



Environmental context elicits behavioural modification of collective state in schooling fish

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Pattern formation and collective behaviour in animal aggregations is highly complex and occurs across many scales, over a wide range of environmental conditions. The patterns found in collective behaviour may be modulated by the environmental habitat in which a group is located. Here, we consider whether habitat context influences the collective behaviour of fish schools under threat of predation in a dynamic salt marsh system. By comparing collective responses of wild forage fish prior to and during predator attack across three environmental contexts, we examine whether schooling state is influenced by the habitat that fish schools reside in. Our results indicate that habitat context had a much stronger effect on collective state relative to predation. The habitats studied (both a marsh edge habitat and a higher complexity habitat) induced changes in the behavioural state of fish schools compared to a free-field context, which demonstrates an alteration of the collective behaviours performed by the school. This suggests that other ecological factors, such as the local environment, plays a larger role than predation risk in structuring the spatial and temporal group level patterns found in collective behaviour.

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Organismal aggregations are found around the world at multiple spatial scales, and are as diverse as swarms of locusts, flocks of birds and schools of fish. Group-living individuals can receive a variety of benefits, such as improved safety, increased foraging and reproductive success (Ioannou, 2017; Krause & Ruxton, 2002). In an aggregation, such as a fish school, each individual responds to its local environment as well as to the behaviour of its neighbours, a process which can elicit emergent collective responses (Couzín, James, Mawdsley, Croft, & Krause, 2006; Herbert-Read, Buhl, Hu, Ward, & Sumpter, 2015), particularly when under threat of predation (Ioannou, Guttal, & Couzín, 2012; Parrish, 1989; Parrish, Viscido, & Grunbaum, 2002; Pitcher, 1983; Rieucau, Fernö, Ioannou, & Handegard, 2015). Collective responses of schooling fish to predation pressure has been well studied, from the aggregative tendency in the presence of predator cues (Hoare, Couzín, Godin, & Krause, 2004) to the dilution of predation risk (Turner & Pitcher, 1986) and decreasing encounter rate (Ioannou, Bartumeus, Krause, & Ruxton, 2011) via grouping. In addition,

behavioural patterns in the antipredator response have also been examined, from the selfish herd mechanism that reduces risk via minimizing distance between conspecifics (Parrish, 1989) and the confusion effect (confusion of predator choice of prey due to prey density) (Jeschke & Tollrian, 2007; Ruxton, Jackson, & Tosh, 2007) to the mechanisms of collective vigilance (Herbert-Read et al., 2015; Herbert-Read, Rosén, et al., 2017; Ward, Herbert-Read, Sumpter, & Krause, 2011) and threat-sensitive responses (Brown, Rive, Ferrari, & Chivers, 2006; Rieucau et al., 2014, 2016) that utilize the transferring of social information about the predator cue throughout the group (Magurran & Higham, 1988). However, it has been shown that environmental effects play a role in structuring predator–prey interactions (Abrahams & Kattenfeld, 1997; Cook & Streams, 1984; Crowder & Cooper, 1982; Higham, Stewart, & Wainwright, 2015), therefore these types of collective antipredator responses may be influenced by local environmental biotic and abiotic factors.

In dynamic marine environments with varying physical and hydrological conditions, including regions of habitat complexity, environmental shifts occur at multiple spatial and temporal scales. The wide array of environmental conditions modulate predator–prey interactions in fish via changes in a number of abiotic factors, including turbidity (Ajemian, Sohel, & Mattila, 2015; De Robertis, Ryer, Veloza, & Brodeur, 2003), temperature

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(Weetman, Atkinson, & Chubb, 1998) and oxygen levels (Domenici, Lefrançois, & Shingles, 2007). Similarly, schooling behaviour (particularly in juveniles and herbivorous species) is ubiquitous across this entire spectrum of environmental conditions, and the social dynamics have been shown to be affected by similar environmental factors, including turbidity (Borner et al., 2015; Kimbell & Morrell, 2015), hypoxia (Domenici, Steffensen, & Marras, 2017) and light level (Ryer & Olla, 1998). The occurrence of schooling across a gradient of environmental conditions suggests robustness in the behavioural schooling state to environmental changes, but may still be altered when coupled with threat of predation. Previous studies have shown how various environmental factors, including turbidity, predation pressure and noise, affect antipredator schooling behaviour. Turbid water promotes risk-averse behaviour and decreases aggregative tendency in favour of individualistic decisions (Chamberlain & Ioannou, 2019), as well as eliciting weaker antipredator responses and higher dispersion within the group (Kimbell & Morrell, 2015), high predation habitats modulate group decision making (Ioannou, Ramnarine, & Torney, 2017) as well as social interactions (Herbert-Read, Rosén, et al., 2017), and the presence of anthropogenic noise destabilizes school structure (Herbert-Read, Kremer, Bruintjes, Radford, & Ioannou, 2017). Habitat complexity has also been shown to influence antipredator behaviour and survival (Crowder & Cooper, 1982; Figueiredo et al., 2015; Lichtenstein et al., 2019), and given the variety of influences environmental factors act on schooling behaviour, it is still unclear whether habitat context modulates the collective antipredator response. An understanding of how different environments affect the collective sensing and decision making of a fish school can thus provide insight on the plasticity and robustness of group behaviour and contribute valuable information to ecosystem management and conservation efforts.

In observing freely behaving groups of fish, a variety of motion and interaction-based metrics have been used to quantify the behavioural state of a school (Delcourt & Poncin, 2012). Schooling state metrics that can be derived from behavioural observations include, for example, the cross-sectional area of the school (Partridge, Pitcher, Cullen, & Wilson, 1980), the average swimming speed (Berdahl, Torney, Ioannou, Faria, & Couzin, 2013; Kent, Lukeman, Lizier, & Ward, 2019; Zienkiewicz, Ladu, Barton, Porfiri, & Bernardo, 2018), fish directional polarization (Cavagna et al., 2008; Viscido, Parrish, & Grünbaum, 2004), angular velocity (Tunstrøm et al., 2013), rotational order (Attanasi, Melillo et al., 2014) and correlation strength as a measure of information transfer rate (Attanasi, Grigera et al., 2014; Cavagna et al., 2008; Cavagna et al., 2010; Handegard et al., 2012). These metrics have been used to characterize internal schooling states (Tunstrøm et al., 2013), determine the behavioural responses to predator threat and evasion (Rieucau et al., 2016), analyse the ability to propagate information to conspecifics (Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015; Strandburg-Peshkin et al., 2013) and propose novel models of collective behaviour that accurately replicate the emergent patterns found in the collective response (Cavagna et al., 2015; Couzin, Krause, James, Ruxton, & Franks, 2002).

The collective response of aggregated animals has been well studied in both simulation and laboratory settings, at both the individual and group level (Gautrais et al., 2012; Lopez, Gautrais, Couzin, & Theraulaz, 2012; Radakov, 1973; Rieucau et al., 2016). However, in situ, remotely observed field level studies, although more difficult to conduct, provide a suitable representation of how the collective behaviour occurs in the natural world (Handegard et al., 2012; King, Fehlmann, Biro, Ward, & Fürtbauer, 2018; Rieucau et al., 2016) and may show the effect of external influences unable to be replicated in the laboratory. In this study, we simultaneously compare the antipredator response to real

predators, directly in their natural environments containing habitat contexts that are common to the ecosystem.

