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Site fidelity and localised homing behaviour in three-spined sticklebacks (*Gasterosteus aculeatus*)

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Abstract

The ability of animals to disperse towards their original home range following displacement has been demonstrated in a number of species. However, little is known about the homing ability of three-spine sticklebacks (*Gasterosteus aculeatus*), an important model species in behavioural ecology. In addition, few studies have examined the role of social facilitation in relation to homing behaviour in fishes. We examined homing behaviour of sticklebacks displaced over distances of between 80 m and 160 m in land-drains with directional water flow. Fish were translocated from their original capture site, tagged and then released either in groups or solitarily. We performed recapture transects either one or two days later. Data provided by recaptured sticklebacks show that the fish dispersed in the direction of their original capture site. Although fish translocated downstream typically moved further than those translocated upstream, both dispersed towards their original capture site. There was no difference between fish released solitarily or in groups in their homing ability and indeed there was little evidence that fish translocated in groups remained together following their release. The homing ability of the fish was demonstrated by the finding that up to 80% of fish returned to their home ranges within two days of release over a distance equivalent to approximately 5000 body lengths of these small fish.

1. Introduction

The movement of individuals within their environment has important implications both for the longer term population dynamics of a species as well

as within shorter time scales for the flow of information, disease, and even genes. Site fidelity, or occupancy of a limited home range, can enable animals to learn and update information about the distribution of resources and threats, potentially allowing them to forage and navigate with greater efficiency relative to conspecifics that show little or no site fidelity (Switzer, 1993). When individuals do display site fidelity, they may attempt to return to their home range following displacement. Such homing behaviour has been recorded in a diverse range of species, including insects (Alcock, 1996), crustaceans (Stone & O'Clair, 2002), molluscs (Cook et al., 1969), fishes (Hert, 1992), amphibians (Crump, 1986), reptiles (Avens et al., 2003), birds (Biro et al., 2002) and mammals (Alyan & Jander, 1994).

Individuals engaged in homing behaviour may use environmental cues and spatial learning to locate a particular habitat (Hasler & Cooper, 1976; Jamon & Bovet, 1987). Local orientation within a habitat likely implies spatial learning of specific areas of habitat, whereas longer range navigation and homing may require that animals use not only spatial learning, but also attend to more generalised cues, including geomagnetic fields, sounds, or smells (Hasler & Cooper, 1976; Hagstrum, 2000; Odling-Smee & Braithwaite, 2003; Bingman et al., 2006; Huijbers et al., 2012).

Animals use social information to improve decision-making in a wide range of contexts (Jackson & Ruxton, 2006; Ward et al., 2011; Laland et al., 2012); social information may also play an important role in homing and navigation (Helfman & Schultz, 1984; Warner, 1988; Reader et al., 2003; Sumpter et al., 2008a; Freeman et al., 2011). One particular example of this is provided in schools of herring (*Clupea harengus*) where experienced, informed individuals tend to play key roles in school movement decisions (McQuinn, 1997; Ferno et al., 1998; Huse et al., 2002). When animals have access to social information in this context, we might, therefore, predict that they will be able to navigate and ultimately to home more effectively. Alternatively, it may argued that if displaced animals are motivated to home because of their unfamiliarity with both their physical and their social environment, then transplanting them in groups with others from their own environment, whom they recognise, may actually make such groups less likely to display homing behaviour.

The three-spined stickleback (*Gasterosteus aculeatus*) is a model species in behavioural ecology (Bell & Foster, 1994) and much is known about their tendency and ability to use social information (Coolen et al., 2003; Sumpter

