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1 Turbidity increases risk perception but constrains collective behaviour
2 during foraging by fish shoals

3

4 **Running header**

5 Shoaling in turbidity

6

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11

12 **Abstract**

13 Turbidity reduces the distance that animals can detect food, predators and conspecifics. How
14 turbidity affects decision making in social contexts has rarely been investigated; moreover, it is
15 unknown whether decreased shoaling in turbid water is due to visual constraints (a mechanistic
16 explanation) or a reduced perception of predation risk (an adaptive explanation). Using a V-shaped
17 decision making arena, we investigated the effect of turbidity on foraging in groups of three-
18 spined sticklebacks (*Gasterosteus aculeatus*). In turbid conditions, fish took longer to leave a
19 refuge, longer to locate the food in one of the arms, and consumed less food once it was found.
20 This increase in risk-averse behaviour was further supported by improved accuracy over repeated
21 trials and a speed-accuracy trade-off only being observed in turbid conditions. Despite evidence of
22 a higher perception of risk in turbid water, the fish to first choose an arm of the maze was more
23 likely to be alone in turbid water, thus this individual lost the anti-predatory and decision making
24 benefits of collective behaviour. This suggests that turbidity acts mechanistically as a visual
25 constraint, shifting decisions away from being made collectively to being made by individuals
26 separated from the group, which could have potential impacts for wild prey populations.

27

28 **Keywords**

29 Antipredator behaviour, collective behaviour, foraging, group decision making, refuge, stickleback.

30

31

32 **Introduction**

33 Turbidity is caused by suspended particles in water that attenuate and increase the scattering of
34 light (Utne & Utne-Palm, 2002). The subsequent decrease in visibility reduces the availability and
35 reliability of visual cues for aquatic animals, limiting the private and social information available
36 for decision making. In addition to some habitats being naturally highly turbid, anthropogenic
37 activity is driving an increase in turbidity via eutrophication and sedimentation from intensified
38 agriculture, deforestation and urbanization (Davies-Colley & Smith, 2001). Accordingly, there is
39 much research interest in quantifying and predicting behavioural responses to increased turbidity
40 as behaviour can mediate the impact of turbidity on wild animal populations and their
41 distributions (Abrahams & Kattenfeld, 1997; Tuomainen & Candolin, 2011; Utne & Utne-Palm,
42 2002).

43 Previous research exploring the effect of turbidity on behaviour has focused on predator-
44 prey interactions, including foraging behaviour by predators and anti-predator behaviour in prey.
45 In turbid water, detection of prey has been shown to be impaired (Pekcan-Hekim & Lappalainen,
46 2006; Quesenberry, Allen, & Cech, 2007; Utne, 1997), which can account for decreased encounter
47 rates between predators and prey (Turesson & Brönmark, 2007) and reduced selectivity regarding
48 prey choice (Abrahams & Kattenfeld, 1997; Kimbell & Morrell, 2016; Sohel, Mattila, & Lindström,
49 2017). A reduced predation rate in turbid water has been used to explain a decrease in risk-averse
50 behaviours in prey (Lehtiniemi, Engström-Öst, & Viitasalo, 2005). Examples include shifts in
51 habitat choice by fathead minnows (*Pimephales promelas*) where the use of more risky areas
52 increases (Abrahams & Kattenfeld, 1997), and in three-spined sticklebacks (*Gasterosteus*
53 *aculeatus*) responding to the sudden appearance of a predator, the use of shelters decreases and
54 fewer individuals show escape responses (Sohel & Lindström, 2015). Other studies, however, have
55 found an increase in anti-predator behaviours, possibly due to the reduced visibility in detecting

56 predators increasing the perception of risk. Also in three-spined sticklebacks, refuge use has been
57 shown to increase in turbid water and reduce activity (Ajemian, Sohel, & Mattila, 2015), with the
58 reduction in activity in turbid water also being demonstrated in guppies *Poecilia reticulata* (Borner
59 et al., 2015) and zebrafish, *Danio rerio* (Suriyampola, Cacéres, & Martins, 2018). Turbidity has also
60 been shown to increase the rate of freezing by guppies in response to detecting a predator
61 (Kimbell & Morrell, 2015) and reduce foraging in spiny damselfish, *Acanthochromis polyacanthus*
62 (Leahy, McCormick, Mitchell, & Ferrari, 2011). These mixed results may be explained by
63 differences in predator hunting modes and the relative visibility of predators and prey in clear and
64 turbid water; they all indicate, however, that turbidity affects both predation and anti-predator
65 behaviour.

