Animal Biotelemetry

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In situ measurement of salinity during seaward migration of Atlantic salmon post-smolts using acoustic transmitters with data-storage capabilities and conventional acoustic transmitters

Hiromichi Mitamura[1,2*], Eva B. Thorstad[2], Ingebrigt Uglem[2] and Finn Økland[2]

Abstract

Background: Development of miniature acoustic transmitters and data-storage tags has provided new insights into ecology of free-ranging aquatic animals. In this study, we used a data-storage-type and a conventional acoustic transmitter, both equipped with a salinity sensor, to measure the in situ salinity experienced by Atlantic salmon post-smolts during the first phase of their marine migration in a Norwegian fjord. The data-storage transmitter conveyed stored salinity data accumulated over a period of up to 27 h prior to moving within the range of a receiver, while the conventional transmitter conveyed only real-time salinity data. Five post-smolts tagged with a conventional transmitter were manually tracked from a boat, and 15 post-smolts tagged with the data-storage transmitter were monitored by six transects consisting of 29 stationary receivers deployed from the river and throughout the fjord.

Results: All tagged post-smolts primarily showed rapid seaward movements. They occasionally stayed in water with salinity below 20.0 psu in the inner part of the fjord, most likely because they were swimming close to the surface, where the salinity was low due to freshwater supply from the river. In the outer fjord, where full-salinity sea water (26.0–32.0 psu) was recorded in the entire water column, half (3 of 6) of the recorded fish still experienced low salinities (<20.0 psu) for periods between 2.25 and 54 h.

Conclusion: Both types of salinity transmitters provided data on ambient salinity of the post-smolts during the seaward movement. In the outer fjord, the post-smolts likely visited one or several river mouths. It is not known whether this behaviour is normal for Atlantic salmon post-smolts during migration, but it might be advantageous in terms of reducing infestation risk from salmon lice, which have low survival in low salinities. The data-storage transmitters provided data on the ambient salinity history of the tagged fish, even when the fish were outside the detection range of receivers. By using this type of transmitters, we were able to collect salinity data during a four times longer period than with conventional transmitters.

Keywords: Smolts, Post-smolts, Seaward migration, Fjord, Salmon lice

Background

Biotelemetry, including the use of small acoustic transmitters, has frequently been applied to provide insight into the ecology of free-ranging aquatic animals, like fishes and sea turtles [1–4]. The tagged animals may be tracked either manually or by using stationary receivers that record presence when within the detection range of a receiver [5–7]. When multiple receivers are deployed in an array, either at locations of particular interest, or across a river or a narrow bay or fjord, the obtained

*Correspondence: mitamura@bre.soc.i.kyoto-u.ac.jp
[1] Graduate School of Informatics, Kyoto University, Kyoto 606-8501, Japan
Full list of author information is available at the end of the article

data may be used for investigating fish movements and migration patterns [5]. Furthermore, by using transmitters equipped with a sensor, it is possible to explore how animals move and respond to variation in environmental conditions. Such sensors may, for instance, allow measurements of swim depth (e.g. [8]), dissolved oxygen [9] and acceleration [10, 11].

The Atlantic salmon *Salmo salar* is an anadromous fish species, of which juveniles (smolt) migrate from the rivers to the ocean for feeding, before they return to the natal river to spawn as adults [12]. During the last century, Atlantic salmon populations have declined [13, 14]. In order to support the wild stocks, hatchery-reared smolts are released into the rivers, where they migrate to the sea more or less simultaneously with their wild conspecifics [15, 16]. During the seaward migration, especially in the estuaries, they are exposed to a considerable predation pressure by larger fishes, such as the gadoids Atlantic cod *Gadus morhua* and saithe *Pollachius virens*, and by birds [17–20]. In addition, the migrating post-smolts are highly susceptible to infections by salmon lice (*Lepeophtheirus salmonis*) during the early part of the marine phase in areas with intensive Atlantic salmon farming [21, 22].

Atlantic salmon post-smolts normally swim in the upper few metres of the water column, most likely to reduce the risk of being preyed upon, as potential predators usually inhabit deeper waters [12]. This behaviour may also reduce the salmon lice infection risk, because salmon lice survive more poorly in the upper usually less saline part of the water column [12, 22]. It has been shown that survival and host infectivity of salmon lice are affected by even short-term exposure to reduced salinity [22, 23]. A preference for low salinities in the first phase of the marine migration may furthermore be related to acclimatization to sea water, because the transfer from freshwater to sea water involves considerable osmoregulatory stress [24]. Although several studies have shown that post-smolts migrate in the upper few metres of the water column [6, 25, 26], little is known about the salinity they actually experience in situ, and how they respond to variation in salinity.

