Disturbed flow in an aquatic environment may create a sensory refuge for aggregated prey

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Predators use olfactory cues moved within water and air to locate prey. Because prey aggregations may produce more cue and be easier to detect, predation could limit aggregation size. However, disturbance in the flow may diminish 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 in disturbed (more turbulent or mixed) and non-disturbed (less mixed) flowing water. We find that increasing odour cue concentration increases predation risk and disturbing the flow reduces predation risk. At high cue concentration fish were able to locate the cue source in both disturbed and non-disturbed flow, but at medium concentrations, predators only located the cue source more often than expected by chance in non-disturbed flow. This suggests that objects disturbing flow provide a sensory refuge allowing prey to form larger groups, but that group sizes may be limited by level of disturbance to the flow.

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14   **Abstract**

15   Predators use olfactory cues moved within water and air to locate prey. Because prey

16   aggregations may produce more cue and be easier to detect, predation could limit aggregation

17   size. However, disturbance in the flow may diminish the reliability of odour as a prey cue,

18   impeding predator foraging success and efficiency. We explore how different cue concentrations

19   (as a proxy for prey group size) affect risk to prey by fish predators in disturbed (more turbulent

20   or mixed) and non-disturbed (less mixed) flowing water. We find that increasing odour cue

21   concentration increases predation risk and disturbing the flow reduces predation risk. At high cue

22   concentration fish were able to locate the cue source in both disturbed and non-disturbed flow,

23   but at medium concentrations, predators only located the cue source more often than expected by

24   chance in non-disturbed flow. This suggests that objects disturbing flow provide a sensory refuge

25   allowing prey to form larger groups, but that group sizes may be limited by level of disturbance

26   to the flow.

27

28   **Introduction**

29

30   To avoid predation, animals use strategies from visual crypsis (Jackson *et al.*, 2005) to

31   increased vigilance in groups (Krause and Ruxton, 2002). In cases where visual interactions

32   between predators and prey are limited, cues such as sound (Obrist *et al.*, 1993) or detection of

33   electric fields (Kajiura and Holland, 2002) are used instead. Olfaction is a key sense used in prey

34   detection and location. Olfactory predators such as crustaceans (Gomez and Atema, 1996;

35   Weissburg and Zimmer-Faust, 1993), fish (Nevitt, 1991), and molluscs (Ferner and Weissburg,

36 2005) can successfully track odour plumes from prey to their source. Animals use many sensing

37 strategies, including time differences in bilateral odour detection (Gardiner and Atema, 2010),

38 time-averaging of odour concentrations (Wilson and Weissburg, 2012), and making

39 simultaneous comparisons of odour concentration (Page *et al.*, 2011; Vergassola *et al.*, 2007). To

40 avoid such detection, prey may try to limit the amount of olfactory cue that they release or

41 otherwise make it difficult for predators to detect them (Ruxton, 2009).

42   To reduce the risk from predators that hunt using vision, prey can group together to

43 increase the time taken for a hunting predator to locate them. This is known as the encounter-

44 dilution effect (Wrona and Dixon, 1991) and favours grouping as an anti-predator strategy in

45 response to visual predators (Jackson *et al.*, 2005; Riipi *et al.*, 2001). However, if increasing

46 group size makes prey increasingly easier for olfactory predators to find (Kunin, 1999), grouping

47 may be counter-productive.

48   Larger or more numerous animals release more odour cue, eliciting a stronger reaction in

49 the receiver (Hawkins *et al.*, 2007; Kusch *et al.*, 2004). When animals aggregate, the odour cues

50 released interact, increasing the size and concentration of the odour plume (Villermaux and

51 Duplat, 2003), which allows receivers to more readily track the plume to its source (Wilson and

52 Weissburg, 2012). Grouping benefits prey avoiding olfactory predators in still water (Johannesen

53 *et al.*, 2014). However, water movement provides a directional cue to the prey, so olfactory cues

54 are more easily taken advantage of in flowing rather than still water (Løkkeborg, 1998).

