Original Article

Depth use and migratory behaviour of homing Atlantic salmon (*Salmo salar*) in Scottish coastal waters

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Knowledge of swimming depths and migration routes of homing Atlantic salmon in open coastal zones is urgently required to inform decisions on managing the species, e.g. for the sustainable development of marine renewable energy. In May–June 2013, pop-up satellite tags programmed to detach from fish after 1–10 d were fitted to 50 adult salmon on the northern coast of Scotland. Most of the tags returned water depth recorded at regular intervals ($n = 47$) and gave a geographic location following detachment ($n = 44$). In general, salmon were found near the surface during the study, with the median number of records at 0–5 m depth ranging from 72 to 85%, depending on the extent of known potential systematic bias. Depth use varied among individuals (8–100% at 0–5 m) and cluster analysis suggested that the sample of fish could be split into two groups, representing different patterns of depth use. These clusters were also associated with pop-up location. There was a small but significant increase in recorded depth at night compared with during the day, contrasting with findings of salmon at sea in other contexts. The mean maximum dive depth was 64 m (range 13–118 m), of similar order to the likely available water column depth. These results suggest that salmon will potentially interact with man-made obstacles, e.g. renewable energy generators, throughout the water column and particularly in surface waters.

Keywords: marine renewables, PSATs, satellite telemetry, tagging.

Introduction

The Atlantic salmon (*Salmo salar* L.) is highly valued in economic, cultural, and biological terms (Hindar *et al.*, 2010) but is in decline across much of its range (Vøllestad *et al.*, 2009). Historically, the fish has supported commercial fisheries in oceanic and coastal regions and both commercial and recreational fisheries within rivers (Mills, 1989). As well as fishery-induced pressures, there are a number of other potential anthropogenic factors which may impact on the species: climate change (Todd *et al.*, 2012), fish-farming (Costello, 2009), pollution (Lower and Moore, 2007; Thorstad *et al.*, 2013), land-use changes (Aarestrup *et al.*, 2007), and barriers to migration (Lundqvist *et al.*, 2008). These factors imply the need for information about the spatial extent and habitat requirements of the species at all stages of its life cycle (Thorstad *et al.*, 2012), yet many aspects of the marine phase of adult Atlantic salmon remain poorly understood (Hansen and Quinn, 1998; Thorstad *et al.*, 2011). This information is particularly important at a time when managers are faced with determining whether marine renewable energy (MRE) development is likely to impact on salmon populations.

MRE may be generated from waves, tidal currents, and wind. Concern has been expressed regarding the potential effects of MRE development on salmon and other aquatic species via direct collisions with tidal turbines and wave devices, noise during the construction and operation of devices, and the electromagnetic fields (EMFs) associated with the cabling for transferring power (Moore *et al.*, 1990; Gill, 2005; Dolman and Simmonds, 2010; Slabbekoorn *et al.*, 2010; Gill *et al.*, 2012). The potential for such interactions depends in the first instance on the spatial distributions of fish in relation to generators and cabling.

Salmon spend their early life stages in freshwater. The fish then metamorphose and migrate to sea as smolts, where they grow rapidly before maturing and returning to rivers to spawn after one (1SW) or more (MSW) winters at sea (Shearer, 1992). In Scotland, most salmon die after their first, or "maiden" homing migration, but some return to sea as kelts after they have spawned and may survive to breed again (Mills, 1989). Thus, both post-smolts and post-kelts that have emigrated from rivers and maturing adults returning from marine feeding areas to spawn are potentially vulnerable to MRE developments, and information on their migration routes and

how they use the available water column is now required to assess potential interactions.

The swimming behaviour of salmon post-smolts at first sea entry is now well described for certain environments (Økland *et al.*, 2006; Davidsen *et al.*, 2008; Hedger *et al.*, 2008; Dempson *et al.*, 2011; Thorstad *et al.*, 2012), but their behaviour in open water remains little known (Thorstad *et al.*, 2012). Still less is known about adults at the marine stage: recently, acoustic tags have been deployed, advancing knowledge on swimming behaviour of post-kelts in relatively enclosed and shallow coastal waters (Hedger *et al.*, 2009), fjords (Halttunen *et al.*, 2009), and in the open ocean using data storage tags (DSTs; Reddin *et al.*, 2011) and pop-up satellite transmitters (PSATs: Lacroix, 2013). However, despite making up most returning adults each year (Shearer, 1992), few studies have investigated the swimming depths of maiden salmon (i.e. those returning to freshwater systems for the first time to spawn) in coastal environments: Davidsen *et al.* (2013) used acoustic tags to record depths of salmon returning to a river within a fjord system; Sturlaugsson (1995) reported depths from ranched fish fitted with DSTs and translocated off shore; and Holm *et al.* (2006) reported depths from four recaptured salmon tagged with DSTs on their marine feeding grounds. Findings from these studies, along with those on swimming depths of post-kelts, suggest that adult salmon are highly surface-oriented. However, sample sizes have been generally small, and swimming depths have often been constrained by coastal topography. Thus, to date, no definitive information has been available on the swimming depths of salmon passing through open coastal waters on their first spawning migration.

