

A novel method for investigating the collective behaviour of fish: introducing ‘Robofish’

Jolyon J. Faria · John R. G. Dyer ·
Romain O. Clément · Iain D. Couzin · Natalie Holt ·
Ashley J. W. Ward · Dean Waters · Jens Krause

Received: 18 January 2010 / Revised: 7 May 2010 / Accepted: 17 May 2010 / Published online: 19 June 2010
© Springer-Verlag 2010

Abstract Collective animal behaviour has attracted much attention recently, but cause-and-effect within interaction sequences has often been difficult to establish. To tackle this problem, we constructed a robotic fish (‘Robofish’) with which three-spined sticklebacks (*Gasterosteus aculeatus* L.) interact. Robofish is a computer-controlled replica stickleback that can be programmed to move around a tank. First, we demonstrated the functioning of the method: that the sticklebacks interacted with Robofish. We examined two types of interaction: recruitment and leadership. We found that Robofish could recruit a single fish from a refuge and could initiate a turn in singletons and in groups of ten, i.e. act as a leader. We also showed that the influence of Robofish

diminished after the first 30 min that fish spent in a new environment. Second, using this method, we investigated the effects of metric and topological inter-individual distance on the influence that Robofish had on the orientation of fish in a shoal of ten. We found that inter-individual interactions during this turn were predominantly mediated by topological, rather than metric, distance. Finally, we discussed the potential of this novel method and the importance of our findings for the study of collective animal behaviour.

Keywords Collective animal behaviour · Leadership · Inter-individual distance · Recruitment · Robot · *Gasterosteus aculeatus*

Communicated by T. Bakker

Electronic supplementary material The online version of this article (doi:10.1007/s00265-010-0988-y) contains supplementary material, which is available to authorized users.

J. J. Faria (✉) · J. R. G. Dyer · N. Holt · D. Waters
Institute of Integrative and Comparative Biology,
University of Leeds,
Leeds LS2 9JT, UK
e-mail: fbsjsf@leeds.ac.uk

R. O. Clément · J. Krause
Department of Biology and Ecology of Fishes,
Leibniz-Institute of Freshwater Ecology & Inland Fisheries,
Müggelseedamm 310,
12587 Berlin, Germany

I. D. Couzin
Department of Ecology and Evolutionary Biology,
Princeton University,
Princeton, NJ 08544, USA

A. J. W. Ward
School of Biological Sciences, University of Sydney,
Sydney, NSW 2006, Australia

Introduction

The study of collective animal behaviour in moving groups has attracted much attention recently with studies on flocking birds (Biro et al. 2006; Ballerini et al. 2008a), marching locusts (Buhl et al. 2006), crowding humans (Dyer et al. 2009b; Faria et al. 2009), shoaling fish (Sumpter et al. 2008; Ward et al. 2008), aggregating cockroaches (Halloy et al. 2007) and social insects (Seeley et al. 2006; Franks et al. 2009). These collective phenomena were the result of animals responding to both their environment and to other group members. Therefore, the nature of interactions between group members is fundamental to group level dynamics (Couzin and Krause 2003).

Theoretical work has shown that group dynamics such as robust cohesion and effective navigation can be caused by interactions between individuals, such as collision avoidance and alignment with particular group members (Couzin et al. 2005; Ballerini et al. 2008b). Further, these types of models

have been successful in predicting the dynamics of animal groups such as the degree of polarisation (Buhl et al. 2006). However, it is often difficult from these studies to determine behavioural cause-and-effect between group members. Therefore, experimenters have controlled the behaviour of an individual in the group by methods such as computer animations (Künzler and Bakker 1998) and remote-controlled robots (Webb 2000). For instance, Halloy et al. (2007) developed a cockroach-like robot which interacted with cockroaches and that allowed a detailed investigation of their aggregation behaviour.

Here, we introduce a novel methodological tool for studying collective animal behaviour in fish: a computer-controlled robotic three-spined stickleback *Gasterosteus aculeatus* L., herein referred to as ‘Robofish’. To test if live fish responded to Robofish as they would to a conspecific, we examined two functionally important interactions between Robofish and the fish: recruitment from a refuge and the initiation of a new swimming direction, also known as leadership (Krause et al. 2000; Krause and Ruxton 2002). To test recruitment and leadership, we observed the behaviour of fish in response to Robofish leaving the refuge and shortly after making a 90° turn. To test recruitment, we compared the duration for the fish to leave a refuge and predicted that fish exposed to Robofish would leave the refuge sooner than those not exposed to Robofish. To test leadership, we compared the orientation of fish before and after Robofish made a 90° turn and predicted that Robofish would be able to initiate a turn.

We also tested a potential limiting factor of the influence of Robofish on other fish: the effect of the duration that the fish had spent in the tank. It has been shown in banded killifish, *Fundulus diaphanous*, that shoaling behaviour is highly context dependent with a low shoaling tendency in absence of danger and high shoaling tendency in its presence (Hoare et al. 2004). Hence, it is likely that an increase in stress, such as movement to a new environment, i.e. from a holding tank to the test tank in this investigation, would also increase the tendency of the fish to shoal. Therefore, we predicted a negative relationship between the time that the fish had spent in the tank and their shoaling tendency with each other and with Robofish.

