Original Article

Where the salmon roam: fjord habitat use of adult Atlantic salmon

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The habitat use of adult Atlantic salmon was evaluated in a fjord complex in western Norway. A representative sample of 9 wild and 29 hatchery origin Atlantic salmon were tagged with acoustic tags and tracked with 28 stationary receivers from June 2012 to river entry. Using a movement-based kernel density estimation, we identified near shore habitat use in relation to a National Salmon Fjord (NSF) and adjoining aquaculture sites. Furthermore, we compared progression rates and vertical distributions among habitat units. Mean residence time for salmon with acoustic tags from marking to river entry was 30 days (range 3–83 days). Moreover, recaptures of individuals with T-bar anchor tags supported the long residency of Atlantic salmon within the fjord (0–63 days). The main habitat use occurred outside the NSF (68%), with 62% of the individuals overlapping with one or more aquaculture sites. Median progression rates ranged from 15 km d^{-1} up to 42 km d^{-1} among the different sections of the fjord with a mean vertical distribution <2 m from the surface. Whereas direct implications from the overlap with aquaculture are unclear, the results illustrate the challenge encountered when evaluating the effectiveness of marine protected areas in close proximity to aquaculture sites.

Keywords: acoustics, adult Atlantic salmon, aquaculture, hatchery Atlantic salmon, marine protected areas, movement based kernel density estimation, near shore habitat use

Introduction

The spawning migration of Atlantic salmon (*Salmo salar*) is one of the best-known migrations in the animal kingdom and historically has been an important source of food and income (Hindar *et al.*, 2007). However, over the last 40 years, Atlantic salmon populations have declined throughout their native range (Friedland, 1998; Parrish *et al.*, 1998; Jonsson and Jonsson, 2004). A wide spectrum of anthropogenic factors are limiting the recovery of Atlantic salmon, ranging from regional scale impacts like climate change (Hare *et al.*, 2016) and acidification (Hesthagen *et al.*, 2011), to localized impacts including aquaculture and habitat degradation (Taranger *et al.*, 2015; Forseth *et al.*, 2017). Throughout their life cycle, Atlantic salmon use a multitude of habitat types alternating from freshwater to marine ecosystems and it is challenging to study and understand how Atlantic salmon interact with their environment (Klemetsen *et al.*, 2003).

Whereas many studies have focused on the distribution throughout the freshwater phase and river entry of the adult salmon, relatively few studies have examined how salmon use near shore habitat prior to entering the rivers to spawn (see Thorstad *et al.*, 2011 and references therein). The marine phase of salmon spawning migration is often perceived as uni-directional, entering the fjord and migrating directly to the river (Davidsen *et al.*, 2013). However, a uniform and direct migration pattern is unlikely and salmon probably reside in the fjords and estuaries searching for the correct natal river (Hasler and Cooper, 1976) or waiting for ideal river conditions (Potter, 1988; Priede *et al.*, 1988). In addition, animals interact with obstacles and the general environment at both spatial and temporal dimensions simultaneously (Horne *et al.*, 2007) and it is likely that valuable information is lost when complex processes in nature are reduced to single dimensions. Therefore, it is necessary to incorporate a

spatiotemporally explicit model that directly assesses the potential overlap between salmonids, their environment, and the pressures that affect them (Lennox et al., 2017; Ogburn et al., 2017).

As the pressure on marine resources increases (Bujnicki et al., 2017), marine spatial planning (MSP) has become one of the most important management tasks. This is central when implementing economic strategies to increase aquaculture production, while simultaneously creating management strategies to limit the potential impacts on native fauna. A relatively new management tool used in Norway to protect wild salmonids is the restriction of aquaculture activities within designated zones called National Salmon Fjords (hereafter called NSF). Legislated for by the Norwegian Parliament in 2003 and then again in 2007 (DKMD, 2006), the Norwegian government created a total of 29 NSFs throughout Norway with the sole purpose of protecting salmonids from anthropogenic impacts, such as genetic introgression of aquaculture, and the spread of disease and parasites (Aasetre and Vik, 2013). It is necessary to understand how populations use the habitat within and around protected areas when evaluating their effectiveness (Pomeroy et al., 2005). This has become evident in recent work along the Norwegian coast where it was concluded that many of the NSFs had minimal effects in protecting wild salmonids against sea lice (Bjørn et al., 2011; Serra-Llinares et al., 2014). However, knowledge is still lacking on how individuals directly use the habitat in relation to different anthropogenic pressures (e.g. aquaculture) and management strategies (e.g. NSFs).

The central objective for this paper is to assess the spatiotemporal distributions throughout the fjord system and to test how different behaviour metrics (progression rates and vertical distribution) change among habitat zones, the potential overlap with aquaculture, and the effectiveness of the NSF. To test how progression rates and vertical distribution change in the different habitat zones, we predict that progression rates will be slower in the estuaries and higher in the outer and inner fjord (Davidsen et al., 2013). In addition, we also predict that depth use will decrease as Atlantic salmon move closer to their natal stream.