Here, our aim is to identify whether habitat context, prior to and in response to predation, affects the behavioural state of schooling juvenile Gulf menhaden, *Brevoortia patronus*. To achieve this objective, we investigated whether schooling state, quantified via six physical metrics, prior to and in response to predator attack is mediated by three different local habitat contexts within a salt marsh pond. The three habitat contexts we compared were (1) a free field, lacking any habitat complexity, (2) a marsh edge habitat, where the topographic profile may restrict potential directions of motion and (3) a habitat of higher complexity, which contained a static physical structure that encompassed the entire water column. We hypothesized that sensory information derived from the habitat context shapes a fish schools' behavioural state, which elicits changes beyond the inherent range of behavioural plasticity that compensates for predator attack. Specifically, we predicted that fish schools located in the marsh edge and complex habitat would exhibit differences in schooling state metrics, particularly area, speed, polarization and correlation strength, between themselves and relative to the free-field habitat context. The restriction in escape directions, as well as physical obstacles in the environment should cause increased school fragmentation (resulting in smaller school sizes and decreased correlation strength) and increased motion coordination (resulting in higher polarization and group speed) relative to schools in the free field. In addition, we predicted that the sensory information difference in heterogeneous habitats compared to the free field would affect the correlative relationships between the six metrics representing the schooling state, causing a decrease in correlation between school area, correlation strength and polarization.

METHODS

Data Collection

We deployed a high-resolution imaging sonar, DIDSON (Sound Metrics Corp., Bellevue, WA, U.S.A.), attached to a tripod approximately 0.4 m above the seafloor. In this deployment, the major axis of the beam was oriented at a tilt angle -0.3° from parallel to the surface, generating a stationary image of the substrate and areal profile of fish schools across each habitat (Fig. 1; Boswell, Miller, & Wilson, 2007, 2019). The DIDSON was operated at a frequency of 1.8 MHz, where a 96-beam transducer array created a $28^\circ \times 14^\circ$ field of view. There are 512 samples along the acoustic axis, with a resolution of ~ 2 cm, which generate a 512×96 sample space. Recordings were collected at a frame rate of eight frames/s, and each frame maps to an image with a range of 10 m.

Sampling

Similar to prior studies that focused on observing schooling behaviour in situ (Handegard et al., 2012; Rieucau et al., 2016), behavioural observations were extracted directly from underwater recordings of shallow estuarine salt marsh ponds (Fig. 1) near Empire, Louisiana ($29^\circ 24' 34''$ N, $89^\circ 37' 48''$ W), U.S.A., between April 2009 and July 2010. The marsh ponds cover $\sim 40\,000$ m² in total area, are intertidal, oligohaline (5–25 ppt), and connect to each other via tidal channels that funnel into a larger water body (Adam's Bay, LA, U.S.A.). Recordings were collected from a total of four ponds, some of which contained both soft substrate and areas of habitat complexity (rocks, logs), creating an adequate experimental setting to compare the influence of environmental context on schooling behaviour of estuarine fishes. Five hour recordings were collected from an individual pond every 2 months, over

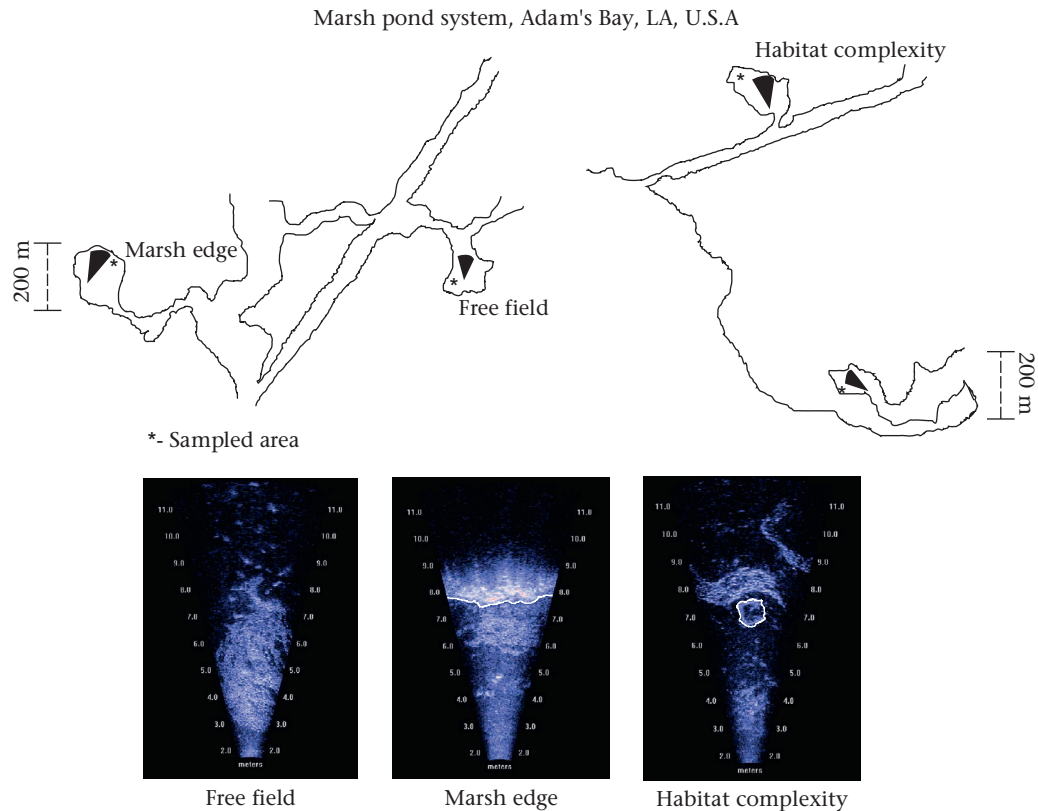


Figure 1. Illustration of marsh pond sample area in Louisiana, U.S.A. Three sonar cone positions represent the three habitat conditions surveyed. Each surveyed condition across the pond was at a shallow depth (<2 m), with no significant tidal currents present. The free-field condition contained a sediment bottom, free of structure and obstacles. The marsh edge condition is equivalent to the free-field condition with the exception of an edge boundary (outlined in white) that impedes movement of swimming organisms. The habitat complexity condition was composed of a sediment bottom, but also contained rocks, wood pilings, crab traps and detritus that served as obstacles towards movement (outlined in white). The habitat complexity condition did not contain an edge boundary, so each direction of movement was preserved.

intervals of four consecutive days, at the same point in the monthly and daily tidal cycle. Direct sampling of the region (Garner, 2012; Handegard et al., 2012; Klotzbach, 2013) conducted concurrently with the collection of these data showed that the schools observed (due to size) were juvenile Gulf menhaden, *B. patronus*, and the predators attacking them were typically (due to size and abundance in area) Atlantic croaker, *Micropogonias undulatus*, or spotted sea trout, *Cynoscion nebulosus*, ensuring species parity across all schooling behavioural observations.

All recordings were analysed, and behavioural interactions between schooling fish and predators were extracted across three habitat conditions present among the four ponds. The three regions consisted of an open free field, a marsh edge and a complex habitat. During analysis of pond recordings collected in the marsh edge and complex habitat, behavioural interactions qualified for inclusion only if they occurred within 0.3 m of the marsh boundary or habitat structure; this threshold distance was chosen to ensure that responses were influenced by the presence of the objects. For each interaction identified, the free-swimming behaviour of each school prior to attack was included in the recording. Over a span of 35 h of recording, partitioned in equal time intervals for each habitat type, 56 interactions between schools and predators were identified and extracted in the free-field habitat, 25 in the marsh edge habitat and 17 in the complex habitat, for a total of 98 individual recordings.

Each observed recording of a behavioural interaction was partitioned into pre- and postpredator attack components. During analysis of the sonar video, the image frame that coincided with the predator attacking the school was marked as the partitioning

threshold. The partitioning criteria was met when one of two conditions occurred: (1) the predator strike directly penetrated the school boundary (identified by the formation of a furrow on the school boundary around the predator), inducing a fast-start escape response from the school, or (2) the school elicited an escape response along the same trajectory as the predator (denoted by movement of the school boundary in the predator's direction of attack), when the predator strike breached the reaction distance of the school (Domenici & Hale, 2019). The attack duration was defined as the time interval from attack to when prey ceased responding to the predator (Pitcher, 1983). For each observed predator attack, the interval of time corresponding to the attack duration was extracted before and after the partitioning threshold. This ensured that all the behavioural phases were split into equal time intervals (~3–6 s before/after) around the partitioning threshold, the first interval representing the prepredator behaviour, and the second representing the midattack response. After partitioning, a total of 196 behavioural observations (98 preattack, 98 midattack) were analysed across the entire sampling period.

