Received: 2 April 2018 | Revised: 20 February 2019 | Accepted: 25 March 2019
DOI: 10.1111/2041-210X.13188

REVIEW

Methods in Ecology and Evolution BRITISH ECOLOGICAL SOCIETY

Current and emerging statistical techniques for aquatic telemetry data: A guide to analysing spatially discrete animal detections

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Funding information
Natural Sciences and Engineering Research Council of Canada; Canada Research Chairs; Ocean Tracking Network; BC Hydro; Killam Trusts; Canadian Statistical Sciences Institute (CANSSI)

Handling Editor: Luca Börger

Abstract

1. Telemetry, or the remote monitoring of animals with electronic transmitters and receivers, has vastly enhanced our ability to study aquatic animals. Radio telemetry, acoustic telemetry and passive integrated transponders are three common technologies that generate detection data — time-stamped, tag-specific records that are logged by receivers.
2. We review current statistical methods and comment on potential future directions for analysing detection data derived from fixed telemetry receiver arrays.
3. To illustrate how different methods may be used to achieve diverse study objectives, we provide a case study dataset collected by an array of 42 acoustic telemetry receivers on 187 bull trout in the Kinbasket Reservoir of British Columbia. To close, we present a decision tree for guiding the selection of a method based on study objectives and sampling design.
4. This paper provides both experienced and novice telemetry researchers with the knowledge and tools to facilitate more comprehensive analysis of detection data and, in so doing, ask a wide variety of ecological questions that will enhance our understanding of aquatic organisms.

KEYWORDS
acoustic telemetry, detection data, movement ecology, Ocean Tracking Network, PIT tag, radio telemetry, statistical methods

1 | INTRODUCTION

Aquatic animals live in habitats that create inherent challenges for those attempting to study their ecology, behaviour and physiology. Telemetry enables the remote monitoring of free-living animals, whereby a signal emanating from a device (i.e., transmitter or tag) carried by an animal transfers information to a receiver. The advent of telemetry tools has provided researchers with effective means of studying aquatic animals in the streams, rivers, lakes, estuaries, and oceans of the world (Hussey et al., 2015; Lucas & Baras, 2000).

Three common telemetry technologies used with aquatic animals are radio and acoustic telemetry, and passive integrated transponders (PIT). Radio telemetry uses radio signals that are detected by an antenna affixed to a receiver, whereas acoustic telemetry uses sound waves to transmit tag information to a hydrophone on a receiver. The transmitters of both technologies are dependent on internal batteries that, along with the tag-animal size ratio and tag settings, limit the duration of data collection. PIT tags rely on external energy derived from an electromagnetic field emitted by receiver antennas, which prolongs the tag lifespan but requires close proximity (Lucas & Baras, 2000). Despite design differences (Cooke, Hinch, Lucas, & Lutcavage, 2012; Lucas & Baras, 2000), these three telemetry technologies all record one specific kind of data: detection data that consist of time-stamped, tag-specific records registered and stored by receivers when tagged animals are within range.

Recently, a shift from mobile tracking towards using fixed receiving stations that automatically log detections has led to a large number of tagged animals and extensive receiver coverage crossing geopolitical boundaries (Donaldson et al., 2014). The collection and aggregation of large aquatic detection datasets has created both challenges and opportunities for the study of wild aquatic animals (Lennox et al., 2017a). Although there have been substantial developments in the statistical analysis of aquatic detection data, to our knowledge, there have been no attempts to synthesize the existing and emerging methods. Our goal is to provide this synthesis. Although the methods we review are the most ubiquitous (today), they are not exhaustive. In particular, because detection data are limited to collection at discrete locations, we do not review methods for spatially continuous data (e.g. movement paths collected by satellite telemetry devices). It is possible to obtain estimates of spatially continuous data from detection data using positioning systems (e.g. Niezgoda, Benfield, Sisak, & Anson, 2002; Smith, 2013) or by calculating centers of activity (Simpfendorfer, Heupel, & Hueter, 2002), in which case other statistical methods not reviewed herein may be used, for example, home range analysis (Marshell, Mills, Rhodes, & McIlwain, 2011), state-space models (Martins et al., 2014), or hidden Markov models (Whoriskey et al., 2017). We also do not discuss software designed primarily for the data management and visualization of aquatic detection data. These developments, e.g. the Ocean Tracking Network Toolbox (otndc@dal.ca), ZoaTrack (Dwyer et al., 2015), the Integrated Marine Observing System's Animal Tracking Facility detection database and quality control procedures (Hoenner et al., 2018), and the R (R Core Team 2018) packages **glatos** (Holbrook, Hayden, & Binder, 2017), and **VTrack** (Campbell, Watts, Dwyer, & Franklin, 2012), provide high-quality standardized methods for handling detection data; however, they typically do not incorporate a stochastic component.