In the current study, our aim was to record the salinity experienced during the early part of the seaward migration of salmon post-smolts, by using two types of transmitters with a conductivity sensor, allowing estimation of in situ salinity. One of the transmitter types was designed for manual tracking and provided real-time data during short-term tracking. The other was a combined data-storage tag and transmitter that was designed to store the in situ salinity for a longer period when the tagged fish were beyond the detection range of receivers. When in range of a receiver, the second tag type allowed transfer of salinity data. More specifically, our aims were to (1) examine the movements of post-smolts in relation to variation in experienced salinity in an estuary by manual tracking and (2) assess to what extent post-smolts stay in low salinity water during the first phase of the marine migration.

Methods

Transmitters

Two types of acoustic transmitters with a conductivity sensor (diameter 9 mm, length 37 mm, mass 7 g in air, output 147 dB, accuracy ± 1470 uS/cm, code set: S256, Thelma Biotel AS, Trondheim, Norway) were designed for this study. One was used for manual tracking (V9-CondTag, battery life: 5 days), and measured conductivity (uS/cm) at a constant time interval (5 s), which subsequently was converted into salinity by using a known linear-conversion formula.

The second type of transmitter also measured conductivity (V9-CondTag, 69 kHz, battery life: 90 days, Table 1) and was used for long-term monitoring with stationary receivers (VR2W, Vemco, Halifax, NS, Canada). In this study, the transmitter recorded a total of 27 h of data per series of signals, including 12 recordings of the average salinity value per 2.25 h. The salinity data were accumulated for a constant scheduled period, and an average value calculated from the data accumulated during this period. The average value was converted to one of eight predefined salinity ranges (salinity-range value 0–7: 0.0–3.9, 4.0–7.9, 8.0–11.9, 12.0–15.9, 16.0–19.9, 20.0–23.9, 24.0–27.9 and 28.0–46.0 psu.). The salinity-range values were stored in cyclic buffer with 12 cells. At the end of the first scheduled period, new salinity data were accumulated during the next scheduled period and then stored in the next cell. After 12 periods, the first/oldest value in the first cell was replaced with the latest value. The latest value was indicated by the write-pointer. The 12 values and the write-pointer were conveyed by the S256 code as a 16-bit payload with an 8-bit ID and a data value in 8 bits. Five S256 codes were implemented in the transmitter, which were able to send five IDs (40 bits) and five data values (40 bits). As a single salinity-range value occupied 3 bits, the cyclic buffer including 12 cells needed 36 bits for transmission. The write-pointer data were assigned to the remaining 4 bits. Conductivity was measured every 45 s. The period during which data were accumulated was set to 2.25 h, which means that the total monitoring period was 27 h. This period was set on the basis of movement speeds of post-smolts documented in a previous study in the same area with the same receiver array [15, 27]. The transmit interval for a series of signals was on average 150 s (range 100–200 s). This means that the same data were transmitted on average 54 times during every 2.25 h.

Table 1 Information of the Atlantic salmon smolts tagged with conventional sensor Transmitters (ID 1-5) and data-storage transmitters (ID 6-20)

Fish ID	Total length (mm)	Body mass (g)	Tagging date	Release date	Last detection date	Last detection site	Tag freq. (kHz)
1	328	330	9 May	11 May	–	–	60
2	303	277	9 May	12 May	–	–	72
3	297	234	9 May	12 May	–	–	75
4	301	267	9 May	13 May	–	–	66
5	312	276	9 May	13 May	–	–	63
6	264	183	10 May	11 May	N	N	69
7	294	218	10 May	11 May	18 May	6	69
8	272	201	10 May	12 May	17 May	6	69
9	286	229	10 May	12 May	14 May	4	69
10	290	239	10 May	12 May	13 May	5	69
11	294	227	10 May	12 May	13 May	2	69
12	292	236	10 May	12 May	13 May	6	69
13	285	213	10 May	12 May	13 May	5	69
14	292	246	10 May	13 May	N	N	69
15	275	229	10 May	13 May	18 May	6	69
16	280	214	10 May	13 May	14 May	2	69
17	287	220	10 May	13 May	15 May	6	69
18	296	228	10 May	13 May	N	N	69
19	302	262	10 May	13 May	16 May	6	69
20	287	241	10 May	13 May	14 May	1	69

N no detection after release

Detection sites refer to sites shown in Fig. 1

Study site and sea water environment

The study was carried out in the River Eira (mean annual water discharge of 17 $m^3\ s^{-1}$) and in the fjords Eresfjord and Langfjord in western Norway (62° 41′ N, 8° 8′ E, Fig. 1). Both Atlantic salmon and anadromous brown trout *Salmo trutta* occur in this river. The annual smolt run of Atlantic salmon has been estimated to 9500–31,500 individuals during 2001–2015. In addition, the power company releases 50,000 hatchery-reared Atlantic salmon smolts annually from the Statkraft Energy AS hatchery in Eresfjord. The wild smolts usually migrate from the River Eira during May, most years with a median migration date between 11 and 17 May.