After we had examined the functionality of the method, we used Robofish to investigate how individuals interact. The influence of one animal over another can be affected by a range of factors that include morphology, individual state and behaviour (Krause et al. 1992; Krause and Ruxton 2002; Rands et al. 2003; King et al. 2009). For instance, Reeb (2001) found that larger fish were more effective than smaller fish at leading a shoal out of a shaded area. A further factor that may affect leadership in animal groups is relative spatial position of individuals. For example, in

three-spined sticklebacks and juvenile roach *Rutilus rutilus*, shoal members tended to be led by individuals at the front of the shoal (Bumann and Krause 1993). Furthermore, distance between individuals is likely to affect the nature of their interaction. Most theoretical studies have made the assumption that interactions between group members are affected by metric distance between individuals, for instance that individuals interact with a subset of other group members within a certain metric distance (Barbaro et al. 2009; Couzin et al. 2002; Romey 1996; but there are exceptions, e.g. Huth and Wissel 1992). However, recent empirical work on bird flocks has suggested that individuals interact with a number of nearest neighbours—referred to as topological distance—largely regardless of metric distance (Ballerini et al. 2008b). We tested the relative importance of metric and topological distance between individuals on interactions. Specifically, we tested whether metric or topological distance was the better predictor of fish behaviour in response to a sudden 90° turn by Robofish.

Description of the method

Robofish design and control

Robofish is a remote-controlled replica fish (Fig. 1a), and the body of the replica was designed following Ward et al. (2008). The body of the replica was made from a mould of a dead three-spined stickleback using chromatic alginate, which was filled with stone plaster to form a cast of the fish (total length (TL) 45 mm). The cast was then painted with acrylics to approximately match the counter-shading of the fish and finished with two coats of waterproof varnish. The fin was made from acetate sheet. This method preserved most of the visible morphological detail from the three-spined stickleback. To attach the replica to its magnetic base, one flat side of a transparent capillary tube (length × diameter 15 × 1.8 mm) was attached (using cyanoacrylate that was cured for at least 24 h) on the ventral side, perpendicular to the anteroposterior (AP) axis of the replica, at the mid-point of the AP axis, and the other flat side was attached to the base. The base comprised a cuboid of Perspex (7 × 7 × 5 mm) mounted (also by cyanoacrylate) on two Neodymium magnets (10 × 3.5 × 2.25 mm (*A*); *A*: axis of polarity). The magnets were positioned so that their longest axis was perpendicular to the AP axis of the fish, and the smallest surface area was parallel with the AP axis. To provide extra balance for Robofish, two pieces of polyethylene sheet (7 × 7 × 1 mm) were attached, by one of the sides with the smallest surface area, to the magnets: one to anterior facing side of the magnet that was closest to the anterior of the fish and one on the posterior side of the

magnet that was closest to the posterior of the fish. The base was painted white to match the bottom of the tank.

The movement of the replica mounted on the magnetic base was controlled by an electromagnet beneath the tank. The electromagnet was mounted on a platform that could be moved in two dimensions directly beneath the tank and was separated from the underside of the tank by a thin layer of greased plastic (<1 mm). Movement was generated by a pulley system, attached to two stepper motors: one for movement along the width of the tank and the other along the length. The stepper motors were operated by control boxes connected to communication ports of a PC. Movement paths could be sent to the control boxes using software packages ‘TestPoint™’, and ‘Microsoft Excel XP™’. The magnet attached to the replica was polar, and only the north pole was attracted strongly to the electromagnet. We mounted the replica on the magnetic base so that the anterior of the replica was aligned with the north pole of the electromagnet. Therefore, the fish always moved anterior first, even after a 180° turn.

To examine the functioning of Robofish and for the subsequent investigation, we programmed Robofish to follow a specific route (Fig. 1b; Online Resource 1).

Robofish was moved at a speed of 12 cm s⁻¹, and the duration between when Robofish left and re-entered the refuge was 13 s. We determined the speed from a set of speeds that the stepper motors could perform and how the fish swam in the test tank. We measured the swimming speed of singletons and group members without Robofish, for a duration of 15 s from when they left the refuge. The swimming speed was extrapolated from the distance between their positions (the mid-point of a line from the fish snout to the base of its tail) at 1-s time intervals. Our focus was on their behaviour excluding edge effects so we excluded time intervals in which a fish moved to within 5 cm of the tank edges. We measured the speed of 20 singletons and 20 group members (one individual was randomly selected from each group). When fish left the refuge, they would often swim to within 5 cm of the side within 15 s (singletons, 17 out of 20; shoal members, 14 out of 20). Therefore, to reduce the effect on fish behaviour caused by the edge of the tank, we selected a speed that was higher than the mean swimming speed of the fish (singletons: mean speed=7.5 cm s⁻¹; mean number of time intervals measured=9; shoal members: mean speed=8.6 cm s⁻¹; mean number of time intervals measured=13), but within an estimated 95% of their swimming speeds (2SD; singletons 8 cm s⁻¹, shoal members 8.1 cm s⁻¹), so that Robofish moved at a similar speed to the fish but made its first turn before any fish reached edge of the tank. Also, fish could easily catch Robofish (e.g. within 3 s) as the Robofish speed was within the limits of the mean maximum speed for three-spined sticklebacks of two morphotypes, which have been

estimated to be 60.72 cm s⁻¹ (mean speed=[mean body length]×[mean body lengths per second]) and 81.6 cm s⁻¹ (Tudorache et al. 2007).

