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FEATURED PAPER

Quantifying Uncertainty in Aquatic Telemetry: Using Received Signal Strength to Estimate Telemetry Error

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Abstract
Telemetry error is not regularly considered in aquatic studies; however, when it is considered, it is generally treated as a static value despite high variation that can occur even within a single tracking event. We describe a simple procedure for using received signal strength (RSS) to estimate telemetry error. We recorded the RSSs of ground- and air-based detections of large (11 g; 11 × 59 mm) and small (8 g; 11 × 43 mm) 172-MHz radio transmitters across a range of distances. Received signal strength was an excellent predictor of the distance to transmitter for ground tracking detections (large transmitter: r^2 = 0.98; small transmitter: r^2 = 0.97) and a fair predictor for aerial detections (large transmitter: r^2 = 0.49; small transmitter: r^2 = 0.57). We also manipulated transmitter antenna lengths and unexpectedly found that both transmitters performed better with shorter antennas relative to factory lengths. With calibrated models relating RSS to the distance to transmitter, RSSs from field-collected data can be used to approximate telemetry error and draw spatial confidence areas around location estimates for analysis and interpretation. During a concurrent movement study, we estimated telemetry error for 2,436 detections of fish at large. Ground tracking error estimates ranged from 1 to 131 m (median = 24 m), and aerial error estimates were most often less than 300 m but were as high as 1 km. The benefits of representing telemetry data as spatial confidence areas guided by the RSS of each detection are discussed. With appropriate caution, this method will provide a more robust alternative to the assumption that error is constant, negligible, or both.

Active transmitters used in radiotelemetry and acoustic telemetry have played an important role in our understanding of fish movement, habitat use, and passage abilities, contributing greatly to both applied and basic fisheries research. They can be detected from long distances, in some cases greater than 1 km (Freund and Hartman 2002; Eiler 2012), making them ideal for long-ranging organisms and those found in environments not conducive to detection with other methods. Furthermore, high detection rates of active transmitters can reduce the sample size of individuals needed to estimate demographic parameters relative to passive transmitters (McMichael et al. 2010). Although the ability to detect organisms from long distances is advantageous, careful attention to spatial accuracy is required.

Telemetry error is inevitable when using active transmitters to estimate locations of fish and includes two components. Animal location error is the difference between the true location of the animal and the estimated location, and mapping error is generated when translating locations to spatial coordinates (Rogers and White 2007). Global Positioning System (GPS) units have greatly reduced

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mapping error, and with differential correction of GPS coordinates, mapping error can be negligible (Roberts and Rahel 2005). Assessing animal location error is more challenging because it is influenced by equipment (Freund and Hartman 2002; Beeman et al. 2007), methods used in tracking and estimating locations (Roberts and Rahel 2005; Taylor and Litvak 2015), variation in environmental conditions (Peters et al. 2008), and personnel experience. Because telemetry error ranges from several to hundreds of meters (Roberts and Rahel 2005; Taylor and Litvak 2015; Lincoln et al. 2016), it is an important consideration when making inferences from telemetry data sets.

High telemetry error can obscure or bias biological conclusions (White and Garrott 1986; Montgomery et al. 2010, 2011), and failure to account for error can lead to subjective or inconsistent interpretation of the data (Figure 1). For example, a time series of telemetry locations for a fish is often represented by points (e.g., exact locations) in a GIS and is used to estimate parameters of interest, such as reach assignment, distance moved, or diel patterns in movement (Rogers and White 2007). If telemetry error is high, the potential for incorrect reach assignments or high error in movement calculations is also high (Figure 1). As the number of data points and spatial resolution of research questions increase, so does the potential for high propagation of error that could influence conclusions (Montgomery et al. 2011). This is especially true in studies using mobile tracking methods (as opposed to fixed telemetry receivers) since error is likely to vary considerably and the fish are often tracked over long distances and long periods of time.

Despite consistent reminders of the importance of considering telemetry error (James et al. 2003; Cooke et al. 2004; Roberts and Rahel 2005; Rogers and White 2007; Koehn et al. 2011; Montgomery et al. 2011), it is not regularly calculated and incorporated into the analysis of telemetry data in fisheries studies. In October 2017, we conducted a literature review using the Web of Science to identify all papers including the keyword "telemetry" that were published between 2010 and 2017 in the *North American Journal of Fisheries Management* and *Transactions of the American Fisheries Society*. From the results, we identified studies that used mobile tracking to record locations of fish. Of the 32 studies meeting these criteria, only 11 (34%) reported an estimate of telemetry error. In the studies that did perform some error measurement, it was often unclear how spatial uncertainty was incorporated into analysis and inferences made from the data. We believe that telemetry error is not more widely addressed in mobile telemetry studies because error is considered small relative to the context of the research question and because simple and robust methods of estimating and incorporating telemetry error are not available. In contrast to fixed acoustic and radio applications (where error seems to be considered more often), we are unaware of any automated software programs or published methods (e.g., Li et al. 2015; Harbicht et al. 2017) that produce error estimates from mobile tracking data. In fact, two of the most widely referenced books on analysis of fisheries data both advise that telemetry error is important, but these books provide little guidance on how to measure it or how to incorporate uncertainty into the analysis and interpretation of telemetry data (Rogers and White 2007; Adams et al. 2012).

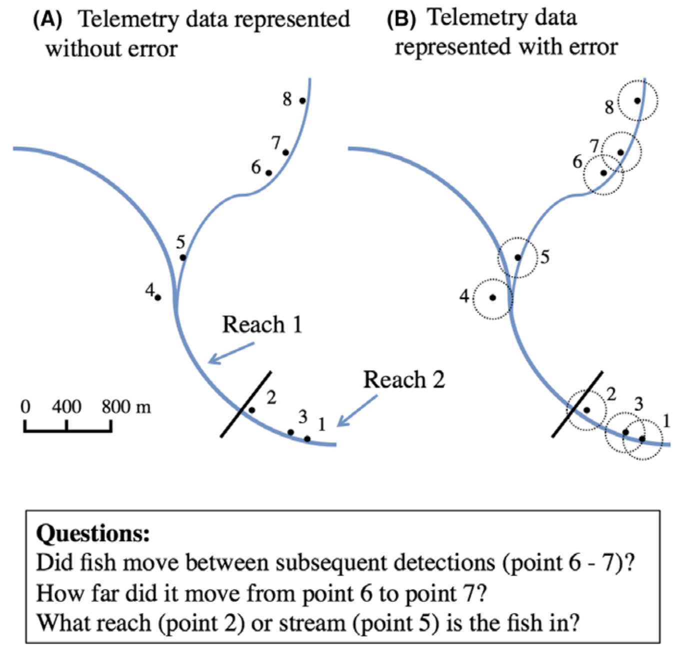

FIGURE 1. Typical treatment of telemetry data (eight aerial telemetry location estimates for an individual fish) plotted **(A)** as exact points and **(B)** with a 200-m radius to represent spatial error. Consider the listed questions and how conclusions may differ based on the different depictions of the data set.

