Does relatedness influence migratory timing and behaviour in Atlantic salmon smolts?

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Aggregating and moving with relatives may enable animals to increase opportunities for kin selection to occur. To gain group-living benefits, animals must coordinate their behaviour. Atlantic salmon, *Salmo salar*, demonstrate both territoriality and schooling: the two key social behaviours performed by fish. In this investigation we compared the migratory timing and behaviour of six distinct full-sibling groups of tagged *S. salar* smolts with a large control sample from the same wild population. The results clearly demonstrate that the incidence of schooling and diel migratory timing is not significantly influenced by relatedness, and this adds further support to the hypothesis that *S. salar* smolt migration is primarily an adaptive response to environmental conditions, rather than a behaviour based solely on genetics or kin-biased behaviour. Used in conjunction with the results of two previous investigations, this is the first study to illustrate that kin discrimination among full-sibling groups of parr does not lead to kin-biased schooling in smolts. Thus, even within the same full-sibling groups, the extent of kin-biased behaviour in fish can both differ within a life history stage under varying ecological conditions and shift from one life history stage to the next.

Aggregating and moving with relatives may enable animals to increase opportunities for kin-biased behaviour to occur. Kin association has been documented in many animals that form social groups: e.g. troops in primates (Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008), herds in mammals (Schuttler, Philbrick, Jeffery, & Eggert, 2014), flocks in birds (Powell, 1974; Tóth et al., 2009), shoals in fish (Alex & Thomas, 2012; van Dongen, Wagner, Moodley, & Schaedelin, 2014; Griffiths & Armstrong, 2001) and colonies of social insects (Queller & Strassmann, 1998).

To gain group-living benefits, social individuals must coordinate their behaviour with other group members (Conradt & Roper, 2009). For example, schools of fish are synchronized and polarized swimming groups (Pitcher & Parrish, 1993) and their formation is believed to have several benefits including facilitating the ability to detect and mitigate a predatory threat and improving prey search efficiency (Pitcher & Parrish, 1993). At the same time, school formation may also entail costs in the form of predator attraction (Botham, Kerfoot, Louca, & Krause, 2005; Ioannou & Krause, 2008) and increased competition (Pitcher & Parrish, 1993). Some teleost fish species form schools during migratory periods (Brehmer, Chi, & Mouillot, 2006). While extensive literature is available to describe patterns of migration in flocks of birds and herds of mammals, fish school migration remains poorly understood due to the difficulties of monitoring wild fish movements (Parrish & Hamner, 1997).

Very few studies have critically investigated the genetic composition of wild fish schools (Fraser, Duchesne, & Bernatchez, 2005). However, two related studies of note found significantly more kin than expected in schools of subadult migratory brook trout, *Salvelinus fontinalis* (Fraser et al., 2005), yet most *S. fontinalis* were found not to associate with kin during the breeding migration (Meli & Fraser, 2013). Taken together, these results illustrate the potential dynamic nature of kin association between consecutive

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life stages, even within the same fish population (Meli & Fraser, 2013).

Atlantic salmon, *Salmo salar*, is an ideal model species for testing kin selection theory in fish since salmon demonstrate both territoriality and schooling: the two key social behaviours performed by fish. During the freshwater parr stage *S. salar* aggressively defend a feeding territory (Keenleyside & Yamamoto, 1962). Nevertheless, kin-biased behaviour has been reported in both laboratory studies (Brown & Brown, 1996) and the wild (Fernandes, Copp, & Riley, 2015; Fernandes, Griffiths, Ibbotson, Bruford, &, Riley, 2015; Griffiths & Armstrong, 2002). Kin discrimination in the wild may facilitate temporal and spatial association (Olsén, Petersson, Ragnarsson, Lundqvist, & Järvi, 2004) and the possibility exists that these abilities, previously only documented over small spatial and temporal scales, are manifest over greater distances and time periods by the formation of schools composed of related individuals.

Salmo salar parr develop into smolts and abandon freshwater territoriality in the spring for migration to the sea (Mills, 1989) to habitats more suitable for feeding and growth. Two discrete processes control the migration of salmon smolts (Baggerman, 1960): first, 'migratory disposition' whereby the juvenile salmon undergo the physiological development and morphological changes associated with smoltification and, second, 'external releasing factors', environmental signals that stimulate downstream movement once smoltification is complete. The initiation, intensity and timing of *S. salar* smolt migrations have been correlated with a variety of external releasing factors (McCormick, Hansen, Quinn, & Saunders, 1998) including river flow and turbidity (Greenstreet, 1992), water temperature (Solomon, 1978) and light intensity (Riley, 2007). Numerous behavioural changes occur in *S. salar* smolts at this time, including increased downstream orientation (Martin et al., 2012) and salinity preference (Hoar, 1988), a decrease in aggressive and territorial behaviour (Godin, Dill, & Drury, 1974; Iwata, 1995) and once migration has commenced it is also commonly believed that smolts migrate in schools (Fångstam, Berglund, Sjöberg, & Lundqvist, 1993; Hvidsten & Johnsen, 1993; McCormick et al., 1998).

