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Disturbed flow may create a sensory refuge for aggregated prey

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Predators use olfactory cues to detect and locate prey, and the movement of water or air both aids dispersal of cues and provides a directional cue. As release of odour cues is related to group size, prey aggregation may be inhibited due to an increased risk of detection. However, disturbance in the flow diminishes the reliability of odour as a prey cue, impeding predator foraging success and efficiency. We explore how different cue concentrations (as a proxy for prey group size) affect risk to prey by fish predators using laminar and disturbed flow. We find that increasing odour cue concentration increases predation risk. However, disturbing the flow reduces the rate at which predators choose the arm of a y-maze containing prey, effectively lowering risk to prey compared to that of prey in non-disturbed flow. This suggests that objects disturbing the flow downstream of prey may provide a sensory refuge, allowing prey to form larger groups than in laminar flow.

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Abstract

Predators use olfactory cues to detect and locate prey, and the movement of water or air both aids dispersal of cues and provides a directional cue. As release of odour cues is related to group size, prey aggregation may be inhibited due to an increased risk of detection. However, disturbance in the flow diminishes the reliability of odour as a prey cue, impeding predator foraging success and efficiency. We explore how different cue concentrations (as a proxy for prey group size) affect risk to prey by fish predators using laminar and disturbed flow. We find that increasing odour cue concentration increases predation risk. However, disturbing the flow reduces the rate at which predators choose the arm of a y-maze containing prey, effectively lowering risk to prey compared to that of prey in non-disturbed flow. This suggests that objects disturbing the flow downstream of prey may provide a sensory refuge, allowing prey to form larger groups than in laminar flow.

Introduction

In order to avoid predation, animals use a range of strategies, from visual crypsis (Jackson *et al.*, 2005) to increased vigilance in groups (Krause and Ruxton, 2002). In cases where visual interactions between predators and prey are limited, other cues are employed, such as nocturnal animals using sound cues (Obrist *et al.*, 1993) or detection of electric fields in sharks (Kajiura and Holland, 2002). For many animals, a key sense used in prey detection and location is olfaction. Olfactory predators such as crustaceans (Gomez and Atema, 1996; Weissburg and Zimmer-Faust, 1993), fish (Nevitt, 1991) and, molluscs (Ferner and Weissburg,

2005) can successfully track odour plumes from prey to their source. To navigate odour plumes, animals adopt a range of sensing strategies, including time differences in bilateral odour detection (e.g. sharks (Gardiner and Atema, 2010)) and time-averaging of odour concentrations (e.g. whelks (Wilson and Weissburg, 2012)), or by making simultaneous comparisons of odour concentration (Gomez and Atema, 1996; Vergassola *et al.*, 2007). In order to avoid such detection, prey may try to limit the amount of olfactory cue that they release or otherwise make it difficult for predators to detect them (Ruxton, 2009).

To reduce the risk from predators that hunt using vision, prey can group together, increasing the time taken for a hunting predator to locate groups, known as the encounter-dilution effect (Wrona and Dixon, 1991), and thus grouping is favoured as part of a predator avoidance strategy when predators hunt using vision (Jackson *et al.*, 2005; Riipi *et al.*, 2001). However, grouping may be counter-productive if increasing group size makes prey increasingly easier for predators to find, as may be the case when predators hunt using olfaction (Kunin, 1999).