We describe a method for estimating telemetry error from received signal strength (RSS), compatible with both acoustic telemetry and radiotelemetry, as well as a framework for incorporating error estimates into analysis. Traditionally, RSS was represented by the audible volume of "pings" or "beeps" made by telemetry receivers. More recently, the numerical output of RSS in modern telemetry equipment has proven to be a valuable piece of data. Received signal strength can be used to estimate activity patterns of aquatic animals (Ryan et al. 2008) and estimate linear stream position using an array of stationary receivers (Harbicht et al. 2017), and it is strongly related to the distance to the transmitter (Cocherell et al. 2010). Because of this relationship, RSS can be used as an indicator of telemetry error (Cocherell et al. 2010). We detail a simple experimental procedure to calibrate the relationship between RSS and the distance to transmitter by using ground- and air-based detection methods, and we describe how this method can be used to estimate telemetry error from detections of tagged fish at large. This calibration procedure can also be used to optimize components of the telemetry system by recording RSS at fixed distances and varying a single telemetry component. We demonstrate this procedure by testing how transmitter size and antenna length influenced the RSS–distance-to-transmitter relationship. Provided with error estimates, we propose a general framework for analysis of imprecise telemetry data that explicitly incorporates telemetry error into inferences made from the data.

METHODS

Representing telemetry error: from points to polygons.— We suggest representing estimates of fish locations as polygons rather than points during analysis because points convey a level of accuracy that is unlikely to be achieved in typical telemetry studies (Figure 1). A location estimate (usually GPS coordinates) and an estimate of telemetry error (proximity of the receiver to the fish) are required for this approach. If telemetry error is assumed to be omnidirectional, then this can be represented as a polygon, defined by a point (GPS coordinates) and a buffer with the radius equal to the estimated error. If polygons are considered the units of analysis, inferences drawn from them will explicitly incorporate telemetry error and will provide consistency in data interpretation. This study offers a method that can be used to estimate an appropriate radius length; however, even if telemetry error estimates are made with other methods, this general framework for representation and analysis of the data will still be applicable.

Study site.— Experiments were conducted during summer 2016 in the Lamar River, Wyoming, and its largest tributary, Slough Creek. The Lamar River (mean annual discharge = 25 m^3/s; U.S. Geological Survey gauging station 06188000) flows 78 km to its confluence with the Yellowstone River. At the sites where we conducted experiments, bank-full widths in the Lamar River and Slough Creek were about 40 and 30 m, respectively. This experimental study was conducted in conjunction with a movement study of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*. Aerial- and ground-based telemetry detections from this study are used to demonstrate the workflow involved in the application of this method. Data were collected mostly from low- to mid-elevation sites on the Lamar River and Slough Creek (bank-full widths ranging from 20 to 80 m) but were also obtained from tributaries (bank-full widths ranging from 1 to 30 m).

Ground tracking and antenna length testing.— Field experiments were conducted to determine (1) how well the distance to transmitter could be predicted from RSS using ground-based tracking methods and (2) how transmitter size and transmitter antenna length influenced RSS. Two models of radio transmitter (Lotek Wireless, Inc.) were tested: MCFT2-3FM (11 g; 11 × 59 mm) and MCFT2-3BM (8 g; 11 × 43 mm), which we henceforth refer to as the "large" and "small" transmitters, respectively. Transmitters were attached to 3-cm-diameter, polyvinyl chloride pipes that were cross-sectioned (to avoid shielding the antenna), mounted on a cinder block, and sunk to a depth of 1 m in the Lamar River. A 100-m-long transect was set up with 16 marked points (2, 4, 6, 8, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 90, and 100 m) that extended from the submerged transmitters. A three-element Yagi antenna (168–172 MHz) was mounted on a tripod at breast height, and a Lotek Wireless SRX 800 receiver was used to make detections of the transmitters at each of the 16 points along the transect. The RSS of five consecutive detections was recorded for each transmitter at each of the distances on the transect (total n = 80 detections per transmitter). Initially, this entire sequence was completed for submerged transmitters with factory-length antennas of 43.5 cm.

To determine how transmitter antenna length influenced RSS, the entire sequence of RSS measurements along the transect was repeated eight more times. At each iteration, the two transmitters were removed, the antennas were trimmed, and the transmitters were placed back into the exact location and orientation in the water. Nine antenna lengths were tested, ranging from factory length (43.5 cm) to 19 cm (43.5, 40.0, 37.0, 34.0, 31.0, 28.0, 25.0, 22.0, and 19.0 cm). The experiment took 11 h to complete; water temperature varied from 13.2°C to 14.4°C, and conductivity was 110 μS/cm. All of the equipment used in these experiments exactly matched the equipment used in our concurrent fish movement study.

Aerial tracking.— An additional test was performed with aerial telemetry. Four transmitters were tested: the two transmitters (one small, one large) that were previously deployed in the Lamar River with antenna lengths of 19 cm; and two additional transmitters (one small, one large) that were placed 1 m deep in Slough Creek. We tested transmitter antenna lengths of 21 cm for Slough Creek because this was the average length of antennas already deployed in live fish. During flights, we used two Lotek Wireless SRX 800 receivers: one was connected to a three-element, 168–172-MHz Yagi antenna, and the other was connected to a three-element, 215–220-MHz Yagi antenna that simultaneously scanned for transmitters. Two different receiving antenna models were used as a matter of convenience since the 215–220-MHz antenna was already affixed to the aircraft we contracted for flights, and we provided the 168–172-MHz antenna specifically for our fish movement study. Both performed well upon initial testing; therefore, we used them both simultaneously for tracking fish in our study. Although this introduced additional variation into our experimental data, it reflected the methods used in our study, so it was appropriate to calibrate our models with similar methods. Test transmitters were detected multiple times while several passes were flown at about 100 m above the river. The GPS coordinates of the aircraft, transmitter ID, and RSS of each detection were digitally recorded by the receiver. The flat-ground horizontal distance from the aircraft position at the time of detection to the known location of the test transmitters was calculated for each detection. The final data set included 99 detections of the two large transmitters and 62 detections of the two small transmitters.