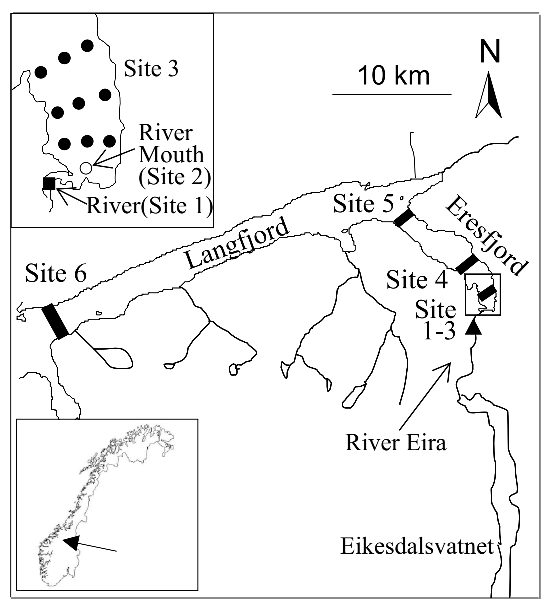

Fig. 1 Eresfjord in western Norway. The smolts tagged with data-storage transmitter were released in the river (*filled triangle*). Stationary receivers were deployed in arrays across the river and fjord, indicated as sites 1–6 (*filled square*: site 1 in the river Eira, *open circle*: site 2 at the river mouth, *filled circles*: site 3 consisting of three arrays in the inner Eresfjord, *lines* in the fjord: site 4–6 named the middle Eresfjord, the outer Eresfjord and the Langfjord, where several receivers were deployed)

Fish tagging and release

Twenty hatchery-reared Atlantic salmon smolts from the Statkraft Energy AS hatchery were tagged. Total body length of the fish ranged from 264 to 328 mm (mean ± SD 292 ± 14 mm) and the body mass from 183 to 330 g (mean ± SD 239 ± 32 g) (Table 1). The transmitter was attached externally as described by Økland et al. [28], under anaesthesia induced with 2-phenoxy-ethanol (Sigma Chemical Co., St Louis, MO, USA, 1 ml per 1 l sea water). The fish were then returned to a holding tank with freshwater for recovery for 1–4 days before release. All handling and tagging was conducted according to the

Norwegian regulations for treatment and welfare of animals (permit ID 2569).

The five fish that were manually tracked were released individually in the fjord close to the river mouth between 11 and 13 May 2010 (Table 1; Fig. 1). Before release, each tagged fish was held in a small net-pen (1 m^3) together with 20 untagged smolts for acclimation to sea water for 2 h at 0.5 m depth. The salinity in the net-pen was on average 22.9 psu (range 16.2–27.5). After acclimation, the net-pen was opened and all fish released. The remaining 15 fish used for long-term monitoring were released in the river 1.1 km upstream from the river mouth between 11 and 13 May (Table 1; Fig. 1).

Manual tracking and long-term monitoring system

Two types of receivers (VR28 and VR100, Vemco) were used from a boat for the manual tracking. The VR28 has four directional hydrophones that detect fish swimming direction by measuring the relative receiving strengths at the four hydrophones. The VR100 was equipped with a global positioning system (GPS) and an omnidirectional hydrophone, and was used to record the ID, salinity, date, time and the boat position. Using these two receivers in combination allowed individual tracking with a precision of approximately 10–20 m. Each fish was tracked for 67–206 min (mean $\pm$ SD 135 + 63 min) (Fig. 1). During manual tracking, the vertical salinity distribution at 0–3 m (0, 0.5, 1, 1.5, 2 and 3 m depth) was measured every 30 min by using a conductivity meter (WTW, KS COND 3).

For the long-term monitoring, 15 fish tagged with the data-storage transmitter were monitored by 29 stationary receivers (VR2W, Vemco), which recorded the five consecutive IDs and data values for the 12 salinity-range values, as well as date and time when the tagged fish were within the detection range. The receivers were deployed at six sites from the river to outermost part of the Langfjord (Fig. 1). At sites 1 and 2, a receiver was deployed at the bottom of the river and the river mouth, respectively. The distance between sites 1 and 2 was 0.4 km. At the remaining sites, the receivers were attached to anchored ropes at 3–5 m depth. At site 3 (inner Eresfjord, 2 km from site 1 in the river mouth), a grid of nine receivers was deployed. At site 4 (middle Eresfjord, 3.5 km from the river mouth), four receivers were distributed evenly in a line across the fjord. At site 5 (outer Eresfjord, 9.9 km from the river mouth), five receivers were distributed in a line across the fjord. The fjord is 1.5 km wide at both sites 4 and 5. At site 6 (Langfjord, 37.4 km from the river mouth), eight receivers were distributed evenly in a line across the fjord (2.6 km wide). The distance between receivers was approximately 300 m at sites 3, 4, 5 and 6. The detection ranges varied between 200 and 450 m in radius at 0.5–3.0 m depth. Data were downloaded on 27 July 2010.

