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Published in:
ICES Journal of Marine Science

Publication date:
2021

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Citation for published version (APA):
McIlvenny, J., Williamson, B., Goddijn-Murphy, L., Del Villar-Guerra, D., & Gauld, N. R. (2021). Combining acoustic tracking and hydrodynamic modelling to study migratory behaviour of Atlantic salmon (*Salmo Salar*) smolts on entry into high-energy coastal waters. *ICES Journal of Marine Science*, 78.
<https://doi.org/10.1093/icesjms/fsab111>

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1 Combining acoustic tracking and hydrodynamic modelling to study migratory
2 behaviour of Atlantic salmon (*Salmo salar*) smolts on entry into high-energy coastal
3 waters

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9

10 Abstract

11 Migration from fresh water to the marine environment is a crucial, transitional stage in the
12 development of Atlantic salmon (*Salmo salar*). This study used a combination of acoustic
13 tracking, instrument data and hydrodynamic modelling to examine behaviour of juvenile
14 salmon (smolts) during their transition from fresh water to the marine environment. The study
15 focuses on a high-energy coastal environment in northern Scotland, which is currently being
16 developed for renewable energy extraction and where there is potential for negative impacts
17 on salmon with energy extraction devices and structures. Thirty-four smolts were captured in
18 the River Wick in Caithness and tagged with acoustic tags transmitting at 69 kHz. The
19 Telemac-Mascaret modelling suite was utilised to construct a 3-dimensional model of the study
20 area and surrounding waters to estimate smolt-current interactions during detection times.
21 Timing of migration was linked to low-light conditions, with smolts mainly exiting the river at
22 night and when the moon was below the horizon. The movement of most of the tags conformed
23 with modelled tidal currents and the tracks matched modelled marine tidal patterns. Smolts
24 were detected only on a single tide suggesting that they rapidly cleared the vicinity of the
25 receiver array.

26 1. Introduction

27 There is a lack of information regarding the behaviour of out-migrating juvenile Atlantic
28 salmon (*Salmo salar*), known as smolts, and their use of coastal waters (McCormack et al.
29 1998; Moriarty et al, 2016; Strøm et al. 2018, Ounsley et al. 2020). This knowledge gap is
30 particularly important because these coastal waters are high-energy environments that are
31 increasingly being developed for generation of marine renewable energy via tidal-flow, wind
32 and wave devices. Numerous productive rivers of high conservation value that also support
33 high-value salmon fisheries discharge into the same coastal waters (Malcolm et al. 2010). There
34 is therefore potential for negative interactions between renewable developments and migrating
35 smolts (Malcolm et al. 2010). Potential impacts are physical impact, acoustic and
36 electromagnetic impacts (Bartlett & Thompson 2012). The extent of this risk is unknown
37 because the full migratory behaviour of the fish is unknown in relation to planned or existing
38 renewable energy developments.

39 In the northern rivers, juvenile salmon spend one or two years in fresh water before entering
40 the smolt stage in early summer when they migrate to the marine environment (Buck &
41 Youngson, 1982; Malcolm et al. 2015). Mortality rates among smolts are reportedly high
42 (Alerstam et al. 2003; Halfyard et al. 2012; Chaput et al. 2018; Lothian et al. 2017, Newton et
43 al. 2016) indicating that migration is a critical stage of the life cycle (Thorstad et al., 2012).
44 Currently, Atlantic salmon are in decline throughout their range for various reasons such as
45 global warming, fisheries impacts and changes in freshwater habitats (Lothian et al. 2017;
46 Nicola et al. 2018) and better understanding of the fishes' behaviour at the critical smolt stage
47 of development may aid improved management.

48 After entering the marine environment, smolts ultimately migrate to feeding grounds in the
49 distant North Atlantic (Holst et al 2000; Haugland et al 2006; Dadswell et al. 2010; Lefèvre et
50 al. 2012). However, the behavioural mechanisms that support smolt migration between their

51 initial entry to the marine environment and their subsequent appearance on the ocean feeding
52 grounds are largely undocumented. Moreover, given the Atlantic salmon's wide range and the
53 disparate characteristics of the various coastal waters that local groups of smolts must traverse,
54 varying forms of behaviour must be invoked. There is a lack of information on smolt movement
55 into and through high-energy coastal waters.

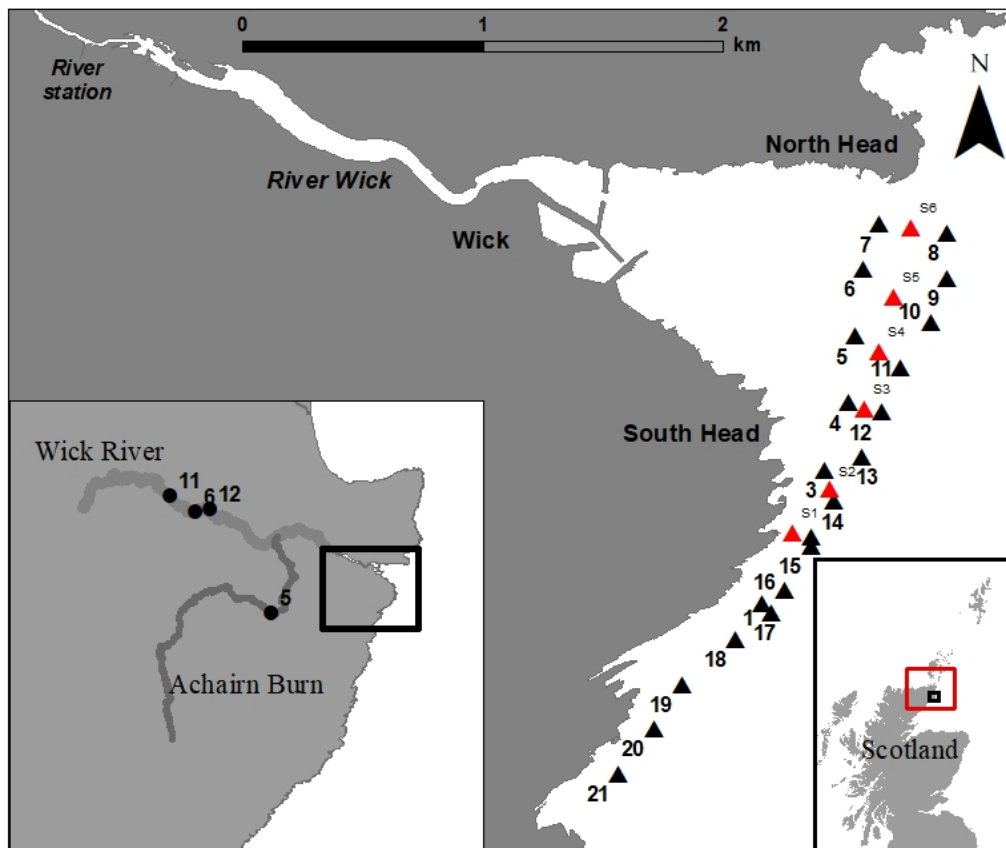
56 To examine potential interactions between renewable energy devices and salmon, contact
57 location and contact duration must be identified. Hydrodynamic modelling offers a means of
58 addressing these questions. This study gathers empirical data of tracks of tagged smolts in a
59 tidally energetic coastal environment and compares observed results with outputs of a 3-
60 dimensional hydrodynamic model to investigate, firstly, if a hydrodynamic model with free
61 drifting particles can simulate tag detection results; secondly, to investigate if smolt are
62 utilising the currents; and thirdly, to investigate the intrinsic directionality of smolt movement.
63 The hypothesis is that the ultimate destination of smolts leaving the Wick river lies far to the
64 west and north of the British mainland (Freidland, 1998; Holst et al. 2000). It is likely therefore
65 that successful completion of the smolt migration is dependent on an intrinsic northwards
66 vector to swimming activity. Additional objectives are to determine the timing of river exit and
67 entry to the marine environment (day/night), and smolt swim depth once in the marine
68 environment.

