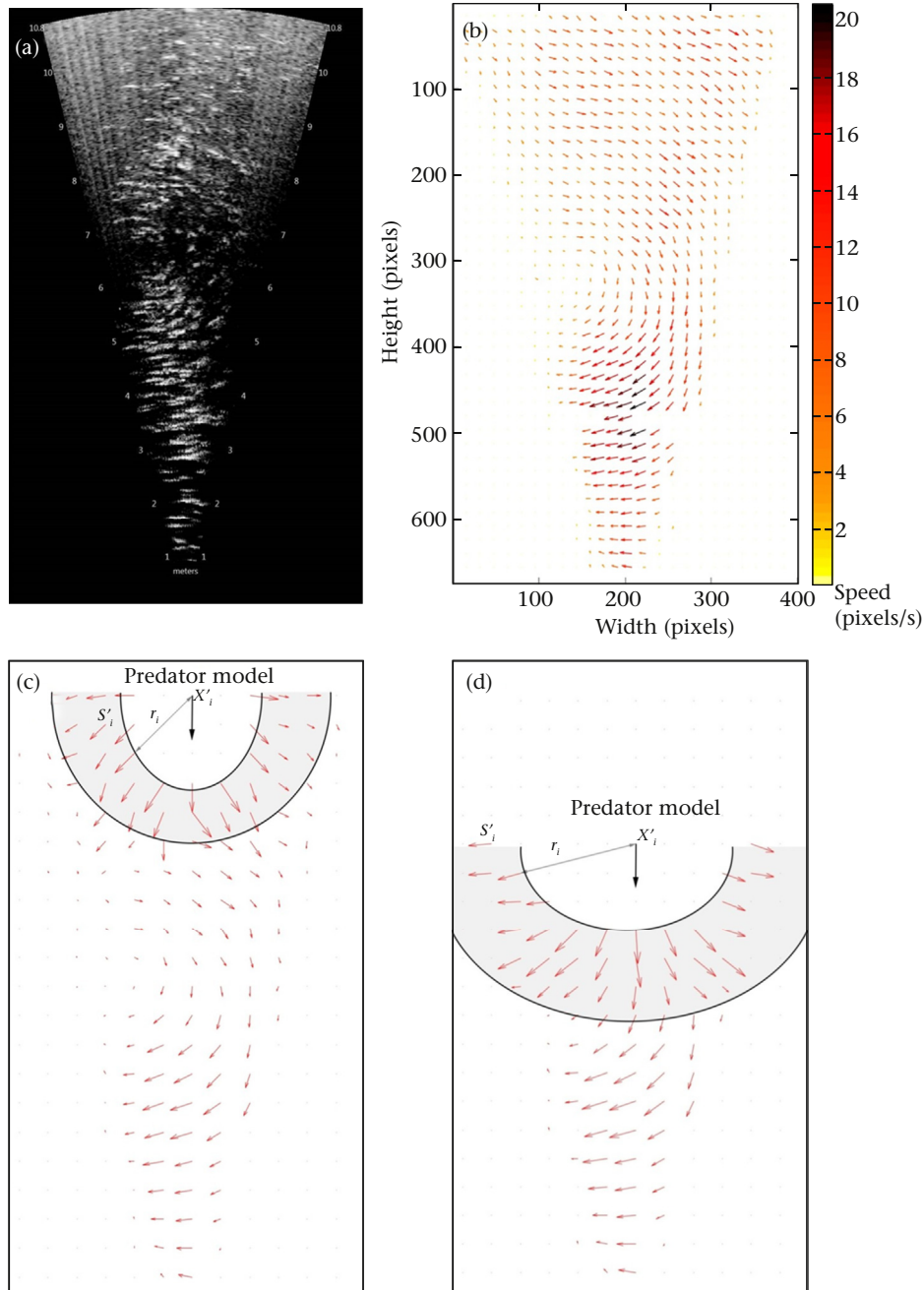


Figure 3. (a) Acoustic frame from the high-frequency imaging sonar (DIDSON) transversely looking across the net pen before exposure to the predator model. (b) Estimation of the swimming speed of herring within the school prior to predator model exposure using a particle image velocimetry (PIV) algorithm. 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 (c) t_i and (d) t_{ij} . The fish velocity component away from the predator model (s'_i) gives the speed of each PIV. The distances from each PIV to the predator model for t_i and t_{ij} are given by r_i and r_{ij} respectively.

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 three 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 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 the behavioural wave (the average s' outside 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 a factor in the behaviour of the fish.

