RESEARCH

A method of spatial correction for acoustic positioning biotelemetry

C. Charles[1,2*], D. M. Gillis[1], L. E. Hrenchuk[2] and P. J. Blanchfield[2,3]

Abstract

Background: It has been stated that there is a certain amount of intrinsic error inherent in all remote sensing methods, including acoustic telemetry, which has gained popularity in both freshwater and marine environments to record fine-scale movements over small spatial scales. We performed stationary tag trials on three freshwater lakes where we placed transmitters at known locations around the lakes and used radio-acoustic positioning and telemetry (RAPT) system-derived location data to assess the measurement and systematic biases of the system. We used a geostatistical technique called ordinary kriging to deal with the systematic errors and a state-space model to represent the measurement error of the data. Furthermore, we applied the kriging correction and a continuous-time correlated random walk model in a state-space framework to predict locations of a lake trout.

Results: The stationary tagging trials produced a complex pattern of spatial error within each lake that could not properly be accounted for by a simple filtering process. Using fivefold cross-validation, positioning error was reduced from 93 to 99 % in three small lakes. We also identified tag depth as a potential source of measurement error. The application of a state-space model resulted in the contraction of home ranges of lake trout by 10–32 % and a 3–32 % reduction in total distance travelled.

Conclusions: Our results indicate that the systematic biases were a greater source of error than the measurement errors using a RAPT system. Consequently, the addition of a state-space model had relatively little effect on the quality of the spatial correction compared with the kriging method. The kriging method was able to compensate for the systematic biases produced by the RAPT systems and in turn increased the quality of data returned.

Keywords: Remote sensing, Kriging, Telemetry, State-space model, Error correction, Radio-acoustic positioning and telemetry (RAPT)

Background

Animal biotelemetry has rapidly evolved in the few decades since its inception. Where once manually locating an individual animal with a telemetry transmitter was a significant milestone, now satellite transmitters and large-scale coastal tracking networks allow for the long-range monitoring of many individuals over large geographic ranges and time spans. In addition, automated positioning systems, often used in aquatic environments, allow for the near-continuous monitoring of multiple animals simultaneously and can provide fine-scale movement data over multiple years [1]. Despite the rapid

technological advances in biotelemetry, and its widespread application by researchers, several inherent issues remain unresolved. Irrespective of the type of telemetry system in use, all locations of telemetry-tagged animals are associated with some degree of positional error (or inaccuracy). Further, because it is not possible to continuously monitor individuals, there are periods of time for which no positional information is available. Both of these issues require the development of analytical tools to make better use of telemetry data.

The use of automated telemetry positioning systems in aquatic environments has allowed for detailed examination of fine-scale spatial patterns in fish and other aquatic biota. Typically these telemetry systems incorporate three or more stationary hydrophone receivers that are positioned in a triangular array. The hydrophone

*Correspondence: colin.charles@hotmail.com; ccharles@iisd-ela.org
[2] IISD-ELA, Winnipeg, MB, Canada
Full list of author information is available at the end of the article

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 2 of 17

receivers continually listen for acoustic transmissions from transmitters at set frequencies, and positions are calculated based on the arrival times of transmitter signals [2]. To test for positional accuracy, stationary acoustic transmitters are placed in varying proximities to the triangular arrays. Despite the rigorous testing of positional error [3–6], little attention has been paid to the systematic errors (bias) introduced by positioning telemetry systems. A limitation of positioning animals with acoustic telemetry systems is that accuracy deteriorates as distance from the monitoring system increases [5], possibly due to signal degradation or echo effects in acoustically complex environments. Unfortunately, this can result in areas that are often biologically important, such as nearshore regions, with positional data of low precision and accuracy. As a result, these data are often excluded from analyses, even after filtering to ensure the highest quality data [7, 8].

The concept of positioning animals by time difference of arrival (TDOA) is employed by a wide variety of systems (Vemco radio-acoustic positioning (VRAP) system, Vemco positioning system (VPS), Lotek, etc.). The basic principle of these types of systems relies on a set of three or more receivers detecting a signal from a transmitter, and based on the difference in arrival time of this signal, a position can be calculated. The complexity of lake basins may affect signal pathways or create echoes such that measurement and systematic errors are not uniformly distributed across the detection range of the hydrophones, and thus, additional analyses may be needed to properly interpret the data. One such method is a geostatistical technique called kriging [9]. Kriging is a well-established method of linear interpolation that can be used to estimate values for random spatial processes, which incorporates any spatial autocorrelation within the model. Kriging is a powerful tool for dealing with sparse spatial data since complete spatial coverage is often unfeasible in real-world situations. In the context of our study, we used kriging to map the error of the radio-acoustic positioning and telemetry (RAPT) system across the lake surface using limited sample sites to estimate RAPT system error at unsampled locations.

We use two technical terms throughout this paper to describe the error structure observed from the RAPT system: systematic error and measurement error. Systematic error describes the expected distance of a calculated location from its true location, while measurement error is defined as the variability of detections around the central detection point, regardless of the transmitter's true location. We can think of spatial detections generated by a remote sensing system as a best guess by the software and hardware used to detect it. As systems continue to detect transmitters and assign spatial coordinates, it is the responsibility of the researcher to understand that these positions are not the absolute true position, but rather a best estimate. The purpose of performing stationary tag trials is twofold: (1) quantify the distance from the actual location of the tag to the position calculated by the software (systematic error) and (2) quantify the error in two dimensions of the RAPT system (measurement error). By placing tags at known coordinates (marked by a hand-held GPS unit) and analysing the resulting detection patterns, we are able to estimate the variability of the system across a spatial gradient.

In order to separate artificial noise (measurement errors) from relevant biological information, it is possible to quantify data quality classes and model them via a state-space model (SSM) [10]. A principle application of SSMs is to analyse time-series data to estimate the state of an unobserved process from observed data. Another advantage of using a state-space model is that the filtering process does not remove "noisy" data points, but instead accounts for noise in the data [10]. In the case of animal tracking data, coordinates (observed state) at an observed time t can be used to estimate an animal's true location (unobserved state) at a future time. Using estimates for the measurement error of a system, we can use the power of a SSM to increase the value of our data by not only retaining more data, but also correcting the error that is inherent in all remote sensing methods. We modelled individual fish movement as a correlated random walk (CRW) using R [11] and the "CRAWL" package [12], which allows the flexibility to model continuous movement with data collected at irregular intervals.

The main objective of this study was to introduce and apply multiple methods for correcting spatial error of a RAPT system. Using telemetry data from a spatial array of stationary tags, we employ kriging [9] to quantify and correct the systematic error of telemetry systems located in three lakes. A secondary objective of this study was to apply a SSM to both the raw and "corrected" telemetry data. SSMs do not directly address spatially biased errors, but they can be used to address random measurement errors introduced by the telemetry system from both a raw and "corrected" data set. We quantify the performance of both kriging and SSM on telemetry data of free-ranging lake trout (*Salvelinus namaycush*) by using movement and habitat usage metrics to assess improvement.

