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The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities

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Abstract

Acoustic telemetry represents the state-of-the-art technology for monitoring behaviour of aquatic organisms in the wild. Yet, the performance of different systems is rarely evaluated across species and environments. In this study, we evaluate two different acoustic telemetry systems; a commonly used analogue Pulse-Position-Modulation based system (Vemco PPM) and a newly developed high-residency digital Binary Phase Shift Key based system (Vemco HR2), in ability to track downstream migrating Atlantic salmon smolt (*Salmo salar*) and European eel (*Anguilla anguilla*) around hydropower facilities. High-precision GPS were used to evaluate precision and accuracy of hyperbolically positioned data derived from each system. The PPM based system had higher detection range than HR2 and generated more positions per transmissions for eels migrating close to bottom than for surface-oriented salmon smolts. HR2 generated ten-fold more positions per time unit than PPM, were less sensitive to noise, achieved sub-meter positional precision and were considerably more accurate than PPM-derived positions after filtering. HR2 was deemed more capable than PPM in fine-scale positioning at moderate distances at hydropower facilities.

Keywords: acoustic telemetry, animal tracking, fish movement, spatial data filtering

Introduction

High-resolution data on fish behaviour and migration are becoming increasingly important in fisheries management and research (Hussey et al. 2015), as well as in aquatic ecotoxicology and conservation (Crossin et al. 2017; Klaminder et al. 2016). Acoustic telemetry is currently the leading technology to track fish with high temporal and spatial resolution in the wild (Cooke et al. 2013; Hellström et al. 2016; Thorstad et al. 2013). The acoustic transmitter is attached to the fish and transmits encoded ultrasound signals, which are received, decoded, and time-stamped by underwater receivers. The signal contains information to identify the unique transmitter, but may also contain information on environmental parameters, such as depth and temperature, if the transmitter is equipped with sensors. If the transmitter signal is detected by three or more hydrophones, the transmitter can be positioned using positioning algorithms based on difference between receivers in the time-of-arrival of the signal (Baktoft et al. 2017; Li et al. 2014; Steig and Holbrook 2012). However, the quality and quantity of the derived position will be impacted by environmental factors, such as noise and temperature, and the technological properties of the system, such as clock resolution, as well as positioning method used (Melnychuk 2012).

In short, the detection range of the transmitter (the distance that a transmitter can be detected by a hydrophone) is particularly sensitive to high levels of background noise close to operating frequency, and to the amount of physical obstruction, such as particles, air-entrapment (bubbles), and vegetation, in the water hindering signal transfer (Melnychuk 2012). Similarly, the technical properties of the signal transfer system, such as the frequency used, the power output (sound level, dB), the technical capabilities of the receiver hardware, and the way information is encoded into the signal, may have profound effects on the quality and resolution of the tracking data (Pincock and Johnston 2012).

A common application of fish telemetry data is to better understand how to optimize fish passage solutions. Increased demand of detailed behavioural data for fish around hydropower facilities has in recent years driven technological advancements in transmission quality and functionality of acoustic telemetry systems. Consequently, a number of different specialized fish tracking system has been developed, using different underlying technical properties regarding operating frequency and signal encoding methods (McMichael et al. 2010; Steig and Holbrook 2012). Each system has clear advantages and disadvantages, when compared to each other, regarding operating requirements, transmission quality, and tracking capabilities, making a successful application of particular systems highly context dependent (Pincock et al. 2010). Understanding specification and capabilities of different acoustic telemetry systems is hence key when designing and setting targets in fine-scale tracking studies.

A very common signal encoding system used in acoustic telemetry is Pulse-Position-Modulation (PPM) (Espinoza et al. 2011; Simpfendorfer et al. 2008; Smith 2013). Information is transmitted using burst of tones spaced in a coded sequence (similar to Morse code), and the resulting "signal train" usually takes a few seconds to transmit. The relative simple coding scheme can be decoded by analogue low-voltage receivers with long operating time and has proven very robust both in sea and freshwater environments. However, due to the signal train taking a few seconds to transmit, there is a risk that two or more transmitters will transmit simultaneously within the range of the receiver. This will interfere with the signal decoding by the receiver and may result in no or false detections (Pincock and Johnston 2012). Such signal collision not only restricts the number of transmitters that can be used in a system (up to a few dozens), but also how often a transmitter can transmit (usually on the scale of minutes), which determine the temporal resolution of the fish tracking. Furthermore, the hardware in the PPM hydrophone listens for signals and records a detection when the signal reaches a certain amplitude, but due to the continuous nature of the signal's amplitude, it is difficult to determine exactly when the signal first reach the hydrophone. This uncertainty in the receiver time-stamp of the signal detection will lower the precision in the positioning capabilities of the system. Hence, in situations where high-resolution tracking data are needed, such as for understanding critical behaviour of fish around entrances to fish passage facilities to optimize their function, guidance, and attraction, the applicability of PPM based systems may be limited (Cooke and Hinch 2013; Coutant and Whitney 2000).

To counter the limitations of PPM-based systems in fish tracking, a recent coding scheme has been adopted in acoustic telemetry (Weiland et al. 2011), and further modified by commercial companies

(Guzzo et al. 2018; McMichael et al. 2010). In this coding-scheme, the information is encoded into the signal by modulating the phase of the tone-wave being transmitted (so called Binary Phase Shift Key, BPSK). The BPSK allows information about transmitter-ID, and even sensor data, to be transmitted in a fraction of a second; hence, minimizing the risk of signal collision. Such high-residency (HR) systems can potentially track a large number of fish (hundreds) simultaneously at very high temporal resolution (on the scale of seconds) (Guzzo et al. 2018). In contrast to the analogue PPM, the digital BPSK enable determining the signals time-of-arrival based on precise phase shifts, which, if combined with high-resolution receiver clocks, can generate a theoretical precision on sub-meter level.

In this study, we compared the performance of two different acoustic telemetry systems, Vemco PPM and Vemco HR2 (BPSK), in their ability to track downstream migrating Atlantic salmon (*Salmo salar*) smolt and adult European eels (*Anguilla anguilla*) around hydropower facilities. Atlantic salmon smolt are known to migrate in the surface (Thorstad et al. 2012), whereas eels are believed to migrated primarily along the bottom (Durif et al. 2003), hence providing species-specific tracking challenges for the systems. We also monitored fixed and mobile transmitters with known, high-precision GPS positions to evaluate system performance based on detection probability, as well as the precision and accuracy of positions derived from both systems based on hyperbolic positioning principles (Smith 2013).

Methods

Study sites

The study was conducted at two sites in Sweden from end of May to early November of 2016. Site 1 was located in Ume River (63°52'45.3"N 20°0'43.0"E), which starts in the Scandinavian mountain range and reaches the Baltic Sea after 470 km. Twenty-three km upstream of the river mouth, the whole river is diverted into a large hydropower plant, leaving 8 km of the natural river bed with just a fraction of the natural water flow (Rivinoja et al. 2001). The acoustic telemetry systems were deployed 3 km upstream of the hydropower plant around a floating guidance structure aimed at directing downstream migrating salmon smolt and kelt into the natural river bed (Figure 1), to prevent passage via the hydropower plant. The guidance structure is 100 m long and covers the upper 2.5 meters of the water column. During the study, the river had a discharge from 300 to 800 $m^3 s^{-1}$, and across its width had water velocities ranging from 0 to 1.5 $m s^{-1}$. The main channel of flow is situated to the east where the shoreline consists mainly of bedrock and boulders, and deeper parts of the river are dominated by soft bottom substrate and sand. Vegetation is scarce at the site and depth ranges from 0 to 16 m. Site 2 was located in Motala River (58°35'19.0"N 16°10'07.6"E), which starts from Lake Vättern in south central Sweden and reaches the Baltic Sea after 100 km. The acoustic telemetry systems were deployed 5 km upstream of the river mouth, where part of the river is diverted into a hydropower plant (Figure 1). Discharge during the study varied between 20 and 40 $m^3 s^{-1}$, and water velocities ranged from 0 to 0.5 $m s^{-1}$ across the width of the river. The southern shoreline consists of shallow areas from 0 to 2 m with soft bottom substrate and macrophytes. The main river channel is located towards the northern shore, also with soft bottom substrate, but with less vegetation and depths from 2 to 7 m. Possible sources of noise included the hydropower station at each site and echoes from the telemetry signals themselves. Boat traffic was close to non-existing at both sites. However, a sonar system (ARIS Explorer 1800; Sound Metrics; Bellevue, Washington, USA) operating at 1.1 MHz was periodically in use (from the 31st of August 2016 to the end of the study) in front of the hydropower intake in Motala River.