Additionally, the migration routes of returning salmon remain unclear. What little is known about the period of migration between location of the UK landmass and river entry, for example, is based on the recovery and reporting of conventional tags at coastal netting stations (Shearer, 1992), constraining knowledge to the nearshore only. Unconstrained samples of locations, such as those provided by PSATs (Musyl *et al.*, 2011; Lacroix, 2013), are necessary for a fuller understanding of salmon migratory pathways, which in turn may have implications for fisheries and conservation.

Scotland has a target to generate the equivalent of 100% of its electricity needs through renewable sources by 2020 (Anon., 2011), partly from tidal energy, particularly in the Pentland Firth, between Orkney and the mainland (Shields *et al.*, 2009). The potential for these developments to impact on salmon has been raised, in part because the Pentland Firth is regarded as an area through which a large proportion of homing Scottish salmon may pass (Malcolm *et al.*, 2010). In the present study, PSATs were deployed to derive the depth distributions and tag pop-up locations of Atlantic salmon captured, tagged, and released in Northern Scotland, close to the Pentland Firth, on their homeward migration.

Material and methods

During the period 29 May–20 June 2013, 50 Atlantic salmon (mean fork length 78.2, range 71–90 cm) were captured in bag nets (Mills, 1989) at Armadale on the north coast of Scotland (Table 1; Figure 1). Salmon were transferred from the net to a holding tank (90 × 60 × 60 cm) on a fishing vessel. To minimize the impact of capture or tagging on subsequent behaviour, any fish in poor condition or <70 cm in length were discarded [although similar PSATs have previously been deployed on fish as small as 50 cm (Lacroix, 2014)]. Assessment of external characteristics suggested that 37 of the 50 fish selected for tagging were female. Three scales were taken from each salmon and their subsequent analysis indicated that 47 of the 50 were maiden fish. Of these, 45 were two-sea-winter fish (2SW)

Table 1. Individual details of Atlantic salmon used in the study, with satellite tag deployments and data returns.

Deployment date	Fork length (cm)	Sex	Sea age (years)	Cluster	Programmed deployment (d)	Depths (n)
Microwave Telemetry X-Tags						
29.05.13	77	m	2	C1	1	5 859
29.05.13	73	f	2	C2	1	5 957
29.05.13	90	m	2	C2	2	5 562
29.05.13	75	f	2	C1	3	7 186
29.05.13	76	f	2	C2	10	6 093
30.05.13	79	f	2	C2	2	6 750
30.05.13	83	f	2	C2	4	4 500
30.05.13	77	f	2	C2	5	6 399
04.06.13	74	m	2	C2	2	981
04.06.13	76	f	2	C1	3	4 401
04.06.13	83	f	2	C1	3	7 245
04.06.13	85	f	3	C1	7	6 435
05.06.13	74	f	2	–	1	0
05.06.13	79	f	2	C1	1	6 038
05.06.13	79	f	2	C2	2	6 854
05.06.13	79	f	2	C1	3	6 154
05.06.13	77	m	2	–	4	54
05.06.13	76	m	2	–	5	108
05.06.13	73	m	2	C1	5	3 136
05.06.13	74	f	2	C1	6	936
06.06.13	77	f	2	C2	1	1 458
06.06.13	77	f	2	C1	2	7 417
06.06.13	79	f	2	C2	3	6 740
06.06.13	78	f	2	C1	4	3 150
06.06.13	83	m	2	C2	6	5 013
06.06.13	80	m	2	C1	7	4 839
11.06.13	80	f	2	–	2	126
11.06.13	90	m	2	C2	3	6 340
11.06.13	78	f	2	C1	4	519
12.06.13	80	f	2	C1	1	5 143
Wildlife Computers MiniPAT						
12.06.13	80	f	2	C1	2	2 718
13.06.13	*74*	*f*	*2*	*C1*	*5*	*187 246*
13.06.13	78	f	2	C2	2	2 447
18.06.13	76	f	2	C1	10	11 907
18.06.13	86	m	3	C1	10	10 856
18.06.13	82	f	a	–	2	0
18.06.13	73	f	2	C2	5	286 037
18.06.13	86	f	2	C2	3	3 338
18.06.13	81	f	2	C1	3	4 091
19.06.13	*77*	*f*	a	*C1*	*2*	*31 462*
19.06.13	73	f	2	C2	10	9 303
19.06.13	74	m	2	C1	3	3 906
19.06.13	88	m	2	C1	5	5 442
19.06.13	71	m	2	–	5	0
19.06.13	76	f	2	–	10	192
20.06.13	*72*	*f*	a	*–*	*5*	*8 500*
20.06.13	80	f	2	C2	2	2 709
20.06.13	78	f	2	C1	3	3 919
20.06.13	74	f	2	C1	3	3 913
20.06.13	*79*	*f*	*2*	*C3*	*10*	*112 834*