The free-field habitat is characterized by a soft sediment bottom, with a depth range of 0.5–1 m (Fig. 1). The edge habitat is characterized as the region where a field habitat abruptly transitions to a physical barrier (e.g., marsh surface), generally with a shallower depth range of 0.1–0.5 m. The edge is composed of solid soil and acts as a boundary that spans the school (Fig. 1). The complex habitat is a free-field habitat, without a boundary, but with either a large rock, or wooden log that encompasses the majority of the water column (Fig. 1).

Data Processing

Each DIDSON frame represents a 512×96 sample space. The raw samples were wavelet denoised (MATLAB R2014b, Image Processing Toolbox) to remove high-frequency artefacts, and converted to distance-based greyscale images via a mapping that accounts for radial beam spread (Fig. 1). We estimated image backgrounds for each behavioural interaction using the 30th percentile for each pixel intensity across all frames in the interaction and subsequently subtracted them from each image. We used particle image velocimetry (PIV), calculated over a 32×32 pixel window, to extract velocity estimates for the school and to estimate the swimming speed and correlation strength (Fleet & Weiss, 2006). In addition to the PIV calculations, school boundary detection was done to extract the position of the school and the school area and to isolate the velocity vectors that contribute to the behaviour of the school. The PIV velocity vectors were additionally filtered temporally over five frames, as well as spatially via a 3-pixel window median filter. The school boundary was obtained via initial thresholding using Otsu's method and pixel area-based filtering (MatLab Image Processing Toolbox, MatLab, Mathworks, Natick, MA, U.S.A.) of small objects in the image to extract a two-dimensional point cloud that represented the school shape (Otsu, 1979). The point cloud was then segmented and labelled based on cluster analysis with a Euclidean norm distance parameter of 0.3 m. The school cluster was then registered via an alpha shape filter, which contained an adaptive alpha value based on cost functions attributed to the area and perimeter of the boundary. The detected school boundary was tracked frame by frame via a Kalman filter and then approximated as a polygon to constrain the PIV velocity vectors to those pertaining to the fish school.

We compared observations from the three different habitats, before and during predator attack, to test whether the schooling state is modulated by the environmental structural gradient. The tests were as follows: (1) whether habitat and predator attack affect schooling state in terms of (a) school area occupied, (b) group speed, (c) angular velocity, (d) polarization, (e) rotational order and (f) correlation strength; (2) effect of habitat context on the relationship between metrics (a–f) that describe the school state.

The school area was calculated based on the school boundary detection algorithm and is a local two-dimensional projection approximation of the total area occupied by the school. In our analysis, we assume constant density of schools, so changes in area represent space utilized as opposed to school size. The group speed was derived by centre-of-mass measurements of the school and its change in position with respect to time. Angular velocity was computed from the curl of the PIV vectors, as follows

$$\omega = \frac{1}{2} (\nabla \times v), \quad (1)$$

where v denotes the velocity vectors located within the detected school. Polarization and rotational order were calculated from the formulas provided in Attanasi, Melillo et al., 2014. In this case, the polarization is the Euclidean norm of the sum of the velocity vectors normalized by magnitude (to isolate direction) divided by the total number of vectors, as shown below:

$$\Phi = \frac{1}{N} \left| \sum_{i=1}^N \frac{\vec{v}_i}{v} \right|. \quad (2)$$

The rotational order, computed as follows,

$$R = \frac{1}{(MN - p)} \left| \sum_{m,n} \frac{\mathbf{x}(m,n) \times \mathbf{v}(m,n)}{|\mathbf{x}(m,n) \times \mathbf{v}(m,n)|} \times \mathbf{e}_z \right|, \quad (3)$$

measures the coherence of rotation in the school, quantified by summing the rotational components (projection of each rotational vector onto the axis orthogonal to the sonar plane, \mathbf{e}_z , relative to the centre of the school) divided by its magnitude, and normalized by the number of vectors (fish) within the school. Integrated correlation strength (the degree to which one fish's behaviour influences its neighbours) was calculated in the same manner as Rieucau et al. (2016), and formulated below:

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

where $c(d)$ is the correlation strength for a given frame i , which measures how the behavioural change of an individual affects its neighbours as a function of distance. The correlation strength for distances greater than 4 m were nearly zero, so it was used as the upper bound of the integration. The correlation strength for each frame was calculated from the spatial autocorrelation of the velocity fluctuations of each school and mapped to metric distance in the sonar image (Handegard et al., 2012; Rieucau et al., 2016).

Statistical Analysis

In the analysis of the behavioural interactions, each individual school is treated as an independent sample, and residual analysis (via $Q-Q$ plot) maintained the assumption of normality. To determine whether predation, habitat, or their interaction explained the variance in the data, we conducted a two-way MANOVA on group speed, school area occupied, angular velocity, polarization, rotational order and correlation strength. We subsequently conducted univariate ANOVAs to test within each schooling metric. Tukey post hoc pairwise comparisons were conducted to determine significance (at 95% significance level) of the mean schooling metrics within predation, habitat, and interaction factors, corrected (Bonferroni) for multiple comparisons. In addition, principal component analysis (PCA), scaled to unit variance, was done to examine the correlation between the schooling metrics before and during predator attack, for each habitat context. All analyses were done using R statistical software (Feather Spray v.3.5.1, R Foundation for Statistical Computing, Vienna, Austria).

Ethical Note

This research was conducted in accordance with the guidelines set forth by the Institutional Animal Care and Use Committee of Louisiana State University (IACUC Protocols No. 10–115 and No. 11–090).

Table 1
Two-way MANOVA table comparing the effect of predation, habitat, and their interaction among the six schooling state variables

MANOVA	df	Wilks' λ	ndf	ddf	P
Predation			6	185	0.37881
Habitat	2	0.80071	12	370	0.00004
Predation:Habitat	2	0.97095	12	370	0.93800
Residuals	190				

RESULTS

Influence of Predation on Schooling State

Predation events had a negligible effect on the behavioural state of the school (MANOVA: $P > 0.35$, Wilks' $\lambda = 0.966$; Table 1, Fig. 2), and did not significantly explain variability in our observations. The effects of predator attack were negligible when each metric of the schooling state was considered individually (Table 2). Pairwise comparisons between preattack and midattack for each schooling metric showed no significant differences in school area (Tukey tests: $P > 0.95$; Table 3), group speed ($P > 0.77$; Table 3), angular velocity ($P > 0.95$; Table 3), polarization ($P > 0.63$; Table 3), rotational order ($P > 0.55$; Table 3) or correlation strength ($P > 0.99$; Table 3), suggesting that schools largely stayed within the same range of behavioural variation prior to and during attack.

Influence of Habitat Context on Schooling State

Habitat context significantly explained the variability in our observations (MANOVA: $P < 0.001$, Wilks' $\lambda = 0.80071$; Table 1, Fig. 2), particularly in schooling area occupied (ANOVA: $F_{2,190} = 6.935$, $P = 0.001$), angular velocity ($F_{2,190} = 9.34$, $P < 0.001$), polarization ($F_{2,190} = 3.61$, $P = 0.0288$), rotational order ($F_{2,190} = 3.98$, $P = 0.0203$) and correlation strength ($F_{2,190} = 6.06$, $P = 0.0028$; Table 3, Fig. 2). In comparison to the free-field habitat, schools in the complex habitat occupied approximately ~40% smaller area ($P = 0.034$) and turned twice as slow ($P = 0.0335$). Schools in the marsh edge, compared to the free field, occupied approximately ~50% less area ($P = 0.003$) and turned ~2.5 times slower ($P < 0.001$). In addition, schools in the marsh edge were ~30% more polarized ($P = 0.025$), contained ~30% higher rotational order ($P = 0.018$) and exhibited a ~20% lower correlation strength ($P = 0.018$) and exhibited a ~20% lower correlation strength

