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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; Rieucau, 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 m^3). 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 $\times$ 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

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