Examination of the method

Experiment setup

We used 350 three-spined sticklebacks (TL 39–49 mm) that were collected from the Great Eau river estuary, UK (53°25′ 07″ N; 08°11′25″ E). Experiments took place in a test tank (Fig. 1b; width×length×water depth 86×18×5 cm; water temperature 14±0.4°C). In the tank, there was a refuge (width×length×height 19×18×10 cm) with one Perspex door that could be raised remotely by fishing line attached to the wall.

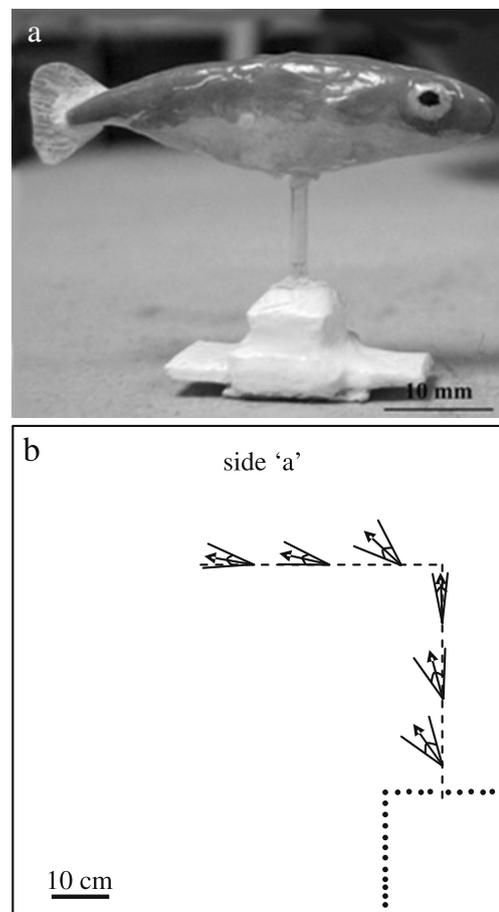


Fig. 1 **a** Photo of the Robofish replica. **b** Plan view of the test tank and response of single fish to Robofish which left the refuge (☉) and followed a pre-programmed route (⚡) and then returned to the refuge by the same route. We measured the orientation, relative to that of Robofish, of the single fish (θ ; $\sqrt{\theta}$; mean \pm 2SE), at six time intervals, 1/1.5/2 s before and 1/1.5/2 s after, Robofish had made the first 90° turn ($n=20$)

The fish were observed using an overhead camera. Footage was captured directly onto laptop and analysed using the following software packages respectively: ‘VirtualDub-MPEG2’ (Lee 2009; version 1.6.19; copyright 1998–2007 by Avery Lee) and ‘ImageJ’ (Abramoff et al. 2004).

Experiment plan

We placed Robofish with one, or a group of ten, fish in the refuge. After 2-min acclimation, we opened the refuge door. When the snout of the first fish reached the perimeter of the refuge, Robofish was activated and moved along its programmed route. In the control, the electromagnet was activated and moved along the programmed route under the tank, but the replica was not added to the tank.

Statistical analyses

Analysis was performed using the software package R 2.10.1 (R Core Development Team 2008). We used a least squares regression approach or Wilcoxon signed-rank tests ($\alpha=0.05$).

Recruitment

We examined the ability of Robofish to recruit followers from the refuge by measuring the time for fish to leave the refuge from when the electromagnet was activated. A fish was considered to have left the refuge when the base of the caudal fin had emerged from beneath the raised refuge door. We analysed the relationship between duration and treatment (test: with Robofish; control: without Robofish) in experiments with one fish and with ten. We measured 20 singletons and 20 group members. For the groups, we compared the duration for the first fish to leave the refuge between test and control treatments.

Singletons, but not groups of ten fish, left the refuge significantly sooner in the presence of Robofish than in controls (one-fish experiment—Wilcoxon signed-rank test (WT): $W=772.5$, $n_{\text{test}}=20$; $n_{\text{control}}=20$; $p<0.0001$, Fig. 2a; ten-fish experiment—WT: $W=155.5$, $n_{\text{test}}=20$; $n_{\text{control}}=20$; $p=0.876$, Fig. 2b).