Methods

Study area
The lakes used in our study are located at the IISD Experimental Lakes Area (ELA) in north-western Ontario (Fig. 1). Stationary tag trials were performed on three lakes to test the accuracy and precision of RAPT systems
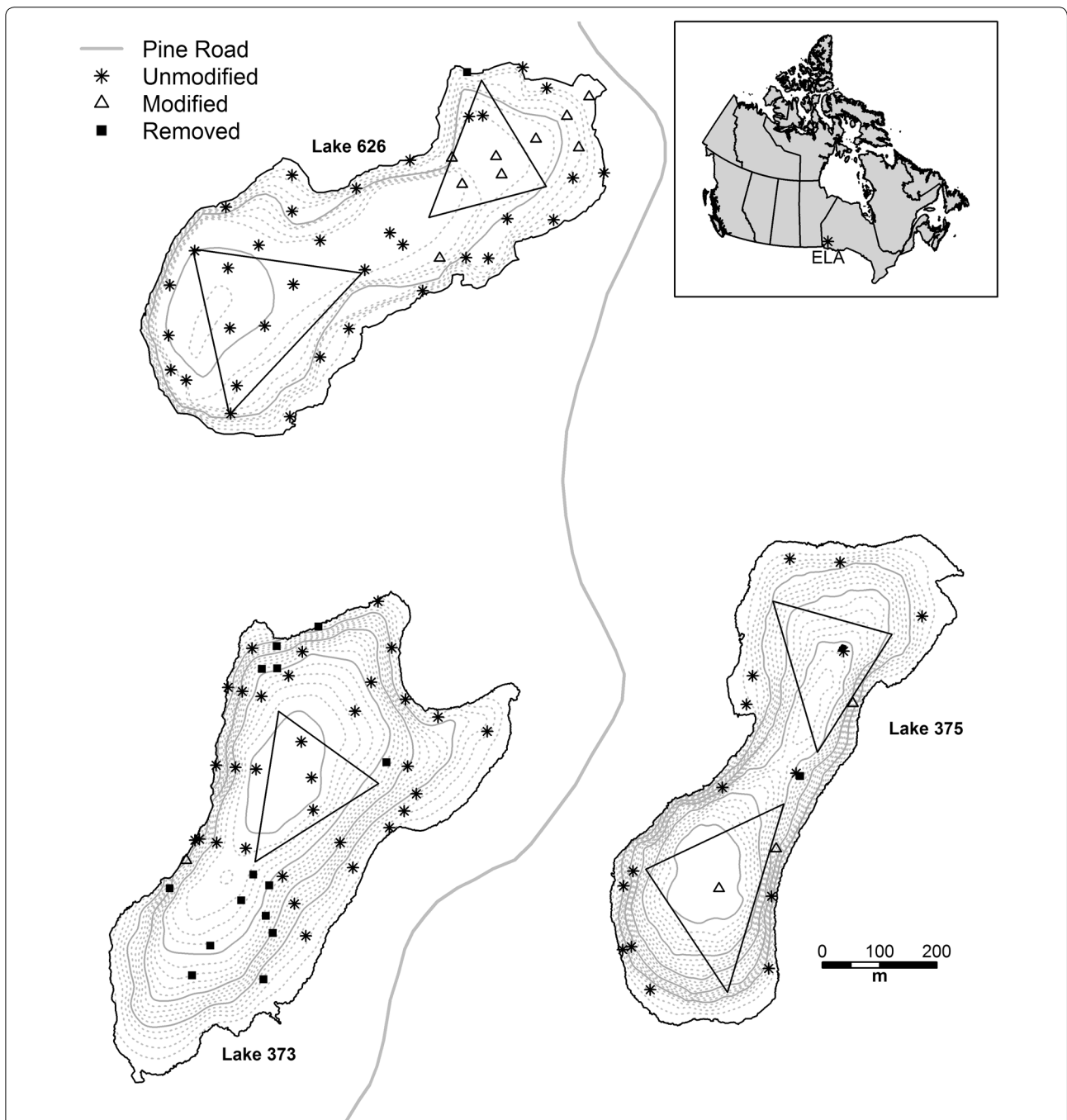
Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 3 of 17

Fig. 1 Location of the three study lakes in relation to each other at the IISD Experimental Lakes Area (ELA) in north-western Ontario, Canada (*inset*). Within each lake, the location of the radio-acoustic positioning and telemetry (RAPT) buoys are shown by the points of the *large triangles*. The locations of the stationary tag trials are shown by the following *symbols*: stations where data were unmodified (*asterisk*); stations where data had to be modified due to inconsistent positioning (*open triangles*); and stations that were removed from analysis (*filled square*) either due to insufficient number of detections or measurement errors not represented by a bivariate normal distribution. Bathymetric contours are shown every 1 m (*grey dashed line*) and every 5 m (*grey solid line*) for each lake

installed in each lake. Each RAPT system consisted of three floating buoys equipped with omnidirectional hydrophones, which were placed 250–300 m apart in the lakes to form a roughly equilateral triangle (referred to as triad hereafter). Each buoy was held in place by a floating dock, which was anchored at four points to minimize

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 4 of 17

potential buoy drift, and GPS coordinates were checked regularly throughout the open water season. The triads were linked to an onshore computer via radio link, which allowed for real-time monitoring of acoustic tag signals. A more complete description of the RAPT systems is provided by Blanchfield et al. [7, 13]. In Lake 375, two separate RAPT systems were in operation, one each in the north and south basins (Fig. 1). A single RAPT system was in operation in Lake 373, positioned over the deepest part of the lake to maximize the number of detections of tagged, cold-water-adapted lake trout (Fig. 1). Two RAPT systems were in operation in Lake 626, one in the west basin and the other in the east basin (Fig. 1). Individual RAPT buoys were re-positioned in the same location as the previous year during each open water period to maintain consistency.

Stationary tag trials
Stationary tag trials were performed to test the accuracy and precision of the RAPT systems (Fig. 1). Each stationary location consisted of an anchor, a line to the surface, and a float. For deployment, a tag was placed in a plastic bottle with holes in it to allow water to flow through, and the bottle was attached to the anchor line at a known depth. Tags were deployed at each location for ~24–72 h except for rare circumstances where tags were left at stations for more than 1 week. The location of each stationary tag trial was recorded using a hand-held GPS unit (GPSMap76 or GPSMap60CSX; measurement error reported by the GPS units for all locations was 2–4 m). Beginning in the fall of 2005, stationary trials were conducted in Lake 375. Three tags were used at 19 stations around the lake, most of which fell outside the RAPT triads. Only one stationary trial was deployed within the north triad in Lake 375, and this tag was placed near an experimental aquaculture cage. Unfortunately, during the early stages of this experiment the focus was to (1) determine whether the RAPT system could detect tags near the shoreline and (2) identify sources of error outside the triads with less attention paid to the error structure within the triad so we have limited information about the error structure within the triads on Lake 375. The spatial trials were improved upon for Lakes 373 and 626 by expanding the number of stations and placing more emphasis within the triads, but nearshore areas were still considered important. The stationary tag trials carried out in Lake 373 (summer 2009 and fall 2013), employed 12 tags and 46 stations. Some stations in Lake 373 were sampled at multiple depths to test whether depth affected positioning. The stationary tag trials performed in Lake 626 in 2010 and 2013 used 15 tags in 45 locations. We retested three locations in the spring of 2015 in Lake 373 to examine potential temporal changes in data quality.
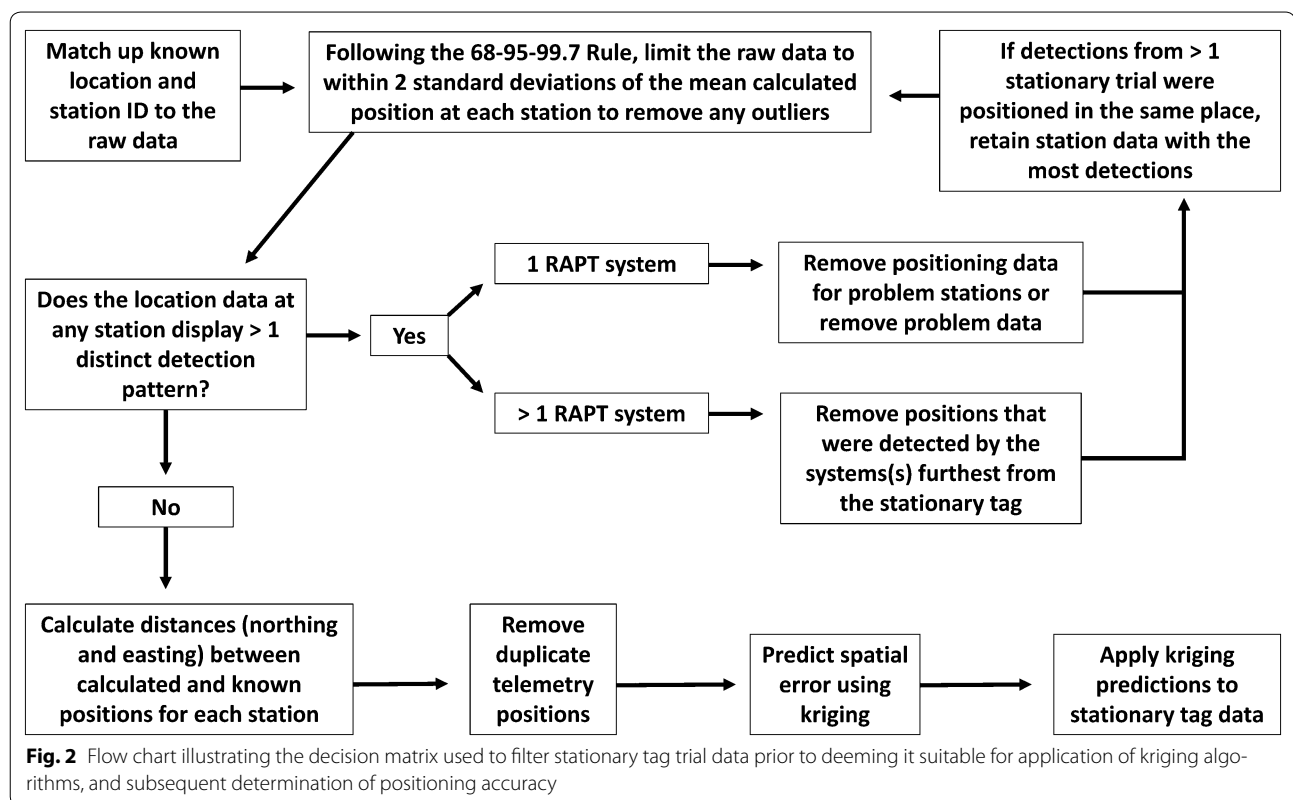
Assumptions
We used the following assumptions for hydro-acoustic systems:

