Animal Biotelemetry

METHODOLOGY

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Using recovered radio transmitters to estimate positioning error and a generalized Monte Carlo simulation to incorporate error into animal telemetry analysis

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Abstract

Background Mobile radio tracking is an important tool in fisheries research and management. Yet, the accuracy of location estimates can be highly variable across studies and within a given dataset. While some methods are available to deal with error, they generally assume a static value for error across all detections. We provide a novel method for making detection-specific error estimates using detections of recovered transmitters (i.e., mortalities or tag expulsion). These data are used to establish the relationship between received signal strength (RSS) and positional error, which can then be used to predict positional error of detections for fish at large. We then show how detection-specific estimates can be integrated into a Monte Carlo framework to analyze movement in ways robust to spatial uncertainty.

Results In a telemetry study in a large river (~ 90 m), we recovered 22 transmitters to estimate and model positional error. Error averaged 94 m (range = 1–727 m) for transmitters tracked by researchers on foot using a Yagi antenna, and 200 m (range = 1–1141 m) for transmitters tracked from vehicles using an omnidirectional whip antenna. Transmitters located near roads were tracked more accurately with both methods. Received signal strength was a strong predictor of positional error ($r^2 = 0.86$, ground tracking; 0.65, tracking from truck) and was thus used to make detection-specific estimates of error for detections of fish at large. Monte Carlo analysis for a binary movement classification revealed that only 18% of location estimates could be confidently assigned to movement ($p < 0.05$); the remainder were associated with stasis or movement that was within the range of positional error. Ignoring positional error led to positive bias of up to 1300% in individual movement estimates and varied seasonally—it was highest when fish were inactive and lowest when fish were most active.

Conclusion Using recovered transmitters and RSS models to estimate telemetry error is a viable alternative to staged 'dummy transmitter' trials and assuming error is a constant. Our proposed approaches to incorporate detection-specific error estimates into analysis are broadly applicable and can 'make the most' out of highly accurate detections while also cautiously extracting spatial information from less-accurate detections.

Keywords Positional error, Monte Carlo simulation, Radio telemetry, Telemetry error, Mobile tracking

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Background

Estimating telemetry error in mobile radio telemetry studies

Mobile radio tracking is an important tool in fisheries research that allows researchers to achieve high spatial resolution of animal locations [1, 2]. Unlike fixed receiver stations, which provide continuous temporal coverage at a single location, mobile tracking can be used to follow animals anywhere. Mobile tracking is useful to identify breeding sites, study habitat use, and identify the date or location of animal mortalities, among many other uses [3–5]. In any of these applications, however, it is necessary to consider the potential influence of positional accuracy on the research questions. For example, if location accuracy is only 100 m, then the data are not suitable to study microhabitat use. At a minimum, researchers using telemetry should characterize positional error and ask how this relates to the spatial scale of their questions. This is particularly important because there is a great deal of variation in positional error reported across many studies.

Positional error can range from meters to kilometers depending on variety of factors such as methods used (e.g., tracking platform, antenna models, receiver type), characteristics of the waterbody, or species being tracked [1, 6–8]. For example, using a directional Yagi antenna and foot-based tracking in small shallow streams, detections can be made with sub-meter accuracy [1]. However, foot-based tracking in a large river system with deep-inaccessible areas can yield higher error in positional estimates (e.g., 24 m in a ~ 40 m wide river [9]). In some cases, aircraft are required to cover remote areas and tracking results in much larger error ranges (e.g., 200–500 m [8, 9]). Additionally, waterbody characteristics like water temperature and conductivity, presence of aquatic vegetation, and depth impact radio signal attenuation and positional error [7, 8]. Indeed, positional error will vary across different studies using different methods; however, positional error also varies substantially within studies.

Even when using consistent methods in the same waterbody, positional error can be highly variable across detections within a dataset. Examples from air-based tracking suggest high ranges in error (e.g., mean error of 177 m (range: 1–842 m) [10], and mean error of 178 m (range: 22–426 m) [8]) which is expected given the speed and altitude typical of aircraft. Examples using ground-based methods generally report lower, put potentially still important, variation in error. Tracking in a small stream using an 'extended reach technique' (i.e., a loop antenna on an extendable pole) yielded an average error of 1 m, but still the range of error in this study was 0.22–4.28 m [11]. Tracking fish in larger streams results in larger ranges around the mean (e.g., 1–131 m [9], and 4–49 m [12]). Moreover, these estimates are from studies *specifically focusing on error estimation using* controlled trials (e.g., dummy transmitter trials). In real fieldwork scenarios, variables like access, weather and conditions, variation in personnel skill, or time availability could lead to additional variation in positional error for detections of fish at large [9]. In this case representing positional error as a constant for all detections could be a consequential and unnecessary oversimplification.

An alternative to assuming error is constant is to use received signal strength (RSS) to estimate error uniquely for every detection [9]. Modern telemetry equipment provides either a reading of decibels (-dB) or a unitless measure of RSS that provides valuable information [13–15]. In controlled trials, RSS explained 98–99% of variation in distance to transmitter, suggesting it could be used to estimate positional error of transmitters detected at large [9, 12]. This method is applicable when 'homing' or the 'gain reduction method' is used, where the transmitter is approached by the researcher and location where RSS peaks is recorded as the animal location [1]. Thus, high RSS means the transmitter is close and low RSS means it is far away—and a fitted RSS model can be used to convert RSS to a distance estimate. Although controlled trials can be used to develop the RSS model [9, 12] another option is to use detections made of recovered transmitters.

If a telemetered fish dies during a research study or a transmitter is ejected, it is likely that it will be tracked on multiple occasions in a final resting place before recovery (Fig. 1). In this sense, recovered transmitters are akin to planting dummy transmitters for positional error testing [1, 2], but with a potential advantage. Field staff conducting telemetry are naïve of the status of the transmitter until the time it is recovered and thus detections are likely more representative than a staff knowingly participating in an accuracy trial. Variation in positioning error from detections made of these transmitters will reflect the skill, conditions, equipment, and effort used in the study. In the first part of our paper, we provide an example of using recovered transmitters for characterizing positional error, exploring bias, and then using these data to build RSS models.