Leadership

In the one-fish and ten-fish experiments, we tested if Robofish could initiate a turn: We compared the absolute orientation of singletons and the closest fish in groups of ten to Robofish, at three pairs of time points (before: after Robofish had turned): 1:1, 1.5:1.5, and 2:2 s. The absolute orientation was the angle between the orientation of the fish (a line from the anteroposterior and lateral mid-point to the

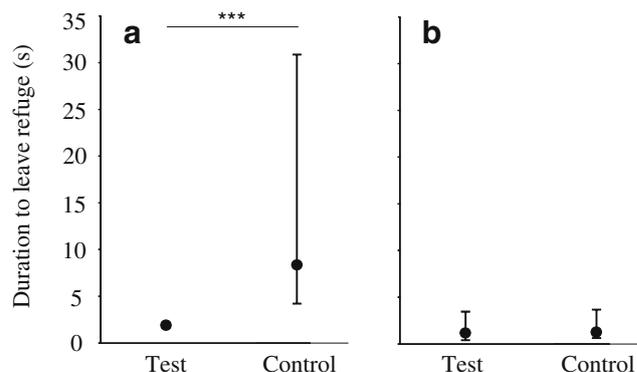


Fig. 2 Duration (median±IQR) for a single fish (a) and the first fish in a shoal of ten (b) to leave a refuge after Robofish had left it, compared to a control ($n=20$). *** $p<0.001$

fish’s snout) with respect to the shortest straight line from the position of the fish to side ‘a’ of the tank (Fig. 1b). We measured 20 singletons and 20 shoal members (one randomly selected from each group).

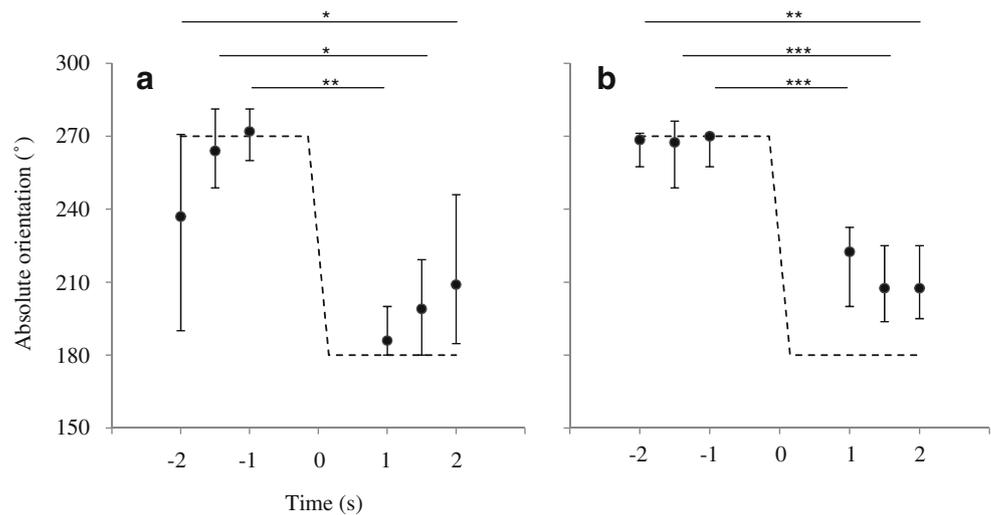
The absolute orientation of single fish and shoal members was significantly different between time points before and after Robofish made the first turn (one-fish experiment: $n_{\text{test}}=20$; $n_{\text{control}}=20$; 1 s—WT: $V=182.5$, $p=0.004$, Fig. 4a; 1.5 s— $V=172$, $p=0.011$; 2 s— $V=159$, $p=0.046$; ten-fish experiment: $n_{\text{test}}=20$; $n_{\text{control}}=20$; 1 s—WT: $V=195.5$, $p<0.001$; 1.5 s— $V=200.5$, $p<0.001$; 2 s— $V=174$, $p=0.002$; Figs. 1b and 3b), and they turned in the same direction as Robofish (see Online Resource 1).

Effect of duration fish had spent in the tank

In the ten-fish experiment, for 27 groups, the fish were left in the tank once Robofish had completed its route for the first time. The trial was then repeated at 5, 30, 60, and 120 min and between 16 and 20 h after the initial test. Between repeats, Robofish was removed from the tank. After the trial, we opened the refuge door and allowed the fish to swim freely in the tank. At the start of the next trial, the fish were shepherded into the refuge using a hand net.