Sixteen receivers were deployed in a network in Ume River from the 5th of May 2016 to the 4th of July 2016 in a depth range from 2 to 16 m. Eight receivers were deployed in a network in Motala River from the 27th of July 2016 to 23rd of November 2016 at a depth range from 1 to 6 m. The receivers (HR2 180 kHz; Vemco Ltd; Bedford, NS, Canada) were mounted on steel bars erected from pyramid-shaped structures, 1.5 m above the bottom, and their positions were taken with a standard GPS (Garmin GPS MAP 60CSx; Garmin Ltd.; Kansas City, Ohio, USA). To withstand water velocities up to 1.5 $m s^{-1}$, the structures were fitted with additional weights at the base, resulting in a total weight of approximately 60 kg for each structure. Each receiver sent out ID-signals that were picked up by the surrounding receivers and used for synchronizing the internal receiver clocks within the receiver network, which is a prerequisite for fine-scale positioning (Espinoza et al. 2011). Within the network of receivers, reference tags were deployed on mooring lines suspended by buoys 1.5 meters above the bottom. The reference tags were used to monitor the performance of the system (see below). Four fixed reference tags were deployed in Ume River, and two reference tags in Motala River. All receivers and reference tags transmitted signals with a power output of 143 dB re 1 µPa @ 1 m in intervals of 30 ± 5 s and 300 ± 30 s for BPSK and PPM, respectively. Transmitters within the network were positioned using a commercial positioning service (Vemco Positioning System, VPS) (Smith 2013), using the time difference of arrival between receivers for each unique transmission to derive positions based on hyperbolic principles.

In Ume River, 50 wild Atlantic salmon smolt were caught in a smolt trap and surgically tagged with a Vemco V5-2x transmitter (weight: 0.77 g, length: 12.7 mm) between the 30th of May and 17th of June 2016. The tag utilized both PPM and BPSK transmissions, transmitting its ID using BPSK at 170 kHz every 0.7 ± 0.1 s, and using PPM at 180 kHz every 30 ± 5 s. The power output of the signal was 143 dB re 1 µPa @ 1 m. The tagged smolt were released 6 km upstream of the receiver network, and their behaviour was tracked as they encountered the guidance structure on their migrations downstream. In Motala River, 70 European eels were surgically tagged with both a Vemco V9-2x transmitters (weight: 3.7 g, length: 25.5 mm) between the 28th of July and the 25th of August 2016. These tags also utilized both PPM and BPSK transmissions, transmitting ID using BPSK every 1.1 ± 0.1 s and PPM every 37.5 ± 12.5 s. The power output of the V9 tags were 143 dB re 1 µPa @ 1 m. To be able to get depth measurements of the eels, the fish were also tagged with a Lotek MM-C-11-SO-TP depth-sensor tag (weight: 11 g, length: 48 mm). The Lotek tags operated on another frequency (76 kHz) and utilized a different coding scheme (Cooke et al. 2005), and was only included in this study to acquire depth measurements of the eels. The tagged eels were released 3.5 km upstream of the receiver network in Motala River, and their behaviour was tracked as they encountered the intake to the hydropower station on their migration downstream. All handling and tagging of fish was approved by the Uppsala Ethical Committee on Animal Research (application DNR C 16/14). All reference tags at each site were identical to the receiver and fish transmitters, respectively, in terms of signal delay and power output. Within the receiver network at each site, a mobile reference tag was towed around from a boat. A high-precision differential GPS (Trimble Geo 7X; Trimble Navigation Ltd.; Sunnyvale, California, USA) mounted above the reference tag was used to get a very accurate track of the transmitter (< 10 cm and << 1 s precision) which then could be compared with the positional data derived from the acoustic telemetry system.

Raw data from the receivers contained the unique ID of the detected signal together with a time stamp and signal strength, as well as a measure of background noise and ambient water temperature recorded every 10 min.

Precision

Precision of the VPS positions was estimated by measuring the distance between each unique position of a transmitter and the median position for that transmitter. All distances were pooled into median values for each system (PPM and BPSK) and background noise level (< 21 and > 21 dB, hereafter referred to as “low” and “high”), resulting in four precision measurements per transmitter. The cut-off value at 21 dB was chosen from being above the baseline noise level at each site (Figure 3). We used transmitters that were deployed at fixed locations with little or no movement, which in our system represented the ID-tags of the receivers and the reference tags. Positions of transmitters located at the perimeters of a receiver array will be less precise than for transmitters located at the center of an array due to the constrained geometry of the receivers used for the hyperbolic positioning (Roy et al. 2014). In this study, we therefore focused only on transmitters located at the center of the receiver arrays. Precision of five receiver tags were evaluated at each site, with an additional four reference tags in Ume River and two reference tags in Motala River. We also calculated hourly median precision for the same receiver tag and reference tag to illustrate variation over time and between transmitter type.

Accuracy

Accuracy, here defined as the distance between VPS positions of the reference tag and GPS positions, was tested both before and after positional filtering. Filtering, i.e. removal of erroneous positions, is a common and often necessary step when analyzing and making sense of fine-scale tracking data

(Meckley et al. 2014). We filtered the VPS positions based on calculated transmitter velocity and turning angles using modified algorithms from the R package argosfilter. The package calculates swimming speed for each position in relation to the most recent, second most recent, next, and second to next position. Comparing each position to the surrounding four, instead of only to the previous position, generates high swimming speeds also for adjacent outliers which otherwise would, wrongly, be associated with low swimming speeds. Turning angles were calculated as the absolute change in bearing from each position to the next (Freitas et al. 2008). This method of filtering out likely erroneous fish positions was also used on VPS reference tracks with corresponding known GPS coordinates (see below).

As discussed by Guzzo et al. (2018), acoustic telemetry positions might have a certain internal precision, but show a spatial offset when compared to absolute GPS positions. We argue that this offset also could be true for the temporal scale, not only due to time drift of internal clocks over long deployments, but because of deviations from true time when initializing and terminating receiver clocks. Hence, tracking data often need to be spatially and temporally adjusted to more accurately reflect the true track. Such adjustment needs true spatiotemporal anchors to be aligned against. In this study, the anchor data consisted of high-precision GPS tracks, which had a spatial precision of < 10 cm and a temporal precision of << 1 s. To spatiotemporally align the filtered VPS reference track to the GPS track, both tracks were imported into QGIS (version 2.14.21) in separate layers and without any internal changes. The VPS reference track was then manually rotated and moved by using the Editing tool to create the best possible fit of the GPS track followed by alignment on the temporal scale where time was either added or removed from the timestamps of the reference track to match the GPS track. To compare spatial and temporal accuracy between the unfiltered and filtered/aligned data, we measured the distance from each VPS position of the reference track to its time stamp correlated (on second level) position from the GPS track.

To evaluate how well the VPS data captured the complexities of the GPS track, we used two measures; 1) track length and 2) dynamic interaction index. By comparing the total track length of filtered data from both systems with the GPS track, one can get an indirect measure of how well the

VPS track reflects the GPS track, as well as an indication of the level of filtering applied to the data (Vanwyck 2018). Dynamic interaction index (DI) is used to quantify the interdependency in the paths of two tracks (usually the movement of two individual animals) by measuring the cohesiveness in direction and speed (Long and Nelson 2013). The index range between -1 to 1, where 1 indicates a perfect positive correlation, -1 indicates a perfect negative correlation, and 0 indicates random movements of the two tracks. DI does not consider the distance between the tracks and hence cannot be used as a measure of accuracy. As DI is influenced by sampling resolution (Long et al. 2014), the gaps in the PPM VPS-track were linearly interpolated to achieve the same temporal resolution as the BPSK VPS track.

Detection range

As defined by Kessel et al. (2014), we evaluated detection range as the relationship between detection probability and the distance between the receiver and tag. To measure this, we deployed two pairs of transmitters 50 m apart with each pair consisting of one transmitter with lower power output (143 dB re 1 μPa @ 1 m) and one with higher power output (147 dB re 1 μPa @ 1 m). Each transmitter sent out PPM and BSK signals at a nominal delay of 300 ± 30 s and 30 ± 5 s, respectively. Proportion of detected signals was calculated in daily bins at 50 m intervals up to 600 m. This test was conducted at Site 1 in Ume River during 9 days at the end of October 2018. To avoid bathymetric interference, i.e. to create free line of sight, all transmitters and receivers were deployed on moorings submerged 4 m below the surface at total depths ranging from 9 to 15 m.