69 2. Methods

70 2.2 Study area

71 The study was conducted on the Wick River in Northern Scotland (Figure 1). The lower reaches
72 of the river have a straight channel with few gentle meanders and a low gradient prior to the
73 river entering Wick Bay, which is delineated by headlands, North Head and South Head, ca.

74 1.8 km distance from the river's junction with the bay. (Figure 1). A line of marine detection
75 stations was placed at the seaward limit of the bay (Figure 1).



76
77 *Figure 1: Wick River in North East Scotland: Red rectangle in in-set indicates hydrodynamic model extent. The position of*
78 *river and marine detection stations are shown (black triangles in large scale map). Sentinel tag locations are shown by red*
79 *triangles. Circular markers in the lower-left inset show fish capture locations with number caught. Black rectangles are extent*
80 *indicators of higher scale maps.*

81 2.3 Acoustic tracking

82 The tracking system comprised Automatic Listening Stations (ALS, Innovasea, Canada; Model
83 VR2) and a mixture of acoustic ID (ID-LP7) and ID-depth (ADT-LP7) transmitter tags
84 (Thelma Biotel, Norway). The ID-LP7 tags transmitted unique codes at 69 kHz and were
85 programmed to transmit at random intervals of between 20 and 40 seconds. The ADT-LP7
86 depth tags transmitted at fixed intervals of 29, 31 and 33 seconds to avoid crosstalk. The battery
87 life of the tags was estimated at approximately 90 days (manufacturer estimate). A single ALS
88 (River Station, Figure 1) was positioned in a linear section of Wick River of uniform channel
89 dimensions just above the limit of saline influence at 58.4487° N, 3.1227° W (Figure 1). The

90 River ALS had unobstructed acoustic reception over the approximately 200-m linear river
91 reach. The River ALS was positioned in mid-water where the river was ca. 0.6 m in depth
92 during the study period and the channel ca. 15 m wide.

93 Twenty-one marine ALS were deployed at spacings of ca. 200 m in a double array design with
94 micro-siting spanning the outer edge of Wick Bay (Figure 1). Previous studies have shown a
95 200-400 m detection range limit for these sensors (Clements et al 2011; Singh et al. 2010,
96 Hedger et al. 2008), therefore the lowest range was assumed for deployment to provide overlap
97 between adjacent ALS. The receivers were buoyed at 2 m above the seabed using a moored
98 configuration of a bottom weight, line and flotation buoy attached above. The array was biased
99 towards the south side of the bay with the aim of optimising fish detection based on a
100 preliminary assessment of the tidal dynamics in Wick bay. All the ALS were in place before
101 fish tagging commenced. Six ID-LP7 sentinel tags were permanently positioned within part of
102 the marine ALS array in order to continuously monitor the operational characteristics of in-
103 range ALS over the natural range of sea and tidal conditions. The sentinel tags were buoyed to
104 1 m above the seabed. The ALS signal detections were downloaded on logger recovery.
105 Innovasea loggers process acoustic signals internally and VUE-software (Innovasea) was used
106 to download and quality control detections before logging in a database. Further post-
107 processing quality control proved necessary and this was carried out as detailed below. A
108 Wald–Wolfowitz runs test was performed on the frequency of detections for the marine ALS
109 stations to test whether the smolt frequency detection differed significantly from random. A
110 binomial generalised linear model (GLM) was used to model probability of detection from the
111 sentinel tag dataset. Explanatory variables were distance from receiver, date and current
112 magnitude and direction, with current data derived from the hydrodynamic modelling data. Site
113 range testing confirmed detection ranges of >80% probability of detection at 200 m from

114 sentinel tag data. 200-meter spacing ensured a large overlap between the detection limits of
115 adjacent stations.

116

117

118 2.4 Fish capture

119 On 23-24 April 2016, 34 smolts were captured by electro fishing over several locations (Figure
120 1) in the Wick River catchment. After capture, fish were placed in an aerated holding tank until
121 they were tagged. Large smolts of greater than 130 mm in length were selected for tagging.
122 Fish were anaesthetised using a 0.4 g l-1 solution of MS222 (Tricaine Pharmaq, Pharmaq Ltd,
123 Fordingbridge, Hampshire, United Kingdom) until the fish no longer responded to external
124 stimuli. The smolts were measured and weighed before being placed on a v-shaped surgical
125 board with the ventral body surface facing upward. An incision approximately 13 mm in length
126 was made just off the ventral midline, anterior to the pelvic girdle. The acoustic tag (ID-LP7.3
127 or ADT-LP7.3, Thelma Biotel, Trondheim, Norway) was inserted through the incision into the
128 body cavity and the incision was closed with two interrupted absorbable vicryl sutures
129 (Ethicon, Johnson and Johnson, Maidenhead, UK, 4-0 suture with a reverse cutting needle).
130 The fish were retained in an in-river recovery box for 1 hr and released at the point of capture.
131 By this point they had fully regained consciousness and responded to external stimuli. All fish
132 were tagged under UK Home Office license by trained personnel.