A two-stage *S. salar* smolt migration theory comprising initial solitary movement followed by schooling was proposed by Bakshtanskiy, Nesterov, and Neklyudov (1980) and Bakshtanskiy, Nesterov, and Neklyudov (1988). They reported that *S. salar* smolts form groups in front of sites of potential danger, subsequently forming schools following a period of mutual learning. However, Olsén et al. (2004) demonstrated in hatchery-reared *S. salar* smolts that siblings migrate closer in time than non-siblings. This was regardless of whether or not the fish were raised together, which led the authors to suggest that salmon migrate as groups, influenced by kinship and not by familiarity. Two recent investigations in neighbouring chalk streams in southern England reported that the initial downstream movement of *S. salar* smolts from their natal stream involved lone fish (Riley, 2007), and that groups of smolts that were observed further downstream came from multiple natal parr tagging sites (a proxy used for possible relatedness; Riley et al., 2014). Working on the same Millstream study site as used in the current investigation, Riley et al. (2014) also reported a significant shift in smolt behaviour, whereby fish detected migrating during the day were often schooling, but those detected migrating at night were not. Lack of evidence for kin structuring has also been found while *S. salar* adults are at sea (Palm et al., 2008). In fact, genetic studies have failed to find evidence of *S. salar* kin aggregation operating in the wild (Fontaine & Dodson, 1999; Mjølnerød, Refseth, & Hindar, 1999).

In this study, we deployed passive integrated transponder (PIT) antenna systems 8.6 km above the tidal limit of the River Frome to continuously monitor the timing of downstream movements of six distinct full-sibling groups of PIT-tagged *S. salar* smolts in 2007 and 2008. Full-sibling group migratory behaviour was compared to that displayed by a large PIT-tagged sample of the wild River Frome *S. salar* smolt population, with particular emphasis on whether time intervals between successive PIT tag detections (the likely occurrence of schooling) and the date and time of day of migration are influenced by relatedness. In doing so, this is the first study to test whether the kin-biased growth and habitat preferences previously documented in the same six distinct full-sibling groups (Fernandes, Copp, et al., 2015; Fernandes, Griffiths, et al., 2015) subsequently lead to kin-biased aggregations/schooling in smolts.

METHODS

Study Area

The River Frome is approximately 70 km long from its source at Evershot (50.50.24N, 2.36.12W) to the tidal limit near Wareham Bypass Bridge (50.40.38N, 2.07.30W). It is a lowland, low-gradient, braided chalk stream that derives most of its discharge directly from the Cretaceous chalk aquifer and man-made bore holes. The River Cerne is a major tributary of the River Frome, with the confluence near Dorchester, in southern England. In the chalk streams of southern England it is generally considered that the majority of juvenile *S. salar* spend 1 year in freshwater before migrating downstream to the sea in the spring as smolts (Riley, 2007; Riley, Maxwell, Ives, & Bendall, 2012).

Fish Data Collection

We created 12 distinct full-sibling groups by fertilizing the eggs of one wild adult female *S. salar* with the milt of one wild adult male ($N = 6$, in 2006 and 2007). We placed each batch of fertilized eggs into a separate incubator (Government of Canada, 1980) at the Watergates Hatchery, Dorchester, U.K. (50.40.59N, 2.22.40W), each supplied from a common source of ground water through an independent siphon to isolate the full-sibling groups from one another.

Within 24 h of the fry dispersing from the incubators, we stocked six groups of full siblings ($N = 3$ each year) into designated sites over a 1.5 km stretch of the River Cerne. Owing to the presence of a weir, located downstream of these sites and impassable for adults on their upstream spawning migration, wild *S. salar* are not present in these stretches of the River Cerne.

After stocking, we gave the fish time to establish territories and grow before sampling using electric fishing, at which time we tagged all juvenile *S. salar* parr caught with PIT tags (as per Ibbotson et al., 2013), to enable the recording of their subsequent migratory timing and behaviour. The tagging took place between 8 and 22 August 2006 and 26 July and 8 August 2007 and included some stream sections not previously reported in Fernandes, Copp, et al. (2015) and Fernandes, Griffiths, et al. (2015). At the time of tagging we took an adipose fin clip (stored in 100% ethanol) for subsequent genetic analyses to enable full-sibling group assignment. We then released all fish back to their site of capture. In 2006, the parr had a mean fork length of 101.5 mm (range 76–134 mm). In 2007, the parr had a mean fork length of 92.4 mm (range 73–199 mm) and a mean wet weight of 12.0 g (range 4.6–98.9 g).

We carried out molecular analysis of the adipose fin tissue to assign juveniles ($N = 428$) to their full-sibling group. We extracted genomic DNA from parental and juvenile adipose fin tissue using the Qiagen tissue DNA extraction kit (catalogue no. 69506, Qiagen, Hilden, Germany). We quantified DNA yield on a 1% agarose gel and visualized on a UV transilluminator, choosing nine loci on the basis of their reliability in the use of parentage assignment based on their

use in previous salmon genetic studies and their allelic size range. The program CERVUS version 3.0.0 (Marshall, 2007) was used to assign each juvenile to its original parent pair. CERVUS compares the candidate parents' genotypes with the offspring's and assesses the relative likelihood (logarithm of odds, LOD) of each offspring's genotype having been inherited from all possible parents. The parent with the highest LOD score is usually assigned as the true parent if its likelihood is significantly higher than the next most likely parent.

In the late summer of 2006 and 2007, we caught 10 882 and 10 712, respectively, wild *S. salar* parr upstream from East Stoke (50.40.47N, 2.11.2W) on the River Frome using electric fishing. We anaesthetized and PIT tagged all the fish and clipped the adipose fin, then returned them to the same section of river from which they had been caught. In 2006, the parr had a mean fork length of 88.9 mm (range 52–187 mm) and a mean wet weight of 8.2 g (range 2–77 g). In 2007, the parr had a mean fork length of 93.3 mm (range 56–200 mm) and a mean wet weight of 10.0 g (range 2.4–108.6 g). In both years, all fish were measured in length to the nearest mm and approximately half of them were weighed. These wild *S. salar* parr were PIT tagged as part of an ongoing international monitored rivers programme, not directly related to the current investigation, to determine natural marine mortality rates, any trends in natural mortality and the level of fishery exploitation, to underpin advice given on the management and conservation of *S. salar* stocks.