We also compared detection probability of PPM and BPSK for tagged fish at both sites. Here, we used the VPS data to calculate the ratio between positioned and transmitted signals. Total amount of animal positions in the time span from each individual's first and last position was divided with the number of transmissions sent out by that specific tag during the same time period. Data from fish that were out of range for longer than two hours, but then returned, were excluded to avoid that missing detections from non-present fish would lower the ratio.

Statistical methods

To examine differences in precision, a two-way general linear mixed model (LMM) was used where precision was treated as a normally distributed response variable, and system (BPSK vs. PPM) and background noise (high vs. low), including their interaction, as two-level fixed effects. Transmitter ID was treated as a random intercept to avoid pseudo replication issues. Precision was analyzed for both sites separately.

The accuracy of the VPS reference tracks in relation to the GPS tracks was tested between the systems before and after spatiotemporal alignment with a Kruskal-Wallis rank sum test on data pooled from both sites.

Detection probability was modeled as a function of distance (0-600 m), system (BPSK vs. PPM) and transmitter power (high vs. low) and their interaction, using a generalized linear mixed model (GLMM), with binomial error and logit link function. Transmitter-receiver pair and day was treated as random effects to avoid pseudo replication issues. Ratios of positioned and transmitted signals for tagged fish were compared between PPM and BPSK with a t-test each for the two sites. All statistical analyses were done in R (version 3.4.3).

Results

Precision

The effect of system on precision was dependent on background noise (significant interaction term, table 1) at both sites. The BPSK system showed a higher precision at both sites, and the difference between the systems was apparent at high levels of noise, with a significant negative effect for PPM but not for BPSK (Figure 2).

The results also showed consistently higher precision for the receiver positions compared to the positions of the reference tags (Figure 3). Precision in Ume River showed little variation over time, whereas corresponding results from Motala River showed higher fluctuations. Correspondingly, there were higher fluctuations in noise levels in Motala River, where peaks in background noise due to sonar operations aligned well with periods of low precision for the PPM system, while the BPSK system seemed unaffected by this (Figure 3B).

Accuracy

The BPSK system generated considerably more VPS positions than did the PPM. The reference tracks at both sites combined generated 8,705 and 89 positions for BPSK and PPM, respectively, with a corresponding accuracy of 24.5 and 29.7 m in relation to the time correlated GPS positions. After removal of erroneous positions with the argosfilter, the number of positions was reduced to 6,159 (BPSK) and 66 (PPM) giving a retention rate of 71% for BPSK and 74% for PPM. GPS and VPS positions showed a clear and systematic spatiotemporal offset at both sites (Figure 4, 5, and A1). In Ume River, the best possible alignment between VPS positions and GPS positions was achieved by configure the VPS track with a 0.7° clockwise rotation, a 6.78 m displacement towards northwest (bearing 276.6°), and a 36 s shift back in time. In Motala River, the best possible alignment between VPS positions and GPS positions was achieved by configuring the VPS track with a 2.0° clockwise rotation, a 5.52 m displacement towards northwest (bearing 270.0°), and a 55 s shift back in time. No significant difference in accuracy was observed between the systems before filtering ($p < 0.070$, Kruskal-Wallis rank sum test; table 1). Accuracy at both sites was significantly improved (21.16 and 29.44 m) for both BPSK and PPM after filtering and spatiotemporal alignment ($p < 0.001$, Kruskal-Wallis rank sum test; table 1). Additionally, after filtering, the accuracy was significant better for BPSK than for PPM ($p < 0.001$, Kruskal-Wallis rank sum test; table 1).

At both sites, the BPSK VPS tracks were longer than the GPS tracks, while the PPM tracks were shorter (table 2). The BPSK VPS track had higher DI compare to PPM VPS tracks at both sites (Ume river DI BPSK = 0.68, DI PPM = 0.60; Motala river DI BPSK 0.73, DI PPM = 0.42).

Detection range

The effect of distance on detection probability was dependent on both system and power output (significant interaction term, $Z = 12.4$, $p < 0.01$). The number of detections was negatively correlated with distance for both systems; however, BPSK signals showed a faster loss of detections over distance compared to PPM (Figure 6). Furthermore, higher power was positive correlated with detection probability for BPSK (most pronounced on distances < 300 m) while higher power had a negative effect on detection probability for PPM across all distances. For BPSK, 50% detection probability was observed between 200 m and 300 m (low power: 226 m, high power: 271 m) whereas PPM was able to detect the same proportion at distances between 400 m and 500 m (low power: 470 m, high power: 427 m).

Fish VPS positions

The number of fish positions in relation to signal transmission was significant higher for PPM than BPSK for eels in Motala River (PPM: 0.76 ± 0.048, BPSK: 0.26 ± 0.030 [mean ± 1 S.E.]; $p < 0.01$), but not for salmon in Ume River (PPM: 0.36 ± 0.023, BPSK: 0.44 ± 0.033 [mean ± 1 S.E.]; $p = 0.38$), showing that PPM signals from eels had a higher chance of being positioned compared to BPSK signals, but no difference between signal type was found for salmon (Figure 7). Depth sensor data confirmed that eels migrate close to the bottom, while behavioural data of smolt close to the guidance structure indicated that salmon smolt were migrating close to surface (Figure 8).

The difference in temporal resolution between the systems had an obvious effect on reflecting fine-scale fish movement, which is illustrated by tagged individuals from each site (Figure 8). Searching behaviour with high numbers of turns was, especially for eel, captured with considerably higher level of detail by BPSK compared to PPM.

Discussion

Our field studies represent two separate long-term tests evaluating the performance of two telemetry systems with different coding schemes in their ability to track downstream migrating European eel and Atlantic salmon around hydropower facilities. Hydropower facilities often represent noisy environments with a lot of reflective surfaces, and hence provide challenging conditions for acoustic telemetry tracking. Further, telemetry data often serve as input for construction or adjustment of e.g. fish passage facilities which sets high demand on the precision and accuracy of the positional data. This, in combination with often fast-moving migrating fish, makes high spatial and temporal resolution of the acoustic telemetry system highly warranted in tracking contexts related to hydropower.

Precision

We found an overall higher precision of the VPS-positions generated from BPSK, where the median error for individual tags was significant smaller compared to PPM. Interestingly, the difference in precision was most apparent in noisy environments, which correlated negative with PPM precision but had no significant effect on BPSK precision. This may reflect the benefit of using the BPSK digital phase shifts to determine a signal's time-of-arrival compared to PPM's analogue threshold, where BPSK evidently is the better alternative to obtain high precision even in noisy environments. Drift in precision over time is rarely accounted for in tracking studies and precision is often only presented as an average over the study period (Baktoft et al. 2015). In this study, there were large variation in precision over time at both study sites, and especially so for the PPM system, highlighting the need for continuously monitoring precision over the entire tracking study. Such variation in precision over time may often be contributed to variation in environmental noise.

The source, magnitude and impact of noise may vary among acoustic tracking studies (Heupel et al. 2006; Simpfendorfer et al. 2008; Voegeli et al. 1998). In our study, the magnitude of noise differed strongly over time and between sites. At both sites, continuous operations of the hydropower regulation could not explain the dramatic increase in the magnitude of noise seen in both sites. In the Ume river, the increase in noise coincide with an increase of number of transmitters residing within the receiver grid. In river Motala, peaks of high noise may correlate to operation of a sonar in close proximity to the receiver grid, although the sonar operated at different magnitudes in the sound spectrum compare to the acoustic telemetry system (180 kHz vs 1.1 MHz). It is noteworthy that BPSK remained robust in positional precision over the entire study period.