66 A handful of recent studies have shown shoaling tendencies in fish are reduced in turbid
67 water (Borner et al., 2015; Fischer & Frommen, 2013; Kimbell & Morrell, 2015). Because shoaling
68 is a key anti-predator behaviour in many fish species (Rieucau, Fernö, Ioannou, & Handegard,
69 2015), this reduction in shoaling in turbid water could represent a lower perception of risk. In
70 contrast, turbidity could act as a visual constraint, reducing the ability of fish to form and maintain
71 groups as vision is a widely used and important sensory modality used in shoaling (Ioannou,
72 Couzin, James, Croft, & Krause, 2011). Despite extensive work on collective decisions in animal
73 groups (Conradt & List, 2009; Ioannou, 2017b), it is unknown how decision making in social
74 contexts is impacted by turbid conditions. Decisions in groups can be made collectively, where a
75 large proportion of the group contribute to a group decision, be led by a single or few individuals,
76 or groups can split where different decisions are made by different subsets, or even individuals,
77 from the group (Ioannou, Ramnarine, & Torney, 2017). Although in this latter case individuals are
78 not constrained by maintaining group cohesion after they have separated from the group
79 (Ioannou et al., 2015), they lose anti-predation benefits of grouping. As with shoaling in general,

80 groups splitting during decision making in turbid water may occur due to a mechanistic constraint
81 in visual information or be an adaptive adjustment of behaviour if the perception of risk is
82 reduced.

83 Three-spined sticklebacks are facultatively group living and widely distributed across a
84 range of habitats, including in clear and turbid water, making them an ideal system for studying
85 the effect of turbidity on decision making in a social context (Quesenberry et al., 2007). In this
86 study we used a V-shaped decision making arena, where the fish start in a refuge at the base of
87 the V and have to choose between two arms, only one of which contained food. Shoals were
88 tested in either clear or turbid water, and given multiple trials per day, to test how turbidity
89 affects foraging and social interactions. In addition to exploring how foraging decisions in a social
90 context are affected by turbidity, we also measured the social cohesion of the individual that first
91 entered an arm of the maze, i.e. the deciding, or 'initiator', individual (Bevan, Gosetto, Jenkins,
92 Barnes, & Ioannou, 2018). Whether turbidity is predicted to have a positive or negative effect on
93 the speed of decision making, the accuracy in which arm was chosen, and cohesion between
94 individuals in the group will depend on whether turbidity increased or decreased the perception of
95 predation risk. By investigating group cohesion in parallel with foraging, we can also infer whether
96 changes in social cohesion are due to altered perception of risk in turbid water (as revealed by the
97 response in foraging), or are more likely to be due to altered visibility of other individuals.
98 Repeated testing within a day allowed testing of how the cumulative effect of habituation, training
99 in the presence and location of food, and satiation (McDonald, Rands, Hill, Elder, & Ioannou, 2016)
100 differs in clear versus turbid environments. We predicted that due to the reduced spatial
101 information in turbid water, e.g. from landmarks (Odling-Smee & Braithwaite, 2003), decision
102 making would improve more slowly in turbid water over repeated trials. We also varied shoal size
103 to test whether the effect of turbidity was sensitive to the number of individuals in the group,

104 which can have multiple effects on decision making such as reducing the perception of risk in
105 individuals, increasing the likelihood that bolder or more cognitively-able individuals are included
106 in the group, and allowing for information transfer and feedback between individuals that results
107 in swarm intelligence (Ioannou, 2017).

108

109 **Materials and methods**

110 **Study subjects and husbandry**

111 Three-spined sticklebacks were caught from the River Cary, Somerset, UK (ST 469 303) in
112 September 2014. The collection site is surrounded by arable land and turbidity varies frequently
113 throughout the year due to variation in agricultural activity and in the weather. Fish were
114 transported to glass stock tanks (40 x 70 x 34 cm) in a temperature controlled room (water
115 temperature: 15-16°C; photoperiod: 12:12 hours). The tanks housed 60-90 fish and were enriched
116 with plastic plants and dark plastic tubing the fish could use as refuges. Fish were not sexed as the
117 water temperature and light cycle prevented reproductive condition. Fish were fed defrosted
118 bloodworms and tropical flake food daily. At the time of testing, the fish in the study had a
119 standard body length mean of 42.3 mm with a standard deviation of 3.9 mm.