Material and methods
Study area
The study area is located on the west coast of Norway 10 km north of the city of Bergen, and consists of an inner and outer fjord (IF and OF, respectively) with multiple rivers and connected estuaries (Arna estuary = AE, Dale estuary = DE, and Vosso estuary = VE) within the IF (Figure 1). By far the largest river system with Atlantic salmon in the study area is the Vosso River, and populations of Atlantic salmon are also found in the Arna, Dale, Ekso, Lone, and Modalen rivers. The IF, Osterfjord, is a deep and narrow fjord that surrounds the large island of Osterøy ($163 \, km^2$ including connected estuaries). Surface waters are brackish (ppt < 20), and usually have a strong thermo- and halocline layer at a depth depending on the discharge from the main rivers and rainfall throughout the catchment (Barlaup, 2013). One of the 29 NSF in Norway is located within the IF and protects $66.76 \, km^2$ of estuarine habitat for salmonids (Figure 1). The OF is an archipelago with several interconnected fjord arms (Byfjorden, Hjeltefjorden, Radfjorden, Herdlefjorden, and Mangersfjorden) and is dominated by more saline surface water (ppt > 20).

Capture, tagging, and tracking
Atlantic salmon populations within the study area consist of both hatchery- and wild conspecifics. Cultivation programs in the Dale and Vosso rivers are used to release smolts, based on genetically distinct brood stock originating from wild fish caught in their respective rivers, to supplement depleted wild populations (for additional details see Barlaup, 2013). To obtain a representative number of individuals to track, it was necessary to tag returning Atlantic salmon both originating from hatchery- and wild conspecifics. For easy identification, all hatchery-reared Atlantic salmon had their adipose fin removed prior to release.

Adult Atlantic salmon capture was conducted at three locations during the summer of 2012. Two capture locations (CL) were in the IF situated between the Dale and Arna rivers (CL 1 and 2; Figure 1) and were active from mid June to mid August 2012. The third location was situated near the entrance to the VE (CL 3; Figure 1) and was active from late May to late September 2012. To compare residence time of individuals with acoustic tags to the broader population of Atlantic salmon, we used individuals caught at CL 1 (wild = 62, hatchery = 359) and CL 3 (wild = 17, hatchery = 171), which are used to assess the number of returning Atlantic salmon to the system. To verify recaptured individuals, all salmon from the three-CL were implanted with a T-bar anchor tag with a unique identification number (FD-94; Floy Tag & Mfg., Inc.).

CL 2 was used to capture individuals to implant with acoustic transmitters. A total of 9 wild and 29 hatchery fish were tagged with acoustic tags (n = 38; Supplementary Table S1). One individual died upon recapture at CL 2 ~5 weeks after tagging. Another fish likely migrated out of the study area as it was last detected in the OF. Finally, we categorized eight individuals as captured during sports fishing prior to entering the river based on their last locations situated in the IF. Compared with the captures at CL 1 and CL 3, the rearing origins of the acoustically tagged individuals appear to be representative of the population of returning adult Atlantic salmon (15, 23, and 9% wild origin for CL 1, CL 2, and CL 3, respectively).

Two models of Vemco acoustic transmitters (VEMCO Ltd, Halifax, Canada) were used during the study, the V13-1L (n = 27, 13 mm × 36 mm, and mass in air = 11 g, battery life ~1117 days) and V13P-1L (n = 11, 13 mm × 48 mm, and mass in air = 13 g, battery life ~727 days). The V13P-1L includes a pressure sensor to measure depth. To implant acoustic transmitters, fish were first anesthetized with benzocaine, and the total length (cm) and wetted mass (g) was recorded. The mean length of tagged individuals was 982 mm (SD = 57 mm) with no difference between individuals tagged with depth tags and standard tags (F-value = 0.997, df = 1, p-value = 0.325). Each tag has a unique ID number and the signal is transmitted randomly every 80–160 s to reduce the chances of tag conflict. Tags were surgically implanted into the body cavity with a ventral incision (3–4 cm in length) just anterior to the pelvic girdle. To close the incision, one suture (4-0 nylon, manufactured by Ethicon) was used in the middle and the ends were secured with tissue adhesive (Braun Histoacryl). Throughout the procedure (~5–8 min per fish), the gills were irrigated with water to maintain oxygen flow. Individuals were then placed in a 1.5 m corrugated culvert (0.5 m diameter) with netting to promote water flow for ~30 min and released once they appeared to recover from the surgery (Norwegian Animal Research Authority approval ID 4141). Tag insertion into the
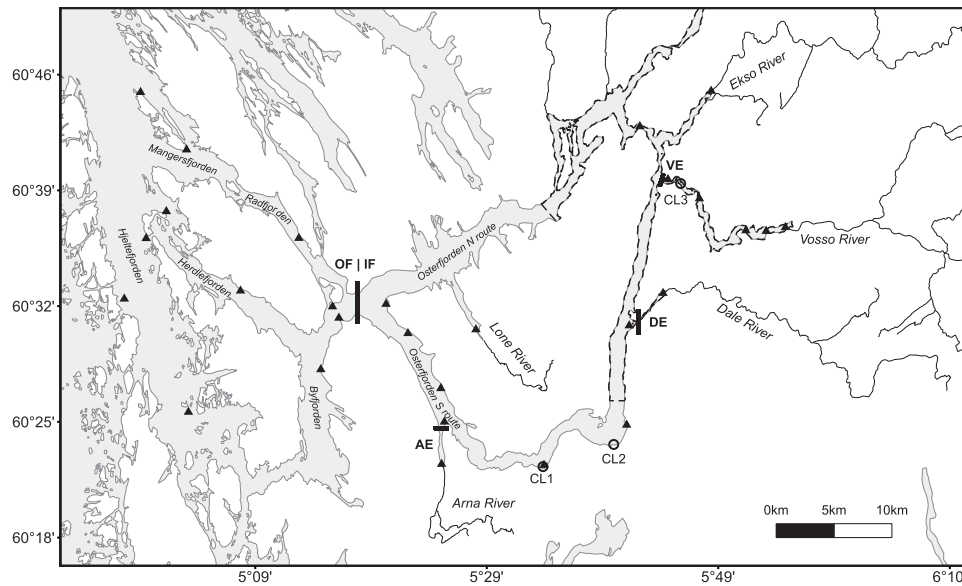
Figure 1. Map of the study area located in western Norway. Solid triangles represent acoustic receivers locations, open circles are the capture locations, solid lines indicate the boundary between different habitat units (outer fjord = OF, inner fjord = IF, Arna estuary = AE, Dale estuary = DE, and Vosso estuary = VE), and the dashed line outlines the National Salmon Fjord.

