


## Original Article

# Regional variation in directed swimming by Atlantic salmon smolts leaving Scottish waters for their oceanic feeding grounds—a modelling study

James P. Ounsley <sup>1\*</sup>, Alejandro Gallego<sup>2</sup>, David J. Morris<sup>1</sup>, and John D. Armstrong<sup>1</sup>

<sup>1</sup>Freshwater Fisheries Laboratory, Marine Scotland Science, Faskally, Pitlochry PH16 5LB, UK

<sup>2</sup>Marine Laboratory Aberdeen, Marine Scotland Science, 375 Victoria Road, Aberdeen AB11 9DB, UK

\*Corresponding author: tel: + 44 131 24 42235; e-mail: [j.ounsley@marlab.ac.uk](mailto:j.ounsley@marlab.ac.uk).

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An understanding of the migratory trajectories and behaviours of Atlantic salmon post-smolts during the early marine phase of their life cycle is needed for effective conservation and marine planning. A simulation study of post-smolt migration from Scottish shores was carried out, combining a high-resolution hydrodynamic model of the Scottish continental shelf with a Lagrangian particle tracking model. Various different notional swimming behavioural scenarios were simulated, including current-orientated and compass-directed movement across a range of swimming speeds. Current-following behaviours did not facilitate migration towards feeding grounds in the North Atlantic. In addition, modelled trajectories resulting from directed-swimming behaviours imply that populations around Scotland need to adopt different locally adapted migratory strategies to successfully reach their feeding grounds.

**Keywords:** Atlantic salmon, individual-based model, migration, particle tracking.

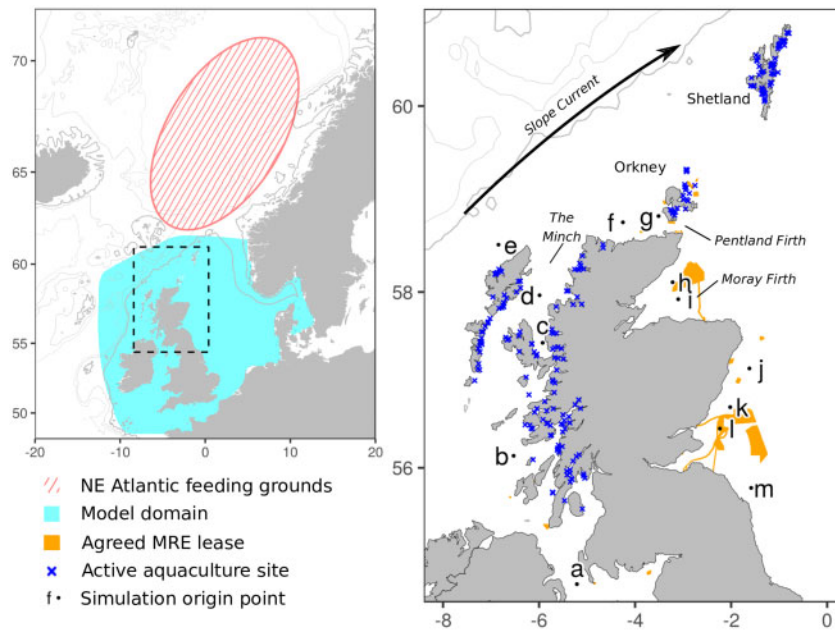
## Introduction

The abundance of Atlantic salmon (*Salmo salar*) has declined across much of the species' range over the last few decades largely due to a reduction in survival during the marine stage of the life cycle (Chaput *et al.*, 2005; ICES, 2009). After smolting, Atlantic salmon enter the coastal marine environment where they face numerous potential hazards (Thorstad *et al.*, 2012) including increased predation (Dieperink *et al.*, 2002), variable ocean climate (Friedland, 1998; Friedland *et al.*, 2000; Jonsson and Jonsson, 2004), and interaction with coastal industries, such as aquaculture (Revie *et al.*, 2009; Finstad *et al.*, 2011) and marine renewable energy (MRE) installations (Pelc and Fujita, 2002; Gill, 2005; Gill *et al.*, 2012).

Estimates from telemetry studies place mortality rates during the early marine phase at 0.3–3.4% per km, (Thorstad *et al.*, 2012) and these are likely to vary depending on the migratory behaviour and ultimate trajectory that a particular population

follows (Furey *et al.*, 2015). A better understanding of the migratory behaviour and marine distribution of salmon post-smolts is a fundamental requirement for effective management and conservation, to both inform impact assessments and facilitate marine spatial planning.

Post-smolt Atlantic salmon of European origin are known to migrate towards rich feeding grounds in the Northeast Atlantic in their first year at sea (Figure 1) (Shelton *et al.*, 1997; Friedland, 1998; Holst *et al.*, 2000) contributing to the Faroese fisheries (Jacobsen *et al.*, 2012). Trawling surveys conducted to the north of Ireland, north west of Scotland, and in the Faroë-Shetland channel found high densities of post-smolts along the slope current (Figure 1) located along the north west European continental shelf edge (Shelton *et al.*, 1997; Holst *et al.*, 2000). By following this current during migration, either actively or under drift, post-smolts may travel towards their feeding grounds in the Northeast Atlantic (Shelton *et al.*, 1997) whilst potentially saving