At the river Motala site, the median precision of VPS-positions from BPSK were well below 1 m, compare to VPS-positions from PPM, which ranged from 1.5 to 2 m. Sub-meter precision is often a much sought after endpoint in tracking studies but seldom achieved (Donaldson et al. 2014; Hussey et al. 2015; Meckley et al. 2014), and our results highlight the ability of the BPSK system to deliver sub-meter precision using non-cabled autonomous receivers time-synchronized only via synchronization tags. The apparent difference in the precision of the positions of the reference tags and the receivers (which both had a power output of 143 dB re 1 µPa @ 1 m), where the reference tags showed a consistent lower precision, is likely explained by the different mooring used for the transmitters. The reference tags were attached to ropes that were held in position 1.5 m over the bottom by a buoy, and hence were able to move in the current, whereas the receivers were mounted on metal rigs that had no or little movement.

Accuracy

Most acoustic telemetry fine-scale tracking studies relies heavily on post-filtering of the raw positional data prior to analyses (Baktoft et al. 2015; Meckley et al. 2014; Roy et al. 2014), and relevant comparison of accuracy between telemetry systems should hence be done on filtered data. The accuracy of both the BPSK and PPM VPS-tracks in our study was greatly improved after filtering (>20 m improvement for both systems). After filtering, BPSK positions was significantly more accurate than PPM with an average median accuracy of 1.3 m over both sites, compared to 3 m for PPM. Accuracy on the scale of 1 meter have to be considered very good in most fish tracking contexts and bodes well for the application of BPSK systems to track fish around hydropower.

A visual comparison of filtered PPM and BPSK tracks overlaid on the GPS-track clearly reveal considerably better alignment of the BPSK track (figure 4 and 5), indicating that the BPSK tracks more accurately capture the complexities of the GPS-track. The higher DI for both BPSK VPS tracks, 70% higher in river Ume and 13 % in river Motala, support this observation and suggests that BPSK indeed produce more detailed and correct data on fish behavior compare to PPM. However, both BPSK and PPM VPS-tracks were substantially off when estimating the true length of the GPS-track, with BPSK overestimating the GPS-track almost 40% and PPM underestimating almost 50%. Overestimating track length may indicate a need to reduce erroneous positions by more aggressive filtering, while underestimating the track length may indicate to much filtering, or too low temporal resolution. Interestingly, both BPSK and PPM had the same retention rate after filtering, i.e. ~70%.

The temporal offset between the VPS-positions and the GPS track are likely explained by an inaccurate internal clock on the laptop used to initiate and offload data from the receivers. This is easily solved by setting the internal clock accurate on the computer used to initiate the receivers, which indeed is suggested by the software. In many studies, a temporal offset up to a few minutes could be neglectable, but when it is important to time synchronize fish movement to events (e.g. sudden shifts in flow regimes) the temporal scale is of great importance.

The spatial offset between the VPS track and the GPS track highlights the importance of precise and accurate reference points, which must be used to fit relative positions to an absolute projection of coordinates in telemetry studies. This is necessary when analyzing animal behavior in relation physical objects, such as guidance structures and turbine inlets in riverine systems. When absolute positions are of importance, we argue that positions of receivers and fixed reference tags should be measured with highest possible precision, e.g. by using differential GPS. If water depth and velocity are high, it can be challenging to obtain accurate coordinates from an object located on the bottom when measuring from a boat on the surface; however, there is always the possibility to use a reference tag mounted directly under the GPS just a meter below the surface to ensure accurate positions in relation to the tag. This reference track should be used to adjust for any possible offset between the geometric positions and the true coordinates, or at minimum, be aware of this possible offset. We argue that the degree of spatial and temporal alignment of the reference tracks to a high-precision GPS track could be directly translated to the fish tracks, and hence that such alignment should be done to all fish tracks post filtering to achieve highest possible accuracy.

Detection range

PPM had higher detection range than BPSK, and PPM's relationship between detection probability and distance supports previous suggested relationships by (Kessel et al. 2014) with high (>75%) detection probabilities up to a certain threshold followed by a rapid drop to under 25%. We observed this drop of around 400 meters for PPM, and 50% detection probability occurred at almost 500 m, compared to <300 m for BPSK. Signal attenuation may depend on frequency and power-output, as well as coding scheme (Pincock and Johnston 2012), and as both power and frequency was similar for both systems in this study, the results suggests that the BPSK coding scheme is less robust over distances compared to PPM. Interestingly though, higher power output from the transmitters improved detection range for BPSK, but not for PPM, which in fact responded negatively on higher power with lower detection probability throughout the range. We interpret this to be an effect of signal collision where the relative long PPM signals is cancelled out by its own echo (Binder et al. 2016).

So far, acoustic telemetry has been used to detect species specific differences in movement and behavior (e.g. Finstad et al. 2005; Hayden et al. 2014; Hussey et al. 2017; Mathes et al. 2009). Yet, to our knowledge, few studies have assessed species-specific impact on the acoustic telemetry performance *per se*. We note that the PPM signals from the bottom migrating eels had a higher chance of being positioned compared to BPSK signals, but no difference between signal type could be observed for the surface-oriented salmon. This result was not expected, as the PPM may need several seconds to transmit a complete signal, in comparison with BPSK which only need a fraction of a second, and hence one would think the PPM to be more susceptible to obstructing structures interfering with signal transmission than BPSK. The lower detection probability for BPSK is however compensated for by the considerably shorter signal interval, which ultimately generates significant more detection per unit of time. For example, even though the probability for positioning tagged eels in Motala River was almost three times higher for each PPM signal (76%) compared to each BPSK signal (26%), the latter one still generated almost twelve times more positions. For PPM to generate as many positions as BPSK in our study, an interval of 3.2 seconds would be required. Although temporal resolution in the PPM system theoretically could be increased to a few seconds, i.e. the length it takes to transmit the signal train, such short signal-delay would severely limit the number of transmitters that could be positioned due to signal collision issues. Commonly therefore, fine-scale positioning in PPM systems often ends up at minute-resolution (e.g. Binder et al. 2016; Klaminder et al. 2016). Low temporal resolution may underestimate activity, and spatially erroneous positions will overestimate both activity and change in swimming direction.

Conclusions

Both BPSK and PPM based acoustic telemetry system perform well in tracking bottom migrating eel and surface oriented migrating salmon smolt around the two hydropower facilities in our study. The higher spatial and temporal resolution of BPSK, and the ability of BPSK VPS-tracks to better capture the potential complexities in fish movement, makes BPSK the preferred system especially if tracking occurs over shorter distance which may often be the case in management contexts related to hydropower. The lower detection probability of BPSK was compensated for by the much higher signal transmission rate. The study also shows the importance of applying filters to remove erroneous positions, as well as the use of high-precision GPS reference tracks to be able to relate VPS-positions to spatial and temporal ground truths.

Acknowledgements

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Tables

Table 1. Results from the linear mixed models from Ume River and Motala River describing the effect of telemetry system and noise on precision.

Site		**Estimate**	**S.E.**	**df**	**t-value**	***p*-value**
Ume River	(Intercept)	1.86	0.32	16	5.79	**<0.001**
Ume River	System	0.40	0.45	16	0.88	0.392
Ume River	Noise	-0.25	0.20	16	-1.20	0.248
Ume River	System:Noise	-0.64	0.29	16	-2.22	**0.041**
Motala River	(Intercept)	0.80	0.35	12	2.30	**0.040**
Motala River	System	1.30	0.49	12	2.63	**0.022**
Motala River	Noise	0.34	0.22	12	1.53	0.152
Motala River	System:Noise	-1.03	0.32	12	-3.24	**0.007**

Table 2. Number of positions, track length and accuracy of GPS and VPS tracks at Ume River and Motala river. Data for both raw and unfiltered VPS tracks from both BPSK and PPM telemetry systems are presented. Letters showing significant differences in median accuracy where A>B, C>D and B<D.