peritoneal cavity has previously been reported as a robust method with minimal effects on behaviour and survival (Davidsen *et al.*, 2013).

To track fish movement throughout the fjord, 28 Vemco VR2W-69 kHz receivers were placed within the study area (from May to December 2012; Figure 1) with one receiver positioned at the river mouths for Arna, Lone, Dale, Ekso, and Vosso rivers. The receivers were set ∼5 m below the surface. Tag range was highly variable depending on the location of the receiver. Normal detection range of the receivers was 300–800 m with the VL13 tags (Espedal, 2015). However between CL1 and CL2, we had simultaneous detections by two or more receivers up to 8 km apart. Therefore, five receivers were removed from the data set (open triangles Supplementary Figure S1) to reduce overlapping detections and to decrease complications with the different levels of analysis (e.g. inflated progression rates; see Supplementary Appendix S1 for more details).

Progression rates and vertical distribution among habitat zones

To assess spatial differences in behaviour throughout the fjord, we focused on rates of movement between receiver locations (referred to as progression rates, m/s) and depth use (m) at receiver locations within the study area. To calculate progression rates between two points, we calculated the difference in time between the last recording of the initial point and first recording of the final point. To measure distance among detections, we calculated the sea distance (20 m raster cells) between each receiver (gdistance package; VanEtten, 2015). Because of unrealistic progression rates (10–99 m/s) at four paired receivers; it was required to omit 380 observations including the habitat unit AE from the progression rate analysis (37% of all observations, see the Supplementary Appendix S1 for further detail).

To match the analysis of progression rates and to account for pseudoreplication (33 022 detections of depth), depth was averaged for each period of receiver detection (from first detection to last detection at a receiver; referred to as depth). This resulted in 11 individuals consisting of 309 depth observations among 25 of the 28 receivers. We used a linear mixed effects model (lme4 package; Bates *et al.*, 2015) to analyse progression rates and vertical movements among the different habitat types (predictor variables). For the progression rate and depth analysis, we had repeated observations between receiver pairs and for each individual. Therefore, we chose to include the nested random variables of receiver pair and individual. A Tukey's post-hoc test was used to determine significant relationships ($\alpha = 0.05$) of progression rates and depth use among the different habitat units (outer and inner fjord and the different estuaries, Figure 1; Hothorn *et al.*, 2008). Because of violations of the model assumptions of linearity and homoscedasticity, we applied a cube root transformation to both models based on a Box Cox transformation assessment (Box and Cox, 1964).

Spatiotemporal analysis of fjord use

We calculated Atlantic salmon habitat use in the fjord by using a movement-based kernel density estimation (MKDE) of biased random bridges (BRB) to analyse Atlantic salmon trajectories (adehabitat package; Calenge, 2006). Trajectories are defined as the successive time ordered movements among receivers. An important attribute of the MKDE is its ability to account for auto-correlation between two successive points (Kranstauber *et al.*, 2012). Because the MKDE is based on time-ordered events (i.e. trajectories) rather than unlinked points, the MKDE improves the overall biological relevance of habitat use estimates (Horne *et al.*, 2007; Benhamou, 2011). To assess near shore habitat use during the spawning migration of Atlantic salmon, it is necessary to place emphasis on the residence time in space by calculating an intensity distribution (ID; Benhamou and Riotte-Lambert, 2012). For a measure of goodness-of-fit for the ID, we used the 30% isopleth areas (ID_{30}) based on recommendations of Benhamou and

Table 1. The median, range, and number of observations (n) for progression rates and depths, and the mean and range for residence time as seen in the outer fjord (OF), inner fjord (IF), Arna estuary (AE), Dale estuary (DE), and Vosso estuary (VE).