[a]Fish identified as repeat spawner.
Lines in italics represent fish where the tag was recaptured allowing all data to be retrieved.

and two were three-sea-winter fish (3SW). The three other fish were identified as having previously spawned (Table 1).

Fish were fitted with either High Rate X-Tags (Microwave Telemetry Inc., dimensions 33 × 125 mm, antenna 184 mm, *n* = 30)
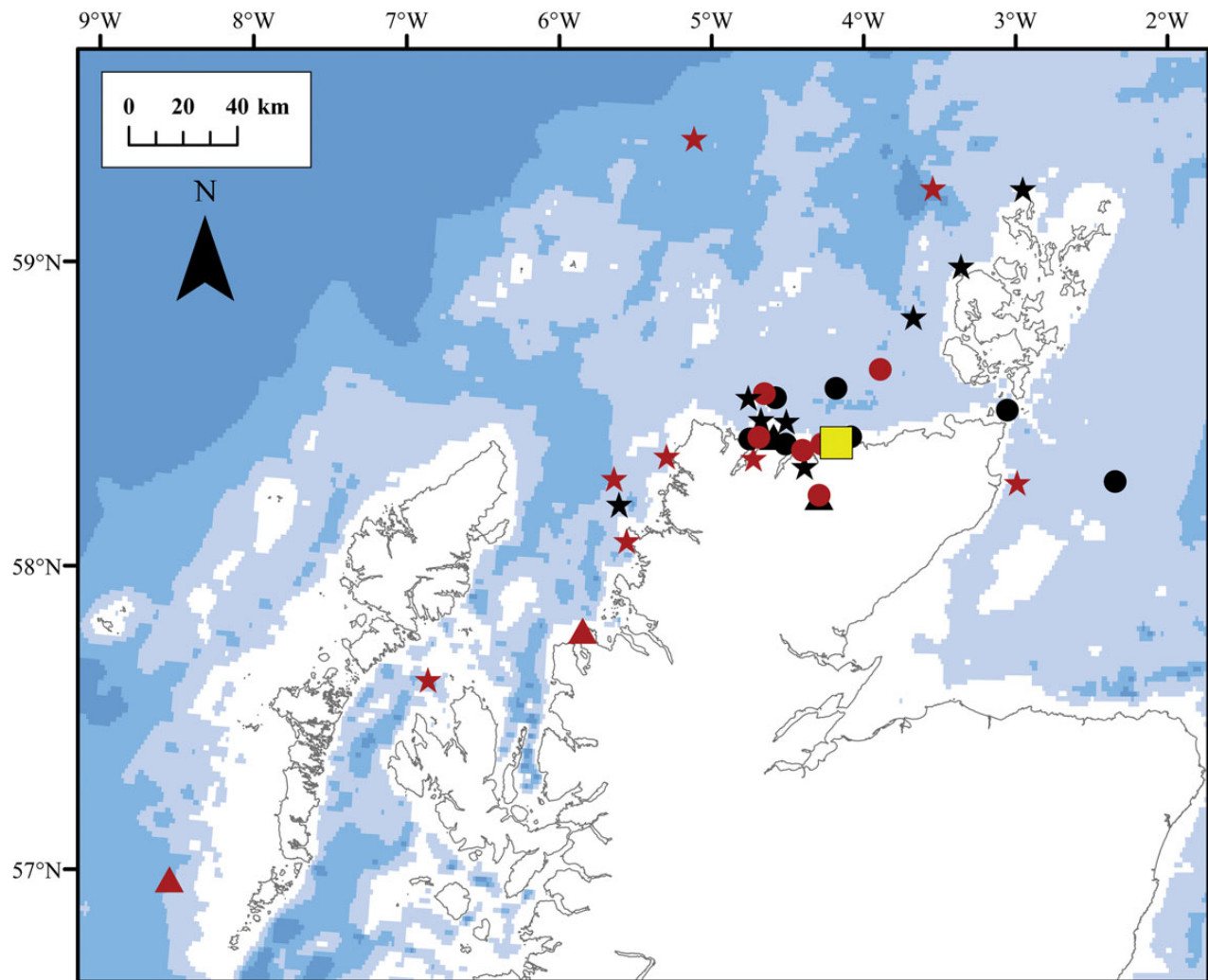
Figure 1. Map of the study area showing locations of satellite tags released from Atlantic salmon 1–2 d (filled circle), 3–5 d (filled star), or 6–10 d (filled triangle) after deployment, with red symbols indicating cluster 1, black symbols cluster 2. The yellow square shows the site of fish capture and release at Armadale. Depth shadings: 0–50 m (white), 50–100 m (light blue), 100–150 m (mid-blue), and >150 m (dark blue). The median error of locations is 5.9 km, maximum error 23.3 km.