Incorporating positional error into analysis of telemetry data

Even if good estimates for positional error are available, an important next step in the analysis of telemetry data is to determine how to incorporate this uncertainty into analysis of animal movement data. Options for incorporating uncertainty include (1) censoring detections with low accuracy; (2) drawing a polygon for each animal

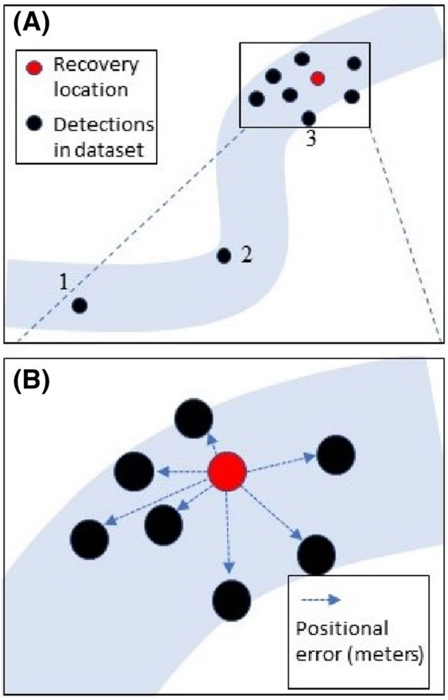

Fig. 1 Example of a detection record (i.e., each dot is an estimated animal location) for a transmitter that is eventually recovered (red dot) where; **a** detections of the transmitter in the final resting place are identified (i.e., after point 3) and these are queried to estimate positional error (**b**). This method assumes that after point 3, the transmitter did not move until it was recovered. Thus, we have (1) a 'true location' and (2) many location estimates (made during regular field-tracking prior to transmitter recovery) to measure positional accuracy

position [1, 16, 17]; (3) modeling error as part of observation error in a state-space framework [18]; (4) or using re-sampling methods to draw points from within an error ellipse and Monte Carlo (MC) simulation to produce analyses incorporating telemetry error [19, 20]. Although each method above has utility, one of the most general is resampling from within telemetry error distributions with MC techniques.

The general MC approach is relatively simple and can be applied to nearly any statistical model [21]. The idea is to simulate many possible versions of a telemetry dataset using recorded locations and estimates of spatial error; each iteration produces a dataset representing where the *animals could have been*. Analysis is then performed on each of these datasets to produce a distribution of feasible results. If conclusions (i.e., movement, habitat preference, etc.) are consistent across the simulated datasets, then those conclusions are robust to uncertainty attributable to telemetry error. While these methods have been used to some extent in the analysis of telemetry data, we are unaware of any studies that incorporate detection-specific estimates of error into a resampling approach. In prior examples, possible 'true' locations are estimated using a static value for positional error [21]; however, this approach fails to fully extract important spatial information from highly accurate detections. Likewise, some detections will be attributed with an unrealistic degree of accuracy.

Here, we provide a simple example of an RSS model integrated with resampling methods to estimate and account for variable positional error in movement analysis. We based the spatial resampling method on the algorithm presented in Openshaw [21]. Although this is a general approach that can be applied to a variety of analyses, we use the question "did the fish move between subsequent detections?" and "how far did it move?" as a demonstration of its utility. We present these methods with a focus on estimating positions using mobile radio tracking but note that the MC method is applicable to any telemetry dataset containing positional error.

Methods

Dataset

We used a mobile tracking dataset from adult landlocked Atlantic salmon (*Salmo salar*) in the Winooski River, Vermont, United States of America (U.S.A.). In this system, a mechanical fish lift is used to capture adult fish at a dam at river kilometer (rKM) 16, and then they are transported 17 rKMs upstream past two additional dams and released into spawning habitat [22]. The upstream extent of habitat access is at rKM 67 where a hydroelectric facility without a passage structure blocks access. Annual mean flow in the Winooski River is 67 m^3/s, it's average bankfull width below rKM 67 (where fish were released and tracked) is about 90 m (range = 40–140 m). Depths are variable across the length of the river ranging from some very shallow riffle sections in braided areas to deep holes in the lower river roughly 10 m deep. A study was initiated in 2018 to assess the behavior of these salmon with a particular focus on fallbacks, which is when fish transported upstream past dams 'fall back' downstream over the dam shortly thereafter [23].

Salmon were captured at the fish lift during the Fall trapping periods (Sept 15 – November 15) from 2018 to 2020 and surgically implanted with radio transmitters. A total of 114 fish were tagged and transported upstream (2018, $n = 21$; 2019, $n = 55$, 2020, $n = 38$) with a mean total length of 771 mm (± 50.12, range = 455–722) and a mean weight of 2.02 kg (± 0.55, 0.74 – 4.28). Fish were anesthetized using electronarcosis and a transmitter (Sigma Eight, TX-PSC-I-450, 46 mm x 12 mm × 12 mm, 8.5 g) was inserted through a small (15 mm) incision which was closed with absorbable sutures. Ping rate of the transmitters was set to 5 s and transmitters frequencies used during the study included 164.290, 164.310, 164.380, 164.480. Fish were transported to sites 20 river km upstream (in 2018) and 33 km upstream (2019, 2020) and released.

Fish were tracked between one to three times a week, including during the winter, using mobile tracking methods. On each tracking event, we drove a pre-determined route along the river in a truck while scanning for fish with a mobile telemetry receiver (Lotek SRX800) attached to a roof-mounted omnidirectional whip antenna. We used one of two methods to record fish locations, (1) we stayed in the truck and marked the location where RSS peaked as the fish location or (2) we got out of the truck and used a directional 3-element Yagi antenna to approach and locate the RSS peak. The first method was used when exiting the truck was not feasible (e.g., private land/no river access, limited time availability of staff, foul weather). When truck tracking, we generally began detecting a transmitter at a weak RSS (which is displayed on the receiver screen and is also indicated by 'chirp' volume from the receiver's speaker), followed by an increase in RSS to a peak before it began decreasing again. We stopped the truck at the location where the RSS peaked, and the RSS and the coordinates (of the truck, as measured using a global positioning system (GPS)) were recorded. When we used the second method, we most often were not wearing waders so were restricted to homing in on the highest RSS signal that could be achieved from the bank. This GPS location, where RSS was highest, was recorded as the fish location.

The GPS coordinates were collected by either handheld units (Garmin Rhino) or the internal GPS on the radio receiver, both of which were enabled with Wide Area Augmentation System (WAAS) and had < 5 m accuracy. This component of positional accuracy is called mapping error [24] and is generally small relative to animal location error in telemetry studies [8], especially those in larger rivers or ones done from aircraft. Given the relatively coarse accuracy of our methods (rarely < 50 m, See Additional File 1: Figure S2) we consider mapping error to be negligible relative to animal location error and do not explicitly account for it.