Data analysis.— Separate models that related RSS to the distance to transmitter were developed for each transmitter size and detection method. The aim of this approach was to calibrate models as closely as possible to the methods and equipment being used in our concurrent fish movement study so that RSSs from live-fish detections could eventually be used to estimate distances to the fish. We therefore only included detections from transmitters with antenna lengths of 19–28 cm from the ground-based tracking experimental data, which reflected the range of transmitter antenna lengths deployed in live fish. All detections of the four test transmitters collected during telemetry flights conducted on July 20 and August 15, 2016, were used for the aerial model (antenna lengths = 19 and 21 cm). The relationship between RSS and the distance to transmitter was nonlinear, so we explored log transformations with linear regression and second-order polynomial regression. Examination of fitted curves, patterns of residuals, and r^2 values were used for model validation.

To assess the influence of transmitter antenna length on RSS, we first plotted RSS as a function of antenna length for each transmitter type at each transect distance. We reviewed these 16 plots visually to explore trends. To display the overall effect of changing transmitter antenna length on RSS, we centered and scaled the RSS values within each subset for each transmitter type so that RSS values could be compared across all transect distances. Scaling was accomplished by calculating the mean and SD of RSS values within a subset and then subtracting the mean from each value and dividing by the SD. All values were plotted together for each transmitter type, and a locally weighted scatterplot smoother was fitted to the data by using R (R Core Team 2017).

RESULTS

Distance-to-Transmitter Models

Received signal strength decreased as the distance to transmitter increased in both ground and aerial tests (Figure 2). Large transmitters consistently had higher RSSs at a given distance to transmitter than small transmitters for both ground and aerial tracking. For the reduced ground-based tracking data set (detections for transmitter antenna lengths of 19–28 cm), RSS averaged 186 ± 5 (mean ± SD) for the large transmitter at a 2-m distance and averaged 165 ± 11 for the small transmitter at 2 m. At a 10-m distance, the mean RSS was 158 ± 7 for the large transmitter and 137 ± 5 for the small transmitter. At a distance of 100 m, the average RSS decreased to 68 ± 10 and 56 ± 7 for the large and small transmitters, respectively.

Differences between large and small transmitter performance were pronounced in the aerial tracking tests (Figure 2). The large transmitter was detected from up to 1,515 m away, whereas the maximum detection distance for the small transmitter was 888 m. There was considerable variation in RSS values at a given distance to transmitter. The average RSS of detections made within 200 m was 89 ± 19 (mean ± SD) for the large transmitter and 77 ± 19 for the small transmitter. The average RSS of detections made between 200 and 600 m was 64 ± 16 for the large transmitter and 50 ± 13 for the small transmitter. The small transmitter was only detected three times at a distance greater than 800 m, whereas the larger transmitter was detected 18 times at such distances.

There was a strong nonlinear relationship between the distance to transmitter and RSS that was best modeled with a second-order polynomial regression of the form

$$\log_e(\text{distance to transmitter}) = \beta_0 + \beta_1\text{RSS} + \beta_2\text{RSS}^2.$$

The $\log_e$ transformation of the response variable was required because of nonconstant variance in residuals, which increased with increasing distance to the transmitter. Received signal strength explained 98% and 97% of the variation in distance to transmitter for large and small transmitters, respectively, using the ground-based tracking data, and 49% and 57% of the variation for the aerial detection data set (Figure 2). Using the ground tracking models, the RSS-predicted distance to transmitter averaged 4 ± 3 m from actual distances (both for large and small transmitters), whereas aerial model predictions averaged 182 ± 156 m from actual distances for the large transmitters and 118 ± 115 m for the small transmitters.

Transmitter Antenna Length Effects

Longer transmitter antennas did not result in higher RSSs, and the relationship between RSS and antenna length differed for the large and small transmitters (Figure 3). We calculated mean RSS for each antenna length at each of the 16 transect distances to determine how changes in antenna length influenced RSS at a given distance to transmitter. The large transmitter performed best with an antenna of 22 cm and consistently performed

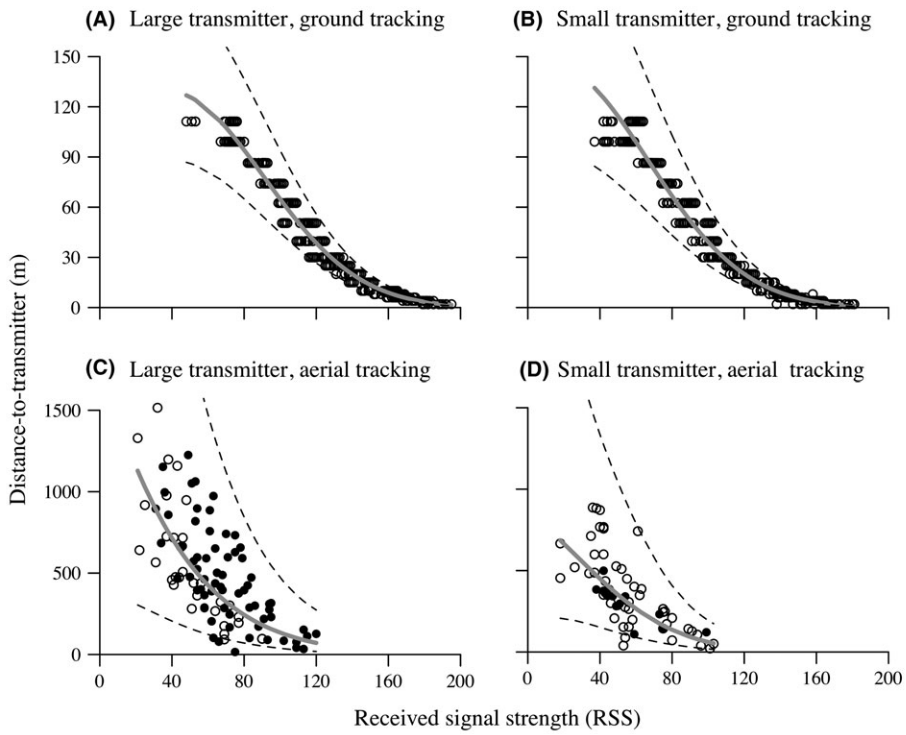

FIGURE 2. Relationship between the distance to transmitter and the received signal strength (RSS) based on experimental data from **(A)** ground tracking of the large transmitter; **(B)** ground tracking of the small transmitter; **(C)** aerial tracking of the large transmitter; and **(D)** aerial tracking of the small transmitter. Gray lines represent polynomial model estimates, and dashed lines represent 95% prediction intervals. The ground tracking experiment used transmitters with antenna lengths ranging from 19 to 28 cm. In panels C and D, the filled points indicate data from transmitters in the Lamar River, Wyoming (antenna length = 19 cm), and the open points represent data from transmitters in Slough Creek (antenna length = 21 cm).