or MiniPATs (Wildlife Computers Inc., dimensions 38 × 115 mm, antenna 165 mm, $n = 20$). The tags were programmed to release across a range of deployment durations (6 × 1, 11 × 2, 11 × 3, 4 × 4, 8 × 5, 2 × 6, 2 × 7, 6 × 10 d) to ensure that a proportion of the sample was not lost as they entered rivers (where tag release systems were not designed to operate). Tags were programmed to record depth (MiniPAT resolution = 0.5 m, X-tag resolution = 1.35 m) and temperature information at intervals of 75 s (MiniPATs) and 10–95 s (X-Tags) depending on deployment duration.

PSATs were attached to fish under anaesthesia (MS222, 80 ppm) using 2 strands of 1 mm diameter polyester twine placed ∼1 cm apart through musculature immediately posterior to the dorsal fin and midway between the lateral line and the back of the fish. When at rest, the tag floated vertically ca. 7 cm above the fish, without touching the dorsal fin. Prior assessment of the tagging system using three adult salmon in a laboratory tank over 2 weeks verified that the tag attachment was secure. Fish tagging was carried out under Home Office Project Licence PPL 60/3566. Fish were allowed to recover in fresh seawater and were released at sea ∼500 m north of the nets, 1–3 h post-tagging.

The tags collected data from activation until the release fired. Transmitted data can be received by satellite only after the release has been fired and the tag is at the surface. Reception of data depends on the timing of satellite overpass and/or environmental conditions at the release point (e.g. presence of cliffs, fouling of the tag antenna, sea state). The maximum possible period of delay between detachment from the fish and first location was calculated for each tag. Subsequent drift of the tag in the equivalent period immediately after first location was then estimated using satellite locations of the drifting tag post-detachment. This was used to estimate location error for each tag, but no attempt was made to use this to postdict the original pop-up location (Chittenden *et al.*, 2013). A further 1.5 km was added to reflect the maximum inherent error in the ARGOS system (max of 1.5 km for class 1 locations, the minimum standard accepted here, see Costa *et al.*, 2010). Locations of tags with estimated errors >25 km were subsequently ignored; the median error of retained locations was 5.9 km.

Patterns of temperature and depth records indicated fish that could be assumed to have died from predation ($n = 2$) by mammals or endothermic fish (Lacroix, 2014), unidentified

factors ($n = 2$), or entered rivers ($n = 5$). Depth data from these individuals were used only up to the point of suspected predation/death or river entry. Depth information was analysed using cumulative information at intervals of 5 m (Lacroix, 2013). Tags returning small numbers of depth records may not accurately represent fish behaviour. To examine this potential bias, the cumulative depth frequency was determined for a random subset of the data received from each tag, and the largest deviation from the actual cumulative frequency for that tag was recorded. This process was repeated 1000 times for each tag and the upper inter-quartile range (IQR—75th percentile) noted for each iteration. The number of depth records in the subset was increased in steps of 50 until the upper IQR was <5% for all tags. This occurred at the level of 200 depth records, and subsequently, any tag containing fewer than 200 depth records was excluded from the analysis.