Vertical profiles of salinity and water temperature in Eresfjord were measured using a conductivity-temperature-depth (CTD) probe (Valeport, mini-CTD) at 0.5-m intervals from the sea surface to 5 m depth and at 1-m intervals between 5 and 25 m depth. A total of 45 profiles at five monitoring transects were obtained. Three profiles at each transect across the fjord were made at sites 3, 4 and 5 on 6, 8 and 11 May 2010 (Fig. 1).

Evaluation of salinity measurements

The precision of salinity transmitters used for the manual tracking was evaluated in a tank experiment, where the transmitters were placed in five different salinities (0.0, 10.1, 20.1, 29.9 and 39.4 psu) with and without water circulation. Signals were transmitted and detected every 5 s, and both ID and salinity data from the transmitters were recorded by a VR100 receiver. Salinity data for 1 min in each solution were used to evaluate precision, and the relationship between salinity and transmitter data investigated with a general linear model. The slopes of the linear relationship with an intercept fixed at 0 were close to 1 (range 0.93–1.23 in circulating water, range 0.85–1.21 in non-circulating water, Table 2). The results indicate

Table 2 Relation between data from conductivity transmitters and salinity with and without circular flow in a laboratory evaluation of the transmitters

Tag	With flow			Without flow		
ID	*a*	2.5%	97.5%	*a′*	2.5%	97.5%
1	1.15	1.135	1.169	1.13	1.110	1.142
2	1.06	1.053	1.063	1.05	1.044	1.056
3	0.93	0.769	1.090	0.85	0.793	0.898
4	1.02	1.008	1.023	1.02	1.011	1.019
5	1.23	1.205	1.262	1.21	1.185	1.244

a and *a′* are slope estimated by general linear model from calibration data with an intercept fixed at 0

2.5% and 97.5% mean 95% confidence interval that the salinity transmitters provided reliable salinity estimates. Data from the manual tracking were calibrated according to these results.

Data analyses

Atlantic salmon post-smolts normally exhibit a distinct and rapid directional outward migration from the river outlets and throughout fjords [15]. Thus, if the tagged fish (1) disappeared between two receiver sites, (2) was detected only at one receiver site without any change in salinity, (3) showed long-term residency or (4) exhibited back-and-forth movements within the fjord, they were characterized as being dead or predated [29]. Only data for fish defined as being alive were used for further analyses. For fish tagged with transmitters that allowed long-term tracking, we defined an individual as being resident at a site if the time lapse between consecutive data was less than 30 min. Movement speeds between monitoring sites were calculated based on first recording at each monitoring site. Statistical analyses were carried out using R (ver. 3.2.1, Foundation for Statistical Computing, Vienna, Austria). A linear mixed model was fitted to explore the effect of distance from the river on swimming speeds of individuals using the *lmer* function in the *lme4* package with individuals as a random effect. The swimming speed was treated as a response variable, and the distance from the river was an explanatory variable. Confidence interval (95%) was calculated for the slope.

Results

Manual tracking

Three tagged fish (IDs 1, 2, 5) showed rapid, directional outward movement from the river mouth, with an average speed of 1.4 body length s^{-1} (±0.4 SD) (Fig. 2). The other two fish (IDs 3, 4) remained near the river mouth during the tracking period (Fig. 2). The fish experienced salinities from 0.0 to 36.0 (psu) during the tracking period (Fig. 2). There was a salinity stratification at the river mouth, with lower salinity water in the upper metres of the water column, and a tendency towards a less clear stratification further away from the river mouth (Fig. 3). The salinities experienced by these five fish showed that they were sometimes swimming in the brackish water (less than 20.0 psu) close to the surface during the first part of their outward migration, but also that they predominantly stayed in sea water (full-salinity around 30.0 psu) (Figs. 2, 3).