During each trial, we recorded the proportion of fish that were shoaling with Robofish during its route every 3 s (time intervals from when Robofish left the refuge—3, 6, 9, 12, and 15 s). An individual was determined to be shoaling with Robofish (or another focal fish) if it had left the refuge and was within five TL of the focal fish or five TL from another individual that was itself within five TL of the focal fish (Gautrais et al. 2008). We analysed the relationship between mean proportion of fish shoaling with Robofish and the time that the fish had spent in the test tank. We also analysed the relationship between the general shoaling tendency of the fish: the mean number of shoals (number of shoals was measured every 5 s for 1 min immediately prior

Fig. 3 Absolute orientation (defined in the body text) of single fish (**a**; median±IQR; $n=20$) and ten fish (**b**; one individual randomly selected from each group; $n=20$) 1, 1.5, and 2 s before and after the first 90° turn by Robofish once it had left the refuge (see Robofish route in Fig. 1b). We analysed the difference in orientation, for each fish, for the following time points (before/after Robofish turned): 1:1, 1.5:1.5, and 2:2 s. * $p<0.05$; ** $p<0.01$; *** $p<0.001$. Absolute orientation of Robofish (dashed line)



to each trial) and the time fish had spent in the tank (at minutes 4, 29, 59, and 119). In both analyses, time was added to the analysis model as a factor.

The proportion of fish shoaling with Robofish decreased with increased time spent in the test tank (linear mixed effects model: $F_{5, 80}=9.981$, $p<0.001$, Fig. 4). Furthermore, the general shoaling tendency of the fish reduced with increased time in the test tank (penalised quasi-likelihood generalised linear mixed effects model: $F_{3, 48}=4.034$, $p=0.012$, error family = quasi-Poisson).

Investigation using the method

Methods

We used the same experimental setup, plan, and analyses, as for the examination of the method. First, in groups of ten fish, we analysed the relationship between the following variables: (a) the metric distance between the position of the closest fish to Robofish and Robofish (1/25 s before

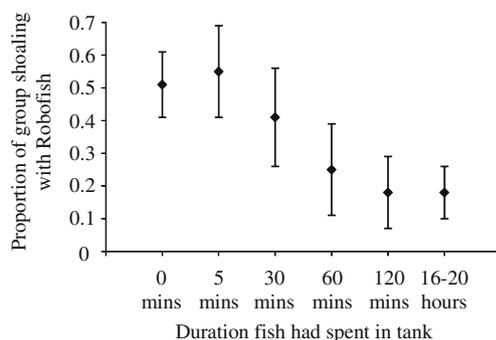


Fig. 4 Proportion (mean ± 2SE) of ten fish shoaling with Robofish during its route after the fish had been left for different periods of time in the test tank ($n=27$)

Robofish began to turn) and (b) the fish's relative orientation (difference between absolute orientation of the fish and of Robofish) 1, 1.5, and 2 s after the turn. We only examined the behaviour of the closest fish to Robofish to control for the effect of topological distance on the interaction between Robofish and each group member. The topological distance was the rank distance of each fish 1/25 s before Robofish began the turn. We used these time points because the fish used in this investigation rarely turned towards Robofish within 0.5 s and had usually stopped turning within 3 s.

Second, we analysed the relationship between the following variables: (a) the topological distance between each fish in the shoal and Robofish and (b) the relative orientation of each fish in the shoal 1, 1.5, and 2 s after the turn (in shoals that varied in the distance between shoal centroid and the position of Robofish.) The shoal centroid was the mean x coordinate and mean y coordinate from the coordinates of the position of each fish in the shoal.

Results

There was no significant relationship between the metric distance of the first fish in a group of ten from Robofish (range 2.1–12.1 cm) and the fish's orientation after the turn (relative orientation at 1 s—LM: $F_{1, 19}=0.016$, $p=0.969$; 1.5 s— $F_{1, 19}=1.199$, $p=0.288$; 2 s— $F_{1, 19}=0.092$, $p=0.764$). This means that the turning behaviour of the nearest neighbour to Robofish could not be predicted by its metric distance from Robofish (1/25 s before Robofish turned).

However, we found a significant linear relationship between topological distance from Robofish and orientation after the turn (relative orientation at 1 s—LME: $F_{1, 179}=101.39$, $r^2=0.42$, $p<0.0001$; 1.5 s— $F_{1, 179}=81.175$, $r^2=0.37$, $p<0.0001$; 2 s— $F_{1, 179}=55.486$, $r^2=0.1$, $p<0.0001$; Fig. 5) despite the fact that the metric distance of the shoal

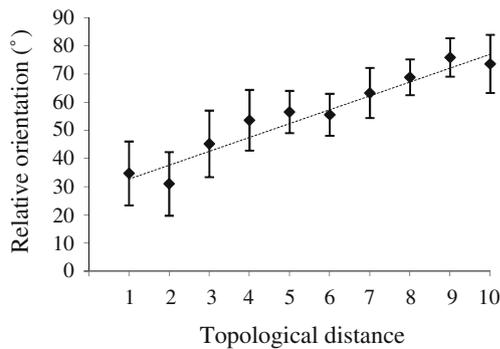


Fig. 5 Relationship between relative orientation to that of Robofish (mean \pm 2SE) 1 s after the first turn by Robofish and topological distance (defined in body text) between each fish and Robofish (1/25 s before Robofish began to turn; $n=20$). Line of best fit (dashed line) was a calculated using a linear mixed effects model

centroid from Robofish varied considerably (range 9.3–33.0 cm). The equation generated by the model for the relationship between topological distance (y) and relative orientation at 1 s (x) was: $y = 4.92x + 37.75$. Therefore, 1 s after Robofish had turned, the individuals closest to Robofish 1/25 s before Robofish turned, had a mean relative orientation of 32.67°, whereas individuals furthest from Robofish had a mean relative orientation of 76.95°.