Habitat unit	OF	IF	AE	DE	VE
Progression rate (km/d)					
Median	25	42	–	28	15
Range	0.5–227	2.1–219	–	5.4–118	0.4–72
n	121	341	–	30	110
Depth (m)					
Median	0.4	0.9	1.1	0.7	1.8
Range	0.0–85.7	0.0–20.7	0.0–14.5	0.0–26.4	0.0–33
n	45	117	66	36	45
Residence (d)					
Mean	4	10	7	3	8
Range	0–19	0.6–24	0–29	0–39	0–44
Presence					
Habitat Total	23(7)	38(11)	29(8)	6(3)	26(9)
River	–	–	21	6	16
River Entry	–	–	9	3	16

The number of individuals present in each habitat type (number of individuals with depth tags in parenthesis) along with the number of individuals that were seen at the river receiver (river) and classified as entering the river (river entry). For presence in the river and river entry, the estuary represents the respective river [e.g. Arna estuary (AE) = Arna river].

Riotte-Lambert (2012). As a result of the smoothing parameters used within this study (outlined below), MKDE outputs often predicted habitat use on land. Therefore, all layers were clipped to the fjord to estimate usable habitat (km^2, rgeos package; Bivand and Rundel, 2017). Finally, to summarize the ID_{30} for all individuals, we calculated the percentage of individuals that had an overlapping ID_{30} at any given point in the fjord (ID_p).

Three smoothing parameters are needed to calculate the ID_{30}. The first is the maximum time threshold that successive location points are not considered linked. Because of the constant and high rate of movement of adult Atlantic salmon seen in this study, movements detected after 12 h ($T_{max} = 43\,200$ s) are unlikely to be representative of two adjacent trajectories (e.g. entering a river and then leaving due to suboptimal conditions). The second is the minimum kernel smoothing parameter ($h_{min} = 4000$ m), which account for all potential locations that an individual can inhabit within a receivers range (Benhamou and Cornélis, 2010). We used 4 km to account for uncertainty associated with the large variation seen for receiver read ranges (e.g. read range up to 8 km). The final smoothing parameter is the minimum distance between two consecutive movements where an individual was considered stationary ($L_{min} = 500$ m). Because the receivers are at fixed positions, any movement between receivers is considered a true movement, and L_{min} of 500 m was less than the minimum receiver distance (620 m) for this study.

To assess the effectiveness the NSF and the potential overlap with aquaculture, we compared the overlap of the ID_p to the NSF and aquaculture sites. While it is possible to extract the ID_p for each point in the study area, the computational requirements were too time consuming to determine the sea distance to the southern border of the NSF for each point. Therefore to obtain a representative sample throughout the study area, we randomly selected 250 points throughout the fjord system (75 points in the NSF, 100 points in the inner fjord excluding the protected area,

and 75 points in the outer fjord). Subsequently, we extracted the ID_p at each point and calculated the sea distance (described above) to the southern border of the NSF. We choose the southern border of the NSF based on the limited presence of individuals seen traversing the northern channel around Osterfjorden (Figure 1). Finally, we calculated the cumulative frequency distribution and identified the ID_{p50} and ID_{p95} (the 50th and 95th percentile of ID_p derived habitat use of Atlantic salmon) based on the proximity to the southern border of the NSF to determine the effective location for the southern border based on the intensity of habitat use. All analyses were conducted in the statistical package R (version 3.5.0; R Core Team, 2018).

Results

The recapture rates of Atlantic salmon with T-bar anchor tags at CL 1 and CL 3 were 8% for both CL and the mean time between recapture was 17 days (range 0–29 days) and 9 days (range 0–63 days), respectively. The recapture rate between CL 1 and CL 3 was 4% (range 3–38 days). The residence times of the recaptured T-bar anchor tagged salmon indicate that they are spending extended periods of time within the IF and estuaries prior to entering the river.

All 38 individuals with acoustic tags from CL2 were detected at least once at one or more receivers with 28 categorized as entering the river (Arna = 9, Dale = 3, and Vosso = 16) based on the last detection at the river receiver. The mean date of river entry for all fish was 13 August (Arna = 14 August, SD = 9 days; Dale = 02 August, SD = 27 days; Vosso = 15 August, SD = 23 days). The mean residence of salmon with acoustics tags was similar to recaptures of salmon with T-bar anchor tags with an average of 30 days from initial tagging to river entry (range 3–83 days). In addition, salmon occupied more time in the IF (mean = 10 days) compared with the other habitat units (Table 1).