**Figure 1.** The study location showing the slope current along the continental shelf. (Left panel) Hashed area—approximate location of feeding grounds for European Atlantic salmon, shaded area—model domain. (Right panel) Crosses—active Atlantic salmon aquaculture sites in Scotland, labeled points—origin locations in the simulation, shaded areas—lease agreements with Crown Estate Scotland for marine renewable projects © Crown Copyright (2019). Bathymetry from Amante and Eakins (2009).

energy (Weihs, 1973) and may have access to rich intermediary feeding grounds (Holst *et al.*, 2000). However, due to the cost and difficulty of tracking or catching salmon at sea, the early stages of the post-smolts migratory trajectories from Scottish shores towards these currents and feeding grounds are still largely unknown. For example, it is unclear at which point post-smolts emigrating from the west coast of Scotland may enter the slope current and what behaviour these post-smolts may adopt to get there. There is even less known about the migration of post-smolts emigrating from the east coast, with an absence of observational data in the North Sea and no clear strong currents flowing in an appropriate direction for post-smolts to utilize. Currents in this region mainly flow in a southerly and south-easterly direction, heading away from the northerly feeding grounds.

Critical to determining the migratory trajectories of post-smolts is an understanding of the types of migratory behaviours that Atlantic salmon may employ in the marine environment. Migratory behaviour in marine organisms is poorly understood (Lohmann *et al.*, 2008). One hypothesis is that juvenile marine organisms will need to rely heavily on passive transport or active movement with the direction of currents to move away from spawning grounds, as a result of limited swimming capabilities relative to the strength of currents and the limited ability to navigate in an environment lacking in navigational cues (Harden Jones, 1968; Dadswell *et al.*, 2010). However, recent research has found that some marine organism, including salmon, may inherit sensory capabilities that enable effective juvenile navigation in the marine environment (Lohmann *et al.*, 2008; Chapman *et al.*, 2011; Putman *et al.*, 2014), and that directional migration, even at relatively slow speeds, can dominate overall movement (Scott *et al.*, 2012).

Technological advances in acoustic telemetry have allowed researchers to obtain movement data on migrating smolts;

however, these studies have mostly been limited to rivers, fjords, estuaries, and coastal embayments due to the requirement for fixed tag detectors or acoustic receiver arrays (Hedger *et al.*, 2009; Martin *et al.*, 2009; Furey *et al.*, 2015; Haraldstad *et al.*, 2017). These studies have revealed that the early stages of estuarine migration occur mostly at night and are characterized by movement with the ebb tide (Moore *et al.*, 1998; Haraldstad *et al.*, 2017). As smolts reach coastal embayments and enter into the sea, a transition in migratory behaviour is observed with a large proportion of post-smolt movement in this early marine stage being driven by active swimming behaviour, which can be independent of the direction of currents (Økland *et al.*, 2006; Hedger *et al.*, 2008; Kocik *et al.*, 2009; Martin *et al.*, 2009). Furthermore, it has been suggested that post-smolts may deploy some form of compass orientation to perform these seaward migrations (Hedger *et al.*, 2008; Martin *et al.*, 2009). Atlantic salmon are also thought to modify their migratory behaviour due to environmental cues such as gradients in salinity and temperature (Hedger *et al.*, 2008; Thorstad *et al.*, 2012). The role of such cues on behaviour in the marine environment is still largely unknown.

Particle tracking simulation studies offer a useful and cost effective tool for developing a predictive understanding of the movement of animals at sea and to identify plausible migration strategies (Byron and Burke, 2014; Li *et al.*, 2014; Chang *et al.*, 2016). In these studies the output from hydrodynamic models is used to drive individual-based models (IBMs) of virtual fish and may additionally include some behavioural component to simulate active migratory movement. There have been a small number of such models used to study the migration of both east and west Atlantic salmon populations, providing insight into possible migration routes, behavioural mechanisms, and the influence of currents at the local scale (Booker *et al.*, 2008; Mork *et al.*, 2012; Byron *et al.*, 2014; Moriarty *et al.*, 2016). Collectively, these

models suggest that different salmon populations may adopt different migratory behaviours to reach their marine feeding grounds (Byron and Burke, 2014), simultaneously supporting both current-following (Booker *et al.*, 2008; Mork *et al.*, 2012) and non-current-following hypotheses of migratory behaviour (Byron *et al.*, 2014; Moriarty *et al.*, 2016). This is potentially indicative of local adaptation (LA), which is generally more likely to be evident at the large geographic scales collectively covered by these models (Fraser *et al.*, 2011).

Whilst to date there are no studies examining migration from Scottish shores, two studies have simulated the migration of European post-smolts in the Northeast Atlantic, specifically looking at populations originating in the west coast of Ireland and the south-west Norwegian coast (Booker *et al.*, 2008; Mork *et al.*, 2012). These studies concluded that, for these populations, behaviours that largely follow local currents but show a preference for particular temperature and salinity conditions are viable behaviours, allowing migrating post-smolts to reach their feeding grounds in the Northeast Atlantic.

In this study we use a recently developed hydrodynamic model of the Scottish continental shelf waters, the Scottish shelf model (SSM), to simulate the trajectories of notional post-smolts migrating from Scotland. We test a range of behaviours and swimming speeds and consider the resultant trajectories with respect to facilitation of migration towards the Northeast Atlantic feeding grounds. Central to the study is a comparison of two hypotheses for post-smolt migration; a predominantly current-following model (Booker *et al.*, 2008; Dadswell *et al.*, 2010; Mork *et al.*, 2012) and a directed-swimming model (Byron *et al.*, 2014; Moriarty *et al.*, 2016). We also investigate the degree to which migratory behaviours are likely to be location- or region-specific by running simulations from origin points distributed around the Scottish coastline and comparing relative success rates under different conditions.