133

134 2.5 Hydrodynamic modelling

135 A hydrodynamic model was used to predict astronomical tidal conditions during the times of
136 tag detections, comprising flow speed, direction and tide height. The TELEMAC-MASCARET
137 suite was used (Galland et al., 1991), comprising an integrated suite of solvers for use in the

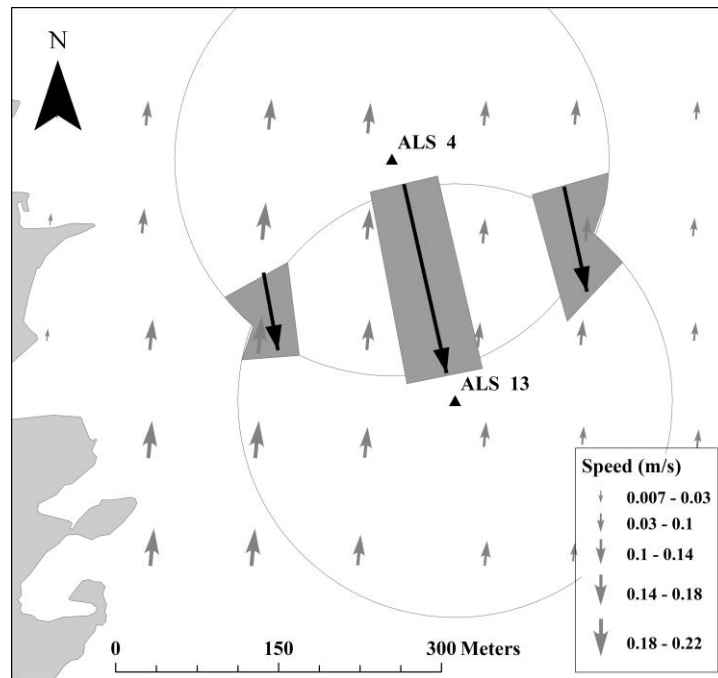
138 field of free-surface flow. A 3-dimensional model was constructed of Wick Bay and
139 surrounding influential waters including the Pentland Firth area (Figure 1). Telemac-3D was
140 utilised with the non-hydrostatic version of the code and the K-E turbulence closure model in
141 both vertical and horizontal directions. Bathymetric data were extracted from the 1 Arcsecond
142 Bathymetry - Marine Themes Digital Elevation Model available from Edina Digimap (©
143 British Crown and OceanWise, 2018. All rights reserved. Licence No. EK001-20180802). The
144 hydrodynamic model was calibrated using the friction coefficient to tidal data available from
145 the Wick tidal gauge (British Oceanographic Data Centre), and bottom-mounted ADCP data
146 collected in the Pentland Firth by the Environmental Research Institute. A Chezy coefficient
147 value of 44 (corresponding to a roughness Cd value of 0.005; Mcilvenny et al. 2020) was found
148 to have the best fit to the data. This agrees with previous suggested values for the Pentland
149 Firth area (Easton et al., 2012; Rahman & Venugopal, 2015). The model was run using an
150 unstructured grid with a spatial resolution of 10 m around the area of Wick Bay. Elsewhere the
151 grid resolution varied from 2 km in open ocean to 200 m near coast and 500 m near open water
152 boundaries. 5 vertical depth layers were used in the grid (supplementary material, Figure 2).

153 Free-floating particles were simulated using the Blue-Kenue Software (Canadian Hydraulics
154 centre) and its in-built 'Psed' Lagrangian sediment transport model. Free floating particles were
155 simulated by creating particles with a neutral buoyancy. Particle models were mobilised using
156 the current data from the TELEMAC-MASCARET model. Previous research has found
157 particle modelling of smolts to be a useful indicator of their behaviour at sea (Mork et al. 2012;
158 Byron et al. 2014; Newton et al. 2017).

159 Several assumptions are necessary to model the movement of a tag based on detections. As the
160 precise location of the first tag detection within a receiver's detection limit is unknown, the
161 starting position for free floating particle insertion must be estimated. In addition, the detection
162 range of each receiver is unknown. This value may be dependent on site-specific conditions at

163 the time of the detection including current low speed, turbulence, and ambient noise from e.g.,
164 sediment movement. A detection range of 200 m was used for each listening station based on
165 the range detection testing done on site prior to fish tagging. For each initial detection time,
166 several locations were tested as the free-drifting particle release point. Particles were released
167 in lines of 500 free-drifting particles with neutral buoyancy at the surface layer orientated
168 across current, to 5 m depth. Several release points were used to determine if currents alone
169 could be responsible for the tag detections patterns observed after initial detection.
170 Hydrodynamic model data were extracted for each tag detection time. Where free particle paths
171 interacted with the tag detection ALS stations within the time frame of tag detections the
172 particle was deemed to have explained the tag detections, thereby model flow only can explain
173 the tag detections. A single free particle was selected from those which explained the tag
174 movement and the particle path length, time and ground speed were calculated. When a tag's
175 timing of detections did not correspond to free drift in tidal current flow indicated by the
176 modelling results, hypothetical movements through the zones of detection were tested. Tidal
177 currents were then averaged over each zone to estimate the maximum and minimum current
178 conditions the tag may have encountered at the surface, the mid-depth and the bed-depth
179 (Figure 2).

180



181 *Figure 2: Example: Tag 102 was first detected in ALS 4 and then in ALS 13, against the flow of tidal current at the time (grey*
182 *arrows). Zones (grey patches) around hypothetical tag movements (large black arrows), were subset and the current averaged*
183 *to estimate maximum flow rates at surface, mid and bottom depth levels. Circles show the maximum expected detection range*
184 *(200 m). Small grey arrows indicate flow during tag detection time.*

185 Tag detection data were compared against wind and visibility data sourced from the Wick
186 weather station (UK MET Office Data) and moon phase. Quality checking resulted in false
187 detections being eliminated from the dataset; these included detections where signals were
188 logged with identity codes which did not correspond to any of the tags, possibly as a result of
189 logger artefacts as well as false positive detections that corresponded to actively used tags but
190 the time and location of the detections were not consistent with other detections of the same
191 tag.