Discussion

In this study, we examined a novel method for studying collective animal behaviour: the use of Robofish. A key question in animal groups is how individuals influence the movement of others. Here, we examined two functionally important inter-individual interactions between Robofish and three-spined sticklebacks: recruitment and leadership.

Robofish was capable of recruiting singletons which normally hesitate to leave the refuge. However, there was no significant influence on groups of ten fish because they rapidly left the refuge even without Robofish. This corroborates previous studies which have shown that refuge use, or shade use, by minnows *Phoxinus phoxinus*, goldfish *Carassius auratus* and golden shiners *Notemigonus crysoleucas* is related to shoal size: Fish in larger groups tended to act bolder (Magurran and Pitcher 1983; Reefs 2000). Using this method, we can further investigate the effect of particular movement patterns of a single or multiple individuals on other group members and resulting collective dynamics across differing ecological scenarios.

Robofish initiated a change in swimming direction in singletons and groups of ten within 2 s and therefore acted as leader. In groups, there are a range of possible mechanisms to account for the turn in the group, which can be seen as a question of who responds to whom (Aoki

1982). All individuals may respond only to Robofish, they may all respond to each other, or individuals may respond to some individuals and not others (or to some to a greater extent than others), e.g. they may only respond to their nearer neighbours (Ballerini et al. 2008b). It is feasible that any of these mechanisms could have resulted in the observed significant change in orientation by group members.

However, there are a number of possible reasons why individuals would respond only to Robofish or respond to Robofish to a greater degree than to others. (1) The behaviour of Robofish: Our model behaves differently to that of other fish in the tank. Robofish moved away from the shoal centre, tended to move faster than other fish and moved without stopping. These behaviours may indicate that Robofish has relatively high quality information (Faria et al. 2010) or that it is relatively bold (Wilson and Godin 2010), which may in turn cause other fish to follow (Dyer et al. 2009a). (2) Group position: Robofish was often at the front of the group. It has been shown that front individuals tended to have relatively high influence over group direction in shoals of three-spined sticklebacks and juvenile roach *R. rutilus* (Bumann and Krause 1993). (3) Robofish morphology: It has been shown in golden shiners (Reefs 2001) that large individuals have greater influence over shoal direction. Although Robofish was no larger than the other subjects, there may have been other components of its appearance that enhanced its influence over others.

We also showed that the influence of Robofish was largely restricted to the first 30 min that fish spent in the test tank. This may have been because fish tended to act in a more risk averse manner (and therefore follow Robofish rather than explore the tank alone) when they are moved to a new tank. The decline in the influence of Robofish may also have been due to increased hunger in the fish or habituation to Robofish. Fish were not fed in the test tank, and it has been shown in banded killifish *F. diaphanous* that hungry individuals have a lower shoaling tendency than satiated individuals (Robinson and Pitcher 1989; Hensor et al. 2004). Finally, information quality of fish is likely to have increased as they spent more time in the tank, which may have reduced their tendency to use public information by following Robofish (Webster and Laland 2008).

Our method provides an effective means to test the effect of individual attributes such as behaviour, individual state (such as nutritional and information quality) and morphology on inter-individual responses in shoals and resultant shoal dynamics. This may provide a better understanding not only of fish behaviour but also contribute to a more general understanding of collective animal behaviour (Sumpter 2006).

Robotic fish have been used successfully in biomechanics and bio-mimetics to investigate fish movement and bio-inspired solutions to engineering problems such as locomotion through water (Streitlien et al. 1996; Liu et al. 2005). In these cases, robots were designed to mimic fish behaviour based on their morphology. In contrast, our Robofish was designed to explore social interactions between fish which requires the robot to be accepted as a conspecific and shoal member.

The technique described for guiding Robofish with a computer-controlled electromagnet opens up many avenues for experimental research on fish. For example, complex behavioural sequences can be programmed, which are beyond the capabilities of previous techniques, for pulling replicas through a tank (Sumpter et al. 2008; Ward et al. 2008). Further, in contrast to virtual fish (Künzler and Bakker 1998), our technique allows for physical interactions between fish and Robofish which enhances the realism of the experimental scenario. Our technique is by no means restricted to fish, or aquatic organisms, but can be used with other animal species if they respond to replicas of conspecifics (however, this method is largely restricted to relatively small organisms). Likewise, our technique has great potential beyond studies of collective behaviour and many different types of behavioural interactions can be investigated including aggressive behaviour, cooperation (e.g. tit-for-tat) and sexual behaviour (Krause and Ruxton 2002).