et al., 2008b). Whether they are able to use social information in order to move long distances in their habitat is less well known. Some populations of this species are migratory, while others remain resident within relatively small areas (Snyder, 1991; Arai et al., 2003; Kume & Mori, 2009). Previous studies have shown that sticklebacks are capable of spatial learning and navigating in short-range (less than 2 metres) foraging tasks (Girvan & Braithwaite, 1998, 2000; Odling-Smee et al., 2008). In addition, sticklebacks from the population described in this experiment show a strong preference for associating with conspecifics from the same local area as themselves on the basis of environmentally-derived cues expressed by the fish themselves (Ward et al., 2005; Webster et al., 2008). This preference is known to be highly specific — fish are able to discriminate between conspecifics taken from connected parts of the same habitat, separated by only 200 m (Ward et al., 2007). This ability to discriminate, and the strong preference of individuals for conspecifics from the same habitat, suggests that sticklebacks may occupy a limited home range and that, if displaced, they would attempt to return to this range. Little is known, however, about the ability of sticklebacks, especially in resident populations, to navigate and home over distances of more than a few metres. In this study we investigated the homing behaviour of sticklebacks that were experimentally displaced from their site of capture. Specifically, we tested three separate hypotheses. First, that fish translocated upstream or downstream of their capture site would disperse in the direction of their original capture sites. Second, that fish translocated in groups would be more likely to be recaptured in the vicinity of another member of the same group than a member of a different group. Third, that fish translocated in groups would show differences in homing behaviour by comparison to fish translocated on their own.

2. Methods

The study was carried out in a linear ditch system connected to the estuary of the Great Eau at Saltfleet, Lincolnshire, UK (Grid reference TF 464 935 GB) in late October/early November across three years: 2008, 2010 and 2011. This time of year is outside the breeding season of the fish (usually April to July in the UK), hence allowing us to minimise disturbance to breeding populations. The ditches are man-made drainage systems, originally constructed in the 17th Century (Darby, 1940). They measure between 1.5 to

2 m in width, with a water depth of 30–50 cm. Flow rate is slow; typically between 2–4 cm/s at the time of sampling. Although the ditches were largely clear of submerged macrophytes at sites A and C, overhanging grasses on the banks of the ditch and floating algal mats provide refuge for the fish. At Site B, there was a considerable amount of emergent vegetation in the channel. Three-spine sticklebacks are the dominant fish species present, although smaller populations of nine-spine sticklebacks (*Pungitius pungitius*) also occur throughout. We used three separate sections of the ditch over the three years. Site A (sampled in 2008) measured 350 m in length. Site B (sampled in 2010 and 2011) measured 220 m in length. Site C (sampled in 2011) measured 240 m in length. Sites were separated by at least 1 km. There were abundant populations of adult (one year old, or greater: 'Y1+') three-spine sticklebacks and indeed juvenile fish (less than one year old: Y0) at all three sites during the time of the studies. For the purposes of this experiment, we used Y1+ fish, which were identifiable as such by their much greater size than Y0 fish at this time of year — greater than 3 cm total length for Y1+ fish compared to less than 2 cm total length in Y0 fish. We did not use Y0 fish in this experiment since their smaller size makes them more difficult to tag effectively. Throughout all experiments, fish were captured using large (1 m × 0.8 m) handnets. We estimate that we caught approximately 30–40-times as many unmarked Y1+ three-spine sticklebacks as marked fish during our recapture transects.