## Methods

We use an IBM, which simulates a population as being composed of discrete individual organisms (DeAngelis and Grimm, 2014), to simulate the migration of Atlantic salmon from the Scottish coast. In the IBM, output from a hydrodynamic model of Scottish waters drives a Lagrangian particle tracking model with behavioural components, all of which are detailed below.

### The SSM

The SSM is a validated three-dimensional hydrodynamic model of the Scottish shelf (Wolf *et al.*, 2016; De Dominicis *et al.*, 2018). The model includes 20 vertical layers, and covers the waters of the Scottish continental shelf out to the 200 m depth contour at the shelf edge. We used a climatological run that represents an “average year.” Meteorological forcing corresponded to the average of a 30-year period (1981–2010). The averaging of forcing data to produce a climatology would smooth out specific meteorological events (e.g. storms) and ongoing work is investigating the effect of averaging on hydrodynamic modelling results. However, short-term meteorological variability is highly unlikely to change the overall patterns of our results, given the geographical and temporal scale of our simulations. Tides were included as an average tidal year (nominally 1993) and freshwater runoff from the land was represented by a 50-year river climatology (1962–2011). This river climatology incorporates only freshwater

sources around Scotland and Northern Ireland. Although the detailed effect of a lack of freshwater input from land elsewhere in the model domain on residual currents and water characteristics is the subject of ongoing analysis, modelled residual circulation and water characteristics compare well with accepted patterns derived from observations (Wolf *et al.*, 2016). The SSM is an implementation of the FVCOM hydrodynamic model, which uses an unstructured grid, allowing for variable horizontal resolution, down to tens- to hundreds of metres per grid element, and therefore a more accurate representation of complex topology than regular or structured grids (Chen *et al.*, 2003). The SSM includes a number of high-resolution nested model areas within a larger low-resolution shelf-wide model, only the shelf-wide model was used in this study. Hourly outputs from the SSM of current velocity, temperature, and salinity were used to drive the offline particle tracking component of the model.

### Particle tracking

To predict salmon migration trajectories the SSM was used to drive an IBM that simulates a range of possible swimming behaviours and biological processes. The IBM is adapted from the offline Lagrangian particle tracking software FISCAM (<https://github.com/GeoffCowles/fiscam>, Liu *et al.*, 2015), developed for the FVCOM framework. The horizontal position ( $x_t, y_t$ ) of each simulated post-smolt at time step  $t$  is updated as follows,

$$x_{t+\Delta t} = x_t + (u + g_x(x_t, y_t))\Delta t + Q\sqrt{2K\Delta t},$$

$$y_{t+\Delta t} = y_t + (v + g_y(x_t, y_t))\Delta t + Q\sqrt{2K\Delta t},$$

where  $u$  and  $v$  are the  $x$  and  $y$  components of velocity from the SSM at the particles' current position,  $\Delta t$  is the length of each time step,  $g_x, g_y$  are the  $x$  and  $y$  components of the active swimming behaviour of the post-smolt,  $Q$  is a random draw from a normal distribution with mean of 0 and standard deviation of 1 and  $K$  is the diffusion constant. Particle positions from time step  $t$  to  $t + \Delta t$  are updated by integrating the velocity field using a 4th-order explicit 4-stage Runge–Kutta scheme (ERK4). The final term adds a Gaussian random walk component to the post-smolt behaviour to take account of random perturbations of the post-smolt's position due to diffusion and stochastic behaviour. Post-smolts are constrained to the surface layer of the hydrodynamic model, consistent with the results from tracking studies and trawl surveys on post-smolt migration (Shelton *et al.*, 1997; Holst *et al.*, 2000; Hedger *et al.*, 2009) and adult homing migration (Godfrey *et al.*, 2015) revealing predominately near-surface habitat use.

For all simulations  $\Delta t$  was set to 1 h, in line with the output from the SSM. The behaviour function  $g$  was varied to simulate a variety of behavioural conditions, detailed below. The implementations can generally be grouped into current-following behaviours and directed-swimming behaviours.

### Current-following behaviours

The first set of behavioural scenarios is those which are dependent only on local physical conditions. All these behaviours have the potential to result in a swimming vector that is largely aligned with the direction of local currents. We include these behaviours to provide a comparison to previous particle tracking studies and migration hypotheses (Booker *et al.*, 2008; Dadswell *et al.*, 2010;

Mork *et al.*, 2012; Byron and Burke, 2014) and consider the required biological mechanisms in the discussion.

#### *Rheotaxis and passive drift*

Rheotaxis is the unconditioned orientation response to water flows and is either positive or negative depending on whether the orientation is away from or towards the direction of flow, respectively. In the rheotaxis condition  $g$  was implemented such that all smolts actively swim in the direction of the local horizontal currents with a specified constant swimming speed, therefore simulating negative rheotaxis. In the passive drift condition the swim speed was 0 and the simulated smolts effectively move only under the influence of the currents creating a pseudo “control” scenario.

#### *Mork*

In the Mork condition  $g$  was implemented to replicate the behavioural model used in the simulation study of Mork *et al.* (2012) whereby post-smolts actively swim in the direction of the local currents with a specified swim speed. In addition, when in regions outside of a preferred temperature range of 8–15°C or preferred salinity of at least 35 PSU, an additional horizontal component was added to particle movement towards the preferred temperature and salinity range, resulting in particles travelling at increased speed. The swim speed increase was directed along the local temperature and salinity gradient with a magnitude linearly determined by the difference between the current and preferred temperature and salinity values, up to a maximum of 0.5 BL s<sup>-1</sup> for a 1°C or 1 PSU difference, respectively.