Positioning error estimation using recovered transmitters

We first used the recovered transmitters to estimate positional error and explore bias. Because (1) we physically recovered 22 transmitters (due to mortalities or tag loss) and collected GPS coordinates of each one (i.e., knew where they were); and (2) we had tracked these transmitters many times to estimate their position during our ongoing study, we unintentionally produced a dataset suitable for estimating positional error. In fact, we produced a 'dummy transmitter' dataset, which refers to a scenario where a transmitter is placed in a known location, then tracked to estimate its position. Detections of these recovered transmitters occurred on 107 unique dates by 10 different field crew so should be reflective of the variation in positional error embedded within our dataset.

We first queried these data to reflect only positional estimates of the transmitters after they had come to a final resting place (i.e., the recovery location, Fig. 1a). When estimating positional error, we wanted to only be using detections recorded of that transmitter in the known location (i.e., the recovery location) and not detections from the fish as it was still alive and moving around. Thus we assume that for all recovered transmitters (1) there was a date the transmitter came to a final resting place, (2) we correctly identified this date, and (3) the transmitter did not move after this date. This method was generally straightforward for most recovered transmitters (e.g., Fig. 1a) but in several cases required a few iterations to determine the appropriate date cutoff. Because the RSS ~ Distance relationship is so strong ($r^2 > 0.95$, $p < 0.05$) [9], if the date cutoff was wrong, clear outliers appeared when reviewing this relationship.

This method resulted in a dataset of 538 estimates of fish locations (432 whip, 104 Yagi) that were each paired with a 'true' location (i.e., the recovery location). We measured the distance from the estimated location to the true location, and considered this a good estimate of positional error. We summarized these data to generate mean estimates of positional error and used ANOVA and Tukey's HSD to determine if positional error varied among transmitters (Table 1). To assess method-specific overall mean error, we fit a linear mixed effects model with the response as distance, antenna type (a two level factor) as a fixed effect, and transmitter ID as a random effect (using the lme4 package in R) [25, 26]. Transmitter ID was used as a random effect because the datasets included many observations made of the same transmitter, which are expected to be correlated. Marginal means and 95% confidence intervals were extracted from the fitted model (using the emmeans package in R) [27]. We also compared the mean positional error of each transmitter to the distance to the nearest road to test the hypothesis that road-proximity was positively correlated to positional error.

Building an RSS model

We then followed the procedures described in [9] and modeled the relationship between distance-to-transmitter (i.e., positional error estimates made from recovered transmitters, described above) and RSS for Yagi and whip antennas (separate models, n Yagi = 104, n whip = 432). We tested five basic models to predict

Table 1 Information on recovered transmitters, including detection equipment and remote positioning data

TagID	Release	Recovered	Last move	At Large (days)	Road dist. (m)	n Yagi	Error yagi	n Whip	Error whip
1	10/19/2020	6/7/2021	11/3/2020	231	16	2	46 (6)	59	26 (8)
2	10/7/2020	6/7/2021	10/27/2020	243	16	2	16 (7)	61	30 (16)
3	11/4/2020	12/16/2020	11/17/2020	42	36	2	5 (0)	8	34 (12)
4	10/22/2019	8/7/2020	12/17/2019	290	63	0	–	21	98 (35)
5	10/22/2019	7/10/2020	1/7/2020	262	53	1	0	20	101 (106)
6	10/15/2019	8/7/2020	12/11/2019	297	65	7	146 (21)	4	116 (59)
7	10/25/2019	8/7/2020	6/24/2020	287	75	1	12	2	126 (26)
8	10/14/2020	4/7/2021	3/22/2021	175	21	1	3	4	142 (118)
9	10/7/2019	8/3/2020	1/7/2020	301	50	8	221 (10)	4	160 (107)
10	10/21/2020	12/16/2020	11/10/2020	56	74	1	3	11	161 (125)
11	11/6/2020	12/28/2020	12/11/2020	52	114	2	73 (78)	3	169 (64)
12	10/22/2019	8/7/2020	11/15/2019	290	134	0	–	37	171 (62)
13	10/23/2019	7/6/2020	6/4/2020	257	89	1	0	8	173 (50)
14	10/26/2020	6/7/2021	2/10/2021	224	148	3	72 (29)	23	183 (59)
15	11/2/2020	6/7/2021	11/10/2020	217	96	8	136 (70)	49	206 (57)
16	10/10/2019	7/10/2020	11/18/2019	274	327	1	0	43	303 (88)
17	10/28/2019	7/29/2020	11/13/2019	275	286	4	265 (176)	24	370 (52)
18	10/25/2019	8/7/2020	11/6/2019	287	333	20	288 (144)	22	377 (90)
19	10/17/2019	8/7/2020	11/18/2019	295	306	11	196 (168)	22	393 (97)
20	10/4/2019	7/6/2020	10/16/2019	276	284	15	202 (299)	7	525 (217)
21	10/10/2019	8/7/2020	3/3/2020	302	388	8	243 (95)	0	–
22	10/2/2020	1/5/2021	12/17/2020	95	35	6	28 (19)	0	–

The Road Dist. (m) column is the distance, in meters, of the recovery location to the nearest road. Columns n Yagi and n whip are the number of unique positional estimates made for the recovered transmitter (before it was recovered). Error Yagi and Error whip are means (followed by standard deviation) of positional error estimates for each transmitter, made with Yagi and whip antennas. Absence of data is indicated by a dash (-) and data are sorted according to the error whip column. Dashed horizontal lines in each panel represent overall means for that antenna type

Distance to transmitter (D) that included (1) D ~ RSS, (2) ln(D) ~ RSS, (3) D ~ RSS + RSS^2, (4) ln(D) ~ RSS + RSS^2, (5) ln(D) ~ RSS + RSS^2 and selected the best using Akaike's Information Criterion (AIC). Polynomial models were orthogonal and fit with the poly() term in in the lm() function (in base R) [25]. We also examined histograms of residuals to examine potential patterns and assess the assumption of homogeneity.

Incorporating telemetry error into analysis: Confidence polygons

In the following two sections we consider a simple analysis of movement using our salmon dataset (detections of fish at large) and use two ways to incorporate estimates of positional error into inferences (polygon approach, and MC approach). Our example research questions are: did the fish move between subsequent detections, and if so, how far? The first approach (confidence polygons) is a two-dimensional analysis and analyzes the location estimates, whereas the second method is one dimensional and assumes that the fish are in the river somewhere near where the location estimates are.