poorly with long antennas, including the factory length of 43.5 cm (Table 1; Figure 3). The difference between the best antenna length (e.g., the length with highest mean RSS) and the worst antenna length (that with the lowest RSS) at a given transect distance ranged from 18 to 36 RSS units and averaged 26 units overall. How an RSS difference of 26 units might influence distance-to-transmitter estimates (based on our fitted model) depends on the magnitude of RSS. Received signal strengths of 140 and 176 would result in distance-to-transmitter estimates of 19.8 and 4.2 m, respectively, whereas RSSs of 80 and 106 would result in distance-to-transmitter estimates of 94.2 and 56.4 m.

An antenna length of 37 cm consistently performed best for the small transmitter (Table 1; Figure 3). The difference between the best and worst antenna lengths at a given transect distance ranged from 12 to 33 RSS units and averaged 20 units. Given our fitted models, RSSs of 140 and 160 would result in distance-to-transmitter estimates of 3.5 and 9.0 m, respectively, and RSSs of 80 and 100 would result in estimates of 39.2 and 66.7 m.

DISCUSSION

We evaluated correlations between RSS and the distance to transmitter, and found strong relationships that can be used to estimate telemetry error from field-based detections. Using ground-based tracking, RSS explained 98% and 97% of the variation in the distance to transmitter for large and small transmitters, respectively; using aerial tracking, RSS explained 49% and 57% of the variation. The two transmitters—which differed only in battery size—performed quite differently. The larger transmitter produced higher RSSs across all detection distances using ground tracking, was detectable from nearly twice as far from an aircraft, and performed best with a short (22 cm) antenna length in our test conditions. In contrast, the smaller transmitter performed best at intermediate antenna lengths and poorly at the factory length of 43.5 cm. Below, we describe how these results can be interpreted and used to estimate telemetry error from field-based fish relocations, how this experimental procedure can be used to guide and optimize equipment choices, and important precautions to take when using this approach.

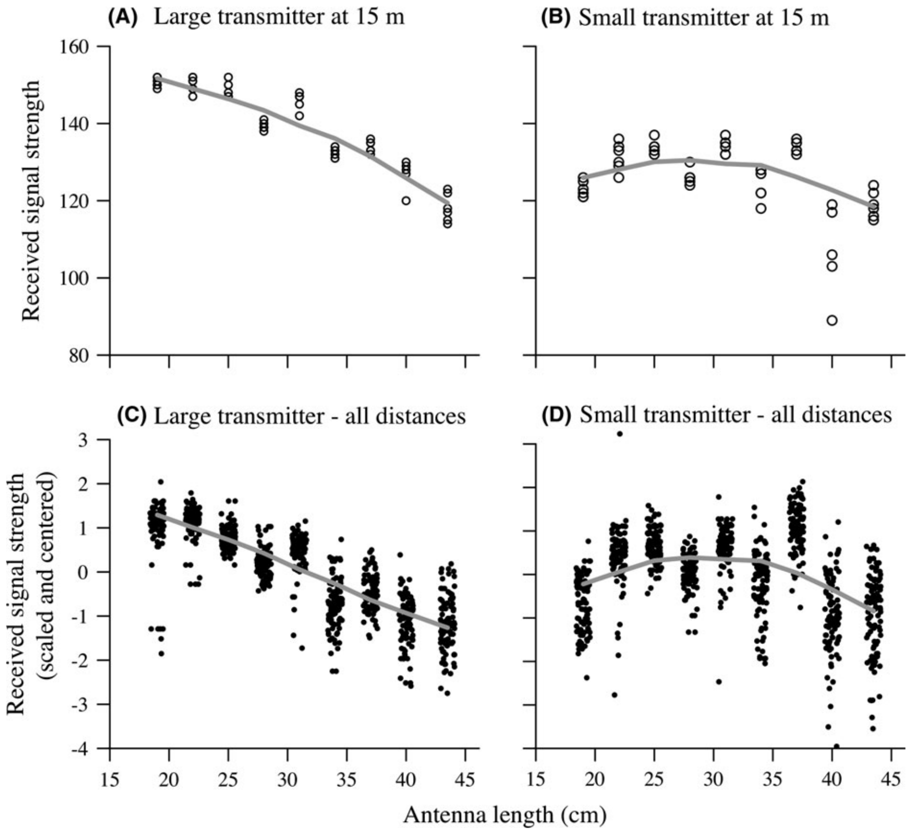

FIGURE 3. Relationship between received signal strength (RSS) and transmitter antenna length for **(A)** the large transmitter from detections made at a distance of 15 m; **(B)** the small transmitter at a distance of 15 m; **(C)** the large transmitter, incorporating measurements collected at all transect distances (2–100 m) using scaled and centered measurements within transect distances; and **(D)** the small transmitter at all transect distances using scaled and centered measurements.

TABLE 1. Performance of different transmitter antenna lengths at 16 different transect distances ranging from 2 to 100 m. Values represent the proportion of trials (16 total) in which a transmitter length performed best (highest RSS) or worst (lowest RSS), as determined by the mean RSS of five detections.

	Antenna length (cm)								
Transmitter size and RSS value	19	22	25	28	31	34	37	40	43.5
Large transmitter									
Highest RSS	0.44	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lowest RSS	0.06	0.00	0.00	0.00	0.00	0.13	0.00	0.31	0.50
Small transmitter									
Highest RSS	0.00	0.06	0.13	0.00	0.19	0.00	0.62	0.00	0.00
Lowest RSS	0.25	0.06	0.00	0.00	0.00	0.13	0.00	0.31	0.25

Application of Received Signal Strength Models to Estimate Telemetry Error

Homing or the "antenna reduction method" appears to be the most common and accurate mobile tracking method (Eiler 2012) used in acoustic telemetry and radiotelemetry. The basic principle is that an observer physically approaches the transmitter and estimates the animal location where the highest RSS is obtained (Koehn et al. 2011). In fact, decreasing the distance between the transmitter and the receiving antenna is the best way to reduce telemetry error (Koehn 2012). In wildlife telemetry, there are complications to this approach, such as safety concerns with physically approaching large carnivores, which has led to the popularity of triangulation. Unfortunately, triangulation is subject to high telemetry error (White and Garrott 1986), is time intensive, and is further complicated in aquatic studies by signal deflection at the water's surface (Kuechle and Kuechle 2012). If homing is to be used to estimate fish locations, then the distance to transmitter is essentially the same as the location error component of telemetry error, and our RSS models will be useful.