At East Stoke (8.6 km above the tidal limit of the River Frome) we installed two full-duplex PIT tag antenna systems (Wyre Micro Design Ltd, Lancashire, U.K.) that span both the main river and a small Millstream (Fig. 1). A full description of these antenna systems can be found in Welton, Beaumont, and Clarke (2002), Ibbotson, Beaumont, Collinson, Wilkinson, and Pinder (2004) and Ibbotson, Beaumont, and Pinder (2011). During April and May 2007 and 2008, we used an acoustic bubble curtain (Welton et al., 2002) to divert downstream-migrating smolts, both those of known parentage from the River Cerne and the general wild population from the River Frome, into the Millstream and past a PIT antenna system in that channel specifically designed for the efficient detection of downstream-migrating PIT-tagged smolts. PIT-tagged smolts migrating in March, and those not deflected by the acoustic bubble curtain, migrated past the second PIT antenna system in the main river channel primarily installed to detect adult *S. salar* returning from the sea on their upstream spawning migration. To be included as a downstream-migrating PIT-tagged smolt, detections had to be recorded between 15 March and 15 May (inclusive), as this time interval has been documented as covering >97% of the smolt migration period for a chalk stream in southern England (Riley, Davison, Ives, & Maxwell, 2013).

Environmental Data Collection

We used the method of Hohenkerk and Yallop (2010) to calculate sunrise, sunset and civil twilight (sun 6° below the horizon) times for the study area. The period between sunrise and sunset is designated as day, the periods of rapidly changing light intensity between the start of civil twilight in the morning and sunrise, and between sunset and the end of civil twilight in the evening, are the crepuscular periods, and the period of darkness between the end of civil twilight in the evening and the start of civil twilight in the morning is designated as night. We calculated the number of intervals (where an interval is the time between two successive downstream-migrating PIT-tagged smolts) within each of the day, night and crepuscular periods based on the period for the second fish in the pair.

Statistical Analysis

Time of migration

We performed circular statistical analyses (Batschelet, 1981) on the time (after sunset) that each smolt migrated downstream past East Stoke, using combined data for both Millstream and main river PIT antenna systems. We calculated mean vector (mean migration time) and mean vector length (*r*, expressed as a value between 0 and 1, with higher values indicating that observations are clustered more closely around the mean) for the wild smolts and for each stocked full-sibling group, for each year of study. We
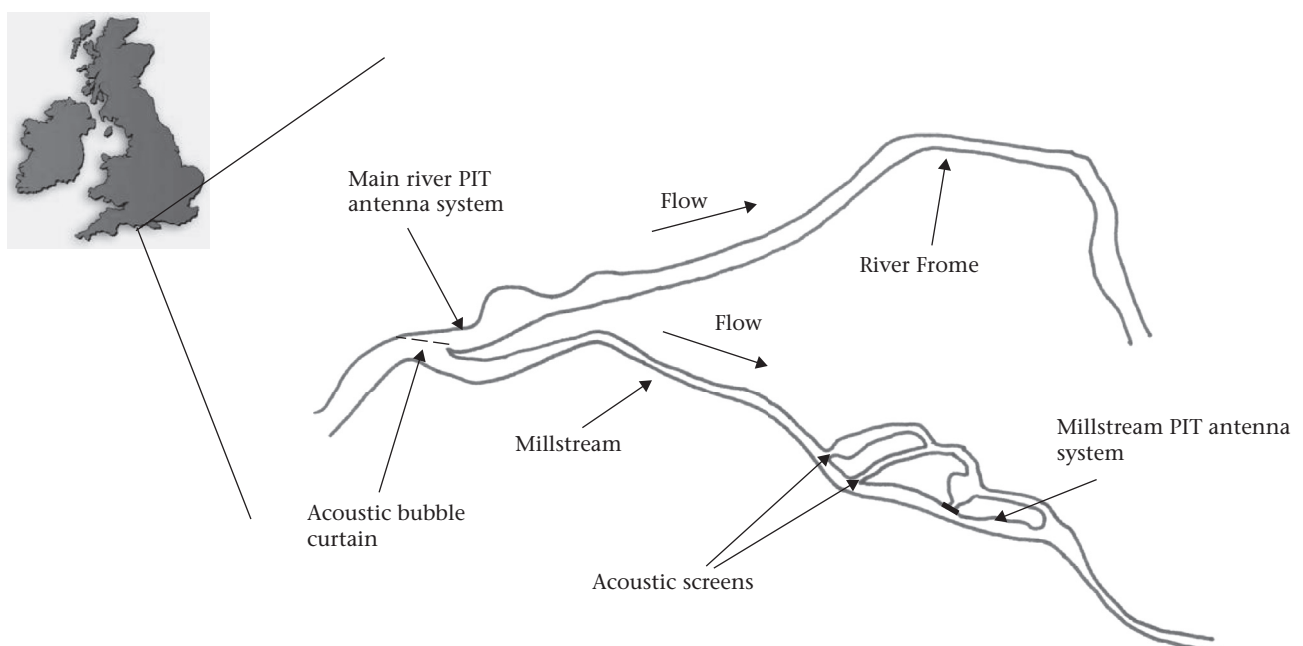
Figure 1. A schematic diagram showing the main River Frome, the Millstream and the positioning of the PIT antenna systems and acoustic bubble curtain at East Stoke.

calculated the probability (P) of the null hypothesis that detections were uniformly distributed throughout the diel cycle, for each year of the study, using Rayleigh's uniformity tests. We assessed the differences between the wild smolts and full-sibling groups and between full-sibling groups using both the 95th percentile confidence limits of the mean vector for each year and nonparametric Mardia−Watson−Wheeler tests (Batschelet, 1981). We used Oriana (2010) to carry out the analysis on time of migration.