120 Trials were carried out January to March 2016. The day prior to being tested, up to three
121 groups consisting of two, four or eight individuals were formed by transferring randomly chosen
122 individuals to three separate breeding nets (16.5 x 12.7 x 12.7 cm) within a glass stock tank, so
123 that up to three groups were tested each day. Fish within each group came from the same stock
124 tank so were familiar with one another and were held overnight in the breeding nets and between
125 trials on the test day that followed. Each group was only tested in one water treatment and
126 individual fish were not tested in more than one group; 132 individuals were exposed to the turbid

127 treatment (groups of two, $N=20$; groups of four, $N=9$; groups of eight, $N=7$) and 116 individuals
128 exposed to the clear treatment (groups of two, $N=20$; groups of four, $N=7$; groups of eight, $N=6$).
129 At the start of testing, fish had not been fed since the previous day to standardise hunger before
130 the start of trials.

131

132 **Experimental apparatus and protocol**

133 Experiments took place in a V-shaped maze constructed from white Perspex plastic (Ioannou &
134 Dall, 2016), ~130cm in length (Fig. 1). Each day, one arm of the maze (left: 130 trials; right: 133
135 trials) was randomly chosen to contain a bloodworm reward inside a petri dish (2 bloodworms per
136 fish per trial). The arm containing bloodworms was kept constant throughout that day of testing.
137 Opaque white plastic covered the front half of the petri dishes to prevent fish seeing the reward
138 prior to swimming into the arm of the maze. Without this visual barrier, the food would have been
139 visible from a greater distance in clear versus turbid water; once past the visual barrier, the
140 bloodworm were visible to the fish even in the turbid water treatment. Trials were recorded with
141 a Panasonic SD800 camera at a resolution of 1920×1080 pixels, mounted 1 metre above the maze
142 on a tripod.

143 The maze was filled with aged water to a depth of 8 cm (42 litres in total). In the morning
144 of turbid treatment days, 4.5 grams (0.11 g/L) of kaolin clay (Trustleaf, Cambridgeshire) was added
145 to the maze water and mixed thoroughly, producing a measurement of 30.98 ± 2.24 NTU (mean $\pm$
146 standard deviation) in line with previous studies (Leahy et al., 2011; Meager & Batty, 2007).
147 Suspended clay particles are frequently a large component of turbidity in natural aquatic habitats
148 (Horppila, Eloranta, Liljendahl-Nurminen, Niemistö, & Pekcan-Hekim, 2009; Rhoton & Bigham,
149 1997), so is an ecologically relevant method for manipulating turbidity. Clear water was measured
150 at 0.36 ± 0.21 NTU (Appendix Fig. A1).

151 For each trial, the fish were transferred to the refuge (an area covered with 5mm black
152 plastic mesh; Fig. 1), acclimatized for 2 minutes, then the door was raised remotely using fishing
153 line, allowing the fish to enter the maze. Trials ended when all bloodworms had been consumed or
154 after 20 minutes if the bloodworms were not all eaten. The group was then returned to their
155 breeding net. After each trial, the water was thoroughly mixed in both water treatments to
156 maintain turbidity. Multiple groups were tested per day (up to 3) and each group was given a
157 maximum of ten trials in one day; no more trials for that group were conducted if no bloodworms
158 were eaten within 20 minutes for two sequential trials for that group. This was to avoid testing
159 groups that were already satiated, and hence unlikely to be motivated to find food. At the end of
160 each day all fish were returned to stock tanks and not reused. The water in the maze was replaced
161 with aged water at the end of each day and filtered overnight using an external Eheim 2213 filter
162 pump, which was turned off during trials.

163 Trials were conducted over 23 days (turbid, $N=12$; clear, $N=11$ days). Water treatment
164 (clear or turbid) was randomised between days. Each group tested that day were each given their
165 first trial, then all groups were given their second trial, then their third, etc. The mean time
166 between consecutive trials starting was 24.64 minutes with a standard deviation of 18.46 minutes.
167 Typically, three groups were tested each day, consisting of one large group composed of four or
168 eight individuals and two groups of two individuals. More trials of smaller groups were conducted
169 as these were expected to be more variable than larger groups (as they are less likely to contain a
170 representative sample of the overall population).