Received signal strength models can be used to convert field-based RSS values into distance-to-transmitter estimates and to represent telemetry error. If one estimates that a fish is located at GPS position A, but the RSS indicates that the fish is still approximately 10 m away (RSS = 137 or 158 in our case), then 10 m is a good estimate for telemetry error. In other words, the real fish location is probably within a 10-m radius of the estimated point (Figure 4). This approach involves several practical oversimplifications. First, because a Yagi antenna is directional, the 10-m estimate is also directional in the compass bearing in which the Yagi antenna is oriented. Attempting to account for this with field-measured compass bearings and projected points is inadvisable and likely to involve issues similar to those experienced with triangulation (Koehn et al. 2011). Second, the experimentally calibrated relationship between RSS and the distance to transmitter does not capture the nuances of field conditions (discussed in detail in the Precautions and Avenues for RSS Model Improvement section). Nonetheless, we believe that this approach is still useful—a detection with an RSS of 180 provides a greater degree of spatial confidence than a detection with an RSS of 30, regardless of the oversimplifications mentioned and the precautions described later on. Detections with low RSS values are not necessarily poor data, but they should be interpreted differently than more accurate locations.

When the predictive power of an RSS model is low, it may be best to avoid making exact predictions for each data point and instead use a categorical approach. The high variation of our aerial test results and the high prediction error (118 and 182 m) suggest that a quantitative treatment (as described for ground-based results) may be inappropriate. Based on examination of the RSS–distance-to-transmitter relationship (Figure 3C, D), we could use a categorical rule-based cutoff approach (Figure 4). Although this may seem subjective, we feel that it represents an improvement over previous error estimates that consider air-based telemetry error to be a static value.

One could identify an RSS cutoff value that would satisfy the accuracy requirements indicated by the biological questions of the project. Ideally, this cutoff value would be identified before data collection so that field personnel could be instructed to achieve the desired RSS value during surveys. A calibrated RSS model could inform these decisions; for example, if our biological questions required 10-m accuracy, we could have chosen an RSS cutoff value of 158 for large tags and a cutoff of 137 for small tags. This approach could save considerable personnel time during tracking surveys because time spent achieving a spatial resolution not required by the research would be avoided. The monetary cost of collecting telemetry relocations is often substantial and underestimated (Winter 2000; cited by Koehn 2012), and with a clearly designated RSS target value, time could be saved during fieldwork. One could also exclude detections below a specified RSS value after the data have been collected (Ertel et al. 2017).

To demonstrate how these results can be used and how variable telemetry data can be, we provide a brief summary of data collected during the first two seasons of our Yellowstone Cutthroat Trout movement study (2015–2016) and highlight how this treatment of the data has been particularly useful. Between August 6, 2015, and October 22, 2016, we conducted 51 ground and 23 aerial telemetry surveys in the Lamar River drainage, resulting in 2,436 detections of 136 fish at large. This total includes only a single detection per fish per day, retaining the detection in which the highest RSS was achieved. We used the methods described above (Figure 4) to assign a telemetry error estimate to each detection based on method- and transmitter-specific RSS values. Before applying polynomial model predictions for ground-based tracking detections, RSS was constrained to within the range of the RSS values that were used to fit the models. This was done because predictions from polynomial functions can be inappropriate beyond the range of data used to fit them. Received signal strength and predicted telemetry error values varied considerably (Figure 5). Median ground tracking error was 24 m overall and was slightly lower for the small transmitter (average = 31 m; range = 1–131 m; median = 17 m) than for the large transmitter (average = 39 m; range = 2–126 m; median = 29 m; Figure 6). Overall, 69% of aerial detections were estimated to have an error of 300 m, 24% had an error of 500 m, 2% had an error of 800 m, and 5% had an error of 1 km (Figure 5). Primary factors precluding consistency in ground tracking accuracy were (1) the fish was on the opposite side of the river and could not be closely approached; (2) inadequate time and variable effort to home in on each transmitter during an exhausting field season; and (3) large-mammal encounters (primarily American bison *Bison bison*) during tracking surveys necessitated detours that led us farther away from the river. Lastly, as described in the Methods, the use of two different models of Yagi antenna from the aircraft likely contributed to the more variable RSS aerial-based data set.

1. How will experimental results be applied?

Ground tracking detections – polynomial model predictions

Aerial tracking detections – rule based
if (RSS >= 80) Error = 300 m
if (RSS >= 60 & RSS < 80) Error = 500 m
if (RSS < 60) Error = 1000 m

2. Apply results to field data

ID	Lat	Long	Method	RSS	Error_pred
1	-110.37	44.92	Air	90	300
2	-110.35	44.92	Ground	145	16.52
3	-110.33	44.92	Air	62	500
4	-110.32	44.93	Ground	67	111
5	-110.33	44.93	Air	84	300
6	-110.38	44.93	Air	45	1000

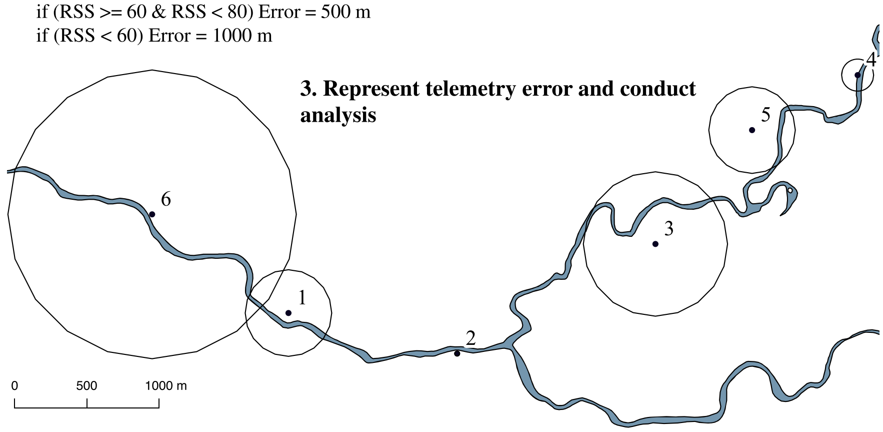

FIGURE 4. Workflow to incorporate telemetry error into aquatic studies. After conducting experiments to determine how received signal strength (RSS) is related to the distance to transmitter, one must determine how to apply results to field-collected data (step 1). After an approach is identified, telemetry error predictions (Error_pred) can be made for each detection (step 2; Lat = latitude; Long = longitude), and telemetry locations can be represented with polygons instead of points to perform analysis and make inferences (step 3). This workflow describes our approach for the larger transmitter; a similar approach was developed for the smaller transmitter, but we used RSS categories of ≥70, 70–50, and <50, with associated error estimates of 300, 500, and 800 m for air-based detections.