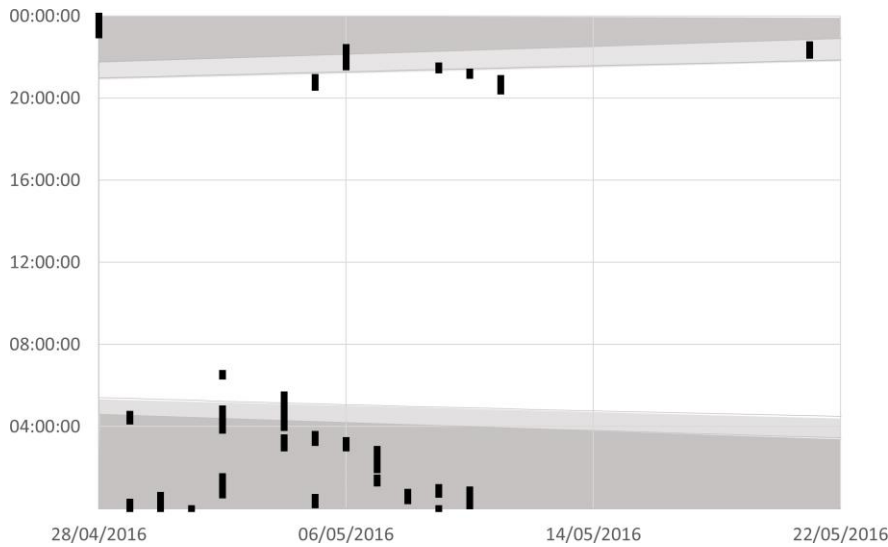
192 3. Results

193 3.1 Fish detection

194 Thirty-four fish were tagged on 23rd-24th April 2016 and 27 were subsequently detected at the
195 River ALS (Table 1). The total period over which individuals were first detected was from 28th
196 April to 21st May. Individuals were continuously present near the River ALS over periods
197 ranging from 2-18 minutes. Two fish (IDs 1121 and 1122) were repeatedly detected over a

198 period of four days although they reached and left the River ALS area on different dates. The
199 range of timings of first detections from the outer marine array was from 20:31 hr to 02:14 hr
200 (UTC) indicating that the fish were not migrating during the main hours of daylight. Twenty-
201 six of the 27 fish detected at the River ALS were subsequently detected in the marine array.
202 One track was discarded (ID 1130) at this stage as a result of quality control issues associated
203 with an unexplained error in the logged timestamp. For the others, the delay between the last
204 detection at the River ALS and the first detection in the marine ALS array (ca. 8 km distance)
205 varied from five hours to 35 days with a median value of 24 hours. 82% of first detections in
206 the marine array were at night and the range of timings was 20:20 to 04:16 UTC (Figure 3).
207 However, four of the tags were detected in daylight times; Tag 1153 was detected 43 minutes
208 before sunset, Tag 1121 detected 1 minute prior to sunset, Tag 1150 detected 19 minutes prior
209 to sunset and Tag 1129 detected 1 hour and 7 minutes prior to sunset. A Wald–Wolfowitz runs
210 test performed on the number of detections at each marine ALS station indicated the results
211 differed significantly from random ($h=1$, $p=0.009$). The binomial GLM model results indicated
212 that probability of detection was most affected by distance from the array ($F(1,24512)=30187$,
213 $p<0.05$). Current magnitude and direction were significant, however, with a lower effect on
214 probability of detection ($F(1,24512)=152$, $p<0.05$ & $F(1,24512)=6$, $p<0.05$ respectively).

215



216

217 *Figure 3: Timing of all marine detections with sunset, dusk and dawn times highlighted in grey.*

218 3.2 Swimming depth

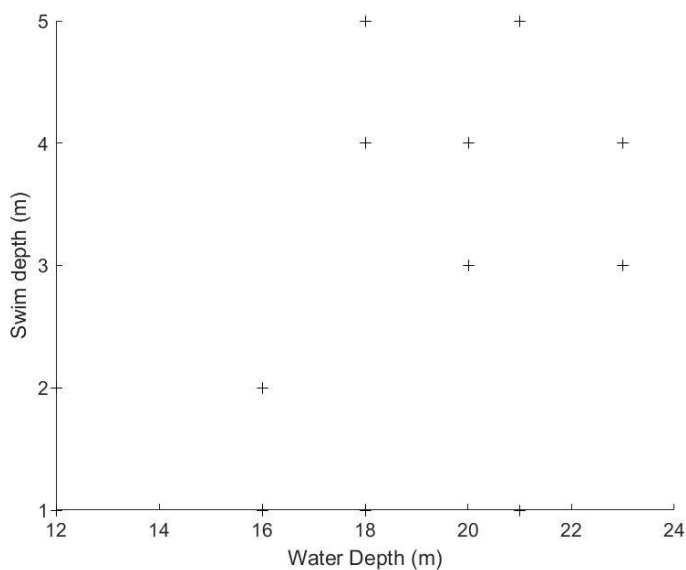
219 Swimming depth was repeatedly logged within in the marine array for three individuals.

220 Swimming depth varied between 1 and 4 m. Water depth within the array varied between 7 and

221 30 m at lowest astronomical tide. Therefore, these smolts utilised the upper part of the water

222 column during their time in the marine array with changes in bottom depth not affecting swim

223 depth (Figure 4).