Grouping may benefit prey avoiding olfactory predators in still water (Johannesen *et al.*, 2014), but in a flowing environment, water movement provides a directional cue to the prey, meaning olfactory cues are more easily taken advantage of than in a still environment (Løkkeborg, 1998). Larger or more numerous animals release more odour cue, eliciting a stronger reaction in the receiver (Hawkins *et al.*, 2007; Kusch *et al.*, 2004). When animals aggregate, the odour cues released interact, increasing the size and concentration of the odour plume (Villermaux and Duplat, 2003), and allowing receivers to more readily track the plume to its source (Wilson and Weissburg, 2012). In a review of olfactory detection distance in insects, Andersson et al (Andersson *et al.*, 2013) indicate that the increase in detection with increasing

size of the source is likely to be asymptotic, although theoretical work indicates accelerating detectability may also be possible (Treisman, 1975). If the risk of predation increases too much with group size, aggregating may be an unsuccessful strategy in species that cannot defend themselves. Therefore, aggregating in flowing environments may be detrimental to prey survival. Here, we explore this question from the perspective of three-spine sticklebacks (*Gasterosteus aculeatus*) locating odour sources of differing concentration (as a proxy for prey group size (Hill and Weissburg, 2014; Schneider *et al.*, 2014) - but see discussion) in flowing water, to test the hypothesis that increasing prey (bloodworm) cue concentration increases the risk to prey in flowing water.

Chemical cues are often detected in pulses because currents, turbulence, and other types of disturbed flow create patches of cue (Finelli and Pentcheff, 1999; Weissburg and Zimmer-Faust, 1993; Zimmer-Faust *et al.*, 1995), which may create 'sensory refuges' (Weissburg and Zimmer-Faust, 1993). In these refuges, predators may be less- or unable to detect prey (Ferner and Weissburg, 2005) (while prey may still be able to detect predators due to back eddies carrying odour cues 'upstream' (Dahl *et al.*, 1998)). Prey animals occupying a sensory refuge would benefit from the reduced predation success, thus potentially leading to aggregation of prey in refuge areas. If animals aggregate in sensory refuges, the sensory refuge may counteract the increased risk of detection due to larger group size. We repeat our experiment in disturbed flow to examine the additional hypothesis that disturbed flow reduces the risk to prey relative to undisturbed flow (as it creates sensory refuges (Webster and Weissburg, 2001)). Our aim is to provide an initial exploration of the possible impact of prey aggregation and flow conditions on the detection of prey by a foraging fish.