Our error estimates generally fell within the range previously reported, yet a small number of our estimates were quite large. Roberts and Rahel (2005) reported an average aerial-based telemetry error of 178 m and a range of 22–426 m; Fraley et al. (2016) reported accuracy within 500 m. For ground-based tracking, reported error ranges from less than 1 m to about 50 m (Broadhurst and Ebner 2007; Cocherell et al. 2010). In our data set, predicted ground and aerial location errors were sometimes as high as 100 m and 1 km, respectively. Because these estimates were based on tagged fish at large, we cannot be sure whether locational error was truly this high or whether these represented detections of particularly deep fish or instances in which transmitting antennas were shielded (by rocks, cover, etc.). Nonetheless, one of the benefits of our method is that these potentially high-error detections can be identified and still used in analysis (described below) rather than excluded. An average or upper boundary of error (e.g., accuracy to within a specified range) does not need to be determined for the entire data set since each data point receives a distinct error estimate based on RSS. Thus, highly accurate detections (which our data set also included) can be represented and analyzed without a loss of spatial accuracy information.

For data analysis and interpretation, we expressed each telemetry detection as a spatial confidence area, defined by a center and a radius equal to the estimated distance to transmitter (Figure 4). Several benefits of this representation relative to expressing data as exact points were readily apparent. First, determining whether a fish moved or not between subsequent detections was unambiguous. Actual movement could be distinguished from "apparent movement" (resulting from telemetry error) when spatial confidence areas did not overlap (Figures 1, 4). This was particularly useful for determining whether fish in remote locations that could only be tracked by aircraft were alive (i.e., dead fish do not move upstream) and also for assigning the spawning migration start date (DeRito et al. 2010). Prespawn fish often remained in the same location for months (many detections with overlapping confidence areas), but an initial spawning movement could be readily distinguished with this method. Second, spatial confidence areas helped to distinguish actual presence within a tributary from "apparent" presence in a tributary (e.g., Figure 1, point 5), in which case we could immediately follow up with ground tracking efforts to confirm location. Finally, we calculated spawning migration distance for each individual and were able to express this value as range that accounted for telemetry error and to perform statistical comparisons that were robust to the influence of telemetry error on conclusions.

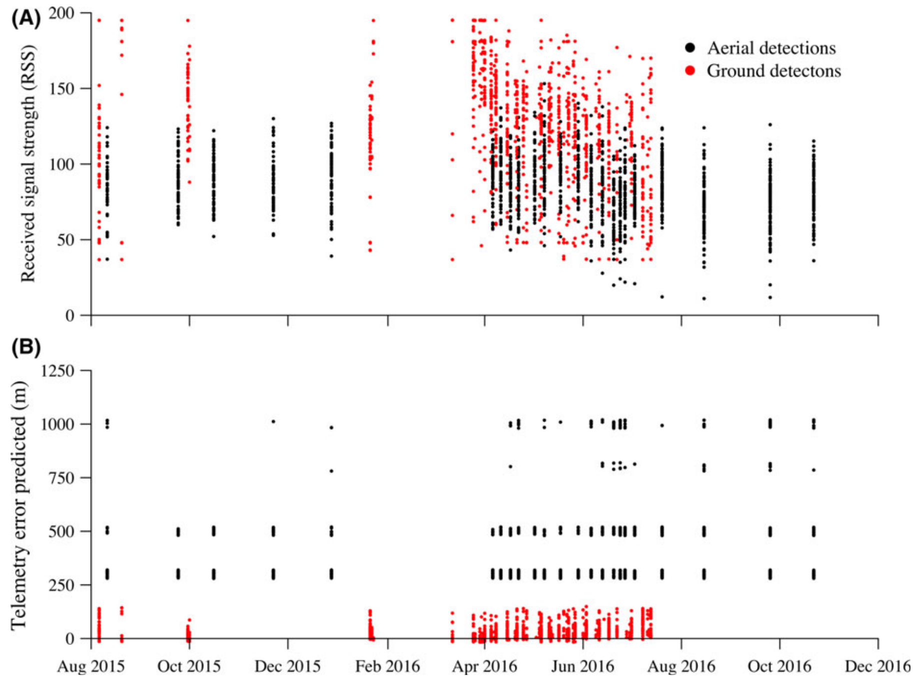

FIGURE 5. **(A)** Received signal strengths (RSSs) for 2,436 unique detections of 136 Yellowstone Cutthroat Trout that were radio tagged in the Lamar River watershed, Wyoming, during 2015 and 2016 and detected by using aerial- and ground-based methods; and **(B)** the estimated telemetry error associated with each of those detections using the models and methods described in Figure 5. In panel B, a small amount of variation was added in the *y*-axis so that overlapping points can be distinguished, as telemetry error estimates were categorical for aerial detections (300, 500, 800, or 1,000 m).

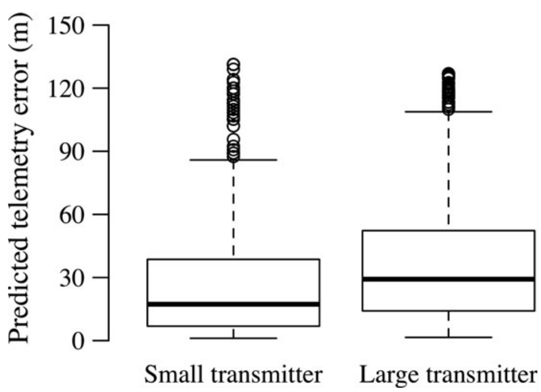

FIGURE 6. Distribution of ground tracking telemetry error predictions (from Figure 5) presented separately for the large and small transmitters. The horizontal line represents the median; the middle 50% of the data (25th to 75th percentiles) are within the box; whiskers indicate 1.5 times the interquartile range, values above this are shown as points.