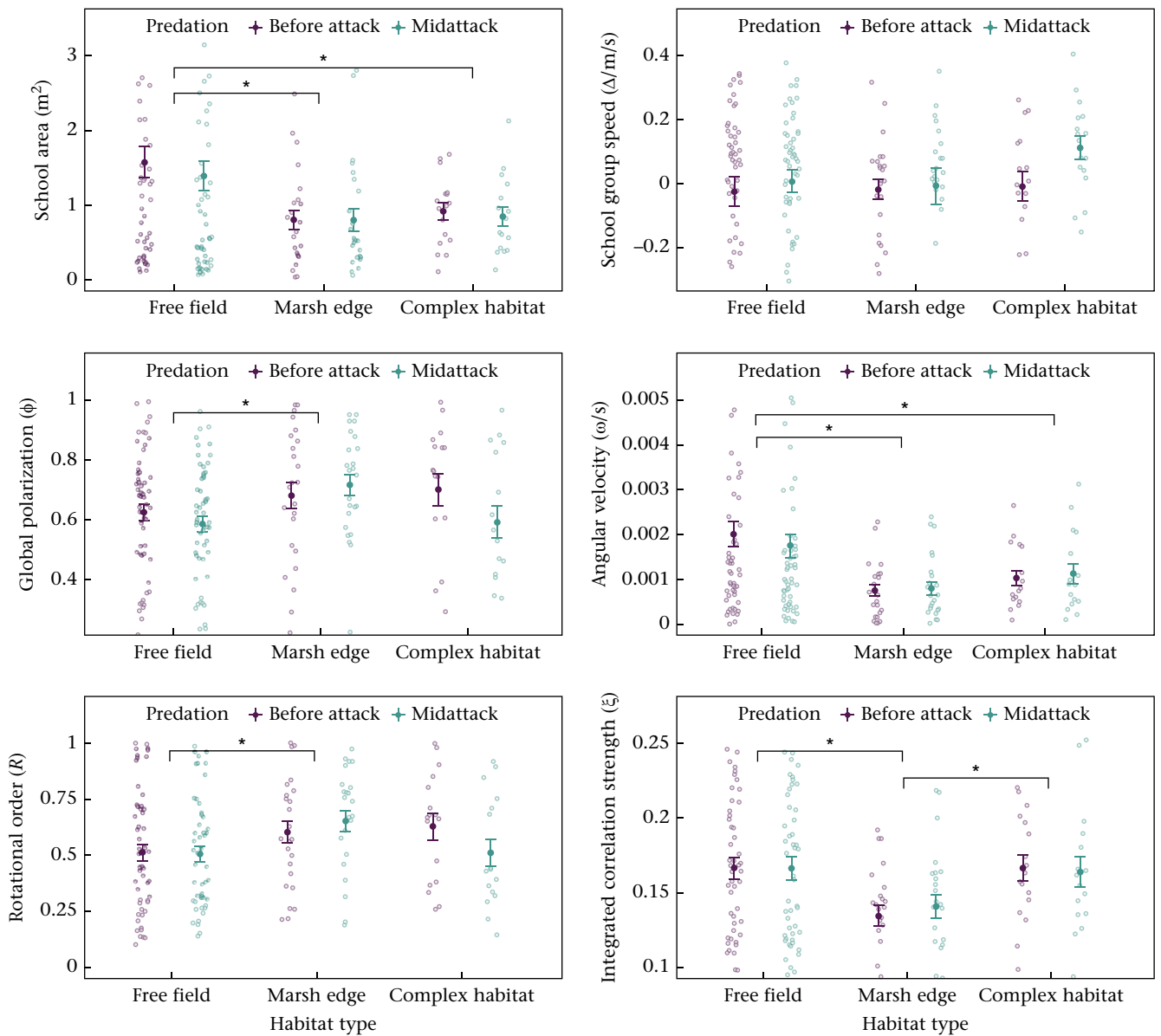


Figure 2. Comparison of behavioural schooling metrics before and during predator attack over an environmental gradient. All conditions before and during predator attack are reported for each habitat context, and are colour-coded within each habitat type. Results show mean values of each schooling state metric, with data distributions represented underneath. Error bars were determined via the standard error, and significant differences between habitat contexts are denoted by an asterisk. Six schooling state parameters were quantified before and during predator attack across three environmental contexts, for a total of 36 unique measurements.

Table 2
Univariate ANOVA tables for each schooling state metric, comparing effects of predation, habitat, and their interaction

ANOVA	df	SS	F	P
School area				
Predation	1	0.6596	0.4521	0.5022
Habitat	2	20.2378	6.9351	0.0012
Predation:Habitat	2	0.3331	0.1141	0.8922
Residuals	190	277.227		
Angular velocity				
Predation	1	0.00001	0.2863	0.5932
Habitat	2	0.00049	9.3401	0.0014
Predation:Habitat	2	0.00001	0.2516	0.7777
Residuals	190	0.00495		
Group speed				
Predation	1	0.0867	1.2196	0.2708
Habitat	2	0.1077	0.7571	0.4705
Predation:Habitat	2	0.0679	0.4775	0.6211
Residuals	190	13.5102		
Rotational order				
Predation	1	0.0058	0.0925	0.7613
Habitat	2	0.5023	3.9803	0.0203
Predation:Habitat	2	0.1400	1.1093	0.3319
Residuals	190	11.9876		
Polarization				
Predation	1	0.0485	1.1529	0.2843
Habitat	2	0.3044	3.6148	0.0288
Predation:Habitat	2	0.1061	1.2596	0.2861
Residuals	190	7.9990		
Correlation strength				
Predation	1	0.0001	0.0221	0.8819
Habitat	2	0.0300	6.0604	0.0028
Predation:Habitat	2	0.0005	0.0969	0.9077
Residuals	190	0.4698		

(~ 0.14 , $P = 0.002$) than schools in the free field. In comparing the complex habitat to the marsh edge, the same $\sim 20\%$ correlation strength decrease was found in comparison to the free field. We found that predation did not significantly influence our observations, so comparisons between habitats within each predation factor (preattack/midattack) did not produce any significant differences in schooling metrics and, thus, in behavioural schooling state.

Influence of Predation and Habitat Context on Schooling Relationships

In the free-field habitat, predation had no effect on the inherent relationships between metrics in the schooling state. Variable

loadings that were highly correlated were split into three uncorrelated groups: (1) polarization/rotational order, which loaded similarly on the first two principal components, (2) area/correlation strength/angular velocity, which loaded strongly on the first principal component and (3) speed, which loaded strongly on the second principal component (Fig. 3, Table A1) and remained uncorrelated even under predator attack. In the marsh edge however, the three uncorrelated groups of variable loadings were affected by predator attack. In the marsh edge, speed remained uncorrelated with the other two groups (due to its strong loading on the third principal component; Appendix, Table A1) prior to predator attack, but it became more correlated with polarization and rotational order during attack (Fig. 3). In contrast to both the free-field and marsh edge habitat contexts, group speed in the complex habitat context remained strongly loaded on the third principal component, yet exhibited higher correlation with polarization and rotational order both prior to and during predator attack (Fig. 3).

In comparison to the free field, the relationships with the strongest coupling between the schooling metrics (polarization/rotational order, area/angular velocity/correlation strength) in the other habitats did not vary at all. The strongest correlations in the marsh edge and complex habitat contexts were equivalent to those in the free-field habitat context both before and during predator attack (Fig. 3). However, habitat context did modulate other strong relationships found in the free field. Polarization and school area were negatively correlated (Fig. 3, Table A1) prior to predator attack in the free-field habitat, but their correlation was no longer evident in the marsh edge or complex habitat context. In addition, the same effect was observed for the relationship between polarization/angular velocity, polarization/correlation strength and rotational order/school area (Fig. 3, Table A1). Each of these relationships became decoupled outside of the free-field habitat context and were not influenced by predator attack.