To estimate the range of the void of fish around the predator model, r_l , 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_l in equation (4),

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

and $\theta = a(r - r_l)$, 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_l 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 nonparametric 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 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). 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 interfish 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 environment 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 $\Delta s' = 1$, $r_0 = 1$, $r_l = 1$ 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_l (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 a conventional level of statistical significance, it is noteworthy that the median values for $\Delta s'$ and r_l were larger in the white net condition than in 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 a 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

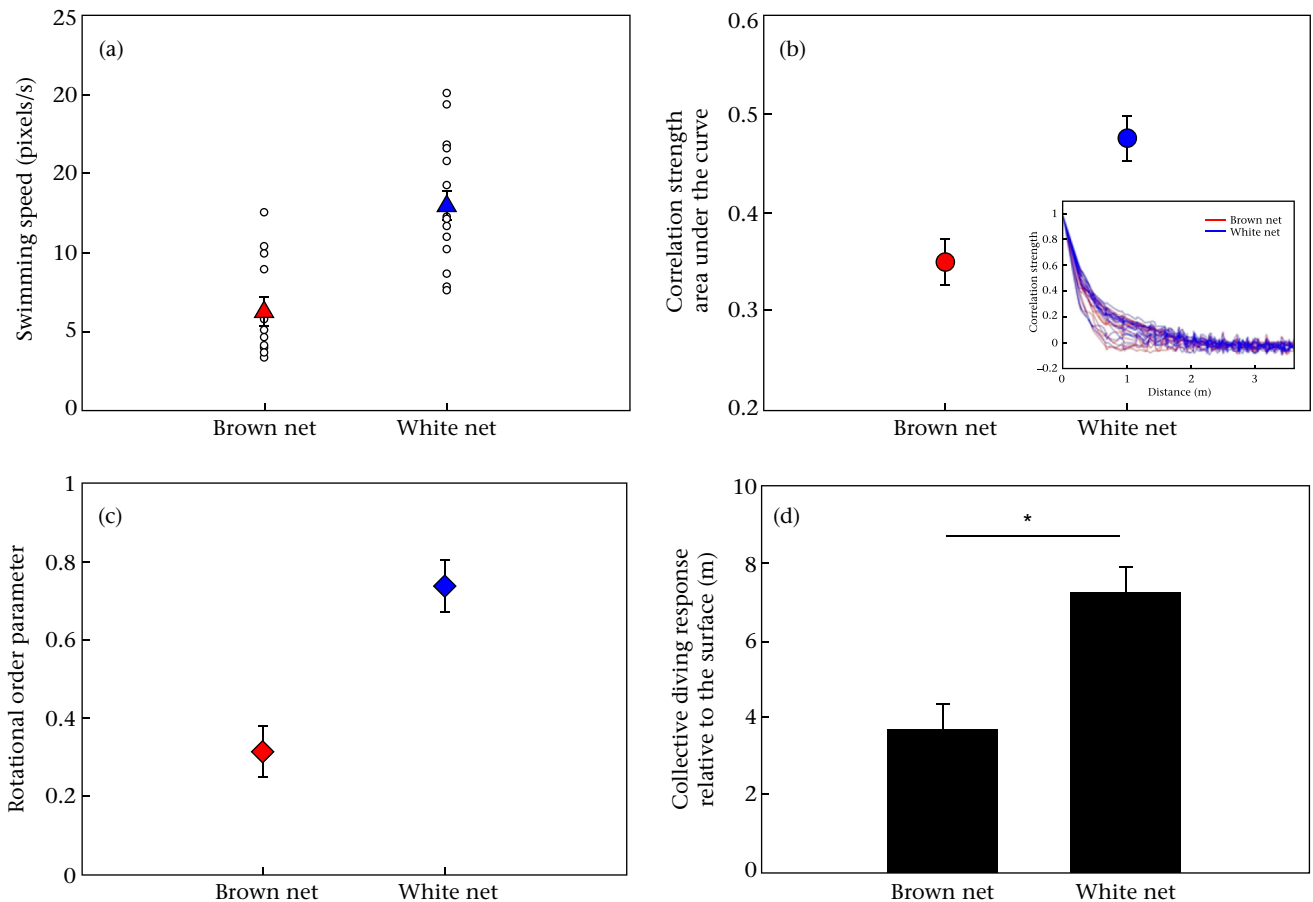


Figure 4. (a) Herring swimming speed in the brown net and white net conditions. Coloured triangles indicate the means \pm SE and open dots show trials. (b) Correlation strength between individual fish (mean \pm SE) prior to predator model exposure in the two experimental conditions. Also presented in (b) is the change in correlation strength as a function of the distance between individuals for each trial 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. * $P < 0.05$.

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 probably more risk-aware, fish. It has previously been found that individuals in large Peruvian anchovy schools are more homogeneously 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 of 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 probably 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 interfish 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 trout, *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 probably an increase in risk; Handegard et al., 2012).