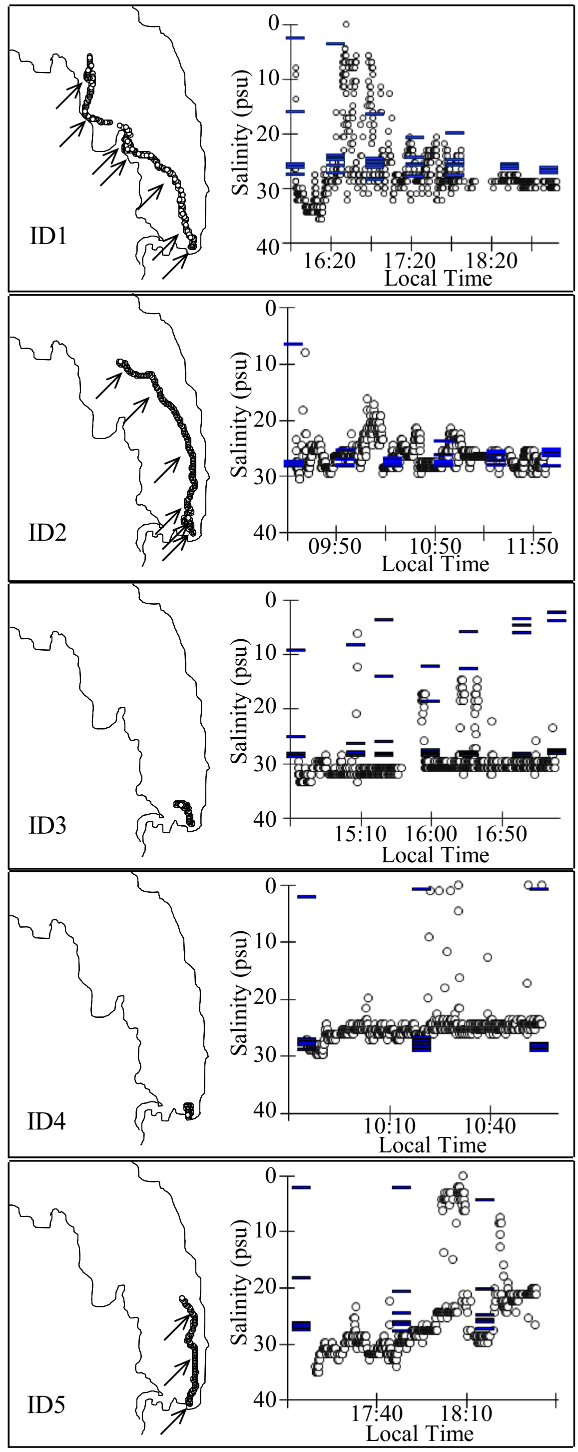

Fig. 2 *Left* and *right panels* show movement paths and salinity (*open circles*) of individual fish in Eresfjord by manual tracking. The fish were released in the river mouth and then tracked by boat. *Arrows* indicate locations where the vertical distributions of salinity (*bars* in the *right panels*) were measured using the salinity meter every 30 min. *Bars* indicate salinity values at every recording. The *top* to the *bottom bars* sequentially show the salinity at the depths of 0–3 m (0, 0.5, 1, 1.5, 2 and 3 m depth) although several bars overlap due to similar measured values

Long-term monitoring with data-storage transmitter

Six (40%) of 15 tagged fish were detected at the outermost receiver site (site 6) within 6 days after release (Fig. 4). The remaining nine fish were likely eaten by predators or died due to other reasons. Seven fish disappeared before

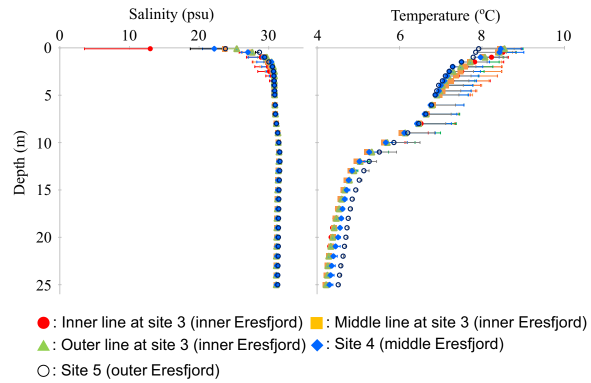

Fig. 3 Vertical distribution of salinity and temperature recorded at five different locations in the fjord, with three locations at site 3 (one at each receiver line, inner Eresfjord), one location at site 4 (middle Eresfjord) and one location at site 5 (outer Eresfjord). At each location, the salinity and temperature were measured at 0.5-m intervals between the sea surface and 5 m depth and at 1-m intervals between 5 and 25 m depth by use of the conductivity-temperature-depth (CTD) probe on 6, 8 and 11 May 2010. The *horizontal bars* indicate the standard deviations