171

172 **Video analysis**

173 Data were extracted from video recordings per trial rather than per individual fish because
174 tracking individual identities in turbid water was too unreliable (Kimbell & Morrell, 2015). The time

175 taken to first leave a refuge is a commonly used method of assessing risk-taking behaviour
176 (Webster, Atton, Ward, & Hart, 2007) and was measured as the latency between the refuge door
177 being raised until the whole body of first fish to leave was past the door. The time taken to make
178 the first decision was the time that elapsed between the first fish leaving the refuge and when the
179 snout of a fish first touched the 'decision boundary' of either arm (Fig. 1). This determined the
180 point in the trial at which a fish first made a decision as to which arm to enter, and this fish was
181 considered the deciding fish by being the first to initiate a movement into an arm. Accuracy of
182 decision making was determined by whether this arm contained the food reward. The time to
183 locate food was measured as the time taken from first crossing a decision boundary to when the
184 first bloodworm was consumed, and foraging success was the proportion of bloodworms
185 consumed within the 20 minutes of the trial starting.

186 The spatial distribution of fish was measured to quantify the social cohesion of the fish to
187 first make a decision (Ioannou et al., 2015). Coordinates were manually recorded from the centre
188 of every fish using ImageJ (Rasband, 2012) at the time of the decision to first enter an arm in each
189 trial. Any fish in the refuge were given the same coordinate, fixed at the centre of the refuge area,
190 as their exact position was unknown. Position coordinates were used to calculate the distance
191 between the first fish that made a decision and its nearest neighbour (Ioannou et al., 2015). The
192 proportion of individuals outside of the refuge was measured from the number of individuals
193 inside and outside the refuge when the first decision was made.

194

195 **Statistical analysis**

196 Time taken response variables (latencies for the first fish to leave the refuge, the first decision to
197 enter an arm, and the first time food was consumed) and nearest neighbour distance (the NND of
198 the individual to first choose an arm, i.e. the deciding fish) were each analysed using a negative

199 binomial Generalised Linear Mixed Model (GLMM; the analyses did not meet the assumptions of
200 normal (Gaussian) or Poisson linear models). Decision making accuracy, the proportion of fish
201 outside the refuge when the decision was made, whether at least one other fish was out of the
202 refuge when the decision was made, and the proportion of bloodworms consumed were each
203 analysed using a binomial GLMM. However, due to convergence warnings in the models with the
204 proportion of bloodworms consumed as the response variable, whether at least 50% of the
205 bloodworm being eaten in each trial was analysed as an alternative measure of food consumed. In
206 79% of trials (271 of 343), all or none of the bloodworm was consumed, suggesting that much of
207 the variation in the proportion of bloodworm consumed was captured by a simple threshold of
208 whether 50% was consumed. To analyse the speed-accuracy trade-off (i.e. the relationship
209 between the decision making time and whether the rewarding arm was chosen first), the time
210 taken to first make a decision (i.e. cross the arena) was used as the response variable and decision
211 making accuracy was included as an additional explanatory variable in a negative binomial GLMM.

212 The initial model for each response variable included all two-way interactions between the
213 water treatment (clear or turbid), the number of fish in the group (a continuous variable: 2, 4 or 8)
214 and trial number (also a continuous variable: 1st to the 10th) terms. Using a stepwise backward
215 elimination approach, models were simplified to remove non-significant interactions ($P > 0.05$),
216 and the final models always included all main effects. Group identity was also always included as a
217 random factor. The dispersion parameter for each statistical model was checked to be
218 approximately equal to one using an equivalent Generalised Linear Model without a random term.
219 Statistical analyses were carried out using R (3.14.2).

220

221 **Results**

222 **Latency to leave the refuge**

223 The latency to first leave the refuge was significantly longer in turbid water and increased over
224 repeated trials (negative binomial GLMM: Appendix Fig. A2a; trial number: $\chi^2_1=44.62$, $P<0.0001$;
225 Appendix Fig. A2b; turbidity: $\chi^2_1=4.93$, $P=0.026$). As expected, the latency to leave the refuge
226 decreased with increasing group size ($\chi^2_1=28.22$, $P<0.0001$).

227

228 **Time taken to make first decision**

229 The time taken to make the first decision, i.e. the time taken from a fish first leaving the refuge to
230 a fish first crossing one of the decision lines into an arm, depended upon a significant interaction
231 between group size and trial number, where repeated exposure over successive trials had no effect
232 on groups of 2 but groups of four and eight became slower over repeated trials (Appendix Fig. A3:
233 negative binomial GLMM: group size $\times$ trial number: $\chi^2_1=9.26$, $P=0.002$). Independent of this
234 effect, the time taken to make the first decision was higher in turbid water (Appendix Fig. A3;
235 $\chi^2_1=27.60$, $P<0.0001$).