					Accuracy (m)		
Site	System	Data	# of positions	Track length (m)	Mean	Median	S.E.
Ume River	GPS	-	5,854	1,526	-	-	-
Ume River	BPSK	Raw	5,470	24,338	23.7	21.4 ^{A}	0.27
Ume River	BPSK	Filtered	3,911	2,235	2.54	1.27 ^{B}	0.11
Ume River	PPM	Raw	55	1,641	27.0	22.9 ^{C}	2.39
Ume River	PPM	Filtered	43	971	4.09	2.51 ^{D}	0.54
Motala River	GPS	-	3,661	799	-	-	-
Motala River	BPSK	Raw	3,235	10,002	26.1	24.1 ^{A}	0.34
Motala River	BPSK	Filtered	2,248	1,060	2.49	1.37 ^{B}	0.11
Motala River	PPM	Raw	34	852	34.2	25.5 ^{C}	7.38
Motala River	PPM	Filtered	23	364	4.76	3.59 ^{D}	1.09

Figures

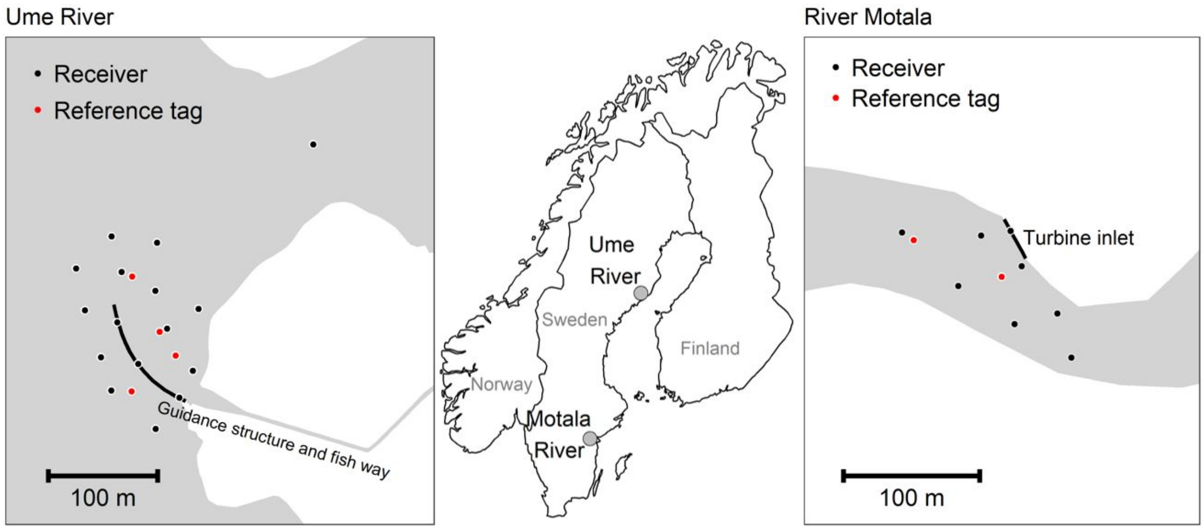


Figure 1. Gray circles in the central map show the location of the study sites Ume River and Motala River. Left and right panels show the main details of each study site in Ume River (left) and Motala River (right). White and grey areas represent land and water, respectively, and receiver (black) and reference tag (red) positions are illustrated with colored circles. The curved black line in Ume River (left) represent a guidance structure (floating louver) leading to a technical fishway. The straight black line in Motala River (right) represent the intake of a tunnel leading to a hydropower plant. Map data: ©The Swedish National Land survey.

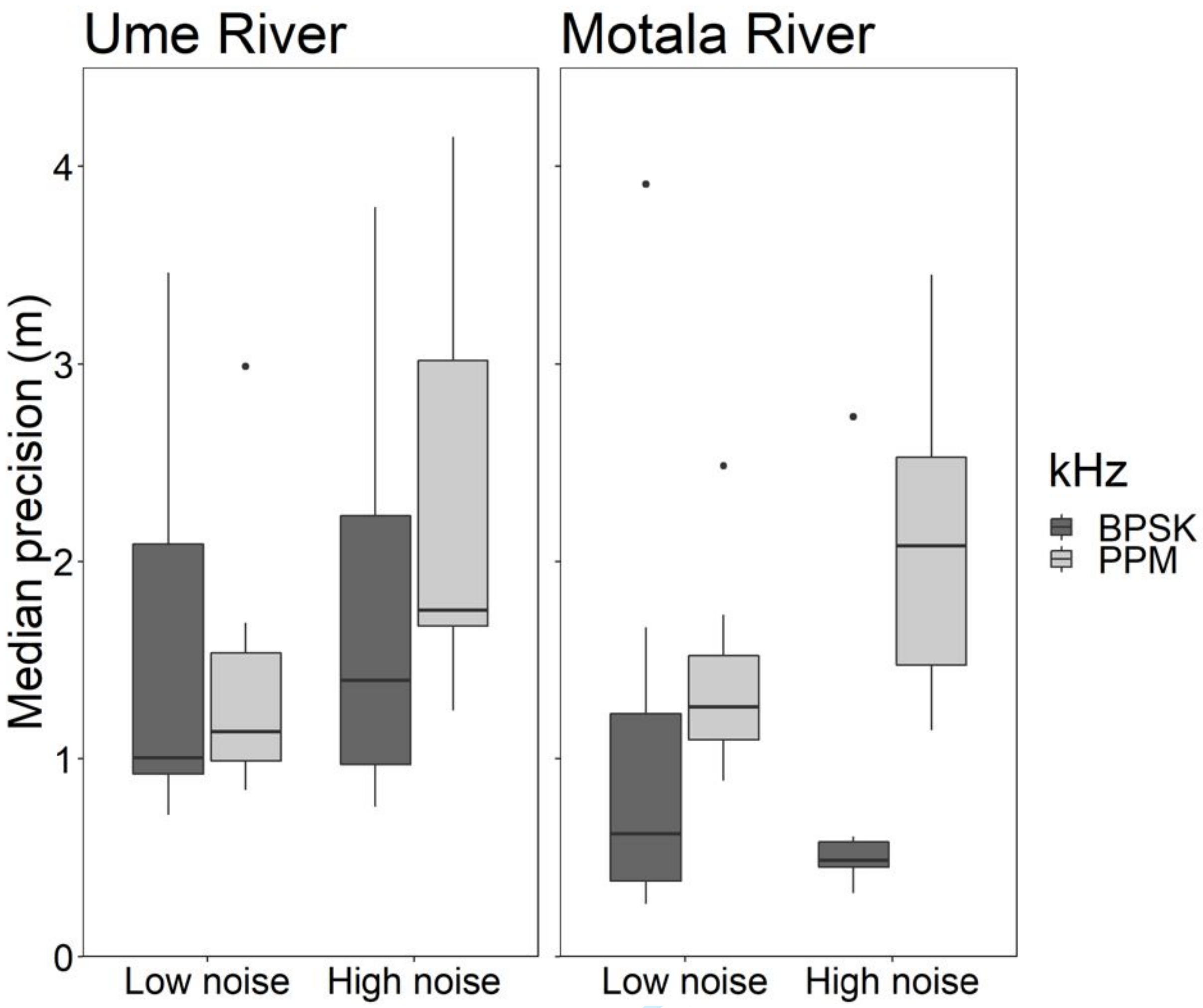
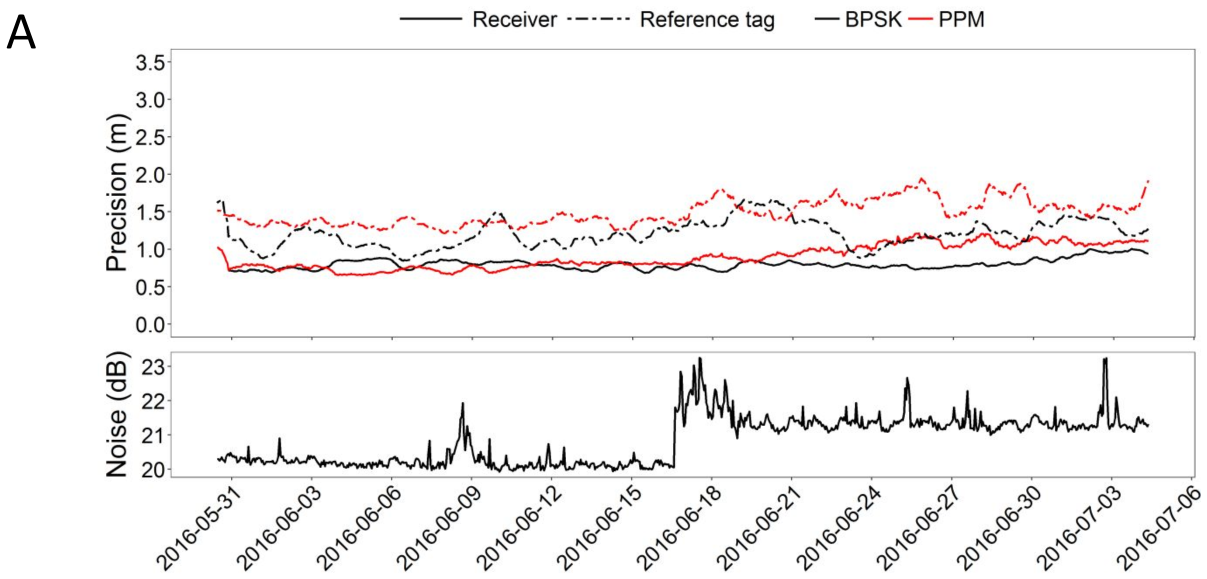


Figure 2. Boxplots showing median precision of VPS positions in Ume River (left, N = 9) and Motala River (right, N = 7) separated by different noise levels (low and high) and telemetry system (dark grey = BPSK and light grey = PPM). Horizontal line within box = median; ends of box = 25th and 75th percentiles; ends of whiskers = 10th and 90th percentiles; black circles = outliers.