First, we represent each detection as a polygon guided by the positional estimate (i.e., a GPS location) and a buffer with radius *r* (Fig. 2). The radius *r* is estimated uniquely for each detection using the fitted RSS model, the observed RSS value for the detection, and the corresponding model prediction for D. We also estimated the upper 80% prediction interval using predict(*model*, interval = "prediction", level = 0.80) as a more conservative (i.e., big) estimate for *r*. This roughly translates to being 80% confident that the fish was within *r* meters of estimated location (Fig. 2). Using these different sized confidence polygons, we then assessed movement (Yes/No, based on overlap of polygons) for every subsequent detection in each fishes' movement history and refer to these metrics as moveSimp (using model prediction for *r*), and moveSimp_80 (using the upper 80% prediction interval for *r*).

Incorporating telemetry error into analysis: Monte Carlo simulation

We also developed a MC simulation-based approach to express confidence in movement direction (Up/Down) and movement distance (estimate and variance) along a

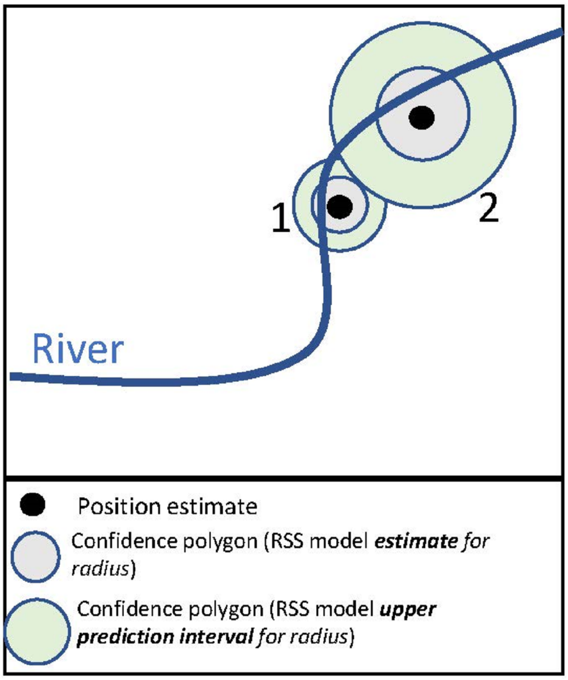

Fig. 2 Example of representing two telemetry detections (1, 2) as polygons with different choices for how to calculate *r* (radius of buffer) from a received signal strength (RSS) model

stream network. We implement the general algorithm presented in [21] which composes of several steps and is generally applicable to a variety of spatial analyses. The steps are:

1) Determine what error is characteristic of a spatial data input (in our example, positional error for fish location estimates)
2) Replace observed spatial data with 'possible' values given the appropriate probability distributions for positional error
3) Perform a sequence of spatial operations or analysis on the data (movement, distance moved, etc.) and save the results
4) Repeat steps 2 to 3 *n sim* times
5) Compute summary statistics or compute MC significance test.

To implement this approach, we developed a user defined function (in R) that produces a possible location using three inputs (1) a positional coordinate (2) an RSS value, and (3) an RSS model that predicts distance to transmitter (i.e., Fig. 2). For this analysis, we converted positional coordinates to Universal Transverse Mercator format (UTM) so units along the X and Y coordinates are measured in units of meters. Now, if point P = (X, Y) is a telemetry detection that is an estimate of a true animal location (Q) with *r* representing the distance between P and Q, then we can acquire a possible value of Q with these steps.

1. Sample a 'possible' distance to transmitter (r_i) using *RSS* and the fitted model
2. Sample an angle (Θ_i) from ~ Uniform(0, 2*π)
3. Calculate Q_i (a possible fish location at X_i and Y_i) as $X_i = X + r_i * \cos(\Theta_i)$ and $Y_i = Y + r_i * \sin(\Theta_i)$

We next consider a pair of points A and B, which represent two detections in a detection history for a fish. We simulated possible locations for A and B to produce Q_a and Q_b. We then used a linear referencing procedure (in the RiverDist R package) [25] to place the Q_a and Q_b on the nearest location within the river (using a river network shapefile) and assigned each a river kilometer value. Importantly, this assumes the fish is in the river and is now a one-dimensional analysis where location can be referenced along the river with a single value. We then repeated this procedure n-sim times and report a p-value test result for upstream movement (US_p) and downstream movement (DS_p). These are the proportion of times (out of all simulations) a given movement did not occur; for example, if in 1000/1000 simulations a fish moved upstream, the UP_p-value would be 0.00. So, a low p-value for UP_p is provides strong evidence for upstream movement and a low value for DS_p provides strong evidence for downstream movement. Note that DS_p is simply1—US_p (i.e., are perfectly correlated) but for demonstration purposes both are presented. We also calculate the distance moved at each iteration and report the mean and sd calculated across all simulations for a given pair of points.

Results

Telemetry error estimated from recovered transmitters

On average positional error was 200 m (lower 95% confidence interval [CI] from mixed model = 148, upper CI 253, min = 1 m, max = 726) with the whip antenna and 94 m (lower CI 39, upper CI 148, min = 1 m, max = 1141) using the Yagi antenna (Fig. 3; Table 1). The preceding estimates are marginal means from the mixed effect model inclusive of transmitter ID as a random effect. Inclusion of transmitter ID was supported by a comparison to a linear model without transmitter ID ($\chi2 = 440.93$, $p < 0.001$). Intraclass correlation of the random effect was 0.59 (random intercept variance = 13009, residual variance = 8928). Furthermore, when using simple ANOVA, positional error differed significantly among recovered transmitters (ANOVA, $F = 33.5$, $p < 0.001$) and in total, 28% of pairwise comparisons among transmitters were significant. This means that some transmitters were