Some uncertainty in depth distributions can be expected due to two potential systematic biases. First, salmon may dive immediately on release (Quinn *et al.*, 1989; Skilbrei *et al.*, 2009) or exhibit other behaviour influenced by capture and handling (Hoolihan *et al.*, 2011). To explore how this bias may impact the results, the depth data were also examined ignoring the first 24 h post-release, reducing the number of tags with sufficient depth records. Second, a tag may release early and then float at the surface until the time of scheduled detachment. The maximum extent of this potential bias was calculated by removing all data indistinguishable from a floating tag (depth ≤1.5 m) that occurred between the last dive (>1.5 m) and the scheduled detachment time.

Potential common trends in swimming depth among individual fish were investigated using hierarchical cluster analysis of the cumulative depth distributions. Clustering was performed in R (R Core Team, 2013) using ward linkage, with the number of clusters being determined by the largest change in distance between consecutive branches (Everitt and Hothorn, 2011). Diving records of individual fish were also examined for diel differences in their diving activity. Paired Wilcoxon tests were used to compare the median recorded depth and coefficient of variation for those fish whose records included both day and night observations. Night was defined as the period between local sunset and sunrise. Analyses were undertaken using the data which accounted for potential early release but which retained the first 24 h. Associations between cluster group and fish/deployment characteristics were tested using a *t*-test (for fish length), Mann–Whitney *U*-tests [for duration of deployment and pop-up location (latitude and longitude in digital format)], and Fisher's exact tests (for sex, sea age, spawning status, and tag type).

Results
In total, 47 of the 50 PSATs reported to the ARGOS network, and 34 provided locations with an acceptable error; these extended across a wide swathe of the north Scotland coastal zone, showing a net westerly directional bias from the release point (westward:eastward ratio of ~2:1; Figure 1). Locations were predominantly near shore, but tags surfaced up to 100 km off the coast. Minimum daily travel rates, based on straight-line swimming routes between release and pop-up locations, were: mean $23.4 \pm$ s.e 2.2 km d^{-1} [range = 3.2–55.5 km d^{-1} (or 0–58.7 km d^{-1} when including estimate of location error)].

Depth data were recovered from 47 PSATs (Table 1). Of these, five tags were recovered from rivers or beaches, and the full dataset could be downloaded. Comparisons of the cumulative depth distributions produced using the full dataset with the subsample received via satellite for each of these tags showed they were broadly similar, with the maximum difference between them being 5.7%. This figure gives an idea of the maximum level of bias that may occur when only part of the depth record is obtained through the satellite records.

The mean maximum dive depth of individuals was $63.9 \pm$ s.e. 3.9 m (range 13–118 m). The cumulative depth distributions are shown in Figure 2, which presents the unadjusted data, and the distributions after accounting for potential biases in post-release behaviour and early release of the tags. The impact of the potential biases on the median values appeared modest: the median cumulative depth distributions indicate that salmon spent 72–86% of time at 0–5 m, 79–90% at 0–10 m, and 6–9% of time at >20 m depth (Figure 2). There was considerable variation among individuals in their distribution of time-at-depth. At one extreme, after discarding the first 24 h data, one fish spent the entire time at 0–5 m; at the other, when accounting for possible early-detachment bias, another spent <10% of time at 0–5 m and 45% at >30 m depth. More detailed information on the depths used by individual fish is provided in the Supplementary data.

There were significant differences between day and night in both the median depths of tagged salmon (Wilcoxon's paired test, $V = 121.5$, $n = 40$, $p = 0.023$) and the coefficient of variation (Wilcoxon's paired test, $V = 178$, $n = 40$, $p = 0.001$). Overall, individuals were deeper during the night than the day, with a median difference of 0.5 m (IQR = −0.13 to 6.04 m). In addition, the coefficient of variation produced by individuals' depth records was greater during the night than the day (median difference = 14.9%, IQR = 3.6–43.7%).

The cluster analysis suggested the presence of two different patterns of cumulative depth use: one deeper, one more surface-orientated (Figure 3). Depth use varied from brief dives to deeper water followed by rapid return to the surface region, which all individuals expressed, to periods of several hours spent at approximately constant depths. Example tracks of individuals from each of the clusters are shown in Figure 4. There were no significant differences in the proportion of the depth records obtained at night between the clusters, indicating that this was not responsible for the observed clustering pattern (Mann–Whitney *U*-test, $U = 175$, $p = 0.545$). There was no detectable relationship of size, sea age, sex, spawning status, subsequent river entry, tag type, or duration of deployment with the clusters ($p > 0.05$). Individuals from cluster 2, the more surface-orientated group, showed a significantly more easterly distribution of pop-up locations (Mann–Whitney *U*-test, $U = 80$, $n = 34$, $p = 0.026$).