236

237 **Decision making accuracy**

238 Confirming that the food was adequately concealed from the fish when they first chose an arm,
239 the fitted probability of choosing the rewarding arm at the start of testing was approximately 0.5
240 (Fig. 2). The probability of the rewarding arm being chosen first increased over successive trials in
241 the turbid treatment but remained close to chance levels (0.5) in clear water (Fig. 2; binomial
242 water treatment $\times$ trial number: $\chi^2_1=7.60$, $P=0.006$). Group size had no significant effect on
243 decision making accuracy ($\chi^2_1=0.80$, $P=0.37$).

244 We then assessed whether the time taken to make the first decision was related to
245 accuracy (choosing the rewarding arm or not), to determine whether the fish showed a speed-

accuracy trade-off during decision making. The time taken to make the first decision (the response variable) depended significantly upon the interaction between water clarity and accuracy of decision making (Fig. 3; negative binomial GLMM: $\chi^2_1=4.80$, $P=0.029$). In clear water, the time taken to make the first decision was not associated with decision accuracy (Fig. 3b), while in turbid water decisions took longer to make if they were accurate compared to incorrect (Fig. 3a). In contrast to the statistical model where accuracy was not included as a main effect, group size and trial number had non-significant effects on time taken to make the first decision (group size: $\chi^2_1=2.07$, $P=0.15$; trial number: $\chi^2_1=3.14$, $P=0.77$).

254

255 **Social cohesion of the fish to first choose an arm**

The nearest neighbour distance (NND) of the first individual to make a decision regarding which arm to choose (the deciding fish) depended significantly on water turbidity, group size and trial number (Fig. 4), although there were no significant interaction terms. Nearest neighbour distances increased as the trials progressed (negative binomial GLMM: $\chi^2_1=24.43$, $P<0.0001$) and, as expected, were lower in larger groups ($\chi^2_1=27.23$, $P<0.0001$). Nearest neighbour distances were significantly greater in the turbid water treatment ($\chi^2_1=5.06$, $P=0.025$), i.e. the fish to first make a decision was further from their nearest neighbour in turbid water.

In the turbid water treatment, there was a significantly smaller proportion of the group out of the refuge when the first decision was made compared to the clear water treatment (Appendix Fig. A4: binomial GLMM: water treatment: $\chi^2_1=19.25$, $P<0.0001$). With increasing group size and trials, the proportion of fish out of the refuge also decreased (group size: $\chi^2_1=14.90$, $P<0.0005$; trial number: $\chi^2_1=52.20$, $P<0.0001$). Although the proportion of fish per group declined with group size, the probability that at least one other fish was out of the refuge increased with group size, as expected ($\chi^2_1=11.98$, $P=0.001$). There was no effect of trial number ($\chi^2_1=2.98$, $P=0.084$). Reflecting

270 the trend of the proportion of the group out of the refuge, the probability that another fish was
271 out of the refuge when the first decision was made was lower in turbid water ($\chi^2_1 = 4.77$, $P=0.029$).

272 These results demonstrate the increased isolation of the fish to make a decision in turbid
273 water, controlling for the number of fish in each trial. To explore these trends further, we
274 repeated the analysis of the deciding fish's NND but only including cases when at least one other
275 fish was out of the refuge (285 trials remained in this analysis, compared to 331 trials in the initial
276 analysis of NND). While the NND still decreased when larger groups were tested (negative
277 binomial GLMM: $\chi^2_1 = 14.89$, $P<0.0005$) and increased as trials progressed ($\chi^2_1 = 27.56$, $P<0.0001$),
278 the effect of water turbidity became non-significant ($\chi^2_1 = 1.13$, $P=0.29$). This suggests that the
279 effect of water turbidity on NND was mainly driven by whether or not there were any other fish
280 out of the refuge, and in cases where there were two or more fish out, the deciding fish could
281 maintain a similar nearest neighbour distance in both clear and turbid water.

282

283 **Time to locate food and proportion of bloodworms eaten**

284 The time taken to locate food, i.e. the latency between first entering an arm and initiating feeding,
285 was significantly longer in turbid water (Appendix Fig. A5a: negative binomial GLMM: water
286 treatment: $\chi^2_1 = 11.42$, $P=0.001$). This included latencies from the incorrect arm being chosen first,
287 although this cannot explain the longer times taken in turbid water as choosing the incorrect arm
288 first was not more frequent in the turbid treatment (Fig. 3). The time taken to locate food also
289 significantly increased with trial number (Appendix Fig. A5b: trial number: $\chi^2_1 = 8.35$, $P=0.004$).
290 Group size had no significant effect (group size: $\chi^2_1 = 0.026$, $P=0.87$).