First, we review statistical methods for detection data derived from fixed telemetry arrays in aquatic environments. To illustrate the differences between statistical methods, throughout the review, we analyse a portion of a dataset collected on acoustically tagged bull trout (*Salvelinus confluentus*). Then, we comment on potential future directions that could help advance our understanding of how aquatic animals interact with each other, their environment, and humans in a rapidly changing world. To close, we present a decision tree to summarize the differences among the statistical methods and to help guide researchers on how to analyse their detection data given the scientific questions of interest and sampling design.

2 | ILLUSTRATIVE DATASET

Between 2010 and 2012, 187 bull trout were acoustically tagged and monitored by an array of 42 receivers deployed in the Kinbasket Reservoir of British Columbia, Canada (Figure 1). The full dataset was previously analysed in Martins et al. (2013) and Gutowsky et al. (2016); for simplicity, we chose to analyse data collected only during January 2011. The resulting dataset comprised three files: receiver metadata, that includes the identities and locations of the deployed receivers, along with environmental information; tag metadata, that consists of the unique tag ID codes and other animal characteristics (e.g. length/weight/sex); and detection data, i.e. the records of tags registered by receivers at a specific date and time. Together, these data (hereafter 'detection data') provide a comprehensive view on individual movements.

For any telemetry study, the question of interest and the spatiotemporal design of the receiver deployments will influence the applicability of various statistical methods. Once a method has been chosen, the detection data will need to be summarized into an appropriate response variable (y). Examples include: counts of detections (Zhang et al., 2015), counts or proportions of receivers visited within a specific time scale (Udyawer, Read, Hamann, Simpfendorfer, & Heupel, 2015), presence/absence data (Dudgeon, Lanyon, & Semmens, 2013; Kessel et al., 2014a), time spent in particular areas

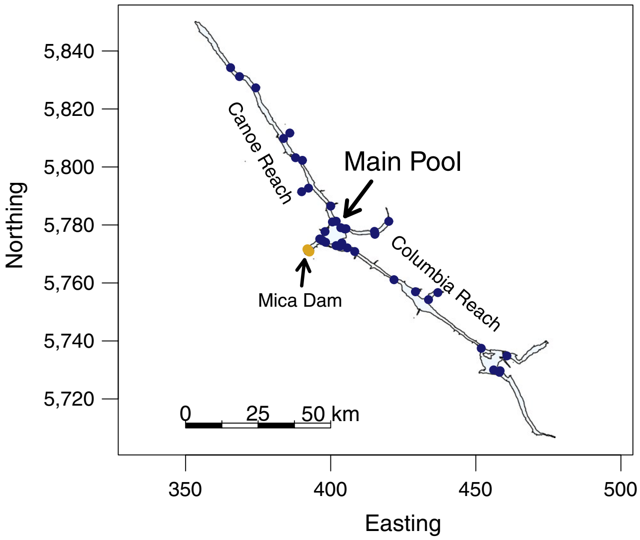


FIGURE 1 Study location of the illustrative dataset, i.e. the Kinbasket reservoir in British Columbia, Canada, with the location of the dam in yellow, and the receiver locations in dark blue. Detection range was assumed to be 500 m, a distance shorter than the width of either Reach in most places

or residency indices (Kessel et al., 2014a; Ketchum et al., 2014), and movement rates (Stich, Kinnison, Kocik, & Zydlewski, 2015). We discuss the form of the response variable for each method reviewed below, and use the Kinbasket dataset to illustrate the versatility of detection data.