55   In a review of olfactory detection distance in insects, Andersson *et al.* (2013) indicate that

56 the increase in detection with increasing size of the source is likely to be asymptotic, although

57 theoretical work indicates accelerating detectability may also be possible (Treisman, 1975). If the

58   risk of predation increases too much with group size, aggregation would be counterproductive in

59   species that cannot otherwise defend themselves. Here, we explore this question from the

60   perspective of three-spine sticklebacks (*Gasterosteus aculeatus*) locating odour sources of

61   differing concentration (as a proxy for prey group size (Hill and Weissburg, 2014; Schneider *et*

62   *al.*, 2014) - but see discussion) in flowing water, to test the hypothesis that increasing prey

63   (bloodworm) cue concentration increases the risk to prey in flowing water.

64   Chemical cues are often detected in pulses because currents, turbulence, and other types

65   of disturbed flow create patches of cue (Finelli and Pentcheff, 1999; Weissburg and Zimmer-

66   Faust, 1993; Zimmer-Faust *et al.*, 1995), which may create 'sensory refuges' (Weissburg and

67   Zimmer-Faust, 1993). When prey are in these refuges, predators may be less- or unable to detect

68   them (Ferner and Weissburg, 2005), while prey may still be able to detect predators as back

69   eddies carry odour cues 'upstream' (Dahl *et al.*, 1998). Prey animals occupying a sensory refuge

70   would benefit from the reduced predation success, leading to aggregation of prey in refuge areas.

71   If animals aggregate in sensory refuges, the sensory refuge may counteract the increased risk of

72   detection due to larger group size. We repeat our experiment in disturbed flow to examine the

73   additional hypothesis that disturbed flow reduces the risk to prey relative to undisturbed flow, as

74   it creates sensory refuges (Weissburg and Zimmer-Faust, 1993). Our aim is to provide an initial

75   exploration of the possible impact of prey aggregation and flow conditions on the detection of

76   prey by a foraging fish.

77   **Methods**

78   *Experimental species, transportation and housing*

79   Two hundred three-spine sticklebacks *Gasterosteus aculeatus* (4-5cm total body length)

80   were caught in a pond in Saltfleet, Lincolnshire in November, 2011 (53°25'59.55"N,

81   0°10'49.41"E) and transported in fish bags (3-5 fish per litre) to aquarium facilities in Leeds (3

82   hour journey). Sticklebacks can detect and locate prey using non-visual cues in still water

83   (Johannesen *et al.*, 2012), but also occupy flowing water environments and may be able to track

84   odour plumes to their source. Fish were housed in grey fibreglass tanks (0.5x0.5x1.0m) with

85   gravel substrate, plastic plants, plant pots and mechanical filters. Light regime was 10:14 hours

86   light:dark, temperature was $14 \pm 2°C$ and fish were fed daily on defrosted frozen bloodworm.

87   Fish were kept for six months to one year for experimentation prior to release where caught in

88   agreement with the Home Office and Defra.

89   *Procedure*

90   Trials were carried out in a flow-through rectangular tank (40 cm by 53 cm, water depth

91   9 cm, flow velocity 3cm s^{-1}) based on a Y maze design (Ward *et al.*, 2011) (Fig 1). The stem of

92   the maze was 33 cm in length including a 20 cm 'release zone' with a removable barrier. Each

93   'arm' was 20 cm long. Conditioned water was pumped from a header tank into the maze, entered

94   the maze over a horizontal barrier in both arms of the Y, and passed through a collimator to

95   create an even water flow ("undisturbed flow"). Flow characteristics were not measured, but

96   pilot trials using dye indicated that the odour cue would move through the water evenly. Water

97   left the flume through 3 mesh-covered exit holes evenly spaced across the base of the stem of the

98   Y, and was not re-circulated. Trials were observed from behind a screen via a webcam to reduce

99   disturbance to the fish.