Date of migration

We compared the average date (including time of day) of migration past East Stoke (combined data for both Millstream and main river PIT antenna systems) for each full-sibling group to the date from other groups and the wild population in the same year using a permutation test on the difference in medians (9999 iterations). Similarly, we compared the spread of migration timing by applying the Ansari−Bradley test for equality of variances to median-centred migration dates (Ansari & Bradley, 1960).

The availability of the large data set of migration dates from the wild population allowed further comparison of the spread of migration timing of each full-sibling group against the wild smolts in the same year. Here, we generated 10 000 simulated data sets by sampling from the set of observed dates for wild smolts, with the number of observations sampled in a set equal to the number in the full-sibling group being tested. For each simulated set of times we calculated the range of migration dates and a 90% interval between the 5th and 95th percentiles. We then compared the range and 90% interval from the observed data to the distribution across the 10 000 simulated data sets (with P defined as (1 + number of simulated values ≤ observed value)/(number of simulated data sets + 1)), to assess evidence of a shorter range or 90% interval in a full-sibling group than the wild population.

Schooling

To compare intervals for full-sibling groups to those from the wild smolts we used a Monte Carlo simulation approach (Manly, 2001), with the analysis undertaken separately for each full-sibling group in each year (2007, 2008) for the Millstream PIT detections only, as this contributed the majority of the observations (Table 1; Riley et al., 2014).

Here, we generated 10 000 simulated data sets by sampling from the set of observed times for wild smolts, with the number of observations sampled in each of the day\night\crepuscular categories set equal to the number in the full-sibling group being tested.

Table 1
A summary of the numbers of *Salmo salar* parr PIT tagged and detected during the study

Year Parr/Smolt	No. parr PIT tagged	No. tagged smolts detected		Wild smolts with PIT tags %
		Millstream	Main river	
Wild population: 2006/2007	10882	1061	190	10.8
Sibling Group 1: 2006/2007	61	16	0	−
Sibling Group 2: 2006/2007	54	18	1	−
Sibling Group 3: 2006/2007	74	19	5	−
Wild population: 2007/2008	10712	996	182	10.8
Sibling Group 4: 2007/2008	184	56	6	−
Sibling Group 5: 2007/2008	17	1	1	−
Sibling Group 6: 2007/2008	38	7	0	−

The table gives the total number of wild parr PIT tagged throughout the *Salmo salar* spawning range on the River Frome, stocked parr (by full-sibling group) PIT tagged on the River Cerne, in 2006 and 2007, individual smolts detected moving downstream past the Millstream and main-river PIT tag antenna systems at East Stoke on the River Frome during the spring in 2007 and 2008 (15 March to 15 May, inclusive) and an estimate of the percentage of the wild smolt run that carried PIT tags each year.

For each simulated set of times, we calculated the intervals between fish and from those appropriate summary statistics. For each statistic we compared the observed value to the distribution across the 10 000 simulated data sets (with P defined as (1 + number of simulated values ≤ observed value)/(number of simulated data sets + 1)), to assess whether there was evidence of shorter intervals in a full-sibling group than the wild population.

We used summary statistics of the 10th percentile to assess short intervals, the median to represent the average interval and H, an index of regularity as described in Riley et al. (2014). H is between 0 and 1, equalling 1 only if all intervals are the same length, with smaller values potentially indicating more clustering, e.g. schooling. When calculating H, we excluded intervals greater than 12 h to avoid skewing the statistic, and we added 0.5 s to the intervals as the times were recorded to the nearest 1 s and any interval of zero would lead to $H = 0$. We used the statistical environment R v3.1.0 (R Development Core Team, 2014) to carry out the analysis.

We also examined the presence of groups of PIT-tagged smolts by selecting all records with ≤12 s between successive detections. We did this for each full-sibling group, the wild smolts and a combined data set. We used 12 s as the criterion because a drop-off in the frequency distribution had previously been observed at this point for wild smolts detected using the same equipment, in the same location, during the smolt migration periods of 2006−2011 (Riley et al., 2014). Therefore, we deemed this time interval between successive detections to be biologically relevant given the proportion of the wild population estimated to be PIT tagged (Table 1; Riley et al., 2014).

Ethical Note

We inserted the PIT tags (12 × 2.12 mm, 0.1 g) into the peritoneal cavity of the parr following the introduction and maintenance of anaesthesia by immersion in 0.4 ml/litre 2-phenoxy-ethanol. Following recovery from anaesthesia we returned all fish, within 1 h of capture, to the same 100 m section of river from which they had been removed. No mortalities were observed as a result of the tagging and there was no effect on survival, compared to control groups, to subsequent capture during migration as smolts the following spring (Ibbotson et al., 2013). All procedures were carried out under the authority of the U.K. Home Office, Animals (Scientific Procedures) Act 1986, Project Licences PPL 80/1851 and PPL 80/1913, and by licensed personnel covered by the Act. The study was performed with the permissions of The Centre for Environment, Fisheries & Aquaculture Science (Cefas) and Centre for Ecology & Hydrology (CEH) Animal Welfare & Ethical Review Committees.