Discussion
The information presented here represents a unique account of depth use by Atlantic salmon principally on their first return migration, during the stage between high seas and final preparation for river entry. These data can be compared with information on depth use by adult salmon in other contexts. The proportion of time spent by salmon tagged as kelts at 0–5 m depths was 94–99% when migrating away from rivers through fjords and estuaries (Halttunen *et al.*, 2009; Hedger *et al.*, 2009) and 60–90% on the high seas (Reddin *et al.*, 2011; Lacroix, 2013). Salmon migrating home through a fjord were closely associated with the surface (mean swimming depths 0.5–2.5 m; Davidsen *et al.*, 2013), but precise depth distributions at this time are likely to depend on local hydrography and its influence on olfactory homing cues (Westerberg, 1982; Døving *et al.*, 1985). Therefore, the general pattern of depth use
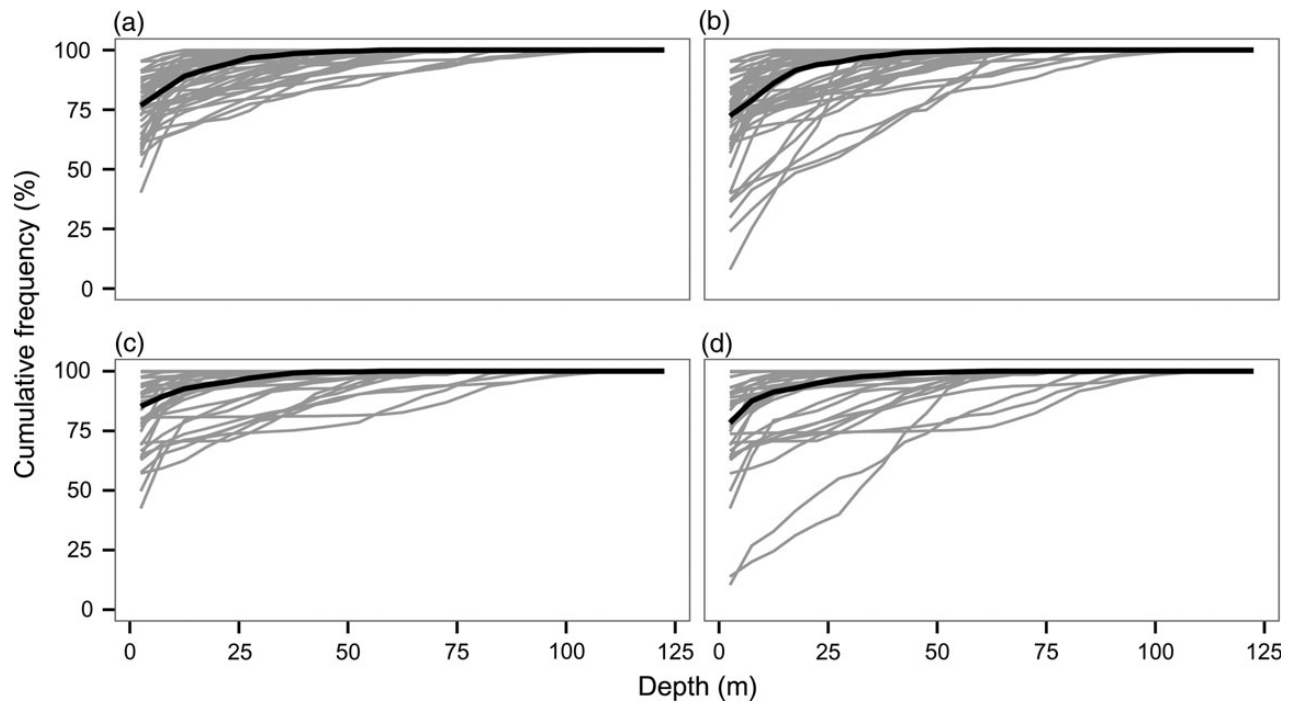
Figure 2. Cumulative depth use by Atlantic salmon on their homing migration through Scottish coastal waters. Thin lines: individual fish, thick line: median (a) unadjusted data ($n = 43$); (b) adjusted for possible early detachment ($n = 43$); (c) adjusted to trim 24 h post-release behaviour ($n = 35$); (d) adjusted by both (b) and (c) ($n = 32$). Individuals with <200 depth readings were excluded from graphs.
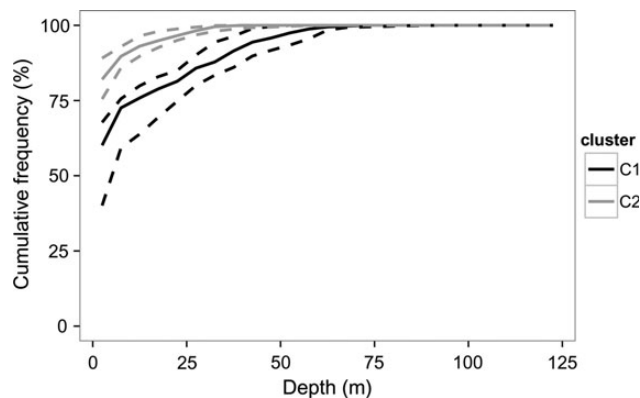