291 Whether at least half of the bloodworm were eaten in each trial was significantly affected
292 by an interaction between group size and trial number (binomial GLMM: $\chi^2_1 = 12.45$, $P<0.0005$) and

an interaction between the water treatment and trial number (GLMM: $\chi^2_1=4.020$, $P=0.045$). Fewer bloodworm were eaten as trials progressed, as expected if the fish became satiated over repeated trials. In earlier trials per group, larger groups were more likely to eat at least 50% of the food compared to smaller groups, although this probability declined to close to zero for all group sizes as trials progressed (Fig. 5). Similarly, fish tended to consume fewer bloodworm in earlier trials in turbid versus clear water, but the difference also declined as the trials progressed.

299

300 Discussion

Our results demonstrate effects of water turbidity at multiple stages of foraging in a social context. The latencies to first leave the refuge, make the first decision, and consume the food after choosing an arm were all slower in turbid water, with these effects being independent of group size and trial order (i.e. there were no interactions with these variables and the turbidity treatment). The higher latencies are consistent with reduced activity in turbid water. This suggests that the perception of predation risk was higher in turbid water in our experiment, with the latency to leave a refuge in particular being commonly used to assay perception of risk in fish (Ajemian et al., 2015; Bevan et al., 2018). The higher perception of risk in the turbid treatment could be a consequence of turbidity being a more novel environment, rather than turbidity being perceived as a higher risk habitat per se. However, we found no evidence that the water treatment affected how the latencies changed over repeated trials, suggesting novelty of a turbid environment, which would decrease with more experience, was not driving the effects on perceived risk. The fish may have reduced their activity to acquire adequate information in the visually-constrained turbid water, but this would not explain why fewer of the available bloodworm were eaten in the turbid water treatment, which also supports the interpretation that the turbid treatment condition was perceived as riskier.

317 Olfactory cues from the bloodworm did not appear to influence the first decision made,
318 where it would be expected that the probability of choosing the rewarding arm would be greater
319 than 0.5 if non-visual cues were being used. Evidence of improved decision making over time,
320 possibly due to learning, came from the fish increasing their probability of choosing the correct
321 (i.e. rewarding) arm as trials progressed, but only in the turbid water treatment. Fish in the clear
322 water treatment tended to choose arms randomly throughout testing. This is particularly
323 surprising because sticklebacks are known to use landmarks during spatial learning (Odling-Smee
324 & Braithwaite, 2003), and the ability to detect landmarks would be constrained in more turbid
325 water (Utne & Utne-Palm, 2002). Together with the apparent increased perception of risk in the
326 turbid water treatment, this result suggests that improved decision making over time occurred
327 only in the turbid water treatment due to the increased cost of making a wrong decision. An
328 increased cost could arise from moving over a greater area than is necessary, which would
329 increase the chance of encountering a predator the fish are unable to detect from a distance in
330 turbid water. This would also explain the reduced activity in turbid water (Ajemian et al., 2015),
331 and could be studied further by measuring the movement of the fish under the different
332 conditions (Ioannou, Ruxton, & Krause, 2008). The cost of making an inaccurate decision is further
333 supported by there only being a speed-accuracy trade-off in turbid water, where choosing the
334 rewarding arm took longer than choosing the incorrect arm. When the risk of making an
335 inaccurate decision is high, speed is typically reduced to maximise accuracy (Chittka, Skorupski, &
336 Raine, 2009). Thus, our results suggest the fish made more careful (i.e. risk averse) decisions that
337 showed patterns typical of other decision making studies (e.g. a speed-accuracy trade-off) when
338 perceived risk was high from being in a turbid environment.

339 Despite these multiple lines of evidence that turbid water conditions were perceived as
340 higher risk, the analysis of the spatial distribution of fish at the point when a fish first chose an arm