The stocking of fry into the River Cerne and subsequent parr removal and return following PIT tagging were authorized by the U.K. Environment Agency.

RESULTS

Smolt Numbers

Table 1 gives the numbers of wild and stocked parr that were PIT tagged in 2006 and 2007, the numbers subsequently detected moving downstream and an estimate of the percentage of the wild smolt run that carried PIT tags each year.

Time of Day of Migration

The Rayleigh tests rejected random migration in favour of one-sidedness or directedness (P < 0.001) for wild River Frome smolts in both years (Table 2). For the *S. salar* stocked in the River Cerne,

Table 2
Summary statistics for migration time after sunset of full-sibling groups and wild smolts

	2007 Wild smolts	2007 All sibling groups	2007 Sibling group 1	2007 Sibling group 2	2007 Sibling group 3	2008 Wild smolts	2008 All sibling groups	2008 Sibling group 4	2008 Sibling group 5	2008 Sibling group 6
N	1251	59	16	19	24	1178	71	62	2	7
μ	19:07	18:54	23:43	15:56	16:52	03:27	02:33	02:22	–	01:31
95% CL (±)	1:31	3:40	2:53	4:31	4:09	0:27	1:36	1:43	–	9:11
r	0.099	0.186	0.435	0.264	0.256	0.338	0.375	0.376	–	0.329
P (Rayleigh test)	**<0.001**	0.129	**0.046**	0.268	0.21	**<0.001**	**<0.001**	**<0.001**	–	0.485

N is number of smolts; μ is mean lapsed time of migration after sunset (mean vector, h:min); r is length of mean vector; P (Rayleigh test) is statistical significance of the Rayleigh test for randomness. Significant results are shown in bold.

the Rayleigh tests rejected random migration in favour of one-sidedness or directedness for full-sibling group 1 ($P < 0.05$) in 2007 and full-sibling group 4 ($P < 0.001$) in 2008 (Table 2).

There was no significant difference between the mean time of smolt migration for wild smolts and full-sibling groups (where $N > 16$) from the same year (in 2007: for full-sibling group 2: $W = 1.468$, $N = 19$, $P = 0.48$; for full-sibling group 3: $W = 1.427$, $N = 24$, $P = 0.49$; in 2008: for full-sibling group 4: $W = 2.190$, $N = 62$, $P = 0.36$; Table 2). However, where sample sizes were small ($N \leq 16$) there were either not enough detections to perform the tests or marginal differences were apparent (e.g. in 2007: for full-sibling group 1: $W = 6.289$, $N = 16$, $P = 0.043$; Table 2).

Circular plots of the data revealed that in 2007 there was a general trend for the majority of wild River Frome smolts and River Cerne stocked smolts to migrate during the day, with another movement of fish following sunset (Fig. 2a). However, in 2008 there

was a general trend for the majority of wild River Frome and stocked smolts to migrate following sunset, with another movement of fish during the afternoon (Fig. 2b).

Date of migration

Table 3 summarizes the median date and spread of dates for wild smolts and different full-sibling groups detected migrating downstream past East Stoke during the spring in 2007 and 2008.