We found that Robofish had a strong directional influence on individuals topologically, but not metrically, for all tested time intervals. We can exclude the explanation that there was insufficient variation in metric distance (to obtain enough test power) because metric distance varied considerably, i.e. by a factor 5.8 for the first fish in a shoal (metric distance range 2.1–12.1 cm). In contrast, ten fish were likely to turn in the order of their relative distance to Robofish (according to whether they were Robofish's first, second, third etc. nearest neighbour) regardless of the absolute distance of the shoal from Robofish (shoal centroid distance from Robofish, 1/25 s before Robofish turned, varied by a factor of 3.5: distance range 9.3–33 cm). This investigation is the first direct comparison, by manipulation, of the effect of metric and topological distance on interactions between individuals in fish shoals, and these findings concur with those from studies of starling flocks (Ballerini et al. 2008b). However, these results are in contrast to some theoretical studies of fish shoaling that use metric distance to determine the nature of inter-individual responses (Couzin et al. 2002; Barbaro et al. 2009). Our findings indicate that modelling individuals with topological, rather than metric, interactions will more closely reproduce and predict the behaviour of shoaling fish.

Acknowledgements JJF was funded by a Biotechnology and Biological Sciences Research Council Doctoral Training Grant. JRGD was funded by a grant from the Engineering and Physical Sciences Research Council to JK. JK also acknowledges funding from the Natural Environment Research Council. We are grateful to Julius Goldthorpe, Daryl van Cauwelaert and Nicola Atton for help with the experiments.

References

- Abramoff MD, Magelhaes PJ, Ram SJ (2004) Image processing with ImageJ. *Biophoton Int* 11:36–42
- Aoki I (1982) A simulation study on the schooling mechanism in fish. *Bull Jpn Soc Sci Fish* 48:1081–1088
- Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, Giardina I, Orlandi A, Parisi G, Procaccini A, Viale M, Zdravkovic V (2008a) Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. *Anim Behav* 76:201–215. doi:10.1016/j.anbehav.2008.02.004
- Ballerini M, Calibbibo N, Candeir R, Cavagna A, Cisbani E, Giardina I, Lecomte V, Orlandi A, Parisi G, Procaccini A, Viale M, Zdravkovic V (2008b) Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. *Proc Natl Acad Sci USA* 105:1232–1237. doi:10.1073/pnas.0711437105
- Barbaro A, Einarsson B, Birnir B, Sigurðsson S, Valdimarsson S, Pálsson ÓK, Sveinbjörnsson S, Sigurðsson P (2009) Modelling and simulations of the migration of pelagic fish. *J Mar Sci* 66:826–838. doi:10.1093/icesjms/fsp067
- Biro D, Sumpter DJT, Meade J, Guilford T (2006) From compromise to leadership in pigeon homing. *Curr Biol* 16:2123–2128. doi:10.1016/j.cub.2006.08.087
- Buhl J, Sumpter DJT, Couzin ID, Hale JJ, Despland E, Miller ER, Simpson SJ (2006) From disorder to order in marching locusts. *Science* 312:1402–1406. doi:10.1126/science.1125142
- Bumann D, Krause J (1993) Front individuals lead in shoals of 3-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*). *Behaviour* 125:189–198
- Couzin ID, Krause J (2003) Self-organization and collective behavior in vertebrates. *Adv Study Behav* 32:1–75. doi:10.1016/S0065-3454(03)01001-5
- Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433:513–516. doi:10.1038/nature03236
- Couzin ID, Krause J, James R, Ruxton GD, Franks NR (2002) Collective memory and spatial sorting in animal groups. *J Theor Biol* 218:1–11. doi:10.1006/jtbi.2002.3065
- Dyer JRG, Croft DP, Morrell LJ, Krause J (2009a) Shoal composition determines foraging success in the guppy. *Behav Ecol* 20:165–171. doi:10.1093/beheco/am129
- Dyer JRG, Johansson A, Helbing D, Couzin ID, Krause J (2009b) Leadership, consensus decision making and collective behaviour in humans. *Philos Trans R Soc B-Biol Sci* 364:781–789. doi:10.1098/rstb.2008.0233
- Faria JJ, Codling EA, Dyer JRG, Trillmich F, Krause J (2009) Navigation in human crowds; testing the many-wrongs principle. *Anim Behav* 78:587–591. doi:10.1016/j.anbehav.2009.05.019
- Faria JJ, Dyer JRG, Tosh C-JK (2010) Leadership and social information use in human crowds. *Anim Behav* 79:895–901. doi:10.1016/j.anbehav.2009.12.039
- Franks NR, Dechaume-Moncharmont FX, Hanmore E, Reynolds JK (2009) Speed versus accuracy in decision-making ants: expediting politics and policy implementation. *Philos Trans R Soc B-Biol Sci* 364:845–852. doi:10.1098/rstb.2008.0224