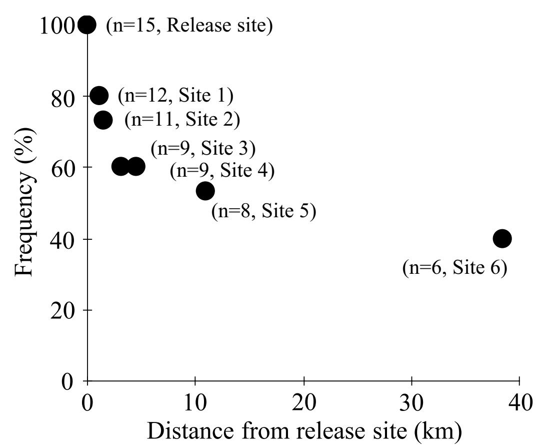

Fig. 4 Proportion of the tagged fish recorded alive at the six different sites with stationary receivers (shown in Fig. 1). *N* indicates the number of tagged fish recorded at each site

reaching the outermost receiver site, and the movement patterns of two fish differed from the normal patterns of post-smolts. Hence, the mortality was large during the first phase of the migration in the river, river mouth and inner fjord (Fig. 4).

The movement speeds at sea during the first 3.5 km (river to site 4), 9.9 km (river to site 5) and 37.4 km (river mouth to site 6) were 1.6 ± 0.86 ($n = 9$), 1.2 ± 0.87 ($n = 8$) and 0.8 ± 0.56 body length s^{-1} ($n = 6$), respectively. The swimming speeds were negatively affected by the distances between the river and each monitoring site (LMM, slope mean = −0.019, 95% CI = −0.0017 to −0.037), indicating that the post-smolts had a slower progression as they moved from the river.

The data-storage transmitters continuously recorded and stored ambient salinity of the tagged fish even when the fish were outside the detection ranges of receivers. The transmitters provided average 46.2 ± 50.7 h (range 0–150.8, $n = 15$ individuals) of consecutive salinity data during the early stage of the marine migration, although the tagged fish spent only 11.6 ± 32.2 h (range 0–127.1) within the detection ranges of receivers.

The ambient salinity experienced by the tagged fish increased during the outward migration, from salinity-range value 0 (0.0–3.9 psu, $n = 12$) to value 6 (24.0–27.9 psu, $n = 8$) and 7 (>28.0 psu, $n = 6$) (Figs. 5, 6). In the inner fjord, mainly low salinities were recorded; salinity-range value 2 (8.0–11.9 psu) was recorded for 173.3 h, and salinity-range value 3 (12.0–15.9 psu) was recorded for 103.5 h (Fig. 6). During the outward migration between the outer Eresfjord (site 5) and Langfjord (site 6), 135 h at salinities above 28.0 psu was recorded by five of the six fish that migrated to site 6. However, three of the six fish experienced relatively low salinities (ID 8, 15 and 19 spent 54, 4.5 and 2.25 h in salinities <20.0 psu, respectively, Figs. 5, 6). The CTD data showed that the salinity was not this low in the sea in the outer Eresfjord,

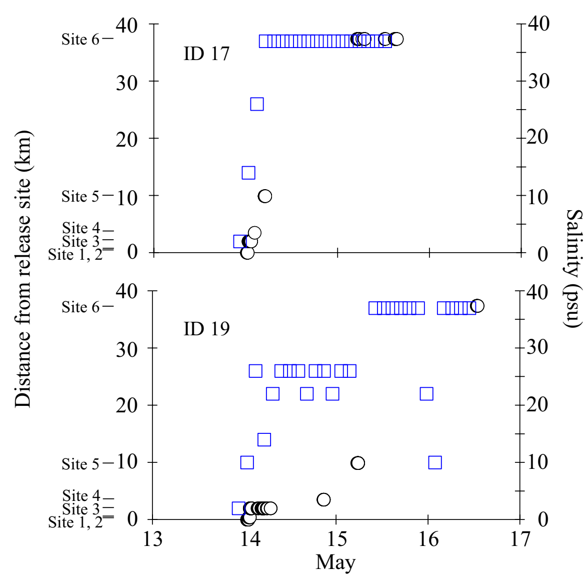

Fig. 5 Typical outward movement patterns of tagged fish with recordings of ambient salinity. *Open circles* indicate the detection at sites 1–6. *Open squares* indicate the salinity range in a 2.25-h period during the outward movement. Salinity-range values used in the figure are average values. For example, salinity data from salinity-range value 2 (8.0–11.9 psu) are shown as 10.0 psu