The median migration date for the full-sibling groups was earlier than the overall wild population in 2007 and later than average in 2008 (except full-sibling group 5). The spread of migration dates in terms of standard deviation was less for the full-sibling groups than the wild population in the associated year, with statistically significant differences ($P < 0.05$) for full-sibling groups 1 and 4. Similarly, the range and 90% interval were shorter for the full-sibling groups which is expected with fewer fish observed. The
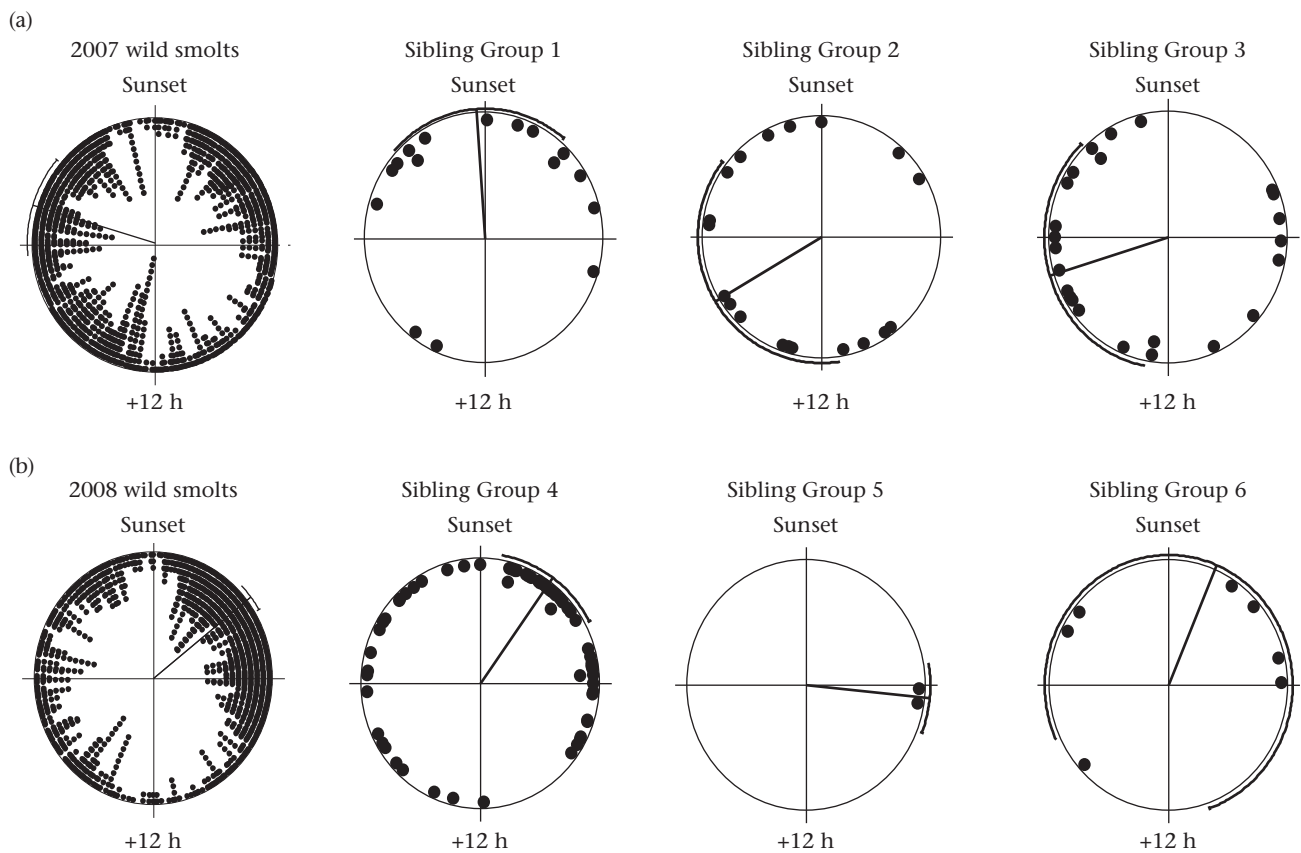
Figure 2. Distributions of smolt movement times relative to time of sunset, in (a) 2007 and (b) 2008. The black line from the origin to the circumference indicates mean time of movement, and the black line parallel to the circumference indicates the bounds of the 95% CI. In the two plots for wild smolts, each black circle represents two fish. In the plots for sibling groups, each circle represents one fish.

Table 3
Summary statistics for migration date and comparisons of full-sibling groups against wild smolts and wild smolts (Sim)

Group	No. of smolts	Migration date (days after 15 March) median	Comparison to wild for median P	Migration date (days after 15 March) SD	Comparison to wild for SD P	Migration date Observed range	Migration date Observed 90% interval	Simulated data Median range	Comparison to Wild (Sim) for range P	Simulated data Median 90% interval	Comparison to Wild (Sim) for 90% interval P
Wild smolts 2007	1251	40.4	–	8.8	–	58.6	28.0	–	–	–	–
Sibling group 1	16	33.8	**0.034**	4.9	**0.009**	18.8	14.3	30.0	**0.021**	24.1	**0.004**
Sibling group 2	19	36.3	0.088	8.4	0.317	32.1	26.4	31.3	0.563	24.4	0.649
Sibling group 3	24	38.8	0.194	6.7	0.053	27.7	17.2	32.8	0.159	25.3	**0.021**
Wild smolts 2008	1178	38.5	–	10.2	–	59.5	33.3	–	–	–	–
Sibling group 4	62	47.0	**<0.001**	6.0	**<0.001**	43.9	16.7	50.5	0.294	31.8	**<0.001**
Sibling group 5	2	31.1	0.214	21.2	0.071	30.0	27.0	8.1	0.950	7.3	0.950
Sibling group 6	7	48.0	**0.044**	4.7	0.106	13.4	12.1	26.8	0.101	22.7	0.113

The 90% interval is from the 5th to 95th percentile of migration dates. Significant results are shown in bold.

median migration date and the spread of migration dates in terms of standard deviation were comparable between full-sibling groups in the same year (Table 4).

The simulation-based test accounting for the number of fish gave a statistically significant shorter range ($P < 0.05$) in four of the 12 comparisons: the range of migration dates for group 1 and the 90% interval for groups 1, 3 and 4 (Table 3).

Schooling

There were no significant differences between the 10th percentile values for the distribution of time intervals (s) between successive smolts from the observed data for full-sibling groups and the 10 000 data sets sampled from the main wild smolt population (P, the proportion of simulated values less than observed value ≥ 0.05; Table 5). Similarly, there were no significant differences between the median values for the distribution of time intervals (s) between successive smolts from the observed data for full-sibling groups and the 10 000 data sets sampled from the main wild smolt population (P, the proportion of simulated values less than observed value ≥ 0.05) during both the day and night periods, and where the number of intervals (N) was >1 (Table 5).

There were no significant differences ($P \geq 0.05$) in the size of H for the distribution of time intervals (s) between successive smolts from the observed data for full-sibling groups and the 10 000 data sets sampled from the main wild smolt population (Table 6), although the values of H were typically smaller during the night for the observed data for full-sibling groups than the data sets sampled from the main wild smolt population.

Five hundred and thirty-nine PIT-tagged smolts were recorded in 202 groups having intervals ≤ 12 s between successive detections from the different individual fish comprising each group. In 2007, groups of wild smolts containing up to 14 PIT-tagged individuals from up to 10 different sites of origin (parr tagging sites) were identified (Riley et al., 2014). In 2008, groups of smolts containing up to six PIT-tagged individuals from up to five different sites of origin (parr tagging sites) were identified. On only one occasion did such groups contain two PIT-tagged individuals from the same full-sibling group (full-sibling group 3). This group contained four PIT-tagged smolts from three different sites of origin; both PIT-tagged smolts from full-sibling group 3 in this group were more closely associated with wild PIT-tagged fish of unknown parentage (4 and 1 s intervals, respectively) than with each other (>8 s interval).