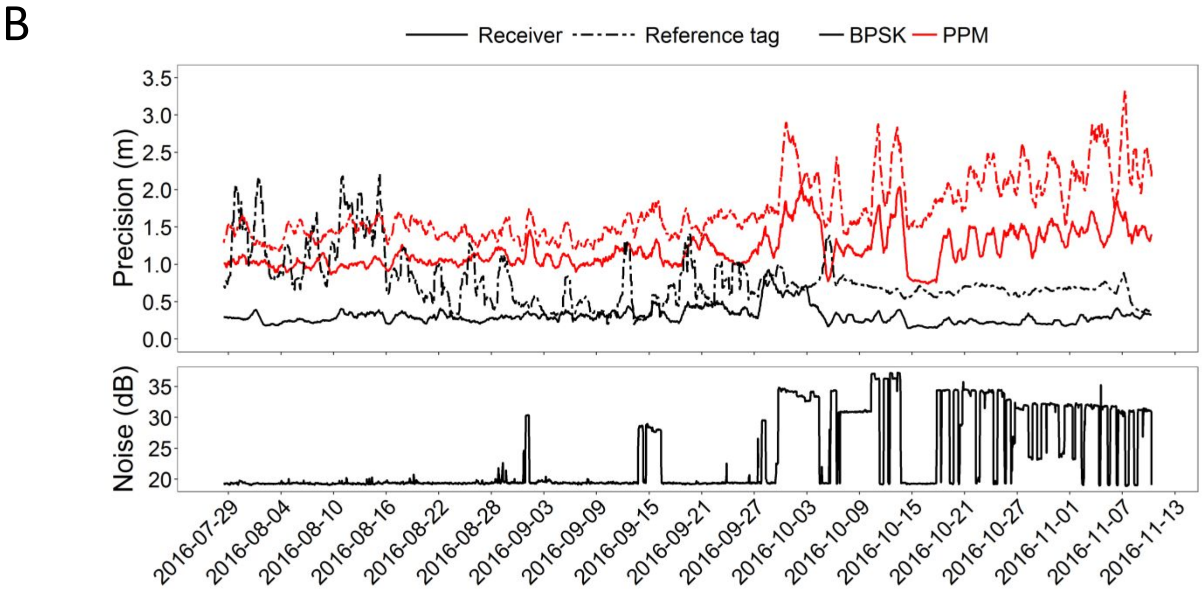


Figure 3. Median values of median precision for each transmitter and background noise in (A) the Ume River study site and (B) the Motala River study site. Results are shown with black lines for BPSK and red lines for PPM, with signals from receivers and reference tags separated with solid and dashed lines, respectively. The measured site-specific noise (in dB) during the study periods is shown in separate graphs under each panel.

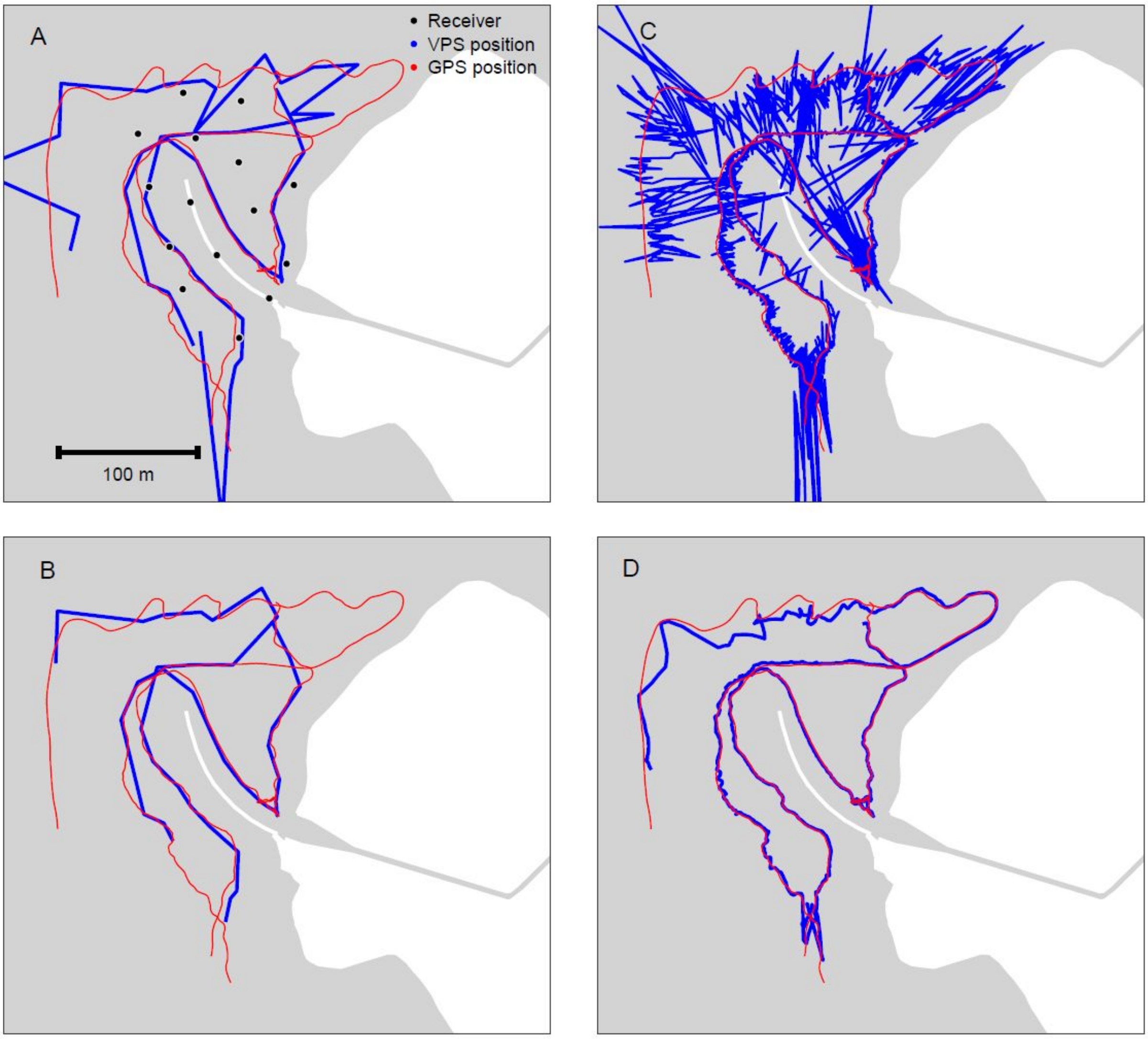


Figure 4. Map showing receiver positions (black circles), GPS tracks (red line) and the corresponding VPS track (blue line) in Ume River consisting of (A) Raw PPM positions, (B) filtered and spatiotemporal aligned PPM positions, (C) raw BPSK positions, and (D) filtered and spatiotemporal aligned BPSK positions. Map data: ©The Swedish National Land survey.