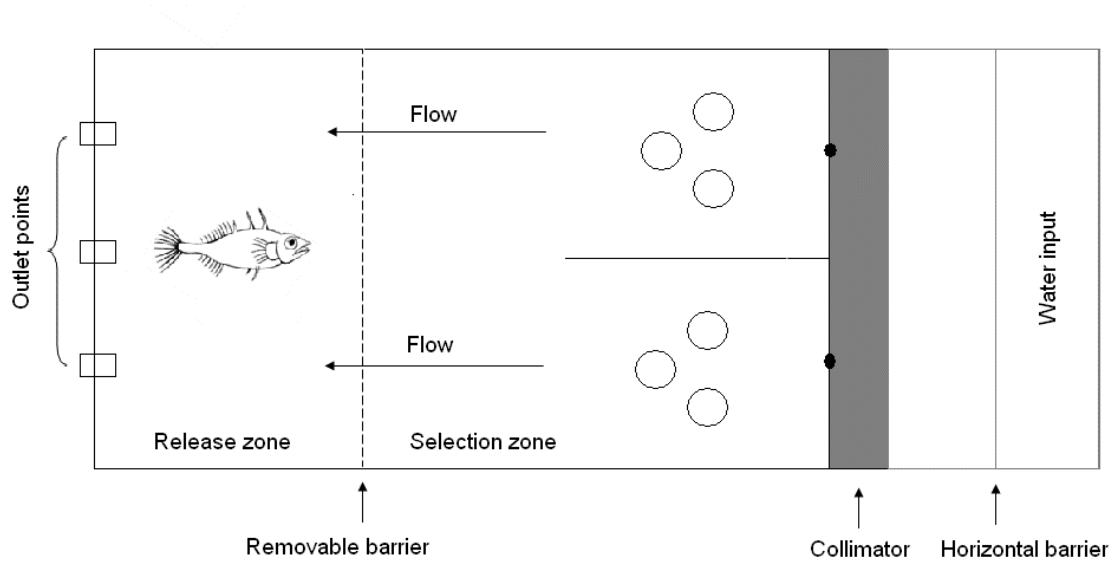
Methods

83 *Experimental species, transportation and housing*

84 Two hundred three-spine sticklebacks *Gasterosteus aculeatus* (4-5cm full body length)
85 were caught in a pond in Saltfleet, Lincolnshire in November, 2011 (53°25'59.55"N,
86 0°10'49.41"E) and transported in fish bags (3-5 fish per litre) to aquarium facilities in Leeds (3
87 hour journey). Sticklebacks can successfully detect and locate prey using non-visual cues in still
88 water (Johannesen *et al.*, 2012), but occupy a range of flowing water environments and may be
89 able to track odour plumes to their source. Fish were housed in grey fibreglass tanks
90 (0.5x0.5x1.0m) with gravel substrate, plastic plants, plant pots and mechanical filters. Light
91 regime was 10/14 hours light/dark, temperature was 14 ± 2°C and fish were fed daily on
92 defrosted frozen bloodworm. Fish were kept for six months to one year for experimentation prior
93 to release where caught in agreement with the Home Office and Defra.

94 *Procedure*

95 Trials were carried out in a flow-through rectangular tank (40 cm by 53 cm, water depth
96 9 cm, flow velocity 3cm s^{-1}) based on a Y maze design (Ward *et al.*, 2011) (Fig 1). The stem of
97 the maze was 33 cm in length including a 20 cm 'release zone' with a removable barrier. Each
98 'arm' was 20 cm long. Conditioned water was pumped from a header tank into the maze, entered
99 the maze over a horizontal barrier in both arms of the Y, and passed through a collimator to
100 approximate laminar flow. Flow characteristics were not measured, but pilot trials using dye
101 indicated that the odour cue would move through the water evenly. Water left the flume through
102 3 mesh-covered exit holes evenly spaced across the base of the stem of the Y, and was not re-
103 circulated. Trials were observed from behind a screen via a webcam to reduce disturbance to the
104 fish.



105

106 **Figure 1**. Layout of the Y-maze (Total dimensions: length 93 cm and width 40 cm). Water flowed over
107 the horizontal barrier (mid-way in the 30 cm long header chamber) before entering the Y-maze through a
108 collimator (10 cm long) to ensure even laminar flow on both sides. The water flowed along the arms of
109 the Y (20 cm long) before entering the stem (33 cm long), which was partitioned with a removable barrier
110 for the release zone (20 cm long). Water flowed through the Y maze at approximately 3 cm s-1 before
111 exiting through the outlet holes (3 cm in diameter). Cue input points are marked by a black dot. Large
112 open circles represent the cylinders (5.5 cm in diameter) added to the tank in the turbulence treatments.

113

114 Olfactory cues were created using filtered macerated bloodworm (cue concentrations
115 low: 5 g l^{-1} medium: 10 g l^{-1} and high: 20 g l^{-1}). We use prey cue concentration as a proxy for
116 size or number of prey, as the interacting odour plumes from multiple prey individuals will
117 increase cue concentration (Hawkins *et al.*, 2007; Villermaux and Duplat, 2003). Cues were
118 delivered to the maze using two peristaltic pumps at a rate of 10 ml min^{-1} (source diameter 4mm,
119 velocity 1.3cm s^{-1}). In each trial, the olfactory cue entered at one arm of the maze, and a

conditioned water control (containing red food dye to copy the tint of the bloodworm cue water) entered at the other at the same rate. Cue side was allocated at random in order to control for side preference. After the trial, the maze was emptied and refilled with conditioned water to remove olfactory cues from the previous trial.