DISCUSSION

The results of the current investigation provide clear evidence that on the River Frome the formation of schools of *S. salar* smolts is not significantly influenced by relatedness. Although the 10th percentile and median interval between successive PIT detections, and the regularity statistic H, were generally smaller (particularly at night) for the full-sibling groups than from the data generated from the general smolt population, these smaller intervals/indices of

Table 4
Comparisons between full-sibling groups for median migration date and variation in migration date

Comparison	Median date P	SD of date P
Sibling group 1 vs 2	0.322	0.081
Sibling group 1 vs 3	0.100	0.160
Sibling group 2 vs 3	0.495	0.686
Sibling group 4 vs 6	0.446	0.641

Full-sibling group 5 was excluded as there were only two observations.

Table 5
10th percentile and median for the distribution of time intervals (s) between successive smolts

Year	Day/night/ crepuscular	Full-sibling group	No. of intervals	10th percentile Observed	10th percentile Sim Median	10th percentile Sim 90% interval	10th percentile P	Median Observed	Median Sim Median	Median Sim 90% interval	Median P
2007	D	1	8	28417	22918	(3656, 65366)	0.61	62039	96677	(38495, 194636)	0.20
2007	D	2	16	6412	6618	(1155, 21924)	0.48	37017	74194	(33127, 110080)	0.06
2007	D	3	14	5661	8729	(1634, 29923)	0.31	42828	75252	(35828, 126248)	0.09
2008	D	4	22	5320	2356	(435, 7766)	0.86	36305	29359	(13007, 50821)	0.68
2008	D	6	3	115626	102781	(18394, 365029)	0.56	309496	213611	(48196, 643824)	0.66
2007	N	1	6	9981	24053	(3512, 88411)	0.20	81257	106857	(30548, 249605)	0.33
2007	N	3	4	14380	32282	(7625, 106475)	0.17	35728	92093	(26662, 260703)	0.11
2008	N	4	32	611	1316	(511, 2990)	0.09	8656	12784	(6071, 35769)	0.21
2008	N	6	3	23424	99172	(8557, 391011)	0.14	90130	229160	(25708, 688945)	0.20
2007	C	1	1	–	–	–	–	8214	76198	(11219, 405133)	**0.02**
2007	C	2	1	–	–	–	–	106243	49555	(9267, 308245)	0.70
2008	C	4	1	–	–	–	–	2022	23030	(3513, 296182)	**0.01**

Columns show the value from the observed data for full-sibling groups, the median and 90% interval from 10 000 data sets sampled from the main population (Sim) and P, the proportion of values less than or equal to the observed value. Significant results are shown in bold.

Table 6
Regularity statistic, H, for the distribution of time intervals (s) between successive smolts

Year	Day/night/crepuscular	Full-sibling group	No. of intervals <12 h	H Observed	H Sim Median	H Sim 90% interval	H P
2007	D	1	2	0.227	0.69	(0.017, 1)	0.19
2007	D	2	8	0.536	0.24	(0.011, 0.778)	0.82
2007	D	3	7	0.053	0.27	(0.011, 0.862)	0.17
2008	D	4	12	0.292	0.13	(0.021, 0.392)	0.87
2008	D	6	0	–	–	–	–
2007	N	1	2	0.685	0.85	(0.087, 1)	0.41
2007	N	3	3	0.505	0.99	(0.14, 1)	0.18
2008	N	4	27	0.054	0.12	(0.049, 0.261)	0.07
2008	N	6	1	1	1	(0.284, 1)	1.00
2007	C	1	1	1	1	(1, 1)	1.00
2007	C	2	0	–	–	–	–
2008	C	4	1	1	1	(1, 1)	1.00

Columns show the value from the observed data for full-sibling groups, the median and 90% interval from 10 000 data sets sampled from the main population (Sim) and P, the proportion of values less than or equal to the observed value.

regularity are not small enough to indicate an increase in schooling behaviour between related individuals. Indeed, these nonsignificant trends can be explained by the significantly shorter migration ranges ('smolt migratory windows'; McCormick et al., 1998) over which several of the full-sibling groups were observed to pass East Stoke compared to that seen in the general wild smolt population. Perhaps one might expect shorter migratory windows for the full-sibling groups as all were stocked into a small section of the River Cerne. All the full-sibling groups, therefore, experienced very similar environments both priming their 'migratory disposition' (zeitgebers) and stimulating downstream migration ('external releasing factors'), and all were migrating very similar total distances prior to detection at East Stoke, compared to the general wild River Frome smolt population. Closely related individuals might also be predisposed to respond to these zeitgebers/releasing factors in a similar way and over a shorter period, However, the comparable median migration date and the spread of migration dates between full-sibling groups in the same year suggest that local environmental conditions in *S. salar* parr nursery areas may have a greater influence on migratory timing than relatedness.