#### *Booker*

In the Booker condition  $g$  was implemented to replicate one of the behavioural models used by Booker *et al.* (2008). Similar to the Mork condition, simulated post-smolts follow horizontal temperature gradients, swimming with a constant speed towards temperatures in the range of 4–8°C. When in their preferred temperature range the simulated post-smolts swim in a randomly selected direction.

### **Directed-swimming behaviours**

In addition to the above current-following behaviours, a set of directed-swimming conditions was also simulated. In these conditions, simulated post-smolts swim along a constant compass bearing, in addition to movement due to the influence of the local currents. Three central compass bearings were chosen, with simulated post-smolts being assigned a constant bearing upon initialization, randomly drawn from a range of ±15° from a central bearing of NW, N, or NE. These bearings were chosen based on the *a priori* assumption that they would allow Scottish post-smolts to leave Scottish waters and head towards their oceanic feeding grounds.

### **Swim speed and growth**

Optimal cruising speeds for migratory fish, based on minimizing swimming costs to cover a given distance, have been estimated to be around 1 BL s<sup>-1</sup> (Weih, 1973; Trump and Leggett, 1980), where BL is body length. However, optimal swimming speeds may be greater than this value when fish are faced with high velocity barriers (Castro-Santos, 2005). Furthermore, it may benefit

post-smolts to swim faster than optimal cruising, and hence use more energy on locomotion, if they benefit from arriving in good feeding areas and/or escape areas of high predation risk sooner. Estimated minimum progression rates for migrating salmon can be as much as 7–30 km per day (Thorstad *et al.*, 2012) corresponding to 0.54–2.3 BL s<sup>-1</sup> for a 15 cm post-smolt. To test the sensitivity of the output from simulations to swim speed, for each of the behavioural conditions repeat simulation sets were run with swimming speeds of 1, 1.5, 2, 2.5, and 3 BL s<sup>-1</sup>. For each combination of swimming behaviour and swim speed, smolt length was determined using a growth model adapted from Mork *et al.* (2012). Under the growth model, the length of a post-smolt after  $d$  days at sea was given by  $l = 0.125e^{\alpha d}$  with  $\alpha = 0.0059$ . The initial body length of 0.125 m corresponds to the estimated average body length of smolts emigrating from Scottish rivers (Malcolm *et al.*, 2015, I. A. Malcolm, pers. comm.).

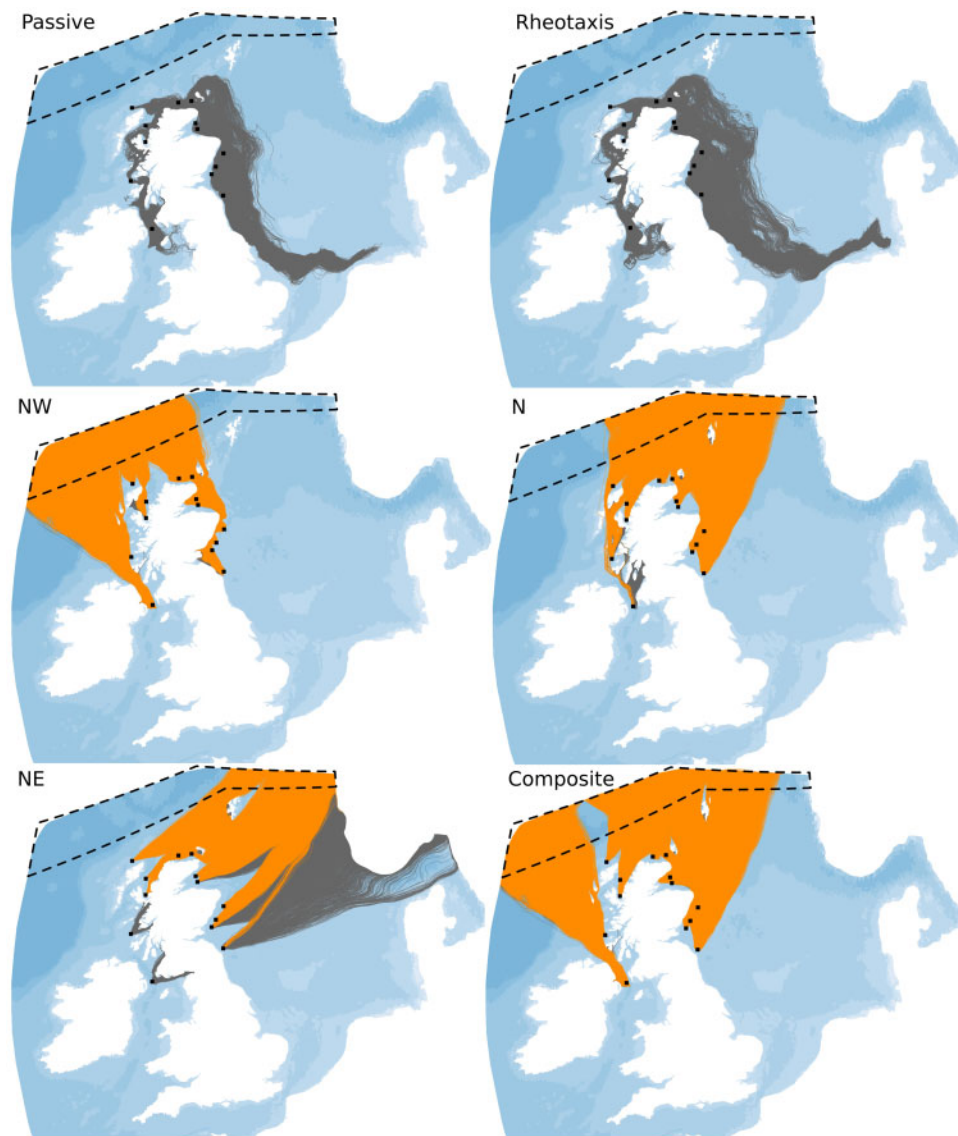
### **Particle origin and collision avoidance**