DISCUSSION

Our results demonstrate that habitat context had a much stronger effect on collective state of free-ranging fish schools than predation. Any type of habitat complexity, due to the presence of a boundary in the marsh edge or an obstacle in the complex habitat, induces changes to the behavioural schooling state. The larger occupied area in the free-field environment relative to the marsh edge and complex habitat, supports previous evidence of larger shoal formation in structurally simple habitats (Orpwood, Magurran, Armstrong, & Griffiths, 2008). When comparing the

Table 3
Tukey post hoc pairwise comparisons testing between each habitat, separating between preattack and midattack

Treatment comparison	P					
	School area	Group speed	Angular velocity	Correlation strength	Polarization	Rotational order
Habitat						
Free field:Habitat complexity	0.034	0.726	0.0335	1.000	0.954	0.654
Marsh edge:Habitat complexity	1.000	0.855	1.000	0.040	0.743	0.900
Free field:Marsh edge	0.003	1.000	0.0002	0.002	0.025	0.018
Preattack/Midattack						
Free field	0.965	0.988	0.9538	1.000	0.928	1.000
Marsh edge	1.000	1.000	1.000	0.998	0.991	0.982
Habitat complexity	1.000	0.772	1.000	1.000	0.637	0.760
Preattack						
Free field:Marsh edge	0.088	1.000	0.0162	0.088	0.855	0.664
Free field:Habitat complexity	0.361	1.000	0.2441	1.000	0.765	0.559
Marsh edge:Habitat complexity	1.000	1.000	0.9932	0.330	1.000	1.000
Midattack						
Free field:Marsh edge	0.338	1.000	0.1422	0.279	0.098	0.153
Free field:Habitat complexity	0.589	0.708	0.7234	1.000	1.000	1.000
Marsh edge:Habitat complexity	1.000	0.719	0.9876	0.678	0.387	0.481

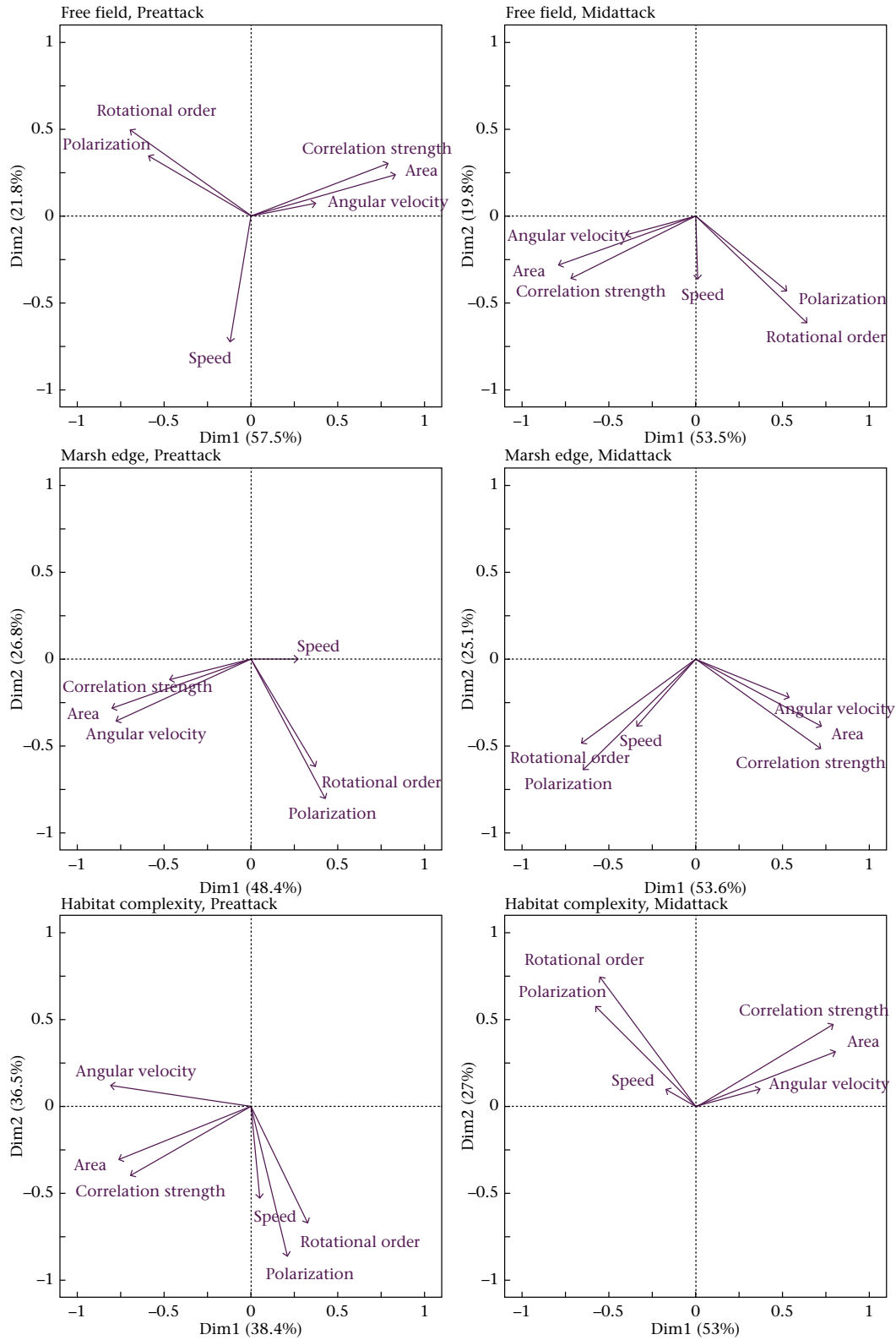


Figure 3. PCA variable loadings for each habitat context and predation status. PCA was scaled to unit variance, with no rotation. The two largest principal components (all captured >75% of the variability) are represented on the X and Y axes. The percentage of the variability explained by each principal component is given in parentheses for each dimension.

impact of the marsh edge context on schooling state, the physical boundary edge appears to have a profound effect on schooling state relative to the free field. The observed decrease in school area, angular velocity and correlation strength seem to be mitigated by a

greater polarization and increased rotational order, where the presence of the physical boundary elicits tighter schooling and directional alignment parallel to the boundary, at the possible cost of a decrease in information transfer rate. This evidence is in line

with the effect of boundaries on driving transitions of schooling state discovered in controlled laboratory experiments (Tunström et al., 2013). Additionally, the presence of the physical boundary constrains the geometry of the school and creates a spatial upper bound on the area that the school can occupy, supported by the decrease in school area and angular velocity. This may be attributed to the safety provided by restricting the direction from which predators may attack, affecting the potential mechanics of predator attack and possibly leading to changes in school vigilance (Higham et al., 2015).

In the complex habitat, the differences in area and angular velocity compared to the free field suggest that the schooling state is being modulated by the presence of obstacles in the environment. The types of structures observed in these environments are uniformly solid and unable to be used as a point of safety for individuals in the school, suggesting that the structures act more like obstacles than areas of refuge. The decrease in area and angular velocity suggests that schools are adopting tighter formations, typical of schools exposed to high predation risk (Magurran & Pitcher, 1987; Orpwood et al., 2008). This may be due to heightened vigilance, derived from the difference in sensory environment compared to a free-field context, requiring the ability to account for any potential obstacles the school may encounter while behaving within the habitat. In these complex environments, the sensory field can confound predator detection by the school via external visual information (in the form of rocks/pilings/traps) that acts as a secondary stimulus or source of noise to the visual information of the impending predator attack. The presence of this type of confounding information, in conjunction with a stimulus that requires a behavioural response, suggests that local environment plays a large role in structuring collective behaviour in response to predator attack.

Our results also indicate that there are few differences in schooling state between the habitats with any type of complexity in the environment. This is likely a reflection of the similarity of the habitat contexts examined. The presence of a boundary or obstacle modulated the schooling state in a similar manner, but further studies are needed to determine whether habitats with high spatial heterogeneity or anthropogenically influenced habitats (e.g., water control structures) differ drastically in their effect on collective behaviour.