2.1. Experiment 1: Do displaced sticklebacks demonstrate homing behaviour?

We conducted the first experiment at Site A (see Figure 1) in 2008. The study was carried out over two days. On the first day, we planted marker posts at 5-m intervals along the length of the section of ditch for a total of 350 m and identified three capture sites. Our middle capture site was positioned halfway along the ditch transect, from 162.5 to 187.5 m. The upstream site was positioned 55 m upstream of this, from 242.5 to 267.5 m. The downstream site was positioned 55 m downstream from the middle site, from 107.5 to 82.5 m. A total of 60 fish were captured from each site, giving a total of 180 fish. All fish used were Y1+. Each fish was then tagged, non-invasively, by attaching an individually identifiable flexible plastic disk measuring 4 mm in diameter and with a thickness of 0.22 mm to the pelvic spine (Webster & Laland, 2009) before being released. Pilot studies have
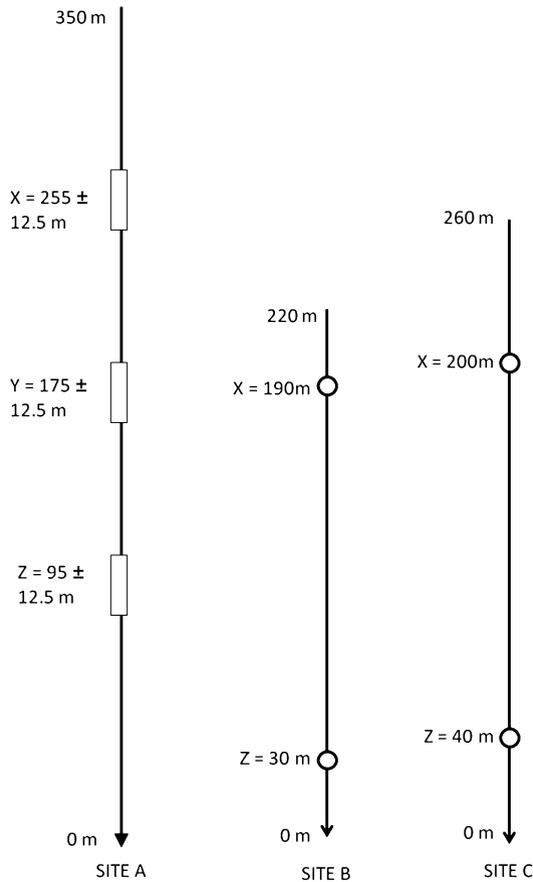
Figure 1. Diagram to show the transects and original capture sites for sites A, B and C. The letter X denotes the upstream capture position, Y denotes the mid-transect capture position, Z denotes the downstream capture position.

shown that these tags do not affect fish locomotion, and tagged fish are just as likely to shoal, and be shoaled with, as untagged fish (Webster & Laland, 2009). Fish captured from the downstream site were translocated to the upstream site and vice versa. As a control, fish captured from the middle site were tagged and re-released at that site. The typical time spent by all fish from being captured to being re-released was approximately 1 h, during which time fish were maintained in 50-l containers filled with water taken from their site of capture. A total of 60 fish were, therefore, released at each site in batches of 10 fish at 5-m intervals.

On the second day we sampled the ditch once, moving from the 350-m marker downstream to the furthest extent of the ditch, where the ditch runs out into a culvert at the 0-m point. Sampling was carried out by two people, each using large (1 m × 0.8 m) hand nets and adopting a stereotypical sweeping method that attempted to ensure that catch effort was even throughout the transect. When a fish was captured its identification tag was read and recorded. The position of each recaptured fish was noted to the nearest 5 m using the marker posts.

2.2. Experiments 2 and 3: Are there differences in homing behaviour between sticklebacks translocated in groups and sticklebacks translocated on their own?

Experiments 2 and 3 were performed using two slightly different protocols in order to minimise the risk that any finding could be an artefact of any given experimental design. In particular, Experiment 2 spatially separated group-released fish and individually-released fish to opposite ends of the transect, but this meant that it had to be performed over two separate years. Experiment 3 intermingled group-released and individually-released fish to an extent, but allowed us to perform the experiment in a single year.

We conducted Experiment 2 across two years (2010 and 2011) at Site B (see Figure 1). In 2010, we captured a total of 100 fish, 50 from each end of the channel. The transect along the ditch was measured with a tape along the bank ranging from the furthest downstream point (0 m) to the furthest upstream point (220 m). Fish at the downstream end of the channel were captured approximately 30 m along the transect, while fish at the upstream end were captured approximately 190 m along the transect. We made 5 groups of 10 fish each from fish that we had captured at the upstream point of the channel and released these at the downstream end of the channel. Each group was tagged with a group-specific marker. The 50 fish that we had caught at the downstream end of the channel were released individually at the upstream end of the channel. Each of these fish had a specific individual mark. The five groups were released, one at each of 5 separate points at 4, 8, 12, 16 and 20 m along the transect. The individual fish were released at 1.2-m intervals from 210 to 151.2 m. Although 1.2 m is a relatively short distance, the environment is relatively structurally complex at Site B and the ditch water is relatively turbid. Furthermore, we observed that on release, the fish tended to dart straight into cover at the water's edge. Thus, while we cannot exclude the possibility that individually-released fish encountered each

other, we can state that it was unlikely to happen immediately following re-
lease.