Although leading to differing conclusions, the results of the current investigation appear moderately consistent with the findings of Olsén et al., (2004) in that they indicate shorter time intervals between migrating *S. salar* smolt full-sibling groups. Where

the interpretations of the respective results diverge is the point at which these shorter intervals become biologically relevant with regard to the formation of kin-structured schools/groups, and the probable cause of these shorter intervals. Olsén et al. (2004) also studied migrating PIT-tagged full-sibling *S. salar* and reported related hatchery-reared smolts being separated by approximately 35 s while unrelated hatchery-reared smolts were approximately 42 s apart, corresponding to a spatial separation of 7.7–15 body lengths (using criteria applied in Griffiths & Ward, 2006). However, these values exceed the customary definition of fish shoal/school membership (3–5 body lengths; Pitcher & Parrish, 1993). In a more recent investigation on wild River Frome smolts (2003–2012, inclusive), at the same study site and using the same PIT detection equipment as in the current investigation, Riley et al. (2014) reported that when approximately 10% of the population was PIT tagged only the shortest intervals (≤ 12 s) between successive smolt detections were likely to be indicative of association (possible schooling), an interval also consistent in terms of body length separation (using the same criteria applied in Griffiths & Ward, 2006) with customary school membership. In both years of the current investigation approximately 10.8% of the wild population was estimated to be PIT tagged, and 31 (out of a possible 117; Millstream only) River Cerne-stocked PIT-tagged smolts of known parentage were observed to form an association with at least one

wild PIT-tagged River Frome smolt of unknown parentage where successive detections between smolts was ≤12 s. Yet on only one occasion did two PIT-tagged individuals from the same full-sibling group form part of such an association using the same criteria. Although the chance of association is clearly dependent on population size, the Monte Carlo simulation analysis undertaken in this investigation clearly demonstrates that the likelihood of schooling is not significantly increased between full siblings. Furthermore, there were no significant differences between the mean time of day of smolt migration for full-sibling groups (where $N > 16$) and wild River Frome smolts from the same year, or the median migration date between the full-sibling groups, further supporting the hypothesis that *S. salar* smolt migration is primarily an adaptive response to environmental conditions (i.e. phenotypic plasticity) rather than a behaviour based solely on genetics or kin-biased behaviour (Olsson, Greenberg, Bergman, & Wysujack, 2006).

The results of the current investigation are consistent with both the recent finding of Riley et al. (2014) regarding the break-up and reforming, at dusk and dawn, respectively, of schools of *S. salar* smolts on the River Frome, and the two-stage *S. salar* smolt migration theory proposed by Bakshtanskiy et al. (1980, 1988) and Riley (2007) comprising initial solitary movement, followed by schooling further downstream following a period of 'mutual learning' in front of sites of danger. Perhaps during these periods the smolts 'learn' not only about the potential dangers of the site, but also about each other in terms of 'personality' (leaders/followers) as they make moment-by-moment decisions on whether to join or leave a group.

Recent work on the collective movements of three-spined sticklebacks, *Gasterosteus aculeatus*, reported that social interaction, like leadership, is associated with individual boldness, but is also subject to social feedback (Jolles et al., 2015), raising the idea that differences in 'personality' between individuals in a group or population (e.g. leaders and followers) may be maintained because of their role in promoting social coordination (Johnstone & Manica, 2011; King, Johnson, & Van Vugt, 2009; Krause, Hoare, Krause, Hemelrijk, & Rubenstein, 2000). Work on birds has suggested similar hierarchical structures, with key individuals contributing disproportionately to group decisions, and the characteristics of individuals and their social system within mixed-species flocks in flight resulting in preferential associations that influence flock structure (Jolles, King, Manica, & Thornton, 2013). If also true for salmonid smolt schools, which by definition are coordinated, heterogeneity (in personality/boldness; genetic) may be a prerequisite in order to maintain collective behaviour, movement and decisions.

Another possible explanation for an apparent lack of a kin-structured migration could be provided by the signal detection theory (Shettleworth, 1998), which describes the capability of an individual to identify important visual and odour cues against a background of unimportant cues ('noise') in the wild. For example, once migration has commenced, darkness, turbidity, density and increased predation threat might impede visual cues, and increased dilution and nearest-neighbour distances might impede the detection of kin recognition odour cues.

It has been suggested that kin structuring might have additional advantages in migratory salmonid species such as *S. salar*, by improving subsequent natal homing to rivers of origin (Olsén, 1989; Quinn & Busack, 1985). However, perhaps the same advantages can be achieved by maintaining population-structured schools. Indeed, although no evidence of kin structuring has been found in *S. salar* adults at sea, a weak tendency for individuals from the same river to co-occur has been reported (Palm et al., 2008).

Different life stages face contrasting pressures that affect survival; therefore, kin interactions in *S. salar* may change throughout their life cycle. The same full-sibling groups (1—6) used in the current investigation were previously reported to occupy differing microhabitat breadths and preferences when parr (Fernandes, Copp, et al., 2015), where their growth was significantly influenced by both full-sibling group and an interaction between relatedness and density (Fernandes, Griffiths, et al., 2015) such that the growth benefits of associating with relatives was most apparent at high density (Fernandes, Griffiths, et al., 2015). However, the results of the current investigation clearly demonstrate that once these full-sibling groups become smolts the incidence of their schooling is not significantly influenced by their relatedness. Taken in conjunction with the results of Fernandes, Copp, et al. (2015) and Fernandes, Griffiths, et al. (2015) the current investigation is the first to illustrate that kin-biased growth and habitat preferences previously documented in the same six distinct full-sibling groups does not lead to kin-biased schooling in smolts. This demonstrates that the extent of kin-biased behaviour in fish can both differ within a life history stage under varying ecological conditions (Fernandes, Griffiths, et al., 2015) and shift from one life history stage to the next, even within the same full-sibling groups.

Acknowledgments

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