341 of the maze shows that a reduced proportion of the group was outside of the refuge in turbid
342 water, the deciding fish was more likely to be alone, and this drove an increased nearest
343 neighbour distance for the deciding fish. Increased shoaling after exposure to predation risk has
344 been demonstrated previously (Hoare, Couzin, Godin, & Krause, 2004), thus the increased
345 perception of risk in turbid water should result in greater cohesion with groupmates. One
346 possibility is that grouping may be a less beneficial anti-predator strategy for individuals in turbid
347 environments, a key issue often ignored in studies comparing anti-predator behaviour in turbid
348 versus clear water conditions. Of the common anti-predatory grouping mechanisms (Ioannou,
349 2017), the confusion effect is less likely to be effective in turbid conditions as the strength of
350 confusion in predators when targeting one of multiple prey from a group should reduce when
351 nearby prey are less visible. However, the increased uncertainty regarding the presence of a
352 predator should increase reliance on group (rather than individual) vigilance, and hence make
353 groups safer compared to solitary individuals in turbid water. The effect of turbidity is distance-
354 dependent, having a greater effect when objects are further away. Thus larger groups will not be
355 as conspicuous as they are in clear water, and encounter rates between predator and prey will
356 instead be more important. As aggregation in prey reduces encounter rates with predators
357 (Ioannou, Bartumeus, Krause, & Ruxton, 2011), turbid water should thus favour larger groups.

358 A more likely explanation for reduced shoaling is that the reduced visibility in turbid water
359 acted as a constraint to social interactions. Vision is a key sensory modality used in the formation
360 and maintenance of shoals in many fish species (Ioannou et al., 2011), and the optical effects of
361 turbidity mean that while individuals in close proximity are visible to one another, visual contact is
362 quickly lost once inter-individual distances increase. This optical property of turbidity is consistent
363 with the results from the nearest neighbour distance: with at least one other fish out of the
364 refuge, the fish to first make a decision was able to maintain visual contact with another fish and

365 maintain similar nearest neighbour distances compared to clear water. Although sticklebacks can
366 shift reliance from visual to olfactory cues (Suriyampola et al., 2018; Webster et al., 2007), our
367 results suggest that they are not able to fully compensate for reduced visual cues in turbid water
368 during shoaling. Previous studies have shown reduced shoaling in turbid conditions (Borner et al.,
369 2015; Fischer & Frommen, 2013; Kimbell & Morrell, 2015); by examining effects of turbidity on
370 other behaviours such as refuge use and foraging in parallel with the social cohesion of the
371 deciding fish, our study provides evidence that turbidity constrains shoaling behaviour, rather than
372 the reduced tendency to shoal being an indirect response to lower perceived risk in turbid
373 environments.

374 We demonstrate the impact of turbidity on foraging behaviour via increased perception of
375 risk which influences decision making, but that turbidity also constrains greater shoal cohesion in
376 response to increased risk. The multiple potential mechanisms underlying our results demonstrate
377 the complexity of understanding behaviour in environments where sensory systems are limited, as
378 both proximate (the reduced ability to detect other group members) and adaptive (the effects of
379 reduced ability to detect, and be detected by, predators) factors operate simultaneously.
380 Improving our understanding of the social responses to turbidity and other changes driven by
381 anthropogenic activity, such as ocean acidification (Duteil et al., 2016) and increasing noise
382 (Herbert-Read, Kremer, Bruintjes, Radford, & Ioannou, 2017; Tidau & Briffa, 2019), is essential in
383 implementing appropriate mitigation strategies for natural populations, given the predicted
384 increase in anthropogenic disturbance in aquatic habitats and potential widespread implication for
385 individual fitness and population viability (Nel et al., 2009). Our study suggests that sticklebacks
386 can respond plastically to increased turbidity by slowing their foraging and making more accurate
387 decisions, which may minimise short-term negative impacts.

388

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520
521

522 Figure legends

523

524 Figure 1: The experimental V-maze used to determine the effects of turbidity on decision making
525 in three-spined sticklebacks. The shaded box represents the refuge where the sticklebacks were
526 released by raising a door on a pulley at the right-hand side of the refuge. The dashed line is the
527 point that determined when a decision had been made (the decision boundary). The circles at
528 both arms represent the petri dishes where food was placed prior to each trial, and the red line
529 represents the opaque plastic used to cover the front half of petri dishes to prevent fish seeing
530 contents of arm. To minimise disturbance and prevent light reflection on the water surface, a
531 white curtain screened the maze during trials. The camera was connected to a monitor beside the
532 maze to allow fish behaviour to be observed remotely without causing disturbance.

533

534 Figure 2: The relationship between water treatment (turbid (a), clear (b)) and trial number on
535 decision making accuracy. Accuracy is measured as whether the arm containing food is chosen
536 first. The line for each treatment represents the fitted values calculated from the GLMM
537 coefficients, whilst controlling for group size at its mean value. The dotted lines around each line
538 of best fit shows $2 \times$ predicted standard error of each line. Jitter has been added to the raw data to
539 allow overlapping points to be visualized.