100

101   Olfactory cues were created using filtered macerated bloodworm (cue concentrations;

102   low: 5 g l^{-1} medium: 10 g l^{-1} and high: 20 g l^{-1}). Although spatial distribution of aggregated prey

103   affects odour plume composition, we use prey cue concentration as a proxy for size or number of

104   prey. This is because the interacting odour plumes from multiple prey individuals will increase

105   cue concentration (Hawkins *et al.*, 2007; Villermaux and Duplat, 2003) and while adding the

106   spatial factor to this experiment would be more realistic, it would also complicate the

107   experiment. Cues were delivered to the maze using two peristaltic pumps at a rate of 10 ml min^{-1}

108   (source diameter 4mm, velocity 1.3cm s^{-1}). In each trial, the olfactory cue entered at one arm of

109   the maze, and a conditioned water control (containing red food dye to copy the tint of the

110   bloodworm cue water) entered at the other at the same rate. Cue side was allocated at random to

111   control for side preference. After the trial, the maze was emptied and refilled with conditioned

112   water to remove olfactory cues from the previous trial.

113   Sticklebacks were placed individually into the release zone and allowed to acclimatise

114   until they resumed normal behaviour (start – stop swimming at moderate speed, five minutes

115   minimum). Following acclimatisation, the water inlet pump was switched on and ran for two

116   minutes (to stabilise flow) before cue pumps were turned on. The behaviour of the test fish was

117   monitored until it had visited both sides of the stem of the Y (two minutes minimum) and the

118   barrier was raised using a pulley system. The fish was allowed five minutes to reach the top of

119   one arm of the Y, where its choice (cue or control) was recorded. The time taken for the fish to

120   acclimatise (begin swimming) and the time taken to reach the top of the chosen arm were also

121   recorded. Fish were excluded from the experiment if they did not resume normal behaviour in

122   the release zone (N=23), did not visit both sides of the stem of the Y within 5 minutes (N = 8

123 fish) or did not make a choice (N = 6). Final sample sizes in undisturbed flow were: low: N = 16,

124 medium: N = 16, high: N = 16).

125   We subsequently investigated the effect of disturbed flow on stickleback choice in the

126 maze. Three cylinders were placed in each arm of the Y maze to create downstream disruption to

127 the flow (see Fig 1). Visualisation of the flow using food dye indicated that the cylinders caused

128 the odour plumes to split and disperse, and that the plumes appeared qualitatively different to

129 those in the experiment with no disturbance to the flow. Methods were the same as in the

130 previous experiment, but investigated only two cue concentrations: medium and high. The low

131 concentration was not used as the first experiment indicated that fish did not show a preference at

132 this concentration (see results). Eight fish were excluded from this experiment, giving final

133 sample sizes of N = 17 for medium cue concentration and N = 17 for high cue concentration in

134 disturbed flow. Each fish was used only once in the experiments, and different fish were used in

135 the two flow conditions to avoid any learning effects. The total sample size for both experiments

136 was N = 82.

137 *Analysis*

138   Data were analysed using R v 2.13.0 (R Core Team, 2013). Cox proportional hazards

139 survival models were used to analyse fish time to acclimatise and time to choose (survival

140 package in R; (Therneau and Lumley, 2011)). Survival models are highly flexible and useful for

141 time-to type data, especially when data do not follow a Gaussian distribution and contain

142 censored times (Therneau and Grambsch, 2000). Preference for prey cue was tested using

143 binomial exact tests against an expectation of random (0.5). A correction for false discovery rate

144 was performed (Benjamini and Hochberg, 1995) on the tests to control for multiple comparisons

145   and the adjusted p values are given in the results section. A binomial GLM with choice as

146   dependent variable (cue, no cue) and cue concentration and flow type as independent variables

147   was used to test the effect of treatments on choice.

148

149   *Ethical statement*

150   As experiments with fish fall outside of the remit of the University of Leeds Ethical

151   Board and no licensed procedures were used, this study was not subject to ethical review.

152   However, laboratory experiments were carried out in accordance with University of

153   Leeds guidelines and in agreement with Home Office licensed technical staff at the animal

154   facility. Great care was taken to ensure optimal welfare for all fish involved in this study.