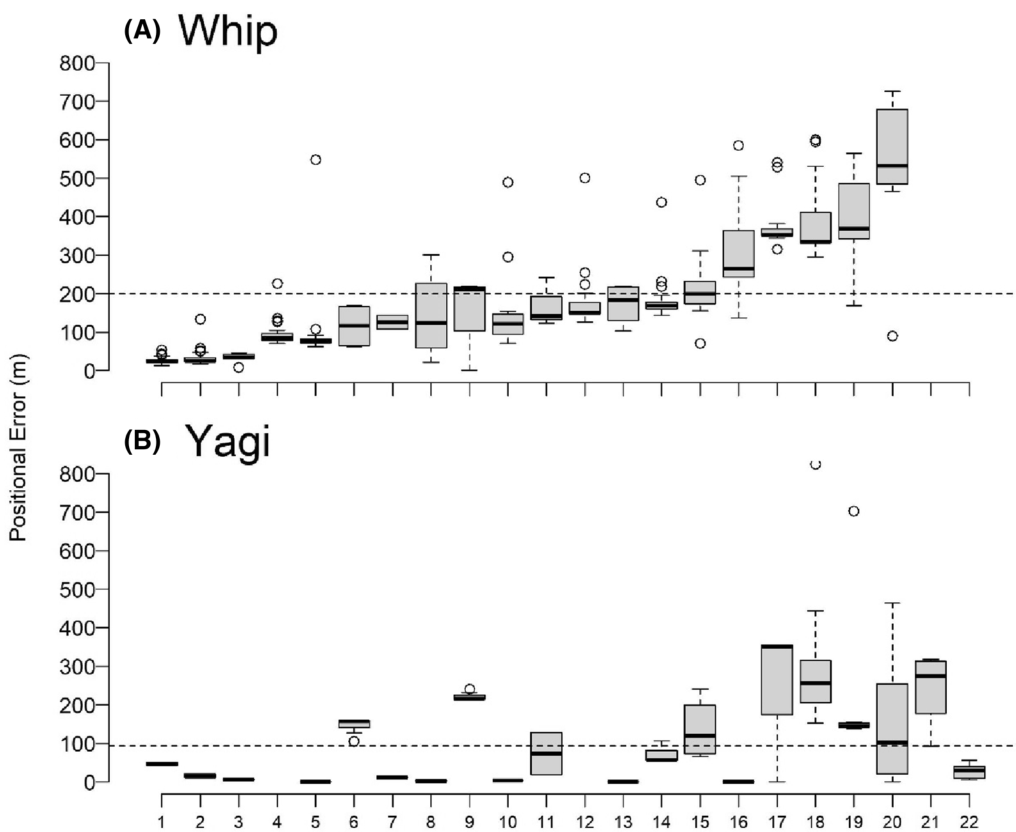

Fig. 3 Variation in positional accuracy of detections made of recovered transmitters using whip (**A**) and Yagi (**B**) antennas. Each box represents a recovered transmitter (x axis labels correspond to Table 1) that was tracked during regular surveys looking for live fish. Transmitters IDs are organized with respect to average error recorded via the whip antenna

consistently tracked more accurately than others, which make sense given that some transmitters were resting in easily accessed areas while others were not.

Indeed, further inquiry revealed that transmitters resting in the water near a road had consistently lower positional error relative to those resting far from a road (Fig. 4). Distance to road explained 82% of variation in mean positional error when using the whip antenna ($r^2=0.82$, intercept = 51.98, slope = 1.01, $p<0.001$). The slope suggests that for every increase in 1 m from a road, telemetry error will increase by 1.01 m, which is sensible because all whip antenna tracking was done from a truck. Distance to nearest road was a weaker, but still significant, predictor of positional error of detections made with the Yagi antenna ($r^2=0.61$, intercept = 47.30, slope = 0.59, $p<0.001$). Convenience of access was thus a strong predictor for telemetry error using both methods.

Received signal strength model development

Second order polynomial models, with a log transformed response variable, fit both the Yagi and whip antenna sets best (Fig. 5). In the Yagi model, RSS explained 86% of variation in distance to transmitter, whereas RSS explained 65% of variation in the whip model. The fitted regression lines and the 85% prediction intervals in Fig. 5 can be viewed as a guide for interpretation of positional error at given levels of RSS. At an RSS of 100 with a Yagi antenna, the transmitter is most likely 99.5 m away (model prediction), and there is an 85% chance it is between 47.4 and 209.2 m (upper and lower prediction intervals). With an RSS of 100 collected with the whip antenna, the transmitter is probably 51.3 m away and there is an 85% chance it is between 13.9 and 189.1 m.

Application of RSS model to detections of fish at large

Our three-year mobile tracking dataset included 87 unique fish detected an average of 31 ± 18 times each (min = 1, max = 67) for a total data set with 2709 unique estimates of a fish location. Application of the RSS model to detections of fish at large indicated a mean error of 149 ± 93 m for Yagi detections and 171 ± 96 for whip detections; however, values ranged widely (See Additional File 1: Figure S2).

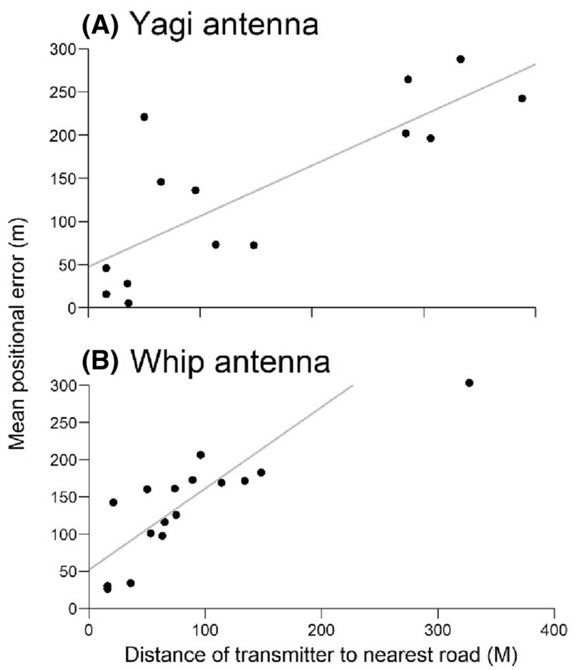

Fig. 4 Linear regression comparing mean positional error for a given transmitter, to the distance that transmitter was from the nearest road using Yagi antennas (**A**) and whip antennas (**B**)

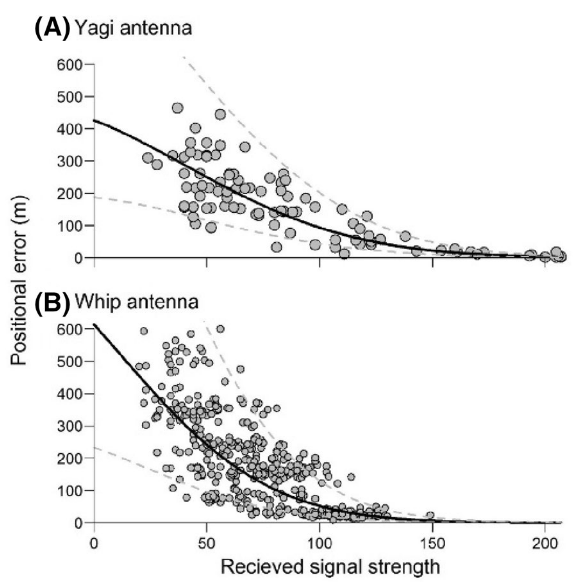

Fig. 5 Received signal strength model results to predict positional error for a Yagi antenna (**A**) and whip antenna (**B**). The solid line shows model estimates, and the dashed lines are the 85% upper and lower prediction intervals. Three points with high error are omitted in panel A

Incorporating error into movement analysis: Confidence polygons and MCMC tests for directional movement

For each sequential pair of detections for each fish, we calculated moveSimp, moveSimp_80, US_p, and DS_p, and movement distance (with SD) with an example for one fish shown in Table 2. This fish was detected on 11/13 and was at large for 7 days relative to its previous detection (11/6) and was estimated to move upstream 2.89 km ± 222. Movement metrics suggest strong evidence for an actual upstream movement (msimp = TRUE, msimp_80 = TRUE and US_p = 0.00) rather than a potential consequence of positional error. These metrics mean that the polygons representing these detections did not overlap using either the model estimate for r (msimp) or the more conservative upper 80% prediction interval (msimp_80). And, in every iteration in the MC procedure, the fish moved upstream (US_p = 0). These are not at all surprising, however, since this movement distance is quite large relative to our mean positional error.