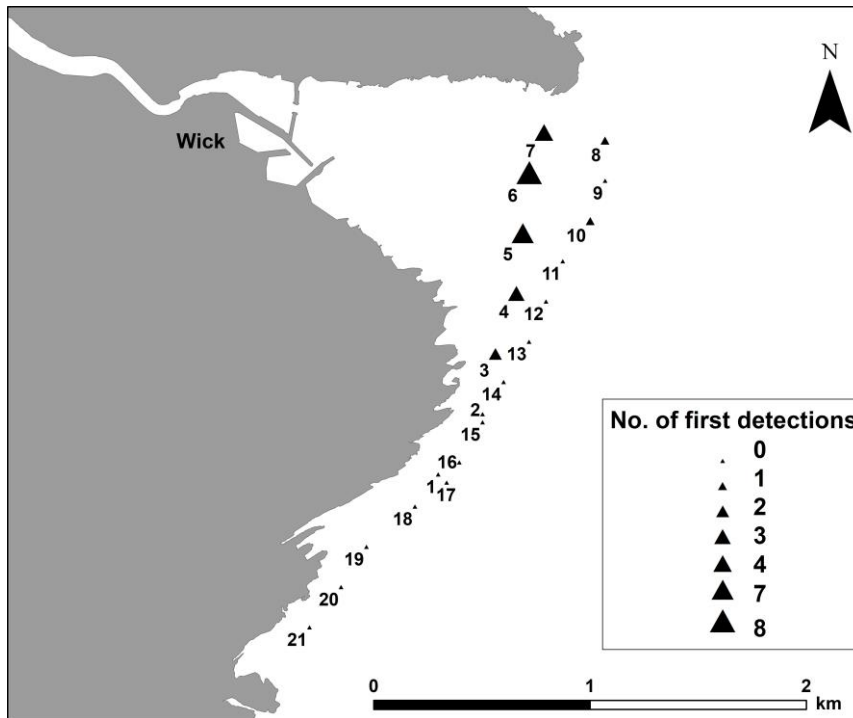
224

225

226 *Figure 4: Swimming depths for three tagged fish in the marine ALS array against bottom depth of receiver stations.*

227

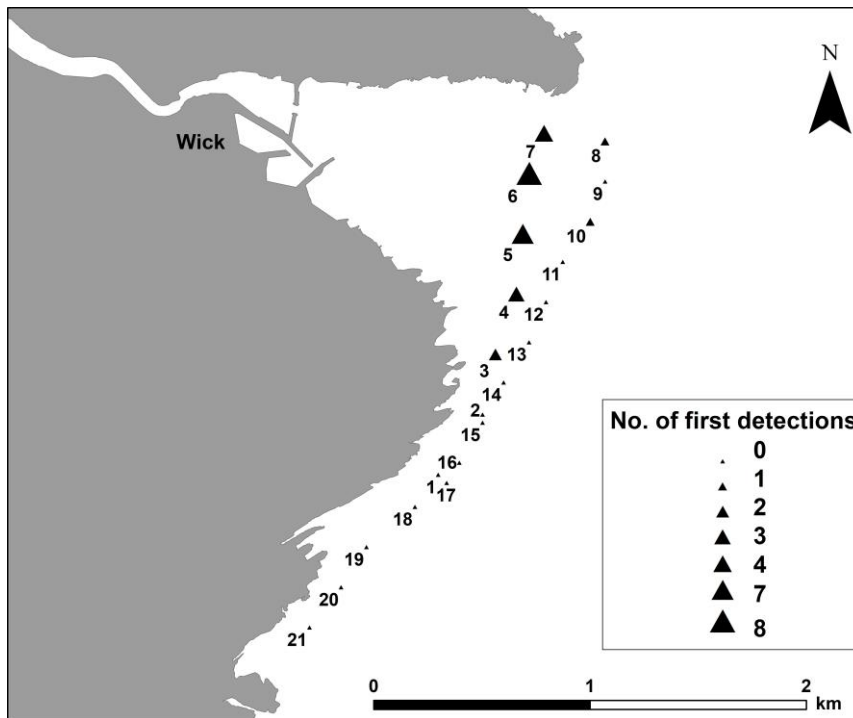
228 3.3 Initial detections



229

230 Figure 5 shows the number of occasions in which single transmitters were first logged at each
231 ALS position. As expected, all first detections occurred in the northern sector of the array by
232 North Headland, between ALS 3 and 7. As also expected, most (24 of 26) first detections
233 occurred in the inner component of the array and only two were logged in the outer component.
234 For occasions in which tags were detected simultaneously at multiple ALS, detection ranges
235 were estimated to be between 200 and 300 meters. Site range detection testing was completed
236 during array deployment showing detection ranges in excess of 200 m in calm conditions.

237



238

239 *Figure 5: ALS locations for initial tag detections where station (triangles) size indicates number of detections, larger triangle*
 240 *for higher number of detections.*

241

242 Tag detections were compared to other variables, tidal conditions, light conditions (including
 243 daylight and moonlight) and whether the tag detection pathway could be attributed to the tidal
 244 currents alone, through experimentation with free particle drift models (Table 1). The results
 245 showed only two tags were detected during times when the moon was above the horizon; Tag
 246 1108: moon phase 60% illumination, 12° above horizon and Tag 1150: moon phase 16%
 247 illumination and 9° above horizon, limited moonlight. Two tags (1111 and 1130) were detected
 248 only once and were eliminated from further analysis as they were only represented by a single
 249 temporal data point. Tidal state showed that 18 tags were detected during or close to slack water
 250 conditions and 6 tags during flood or ebb tides, 16 tags were associated with ebb tide conditions
 251 whilst 8 tags were associated with flood tide conditions.

252

253 Table 1: Tag detection summary. The date, time, and duration of the first detection of each tag are shown. "Explained by model Flow only" denotes if the tag detection pathway is satisfactorily
 254 explained by modelled tidal current movements. Detections which included an additional vector of the fish swimming within the flow vector (Flow only = No) are highlighted in light grey. The
 255 mean model flow along the particle path is shown along with free particle calculated ground speed for path and time and distance for particle to complete path for tag detections. The night column
 256 denotes whether the tag detections occurred during daylight (no) or dark conditions (yes). Whether or not the moon was above the horizon at the time of the detections is included in brackets in
 257 the same column whereby; (m) moon above the horizon and visible.