Figure 3. Median cumulative depth use of two groups of salmon identified by cluster analysis, showing IQRs. Data used are trimmed for early detachment bias.

by salmon returning through Scotland's northern coastal waters (median 72–85% of time at 0–5 m depths, mean 67–81%) is more similar to that of kelts that had returned to feed at sea, and less surface-orientated than that of homing salmon migrating through certain estuarine/fjordic environments towards local rivers. The range of maximum diving depths (13–118 m) of adult salmon in the coastal waters around northern Scotland was similar to the depths present at the pop-off locations (0.5–151 m) and around the study area (Figure 1). The data collected are therefore consistent with most salmon using the full extent of the available water column. Dives of over 600 m were recorded in the Labrador Sea for salmon tagged as kelts (Lacroix, 2013).

Salmon on their homeward migration in the coastal zone were predominantly surface-dwelling, but most passed regularly through the water column, and some spent extensive time at depth. Among this general pattern, there was evidence for two different groups of cumulative depth use, representing shallower and deeper swimming fish. We were unable to find evidence for any association of particular clusters with available individual fish metrics, although there was an association between clusters and pop-up location, with the deeper swimming group having a more westerly distribution. While different patterns of diving behaviour have previously been noted for Atlantic salmon (Sturlaugsson, 1995), the reasons for different uses of the water column are unclear. Diving may be associated with feeding (Reddin *et al.*, 2004; Lacroix, 2013), predator avoidance (Hastie *et al.*, 2006, Lacroix, 2014), sampling the water column in search of olfactory cues from the home river (Westerberg, 1982; Døving *et al.*, 1985), and behavioural thermoregulation (Tanaka *et al.*, 2000; Reddin *et al.*, 2011). The behaviour of fish is likely to depend on the relative importance of different processes at any given time, which may vary depending on the phase of migration (Middlemas *et al.*, 2009) and the geographic location of the fish (Lacroix, 2013). For example, while two distinct clusters were found in the data from this study, all fish alternated between periods at the surface and periods of diving (e.g. Figure 4). Examination of longer deployments will be required to determine the periods over which individuals may switch between different patterns of depth use, or whether the differences found here are stable over extended periods during migrations in coastal waters.