A more subtle movement is seen on 11/21. The distance moved along the river is 63 ± 11 m yet the movement metrics msimp, msimp_80, and UP_p still provide strong support for an actual movement. Confidence in movement is high—despite such a short distance moved—because the underlying detection data have low positional error. The two detections were made with a Yagi antenna with RSS of 175 (predicted positional error = 9.3 m, see Fig. 5) and 206 (error = 2.7 m).

Alternatively, some long-distance movements still provide insufficient evidence to distinguish movement from positional error. For example, though the movement detected from 12/12 to 12/16 was downstream 1.01 km ± 859, there is insufficient evidence to conclude movement occurred in either direction at the $\alpha = 0.05$ level (Up_p and Down_$P > 0.05$). Here DS_p is 0.12 which means 88% of simulations suggested a downstream movement, though 12% of simulations suggested upstream movement. The polygon-based approach also suggests insufficient evidence is available to conclude movement in two-dimensional space using MoveSimp_80, though the version using the model fit (moveSimp) does suggest movement. Here, a Yagi antenna detection with RSS of 57 (error ~ 153) and a whip antenna detection with RSS of 30 (error ~ 378 m) are the underlying reason for inconclusive movement results.

Taken collectively (84 unique fish and 2599 pairs of detections), the MC test for directional movement along the river suggested 472 movements (out of 2599, 18%) could be distinguished from positional error at the $\alpha = 0.05$. The metrics moveSimp suggested 614 movements were TRUE (24%), and moveSimp_80 was the most conservative estimate with 343 movements classified as TRUE (12%).

Table 2 Movement information based on sequential pairs of detections for a fish at large

Date	Days BTW	Det1	Det2	Distance	Distance SD	US_p	DS_p	MoveSimp	MoveSimp_0.8
11/6	2	Whip-117	Yagi-137	− 75	36	0.994	0.006	True	True
11/13	7	Yagi-137	Yagi-78	2893	222	< 0.001	1.00	True	True
11/14	1	Yagi-78	Yagi-73	254	309	0.162	0.838	False	False
11/15	1	Yagi-73	Yagi-120	− 285	186	0.950	0.050	True	False
11/18	3	Yagi-120	Yagi-75	245	172	0.064	0.936	True	False
11/20	2	Yagi-75	Yagi-175	157	251	0.164	0.836	True	False
11/21	1	Yagi-175	Yagi-206	− 63	11	1.00	< 0.001	True	True
11/27	6	Yagi-206	Yagi-111	− 112	107	0.932	0.068	True	False
12/3	6	Yagi-111	Yagi-54	195	241	0.216	0.784	False	False
12/5	2	Yagi-54	Yagi-100	− 586	249	0.992	0.008	True	False
12/9	4	Yagi-100	Whip-59	171	254	0.228	0.772	False	False
12/10	1	Whip-59	Yagi-125	− 117	223	0.726	0.274	False	False
12/11	1	Yagi-125	Yagi-104	82	104	0.208	0.792	False	False
12/12	1	Yagi-104	Yagi-57	322	263	0.108	0.892	False	False
12/16	4	Yagi-57	Whip-30	− 1013	859	0.880	0.120	True	False

Each row shows a comparison of the prior detection in the time series to the detection on the date shown. Days BTW = days between the two sequential detections; Det1 = type of antenna used in the first detection and received signal strength of detection; Det2 = type of antenna used in the second detection and received signal strength; Distance = estimated distance traveled along the river (downstream is negative) based on Monte Carlo (MC) simulation; SD = MC-based standard deviation for distance moved; US_p = MC-based p-value for upstream movement; DS_p = MC-based p-value for downstream movement; MoveSimp = polygon-based assessment of movement; MoveSimp_0.8 = polygon-based assessment of movement using upper 80% prediction interval

The relationship between distance moved along the river and the MC p-value for directional movement reveals several important points (Fig. 6A). First, movements longer than 1.1 km are all considered significant (i.e., true movement) based on US_p or DS_p ($\alpha = 0.05$). This implies that if a 'distance cutoff' were to be used ensure 95% probability that movements were classified correctly as distinguishable from error, it would need to be quite large. However, such a cutoff would fail to adequately classify a large number of movements estimated with more accurate positions. Indeed, there are many movements under 1.1 km that can reliably be distinguished from positional error (Fig. 6B). Out of 472 significant directional movements ($\alpha = 0.05$) 203 were under 1 km, 90 were under 500 m, 18 were under 200 m, and 6 were under 100 m.

By examining monthly movements ignoring error, and then using only movements classified with our MC test, we found that bias associated with ignoring error was substantial and varied seasonally (Table 3). This table shows movement calculated disregarding error (i.e., all location estimates are exact) and compares it to movements calculated only using movements that are distinguishable from positional error with the MC test. These movement sums ignoring error overestimate actual movement by as much as 1388%. For example, in April we documented 81 'presumed upstream movements' (e.g., any sequential pair of detections, for a fish) but only 1/81 (1%) of these was confirmed by the MC test for directional movement. Thus, we only have confidence in movement of 501 m during April (rounded to 1 km in Table 3), but the summation of all movements ignoring positional error is 7 km (e.g., 1388% of confirmed movements). Trends present in Table 3 suggest (1) actual movement was more common in Fall months when salmon were migrating, and (2) bias created by ignoring error was highest when overall rates of movement were low. These results are intuitive because long movements are also more likely to be 'real' (Fig. 6) and thus during periods of high animal activity, relative bias created by positional error is diminished. In contrast, when actual movement rates are low then then positional error accumulates and creates an illusion of apparent movement.