Precautions and Avenues for Received Signal Strength Model Improvement

As our antenna length results indicate, there are many variables that might influence the relationship between RSS and the distance to transmitter, and such factors should be carefully considered. The lack of a consistent increase in RSS with antenna length was, however, unexpected. It is well known that external antennas have the potential to negatively influence swimming performance (Murchie et al. 2004), become tangled (Adams et al. 1998), or lead to infection at the exit wound (Knights and Lasee 1996), but we initially assumed that a shorter antenna length would decrease RSS (and detectability). However, we found that longer transmitter antennas did not increase RSS and that factory-length antennas were longer than necessary for our application. Transmitter size, shape, antenna material, and frequency all interact to influence the optimum antenna length for a given radio transmitter (Beeman et al. 2007; Peters et al. 2008; Kuechle and Kuechle 2012). Additionally, optimum antenna length will also be influenced by water chemistry (Beeman et al. 2007). Determining the optimal antenna length for a given transmitter by using theoretical calculations is possible (see Kuechle and Kuechle 2012 [their Appendix] for a detailed discussion) but is beyond the scope of general application by fisheries biologists. Our recommendation is to perform the “test” described here and trim antennas consistently to an optimal length prior to deployment. This would both optimize transmitter performance and lead to lower prediction error if RSS models are used to estimate telemetry error.

Telemetry projects often cost considerable amounts of money (Rogers and White 2007), and small technical differences in equipment can increase performance and the overall success of a telemetry project (Evans and Stevenson 2012). For example, an optimized transmitter antenna might lead to a greater number of relocations and an overall higher-quality data set. Using this experimental design and RSS as a benchmark of performance, other aspects of the telemetry system (receiving antenna type, receiver settings, etc.) could be empirically tested to optimize performance prior to beginning a project. Testing the RSS at fixed transmitter distance points can also provide a valuable measurement tool for troubleshooting equipment problems.

Care should be taken when extrapolating the results of an RSS experimental model to transmitters deployed in live fish because environmental conditions are constantly changing. Our models are calibrated to a transmitter in fixed conditions and with equipment specific to our study. Variation in environmental conditions or equipment will likely alter the relationship between RSS and the distance to transmitter (Freund and Hartman 2002; Rogers and White 2007; Peters et al. 2008), and telemetry error estimates derived from RSS models could be inaccurate. It is important to recognize that each study using this method would require an experimental calibration with the equipment and conditions specific to that project. The experiment could be conducted annually during training of new technicians or field staff, providing valuable data for an RSS model as well as supervised experience for fieldworkers. Additionally, the accuracy of the GPS or mapping method (e.g., mapping error) will vary from study to study and should also be estimated and potentially added to the estimate of location error.

Perhaps the most influential factor is transmitter depth, which can make it challenging to home in closely to a fish and which exponentially decreases the reception range of transmitters because of signal attenuation (Freund and Hartman 2002). Fish located in larger and deeper waterbodies will be inherently more difficult to approach closely than fish in smaller and shallower waterbodies. In small streams, homing techniques can result in sub-meter accuracy (Broadhurst and Ebner 2007), but the large size of our study system (and time constraints) prevented us from consistently attaining this level of accuracy. When we tracked fish spawning in small tributaries, we could sometimes approach within 1 m, achieving an RSS of over 200. There is probably a correlation between stream size and telemetry error, but our method of recording RSS effectively captured error variation without a need to measure physical variables (although see Discussion below, as these could help to refine estimates). Aside from accessibility, variation in transmitter depth is also an important consideration since it will influence the RSS–distance-to-transmitter relationship because of attenuation. With this in mind, we parameterized our RSS models under conditions most relevant for our field situation and project goals. Our ongoing study focuses on spawning location and timing of Yellowstone Cutthroat Trout, which generally spawn at depths less than 1 m (Gresswell 2011). We therefore calibrated models with transmitters at a depth of 1 m to reflect the conditions under which our most important detections would be made. An important point is that if a fish was deeper than 1 m, signal attenuation would reduce the RSS, and therefore the distance-to-transmitter estimates using our calibrated models would also increase. In other words, our telemetry error estimates will conservatively large when fish are in deep water. We consider this to be better than overconfidence in spatial accuracy, and we suggest that the conditions used for model calibration should be carefully considered.

In highly variable environments or in large lakes where fish inhabit a wide range of depths, an RSS model could be calibrated under a range of conditions, and these variables could be included as additional model covariates. For example, replicating this experiment at multiple depths, turbidity levels, or conductivity levels could inform a more nuanced RSS model. These environmental conditions could be recorded during field tracking and used in estimation of telemetry error. Especially useful would be incorporating data from transmitters that provide information on fish depth (Cooke et al. 2004) to disentangle the effects of changing environmental conditions on observed RSS values in live fish. For example, a low RSS for a tagged Lake Trout *Salvelinus namaycush*, which are often found deep in the water column (Koel et al. 2005), could reflect an accurate detection of a fish in a deep area or an inaccurate detection of a fish in a shallow area. With an RSS model calibrated at different depths and given known depth information from the fish, a more accurate estimation of telemetry error could be made.

Active transmitters continue to be valuable tools in aquatic research, and we recommend explicitly incorporating estimates of telemetry error into analysis as others have done (James et al. 2003; Cooke et al. 2004; Roberts and Rahel 2005; Koehn et al. 2011; Montgomery et al. 2011). Along with our recommendation, we provide a simple method for estimating telemetry error. Received signal strength models can inform detection-specific telemetry error estimates, providing a better understanding of the spatial accuracy and variability of telemetry systems. Incorporating these estimates into analysis will lead to more repeatable and robust biological inferences regarding aquatic animal habitat use and movement.

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REFERENCES

Adams, N. S., J. W. Beeman, and J. H. Eiler. 2012. Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.

Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly. 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile Chinook Salmon. Transactions of the American Fisheries Society 127:128–136.

Beeman, J. W., N. Bower, S. Juhnke, L. Dingmon, M. Van Den Tillaart, and T. Thomas. 2007. Effects of antenna length and material on output power and detection of miniature radio transmitters. Hydrobiologia 582:221–229.

Broadhurst, B., and B. Ebner. 2007. An improved technique for small-scale radio-tracking of crayfish and benthic fishes in upland streams. Transactions of the American Fisheries Society 136:423–427.

Cocherell, S. A., G. J. Jones, J. B. Miranda, D. E. Cocherell, J. J. Cech, L. C. Thompson, and A. P. Klimley. 2010. Distribution and movement of domestic Rainbow Trout, *Oncorhynchus mykiss*, during pulsed flows in the South Fork American River, California. Environmental Biology of Fishes 89:105–116.