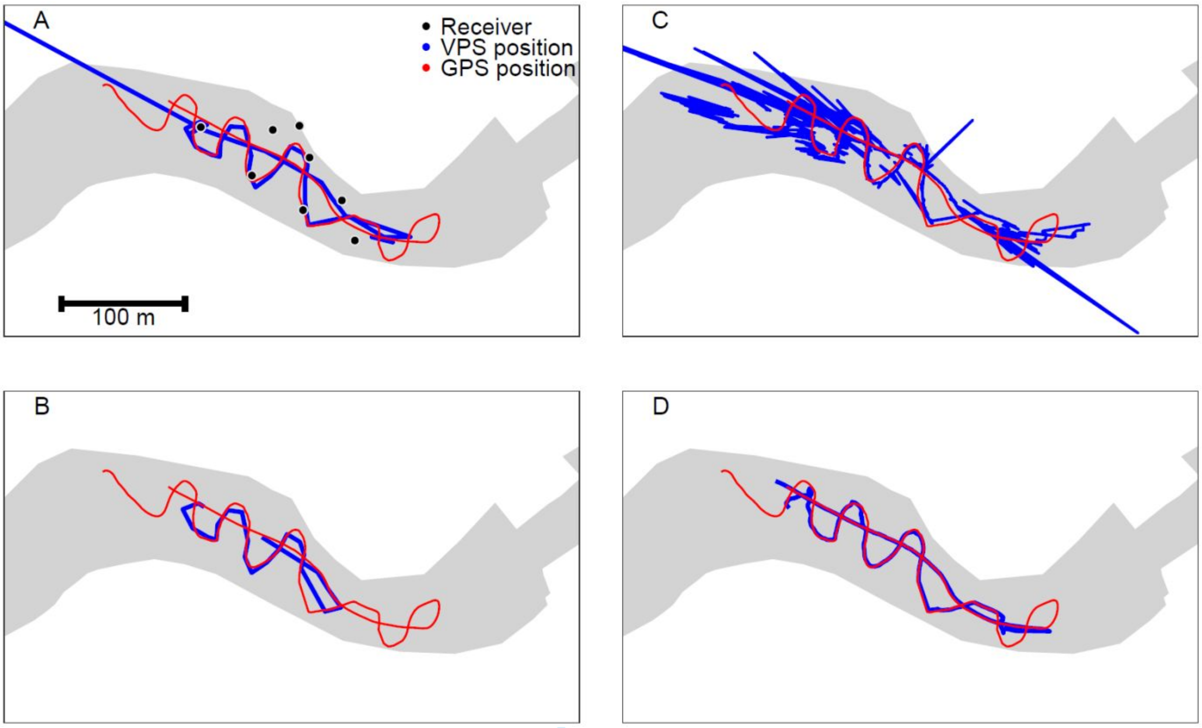


Figure 5. Map showing receiver positions (black circles), GPS tracks (red line) and the corresponding VPS track (blue line) in Motala River consisting of (A) Raw PPM positions, (B) filtered and spatiotemporal aligned PPM positions, (C) raw BPSK positions, and (D) filtered and spatiotemporal aligned BPSK positions. Map data: ©The Swedish National Land survey.

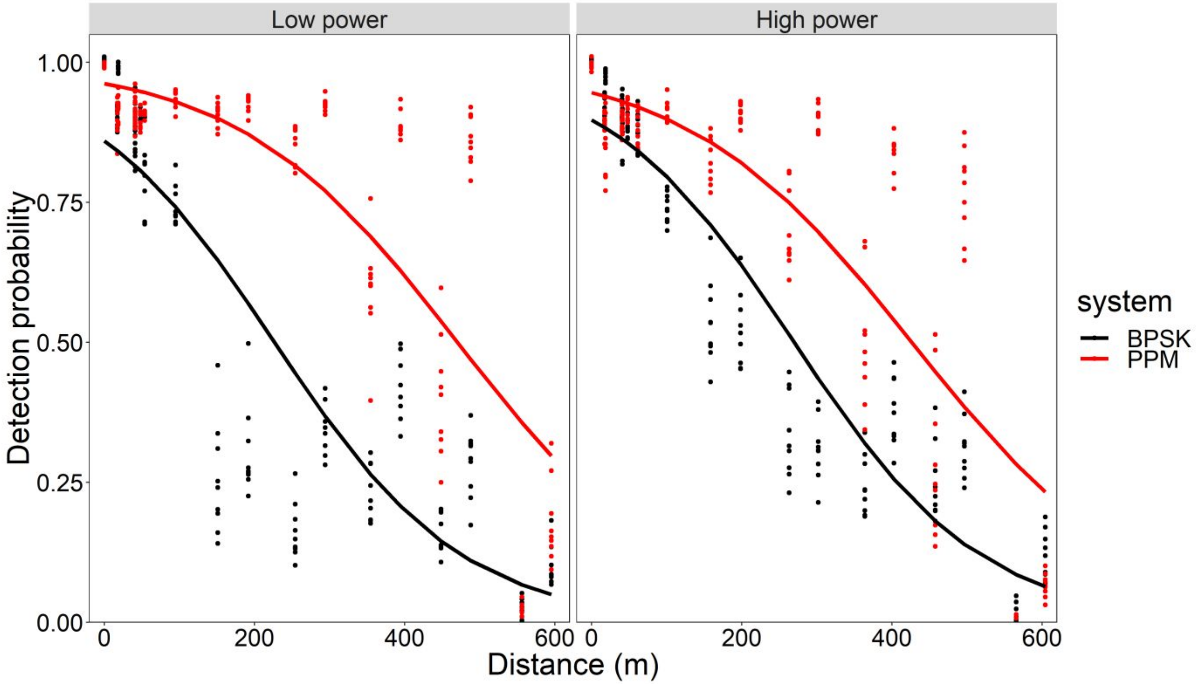


Figure 6. Results from the range test at Ume River. Daily measurements of detection probability over distance for each telemetry system is shown in colored points (black = BPSK and red = PPM) at low power output (left) and high power output (right). Solid lines (black = BPSK and red = PPM) represents predictions from the binomial regressions.

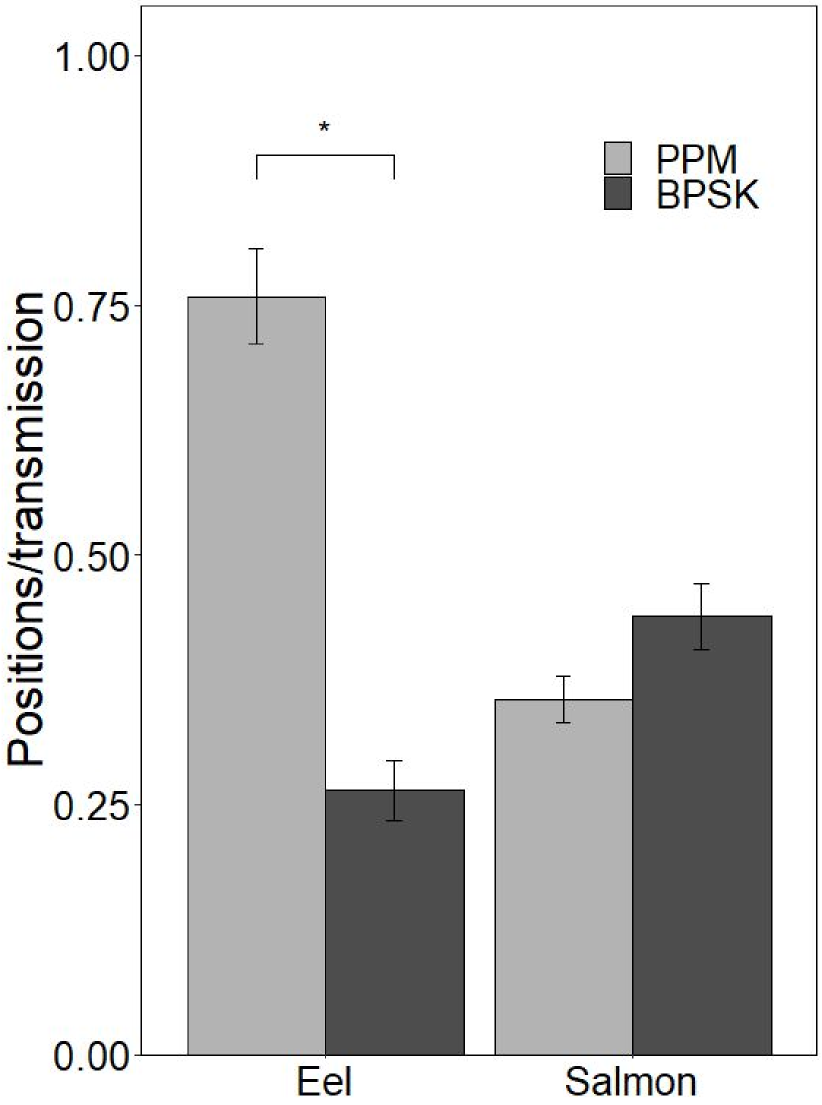
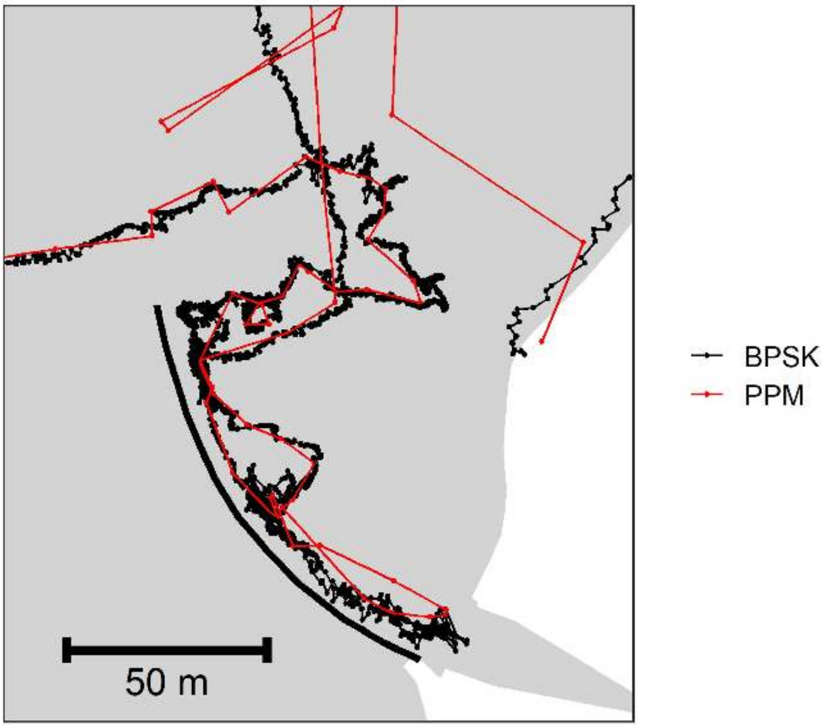