Discussion

Using a novel method that uses recovered transmitters, we found positional error in a mobile tracking dataset was large, highly variable, correlated with method used (ground-based Yagi or truck-based tracking), and associated with road proximity. We then demonstrated two methods to incorporate detection-specific estimates of positional error into analysis and interpretation of telemetry data. The polygon-based approach and MC-based test both provide a means to distinguish movement from 'apparent' movement propagated by positional error. While we demonstrated a simple binomial test for movement, these approaches are flexible and could be applied

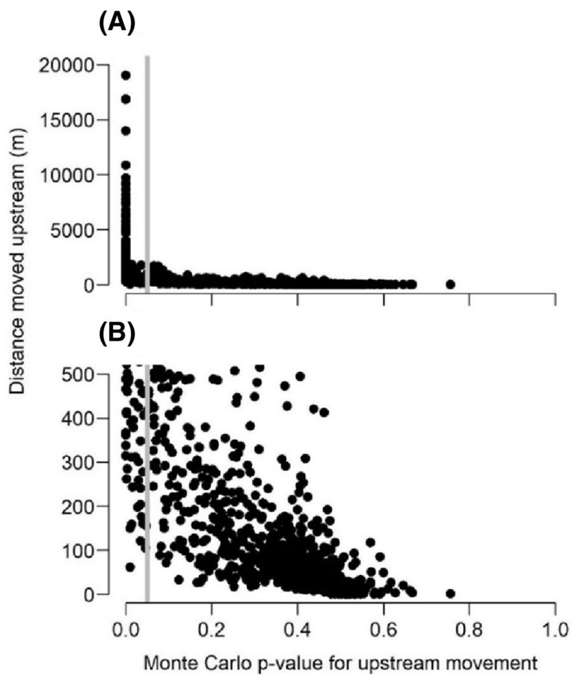

Fig. 6 Relationship between movement distance upstream and the Monte Carlo p-value test for upstream movement; each point represents the estimated movement distance for a fish, based on two sequential detections. The $\alpha = 0.05$ is shown as a gray vertical bar, points to the left of this bar show sufficient evidence to distinguish movement from apparent movement created by positional error; points to the right of the bar do not provide sufficient evidence to conclude movement has occurred at the 0.05 level. Panels A and B represent the same data but are shown with different ranges on Y-axes

to a variety of other analyses conducted with telemetry datasets in aquatic and terrestrial systems.

Positional error estimates using recovered transmitters

There are several benefits to estimating error from detections of recovered transmitters. First, in the absence of a single-blind hidden transmitter trial (i.e., staff tracking transmitters do not know they are tracking planted transmitters), these data may be generated un-intentionally and require little effort. We spent time recovering transmitters to confirm mortalities and get expensive transmitters back and had not initially considered making estimates of positional accuracy using them. However, we later realized the need to characterize our error, and that we had collected excellent data to make error estimates. Thus, the technique described here might be useful as an opportunistic means to assess and model error if transmitters are recovered during a study.

Additionally, a benefit of this method is that the estimated detection accuracy should reflect realistic variation in conditions (e.g., season, water chemistry), staff participation, and effort to locate transmitters. Indeed, we used 22 recovered transmitters with known locations that were tracked 538 times, on 107 unique dates, by ten different staff members to estimate positional error. In contrast, typical 'hidden transmitter' studies generally use far fewer transmitters deployed in a narrower window of conditions than this study. For example [9] used 4 transmitters, [2] used 10, and [10] used 5. Using our approach, the estimates of positional error are truly reflective of the typical 'efforts' made by field personnel to locate transmitters under real-world fieldwork conditions. To make highly accurate detentions of fish using homing or the gain-reduction-method takes quite a bit of time, and we strongly expect there to be a strong relation between 'time spent looking' and positional accuracy. For example, working in a river ~ 50 m wide and tracking from a boat, Koehn et al. [2] report 0.19 (± 0.13) meter accuracy and note that transmitter location estimates took an average of 26 min (per transmitter). Working in an 8 m wide stream, Sullivan et al. [1] report 0.91 (± 1.4) meters and an average time to track a transmitter of 21 min. These studies show that achieving very low error is possible, but it takes time. In real fieldwork scenarios, this time commitment might not be maintained in which case error estimates from a staged trial could be biased low. In our study over several years, we had many crew members, working year-round, and there was undoubtedly wide variation in effort made across detections. This variability underscores the utility of using RSS as an indicator of positional error, since it will provide similar information on proximity to transmitter regardless of effort or personnel skill.

Our estimates of mean positional error using the Yagi antenna (94 m) and the 'gain reduction method' [5] are quite high relative to other published studies. As mentioned, some studies report sub-meter accuracy while others report accuracy up to about 50 m using similar foot-based methods [16, 29]. The fact that we were restricted to the bank on most tracking events, and we were tracking a large river (~ 90 m wide) are the best explanations for this large degree of error. Moreover, as we had many transmitters to track on a weekly basis, we did not commit a large amount of time to tracking each individual transmitter. The important conclusion is that the estimates of positional error should be made specifically for a given study, not inferred based on previous studies using different methods in a different environment, with different people.

If a specific 'target' level of accuracy is required by a study, we strongly recommend that an RSS target be developed and conveyed to field crews prior to field data collection. For example, if we knew our research questions required 30 m accuracy, we could use an RSS model

Table 3 Monthly movement estimates of Atlantic salmon (*Salmo salar*) tracked with mobile methods

Direction	Month	n movements (actual: total)	Actual movement (km)	Total movement (km)	Bias (%)
Upstream	January	23: 212 (0.11)	19	40	209
	February	20: 168 (0.12)	29	44	151
	March	10: 136 (0.07)	53	66	125
	April	1: 81 (0.01)	1	7	1388
	May	2: 68 (0.03)	3	8	265
	June	5: 140 (0.04)	9	19	204
	July	2: 8 (0.25)	99	100	101
	October	19: 31 (0.61)	72	76	106
	November	69: 200 (0.35)	241	260	108
	December	46: 233 (0.2)	110	133	120
Downstream	January	42: 242 (0.17)	234	255	109
	February	13: 138 (0.09)	131	144	109
	March	27: 145 (0.19)	129	142	110
	April	10: 81 (0.12)	133	139	104
	May	5: 74 (0.07)	65	69	107
	June	12: 139 (0.09)	147	158	107
	July	0: 5 (0)	0	1	NA
	October	15: 26 (0.58)	111	113	102
	November	82: 212 (0.39)	269	287	107
	December	72: 260 (0.28)	440	459	104

'Actual' movements are determined by the Monte Carlo method (MC), whereas any pair of detections not in the same location are considered in the 'total' column. Actual movement (km) is the sum of monthly movement distances that pass the MC test (upstream or downstream at $\alpha = 0.05$), whereas total movement is the sum of all potential movements. Bias is the ratio total movements to actual movements

to determine a target RSS value of 140 (Fig. 5). Based on our model, an RSS of 140 means you are probably 30 m away from the transmitter. In a fieldwork setting, this 'cutoff' could be quite useful to provide consistency in accuracy but also save time; once a detection with a target RSS was achieved, the field staff could proceed to tracking the next transmitter.