3 | REVIEW OF CURRENT STATISTICAL METHODS

3.1 | Generalized modelling framework

Researchers who use telemetry are often interested in determining whether there is a relationship between animal movement patterns and a set of putative explanatory variables or covariates. Because many of the possible response variables are non-Gaussian, traditional statistical methods like analysis of variance and linear regression are not directly applicable. Generalized linear models (GLMs) enable the modelling of non-Gaussian response variables provided they follow a distribution belonging to the exponential family (Wood, 2006). A GLM links an observation y_i to a set of covariates $\mathbf{X}_i$:

$$\begin{aligned}\mu_i &\equiv \mathrm{E}\left[y_i\right], \\ g\left(\mu_i\right) &= \mathbf{X}_i\boldsymbol{\beta} = \beta_0 + \beta_1 x_{i,1} + \beta_2 x_{i,2} + \cdots + \beta_k x_{i,k}\end{aligned}, \tag{1}$$

where E[•] denotes the expectation of a random variable, $g(\bullet)$ is a monotonic link function, and the vector β contains $k + 1$ entries that describe the relationship between μ_i and the k covariates (plus an intercept) contained in each row vector $\mathbf{X}_i$ (Wood, 2006).

Because telemetry does not directly measure animal absence, researchers must decide whether to interpret a lack of detections as absence and encode them as zeros within a dataset. The temporal resolution of the study directly affects the number of zeros in the response, whereby many zeros will be included if animals are rarely detected over numerous short time intervals. Furthermore, environmental features like topography, weather, and biological noise, as well as collisions with other telemetry transmissions, can lead to false absences (Cagua, Berumen, & Tyler, 2013). A dataset will be more difficult to accurately model when the number of observed zeros is substantially greater than the number predicted; such models may show evidence of overdispersion (when the response variance is larger than expected) or lack of fit (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In these cases, zero-inflated models may provide more accurate results (Zuur et al., 2009).

Both discrete and continuous covariates can be included in GLMs if they are linearly related to the response. For nonlinear relationships, generalized additive models (GAMs) relate the response and covariates using a sum of smooth functions $f(\bullet)$ of the variables (Wood, 2006), e.g.

$$g\left(\mu_i\right) = f_1\left(x_{i,1}\right) + f_2\left(x_{i,2}, x_{i,3}\right) + \cdots \tag{2}$$

Detection data have been related to covariates like lunar phase and tidal stage (Dudgeon et al., 2013), water temperature (Kessel et al., 2014a; Udyawer et al., 2015), discharge (Richard, Bernatchez, Valiquette, & Dionne, 2014; Stich et al., 2015), and diel period (Ketchum et al., 2014; Zhang et al., 2015). Temporal data can also be used, often by summarizing the response into temporal blocks and including the blocks as a covariate. Blocks can be defined based on species ecology (e.g. reproductive timing), or anthropogenically (e.g. by monthly intervals; Matich & Heithaus, 2014). When investigating a temporal trend in the response, temporal autocorrelation should be checked and accounted for if the assumption of independence is violated, e.g. by incorporating lagged temporal variables (Kessel et al., 2014a) or including a correlation structure (Börger et al., 2006).

Because most detection data are collected under the largely uncontrolled conditions of the natural environment, some responses may only be independent when conditioned upon other variables. These variables, also known as random effects, can be accounted for by incorporating a second stochastic term into GLMs and GAMs to form generalized linear mixed models (GLMMs) and generalized additive mixed models (GAMMs; Wood, 2006). In practice, random effects are often included to account for variation within and among sampling units. For example, detection data are usually collected on a random subset of individuals from a population. To conduct population-level inference, individual ID can be included as a random effect with either, or both, an intercept and slope (Bolker et al., 2009). Random effects can also be associated with space or time, e.g. receiver location (Ketchum et al., 2014) or age and sampling year (Börger et al., 2006).