155

156   **Results**

157   Fish tested in the disturbed flow condition took less time to acclimatise than those in the

158   non-disturbed flow condition (coxph: Chi-squared = 25.81, df = 1, p < 0.001), but there was no

159   effect of cue concentration or flow type on time to choose once acclimatised (coxph: Chi-squared

160   = 6.22, df = 5, p = 0.29).

161   In the 'undisturbed flow' condition, fish selected the cue arm over the control arm at

162   medium (N = 13/16, P(success) = 0.8125, p = 0.035) and high (N = 15/16, P(success) = 0.938, p

163   = 0.003) cue concentrations, but not at the low cue concentration (N = 11/16, P(success) = 0.688,

164   p = 0.26). When flow disturbance was added, fish preferentially selected the cue arm at high (N

165   = 14/17, P(success) = 0.824, p = 0.033) but not medium (N = 10/17, P(success) = 0.588, p =

166   0.629) cue concentrations (Fig 2).

167   In a test of the effects of cue concentration and flow regime, cue concentration

168   significantly affected choice (Binomial GLM; z = 2.235, N = 82, p = 0.025) while the effect of

169   water regime fell short of significance (Binomial GLM; z = -1.814, N = 82, p = 0.070).

170

171   **Discussion**

172   Our results suggest that in a Y-maze with olfactory cue presented in one arm only, fish

173   predators can successfully choose the arm containing the cue more often than expected by

174   chance if the concentration of the cue is high enough. At the low cue concentration, fish did not

175   choose the cue arm more often than the non-cue arm. Interpreted in the context of our question of

176   how increasing group size affects detection, this suggests that grouping in prey (increased cue

177   concentration) may increase risk from olfactory predators. Adding objects to the maze to disturb

178   the flow (i.e. create more turbulent mixing) decreased the number of successful choices,

179   particularly at the medium cue concentration, suggesting that 'sensory refuges' created by

180   disturbed flow (Weissburg and Zimmer-Faust, 1993) allow larger groups to form by countering

181   the increased risk of detection. However, at higher cue concentrations, the benefit gained from

182   flow disturbance may decrease, and larger groups would be more easily detected. While we did

183   not compare multiple disturbance levels, we suggest that the level of disturbance may also

184   influence the detection of prey cues of different concentrations.

185   We used concentration as a proxy for group size, following previous work (Schneider *et*

186   *al.*, 2014), although the effect of group size on odour plumes is more complex. When individuals

187   group together, they produce a greater number of odour filaments (Monismith *et al.*, 1990;

188   Wilson and Weissburg, 2012) that cover a wider area (Webster and Weissburg, 2001). When

189   prey are spaced sufficiently far apart, individual odour filaments do not interact and would not

190   result in an increase in cue concentration. In that case, the risk of detection by predators who are

191   unable to detect any individual filament, but would detect a more concentrated one, remains low

192   regardless of group size. However, in cases of tightly aggregated prey, filaments are likely to

193   interact and increase the time-averaged concentration (Villermaux and Duplat, 2003) used by

194   some predators to track plumes (Ferner and Weissburg, 2005) as well as filament concentration

195   (Villermaux and Duplat, 2003). Therefore, tightly packed prey increase risk of detection with

196   group size, particularly by predators who would not have detected a single individual's odour

197   plume.

198   Concentration may reflect a number of other features of the prey landscape in addition to

199   group size in tight aggregations. As cues become more diluted over distance and time, cue

200   concentration may signal distance to prey (but see Bytheway *et al.*, 2013), or if larger individuals

201   release more cue, the concentration could signal size of prey. Thus, predators could move

202   towards higher concentrations because they represent better value predation opportunities, rather

203   than because they are easier to detect. However, while the results in this experiment could reflect

204   a perceived value of cue in the fish rather than simple detection, there is no indication of this in

205   the latency to choose a cue arm in our data.