In contrast to habitat context, behavioural schooling state in fish schools appear to be robust to predator attack, which implies that there exists a plasticity in the schooling behaviours that can account for the sudden presence of external stimuli. More importantly, this pattern is conserved within habitat context, since no differences were found in schooling state before and during predator attack in both the marsh edge and complex habitat contexts. Predation pressure was largely equivalent across all habitat contexts (based on catch ratios of predator to prey abundance) (Klotzbach, 2013), suggesting that prey schools were not influenced by environmental adaptation to the inherent risk level (Ioannou et al., 2017). Habitat complexity typically decreases predation due to the increase in refuges (Crowder & Cooper, 1982; Holbrook & Schmitt, 2002), but the lack of differences in the schooling state response before and after predator attack even in the marsh edge and complex habitats suggests that local environment plays a much larger role in structuring collective behaviour than predation.

When examining the relationships between the schooling state metrics, our results indicate that changes in the presence and strength of correlation provide further insight into whether predation and environment modulate group behaviour of fish schools. In the free field, we saw no changes in the relationships between

schooling metrics during predator attack, but we did find that the marsh edge and complex habitat contexts influenced the relationship between group speed and orientational polarization/rotational order. The appearance of coupling between speed and polarization/rotational order during predator attack in the marsh edge is consistent with the idea that the edge boundary affects the school state, promoting alignment with the boundary as the school is quickly escaping from predators. The tighter coupling between speed and polarization of schools when attacked by predators is consistent with prior investigations into the mechanisms controlling the collective response (Calovi et al., 2014; Lecheval et al., 2018; Tunström et al., 2013; Viscido et al., 2004). This further supports the premise that the local environment (such as the presence of an obstacle) strongly influences collective patterns and antipredator schooling behaviour.

When comparing schooling state relationships within environmental contexts, we found a combination of robustness as well as modulation in the schooling state. In the free-field condition, the strongest schooling metric relationships (rotational order/polarization, area/angular velocity, correlation strength/angular velocity, area/correlation strength), remained consistent regardless of predator attack. This provides further evidence to support the idea that the antipredator response falls within the range of behavioural plasticity. However, these relationships were conserved in both the marsh edge and complex habitat contexts, implying that certain aspects of the collective behaviour are inherently robust to any type of outside sensory stimuli perceived by the school.

As a complement to robust relationships found across all habitat types, the fact that some relationships decoupled outside of the free field suggests that the schooling state in the marsh edge and complex habitats was altered directly by the habitat context itself. The loss of negatively correlated relationships (school area/polarization, polarization/angular velocity, school area/rotational order, correlation strength/polarization) in both the marsh edge and complex habitat context shows that the physical differences in the environment directly modulate collective behaviour. The habitat context, in this case, seems to influence the trade-off between area and polarization/rotational order, as well as polarization and correlation strength/angular velocity; the loss of this trade-off may allow looser schooling without loss of directional and rotational coherence, as well as information transfer. This is in contrast to the effect of other environmental factors, such as turbidity (Chamberlain & Ioannou, 2019) and anthropogenic noise (Herbert-Read, Kremer, et al., 2017), which act to weaken school structure and responses. The purpose and mechanism underlying habitat influences on collective behaviour remains unclear, and our results call for further investigation of the functional explanations of changes in collective state of fish schools at the face of habitat complexity in natural settings.

In this study, we examined the influence of habitat context on the state and structure of freely behaving fish schools before and during predator attack. We found that, in general, habitat context, not predation, caused changes in schooling state relative to a free-field environment. The type of habitat affected the schooling state, where the presence of a boundary or finite-sized obstacles caused direct changes in schooling behaviour. These results demonstrate, in concert with studies of other environmental factors, that the surrounding environmental context, regardless of predation, is largely influential in the modulation of collective behaviour in fish schools. In the face of global climate change, habitat modification and potential destruction may then influence movement, foraging and local behaviour patterns of large groups of prey fish of critical and commercial importance. Knowledge of the environmental

impacts on the behavioural dynamics of these animal aggregations will help refine our understanding of the patterns of collective behaviour.

Author Contributions

I.R.-P. conceived of the study, extracted the data from observations, processed the data, analysed the data, carried out the statistics and drafted the manuscript; G.R. conceived the study and critically revised the manuscript; N.O.H. conceived the study, assisted in data processing and analysis and critically revised the manuscript. K.M.B. collected the data, assisted in data processing and analysis, assisted in the statistical analysis and critically revised the manuscript. All authors contributed critically to the drafts.