(1) There is no inter-tag variation in detection quality
(2) Depth does not affect telemetry positioning
(3) Water temperature (seasonal effect) or thermocline does not affect acoustic signals travelling through the water
(4) The errors will display temporal consistency, and thus, a single stationary tag trial is sufficient for correcting multiple years of data
(5) The error structure of the detections follows a bivariate Gaussian distribution

Correcting the data
Figure 2 depicts a flow chart for the decision-making process used when examining the stationary tag trial data. During the tag trials, multiple stations were tested simultaneously, and each RAPT system was also monitoring the activities of multiple live fish. Only positional data that met the highest detection criteria by the RAPT software were used for analysis. In statistical quality control, it is common for users to employ what is termed the three-sigma rule. The three-sigma rule states that for a Gaussian process with mean μ and standard deviation σ, it is expected that approximately 68, 95, and 99.7 % of the observation will fall within 1, 2, and 3 standard deviations of the mean, respectively. Upon retrieving the data, our first step towards measuring spatial error was to isolate the positioning data for each tag and station. Next, we removed occasional outliers by limiting the detections at each station to within two standard deviations of the mean easting and northing coordinates so as to retain ~95 % of detections. Further, all stations where tags were detected less than 100 times were removed from further analysis (denoted by filled square symbol and termed "Removed" in Fig. 1). During the analyses, it became evident that in lakes with two RAPT systems (Lake 375 and Lake 626) some of the stationary tags were detected by both systems, which we have termed compound errors. These compound errors invoke spatial error because the detection patterns by each system produced two distinct groupings. In these cases, to reduce variation during the kriging process, only positions reported by the RAPT system closest to the actual position of the stationary tag were retained for analysis (location denoted by open triangle symbol and termed "Modified" in Fig. 1). Additionally, during the stationary trials it was common for the RAPT software to record duplicate spatial coordinates (on the scale of 1 m) to multiple detections over time. Duplicate positions were removed from analysis because the kriging procedure would not accept spatially duplicate entries. Each remaining detection was assigned

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 5 of 17

Fig. 2 Flow chart illustrating the decision matrix used to filter stationary tag trial data prior to deeming it suitable for application of kriging algorithms, and subsequent determination of positioning accuracy

easting and northing Euclidean distances in relation to the actual position of the stationary tag. To quantify the spatial error of the RAPT systems, ordinary kriging (simply termed kriging hereafter) was employed through the use of the R statistical package geoR [14].

Validation of the kriging method

We used a fivefold cross-validation to test the predictability of the kriging method. In fivefold cross-validation, the data set gets partitioned randomly into five equally sized subdata sets, and one subsample is taken as the testing set and the remaining subsamples are used as the model training set. The training set is used as input into the kriging method, and the testing set is used to test the predictability of the model. The process is repeated five times to independently use each subsample as the testing set. Further validation was performed in Lake 373 by a "leave-one-out" procedure "Appendix"). This procedure involved sequentially removing one station from the data set, performing the kriging method, and calculating the spatial error on the raw and corrected data.

Depth comparison

During the course of the stationary tag trials, efforts were made to test whether tag depth affected the positioning ability of the RAPT systems. Depth tests were conducted in both Lake 373 and Lake 375, but no thermocline was

present in Lake 375 during the test. We felt it was most important to present results with tags set above and below a thermocline to show whether changes in water density has an effect on signal propagation, and thus, we have only included depth test results from Lake 373. To measure spatial overlap between tags set at different depths, we calculated the 95 % kernel home range for each depth and measured home range overlap using the volume of intersection statistic (VI). The VI was introduced by Seidel [15] and compares the utilization distribution (UD) overlap between two animals (from Fieberg and Kochanny [16]):

$$VI = \int\limits_{-\infty}^{\infty}\int\limits_{-\infty}^{\infty} \min\left[\widehat{UD}_1(x,y), \widehat{UD}_2(x,y)\right] \mathrm{d}x\mathrm{d}y$$

The VI ranges from zero (for 2 home ranges with no overlap) to 1 (for 2 home ranges with overlapping uniform UDs). The VI has been suggested as a preferred method of assessing UD overlap based on theoretical grounds as well as from a simulation performed by Fieberg and Kochanny [16].

State-space models

State-space models are used to estimate the state of unobserved processes from observations while accounting for measurement errors and stochasticity in the process [17].

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 6 of 17

In the present case of this study, the true location is the unobserved process. As is common with many remote sensing methods for geolocation data, there are latitudinal and longitudinal variances (measurement errors) associated with the observed location. We can use a SSM to account for the variances of the observed locations while simultaneously using maximum likelihood to estimate an animal's true position. In the context of this study, we have assumed that the measurement errors follow a bivariate normal distribution around the mean spatial coordinates from each stationary tag trial. To model telemetry positions in continuous time, we followed methods described by Johnson et al. [18] to put a continuous-time correlated random walk model into a SSM framework. The telemetry data collected for this study differ from Argos data in that the quality class for each detection is not recorded, and thus, we assume measurement errors display a Gaussian structure for all detections within the SSM framework where the mean and standard deviation are fixed. Although we understand that telemetry systems can be subject to dilution of precision, in the context of our study we decided to treat all detections with equal weight since only the highest quality data were retained during processing. In order to estimate the SSM parameters, we used the crawl package [12].

Performance of correction techniques

To assess the quality of data, we spatially quantified systematic errors using kriging and used the SSM to correct measurement errors. We tested the performance of each method independently and simultaneously and quantified the improvements. Using observed telemetry data from a tagged lake trout in each of the three study lakes, we present four scenarios: (1) raw data, (2) data corrected for measurement error (only SSM), (3) data corrected for systematic error (only kriging), and (4) data corrected for both measurement and systematic errors. In order to compare the performance of each scenario, we used three indicators to measure activity and space use: total distance travelled, 100 % home range size calculated using the minimum convex polygon (MCP) [19], and 50 % kernel density estimator (KDE) [20]. We used the adehabitatHR library [21] to calculate the MCP and KDE using the R statistical language. We chose to use the MCP method to describe the absolute home range and a KDE for detecting biologically important areas [22]. Total distance travelled was used to show how biases in the telemetry data can influence calculations in animal behaviour and bioenergetics. For the purpose of this study, we have assumed that there is no spatial variation in detection quality among stationary tag locations. Thus, we model bias as varying in space and treat measurement error as equal among all locations.
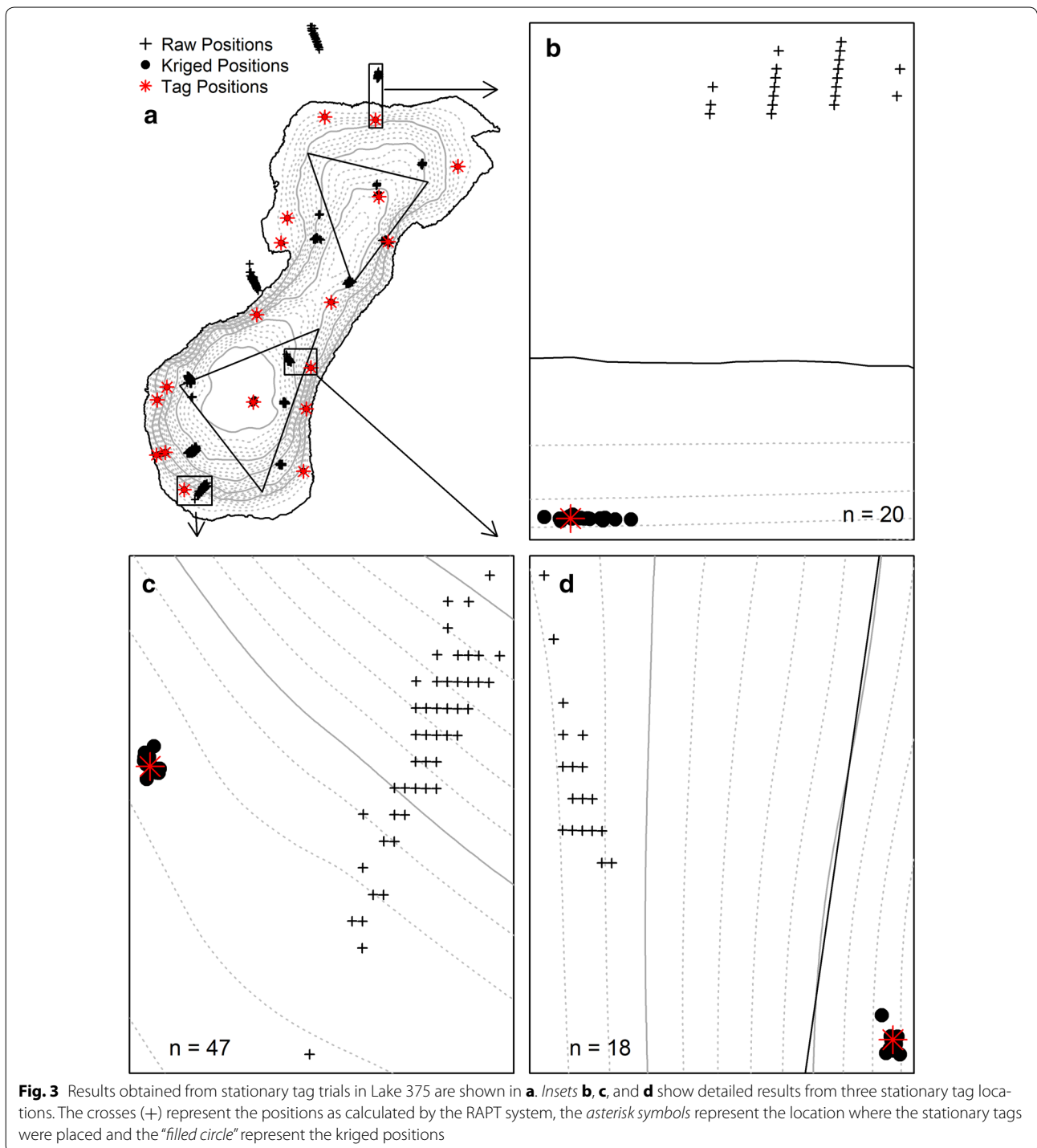
Results