Movement patterns of the 38 Atlantic salmon tagged with acoustic transmitters demonstrated various patterns ranging from unidirectional movements terminating in a river (Figure 2a) to broad bi-directional movements spanning multiple habitat types (Figure 2c). Median progression rates while inhabiting the fjord area and connected estuaries was 0.36 m/s with a range of <0.01–2.63 m/s. Habitat specific progression rates where fastest in the IF (median = 0.50 m/s) and slowest in the VE (median = 0.18 m/s, Table 1). While we compared all combinations of progression rates among the different habitat types (Figure 3), a statistically significant increase in progression rates were seen between the OF and IF and statistically significant decreases were observed between the OF and VE, and IF and VE (Figure 3). Prior to accounting for pseudoreplication, depth ranged from <0.01 (all habitat units) to 85.74 m (Mangersfjorden of the OF, Table 1). In addition, the median depth during the study was 0.97 m with the shallowest median depth seen in the OF (0.4 m) and the deepest median depth seen in the VE (1.8 m, Table 1). However, a significant increase in depth was observed for individuals that migrated through the VE compared with the other habitat types (Figure 3).

Spatiotemporal analysis of fjord use

Adult Atlantic salmon movements were concentrated throughout the southern corridor of the IF and extending from the VE to the OF (Figure 4). Conversely, Atlantic salmon had minimal use of the northern corridor of the IF with only one individual moving through this area. Atlantic salmon habitat use (ID_{30}) consisted of
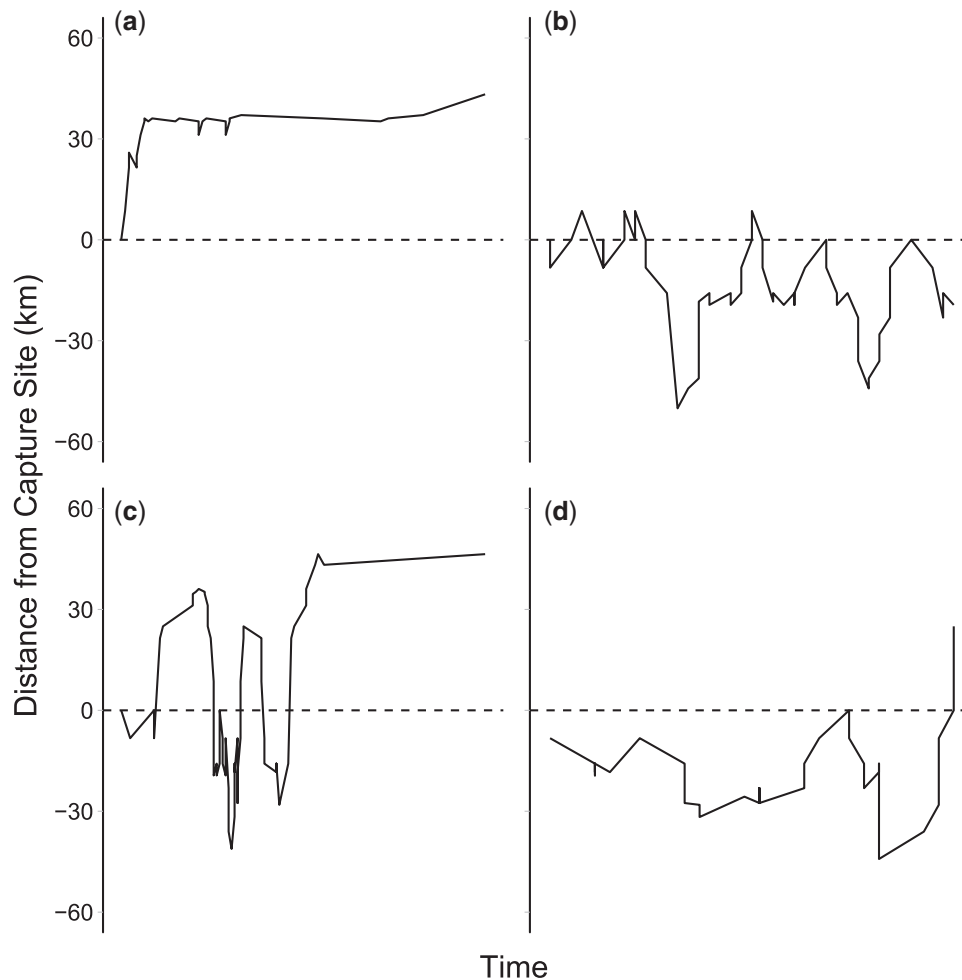
Figure 2. Here are four examples of the different movement patterns observed in this study. The fjord residence time for these individuals ranged from 6 days (a) to 62 days (c) with two individuals entering the Vosso River (a and c), one entering the Arna River (b), and one classified as captured during sports fishing (d).

relatively small spatial extents with a median habitat size of 25 km^2 and ranged from 12 to 56 km^2. In relation to the NSF, the median ID$_{30}$ overlap with the NSF was 17% with a range of 0–98%. The cumulative habitat use (ID$_p$) across individuals found that as much as 32% of the habitat use (cumulative ID$_p$) occurred in the NSF with 50% of the cumulative habitat use (ID$_{p50}$) occurring ~8.5 km from the southern border of the NFS and the ID$_{p95}$ occurring 25 km from the southern border of the NSF (Figure 4). Aquaculture sites also overlapped spatiotemporally with Atlantic salmon ranging from 0 to 62% (mean ID$_p$ = 8%). Individuals had a higher frequency of overlap at aquaculture sites located in the IF (mean ID$_p$ = 23%) compared with the OF (mean ID$_p$ < 1%; Figure 4).