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References

- Abrahams, M. V., & Kattenfeld, M. G. (1997). The role of turbidity as a constraint on predator–prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology*, *40*(3), 169–174.
- Ajemian, M. J., Sohel, S., & Mattila, J. (2015). Effects of turbidity and habitat complexity on antipredator behavior of three-spined sticklebacks (*Gasterosteus aculeatus*): Antipredator behavior in sticklebacks. *Environmental Biology of Fishes*, *98*(1), 45–55. <https://doi.org/10.1007/s10641-014-0235-x>.
- Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Grigera, T., Jelić, A., et al. (2014). Information transfer and behavioural inertia in starling flocks. *Nature Physics*, *10*(9), 691–696. <https://doi.org/10.1038/nphys3035>.
- Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Melillo, S., Parisi, L., et al. (2014). Collective behaviour without collective order in wild swarms of midges. *PLoS Computational Biology*, *10*(7), e1003697. <https://doi.org/10.1371/journal.pcbi.1003697>.
- Berdahl, A., Torney, C. J., Ioannou, C. C., Faria, J. J., & Couzin, I. D. (2013). Emergent sensing of complex environments by mobile animal groups. *Science*, *339*(6119), 574–576.
- Borner, K. K., Krause, S., Mehner, T., Uusi-Heikkilä, S., Ramnarine, I. W., & Krause, J. (2015). Turbidity affects social dynamics in Trinidadian guppies. *Behavioral Ecology and Sociobiology*, *69*(4), 645–651. <https://doi.org/10.1007/s00265-015-1875-3>.
- Boswell, K. M., Kimball, M. E., Rieucou, G., Martin, J. G. A., Jacques, D. A., Correa, D., et al. (2019). Tidal stage mediates periodic asynchrony between predator and prey nekton in salt marsh creeks. *Estuaries and Coasts*, *42*(5), 1342–1352. <https://doi.org/10.1007/s12237-019-00553-x>.
- Boswell, K. M., Miller, M. W., & Wilson, C. A. (2007). A lightweight transducer platform for use in stationary shallow water horizontal-aspect acoustic surveys. *Fisheries Research*, *85*(3), 291–294.
- Brown, G. E., Rive, A. C., Ferrari, M. C. O., & Chivers, D. P. (2006). The dynamic nature of antipredator behavior: Prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. *Behavioral Ecology and Sociobiology*, *61*(1), 9–16. <https://doi.org/10.1007/s00265-006-0232-y>.
- Calovi, D. S., Lopez, U., Ngo, S., Sire, C., Chaté, H., & Theraulaz, G. (2014). Swarming, schooling, milling: Phase diagram of a data-driven fish school model. *New Journal of Physics*, *16*(1), 015026. <https://doi.org/10.1088/1367-2630/16/1/015026>.
- Cavagna, A., Cimorelli, A., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A., et al. (2008). New statistical tools for analyzing the structure of animal groups. *Mathematical Biosciences*, *214*(1–2), 32–37. <https://doi.org/10.1016/j.mbs.2008.05.006>.
- Cavagna, A., Cimorelli, A., Giardina, I., Parisi, G., Santagati, R., Stefanini, F., et al. (2010). Scale-free correlations in starling flocks. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(26), 11865–11870. <https://doi.org/10.1073/pnas.1005766107>.
- Cavagna, A., Del Castello, L., Giardina, I., Grigera, T., Jelic, A., Melillo, S., et al. (2015). Flocking and turning: A new model for self-organized collective motion. *Journal of Statistical Physics*, *158*(3), 601–627.
- Chamberlain, A. C., & Ioannou, C. C. (2019). Turbidity increases risk perception but constrains collective behaviour during foraging by fish shoals. *Animal Behaviour*, *156*, 129–138. <https://doi.org/10.1016/j.anbehav.2019.08.012>.
- Cook, W. L., & Streams, F. A. (1984). Fish predation on *Notonecta* (Hemiptera): Relationship between prey risk and habitat utilization. *Oecologia*, *64*(2), 177–183. <https://doi.org/10.1007/BF00376868>.
- Couzin, I. D., James, R., Mawdsley, D., Croft, D. P., & Krause, J. (2006). Social organization and information transfer in schooling fishes. In C. Brown, K. Laland, & J. Krause (Eds.), *Fish cognition and behavior* (pp. 166–185). Oxford, U.K.: Blackwell.
- Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002). Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology*, *218*(1), 1–11.
- Crowder, L. B., & Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, *63*(6), 1802–1813. <https://doi.org/10.2307/1940122>.
- De Robertis, A., Ryer, C. H., Veloza, A., & Brodeur, R. D. (2003). Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(12), 1517–1526. <https://doi.org/10.1139/f03-123>.
- Delcourt, J., & Poncin, P. (2012). Shoals and schools: Back to the heuristic definitions and quantitative references. *Reviews in Fish Biology and Fisheries*, *22*(3), 595–619. <https://doi.org/10.1007/s11160-012-9260-z>.
- Domenici, P., & Hale, M. E. (2019). Escape responses of fish: A review of the diversity in motor control, kinematics and behaviour. *Journal of Experimental Biology*, *222*. <https://doi.org/10.1242/jeb.166009>.
- Domenici, P., Lefrançois, C., & Shingles, A. (2007). Hypoxia and the antipredator behaviours of fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1487), 2105–2121. <https://doi.org/10.1098/rstb.2007.2103>.
- Domenici, P., Steffensen, J. F., & Marras, S. (2017). The effect of hypoxia on fish schooling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1727), 20160236. <https://doi.org/10.1098/rstb.2016.0236>.
- Figueiredo, B. R. S., Mormul, R. P., & Benedito, E. (2015). Structural complexity and turbidity do not interact to influence predation rate and prey selectivity by a small visually feeding fish. *Marine and Freshwater Research*, *66*(2), 170–176. <https://doi.org/10.1071/MF14030>.
- Fleet, D., & Weiss, Y. (2006). Optical flow estimation. In N. Paragios, Y. Chen, & O. Faugeras (Eds.), *Handbook of mathematical models in computer vision* (pp. 237–257). New York, NY: Springer.
- Garner, S. B. (2012). *Effects of mimic artificial oyster reefs on the ecology of juvenile fishes in marsh ponds: A before-after-control-impact analysis* (M.Sc. thesis). Baton Rouge, LA: Louisiana State University and Agricultural and Mechanical College.
- Gautrais, J., Ginelli, F., Fournier, R., Blanco, S., Soria, M., Chaté, H., et al. (2012). Deciphering interactions in moving animal groups. *PLoS Computational Biology*, *8*(9), e1002678. <https://doi.org/10.1371/journal.pcbi.1002678>.
- Handegard, N. O., Boswell, K. M., Ioannou, C. C., Leblanc, S. P., Tjøstheim, D. B., & Couzin, I. D. (2012). The dynamics of coordinated group hunting and collective information transfer among schooling prey. *Current Biology*, *22*(13), 1213–1217. <https://doi.org/10.1016/j.cub.2012.04.050>.
- Herbert-Read, J. E., Buhl, J., Hu, F., Ward, A. J., & Sumpter, D. J. (2015). Initiation and spread of escape waves within animal groups. *Royal Society Open Science*, *2*(4), 140355.
- Herbert-Read, J. E., Kremer, L., Bruintjes, R., Radford, A. N., & Ioannou, C. C. (2017). Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1863), 20171627. <https://doi.org/10.1098/rspb.2017.1627>.
- Herbert-Read, J. E., Rosén, E., Szorkovszky, A., Ioannou, C. C., Rogell, B., Perna, A., et al. (2017). How predation shapes the social interaction rules of shoaling fish. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1861), 20171126. <https://doi.org/10.1098/rspb.2017.1126>.
- Higham, T. E., Stewart, W. J., & Wainwright, P. C. (2015). Turbulence, temperature, and turbidity: The ecomechanics of predator–prey interactions in fishes. *Integrative and Comparative Biology*, *55*(1), 6–20. <https://doi.org/10.1093/icb/052>.
- Hoare, D. J., Couzin, I. D., Godin, J.-G. J., & Krause, J. (2004). Context-dependent group size choice in fish. *Animal Behaviour*, *67*(1), 155–164. <https://doi.org/10.1016/j.anbehav.2003.04.004>.
- Holbrook, S. J., & Schmitt, R. J. (2002). Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology*, *83*(10), 2855–2868. [https://doi.org/10.1890/0012-9658\(2002\)083\[2855:CFSSCD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2855:CFSSCD]2.0.CO;2).
- Ioannou, C. C. (2017). Grouping and predation. In T. K. Shackelford, & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of evolutionary psychological science* (pp. 1–6). New York, NY: Springer International. https://doi.org/10.1007/978-3-319-16999-6_2699-1.
- Ioannou, C. C., Bartumeus, F., Krause, J., & Ruxton, G. D. (2011). Unified effects of aggregation reveal larger prey groups take longer to find. *Proceedings of the*