Stationary tag trials

Stationary tag trials were used to assess spatial error of RAPT systems, and a spherical covariance model was used to describe the easting errors and northing errors in the study lakes (Fig. 3). Table 1 summarizes data from the stationary tag trials in all three test lakes. Of 24 338 detections in Lake 375, a total of 12 995 positions were removed from the analysis. Although this is a large number of detections, closer inspection reveals that a single station in Lake 375 was removed from analysis with a total of 11 616 detections (47.7 % of total detections). In this case, three tags were simultaneously deployed at the same station in an area between two RAPT systems and left for 29 days, but the RAPT systems were not able to consistently position the tags during this trial; thus, the accumulated data were omitted. It is expected that these tags were in a "shadow zone" where the tag could be detected, but the receivers were not able to cleanly pick up the signal, and the distribution of detections resembled a long-axis along the fetch of Lake 375. Of the remaining positions in Lake 375, a total of 10 960 (96.6 %) detections were spatial duplicates. In Lakes 373 and 626, the percent of spatially duplicate detections were 94.6 and 97.7 %, respectively. This high proportion of duplication indicates that the RAPT systems are able to position tags with a high degree of precision.

In Lake 375, the mean northing error was 33.35 m and the mean easting error was 32.93 m from the true tag locations. Overall, the mean systematic error (Euclidean distance) in Lake 375 was 50.15 m. The RAPT positions of stationary tags display a high degree of precision (the data points are clustered), but there was considerable systematic error (the clusters of points do not match the known tag locations) (Fig. 3a). Closer inspection of three stations within Lake 375 (Fig. 3b–d) illustrates the spatial distribution of the positioning errors. In each case, the RAPT systems show low accuracy but good precision. Similar results were obtained in Lakes 373 and 626 in relation to the precision of the systems, but the systematic errors were much different. Of the three lakes studied, the system on Lake 373 produced the most systematic bias, which was most likely due to a combination of bathymetry and distance of stationary tags from the centre of the triad.

Correcting spatial error

We used kriging with telemetry information from the stationary tag trials to quantify systematic error of the RAPT systems in our three study lakes. The spatial error generated by the RAPT systems was not constant over the study areas, but rather produced a complex spatial pattern, which need to be addressed by kriging (Fig. 4).

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 7 of 17

Fig. 3 Results obtained from stationary tag trials in Lake 375 are shown in **a**. *Insets* **b**, **c**, and **d** show detailed results from three stationary tag locations. The crosses (+) represent the positions as calculated by the RAPT system, the *asterisk symbols* represent the location where the stationary tags were placed and the "*filled circle*" represent the kriged positions

When we applied the northing and easting corrections generated by the kriging technique to the raw data produced by the RAPT systems, the accuracy of the spatial positions improved considerably (Table 2, kriged positions). The corrected data in Lake 375 had a mean northing error of 0.28 m and a mean easting error of 0.35 m.

The mean Euclidean distance between actual tag location and calculated tag location decreased to 0.47 m, a change (ΔEuc Dist) of 49.68 m (an improvement of 99 %) from the raw to the corrected data. Positional data from Lake 373 showed the greatest improvement in mean tag Euclidean distance going from 57.56 m (raw) to 1.98 m

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 8 of 17

Table 1 Summary of stationary tag trial data for RAPT systems in Lakes 373, 375, and 626 at the Experimental Lakes Area

Lake	Maximum depth (m)	Area (ha)	# tags	# stations	# stations used in kriging	# detections	# detections removed	# duplicate detections
373	21	27.3	14	47	33	39,708	15,826	22,583
375	26	23	3	19	18	24,338	12,995	10,960
626	12	26.2	15	45	44	97,963	45,065	51,671

(kriged; an improvement of 97 %). During the initial analysis of Lake 626, we found that the performance of the RAPT systems was superior to that of the other two lakes with a mean systematic error of 12.2 m. The kriging technique was able to position stationary transmitters to 0.79 m away from their known location, for an improvement of 94 %. Although the percent improvement on Lake 626 was the smallest of the three study lakes, the initial performance was very high compared to the other lakes.

Depth comparison

System performance was affected by the depth of tag placement (Tables 3, 4). Accuracy of the system was affected less than precision, as tags set at different depths still displayed VI index values ≫0 in most cases. The only location where tags displayed a relatively low overlap values is where the tag was set at 3.2 m at centre buoy in

Lake 373 ("Cen" station). For all other depths and locations around Lake 373, the VI values ranged from 0.26 to 0.32. Although these values are much lower than a complete overlap as indicated by a value of 1, the size of the 95 % UD used to calculate the VI index varied greatly (Table 3). Since the UD can be thought of a three-dimensional representation describing where an animal can be found at any point in time, centres of high use receive added weight during comparisons. We can see from Fig. 5 that a tag does behave slightly differently at various depths. Interestingly, for the depth comparisons conducted on Lake 373 the tags set at the deepest depth all exhibited the smallest home range (Table 4). It is possible that signals emitted from tags located near the surface are exposed to a certain degree a backscatter, resulting in higher degree of inaccuracy. Our depth trials were conducted over multiple years in Lake 373 as well as above and below a thermocline (Fig. 5). The results from our
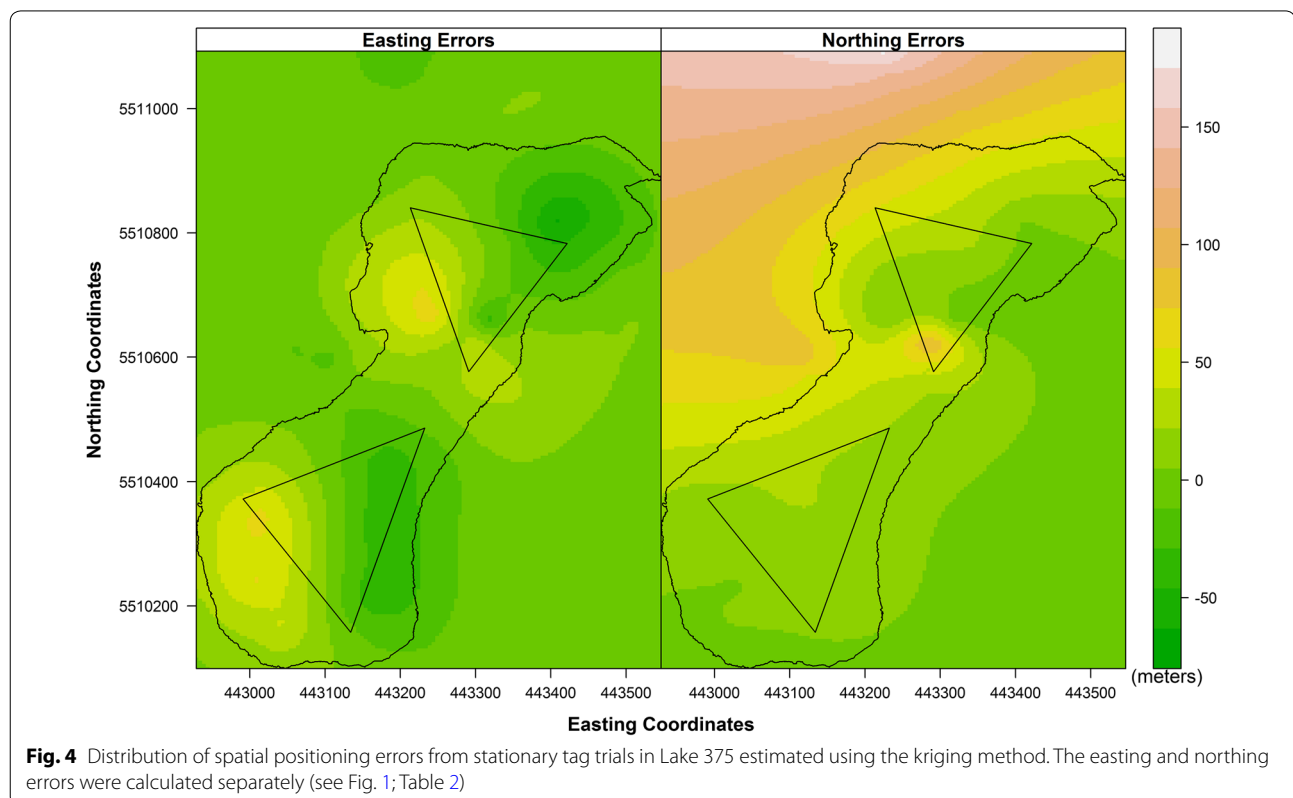