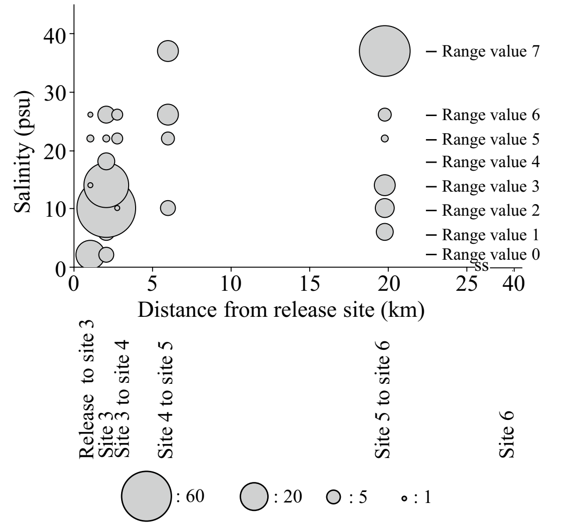

Fig. 6 Number of recordings for each salinity-range value (0–7) of the tagged fish between the release site and the outermost monitoring site (site 6, Langfjord). Release site and sites 1–6 are shown in Fig. 1. The *smallest bubble* represents one data point (2.25 h), while the *largest* at the site 3 represents 77 data points (173 h)

with 23.8 psu even in the surface layer (Fig. 3). These results may indicate that the tagged fish not exclusively showed a continuous rapid outward movement, but also that they occasionally stayed in water with low salinities, most likely in rivers or close to river mouths since the freshwater influx to the outer fjord area is much lower than in the inner part of the fjord.

Discussion

The salinity transmitters used in this study provided data on ambient salinity of Atlantic salmon post-smolts during the seaward movement. The manual tracking demonstrated that three tagged fish showed rapid directed seaward movement, while two remained at the river mouth during the first hours after release. The ambient salinity of the migrating post-smolt ranged from 0.0 to 36.0 psu and tended to be higher furthest away from the river mouth. This was also found during the long-term monitoring of 15 smolts by automatic receivers. Comparison of salinity profiles in the water column and the salinity experienced by the fish indicated that the post-smolt migrated in the upper few metres of the water column during the first part of the marine migration. These results concur with previous studies, showing that Atlantic salmon post-smolts display rapid directed seaward movement, swimming close to the surface [15, 25]. The swimming speeds recorded both during manual tracking and by stationary receivers did not differ from those of a previous study in the fjord [30], and were within the range of swimming speeds recorded in earlier studies, although some studies have also shown slower migration speeds [12]. The relatively fast migration of the Atlantic salmon smolts in the present study could be related to their larger size compared to wild smolts [12]. Rapid movements through a fjord would be advantageous for migrating post-smolts, by reducing the possibility of being eaten by predators, such as Atlantic cod and saithe [19]. There is a general tendency for post-smolts to increase their feeding intensity when migrating away from the estuary and in the direction of the open ocean [12]. Hence, it might be that the post-smolts in the present study reduced the migration speeds in the outer parts of the study area because of foraging. The two types of transmitters used in this study complement each other to provide new insight in salmon post-smolt ecology. The conventional transmitter provided real-time data with high time resolution (every few seconds) although the fish were tracked for a short period, while the data-storage transmitter provided long-term data even if the tagged fish were beyond the detection range of receivers, although the time resolution was lower (every 2.25 h).

Previous studies have attempted to reveal how post-smolts find the seaward direction, and a variety of mechanisms have been proposed, including using water currents [12]. However, other studies have demonstrated that water currents are not systematically used as an orientation cue, because smolts often show random movements compared to the water current direction [27, 31]. It has also been suggested that positive salinity gradients may be one of the key factors for seaward movements [6, 26]. Our results support that post-smolts may exploit variation in salinity cues for navigation purposes.

The data-storage transmitters provided ambient salinity histories of the tagged fish, even when the fish were beyond the detection ranges of receivers. Hence, these transmitters provided data for much longer periods than conventional sensor transmitters would have done. Data-storage tags (also termed archival tags), which store data in a memory, are widely used to understand behaviour and movement of aquatic animals, for example sea turtles [32] and penguins [33]. However, the tag must normally be recovered for data retrieval, which often may be difficult for free-swimming fish [34], especially at sea and in other large water bodies. A data-storage transmitter that does not require recovery for data retrieval may therefore be more useful in studies of fish. It is, nevertheless, essential to design such transmitters with an adequate sampling period for the actual study. In this study, the period during which data were accumulated by the transmitters (2.25 h) was decided on the basis of previous knowledge about post-smolt movement speeds in the relevant area. Thus, the salinity history of the tagged fish between release and last detections was obtained for most of the migration period. Furthermore, other sensors (e.g. depth) could also be implemented in such transmitters. The concept of such transmitters, in which the sensor data are measured, stored, compiled and conveyed, could provide new information on many fish species, both in marine and in freshwater systems.