Two days following release we sampled the transect unidirectionally from
0 m (downstream) to 220 m (upstream). The ditch was sampled in the same
manner as previously described, again standardising catch effort as far as
possible. Where fish were recaptured, their identity and the location of cap-
ture, to the nearest metre, was recorded.

The following year, 2011, we repeated the procedure but this time with
the difference that the fish later to be released in groups were caught at the
downstream end of the transect at approximately 30 m and released in five
groups of 10 fish at the upstream point of the transect, at 170, 175, 180, 185
and 190 m, while fish to be released individually were caught at the upstream
point of the transect at 190 m and released at the downstream point at 1.2-m
intervals from 4 to 62.8 m. Again, the transect was sampled two days later
from 0 to 220 m. By performing the transects over two separate years, we
ensured that group-released and individually-released fish that were moving
back towards their original capture sites would always be travelling in oppo-
site directions.

Experiment 3 tested the same hypothesis as Experiment 2, but used a dif-
ferent experimental protocol. We performed this experiment at Site C (see
Figure 1) in 2011, again releasing fish in groups or individually. We cre-
ated a transect from 0 (downstream) to 260 m (upstream). We caught 40
fish downstream, at 40 m along our transect, and 40 fish upstream, at 200 m
along our transect. All fish were then individually tagged. The fish caught at
the downstream end of the transect were released upstream, and vice versa.
We released four groups of 10 fish, two groups were released downstream
of their original capture site at 55 and 75 m along our transect, and two fur-
ther groups were released upstream of their original capture site, at 169 and
209 m. Twenty fish were released individually downstream of their origi-
nal capture site at 1-m intervals from 36 to 45 m, and from 85 to 94 m.
Twenty fish were released individually upstream of their original capture
site, again at 1-m intervals from 150 to 159 m and from 219 to 228 m. In this
way we ensured a minimum 10-m interval between individually-released and
group-released fish and ensured that individually-released fish were released
both upstream and downstream of the group-released fish in all cases. While
we cannot of course be certain that individually-released fish did not locate
group-released fish, this spacing ensured that this would not happen immedi-

ately. Furthermore, the large populations of three-spine sticklebacks present in the ditch meant that tagged fish would encounter many potential group-mates. Again we sampled along the ditch unidirectionally 2 days following the fish's release from -50 m at the furthest downstream extent of our transect up to 310 m at the furthest upstream extent.

2.3. Data analysis

For Experiment 1, we analysed the distance and the direction that fish travelled using ANOVA. The number of metres that a fish was recaptured upstream of its release point was recorded as a positive value, whereas the number of metres that a fish moved downstream was recorded as a negative value. The release treatment (translocated upstream, translocated downstream and control) was used as the single factor in the analysis.

For Experiments 2 and 3, we investigated the dispersal behaviour of the fish with respect to the physical environment, specifically the distance and direction moved following release, using ANOVA. We used whether a fish was released on its own or in a group as one factor and whether it was released upstream or downstream of its original capture point as another factor. We examined two response variables separately: the absolute distance that a fish moved from its original release point, and the distance that the fish moved with respect to its original capture point — if it moved toward the original capture point, this was a positive value, if it moved away from the original capture point, this was a negative value. We analysed Experiments 2 and 3 separately.

In determining whether a fish had 'homed' we defined this as having been recaptured within 20 m of its original capture point.

To test social cohesion following release, i.e., whether fish that were released in proximity (or together in the case of group-released fish) were caught in closer proximity than could be expected by chance, we used a simple randomisation procedure (Ward et al., 2002; Sundaresan et al., 2009). For individually-released fish, we counted all the pairs of fish that were released within a given distance, X. We then found the distance apart that such fish were recaptured. The test statistic, d, is the mean of these distances over all such pairs. This was then compared with the mean distances when the observed recapture positions are shuffled randomly among the recaptured fish. For group-released fish, we followed the same procedure with the exception that we could obviously dispense with the parameter, X. We would expect

d to be significantly less than the population mean if proximity at release were driving proximity at recapture. We tested the entire recapture set for Experiments 2 and 3 separately, using 10 000 randomisations each time.

