



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.

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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 Bakhtanskiy, Nesterov, and Neklyudov (1980) and Bakhtanskiy, 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

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