In each simulation, 5000 simulated post-smolts were initialized at 13 origin points near river systems of interest around the Scottish coast (Figure 1). The focus of this study was to make predictions about the marine migration of salmon post-smolts; consequently, each release point was deliberately displaced a small distance out to sea from the coastline to reduce the risk of simulated post-smolts failing to escape near shore topography. Despite this displacement, collisions with the coastline were found to be quite frequent for some origin points when a directed-swimming behaviour was used. Consequently, a collision avoiding mechanism was implemented to mitigate this issue. For a time step in which a particle was within a boundary element, or would have exited the SSM domain as a result of the behavioural movement function ( $g$ ), movement for that particle was switched to be in the direction of the local currents for that time step. This was found to be an effective general collision avoiding mechanism and included in all directed-swimming behaviours (Supplementary Text).

The simulated post-smolts were released at times randomly drawn from a normal distribution with mean of 3 May (DOY 124) and standard deviation of 31 days, truncated at 12 April (DOY 103) and 24 May (DOY 145), being ~25 and 75% quantiles of the distribution. These release times were chosen to match those found for emigrating post-smolts from Scottish shores (Malcolm *et al.*, 2015).

### **Model assessment**

To evaluate the relative performance of the different behavioural models and swimming speeds, a “successful migration criteria” was devised based on the requirement that Scottish post-smolts leave the Scottish continental shelf for the Norwegian Sea within the first few months of migration (Shelton *et al.*, 1997; Holst *et al.*, 2000; Ó Maoiléidigh *et al.*, 2018). The SSM domain is limited to the Scottish continental shelf and does not cover the Northeast Atlantic feeding grounds, consequently a region was delineated along the northerly and north-westerly edge of the SSM domain with the assumption that migrating post-smolts would be required to pass through this region en route to the feeding grounds. The region was defined by an east-west line from the Norwegian coast at a latitude of 61 degrees and a south-west to north-east line to the north-west of the continental shelf edge (Figure 2). A particle crossing either of these lines



**Figure 2.** Traces of particles in the passive, rheotaxis, NW, N, and NE condition with a swim speed of  $2 \text{ BL s}^{-1}$ . The dashed lines denote the “boundary for migration,” light traces are for particles crossing the boundary within a 100-day simulation run, dark traces give a sample of particles not crossing the boundary. Black squares show origin points. The composite plot shows trajectories when particles adopt the most successful behaviour for each origin.

within a 100-day simulation was deemed to have crossed the “boundary for migration” and emigrated successfully. For each of the behavioural conditions and swim speeds the proportion of particles reaching the boundary for migration for each origin was calculated.

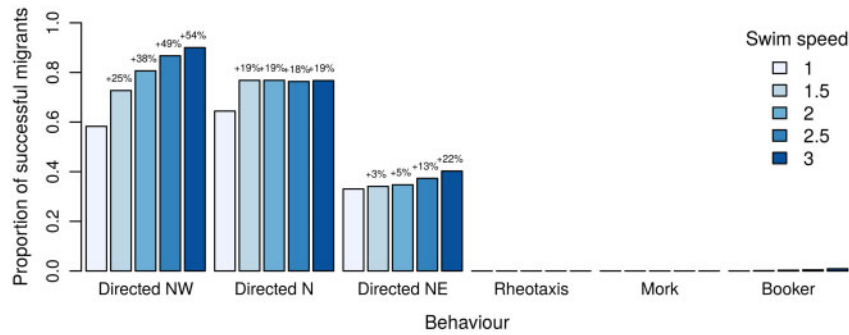
## Results

### Migration trajectories

The trajectories of particles in the rheotaxis condition show a distinctive pattern whereby most particles, irrespective of origin, move towards the south-east coast of Scotland, and are restricted to the North Sea (Figure 2). For the majority of particles originating from the west coast this requires traversing along the north coast of Scotland, either around the north of Orkney or through the Pentland Firth. Particles originating from the south-west

(origin a) are an exception to this pattern remaining local to their origin between Scotland and Northern Ireland. Qualitatively similar trajectories are observed with the passive drift, Mork, and Booker behavioural models.