Fig. 4 Distribution of spatial positioning errors from stationary tag trials in Lake 375 estimated using the kriging method. The easting and northing errors were calculated separately (see Fig. 1; Table 2)

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 9 of 17

Table 2 Summary of fivefold cross-validation of the kriging model

Location	Run #	Raw positions (m)			Kriged positions (m)			Difference
		$\bar{x}North$	$\bar{x}East$	*Euc Dist*	$\bar{x}North$	$\bar{x}East$	*Euc Dist*	Δ *Euc Dist*
Lake 373	1	23.68	44.53	57.27	0.84	1.59	1.94	55.33
	2	24.57	43.99	57.32	0.87	1.72	2.07	55.25
	3	25.41	44.71	58.86	0.91	1.75	2.11	56.76
	4	23.56	44.19	56.80	0.91	1.62	2.00	54.80
	5	25.25	43.30	57.55	0.78	1.42	1.76	55.80
Mean		24.94	44.14	57.56	0.86	1.62	1.98	55.59
Lake 375	1	33.28	32.80	50.06	0.27	0.33	0.45	49.61
	2	33.26	33.27	50.34	0.28	0.36	0.48	49.87
	3	33.42	32.83	50.13	0.28	0.34	0.46	49.67
	4	33.75	32.92	50.35	0.28	0.36	0.47	49.87
	5	33.05	32.83	49.86	0.27	0.35	0.47	49.40
Mean		33.35	32.93	50.15	0.28	0.35	0.47	49.68
Lake 626	1	9.47	6.07	12.21	0.62	0.27	0.76	11.45
	2	9.61	6.24	12.44	0.62	0.30	0.79	11.66
	3	9.41	6.13	12.21	0.63	0.31	0.80	11.41
	4	9.33	5.96	12.03	0.63	0.29	0.78	11.25
	5	9.39	6.02	12.10	0.65	0.30	0.81	11.29
Mean		9.44	6.08	12.20	0.63	0.30	0.79	11.41

Mean northings ($\bar{x}$ North) and eastings ($\bar{x}$ East) are distances of detections from known tag locations. The Euclidean distance (Euc Dist) is distance between locations calculated by the RAPT system and the actual tag location. The change in Euclidean distance (ΔEuc Dist) is the difference between the raw and kriged tag positions

Table 3 Comparison of 95 % kernel home range overlap for tags set at different depths using the volume of intersection statistic (VI) for four stations in Lake 373

Station	Depth 1 (m)	Depth 2 (m)	VI
b1-1	7.4	15.8	0.26
b3-1	2.4	16	0.30
	2.4	15	0.35
	15	16	0.12
b3-2	8.8	15	0.28
	8.8	14.8	0.08
	14.8	15	0.15
Cen	3.2	9.5	0.06
	3.2	15	0.71
	3.2	16.9	0.003
	9.5	15	0.05
	9.5	16.9	0.31
	15	16.9	0.006

Tags were set at identical spatial locations, but depth of the tag in the water column was different for each trial. Depths 1 and 2 represent the comparison used to attain each VI value (0 = no overlap, 1 = for 2 home ranges with overlapping uniform UDs)

Table 4 95 % kernel home range for each depth trial at each station in Lake 373

Station	Tag depth (m)	Area (m²)
b1-1	7.4	104
	15.8	18
b3-1	2.4	670
	15	424
	16	140
b3-2	8.8	278
	14.8	169
	15	154
Cen	3.2	51
	9.5	40
	15	69
	16.9	17

depth trials indicate that depth does have an effect on the RAPT systems, but this effect is not significant enough to suggest that either assumption 2 or assumption 3 was violated. The performance of the system from year to year is consistent, and therefore, we also assume that assumption 4 is valid.

Comparing correction techniques

We used tracking data from a tagged lake trout in each of the three study lakes to demonstrate how different scenarios for error correction can influence data collected irregularly through time (Table 5). Using the raw data reported by the RAPT system in Lake 375, the total
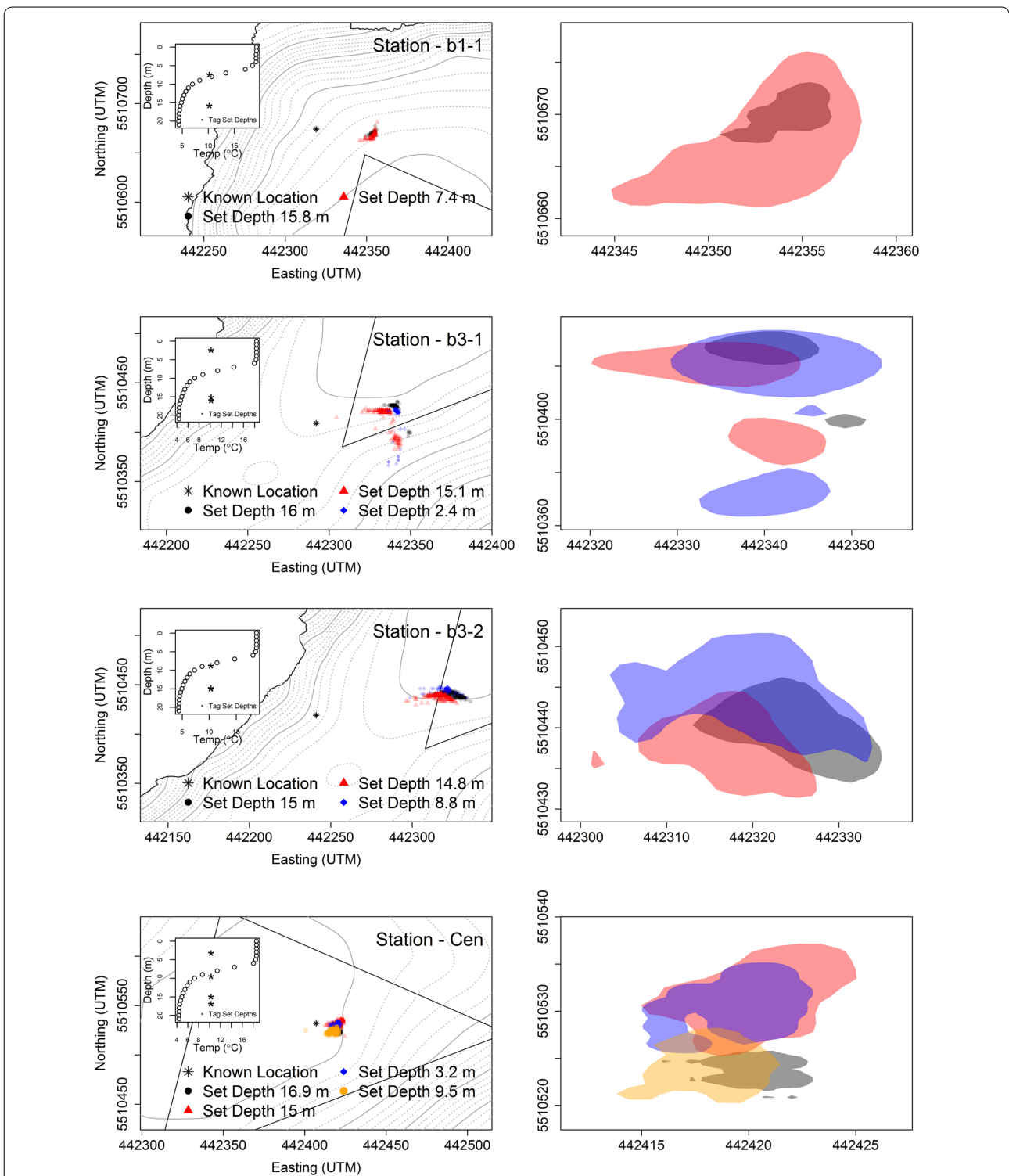
Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 10 of 17

Fig. 5 Summary of 4 stations on Lake 373 where stationary tag trials were conducted at multiple depths. The *panels on the left* show the locations of the stationary tag along with the raw detections from each depth. The *insets* in the *plots on the left* show temperature profiles during the tag trials with clearly established thermoclines. The *plots* on the immediate *right* show the 95 % kernel home range for the pattern of detection at each depth. The *colours* of the home range correspond to the tag depths listed on the *plots on the left*. A transparency factor was added to the *colours* to make overlap more evident. Temperature profiles for 2015 are not included, but trials were conducted under similar conditions where a thermocline was present