- Royal Society B: Biological Sciences, 278(1720), 2985–2990. <https://doi.org/10.1098/rspb.2011.0003>.
- Ioannou, C. C., Guttal, V., & Couzin, I. D. (2012). Predatory fish select for coordinated collective motion in virtual prey. *Science*, 337(6099), 1212–1215. <https://doi.org/10.1126/science.1218919>.
- Ioannou, C. C., Ramnarine, I. W., & Torney, C. J. (2017). High-predation habitats affect the social dynamics of collective exploration in a shoaling fish. *Science Advances*, 3(5), e1602682. <https://doi.org/10.1126/sciadv.1602682>.
- Jeschke, J. M., & Tollrian, R. (2007). Prey swarming: Which predators become confused and why? *Animal Behaviour*, 74(3), 387–393. <https://doi.org/10.1016/j.anbehav.2006.08.020>.
- Kent, M. I. A., Lukeman, R., Lizier, J. T., & Ward, A. J. W. (2019). Speed-mediated properties of schooling. *Royal Society Open Science*, 6(2), 181482. <https://doi.org/10.1098/rso.181482>.
- Kimbell, H. S., & Morrell, L. J. (2015). Turbidity influences individual and group level responses to predation in guppies, *Poecilia reticulata*. *Animal Behaviour*, 103, 179–185.
- King, A. J., Fehlmann, G., Biro, D., Ward, A. J., & Fürtbauer, I. (2018). Re-wilding collective behaviour: An ecological perspective. *Trends in Ecology & Evolution*, 33(5), 347–357.
- Klotzbach, K. E. (2013). *Impacts of artificial reef addition on the nekton community of Louisiana marsh ponds: a before-after-control-impact analysis* (M.Sc. thesis). Baton Rouge, LA: Louisiana State University and Agricultural and Mechanical College.
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, U.K.: Oxford University Press.
- Lecheval, V., Jiang, L., Tichit, P., Sire, C., Hemelrijk, C. K., & Theraulaz, G. (2018). Social conformity and propagation of information in collective U-turns of fish schools. *Proceedings of the Royal Society B: Biological Sciences*, 285(1877), 20180251. <https://doi.org/10.1098/rspb.2018.0251>.
- Lichtenstein, J. L., Daniel, K. A., Wong, J. B., Wright, C. M., Doering, G. N., Costa-Pereira, R., et al. (2019). Habitat structure changes the relationships between predator behavior, prey behavior, and prey survival rates. *Oecologia*, 190(2), 297–308. <https://doi.org/10.1007/s00442-019-04344-w>.
- Lopez, U., Gautrais, J., Couzin, I. D., & Theraulaz, G. (2012). From behavioural analyses to models of collective motion in fish schools. *Interface Focus*, 2(6), 693–707. <https://doi.org/10.1098/rsfs.2012.0033>.
- Magurran, A. E., & Higham, A. (1988). Information transfer across fish shoals under predator threat. *Ethology*, 78(2), 153–158.
- 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, Series B: Biological Sciences*, 229(1257), 439–465. <https://doi.org/10.1098/rspb.1987.0004>.
- Orpwood, J. E., Magurran, A. E., Armstrong, J. D., & Griffiths, S. W. (2008). Minnows and the selfish herd: Effects of predation risk on shoaling behaviour are dependent on habitat complexity. *Animal Behaviour*, 76(1), 143–152. <https://doi.org/10.1016/j.anbehav.2008.01.016>.
- Otsu, N. (1979). A threshold selection method from gray-level histograms. *IEEE Transactions on Systems, Man, and Cybernetics*, 9(1), 62–66.
- Parrish, J. K. (1989). Re-examining the selfish herd: Are central fish safer? *Animal Behaviour*, 38(6), 1048–1053.
- Parrish, J. K., Viscido, S. V., & Grunbaum, D. (2002). Self-organized fish schools: An examination of emergent properties. *Biological Bulletin*, 202(3), 296–305.
- Partridge, B. L., Pitcher, T., Cullen, J. M., & Wilson, J. (1980). The three-dimensional structure of fish schools. *Behavioral Ecology and Sociobiology*, 6(4), 277–288.
- Pitcher, T. J. (1983). Heuristic definitions of fish shoaling behaviour. *Animal Behaviour*, 31, 611–613.
- Radakov, D. V. (1973). *Schooling in the ecology of fish*. New York, NY: J. Wiley.
- Rieucou, G., Boswell, K. M., De Robertis, A., Macaulay, G. J., & Handegard, N. O. (2014). Experimental evidence of threat-sensitive collective avoidance responses in a large wild-caught herring school. *PLoS One*, 9(1), e86726. <https://doi.org/10.1371/journal.pone.0086726>.
- Rieucou, G., Fernö, A., Ioannou, C. C., & Handegard, N. O. (2015). Towards of a firmer explanation of large shoal formation, maintenance and collective reactions in marine fish. *Reviews in Fish Biology and Fisheries*, 25(1), 21–37. <https://doi.org/10.1007/s11160-014-9367-5>.
- Rieucou, G., Holmin, A. J., Castillo, J. C., Couzin, I. D., & Handegard, N. O. (2016). School level structural and dynamic adjustments to risk promote information transfer and collective evasion in herring. *Animal Behaviour*, 117, 69–78. <https://doi.org/10.1016/j.anbehav.2016.05.002>.
- Rosenthal, S. B., Twomey, C. R., Hartnett, A. T., Wu, H. S., & Couzin, I. D. (2015). Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proceedings of the National Academy of Sciences of the United States of America*, 112(15), 4690–4695. <https://doi.org/10.1073/pnas.1420068112>.
- Ruxton, G. D., Jackson, A. L., & Tosh, C. R. (2007). Confusion of predators does not rely on specialist coordinated behavior. *Behavioral Ecology*, 18(3), 590–596. <https://doi.org/10.1093/beheco/arm009>.
- Ryer, C., & Olla, B. I. (1998). Effect of light on juvenile walleye pollock shoaling and their interaction with predators. *Marine Ecology Progress Series*, 167, 215–226. <https://doi.org/10.3354/meps167215>.
- Strandburg-Peshkin, A., Twomey, C. R., Bode, N. W., Kao, A. B., Katz, Y., Ioannou, C. C., et al. (2013). Visual sensory networks and effective information transfer in animal groups. *Current Biology*, 23(17), R709–R711.
- Tunstrøm, K., Katz, Y., Ioannou, C. C., Huepe, C., Lutz, M. J., & Couzin, I. D. (2013). Collective states, multistability and transitional behavior in schooling fish. *PLoS Computational Biology*, 9(2), e1002915. <https://doi.org/10.1371/journal.pcbi.1002915>.
- Turner, G. F., & Pitcher, T. J. (1986). Attack abatement: A model for group protection by combined avoidance and dilution. *American Naturalist*, 128(2), 228–240. <https://doi.org/10.1086/284556>.
- Viscido, S. V., Parrish, J. K., & Grunbaum, D. (2004). Individual behavior and emergent properties of fish schools: A comparison of observation and theory. *Marine Ecology Progress Series*, 273, 239–250.
- Ward, A. J. W., Herbert-Read, J. E., Sumpter, D. J. T., & Krause, J. (2011). Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America*, 108(8). <https://doi.org/10.1073/pnas.1101616108>. E27–E27.
- Weetman, D., Atkinson, D., & Chubb, J. C. (1998). Effects of temperature on anti-predator behaviour in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 55(5), 1361–1372.
- Zienkiewicz, A. K., Ladu, F., Barton, D. A. W., Porfiri, M., & Bernardo, M. D. (2018). Data-driven modelling of social forces and collective behaviour in zebrafish. *Journal of Theoretical Biology*, 443, 39–51. <https://doi.org/10.1016/j.jtbi.2018.01.011>.

Appendix

Table A1
PCA variable loadings for each habitat and attack condition

	PC1	PC2	PC3	PC4
Free field, Preattack				
Speed	-0.0687	-0.6718	-0.7364	-0.0370
Area	0.4935	0.2281	-0.2730	0.0948
Angular velocity	0.4775	0.1566	-0.2094	0.6590
Polarization	-0.4116	0.4333	-0.3433	-0.0642
Rotational order	-0.3935	0.4552	-0.3966	0.1728
Correlation strength	0.4465	0.2777	-0.2536	-0.7221
Free field, Midattack				
Speed	0.0066	-0.3701	-0.9011	-0.1768
Area	-0.5125	-0.3060	0.1108	0.1799
Angular velocity	-0.5074	-0.2051	-0.0367	0.6120
Polarization	0.3775	-0.5116	0.3187	0.0084
Rotational order	0.3726	-0.5884	0.0970	0.2181
Correlation strength	-0.4456	-0.3455	0.2520	-0.7170
Marsh edge, Preattack				
Speed	0.1861	-0.0012	0.9201	-0.2721
Area	-0.5461	-0.1926	-0.0064	0.1940
Angular velocity	-0.4927	-0.2808	0.2859	0.3666
Polarization	0.2629	-0.6636	0.1130	0.3828
Rotational order	0.2670	-0.6383	-0.2426	-0.4217
Correlation strength	-0.5329	-0.1906	-0.0018	-0.6553
Marsh edge, Midattack				
Speed	-0.2606	-0.3984	-0.7988	0.2130
Area	0.4945	-0.2982	0.1617	-0.0848
Angular velocity	0.4663	-0.2969	-0.2325	-0.6545
Polarization	-0.3792	-0.5447	0.1287	-0.2467
Rotational order	-0.3868	-0.4163	0.4947	-0.0673
Correlation strength	0.4203	-0.4410	0.1435	0.6735
Habitat complexity, Preattack				
Speed	0.0413	-0.4393	0.8787	-0.0877
Area	-0.5702	-0.2512	-0.1224	-0.2249
Angular velocity	-0.5935	0.0867	0.0826	-0.4708
Polarization	0.1477	-0.6241	-0.1675	0.2196
Rotational order	0.2360	-0.5158	-0.4023	-0.5130
Correlation strength	-0.4933	-0.2843	-0.1269	0.6393
Habitat complexity, Midattack				
Speed	-0.0971	0.1400	-0.9844	0.0435
Area	0.5148	0.2628	-0.0245	-0.0919
Angular velocity	0.5259	0.1981	-0.0435	-0.5435
Polarization	-0.3509	0.5882	0.1312	0.3011
Rotational order	-0.3292	0.6116	0.0985	-0.4756
Correlation strength	0.4664	0.3900	0.0395	0.6143

Schooling state parameter measurements are given for each habitat and attack condition. Scree plot analysis showed that the first four principal components explain >95% of the variability in the data.