3. Results

3.1. Experiment 1

After 24 h, 47.5% of translocated and subsequently recaptured fish had homed; 31% of fish translocated upstream and subsequently recaptured had homed, whereas 62.5% of fish translocated downstream and subsequently recaptured had done so. Fish released at different sites differed in the distance and direction of movement following release (ANOVA: $F_{2,87} = 68.9$, $p < 0.001$; see Figure 2). Fish translocated downstream moved further than fish translocated upstream although both tended to travel towards their original capture point. Translocated fish moved further than control fish, and while both downstream and upstream translocated fish showed a significant departure from a null expectation of zero movement from their release site,
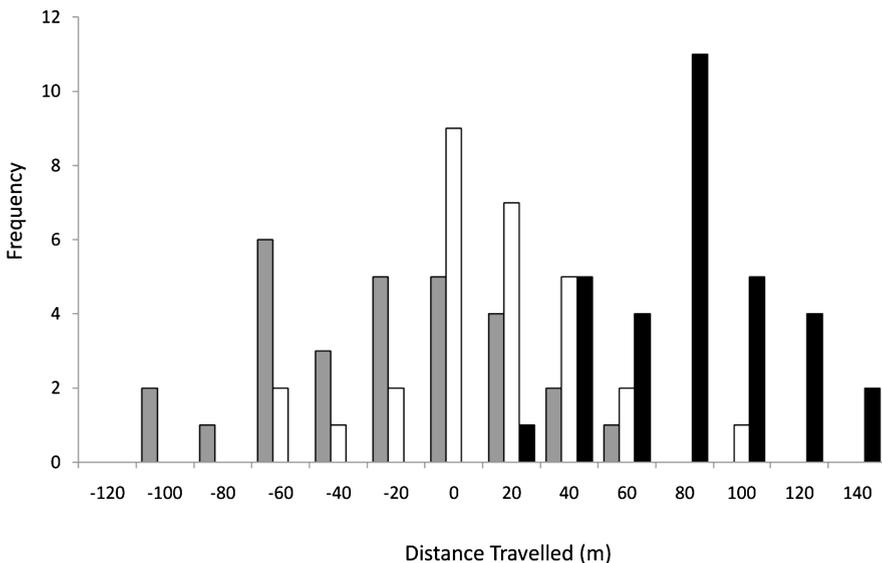
Figure 2. Frequency distribution of distances travelled by fish captured and translocated approximately 80 m upstream (grey bars), 80 m downstream (black bars), or captured and returned to their capture site as a control (white bars). Distances travelled are indicated as positive when fish moved upstream and as negative when fish moved downstream.

Table 1.
Direction and distance travelled by fish following translocation in Experiment 1.

Release site	Mean distance moved in 24 h (m)	SE	*t*	df	*p*
Upstream	−30.17	7.5	4.02	28	<0.001
Control	4.66	6.5	0.72	28	0.48
Downstream	67.66	5.49	12.31	31	<0.001

Positive distance values indicate fish travelling upstream, negative distance values indicate fish travelling downstream. Results of a one sample *t*-test are shown comparing distance travelled against a null expectation of zero.

control fish did not show any departure from zero overall mean movement (see Table 1).

3.2. *Experiments 2 and 3*

In both Experiment 2 and 3, translocated fish tended to move back towards the site where they were originally captured (see Figure 3(a) and (c)). In total, 28.7% of fish homed in Experiment 2, whereas 80% of fish did so in Experiment 3.

In Experiment 2, there was a significant difference between fish released upstream and fish released downstream both in terms of the absolute distance travelled and in terms of the distance travelled towards their original capture site, with fish translocated downstream moving further overall and further towards their original capture site. There was no difference between the post-release behaviour of fish according to whether they were released on their own or released in a group. However, there was a strongly significant interaction between the two factors (see Table 2 (a)–(b), Figure 3(a)–(b)). Among the recaptured fish, 45% of the downstream translocated fish had homed against 9.1% of upstream translocated fish. Overall, 46.9% of recaptured solitary-released fish and 14.6% of recaptured group released fish had homed.