The trajectories of particles in the directed-swimming conditions are substantially different from one another depending on the direction of swimming and also greatly diverge from the pattern seen in the current-following behaviours. In the NW condition (Figure 2), west and north coast particles (origins a–g) generally move rapidly away from the coast towards the slope current, with particles from the south-west (origins a and b) avoiding the Minch and travelling west of the Hebrides to enter the slope current at a relatively low latitude. East coast particles (origins h–m) stay close to the coast, following the shoreline north through the Pentland Firth and west of the Orkney and Shetland islands. In the N condition (Figure 2), particles from



**Figure 3.** The proportion of particles crossing the boundary for migration within a 100-day simulation run for each of the behavioural conditions and swim speeds. The percentage increase relative to  $1 \text{ BL s}^{-1}$  is shown for each condition when the  $1 \text{ BL s}^{-1}$  success rate is non-zero.

south-west origins (a–d) head through the Minch and enter the slope current off the north coast of Scotland. East coast particles are further removed from the shoreline than in the NW condition, with some particles from the south-east (origins j–m) heading north-east and passing west of the Shetland Islands. In the NE condition (Figure 2), particles from the south-west (origins a and b) become trapped against the west coast and do not head north. For particles from the north and east (origins c–m), most head towards the Norwegian coast, traversing south of the Shetland Islands (with the exception of some particles from origin e).

### Successful migration

When comparing the different behavioural models with the successful migration criteria a clear difference between the current-following and directed-swimming conditions is observed. In all simulations with a current-following behaviour (passive drift, Mork, Booker, or negative rheotaxis)  $<0.5\%$  of particles fulfilled the successful migration criteria. For the directed-swimming behaviours, however, migration rates were substantially higher. The percentage of particles reaching the region for migration ranged from 33 to 87% conditional on the direction of swimming and the swimming speed (Figure 3).

In light of the near-zero success rates and resultant trajectories of the current-following behaviours after a 100-day simulation, an extended simulation was run with 1000 particles originating at origin j adopting the rheotaxis behaviour for a total of 255 days at  $2 \text{ BL s}^{-1}$ . The aim was to verify whether east coast particles could successfully migrate by following currents in the North Sea given enough time. Even after the extra run time, none of the particles reached the boundary for migration, remaining in the south-east of the North Sea. It should be noted that the SSM has much lower resolution in this region than around the Scottish coast line and so may not fully capture the local hydrodynamics leading to greater uncertainty in the tail end of the particle trajectories.

Of the different swimming directions tested, the highest proportion of particles crossing the boundary for migration was achieved in the N and NW conditions, with higher success rates in the NW than in the N condition at faster swim speeds. Performance in the NE condition was the worst out of the directed-swimming behaviours for all swim speeds (Figure 3). A swimming speed of  $1 \text{ BL s}^{-1}$  consistently lead to the lowest success rates in all conditions. For the NW and NE conditions success rates consistently improved with swimming speed but plateaued for the N condition at speeds of  $1.5 \text{ BL s}^{-1}$  and above.

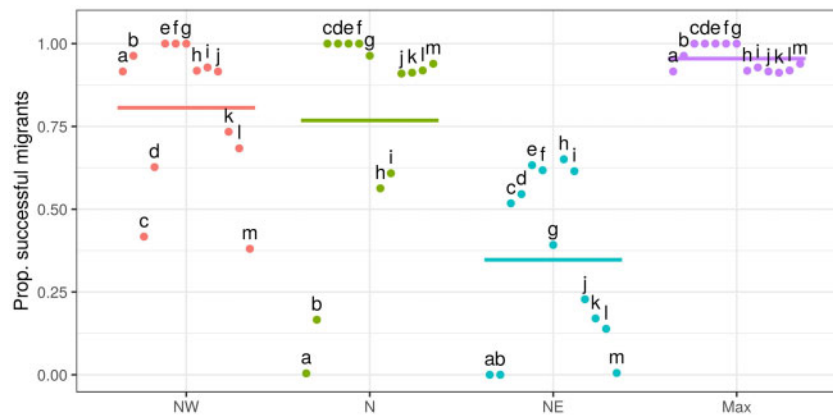
Swimming speeds in excess of  $1 \text{ BL s}^{-1}$  are consistent with previous research (Thorstad *et al.*, 2012).

For the directed-swimming behaviours there was substantial variation in meeting the successful migration criteria among origins, with no single condition leading to the highest success rate for all origin points (Figure 4). A clustering analysis of the successful migration rates across the directed-swimming conditions for each origin point reveals that the migratory success rates for different behaviours was region specific (Figure 5, Supplementary Text). Origin points could be generally grouped into five geographically related clusters based on performance across the conditions. Particles from origins a and b in the south-west predominately performed well in the NW condition only. Particles from origins c and d within the Minch performed strongly in the N condition and reasonably well in both the NE and NW condition. Particles from origins e–g in the north together with particles from j in the east generally performed well in both the NW and N conditions, with reasonable performance in the NE condition also. Particles from origins h and i within the Moray Firth in the north east have similar pattern to particles from e–g and j, but with relatively worse performance in the N condition. Finally particles from origins k–m in the south-east performed well predominately in the N condition with reasonable success in the NW condition.