540

541 Figure 3: The relationship between speed and accuracy of decision making in turbid (a) and clear
542 (b) water treatments. Speed is measured as the time taken to make the first decision. Medians are
543 illustrated by thick black lines, the interquartile range (IQR) is shown within the boxes and the
544 whiskers represent data points within $1.5 \times$ IQR. The open circles represent data points outside of
545 the whiskers. The y-axes show natural log transformed time taken to make the first decision for
546 visual clarity in plotting.

547

548 Figure 4: The effect of group size (2 (a), 4 (b) and 8 (c) fish) and trial number on the nearest
549 neighbour distance of the fish making the first decision at the time the first decision is made in
550 clear (dash line, filled circles) and turbid (solid line, crosses) water treatments. Lines are the
551 predicted trends calculated from GLMM coefficients. The y-axes show natural log transformed
552 nearest neighbour distance for visual clarity in plotting.

553

554 Figure 5: The effect of group size (2 (a), 4 (b) and 8 (c) fish) and trial number on whether 50% of
555 the bloodworms were eaten in clear (dash line, filled circles) and turbid (solid line, crosses) water
556 treatments. The lines are the predicted values calculated from GLMM coefficients. Jitter has been
557 added to the raw data to allow overlapping points to be visualized.

558

559 Appendix figure legends

560

561 Figure A1: Turbidity levels in the experimental V-maze remained stable between the front (open
562 circles) and back (crosses) of the arena, across each day in both the turbid (high NTU values) and
563 clear (low NTU values) treatments. Water samples were taken from both ends of the maze at the
564 start and end of each day to monitor turbidity, which was determined using a calibrated
565 spectrophotometer. Turbidity did not vary significantly within each treatment at different
566 locations or start or end of the testing days (two-way ANOVA for each turbid and clear treatments:
567 start or end of day: turbid: $F_{1,45}=1.8$, $P=0.18$; clear: $F_{1,40}=0.25$, $P=0.62$; position in maze: turbid:
568 $F_{1,45}=0.001$, $P=0.98$; clear: $F_{1,40}=0.14$, $P=0.72$).

569

570 Figure A2: The latency to leave the refuge across trials (a) and between water treatments (b).
571 Medians are illustrated by thick black lines, the interquartile range (IQR) is shown within the boxes
572 and the whiskers represent data points within 1.5 x IQR. The circles represent data points outside
573 of the whiskers. Y-axes show natural log transformed latency to leave the refuge for visual clarity
574 in plotting.

575

576 Figure A3: The effect of group size (2 (a), 4 (b) and 8 (c) fish) and trial number on the time taken to
577 make the first decision from the first fish leaving the refuge for both clear (dash line, filled circles)
578 and turbid (solid line, crosses) water. The fitted lines are calculated from the coefficients of the
579 GLMM. Y-axes show natural log transformed latency to cross the arena for visual clarity in plotting.

580

581 Figure A4: The effect of group size (2 (a), 4 (b) and 8 (c) fish) and trial number on the proportion of
582 fish outside the refuge at the moment the first decision was made, across clear (dash line, filled
583 circles) and turbid (solid line, crosses) water treatments. The fitted lines are calculated from the
584 coefficients of the GLMM.

585

586 Figure A5: The effect of water treatment (a) and trial number (b) on the time taken to find food
587 after an arm was chosen for the first time. Medians are illustrated by thick black lines, the
588 interquartile range (IQR) is shown within the boxes and the whiskers represent data points within
589 1.5 x IQR. The cross represents a data point outside of the whiskers. The y-axes show natural log
590 transformed latency to leave the refuge for visual clarity in plotting.

591

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Ethical note

All procedures were approved by the University of Bristol Ethical Review Group (UIN UB/11/042 and UB/14/045). Manipulating turbidity using dissolved clay powder is a common method in laboratory experiments (Ferrari, Lysak, & Chivers, 2010), and has been used in previous behavioural studies of fish with no observed ill effects (Vollset & Bailey, 2011). Turbidity less than 40 NTU was used which is within ecologically realistic limits in the habitats of sticklebacks where turbidity can change rapidly due to increased precipitation and run-off from surrounding land. A number of studies have shown the use of clay powder to induce turbidity has no significant effect on water pH (Johannesen, Dunn, & Morrell, 2012; Leahy, McCormick, Mitchell, & Ferrari, 2011). After use in the laboratory, fish were rehomed in a pond unconnected to other water bodies, in accordance with the U.K.'s Environment Agency regulations.

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