Generalized models were used to assess the factors affecting spatial distribution and movement of bull trout in the full complement of the illustrative dataset (Gutowsky et al., 2016). Using a GLMM, Gutowsky et al. (2016) assessed the effects of year, season, sex, and body size (covariates in **X**) on home range size (response **y**; 95% minimum convex polygon). A GAMM was used to quantify the relationship between total displacement (response **y**; sum of distances between receivers) and sex, body size, and smoothed month. Larger β coefficient values for spring and fall suggested that bull trout home ranges were larger in those seasons than in winter and summer. Additionally, a positive sex-size interaction term suggested that larger females moved farther than smaller females.

3.2 | Survival (time-to-event) analysis

Telemetry measures animal positions over time and changes in position can be related to important ecological events. For example, tagged animals may disperse or migrate (Kawabata et al., 2010), interact with humans (Thorley, Youngson, & Laughton, 2007), pass an obstacle (Castro-Santos & Haro, 2003; Martins et al., 2013; Naughton et al., 2005), be depredated (Danylchuk et al., 2007; Lennox et al., 2017b), or die (Curtis, Johnson, Diamond, & Stunz, 2015). These events can be analysed with GLMs using a binomial response, where study animals are grouped into those that experience an event and those that do not. Survival analysis extends the response by incorporating the time it takes for the event to occur (e.g. y = 2 days) and estimates the survival function, $S(t)$,

$$S(t) = \Pr\left(T > t\right), \tag{3}$$

which describes the probability, Pr(•), that an event will occur at some random time T after the set time t (Klein & Moeschberger, 2003; Pollock, Winterstein, Bunck, & Curtis, 1989). Two common survival function estimators include the non-parametric Kaplan–Meier and Nelson-Aalen estimators (Klein & Moeschberger, 2003). A log-rank test can be used to compare the estimated survival curves of different groups (e.g. sex and reproductive state or moult stage; Pollock, Winterstein, et al., 1989; Huserbråten et al., 2013).

Further inference is possible with the hazard function $h(t)$, which describes the conditional rate of an event occurring during a period of time $\{t, t + \Delta t\}$ given that it has not already been experienced (Klein & Moeschberger, 2003):

$$h(t) = \lim_{\Delta t \to 0} \frac{P[t \le T < t + \Delta t \mid T \ge t]}{\Delta t} \tag{4}$$

When the shape of the hazard or survival function is assumed, parametric survival analysis can be performed with error distributions (e.g. Weibull) and this allows for predictive extrapolation (Benoît et al., 2015). However, selecting a parametric hazard function requires accurate knowledge of the true shape, which is not often known (Murray, 2006; White & Garrott, 1990). Consequently, using semi-parametric Cox proportional hazards regression can be advantageous because there is no assumption about the hazard shape, yet the response can still be compared to a set of covariates $\mathbf{X}$ (Harrell, 2015; Murray, 2006),

$$h(t_i) = h_0(t_i)\, c(\mathbf{X}_i \boldsymbol{\beta}). \tag{5}$$

The hazard $h(\bullet)$ is related to an arbitrary baseline hazard $h_0(\bullet)$ that is treated non-parametrically, and a known parametric function $c(\bullet)$ of the covariates and their coefficients (Klein & Moeschberger, 2003). The Cox proportional hazards model is also less sensitive to outlying observations than parametric models, but does require hazard proportionality which can be verified graphically or by testing for independence between Schoenfeld residuals and time (Harrell, 2015). Violations of this assumption may be compensated for by fitting stratified models (Harrell, 2015).

In telemetry studies, animals often go undetected for extended periods, either because they leave the detection range of the array or because they are inactive. The resulting monitoring gaps can cause discontinuity in the hazard function (Murray, 2006) and bias survival estimates (Bunck, Chen, & Pollock, 1995). The Andersen–Gill estimator (Andersen & Gill, 1982) is a variation of the Cox proportional hazards model that uses a counting process to account for discontinuous monitoring (Murray, 2006; see e.g. Johnson, Boyce, Schwartz, & Haroldson, 2004). In addition, individuals that fully drop out of the study before the event occurs can be censored from survival analysis techniques without having to be removed entirely (Pollock, Winterstein & Conroy 1989). For example, Topping and Szedlmayer (2011) used survival analysis to study the residency time (event = emigration) of red snapper (*Lutjanus campechanus*), and censored fish that either died before emigration or did not emigrate in order to retain them in the analysis.