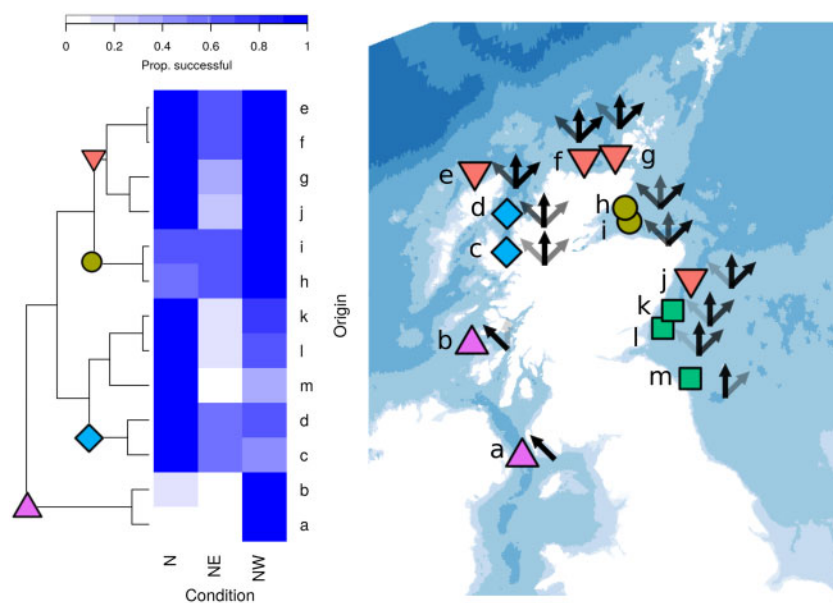
If we consider a “best case scenario” in which particles from each origin adopt the behaviour which leads to the maximum success rate for that origin point we see a significant increase in the mean success rate relative to homogeneous behaviour across origin points, when measuring migration as the proportion of particles crossing the migration boundary (Figure 4). In this “max” condition with a swim speed of  $2 \text{ BL s}^{-1}$  95% of all particles crossed the boundary within the 100-day simulation, compared to 81% in the NW condition. The composite traces of particles resulting from this “max” condition are shown in Figure 2.

### Discussion

The results from this simulation study lead to the inference that Scottish Atlantic salmon cannot rely on purely current-following behaviours to reach their feeding grounds in the Northeast Atlantic. This is particularly true for populations on the east coast, where prevailing currents tend to result in migration to the south and then the east. Actively swimming in a fixed direction was found to be a plausible hypothesis for post-smolt migratory



**Figure 4.** The distribution and mean (horizontal bar) proportion of particles meeting the successful migration criteria by origin point for each of the directed-swimming behaviours and for a “best case scenario” in which particles from each origin adopt the directed-swimming behaviour that leads to the maximum success rate for that origin. Results are from simulations with a swim speed of  $2 \text{ BL s}^{-1}$ .



**Figure 5.** (Left panel) The proportion of particles crossing the boundary for migration in the directed-swimming conditions with swim speed of  $2 \text{ BL s}^{-1}$ . Origins are grouped by similarity of outcome across conditions using an Euclidean distance metric. (Right panel) The groupings mapped to origin, with success rates in each directed-swimming condition indicated by the darkness of the associated arrow.

behaviour. The swimming direction that led to the highest proportion of particles meeting our successful migration criteria varied with the location of origin of simulated smolts, with geographically close origin points having similar success profiles.

Our findings are consistent with the results of previous simulation studies on north west Atlantic salmon in that directed-swimming behaviour during post-smolt migration is supported over current-following migration or passive drift (Moriarty *et al.*, 2016). This is in contrast to output from models of European Atlantic salmon migration, which support some variation of current-following behaviour (Booker *et al.*, 2008; Mork *et al.*, 2012). An explanation for this discrepancy is that the characteristics of the Scottish marine environment require a different behavioural strategy, particularly in the early stages of migration following escapement from the coast, to that of the Irish and Norwegian populations that were the focus of these previous

studies. The presence of regional differences in migration behaviour is supported by previous research (Lacroix, 2008; Lacroix and Jonsson, 2013; Byron and Burke, 2014). Furthermore, given that no single behaviour modelled in this analysis led to high rates of successful migration for all the tested origin points, our results suggest that there will be benefits to location- or region-specific migratory behaviours, which could be locally adaptive. Indeed, when considering a best case scenario, allowing for origin specific behaviours, nearly all particles successfully crossed our boundary for migration.

In this study, we used a climatological run representing an “average year” and so did not investigate the impact of year-to-year-variation in the hydrodynamics. Previous studies have shown that inter-annual variability in climatic conditions can have important implications for migration trajectories (Mork *et al.*, 2012; Reddin *et al.*, 2012; Byron *et al.*, 2014).

However, it is unlikely that such variation would change our model output sufficiently so as to alter our main conclusions that Scottish Atlantic salmon cannot rely on current-following behaviour alone and that geographically specific directed-swimming behaviour is the most likely requirement to allow post-smolts to reach their feeding grounds.

The predicted trajectories provide useful insight for management purposes. In both the N and current-following conditions, post-smolts originating from the south-west of Scotland are predicted to traverse through the Minch, an area with a high density of aquaculture development (Figure 1). This is not the case in the NW condition, where the same post-smolts are predicted to travel west of the outer Hebrides. This implies that differences in post-smolt migratory behaviour could have significant implications for the risk to Scottish salmon of potentially hazardous interactions with aquaculture, in particular due to increased risk of sea-lice infestation which in some cases can reduce the physical condition of salmonids and ultimately increase mortality (Finstad *et al.*, 2011). By understanding the migration routes of post-smolts in this region, any hazardous interactions between salmon and aquaculture could potentially be mitigated through strategic placement of future aquaculture development. Similarly, in both the current-following and NW conditions a large proportion of emigrating smolts traverse through the Pentland Firth (Figure 1) from west to east and east to west respectively, whilst in the N and NE conditions the proportion of particles using this route is greatly reduced. This region is of interest as it is a proposed site of large-scale tidal stream MRE developments, which have been subject to consideration in terms of potential hazard to salmon (Gill, 2005; Malcolm *et al.*, 2010; Gill *et al.*, 2012). Whilst the current level of MRE development within Scottish seas is relatively minor, the extent of agreed leases for future MRE development is significant (Figure 1). Our results highlight how the spatial overlap of post-smolts and coastal developments may greatly depend on the combination of river of origin and the migratory behaviour.