In Experiment 3, there was no significant difference in either absolute distance travelled or distance travelled towards home between fish released upstream and fish released downstream, nor was there any significant differences according to whether fish were released on their own or released in a group (see Table 2 (c)–(d), Figure 3(c)–(d)). Among recaptured fish in Experiment 3, 78.3% of the downstream translocated fish had homed against 83.3% of upstream translocated fish. Overall, 84.6% of recaptured solitary-released fish and 80% of recaptured group released fish had homed.
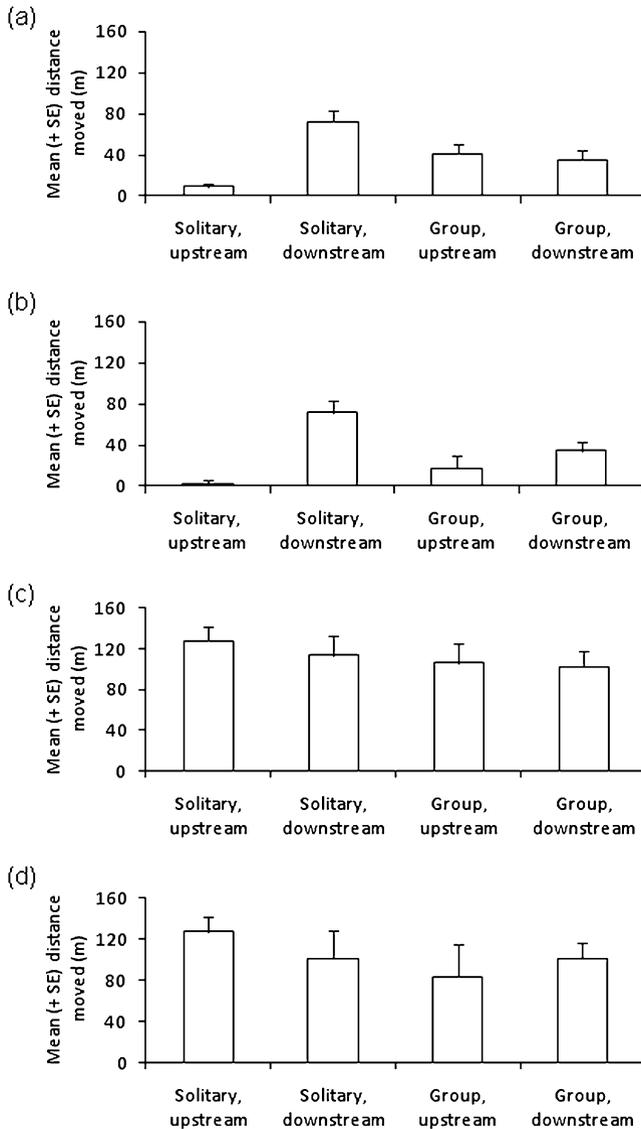
Figure 3. Mean (+ SE) distance in metres travelled by fish in two days following translocation upstream or downstream from their capture site and released either solitarily or in a group; (a) absolute distance travelled by fish in Experiment 2, (b) distance travelled by fish towards original capture point in Experiment 2, (c) absolute distance travelled by fish in Experiment 3, (d) distance travelled by fish towards original capture point in Experiment 3.

Table 2.
Output of two factor ANOVA analysing the movement of fish following translocation; (a) absolute distance travelled by fish in Experiment 2, (b) distance travelled by fish towards original capture point in Experiment 2, (c) absolute distance travelled by fish in Experiment 3 and (d) distance travelled by fish towards original capture point in Experiment 3.