206   While turbulence or other disturbance to flow can cause odour plumes to break up

207   (Webster and Weissburg, 2001) it can also act to mix the plumes and dilute the cue to

208   background levels with only intermittent spikes (Webster and Weissburg, 2009) that may not be

209   worth exploring. Either mechanism would act to make tracking the cue to the source more

210   difficult for the predator (Robinson *et al.*, 2011), although this may depend on the predator's

211   sensing strategy and sensitivity (Ferner and Weissburg, 2005). Our observations with food dye

212   suggest that the plume in disturbed flow split primarily into two meandering plumes. Assuming a

213   fish was only exposed to one arm of the split plume, the decreased amount of cue could mean

214   fewer or smaller prey, greater distance to prey, or the concentration might be below a detection

215   threshold. A meandering plume will, in addition to the perceived lower reward, be more difficult

216   to track for fish and other filament samplers, making the effort greater. While a time-averaging

217   predator may be able to compensate for meandering plumes (Page *et al.*, 2011), a diluted and

218   split plume signals lower reward, so inhabiting turbulent water can also benefit tightly packed

219   prey hiding from a time-averager. However, as sticklebacks most likely do not use time-

220   averaging sensing strategies (Nevitt, 1991; Webster and Weissburg, 2001), this has not been

221   explicitly tested here.

222   Our study did not investigate the fluid mechanics and transport of olfactory cue in the

223   different flow regimes, focusing instead on the response of the predator. Thus, we cannot

224   speculate on the sensory mechanism, motivation, or features of water flow and cue transport that

225   cause the different behaviours shown by our fish predators. However, the end result for the prey

226   remains the same. If an olfactory prey cue is highly concentrated, indicating either great reward

227   (many or large prey) or easy reward (close proximity) a predator is more likely to pursue that

228   cue. Conversely, if the olfactory prey cue plume is somehow broken down, indicating small

229   reward (few or small prey) or difficult reward (long distance, a plume that is difficult to track) a

230   fish predator is less likely to pursue that cue. In the context of our question regarding

231   aggregation, this suggests prey are able to aggregate into larger groups by taking advantage of a

232   sensory refuge and either fooling the predator into thinking they are not worth the effort (small

233   reward/high effort) or decreasing the cue to avoid detection. Individuals in such aggregations

234   would in turn benefit from greater survival chance if found due to other benefits of grouping,

235   such as predator satiation.

236   The study of anti-predator aggregation has primarily focused on predators that use vision

237   to detect their prey (Ioannou and Krause, 2008), while the effect of olfactory predators on the

238   evolution of aggregation is less well understood. Our work suggests that group size may interact

239   with environmental parameters, and that the evolution of grouping in response to olfactory

240   predators may be dependent on the flow environment. However, further work is needed to fully

241   investigate the relationship between grouping prey, detection by predators, and environmental

242   conditions. Prey are known to aggregate in streams (Rasmussen and Downing, 1988), but

243   aggregation decisions may depend on factors other than risk from olfactory predators, including

244   foraging opportunities, flow speed and risk from predators relying on other sensory modalities

245   (Ioannou and Krause, 2008; Krause and Ruxton, 2002). Experimental manipulation and

246   characterisation of flow regimes and the response of predators and prey may help disentangle the

247   interacting effects of group size, flow regime and aggregation in response to other resources.

248

249   **Data Accessibility Section**

250   The data presented in this paper can be found on Figshare

251   (http://dx.doi.org/10.6084/m9.figshare.985515).