The depths used by salmon in this study were greater during the night than the day. This contrasts with previous studies which have found that both Atlantic salmon post-kelts and post-smolts tended to be closer to the surface of the sea at night (Davidsen *et al.*, 2008; Hedger *et al.*, 2009; Reddin *et al.*, 2011; Lacroix, 2013). These behavioural variations may be due to differences in the local environments and/or the salmon, for example, whether they are actively feeding.
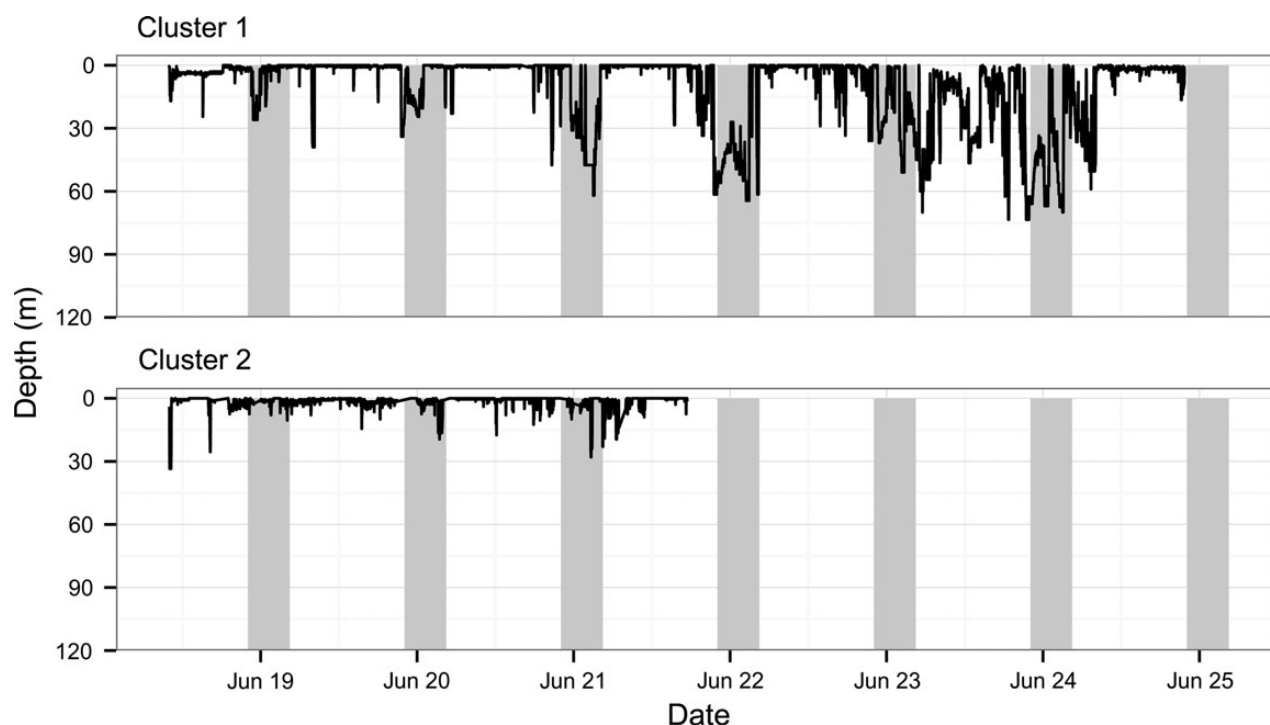
Figure 4. Example depth tracks with time of an individual from each of the two groups identified in the cluster analysis. Grey bars indicate the period between local sunset and sunrise.

The locational information provided by this study suggest that salmon may typically follow coastal swimming routes, but are by no means restricted to this zone. Minimum daily travel rates (23.4 km d^{-1}) are similar to those of homing salmon estimated by mark-recapture in the Norwegian sea and fjords (Hansen *et al.*, 1993) and of those in open sea off Scotland's east coast estimated either by mark-recapture (Pyefinch and Woodward, 1955) or by acoustic tracking (Hawkins *et al.*, 1979; Smith *et al.*, 1981), though direct comparisons with these studies are difficult. They are somewhat slower than the 38 km d^{-1} reported for post-kelts on their seaward migration through a fjord (Halttunen *et al.*, 2009). However, interpretation of minimum daily travel rates is difficult since, depending on swimming behaviour, they may have little relationship with actual distance travelled.

The results of this study have several general implications in relation to development of MRE. First, salmon may come into contact with devices throughout the water column. Second, some individual fish are more likely to use deep and midwater zones than others, but the use of the upper layers (<20 m) predominated usually. Third, wave energy generators in near-surface waters might be particularly likely to interact extensively with homing salmon. Such devices may also have exposed cabling generating EMFs that might be experienced by migrating salmon.

This study also has specific implications for the deployment of tidal turbines within the Pentland Firth. The turbines so far licensed for this area have a minimum clearance of 8 m between the turbine blade and the water surface (Anon., 2012). All the tagged salmon were recorded at depths below 8 m and therefore had the potential to be impacted by the proposed turbines, should they traverse the development area within the Pentland Firth. Accounting for potential early release, individuals spent a median of 24.2% of their time below this depth (IQR 14.6–32.7). However, the scatter in pop-up

locations (Figure 1) suggests that salmon do not have well-defined routes in the region and it is not currently possible to predict what proportion of the population passes across specific zones within the Pentland Firth. While the data can be used to help model the co-occurrence of salmon and turbines, information on avoidance behaviour will be required to assess impact. Assessment of avoidance behaviour and understanding the possible impact of EMFs are therefore further priorities in assessing requirements for mitigation.

Supplementary data

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

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