Source	Type III sum of squares	df	Mean square	*F*	*p*
(a)					
Corrected Model	31 848.849	3	10 616.283	6.729	<0.001
Solitary or group release	107.168	1	107.168	0.068	0.795
Translocation site	13 899.691	1	13 899.691	8.81	0.004
Interaction	20 569.849	1	20 569.849	13.037	0.001
Error	108 867.986	69	1577.797		
(b)					
Corrected Model	46 524.208	3	15 508.283	7.49	<0.001
Solitary or group release	1993.745	1	1993.745	0.963	0.33
Translocation site	32 603.693	1	32 603.693	15.748	<0.001
Interaction	12 181.812	1	12 181.812	5.884	0.018
Error	142 856.806	69	2070.388		
(c)					
Corrected Model	2609.452	3	869.817	0.325	0.807
Solitary or group release	2022.948	1	2022.948	0.755	0.391
Translocation site	565.326	1	565.326	0.211	0.649
Interaction	199.119	1	199.119	0.074	0.787
Error	83 014.433	31	2677.885		
(d)					
Corrected Model	5766.61	3	1922.203	0.43	0.733
Solitary or group release	3758.811	1	3758.811	0.842	0.366
Translocation site	123.034	1	123.034	0.028	0.869
Interaction	3636.826	1	3636.826	0.814	0.374
Error	83 014.433	31	2677.885		

Group-released fish did not remain in proximity in either experiment, while there was only weak evidence for solitary-released fish to remain in proximity with others released nearby (see Table 3).

4. Discussion

Together our experiments provide evidence for localised homing behaviour in three-spine stickleback. In the first experiment, translocated fish homed

Table 3.
Results of randomisation procedure examining whether fish that were released in proximity (or together in the case of group-released fish) were caught in closer proximity than could be expected by chance.

Experiment	Solitary or group release	X, the distance between pairs of fish at release (m)	No. of recaptures	d, the mean observed distance between pairs (m)	Mean expected distance between pairs (m)	Probability observed distance is less than expected distance
2	Solitary	2.4	24	40.71	43.87	0.31
2	Solitary	4.8	44	38.02	41.71	0.52
2	Solitary	12	96	43.09	40.96	0.22
2	Group	0	76	49.72	49.49	0.47
3	Solitary	2	6	26.50	53.23	0.12
3	Solitary	4	10	37.30	60.63	0.04
3	Solitary	10	13	35.69	54.94	<0.01
3	Group	0	58	69.74	67.05	0.65

For each solitary release, we consider three initial distances between fish, relating to separations of 2, 4 and 10 release points. As we increase this distance, we increase the number of fish in the analysis.

toward their original site of capture, while control fish remained at their site of release, which was located at their site of capture. In the second and third experiments, both individually-released fish and group-released fish moved towards their original site of capture following experimental displacement, with no obvious effect either of social facilitation or social inhibition of homing behaviour.

The ability and willingness of fish to return to their home range following displacement indicates that there must be clear benefits associated with occupation of such a home range (Papi, 1992; Stamps, 1995; Piper, 2011). A number of potential benefits suggest themselves, including local adaptation to site-specific conditions (Bolnick et al., 2003; Moore & Hendry, 2009; Webster et al., 2011), and familiarity with the location of resources including prey patches and refuges (Yoder et al., 2004). Moreover, where social animals inhabit a home range, they are likely to interact repeatedly with the same individuals. Such stable group membership potentially increases the benefits of sociality to group members (Krause & Ruxton, 2002). Association preferences for familiar individuals have been documented in a number of shoaling fish species (Ward & Hart, 2003) and interaction with familiar individuals is known to enhance foraging and social learning (Swaney et al., 2001; Ward & Hart, 2005). This interrelationship between the physical and the social environment is also suggested by recent work in this population of sticklebacks, amongst others, revealing that individuals preferentially associate with conspecifics from the same local environment as themselves, which they recognise on the basis of temporally labile, habitat-specific chemical cues (Ward et al., 2004, 2005, 2007; Webster et al., 2007). This may also influence their movement patterns, since preferentially associating with individuals that produce similar habitat-based cues is likely to increase site fidelity as a by-product.