Sticklebacks were placed individually into the release zone and allowed to acclimatise until they resumed normal behaviour (start – stop swimming at moderate speed, five minutes minimum). Following acclimatisation, the water inlet pump was switched on and ran for two minutes (to stabilise flow) before cue pumps were turned on. The behaviour of the test fish was monitored until it had visited both sides of the stem of the Y (two minutes minimum) and the barrier was raised using a pulley system. The fish was allowed five minutes to reach the top of one arm of the Y, where its choice (cue or control) was recorded. The time taken for the fish to acclimatise (begin swimming) and the time taken to reach the top of the chosen arm were also recorded. Fish were excluded from the experiment if they did not resume normal behaviour in the release zone (N=23), did not visit both sides of the stem of the Y within 5 minutes (N = 8 fish) or did not make a choice (N = 6). Final sample sizes were: low: N = 16, medium: N = 16, high: N = 16).

We subsequently investigated the effect of disturbed flow on stickleback choice in the maze. Three cylinders were placed in each arm of the Y maze to create downstream disruption to the flow (see Fig 1). Visualisation of the flow using food dye indicated that the cylinders caused the odour plumes to split and disperse, and that the plumes appeared qualitatively different to those in the experiment with no disturbance to the flow. Methods were the same as in the previous experiment, but investigated only two cue concentrations: medium and high. The low concentration was not used as the first experiment indicated that fish did not prefer this

143 concentration, see results. Eight fish were excluded from this experiment, giving final sample sizes
144 of N = 17 for medium cue concentration and N = 17 for high cue concentration. Each fish was
145 used only once in the experiments, and different fish were used in the two flow conditions to
146 avoid any learning effects.

147 *Analysis*

148 Data were analysed using R v 2.13.0 (R Core Team, 2013). Cox proportional hazards
149 survival models were used to analyse fish time to acclimatise and time to choose (survival
150 package in R; (Therneau and Lumley, 2011)). Survival models are highly flexible and useful for
151 time-to type data, especially when data do not follow a Gaussian distribution and contain
152 censored times (Therneau and Grambsch, 2000). Choice of side was analysed using binomial
153 exact tests (proportion of fish choosing the cue side over the control side against a random
154 expectation of 0.5).

155 *Ethical statement*

156 As experiments with fish fall outside of the remit of the University of Leeds Ethical
157 Board and no licensed procedures were used, this study was not subject to ethical review.

158 However, laboratory experiments were carried out in accordance with University of
159 Leeds guidelines and in agreement with Home Office licensed technical staff at the animal
160 facility. Great care was taken to ensure optimal welfare for all fish involved in this study.