Cooke, S. J., S. G. Hinch, M. Wikelski, R. D. Andrews, L. J. Kuchel, T. G. Wolcott, and P. J. Butler. 2004. Biotelemetry: a mechanistic approach to ecology. Trends in Ecology and Evolution 19:334–343.

DeRito, J. N., A. V. Zale, and B. B. Shepard. 2010. Temporal reproductive separation of fluvial Yellowstone Cutthroat Trout from Rainbow Trout and hybrids in the Yellowstone River. North American Journal of Fisheries Management 30:866–886.

Eiler, J. H. 2012. Tracking aquatic animals with radio telemetry. Pages 163–204 *in* N. S. Adams, J. W. Beeman, and J. H. Eiler, editors. Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.

Ertel, B. D., T. E. McMahon, T. M. Koel, R. E. Gresswell, and J. C. Burckhardt. 2017. Life history migrations of adult Yellowstone Cutthroat Trout in the upper Yellowstone River. North American Journal of Fisheries Management 37:743–755.

Evans, S. D., and J. R. Stevenson. 2012. Optimization of radio telemetry receiving systems. Pages 139–162 *in* N. S. Adams, J. W. Beeman, and J. H. Eiler, editors. Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.

Fraley, K. M., J. A. Falke, R. Yanusz, and S. Ivey. 2016. Seasonal movements and habitat use of potamodromous Rainbow Trout across a complex Alaska riverscape. Transactions of the American Fisheries Society 145:1077–1092.

Freund, J. G., and K. J. Hartman. 2002. Influence of depth on detection distance of low-frequency radio transmitters in the Ohio River. North American Journal of Fisheries Management 22:1301–1305.

Gresswell, R. E. 2011. Biology, status, and management of the Yellowstone Cutthroat Trout. North American Journal of Fisheries Management 31:782–812.

Harbicht, A. B., T. Castro-Santos, W. R. Ardren, D. Gorsky, and D. J. Fraser. 2017. Novel, continuous monitoring of fine-scale movement using fixed-position radio telemetry arrays and random forest location fingerprinting. Methods in Ecology and Evolution 8:850–859.

James, D. A., J. W. Erickson, and B. A. Barton. 2003. Using a geographic information system to assess the accuracy of radio-triangulation techniques for fish telemetry. North American Journal of Fisheries Management 23:1271–1275.

Knights, B. C., and B. A. Lasee. 1996. Effects of implanted transmitters on adult Bluegills at two temperatures. Transactions of the American Fisheries Society 125:440–449.

Koehn, J. D. 2012. Designing studies based on acoustic or radio telemetry. Pages 21–44 *in* N. S. Adams, J. W. Beeman, and J. H. Eiler, editors. Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.

Koehn, J. D., J. H. Eiler, J. A. McKenzie, and W. G. O'Connor. 2011. An improved method for obtaining fine-scale location of radio tags when tracking by boat. Pages 379–384 *in* J. McKenzie, B. Parsons, A. Seitz, R. Kopf, M. Mesa, and Q. Phelps, editors. Advances in fish tagging and marking technology. American Fisheries Society, Symposium 76, Bethesda, Maryland.

Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and D. L. Mahony. 2005. Nonnative Lake Trout result in Yellowstone Cutthroat Trout decline and impacts to bears and anglers. Fisheries 30(11):10–19.

Kuechle, V. B, and P. J. Kuechle. 2012. Radio telemetry in fresh water: the basics. Pages 91–137 *in* N. S. Adams, J. W. Beeman, and J. H. Eiler, editors. Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.

Li, X., Z. Deng, J. J. Martinez, T. Fu, P. S. Titzler, J. S. Hughes, M. A. Weiland, R. S. Brown, B. A. Trumbo, M. L. Ahmann, and J. F. Renholds. 2015. Three-dimensional tracking of juvenile salmon at a mid-reach location between dams. Fisheries Research 167:216–224.

Lincoln, K. J., D. D. Aday, and J. A. Rice. 2016. Seasonal mortality and movement patterns of White Bass in a southeastern U.S. reservoir. Transactions of the American Fisheries Society 145:1035–1046.

McMichael, G. A., M. B. Eppard, T. J. Carlson, J. A. Carter, B. D. Ebberts, R. S. Brown, M. Weiland, G. R. Ploskey, R. A. Harnish, and Z. D. Deng. 2010. The juvenile salmon acoustic telemetry system: a new tool. Fisheries 35:9–22.

Montgomery, R. A., G. J. Roloff, and J. M. Ver Hoef. 2011. Implications of ignoring telemetry error on inference in wildlife resource use models. Journal of Wildlife Management 75:702–708.

Montgomery, R. A., G. J. Roloff, J. M. Ver Hoef, and J. J. Millspaugh. 2010. Can we accurately characterize wildlife resource use when telemetry data are imprecise? Journal of Wildlife Management 74:1917–1925.

Murchie, K. J., S. J. Cooke, and J. F. Schreer. 2004. Effects of radio-transmitter antenna length on swimming performance of juvenile Rainbow Trout. Ecology of Freshwater Fish 13:312–316.

Peters, L. M., U. G. Reinhardt, and M. A. Pegg. 2008. Factors influencing radio wave transmission and reception: use of radiotelemetry in large river systems. North American Journal of Fisheries Management 28:301–307.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: https://www.R-project.org/. (September 2018).

Roberts, J. J., and F. J. Rahel. 2005. Accuracy of aerial telemetry in fisheries studies. North American Journal of Fisheries Management 25:660–666.

Rogers, K., and G. C. White. 2007. Analysis of movement and habitat use from telemetry data. Pages 625–676 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Ryan, K. A., B. C. Ebner, and R. H. Norris. 2008. Radio-tracking interval effects on the accuracy of diel scale crayfish movement variables. Freshwater Crayfish 16:87–92.

Taylor, A. D., and M. K. Litvak. 2015. Quantifying a manual triangulation technique for aquatic ultrasonic telemetry. North American Journal of Fisheries Management 35:865–870.

White, G. C., and R. A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. Journal of Wildlife Management 50:509–513.

Winter, J. D. 2000. Designing telemetry studies and other technical and analytical considerations. Pages 229—248 *in* J. H. Eiler, D. J. Alcorn, and M. R. Neuman, editors. Biotelemetry 15: proceedings of the 15th International Symposium on Biotelemetry. International Society on Biotelemetry, Wageningen, The Netherlands.