258

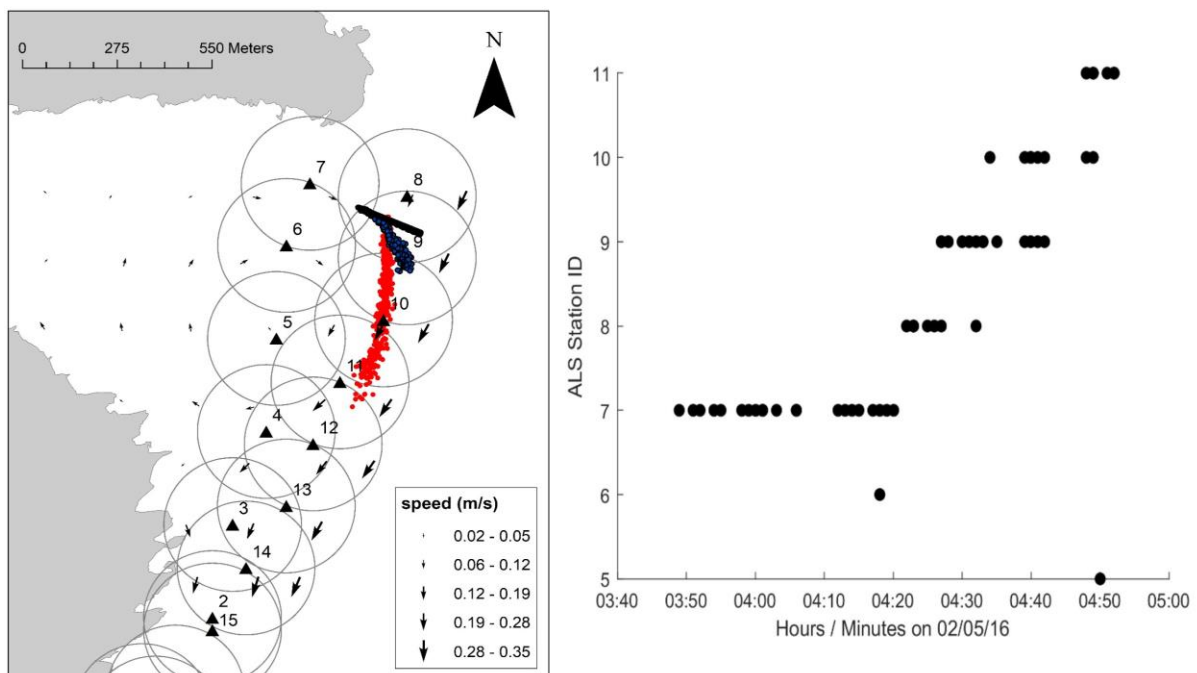
Tag ID	First detection date	First detection time (UTC)	Detection duration (minutes)	Explained by model flow only	Model flow mean	Model free particle ground speed (m/s)	Mean particle ground direction	Tide state	Night	Free particle distance	Free particle time to reach time (mins)
101	08/05/2016	00:23	48	Yes	0.31	0.27013889	North	Ebb-Slack	Yes	778	48
102	21/05/2016	22:05	31	No	0.128	>0.128	South	Flood-slack	Yes	NaN	NaN
103	02/05/2018	00:53	342	Yes	0.14	0.04917617	East	Ebb-slack	Yes	776	263
1106	09/05/2016	00:00	62	Yes	0.28	0.27373737	North	Flood-slack	Yes	542	33
1107	06/05/2016	02:57	22	Yes	0.007	0.06363636	North	Ebb-slack	Yes	84	22
1108	29/04/2016	04:16	20	No	0.18	>0.018	South	Slack-ebb	Yes(m)	NaN	NaN
1109	28/04/2016	23:53	16	Yes	0.24	0.22291667	south	Slack-ebb	Yes	214	16
1110	28/04/2016	23:04	75	Yes	0.28	0.20895522	South	Flood -slack	Yes	840	67
1111	10/06/2016	04:09	n/a	Single Detection	NaN	NaN	NaN	Flood	Yes	NaN	NaN
1112	05/05/2016	0.0076389	22	Yes	0.18	0.16742424	North	Ebb	Yes	221	22
1119	07/05/2016	01:53	60	Yes	0.03	0.04482759	North	Ebb	Yes	156	58
1121	09/05/2016	21:22	12	Yes	0.3	0.24242424	East	Flood	No	160	11
1122	10/05/2016	00:08	47	Yes	0.18	0.09503546	East	Flood-slack	Yes	268	47
1123	06/05/2016	21:31	36	Yes	0.19	0.10075758	East	Flood-slack	Yes	133	22
1124	07/05/2016	01:15	15	Yes	0.35	0.34666667	North	Slack-Ebb	Yes	312	15
1125	30/04/2016	00:00	39	No	0.22	>0.22	South	Slack-flood	Yes	947	81
1126	29/04/2016	00:02	16	Yes	0.34	0.290625	South	flood	Yes	279	16
1127	06/05/2016	21:37	45	Yes	0.16	0.13809524	North	Flood-slack	Yes	290	35
1128	05/05/2016	03:13	24	Yes	0.04	0.03819444	South	Slack-flood	Yes	55	24
1129	11/05/2016	20:20	37	No	0.05	>0.05	North east	Slack-flood	No	NaN	NaN
1130	01/05/2016	00:00	n/a	Single detection	NaN	NaN	NaN	flood	Yes	NaN	NaN
1147	02/05/2016	03:49	63	Yes	0.18	0.15327381	South	flood	Yes	515	56
1148	06/05/2016	22:04	24	Yes	0.18	0.17222222	North	flood-slack	Yes	186	18
1150	10/05/2016	21:06	10	Yes	0.39	0.37037037	South	Slack-flood	No(m)	200	9
1151	02/05/2016	00:40	21	No	0.03	>0.05	North	Slack-flood	Yes	NaN	NaN
1152	04/05/2016	02:57	155	Yes	0.07	0.0625	South	Slack-flood	Yes	450	120
1153	05/05/2016	20:31	29	Yes	0.17	0.12666667	East	flood	No	38	5

259

260

261 3.4 Particle modelling

262 Although the model used in this study only used astronomical forcing, wind data from the Met
263 Office MIDAS land surface observations shows no extreme high wind forcing events during
264 the detection times. Modelling showed tag detection timings for the initial first pass through
265 the marine array were consistent with tidal current patterns; however, after the tags left the
266 marine array, they were not detected on subsequent tides. Tag 1147 (