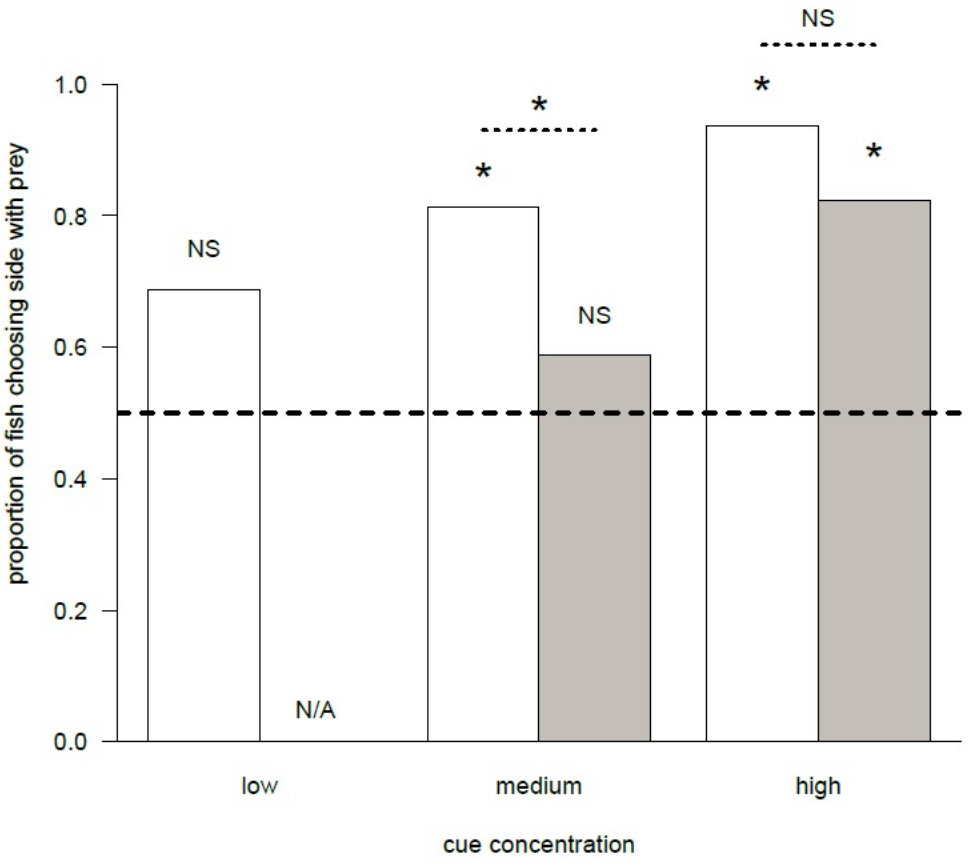
161

162 **Results**

163 Fish tested in the disturbed flow condition took less time to acclimatise than those in the
164 laminar flow condition (coxph: Chi-squared = 25.81, df = 1, $p < 0.001$), but there was no effect
165 of cue concentration or flow type on time to choose once acclimatised (coxph: Chi-squared =
166 6.22, df = 5, $p = 0.29$).

167 In the 'undisturbed flow' condition, fish selected the cue arm over the control arm at
168 medium (N = 13/16, P(success) = 0.8125, $p = 0.021$) and high (N = 15/16, P (success) = 0.938, p
169 < 0.001) cue concentrations, but not at the low cue concentration (N = 11/16, P(success) = 0.688,
170 $p = 0.21$). When flow disturbance was added, fish preferentially selected the cue arm at high (N
171 = 14/17, P(success) = 0.824, $p = 0.013$) but not medium (N = 10/17, P(success) = 0.588, p =
172 0.629) cue concentrations (Fig 2).

173



174

175 **Figure 2.** Proportion of fish choosing the prey side in a y-maze. Stars above bars signify significant
176 differences (binomial exact tests) from random choice of side while stars above dashed lines signify
177 differences between treatments. White bars are laminar flow treatments and grey bars are disturbed flow
178 treatments. The horizontal dashed line indicates no preference.

179

180 At medium cue concentration, proportion of predators choosing the prey cue arm was
181 significantly reduced in disturbed flow (comparison with P(success) = 0.8125; N = 10/17, p =
182 0.027). There was no difference at high cue concentrations (comparison with P(success) = 0.938;
183 N = 14/17, p = 0.086; Fig 2).

184

185 **Discussion**

186 Our results suggest that in a Y-maze with olfactory cue presented in one arm only, fish
187 predators can successfully choose the arm containing the cue more often than expected by
188 chance when the concentration of the cue is high. At low cue concentration, fish did not choose
189 the cue arm more often than the non-cue arm. Interpreted in the context of our question of how
190 increasing group size affects detection, this suggests that grouping in prey may increase risk
191 from olfactory predators. Adding objects to the maze to disturb the flow decreased the number of
192 successful choices, particularly at the medium cue concentration, suggesting that 'sensory
193 refuges' created by disturbed flow (Weissburg and Zimmer-Faust, 1993) could allow larger
194 groups to form relative to undisturbed flow, without an increased risk of detection from olfactory
195 predators..