Discussion

Comparisons of Atlantic salmon with T-bar anchor tags and acoustic tags demonstrated that returning Atlantic salmon spend considerable time within the fjord prior to entering the river (up to 63 and 83 days observed in this study between the two methods, respectively). Residency times observed in this study are likely underestimated because the CL are situated in the IF and adult Atlantic salmon have to occupy the IF prior to capture. In addition, the NSF was limited in encompassing the spatiotemporal distribution

routinely used by Atlantic salmon and resulted in an increased overlap with aquaculture sites within the IF.

Understanding the spatiotemporal use of near shore habitat by Atlantic salmon can provide valuable insight during MSP. For instance, identifying the spatial locations of new technologies (Godfrey *et al.*, 2014), future aquaculture locations, or with current and future management strategies. One management strategy used to protect salmonids within near shore habitat is the use of protected areas. The present study is the first to directly evaluate the NSF in relation to returning adult Atlantic salmon. The current area of conservation protects ~40% of the IF, while, the main concentration of adult salmon in this study resided outside the NSF. To be an effective marine protected area (MPA), it is generally accepted that larger MPAs have a greater chance of being successful (Claudet *et al.*, 2008; Edgar *et al.*, 2014). This is in line with previous studies assessing the NSF in Norway that found that the smaller protected areas have limited effectiveness to protect sea trout against sea lice infestations (Bjørn *et al.*, 2011; Serra-Llinares *et al.*, 2014). Extending the southern border to the ID$_{p95}$ threshold would add an additional 45 km^2 of habitat and create a biologically meaningful MPA by incorporating habitat use that is routinely used by individuals in the system.
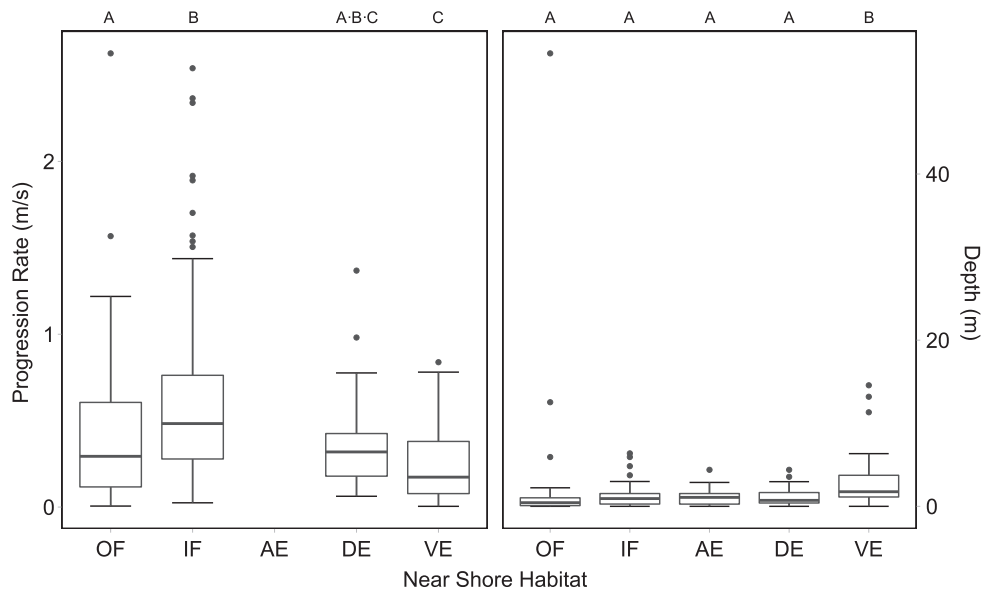
Figure 3. Progression rates (left) and depth (right) comparisons among outer fjord (OF), inner fjord (IF), Arne estuary (AE), Dale estuary (DE), and Vosso estuary (VE). The solid line denotes the median value, the box is the interquartile range, whiskers are 1.5 times the interquartile range, and points are outliers. Letters denote comparisons of non-significant relationships.
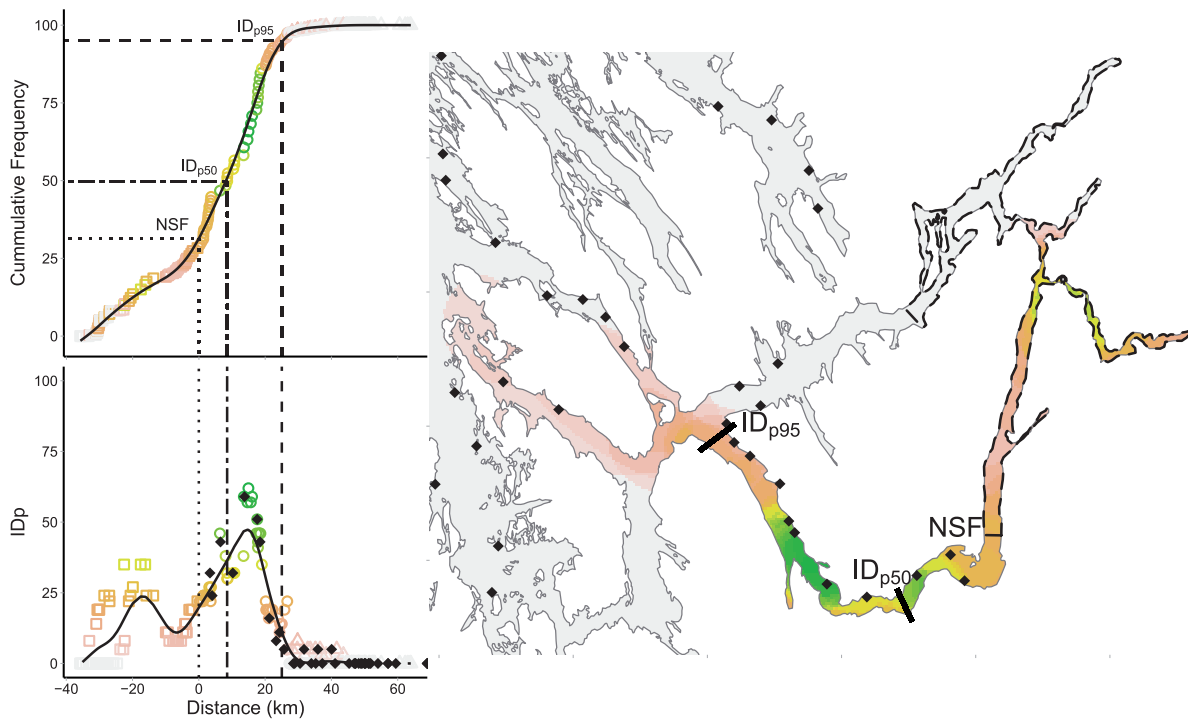
Figure 4. Map illustrating the habitat use of adult Atlantic salmon (grey is low intensity use and green is high intensity use) in relation to the National Salmon Fjord (dashed line polygon; NSF) and aquaculture sites (black diamonds). Bottom left figure is the percentage of individuals that had overlapping intensity distribution (ID_p) in relation to the bottom border of the NSF (NSF in map and plots). Top left figure is the cumulative frequency of the overlapping intensity distribution. The dotted line is the southern border of the NSF, the two dashed line is the distance that 50% of the overlapping intensity distribution (ID_{p50}), and the dashed line is the 95% overlapping intensity distribution (ID_{p95}). The map shows where the ID_{p50} and ID_{p95} points are located in space (solid black line). Negative values indicate locations within the NSF (open squares) and positive values indicate values outside the NSF (open circles are in the inner fjord and open triangles are located in the outer fjord). The intensity of the heat map corresponds to the the point coloration in the two graphs.