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 11 of 17

distance travelled by a lake trout was 4839 m, the kernel home range size was 12.13 ha, and the MCP home range size was 18.55 ha (Fig. 6a, Table 5). Where we used a SSM to correct the measurement errors (scenario 2), the total distance travelled was 3294 m, the kernel home range size was 10.93 ha, and the MCP home range was 12.63 ha (Fig. 6b). In the third scenario, where the raw data were corrected by kriging, we observed a total distance travelled of 4676 m, a kernel home range of 13 ha, and a MCP home range of 17.53 ha (Fig. 6c). When we applied a SSM to the kriged data, (scenario 4), total distance travelled by the lake trout was 3251 m, the kernel home range was 11.67 ha, and the MCP home range was 13.89 ha (Fig. 6d). Depending on the error correction scenario applied, estimates of distance travelled by lake trout ranged from 32 % lower to 20 % greater than calculated from raw data. Similarly, MCP of lake trout ranged from 32 % smaller to 40 % larger than that calculated from raw data, and core-use areas were up to 10 % smaller and 26 % larger than estimates from raw telemetry data. Results from each lake suggest that only applying a SSM to raw data results in a contraction in all three of our performance indicators. The application of kriging (scenario 3) and the combination of kriging and a SSM (scenario 4) produced more complex results. In Lake 373, the MCP and kernel density area increased in scenarios 3 and 4, but the total distance increased in scenario 3 and decreased in scenario 4. In Lake 375, all three of our performance indicators decreased with the application of correction techniques. In Lake 626, the lake where the systems produced the highest quality results from the raw data, the correction techniques produced similar results to the raw data. Scenario 3 showed increased values for all three performance indicators, while scenario 4 had decreased distance travelled and core area use, but greater MCP area (Table 5).

Discussion

Acoustic telemetry is a widely used method of gathering spatial distribution data for organisms in aquatic environments. It is generally accepted that RAPT systems have a certain amount of intrinsic error associated with them likely resulting from deployment in complex acoustic environments. When assessing important ecological questions like an animal's home range, it is important to use accurate spatial positioning information. As such, we have identified a need to quantify and correct systematic biases produced by acoustic telemetry systems. Through the use of stationary tag trials and kriging, we have successfully modelled errors inherent in acoustic telemetry methods using systems from three lakes in the Canadian boreal shield, removing systematic biases and improving the accuracy of the spatial data. We chose kriging because it is well documented in the literature, straightforward to use, and worked well for our purpose. Other spatial interpolation methods such as a general additive model [23] could be explored by other researchers depending on their data structure and experimental design. Furthermore, we have shown that kriging can be combined with SSMs to correct measurement errors as well. The general conclusion of this study is that the systematic errors produced by the RAPT systems have a greater effect on the quality of the data compared to the measurement errors and so we believe that more effort should be applied to

Table 5 Performance of error correction techniques applied to raw RAPT data of an acoustically tagged lake trout (*Salvelinus namaycush*) in three different lakes at the Experimental Lakes Area

Location	Scenario	Distance travelled (m)	100 % MCP area (ha)	Core area (ha)
Lake 373	Raw data	4089.8	5.95	3.6
	SSM only	3278.3	5.38	3.47
	Kriged data	4924.8	8.31	4.53
	Kriged and SSM	4051.1	7.74	4.36
Lake 375	Raw data	4839.2	18.55	12.13
	SSM only	3294.2	12.63	10.93
	Kriged data	4675.9	17.53	13
	Kriged and SSM	3250.5	13.89	11.67
Lake 626	Raw data	5672.1	24.38	8.89
	SSM only	5462.5	23.98	8.75
	Kriged data	5847.3	25.56	9.31
	Kriged and SSM	5392.1	24.88	8.75

Each of the four scenarios is quantified by the total distance travelled by a fish, the 100 % minimum convex polygon (MCP) to indicate total space use, and the kernel density core area use (50 %) to quantify areas of high importance

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 12 of 17

performing stationary tag trials to identify problem areas in study systems. We feel that the measurement error displayed by the RAPT systems in our study lakes is of lesser concern and that the quality of the data is most affected by systematic biases.

The depth of a stationary tag clearly affected the detection quality during the tag trials, but this effect had greater implications for precision than accuracy. The low degree of overlap calculated by the VI should not be a cause for concern because the VI uses three-dimensional space use in its calculation. Even at centre buoy where the shallow tag did not have high overlap with the deeper tags, the absolute difference between the mean software-derived locations for each depth was within ~5 m of each other. On an ecosystem level, an error of 5 m would not have a dramatic impact on space use and home range size. Signals that are transmitted from tags near the surface are likely subject to reflections from the surface waters. Signals in an aquatic environment are analogous to signals travelling down a canyon, where the canyon walls can reflect signals, but in the case of a freshwater or marine system one of the "walls" (the surface of the water) is a dynamic interface affected by wind and other environmental factors [24]. Similar results were obtained by Baktoft et al. [25], where the authors tested an acoustic telemetry system on two lakes. The depth trials suggest that space use of tagged animals that inhabit the upper water column may be considerably overestimated compared to those living deeper in the water column. Furthermore, detections from the depth trials (Fig. 5, Table 4) show that the presence of a thermocline did not have a negative effect on the acoustic signal; therefore, we did not violate assumptions 2 or 3. In our case, the acoustic signals were unaffected by a thermal barrier, but perhaps the signals may be more sensitive in systems with a chemical barrier or other physical barrier; if so, a separate stationary tag trial may need to be conducted above and below the disturbance to determine whether separate corrections would be required.

For our purposes, we have defined our errors using an absolute measure of error in metres in two dimensions (northing and easting). An additional way to report errors currently in use by VPS is termed horizontal positioning error (HPE). In the framework of HPE, the arrival time of a signal from a transmitter to two receivers defines a branch of a hyperbola; this branch is commonly termed a hyperbolic line of position (LOP). A transmitter can be located along any point of this LOP with the actual transmitter location unknown. In order to calculate a transmitter location, a second hyperbola is calculated from a third receiver. The intersection point of these two LOPs is the location of the transmitter. See Smith [2] for further details about the hyperbolic positioning sensitivity,

especially Figs. 4, 5 and 6. One of the main drawbacks of using HPE is that it should only be interpreted as a unit-less estimate of error sensitivity while HPEm (measured horizontal position error estimate in metres) should only be used for informal purposes [2]. The performance of the VPS system was tested in marine, estuary, and riverine environments with median HPEm of 3.3 m and less although system performance was not tested outside of the arrays [26]. In the context of our study, we were able to specifically quantify the positioning error in two dimensions, which allowed us to use the kriging method to create the error maps in Fig. 4. We did not, however, have access to estimates for error sensitivity for our analysis. Although HPE cannot be used for error correction purposes, it does provide researchers information regarding the quality of the detections and can be used to identify areas where more receivers could be placed. Many aquatic species use nearshore areas for breeding and foraging. These areas often have important biological implications, but depending on receiver or RAPT buoy placement, these areas may receive relatively poor coverage, and thus, the error sensitivity (HPE) may be high. The kriging method returns much more informative error information than HPEm because although HPEm returns information relative to the accuracy of a detection it does not provide anything about the directionality of the error. The kriging method can quantify the precision error in two dimensions, which in turn can be used to identify complex habitat or problem areas.

In multi-species systems, researchers may want to monitor more than one species at a time using acoustic telemetry. Different species may have different physiological constraints, and in turn they may need to inhabit different niches within the water column. The depth trials we performed showed that tags detected closer to the surface were subject to "backscattering" issues, which caused higher detection variation. Consider a hypothetical system that contains two distinct species where one is a warm-water-adapted species (species A) and a second cold-water-adapted fish (species B). During periods of stratification when species B is driven deeper into the lake due to metabolic requirements and species A is unaffected, based on our results, data quality from species A would be considerably less, with respect to transmitter precision, than that of species B, and it is likely that energetic estimates would also be overestimated for species A. This type of scenario deserves some consideration when designing a study monitoring species with different habitat and metabolic requirements.

Espeland et al. [5] suggest that home ranges extending far beyond RAPT triads may be overestimated. While in partial agreement with this statement, we also urge researchers to use caution with this assertion as our

Fig. 6 A comparison of raw data three corrections applied to acoustic positioning telemetry data of a free-ranging lake trout (*Salvelinus namaycush*) in Lake 375 at the Experimental Lakes Area, monitored by two RAPT systems (see Fig. 1) over a period of approximately 24 h. The *panels* show: **a** raw telemetry data; **b** a SSM was applied to correct for measurement errors; **c** a correction for systematic bias (determined by kriging); **d** systematic (kriging) and measurement errors (SSM) were accounted for

results suggest that home ranges can also be underestimated. In our study, the RAPT systems did not have a consistent bias throughout the lake. RAPT systems either incorrectly positioned tags closer to or further from the centre of the triad, but not in a consistent fashion. In addition, RAPT systems are used in both freshwater [8] and marine systems [27, 28], but it is presently unknown whether RAPT systems deployed in marine systems produce the same patterns of bias that are present in freshwater systems. The method we developed in this paper aims to reduce the effects associated with telemetry errors by increasing the accuracy of the estimated positions and to simultaneously quantify and correct any

biases produced by the system. In small lakes like the ones commonly present in the boreal and arctic regions, this underestimation could have a large impact on the ratio of surface area to core space use.