196 We used concentration as a proxy for group size, following previous work (Schneider *et*
197 *al.*, 2014). When individuals group together, they produce a greater number of odour filaments
198 (Monismith *et al.*, 1990; Wilson and Weissburg, 2012) that cover a wider area (Webster and
199 Weissburg, 2001). Aggregation, particularly where animals group tightly together, as they might
200 in a refuge, may also act to increase the time-averaged concentration (Villermaux and Duplat,
201 2003) used by some predators to track plumes (Ferner and Weissburg, 2005) as well as filament
202 concentration from interacting odour sources (Villermaux and Duplat, 2003). However,
203 concentration may reflect a number of other features of the prey landscape in addition to
204 aggregation levels, such as size or distance of prey (but perhaps not very long distances
205 (Bytheway *et al.*, 2013)), and therefore the cue concentrations used in this experiment might

206 indicate to the fish whether the cue arm is worth the effort of investigating (i.e. that it indicated
207 closer prey rather than a larger group pursuing), but there is no indication of this in the latency to
208 choose a cue arm in our data.

209 While turbulence or other disturbance to flow can cause odour plumes to break up
210 (Webster and Weissburg, 2001) it may also act to mix the plumes and dilute the cue to
211 background levels with only intermittent spikes (Webster and Weissburg, 2009) that may not be
212 worth exploring. Either mechanism would act to make tracking the cue to the source more
213 difficult for the predator (Robinson *et al.*, 2011) (although this may depend on the predator's
214 sensing strategy and sensitivity (Ferner and Weissburg, 2005)). Our observations with food dye
215 suggest that the plume in disturbed flow split primarily into two meandering plumes. Assuming a
216 fish was only exposed to one arm of the split plume, the decreased amount of cue may suggest
217 there are fewer or smaller prey, or that prey were at greater distance than was the case, or the
218 concentration may drop under a detection threshold. A meandering plume will, in addition to the
219 perceived lower reward, be more difficult to track, making the effort greater. However, turbulent
220 or disturbed flow in the wild could also have this effect, meaning that regardless of the
221 mechanism, a group producing more cue, and many individual and mixing odour plumes
222 (Wilson and Weissburg, 2012) would be less likely to be detected, or detection less likely to be
223 followed up, in disturbed flow.

224 Our study did not investigate the fluid mechanics and transport of olfactory cue in the
225 different flow regimes, focusing instead on the response of the predator. Thus, we cannot
226 speculate on the mechanical cause of the different behaviours shown by our fish predators.
227 However, the end result for the prey remains the same. If an olfactory prey cue is highly
228 concentrated, indicating either great reward (many or large prey) or easy reward (close

proximity) a predator is more likely to pursue that prey. Conversely, if the olfactory prey cue plume is somehow broken down, indicating small reward (few or small prey) or difficult reward (long distance, a plume that is difficult to track) a fish predator is less likely to pursue that cue. In the context of our question regarding aggregation, this suggests prey may able to aggregate into larger groups if they can take advantage of a sensory refuge and thus either fool the predator into thinking they are not worth the effort (small reward/high effort) or successfully decrease the cue to avoid detection. Individuals in such aggregations would in turn benefit from greater survival chance if found, due to predator satiation.

The study of anti-predator aggregation has primarily focused on predators that use vision to detect their prey (Ioannou and Krause, 2008), while the effect of olfactory predators on the evolution of aggregation is less well understood. Our work suggests that group size may interact with environmental parameters, and that the evolution of grouping in response to olfactory predators may be dependent on the flow environment, but further work is needed to fully investigate the relationship between grouping prey, detection by predators, and environmental conditions. Prey are known to aggregate in streams (Rasmussen and Downing, 1988), but aggregation decisions may depend on factors other than risk from olfactory predators, including foraging opportunities, flow speed and risk from predators relying on other sensory modalities (Ioannou and Krause, 2008; Krause and Ruxton, 2002). Experimental manipulation and characterisation of flow regimes and the response of predators and prey may help disentangle the interacting effects of group size, flow regime and aggregation in response to other resources.

Data Accessibility Section

The data presented in this paper can be found on Figshare (http://dx.doi.org/10.6084/m9.figshare.985515).

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