There was no clear difference between the dispersal behaviour and homing ability of fish according to whether they were released solitarily, or in groups. Clearly, this may be linked to our finding that fish that were released in groups did not appear to remain in any kind of association with their former group-mates. This may partly be due to the large populations of sticklebacks present at these sites — there would clearly have been no shortage of potential fish with which to shoal, and for many species of small shoaling fish that occur at high densities, high turnover in group composition through fission and fusion processes is thought to be common (Ward et al.,

2002; Croft et al., 2003; Hoare et al., 2004). In addition to this, the way in which we allocated fish to groups was somewhat arbitrary in that while the fish were caught at a similar location, we had no information on their patterns of social association prior to capture. Our results here suggest that individuals are capable of homing independently and are able to act primarily on their own information.

We found some slight differences in the dispersal behaviour of fish and in their ability home according to the direction of flow. Fish that were translocated downstream moved further than those translocated upstream in Experiments 1 and 2, while there was no difference in Experiment 3. This is generally in line with previous studies on other species of fish, where individuals displaced downstream are able to home more effectively than those displaced upstream (Harcup et al., 1984; Belanger & Rodriguez, 2001). This may be due to the fact that displacement through natural events, such as a sudden spate, is far more likely to be in a downstream direction; therefore, fish may simply respond to displacement by swimming upstream (Garcia de Leaniz, 1989), although see Armstrong & Herbert (1997). However, fish translocated upstream in the present study did tend to move downstream rather than upstream. Another possible explanation may be that our sampling regime affected the outcome, however since we sampled with the current in Experiment 1, and against the current in Experiments 2 and 3, this seems unlikely. Rather, this finding may reflect the availability of cues for navigation. Chemical cues have been shown to be of particular importance in locating both short and longer range sites in some fish species (Gunning, 1959; Hasler & Cooper, 1976; Halvorsen & Stabell, 1990; Mitamura et al., 2005). It may simply be that chemical cues may be more easy to assess downstream of their source, thereby facilitating upstream movement in a homing context. Given that fish were also able to navigate downstream, it seems unlikely that chemical cues tell the whole story (although see Dahl et al., 1998 and Wisenden et al., 2010). It is known that fish may attend to multiple sensory cues in navigation and movement decisions (Braithwaite et al., 1996; Huijbers et al., 2012), and that they may learn topography and landmarks (Odling-Smee & Braithwaite, 2003; Odling-Smee et al., 2008). The remarkable accuracy of displaced fish to home either partially or completely in a relatively short space of time, over a considerable distance (relative to their size) and in a turbid and cluttered environment warrants further work to examine the mechanisms used.

In addition to the differences in fish dispersal and homing ability between upstream and downstream translocated fish, we also found apparent differences across different sites, as almost three times as many fish homed successfully in Experiment 3 than in Experiment 2. This finding is harder to account for, given that the sites are within the same ditch system and separated only by a relatively short distance of approximately 1 km. Perhaps the most likely explanation here is that the greater complexity produced by the greater abundance of emergent vegetation in Site B restricted the movement of fish in Experiment 2.

In summary, the current experiments demonstrate that sticklebacks possess impressive homing abilities, extending to displacement distances of up to 200 m. But while we are able to document this ability, the functional explanations for this behaviour remain largely unresolved. One possibility is that in first capturing and then handling the fish in order to tag them, we induced stress akin to an encounter with a predator and thereby provided a strong stimulus to move away from the release site (Wisenden et al., 1995; Wisenden, 2008). This argument is perhaps partially countered by the fact that the fish dispersed in a directed manner, towards their original sites of capture, rather than simply away from the release point in any direction. Nonetheless, it would be extremely interesting to hold the fish in situ at their release point to determine whether their motivation to move is affected by a period of recuperation following this initial stimulus since animals are known to be responsive to changes in the levels of risk in time and space (Lima & Dill, 1990; Wisenden, 2008). The possibility exists that the tendency to disperse will reduce as their perception of proximate risk diminishes. In addition, while a negative experience could increase the motivation to disperse, positive local stimuli at the release site could increase the motivation to remain. For example, if fish are transplanted to an area of habitat with excellent foraging opportunities, dispersal and homing behaviour may be curtailed. Such considerations represent interesting avenues for further research.

Acknowledgements

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