267

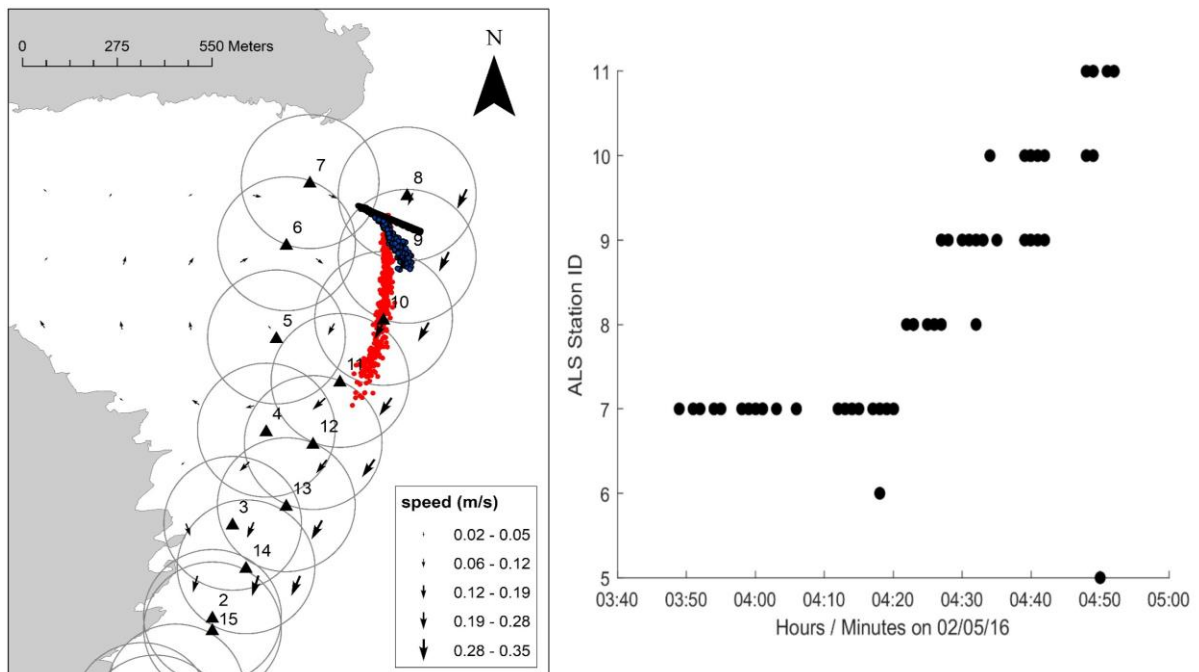
268 Figure 6) is an example of where a detection path could be explained by a free drifting particle.

269 In all cases free drifting particles were released into the model on a line in approximate region
270 of first detection and under the influence of the tidal currents until the last detection time.

271 Tag detection paths followed currents when tidal currents in the vicinity of the ALS exceeded
272 approximately 0.2 m/s in all but two cases, based on an estimated 200-m detection radius of
273 receivers. Tag 1107 and Tag 1128 movement paths were also explicable by the currents alone
274 although the currents speeds were relatively low (0.1 and 0.09 m/s maximum current speed at
275 times of detection within vicinity of free moving particles, Table 1). After initial tag detection,

276 for the tags explained by the current, 7 moved south, 7 moved north and 5 moved eastwards.

277 Of the tags not explained by the current, 3 moved south and 2 moved northwards.



278

279 *Figure 6: Tag 1147; (left) particle modelling showing the particle release location, Note particles released equally along line*
280 *length (straight line), particle locations at half the run-time (blue dots) and final particle positions (red dots) the maximum*
281 *ALS detection range (200 m, black circles) and the flow speed / direction, (right) tag detection timings at ALS stations for tag*
282 *1147.*

283 3.5 Drift over subsequent tides

284 Particle modelling also showed free-drifting particles trapped by the tidal current would have

285 been detectable in the marine array for several tides as the flowed through the marine array in

286 subsequent ebb and flood tides; all of the fish detected in the marine array were detected only

287 on one tide suggesting that they left the area rapidly after passing through the array immediately

288 after leaving the river. Particle-drift simulations were run over several tidal cycles beyond the

289 last detection of each tag to estimate what paths particles may take by astronomical tidal action

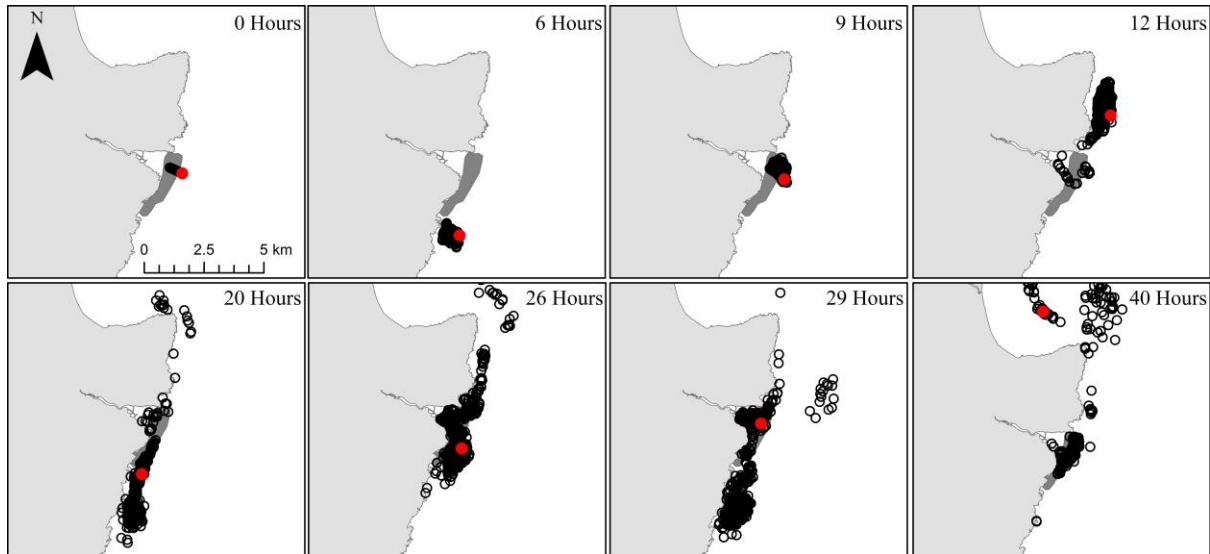
290 alone. The example in Figure 7 is a 48-hour simulation for Tag 1125. One of the 500 particles

291 injected into the model is highlighted as an example. The particle highlighted is on the extreme

292 east of the particle injection line at a position where tidal currents have the highest influence.