Interindividual 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 interfish distances (Rieucau, De Robertis et al., 2014). Research has 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 (ca. 0.2 fish/m³, Makris et al., 2009). These compressional waves can be one order of magnitude

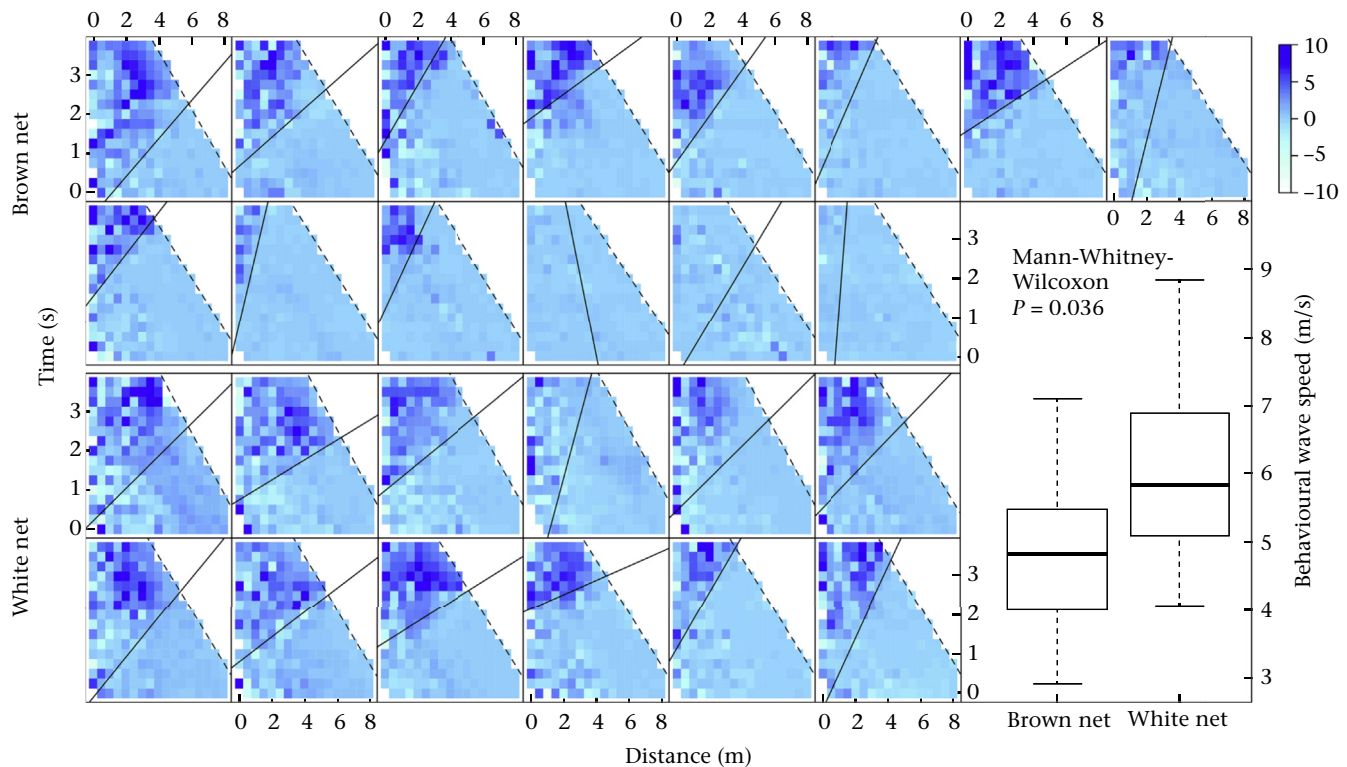


Figure 5. Average velocity component away from the predator model, s' , in range and time bins of width 0.5 m and 0.25 s, respectively, plotted against distance on the x axis and time on the y axis. An increase in saturation of blue colour indicates an increase in velocity component, s' , and the fitted 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 is a box plot, with interquartile range (IQR), whiskers (lower quartile + $1.5 \times \text{IQR}$, upper quartile + $1.5 \times \text{IQR}$) and median, showing the speed of the behavioural wave ahead of the predator model in the brown net and white net conditions.

faster than herring swimming speed and can span 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 to explore how large marine schools evaluate the level of, and respond to, predation risk from different types of predator cues such as acoustic (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 in the face of biotic (e.g. consumptive and nonconsumptive predator effects; Langård et al., 2014) or abiotic factors (e.g. thermocline, pycnocline or light level; Fernö et al., 1998; Mackinson, 1999). We foresee the context-dependent response of marine schools as being a valuable source of information to develop nonintrusive 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 ameliorate housing conditions and practices in fish farms or to 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.

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APPENDIX

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

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

where p is the number of NaN's that were replaced by zeros, and M and N are the sizes of the PIV matrix. For each component of \mathbf{u} , the two-dimensional spatial autocorrelation was calculated using `xcorr2` in MATLAB (The Mathworks, Natick, MA, U.S.A.),

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

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 replacing u_x by u_y , the correlation on the y direction, c'_y , was similarly calculated. The $u_x(m, n)$ were set to zero outside the original domain for the PIV (e.g. when $m - k < 0$, etc). The correlations were normalized using the standard deviation defined as

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

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

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

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

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

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

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

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

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

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

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

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 sonar plane, and $\mathbf{v}(m, n)$ is the PIV vector with a zero padded for the vertical dimension (along \mathbf{e}_z).