Figure 7. Mean derived positions per transmission for eel in Motala River and salmon in Ume River. Light and dark grey shows PPM and BPSK signals, respectively, error bars represent ± 1 S.E., and * indicates a significant difference ($p < 0.05$).



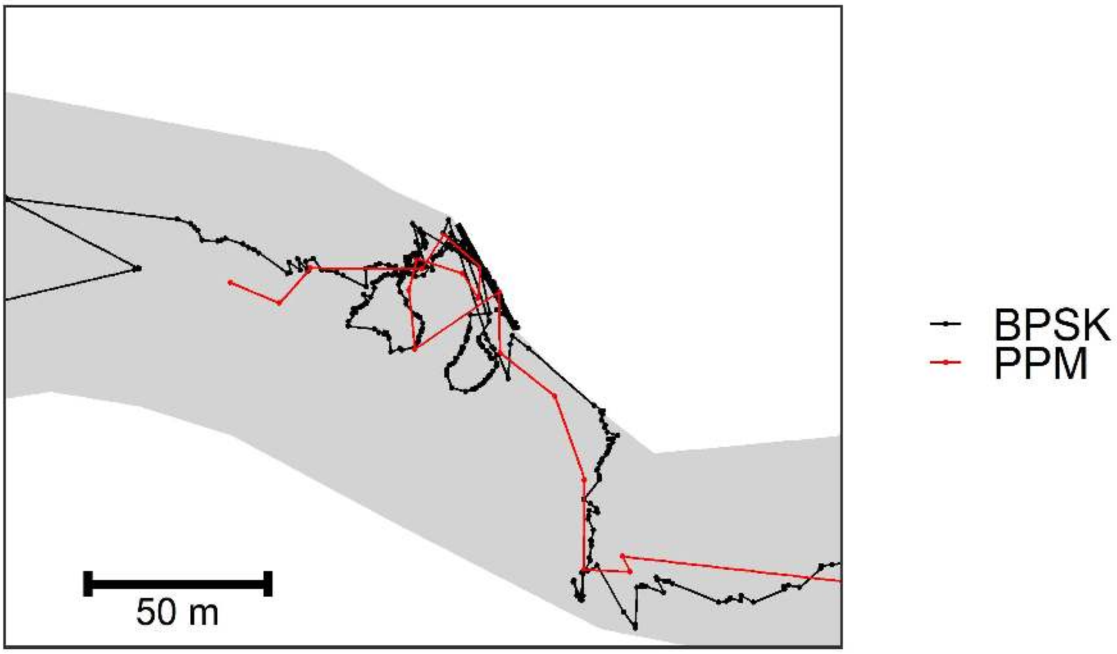


Figure 8. Two examples showing filtered and spatiotemporal aligned PPM positions (red) and BPSK positions (black) for a tagged salmon smolt (top) and eel (bottom). Each position is illustrated with filled circles and connected to the last and next positions with solid lines. The salmon tags transmitted BPSK signals at an average delay of 0.7 s, and PPM signals at an average delay of 30 s, whereas the eel tags transmitted BPSK signals at an average delay of 1.1 s, and PPM signals at an average delay of

37.5 s. Note the searching behaviour along the guidance structure (top, black line) and in front of the turbine intake (bottom, black line). Map data: ©The Swedish National Land survey.

Appendix

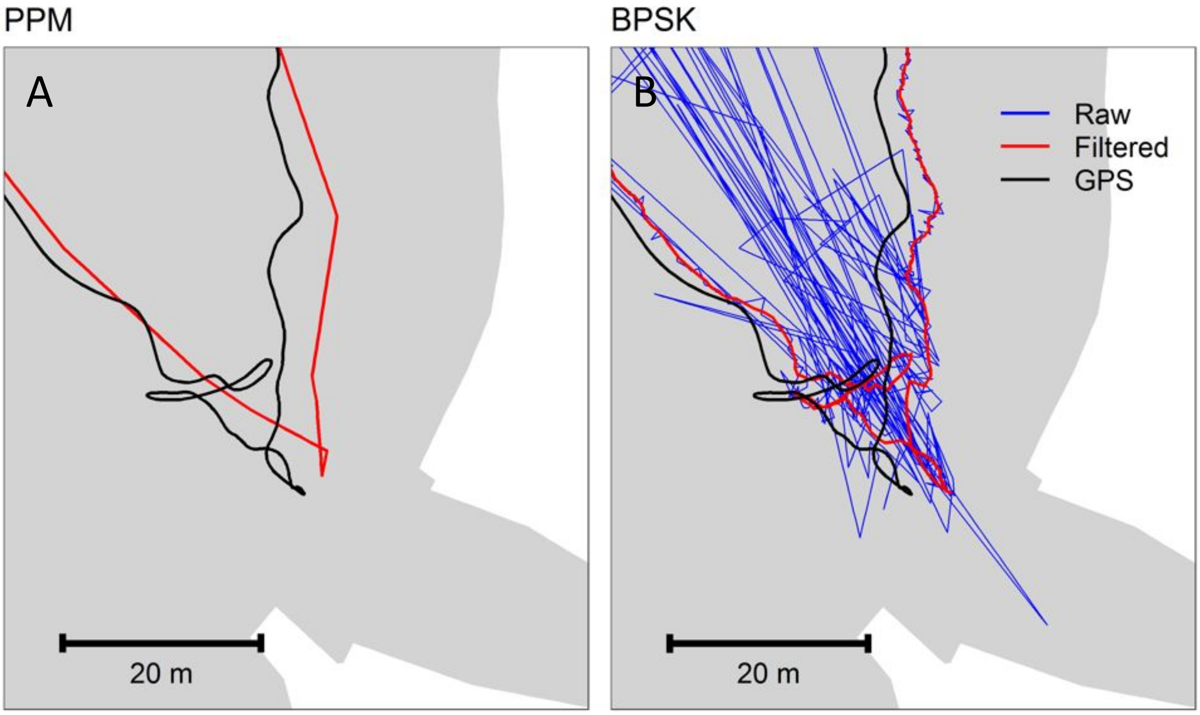


Figure A1. Zoomed in map showing GPS positions (black line), raw VPS positions (blue line), and filtered (but not spatiotemporal aligned) VPS positions (red line), for moving reference tag in Ume River. (A) PPM positions and (B) BPSK positions. Map data: ©The Swedish National Land survey.