The utilization of a SSM is meant to account for the measurement errors of the detections. In some cases, it became apparent that the measurement errors became more variable along one axis, and in these cases the northing errors were different from the easting errors (e.g. Fig. 3b vs. c). This phenomenon was shown by Espinoza et al. [1] regarding tag placement inside and outside an array. The pattern detected by their VPS system is very similar to patterns detected by the RAPT systems in our

study when transmitters were located far from the centre of the triads. In our study, a normal distribution was used to describe the error structure of the detections in the SSM, but [25] used a hidden Markov model (HMM) and a t-distribution to model measurement errors (the authors refer to them as observation errors). Although this technique did not address any systematic biases that may have been present, this approach did improve the data (with some residual scattering around the true positions). Perhaps in the future a combination of kriging to address the systematic bias and a t-distribution in a SSM to address the measurement errors may further improve telemetry data by accounting for spatial differences in measurement errors. Although we feel the need to account for measurement errors in RAPT data is relatively low due to the high precision as seen in the stationary tag trials, the fact that this type of data is collected irregularly through time presents yet another statistical challenge for analysis.

The principle of RAPT systems relies on arrival times of acoustic signals from tags to hydrophones. In our system in order for a tag to be positioned, the signal from a tag is detected by three omnidirectional hydrophones, and the arrival times of the acoustic signals are processed and run through "signal-arrival-time" difference equations, which are used to calculate the tag position [28, 29]. Some of the factors that must be taken into consideration in the origin of measurement errors are the speed of sound through water and arrival-time differences [30]. Environmental variables may also contribute to measurement errors. Wind action causes waves, which can distort sound signals and cause anchored buoys to shift from their recorded. In our study, any unrecorded small-scale movement of the hydrophones could potentially add more noise during the signal arrival time, but the method by which the buoys were anchored limited their movement. All telemetry systems are subject to these disturbances; we controlled these variables as much as possible by mooring the buoys solidly. Receiver locations should be chosen to maximize lake coverage while minimizing potential interactions of acoustic signals (e.g. cliffs or large boulders) while continuing to maximize detection probability of the study species.

Recommendations

The kriging methodology proposed in this paper is a simple, yet powerful way to correct systematic errors in acoustic telemetry systems. Though some time and effort must be expended to perform a stationary tag trial in an experimental system, in our opinion the benefits outweigh the costs in order to achieve the most accurate telemetry data for aquatic species that are otherwise difficult to study on a continuous timescale. The results from

the kriging analyses are likely to be robust and could be used to correct systematic errors over multiple years. The application of this method affects research areas such as bioenergetics, habitat utilization, and resource use. The ability and flexibility of this method to be used in lakes with one or more RAPT systems should allow other researchers to reduce the influence of problem telemetry data and thus increase the accuracy of inferred fish positions and movement. Regarding our three scenarios of spatial correction, we found that the kriging method had the best performance with regard to spatial correction. On its own, the SSM was not able to identify or compensate for the bias present in our study systems. At this point, it is unknown whether there is any advantage to combining the kriging and SSM solely on the reality that detection quality was not returned with the system presented in this paper. Temporal stability should be further tested by leaving tags at stationary locations for longer periods of time, possibly for the length of the study or just a single year. This would allow researchers to adjust for seasonal effects that were not apparent during the deployment of our tags. Alternately, researchers could conduct multiple short-term trials throughout the year (e.g. 1 week per month); this would yield stationary tag data that are temporally spaced, but would reduce the load on the telemetry system and the effort required on the part of the researcher to process the data.

In closing, we found that the systematic errors were more likely to influence the recorded position of the stationary tags rather than measurement errors. Although SSMs can be used to correct measurement errors, in the context of our study the SSM on its own was not able to compensate for biases introduced by the interaction between the physical environment and the telemetry system. Therefore, we recommend that any future telemetry studies should perform at least a rudimentary stationary tag trial in order to assess the performance of their system. Any such trials should attempt to cover as much of the study area as possible, with multiple stations located within each triad of receivers and many nearshore locations. It is especially important to conduct trials near areas of expected biological importance in order to draw accurate biological conclusions.

Author details
[1] University of Manitoba, Winnipeg, MB, Canada. [2] IISD-ELA, Winnipeg, MB, Canada. [3] Fisheries and Oceans Canada, Winnipeg, MB, Canada.

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 15 of 17

Appendix

"Leave-one-out" kriging performance test

In order to validate the kriging method further, we also tested it using a "leave-one-out" quality control. This method involves sequentially removing one station from the data set, running the kriging process with the remaining stations, and applying the resulting correction map to the data from the removed station. This was performed on all stations within the lake. This allowed us to test the kriging method on data from "unknown" data points, while still having access to the known transmitter location, thus allowing us to quantify the accuracy of the kriging process.

The "leave-one-out" method showed bias improvement at all but 5 stations on Lake 373. Further, at 3 of these 5 stations tags were displaced less than 4 m; the maximum value for stations where the kriging method did not improve the raw data was 19.6 m (Fig. 7). The kriging method was able to improve the data quality for the remaining 28 stations (85 % of all stations). Mean improvement was 50.8 m (median of 50.83 m), while the mean error at stations where the kriging method did not improve the data quality was 8.4 m (median of 3.8 m).
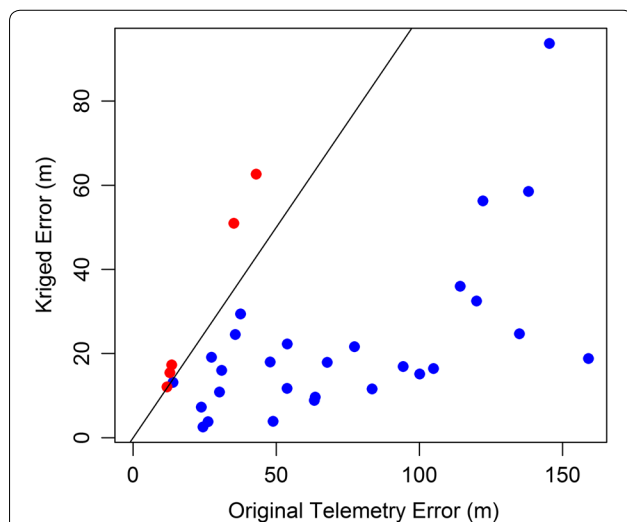

Fig. 7 This figure shows the results of the "leave-one-out" method. The *black line* shows the 1:1 ratio for the original error and the kriged error. All *points* which lie to the *right* of the 1:1 *line* show an improvement in Euclidean distance from the actual tag position compared to the raw data (*blue points*), while points to the *left of the line* were made worse by kriging (*red points*)
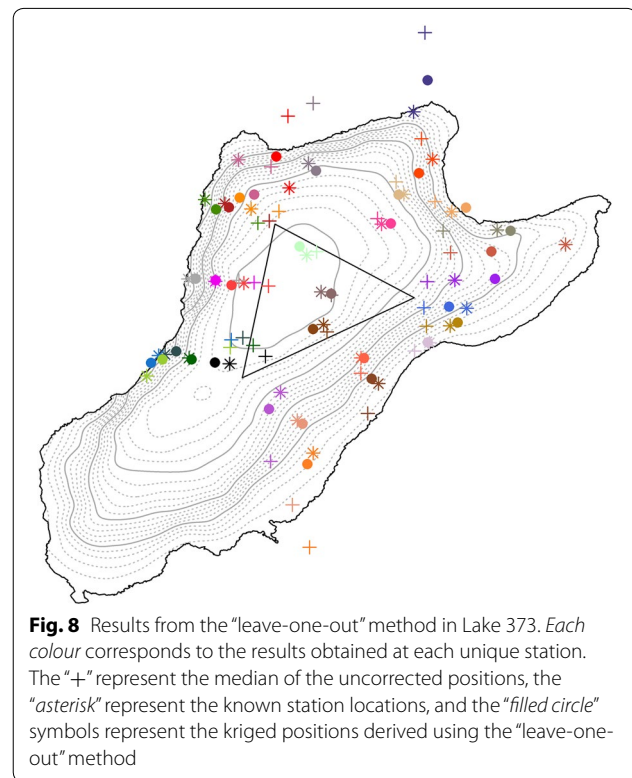

Fig. 8 Results from the "leave-one-out" method in Lake 373. *Each colour* corresponds to the results obtained at each unique station. The "+" represent the median of the uncorrected positions, the "*asterisk*" represent the known station locations, and the "*filled circle*" symbols represent the kriged positions derived using the "leave-one-out" method