293 The point shows multiple interactions with the marine array (dark grey area, Figure 7) over the

294 period of 48 hours, all other simulated particles had similar multiple interactions with the
295 marine array. A similar pattern occurred for all other simulations where particles had multiple
296 interactions with the marine array over several tidal cycles. Simulations showed few particles
297 eventually escaping to the north, whilst the majority became trapped for longer periods in near
298 coastal tidal currents and bay eddies.



299

300 *Figure 7: 48-hour simulation of 500 particles released perpendicular to current in estimated position of first detection of Tag*
301 *1125. Dark grey zone indicates 200 m buffer around marine array vicinity. Example point, single drifting particle (red) shows*
302 *multiple interactions with tidal array assuming 200-m detection range.*

303

304 3.6 Anomalies

305 Five of the 27 detection tracks were not explicable by tidal current movements from model
306 results (Table 1, Tag IDs 102, 1108, 1125, 1129 and 1151). Of these 5 tags, 4 occurred in low-
307 flow velocities (<0.2 m/s), these 4 tags moved in different directions to the mean current flow
308 suggested by modelling results. The 5th tag which could not be explained by currents alone
309 was associated with currents from 0.22-0.27 m/s (Tag 1125); however, the direction of travel
310 was with the tidal flow. This tag also exhibited the fastest rate of movement at up to 0.48 m/s
311 (1.72 km/hr) estimated by initial detection time to final detection time.

312

313 4. Discussion

314 This study used a 3-dimensional hydrodynamic model to improve understanding of how an
315 array of receivers detects the movement of tagged fish. The model proved an important tool in
316 understanding smolt behaviour from tag movements in relation to hydrodynamics of the bay.
317 The model agreed with the majority of tag movements (77.7%). Of the tracks which are
318 explained by tidal currents, the model indicated these experienced current speeds in excess of
319 0.2 m/s.

320 After last detection at the River ALS, smolts rapidly migrated to the marine environment as
321 indicated in previous studies (Halfyard et al. 2012; Lothian et al. 2016; Nicola et al. 2018).
322 Marine detection mostly occurred after sunset and prior to sunrise. Four exceptions were first
323 registered close to sunset. These findings are in line with other published results (Thostad et al.
324 2016; Lothian et al. 2017). Haraldstad et al. (2016) found most river and marine migration
325 success linked to night, potentially due to predator avoidance.

326 Three of the smolts were monitored for depth. This showed they stayed near the surface whilst
327 detected in the outer marine array. This agrees with other studies finding that after initial marine
328 migration, smolt stay near the surface (Thorstad et al. 2012). Estimated tag movement speeds
329 show faster than maximum suggested smolt swim speed, 0.25 m/s (0.9 km/hr) but comparable
330 with other studies where smolt utilize currents (Thorstad et al. 2012; Lothian et al. 2017;
331 Newton et al. 2017).

332 Two hypotheses have been suggested previously of migratory behaviour in juvenile Atlantic
333 salmon in the marine environment, either they rely heavily on passive transport, or they have
334 directional component to their migration (Ounsley et al. 2020). All tags which were detected
335 by the marine array are only detected on the same tidal phase as the initial detection and are
336 not detected in subsequent tidal phases. Passive particle modelling suggests particles would

337 interact with the marine array several times over subsequent tidal cycles, becoming trapped in
338 the ebb and flood currents which flow approximately north to south. On the contrary, the tags
339 were not detected in the marine array in subsequent tidal phases, suggesting either the smolt
340 were actively altering their vector by swimming, or they were prevented returning to the array
341 (predation).

342 These results point to transitional behaviour of the smolt. A first stage of river migration
343 behaviour is defined by active swimming during a narrow time window to enter the marine
344 environment. Once in the marine environment, during an initial marine behaviour stage, the
345 smolt may remove themselves from the influence of coastal waters. This raises questions as to
346 whether there are further behaviour changes occurring proceeding this. No strong evidence of
347 a preferred north or south trajectory was found with 66% of the tags were associated with ebb
348 tide whilst 34% were associated with flood tide conditions. However, this may be a subsequent
349 behaviour at a later point in migration, possibly changing direction after leaving the influence
350 of near-shore coastal waters for migratory routes leading to feeding grounds in the Northeast
351 Atlantic (Ounsley et al. 2020). It is not known whether smolt will continue to avoid near-shore
352 conditions or use them intermittently, such as returning to stronger currents when direction is
353 favourable, for example using only ebb currents and returning to deeper water for the flowing
354 flood tide with a net north movement, or if tidal channels with extreme conditions like the
355 Pentland Firth are utilised or avoided. If they salmon continue to utilise currents during their
356 migration it may bring them into direct contact with renewable energy developments.
357 Renewable energy developments are increasing worldwide with a 13% increase in growth in
358 2019 (Chowdhury et al. 2020). There are several developments planned and at early stages
359 around Scottish waters including the Pentland Frith and Orkney waters, where strong tidal
360 currents are present. Travel through these areas would provide a low-energy path for smolt to

361 reach richer feeding grounds. In addition, in deeper waters with low flow, offshore wind energy
362 developments exist, with smolts potentially interacting with high voltage subsea cables.

363 Subsequent tagging and modelling work are required to investigate smolts' movements after
364 leaving the area of their initial marine migration. Smolt interactions with marine renewable
365 developments are poorly understood due to poor understanding of how and where the smolt
366 move during their migration. This study was an attempt to track the first stage of this journey.
367 The results will be used to inform initialisation of further tagging efforts and marine listening
368 station array design to track the route of smolts as they migrate along the Scottish coastline,
369 together with high-resolution particle drift models using particles which mimic fish behaviour,
370 for example with traits of preferred swimming direction, swimming depth, and starting position
371 (nearest point offshore removed from near-shore current influence) and with current utilisations
372 preferences.

373 In future, it may prove possible to extrapolate from modelling studies to guide sequential
374 studies of the dispersal of migrants, focussing necessarily limited technical resources for
375 tracking on the predicted pathways of fish moving through very large areas of sea. In order to
376 achieve this, adequate hydrodynamic models and realistic biological inputs for the point and
377 timing of entry of fish to the model domain and their subsequent behaviour in the domain will
378 be needed at each stage.

379

380 5. Acknowledgements

381 The involvement of the community through the FCRT demonstrated high levels of local
382 interest extending to practical advice and material support from both commercial and sports
383 fishermen. Beatrice Offshore Windfarm Ltd. Community Fund contributed to the receiver
384 deployments.

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