As suggested in [9] we modeled the relationship between RSS and distance to transmitter and found strong relationships ($r^2 = 0.86$, 0.65) that were useful to extrapolate to RSS values of detections made of fish at large. Whereas [9] used a controlled trial occurring on a single day, using two transmitters, to establish the relationship between RSS and distance ($r^2 = 0.98$), here we used data collected on many unique days and 22 transmitters at large in a river. That our models' explanatory power is lower is not surprising given the underlying variability of our data. We consider a RSS model built on this variable data to be more useful, since model predictions (and underlying prediction error surrounding the predictions) applied to animals at large will be more realistic. For example, the model distance ~ RSS is useful, but clearly too simple as things like depth, water chemistry, or other factors influence signal attenuation in water [6, 7]. A 'field-based' RSS model—collecting data over a broad range of conditions—will incorporate this inherent variation into the model and thus the extrapolations also made from the model. Thus, prediction intervals extrapolated to animals at large will be larger but a better representation of underlying uncertainty.

We found that distance to the nearest road was strongly correlated with positional error estimates, which is an important factor to consider when interpreting and analyzing telemetry datasets. The potential consequences of this on positional inference will depend on the research question being addressed; for example, in a habitat use study one might have increased confidence near roads to assign locations to habitat types. Habitat features colinear with road proximity (e.g., culverts, stream crossings, or canyons with adjacent roads) might appear to be used more frequently than other habitats where detections were not made (because they were too far from a road) or detection accuracy is limited, preventing assignment to that habitat type. This topic is commonly considered in GPS – collar telemetry, where GPS fix rate can be biased by habitat features (e.g., canopy, topography) [19]. For example, acquiring GPS fixes of large mammals was strongly influenced by topography in [26] and these researchers suggest correction measures are important to reduce bias in habitat selection analysis when fix-rate is non-random. Further research is warranted in aquatic telemetry studies to assess how detection probability or accuracy is related to habitat features and how to account for this in analysis.

Incorporating positional error into analysis

The benefits of incorporating error via a polygon-based approach or MC simulation are described in more detail elsewhere; however, an important advancement of this paper is the combination of these methods with detection-specific estimates for error. Rather than drawing from a single 'characteristic' positional error distribution for all detections, the use of RSS and a fitted RSS model allows for a unique error distribution to be used for each detection. Although this methodology adds a level of complexity to analysis, it provides a more nuanced and realistic approach to capturing uncertainty. However, our method does involve making some choices with regards to what radius to use (e.g., in moveSimp) or what p-value to use in the MC tests, that will depend on the research question being asked.

Increasingly large polygons (as determined by upper prediction intervals at different levels of α) will be increasingly conservative *against* detecting movement when using moveSimp. For example, using an upper 95% prediction interval will give large polygons indicating '95% confidence the true locations are within these two polygons" and thus be conservative against confirming movement via non-overlapping areas. Higher α is associated with more stringent measures required by the analyst to confirm movement. Similarly, with the MC test for directional movement, the simulation-based p-value establishes a threshold for establishing movement. A lower α is associated with a test more conservative against movement than one with a higher α. Which test and at what significance level should be guided by carefully considering the research questions being asked. Finally, it is important to recognize that these methods provide a way to establish a level of confidence that movement *has occurred* but cannot ever confirm that movement *has not* occurred.

The polygon-based approach and MC routine have potential applications for a wide variety of analyses. For example, determining mortality status or date of death could be assessed in a quantitative manner based on the cessation of movement [27, 28]. Although cessation of movement does not necessarily imply death, or movement always indicate the animal is still alive [29], the p-value-based test for directional movement will provide a level of confidence in the determination of movement. Other applications of the MC test include habitat selection models, which could be run on a high number of simulated datasets, and variation in selected top models and coefficient values could be assessed. Also, comparisons of movement rates among seasons, study groups, or animals with different traits could all be done in a way that incorporates error using the methods presented here.

Conclusion

In mobile telemetry studies, some detections are more accurate than others. This is inevitable when conducting fieldwork and should not be ignored. Thus, if detection-specific estimates of positional error are available (e.g., via a RSS model) then they can be highly useful. Accurate detections can be used to answer some questions (e.g., did this fish move upstream at least 10 m) that inaccurate ones cannot, yet, inaccurate detections still provide useful data. The polygon and MC-based methods for incorporating error 'make the most' out the inherent information of the data and can provide conclusions robust to the influence of telemetry error.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-023-00337-y.

Additional file 1: Figure S1. Trigonometry employed in determining range of 'possible locations' given (1) an estimated location made in the field (2) received signal strength (RSS) of the detection used to estimate location and (3) a fitted RSS model relating RSS to distance to transmitter. From an estimated point P (i.e., an X, Y coordinate) possible locations (Q) are estimated using the *r* (predicted distance-to-transmitter given the observed RSS and the RSS model) and a random angle. **Figure S2**. Distribution of recorded received signal strength (RSS) values for detections of transmitters at large (A, B) and the resulting positional error estimates for those detections based on the best fitting model (C, D).

Additional file 2. This additional file contains data and R scripts to demonstrate methods.

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Author contributions

KCH and WRA conceived the idea to use recovered transmitter detections to estimate positional error. KCH conducted the analysis, developed methods, and wrote the manuscript. TCS and WRA oversaw collection of example dataset used for demonstration of methods. All authors contributed critically to drafts of the manuscript and provided final approval for publication. Any use of trade, product, or firm names is for descriptive purposes and does not imply endorsement by the U.S. Government.

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Availability of data and materials
The R code to perform the methods developed here is demonstrated in the additional file 2 available on the journal webpage. Additionally, example datasets are provided to run the code. Data and R code are also available at https://github.com/KurtHeim/Heim-et-al-2023-Animal-Biotelemetry

Declarations

Ethics approval and consent to participate
Fish were collected and sampled by USFWS according to accepted guidelines for the use of fish in research (AFS, AIFRB, & ASIH, 2014).

Consent for publication
Not applicable.

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

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