Whilst this analysis can help rule out some behaviours, the methods do not allow us to determine whether a given modelled migratory behaviour is actually used by post-smolts. First, modelling salmon behaviour in all its complexity is not possible in a computer simulation, furthermore multiple behaviours may lead to similar outcomes and the lack of observational data makes differentiating among behaviours difficult (Byron *et al.*, 2014). However, our results support a directional active swimming behaviour as a plausible and likely candidate for early Scottish post-smolt migration and demonstrate that there are clear benefits for location-specific swimming headings. Although there is uncertainty about the biological mechanisms used by migrating salmon (Lohmann *et al.*, 2008), they have been shown to be sensitive to magnetic and celestial cues (Quinn, 1980), which could facilitate such an outward directed migration.

It is plausible that Scottish salmon may change migratory behaviour, for example to follow currents as their migration progresses. A switch to rheotaxis upon reaching the slope current would result in north-easterly movement towards the Norwegian Sea, coinciding with the migratory pathways predicted in the Booker and Mork studies. A transition to current-following or passive drift behaviour once in the open ocean would also align with the hypothesis that Atlantic salmon utilize the North Atlantic subpolar gyre during their long-term migration (Dadswell *et al.*, 2010). To date, there is no widely accepted

mechanism through which pelagic organisms may be able to directly detect and follow currents in the open ocean, where there is an absence of stationary reference points (Lohmann *et al.*, 2008; Chapman *et al.*, 2011). This broadly aligns with our conclusions that directed swimming is a more likely migratory behaviour. However, one hypothesis for a mechanism which might enable open ocean current-following behaviour in salmon is based on evidence that they are sensitive to differences in the movement between vertical oceanic layers (Døving and Stabell, 2008). It is likely that salmon exhibit location-specific behaviours to escape from the immediate coastal zone, and these may be quite different from subsequent trajectories. For example, post-smolts from Loch Linnhe (a sea loch on the west coast of Scotland) first move approximately south-west to swim rapidly out of the loch (Middlemas *et al.*, 2017) and must then traverse around the Isle of Mull before escaping to open water.

The requirement for region- or location-specific migratory behaviour in Scottish salmon suggested by our analysis raises the question of whether such behaviours could result from LA. The presence of a spatially heterogeneous phenotype alone is not necessarily indicative of LA, which could also result from mechanisms such as phenotypic plasticity or selective mortality. Furthermore, LA is likely to be prevented under high levels of gene flow, resulting from variable homing for example, or genetic drift (Fraser *et al.*, 2011). However, the Scottish salmon population displays significant genetic structuring at the regional level (Gilbey *et al.*, 2016) reflecting, at least in part, the original colonization of the rivers (Cauwelier *et al.*, 2018b). In addition, tributary-specific run-timing behaviour in Scottish salmon has been found to be strongly heritable through translocation experiments (Stewart *et al.*, 2002), and genetic markers linked to differences in run-timing have been identified (Cauwelier *et al.*, 2018a). Together this supports the hypothesis that migratory behaviour in Scottish salmon could be locally adapted.

The effect of swim speed on success is difficult to interpret for the directed-swimming behaviours due to the frequent requirement for navigation of the coastline, particularly for particles originating in the south-east in the NW condition and particles in the south-west in the NE condition. Whilst the general collision avoidance mechanism deployed was effective in increasing success rates (Supplementary Text), particles inevitably travelled more slowly around the coastline than would be expected had a more optimum route been utilized. As a result the marked increase in success rate with swim speed in the NW condition, for example, was largely driven by particles from origins j–m in the south-east for which fast swim speeds compensated for slowed traversal due to the collision avoidance mechanism. In addition, due to a lack of information on arrival times at different locations at sea we could not penalize early arrival resulting from travelling too quickly.

Further research is required to improve our understanding of post-smolt migration from the Scottish coast. A cautionary note is that although our analysis suggests that a current-following behaviour is unlikely for Scottish post-smolts, to date there has been no published systematic sampling of the North Sea to confirm that post-smolts do not indeed follow local currents south-east along the Scottish coast. More generally, further information on the spatial and temporal distribution of migrating post-smolts would greatly aid model validation. Whilst previous particle tracking studies have used existing data from trawling surveys to ground-truth model output (Mork *et al.*, 2012), there is little data



available within the SSM domain with appropriate spatial and temporal coverage to allow for differentiation between the competing behavioural hypotheses presented in this study. A key requirement of further data collection is to differentiate between behaviours to escape from the coast and those subsequently associated with the location of northerly high seas feeding areas.

Structured experimental work may provide a greater insight into Atlantic salmon migration from Scottish shores. For example, the extent of LA of migratory behaviour may be tested through transplantation studies that allow for a direct comparison of the swimming behaviour of fish from different rivers of origin (Godø, 1995). Such methods would also be useful for examining the flexibility of migration behaviour to local conditions and currents. In addition, there is scope for the strategic deployment of acoustic receivers for use in tracking smolts carrying acoustic emitting tags, informed by model outputs such as those presented here, to test hypotheses about location-specific migratory routes (Hedger *et al.*, 2009; Plantalech Manel-La *et al.*, 2011; Furey *et al.*, 2015; Lothian *et al.*, 2017). In combination with modelling, these methods will provide valuable tools for understanding salmon migration, managing coastal development, and directing future research effort.

### Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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