- Gautrais J, Jost C, Theraulaz G (2008) Key behavioural factors in a self-organised fish school model. *Ann Zool Fenn* 45:415–428
- Halloy J, Sempo G, Caprari G, Rivault C, Asadpour M, Tache F, Said I, Durier V, Canonge S, Ame JM, Detrain C, Correll N, Martinoli A, Mondada F, Siegwart R, Deneubourg JL (2007) Social integration of robots into groups of cockroaches to control self-organized choices. *Science* 318:1155–1158. doi:10.1126/science.1144259
- Hensor EMA, Godin J-GJ, Hoare DJ-JK (2004) Effects of nutritional state on the shoaling tendency of banded killifish, *Fundulus diaphanus*, in the field. *Anim Behav* 65:663–669. doi:10.1006/anbe.2003.2075
- Hoare DJ, Couzin ID, Godin J-GJ, Krause J (2004) Context-dependent group size choice in fish. *Anim Behav* 67:155–164. doi:10.1016/j.anbehav.2003.04.004
- Huth A, Wissel C (1992) The simulation of movement of fish schools. *J Theor Biol* 156:365–385. doi:10.1016/S0022-5193(05)80681-2
- King AJ, Johnson DDP, Van Vugt M (2009) The origins and evolution of leadership. *Curr Biol* 19:R911–R916. doi:10.1016/j.cub.2009.07.027
- Krause J, Bumann D, Todt D (1992) Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (*Rutilus rutilus*). *Behav Ecol Sociobiol* 30:177–180. doi:10.1007/BF00166700
- Krause J, Hoare D, Krause S, Hemelrijk CK, Rubenstein DI (2000) Leadership in fish shoals. *Fish Fish* 1:82–89
- Krause J, Ruxton GD (2002) *Living in groups*, 1st edn. Oxford University Press, Oxford
- Künzler R, Bakker TCM (1998) Computer animations as a tool in the study of mating preferences. *Behaviour* 135:1137–1159
- Lee A (2009) VirtualDub home page. <http://www.virtualdub.org>. Software hosted by 'SourceForge.net'
- Liu J, Dukes I, Hu H (2005) Novel mechatronics design for a robotic fish. In: IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS05), Edmonton, Canada, pp 2077–2082
- Magurran AE, Pitcher TJ (1983) Foraging, timidity, and shoal size in minnows and goldfish. *Behav Ecol Sociobiol* 12:147–152. doi:10.1007/BF00343206
- R Core Development Team (2008) R: a language and environment for statistical computing. In: *Computing RFFS* (ed), Vienna, Austria
- Rands SA, Cowlshaw G, Pettifor RA, Rowcliffe JM, Johnstone RA (2003) Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423:432–434. doi:10.1038/nature01630
- Reebs SG (2000) Can a minority of informed leaders determine the foraging movements of a fish shoal? *Anim Behav* 59:403–409. doi:10.1006/anbe.1999.1314
- Reebs SG (2001) Influence of body size on leadership in shoals of golden shiners, *Notemigonus crysoleucas*. *Behaviour* 138:797–809. doi:10.1163/156853901753172656
- Robinson CJ, Pitcher TJ (1989) The influence of hunger and ration level on shoal density, polarization and swimming speed of herring, *Clupea harengus* L. *J Fish Biol* 34:631–633. doi:10.1111/j.1095-8649.1989.tb03341.x
- Romey WL (1996) Individual differences make a difference in the trajectories of simulated schools of fish. *Ecol Model* 92:65–77. doi:10.1016/0304-3800(95)00202-2
- Seeley TD, Visscher PK, Passino KM (2006) Group decision making in honey bee swarms. *Am Sci* 94:220–229
- Streitlien K, Triantafyllou GS, Triantafyllou MS (1996) Efficient foil propulsion through vortex control. *American Institute of Aeronautics and Astronautics* 34:2315–2319. doi:10.2514/3.13396
- Sumpter DJ (2006) The principles of collective animal behaviour. *Philos Trans R Soc Lond B Biol Sci* 361:5–22. doi:10.1098/rstb.2005.1733
- Sumpter DJ, Krause J, James R, Couzin ID, Ward AJ (2008) Consensus decision making by fish. *Curr Biol* 18:1773–1777. doi:10.1016/j.cub.2008.09.064
- Tudorache C, Blust R, De Boeck G (2007) Swimming capacity and energetics of migrating and non-migrating morphs of three-spined stickleback *Gasterosteus aculeatus* L. and their ecological implications. *J Fish Biol* 71:1448–1456. doi:10.1111/j.1095-8649.2007.01612.x
- Ward AJW, Sumpter DJT, Couzin LD, Hart PJB, Krause J (2008) Quorum decision-making facilitates information transfer in fish shoals. *Proc Natl Acad Sci USA* 105:6948–6953. doi:10.1073/pnas.0710344105
- Webb B (2000) What does robotics offer animal behaviour? *Anim Behav* 60:545–558. doi:10.1006/anbe.2000.1514
- Webster M, Laland KN (2008) Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proc R Soc Lond B Biol Sci* 275:2869–2876. doi:10.1098/rspb.2008.0817
- Wilson ADM, Godin J-GJ (2010) Boldness and intermittent locomotion in the bluegill sunfish, *Lepomis macrochirus*. *Behav Ecol* 21:57–62. doi:10.1093/beheco/arp157