Figure 8 illustrates the results of the leave-one-out procedure for each station on Lake 373.
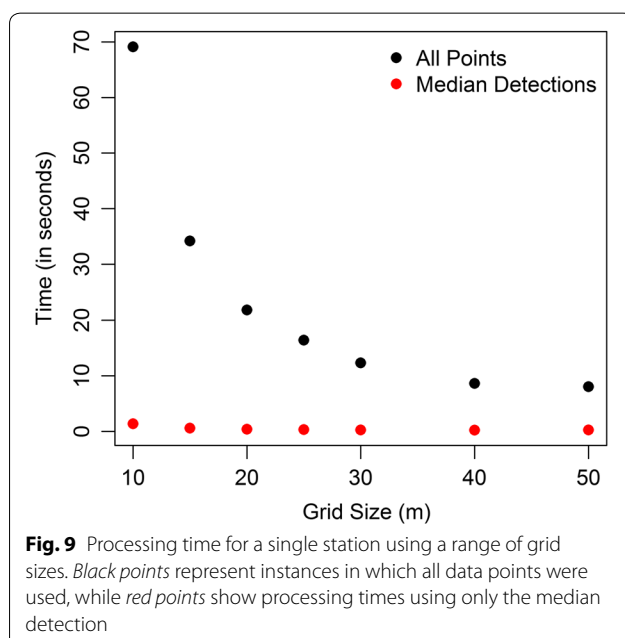
Although the performance was not improved at all stations, the benefits of applying the kriging procedure outweigh the costs. Stations within the triad were not improved by the kriging process, but these stations generally provided the most reliable positioning data. This suggests that correction by kriging is less important for positions detected within the buoy triad. The "leave-one-out" method clearly showed that stations near the perimeter of the lake were more likely to be influenced positively by the kriging method where there is strong evidence for over- or under-correction. These results show that kriging produces much more reliable data outside of the triad (vs. raw data); the "kriged" positions are much closer to the actual tag position than the "raw" data. This method of quality control reinforces that stations must be tested outside of the triads, especially near shore where biologically important habitats may be located in order to properly address and assess telemetry errors. The leave-one-out procedure showed that kriging is essential to yield accurate data outside the triad and that kriging has minimal effects on high-quality data within the triads.

Effect of grid size and detection filtering

During the development of our correction technique, we identified two crucial factors, which directly affect

Charles *et al. Anim Biotelemetry (2016) 4:5*

Page 16 of 17

processing time: (1) number of detections and (2) grid size. The kriging method required creating a spatial grid over the study area in order to assign error estimates to each grid. This grid was used for linear interpolation of spatial bias from the RAPT system. The choice of grid size and the number of accumulated points at each station affected the processing time. Improvements in technology, including battery life, receiver memory storage, and tag ping intervals of <30 s, have increased the potential for long-term remote telemetry studies to yield massive data sets. Even in this study where the tags emitted signals every 120–300 s and detections were filtered to only include data within 2 standard deviation of the mean at each station (~95 % of the data), each station still produced a high number of detections (up to 2000 detections at a single station). Using these detections, the limiting factor was selecting grid size for interpolation (Fig. 9). Processing times ranged from ~10 s per station using a 50-m grid to 70 s per station using a 10-m grid. Increasing the grid size led to an exponential decline in processing time, and these limitations were readily evident when using the "leave-one-out" method. In Lake 373 where we used 33 stations, the total processing time could take longer than 40 min.

In future large-scale studies that involve stationary tag trials, processing time will become the limiting factor. One way to improve processing time would be to use the median detection location for each stationary tag rather than the entire cloud of detection points when producing the kriging map. The median detection location represents the central tendency of the data, and it is less sensitive to outliers and could be used to represent all detections at that stationary location. In our study, the use of the median location for each station in the kriging technique yielded processing times of only a few seconds per station for all grid sizes and produces a 51-fold improvement in processing time using a grid size of 10 m.

References
1. Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res. 2011;108:364–71.
2. Smith F. Understanding HPE in the VEMCO positioning system (VPS) V1.0, September 27, 2013. http://vemco.com/wp-content/uploads/2013/09/understanding-hpe-vps.pdf. Document #: DOC-005457-01. Retrieved 15 Jan 2015.
3. Begout Anras ML, Cooley PM, Bodaly RA, Anras L, Fudge RJP. Movement and habitat use by lake whitefish during spawning in a boreal lake: integrating acoustic telemetry and geographic information systems. Trans Am Fish Soc. 1999;128:939–52.
4. Zamora L, Moreno-Amich R. Quantifying the activity and movement of perch in a temperate lake by integrating acoustic telemetry and a geographic information system. Hydrobiologia. 2002;483:209–18.
5. Espeland SH, Gundersen AF, Olsen EM, Knutsen H, Gjøsæter J, Stenseth NC. Home range and elevated egg densities within an inshore spawning ground of coastal cod. ICES J Mar Sci. 2007;64:920–8.
6. Andrews KS, Tolimieri N, Williams GD, Samhouri JF, Harvey CJ, Levin PS. Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. Mar Biol. 2011;158:2377–87.
7. Blanchfield PJ, Flavelle LS, Hodge TF, Orihel DM. The response of lake trout to manual tracking. Trans Am Fish Soc. 2005;134:346–55.
8. Blanchfield P, Tate L, Podemski C. Survival and behaviour of rainbow trout (*Oncorhynchus mykiss*) released from an experimental aquaculture operation. Can J Fish Aquat Sci. 2009;66:1976–88.
9. Journel AG, Huijbregts CJ. Mining Geostatistics. New York: Academic Press; 1978.
10. Jonsen I, Flemming J, Myers R. Robust state-space modeling of animal movement data. Ecology. 2005;86(11):2874–80.
11. R Core Team. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; 2014. http://www.R-project.org/.
12. Johnson DS. crawl: Fit continuous-time correlated random walk models to animal movement data. R package version 1.4-1.2013. http://CRAN.R-project.org/package=crawl.
13. Blanchfield PJ, Tate LS, Plumb JM, Acolas M-LA, Beaty KG. Seasonal habitat selection by lake trout (*Salvelinus namaycush*) in a Canadian shield lake: constraints imposed by winter conditions. Aquat Ecol. 2009;43:777–87.
14. Ribeiro PJ Jr, Diggle PJ. geoR: a package for geostatistical analysis. R-NEWS. 2001;1(2):15–8.
15. Seidel KS. Statistical properties and applications of a new measure of joint space use for wildlife. Thesis, University of Washington, Seattle, USA. 1992.
16. Fieberg J, Kochanny CO. Quantifying home-range overlap: the importance of the utilization distribution. J Wildl Manage. 2005;69(4):1346–59.
17. Jonsen I, Myers R, Flemming J. Meta-analysis of animal movement using state-space models. Ecology. 2003;84:3055–63.
18. Johnson DS, London JM, Lea MA, Durban JW. Continuous-time correlated random walk model for animal telemetry data. Ecology. 2008;89:1208–15.
19. Mohr CO. Table of equivalent populations of North American small mammals. Am Mid. Nat. 1947;37:223–49.
20. Worton BJ. Kernel methods for estimating the utilization distribution in home-range studies. Ecology. 1989;70:164–8.
21. Calenge C. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model. 2006;197:516–9.

Fig. 9 Processing time for a single station using a range of grid sizes. *Black points* represent instances in which all data points were used, while *red points* show processing times using only the median detection

Charles *et al. Anim Biotelemetry* (2016) 4:5

Page 17 of 17

22. Nilsen EB, Perdersen S, Linnell JDC. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecol Res. 2008;23:635–9.
23. Wood SN. Generalized additive models: an introduction with R. London: Chapman and Hall/CRC; 2006.
24. Caley M, Duncan A. Conceptual development of a dynamic underwater acoustic channel simulator. Paper number 134. Proceedings of ACOUSTICS 2011. 2011.
25. Baktoft H, Zajicek P, Klefoth T, Svendsen JC, Jacobsen L, Pedersen MW, Morla DM, Skov C, Nakayama S, Arlinghaus A. Performance assessment of two whole-lake acoustic positional telemetry systems—Is reality mining of free-range aquatic animals technologically possible? PLoS One. 2015;10(5):20.
26. Steel AE, Hearn AR, Klimley AP. Performance of an ultrasonic telemetry positioning system under varied environmental conditions. Anim Biotelem. 2014;2(15):1–17.
27. Rigby PR, Andrade Y, O'Dor RK. Interpreting behavioural data from radio–acoustic positioning telemetry (RAPT) systems. Afr J Mar Sci. 2005;27(2):395–9.
28. Voegeli FA, Smale MJ, Webber DM, Andrade Y, O'Dor RK. Ultrasonic telemetry, tracking and automated monitoring technology for sharks. Environ Biol Fish. 2001;60:267–81.
29. O'Dor RK, Andrade Y, Webber DM, Sauer WHH, Roberts MJ, Smale MJ, Voegeli FM. Applications and performance of radio–acoustic positioning and telemetry (RAPT) systems. Hydrobiologia. 1998;371(372):1–8.
30. Ehrenberg JE, Steig TW. Improved techniques for studying the temporal and spatial behavior of fish in a fixed location. ICES J Mar Sci. 2003;60:700–6.