One consequence of extending the southern border of the NSF would be the removal of 10 aquaculture facilities. While it is certain that Atlantic salmon overlap spatiotemporally with aquaculture sites, it is unknown what impact farms have on returning adult Atlantic salmon. One concern that has been raised related to the interaction between migrating wild salmonids and fish farms is the potential spread of disease and parasites between returning Atlantic salmon and farmed fish (Garseth *et al.*, 2013b). Transmission between aquaculture facilities and wild salmonids has been seen in the past but the frequency and consequence of infections are largely unknown (Garseth *et al.*, 2013b; Madhun *et al.*, 2015). It may be difficult to quantify the proportion of infected wild individuals, as they tend to be less catchable and are more likely to be preyed upon (Madhun *et al.*, 2015). In general though, wild adult salmon have been seen as an unlikely vector for infecting farmed fish due to their low densities (Garseth *et al.*, 2013a) and limited residence time around aquaculture. However, the temporal and spatial overlap with a high concentration of aquaculture sites ($\sim$62 ID$_P$ overlap) combined with the long residence times observed (0–83 days) within this study may create a situation where infections may occur from wild to farmed salmon and from farmed to wild salmon (Garseth *et al.*, 2013a). Therefore, prior to altering existing NSF boundaries, it is prudent to further explore to what extent aquaculture sites can have, if any, on returning Atlantic salmon.

While the strength of this study is the direct quantification of Atlantic salmon spatial and temporal scale of habitat use, it may not be representative of all the populations that reside within the Osterfjord system. For instance, we failed to see individuals enter the Lone, Ekso, and Modalen rivers and only one individual was observed migrating through the northern route of the inner fjord. Sampling in the southern corridor seems to only represent the populations that migrate through this area. It is therefore likely that the populations in the northern corridor of Osterfjord interact differently, both spatially and temporally, compared with populations in the southern corridor. In addition, this study focused on large two- and three-sea winter (2SW and 3SW respectively) adult Atlantic salmon. However, differences in time-at-sea have been seen in previous studies where younger one-sea winter (1SW) fish demonstrated a lower straying rate compared with 2SW fish (Jonsson *et al.*, 2003). It is therefore important to acknowledge that the current study potentially underrepresents the habitat use, as it is likely that differences exist based on time-at-sea age determinates (e.g. 1SW vs. 2SW; Jonsson *et al.*, 2003) and populations when assessing potential management implications.