The salinity history of the tagged fish indicated that the post-smolts occasionally spent time in sea water with lower salinity than 20.0 psu, especially in the inner part of the fjord. The utilization of salinities below 20.0 psu may reduce infestation risk by salmon lice [22, 23], and the probability of infestation is generally shown to decrease with increasing freshwater influence [35]. Salmon louse is a marine parasite, which can severely reduce Atlantic salmon populations in farm-intensive areas [36, 37]. Whether the fish actively preferred lower salinity waters or unintentionally experienced low salinity because they were swimming close to the surface for other reasons (for instance, avoiding predation) is not known, but nevertheless, this behaviour might reduce the salmon lice infestation risk. In the outer fjord, the ambient salinity of the tagged fish was basically stable within the higher salinity range recorded by the transmitter, which indicate that the fish would be exposed to salmon lice. However, the higher salinity recordings in this area do not reflect a larger swimming depth, because the salinity was high in the entire water column.

Unexpectedly, the recorded salinity history showed that half of the tagged fish (3 of 6) detected at the outermost site occasionally had stayed in lower salinity waters in this area (<20.0 psu). Two fish spent several hours in low salinity waters (<20.0 psu), whereas one fish stayed for more than 2 days (54 h). This was not expected, because such low salinities were not recorded in this area of the fjord either in this study or in previous years (own unpublished data). The most probable explanation is that the fish visited one or several river mouths in the outer part of the fjord. The smolts normally show rapid and directed seaward movements in a fjord system, and during the seaward movements little is known about visits to freshwaters and brackish waters. Swimming speeds normally increase with the distance from the natal river [6, 12]. However, in the present study, the swimming speeds became slower as the post-smolts moved further away from their home river. This could be related to visits to freshwater and brackish water by half of the fish.

Especially for sea trout, premature return to freshwater of individuals carrying large numbers of salmon lice has been interpreted as an adaptive behavioural response to salmon lice-induced osmoregulatory dysfunction [38–40]. Even short-term exposure to reduced salinity levels severely compromises survival and host infectivity of salmon lice [22, 23]. The fish in the present study had been too short time in the sea for development of adult salmon lice [41], but high levels of copepodids alone also caused premature freshwater return of sea trout [39]. We do not know the salmon lice infestation pressure in the study area at the time the study was performed, but it has earlier been characterized as moderate [42]. Hence, we do not know whether the unexpected visits by Atlantic salmon post-smolts to lower salinity waters in this study were linked to salmon lice infestations and osmoregulatory dysfunction or whether it reflects a behaviour normally performed by migrating post-smolts.

Hatchery-reared fish were tagged in the present study instead of wild fish, because they were easily accessible, and larger than wild smolts in this area, which reduced the likelihood of any negative impact by being tagged with acoustic transmitters. Previous studies have shown that the total sea survival of hatchery-reared Atlantic salmon, from the pre-smolt stage to return as adults, is lower than that of wild Atlantic salmon from this river [17]. However, the difference seems to occur in later stages of the migration, because the survival and behaviour of wild and hatchery-reared post-smolts did not differ in the first phase of the marine migration in previous studies in the same study area [27, 30, 31]. Hence, we suggest that the behaviour of the hatchery-reared post-smolts in the present study was representative for that of wild post-smolts, but direct comparisons are missing.

Conclusion

Our results showed that the use of salinity sensor transmitters provided new insights regarding the early seaward migration of Atlantic salmon post-smolts, despite this being a well-studied life stage due to the development and use of small conventional acoustic transmitters during the last two decades. As expected, the post-smolts experienced lower salinities in the inner part of the fjord, close to their home river. However, some of the fish also stayed in low salinity waters in the outer part of fjord during their seaward migration. This finding was unexpected and may indicate that some post-smolts actually visit river mouths also in outer fjord areas. Thus, our study illustrate that data-storage transmitters have a substantial potential as a means to better understand movements and behaviour of free-swimming fish. Biotelemetry has been a powerful tool in studies of aquatic animals, including fish, and has provided substantial insights into their ecology and behaviour [1, 3, 4].

Authors' contributions
All authors designed the experiment and performed field work. HM analysed the data and drafted the manuscript. All authors completed the manuscript. All authors read and approved the final manuscript.

Author details
[1] Graduate School of Informatics, Kyoto University, Kyoto 606-8501, Japan. [2] Norwegian Institute for Nature Research, P.O. Box 5685, Sluppen, 7485 Trondheim, Norway.

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Competing interests
The authors declare that they have no competing interests.

Availability of data and materials
Please contact the corresponding author for data requests.

Ethics approval and consent to participate
All handling and tagging was conducted according to the Norwegian regulations for treatment and welfare of animals (permit ID 2569).

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