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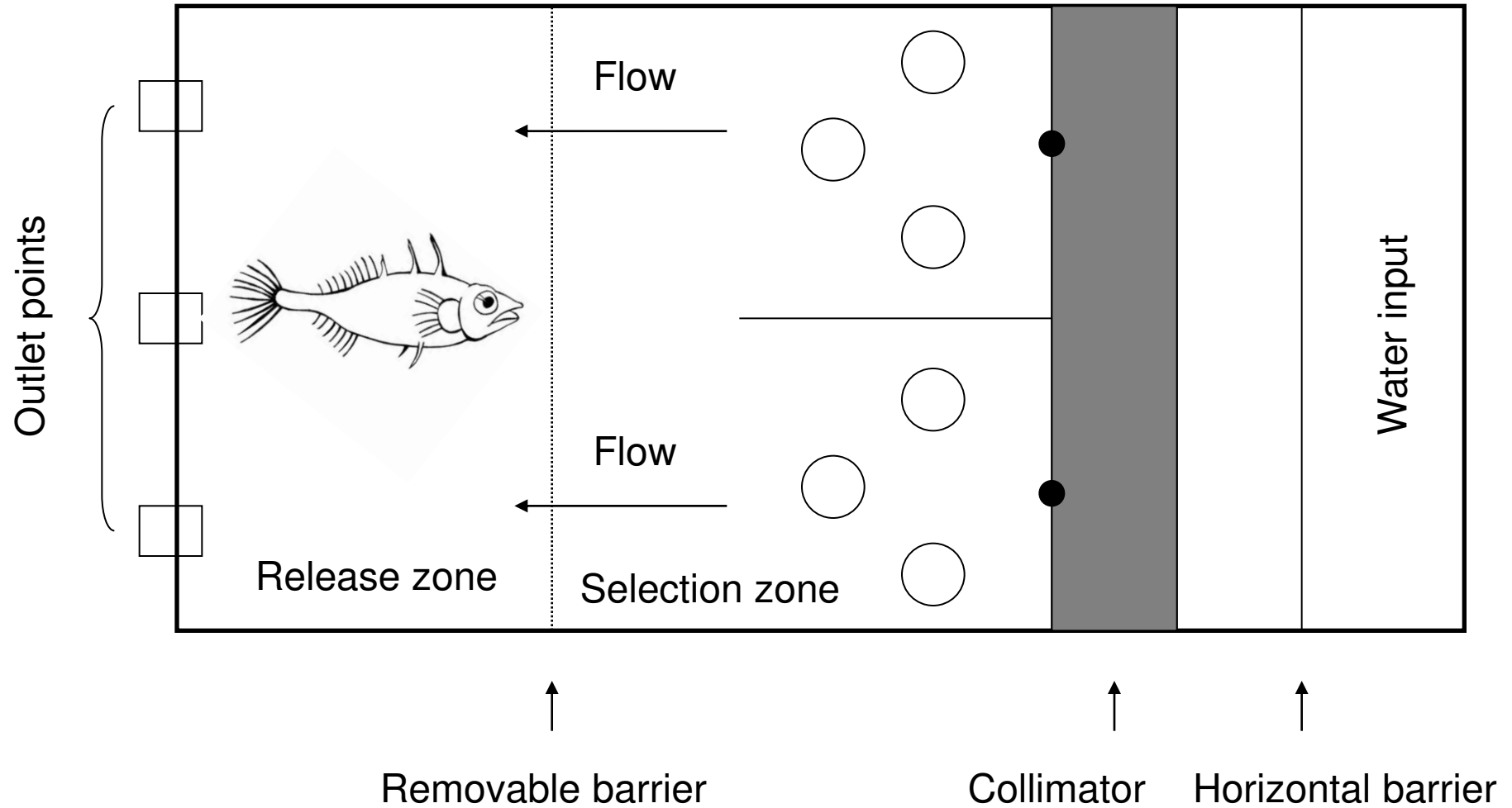
360

Layout of the Y-maze (Total dimensions: length 93 cm and width 40 cm).

Water flowed over the horizontal barrier (mid-way in the 30 cm long header chamber) before entering the Y-maze through a collimator (10 cm long) to ensure even flow on both sides. The water flowed along the arms of the Y (20 cm long) before entering the stem (33 cm long), which was partitioned with a removable barrier for the release zone (20 cm long). Water flowed through the Y maze at approximately 3 cm s-1 before exiting through the outlet holes (3 cm in diameter). Cue input points are marked by a black dot. Large open circles represent the cylinders (5.5 cm in diameter) added to the tank in the 'disturbed flow' treatments.

Proportion of fish choosing the prey side in a y-maze.

Stars above bars signify significant differences (binomial exact tests) from random choice of side. Dark bars are non-disturbed flow treatments and light bars are disturbed flow treatments. The horizontal dashed line indicates no preference.