Assessing the habitat use of an individual can provide valuable information into when and where Atlantic salmon can be found in the fjord, it is, however, not clear why salmon spend extended periods of time in the inner fjord (Powell and Mitchell, 2012; Quinn *et al.*, 2016). Several explanations may clarify why salmon use the habitat observed in this study, such as the difference between hatchery and wild conspecifics (Jonsson *et al.*, 1991), environmental factors affecting river entry (Quinn *et al.*, 2016), and natal stream identification. For instance, the salmon tagged in this study were predominantly salmon ($\sim$75%) from the Vosso hatchery that were released as smolts to help restore the Vosso Atlantic salmon population (Vollset *et al.*, 2016). Furthermore, a large portion of hatchery individuals was detected at the Arna river receiver at some point indicating a potentially high straying rate if river conditions were adequate for stream entry. Because the cues needed to migrate back to natal streams are not

necessarily fully imprinted onto hatchery Atlantic salmon, it is possible that hatchery individuals spend more time searching for the correct river and therefore could overinflate the residence time in the fjord prior to migrating to the river. Numerous studies have found differences between wild and hatchery salmon and particularly with straying rates from the intended release streams (Jonsson *et al.*, 1991). A large amount of variation in residence time was observed in both conspecifics and there may be significant differences between wild and hatchery fish. However, the number of wild salmon in our study was too small to test any potential difference between them. Given this limitation, the results from this study are still valid due to the large proportion of hatchery fish to wild fish present throughout the system.

Previous studies observed Atlantic salmon in the estuary for extended periods (Potter, 1988; Davidsen *et al.*, 2013), and one of the main attributing factors to time spent in the estuary prior to river entry is the river condition. Potter (1988) found that low river discharge delayed river migration. River entry for Atlantic salmon in the Arna River was within a relatively small time window compared with the Dale and Vosso Rivers where river entry was spread out across a month or more. This difference in river entry may be attributed to river conditions where Dale and Vosso rivers are larger rivers (watershed size is 198 km^2 and 1496 km^2, respectively) that have base flows that are adequate for upstream migration throughout the season. On the other hand, the Arna River is the smallest (51 km^2) and salmon potentially need higher-sustained discharges in order to migrate to spawning areas.

In addition to assessing the temporal and spatial distribution of returning Atlantic salmon, we also compared how progression rates and vertical distribution changed through the predefined fjord zones. We saw progression rates increase as Atlantic salmon entered the IF but no difference was seen between the IF and two of the three estuaries. Partially supporting our expectations, we observed a decrease in progression rates through the VE, which was also reported in Davidsen *et al.* (2013). Unlike Davidsen *et al.* (2013) though, we believe this may be attributed to several relatively narrow and shallow sections of the VE that act more like rivers than calm estuaries and the decrease in progression rate likely reflect the change in water velocity in these sections.

One interesting aspect from our study was that progression rates for Atlantic salmon were similar to flume tank testing of wild Atlantic salmon swim speeds (Colavecchia *et al.*, 1998) and were overall greater when compared with previously reported progression rates in near shore habitats (Hansen *et al.*, 1993; Davidsen *et al.*, 2013). Davidsen *et al.* (2013) reported mean progression rates in the Alta fjord of 9.7 km/d compared with the median progression rate of 31.1 km/d in this study. Overall, the median rates observed in this study are comparable to the maximum rates observed by Hansen *et al.* (1993) in fjords and more closely resemble rates in the coastal waters of Norway rather than the near shore habitat in the same study (Hansen *et al.*, 1993). These differences may be the result of the narrow Osterfjord system that may serve to direct the movements in a conserved and focused direction thereby increasing the progression rates between points. Fjords in previous studies were more open and allowed for greater orthogonal movement between points, thereby decreasing progression rates (Hansen *et al.*, 1993; Davidsen *et al.*, 2013).

Contrary to our expected results, individuals swam at greater depths when transiting the VE. This also differed from Davidsen

et al. (2013), where they reported that Atlantic salmon swam closer to the surface as they approached the river. It has also been shown that Atlantic salmon use vertical movements to help identify specific navigational cues (Døving *et al.*, 1985) and we expected more variation in depth use at locations further from the targeted river. While it is possible that such differences in depth use exist, the small number of individuals ($n = 11$) with depth sensor tags and the broad spatial placement of the receivers in the outer fjord could easily miss such fine scale movement patterns among locations. It is therefore necessary to further investigate how individuals use the vertical profile of the fjord during return migrations.

We showed, for the first time, how returning Atlantic salmon use habitat in a complex fjord system and demonstrated the propensity of Atlantic salmon to use habitat outside the NSF where aquaculture sites are present. By directly quantifying habitat usage, we can apply biologically relevant information into MSP practices for the species of concern and in-turn, enhance our ability to manage marine systems. Because it is unclear why Atlantic salmon spends prolonged time periods in the fjord, it is necessary to broaden the scope of future studies to include the dynamic nature of the focal species so as to improve our understanding of if and/or why populations use spatial resources differently.

Supplementary data

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

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