An example of survival analysis using detection data can be found in Martins et al. (2013), where the Kaplan–Meier estimator was used to compute the risk of bull trout unintentionally passing through hydro-electric dam turbines (the event of interest) from the full Kinbasket dataset. The Kaplan–Meier estimator exhibits larger jumps in the survival curve for the fall and winter, suggesting that the risk of passing through the dam was higher during those seasons.

3.3 | Mark-recapture models

Mark-recapture models are used for estimating movement or demographic attributes, e.g. abundance or survival. These models are fitted to data collected by capturing and marking a sample of animals from a population, subsequent release, and resampling such that additional samples can include both marked and unmarked animals (Amstrup, McDonald, & Manly, 2005). When using telemetry, mark-recapture models are applicable if the tagging procedure is considered the marking process, and detections are the recaptures. Few telemetry studies record the presence of untagged animals (but see Dudgeon, Pollock, Braccini, Semmens, & Barnett, 2015), therefore the most applicable mark-recapture models incorporate data collected on tagged animals only, which include known-fate, live-recapture, and recovery models (Lindberg, 2012).

Known fate models (related to survival analysis) assume perfect detection probabilities, which rarely occur in telemetry. Alternatively, live-recapture models are highly applicable for analyzing detection data because they enable the joint estimation of detection probability and demographic quantities. Among live-recapture models, the Cormack–Jolly–Seber model is frequently used, often to estimate survival along migratory routes (e.g. Moore et al., 2015; Welch et al., 2009). The Cormack–Jolly–Seber model is fitted using a product of probabilities with two basic parameters: ϕ is the probability that an individual survives between detections, and p is the probability that an individual is detected if alive and marked (Amstrup et al., 2005). The response variable consists of a binary encounter history (absence = 0 and presence = 1) for every marked animal that is recorded on a discrete temporal scale chosen by the researcher. If a single animal's encounter history is encoded as 1101, where the first digit is the initial capture and tagging, then the associated encounter probability would be

$$\phi p \phi (1 - p)\, \phi p, \tag{6}$$

if ϕ and p are assumed constant through time, or

$$\phi_1 p_2 \phi_2 (1 - p_3)\, \phi_3 p_4, \tag{7}$$

if these probabilities are allowed to vary. Because the Cormack–Jolly–Seber model cannot distinguish between mortality and emigration, survival estimates are more appropriately termed apparent survival (Williams, Nichols, & Conroy, 2001).

A useful extension of the Cormack–Jolly–Seber model is the multi-state Arnason–Schwarz model, which estimates survival and detection probabilities as a function of an observed animal state

(Schwarz, Schweigert, & Arnason, 1993; Amstrup et al., 2005). The states are assumed to follow a first-order Markov process governed by transition probabilities (Amstrup et al., 2005). It has been applied to detection data to estimate daily probabilities of horseshoe crab spawning (*Limulus polyphemus*; reproductive state; Brousseau, Sclafani, Smith, & Carter, 2004), survival of downstream migrating Atlantic salmon (*Salmo salar*; location state; Holbrook, Kinnison, & Zydlewski, 2011), and movement probabilities along walleye (*Sander vitreus*) migratory routes (location state; Hayden et al., 2014).

Recovery mark-recapture models are useful when the recapture process is terminal (Lindberg, 2012). Information on deceased individuals can be jointly modeled with live detection data using the Burnham model (Burnham, 1993), which has been used to provide more precise survival estimates (Sollmann, Furtado, Jácomo, Tôrres, & Silveira, 2010) and to estimate the joint probability that tagged individuals were caught and reported (Martins et al., 2011). The Barker model is an extension of the Burnham model useful for analysing temporally continuous detection data (Barker, 1997), and has been used to estimate the effects of gastric lavage on common snook survival (*Centropomus undecimalis*; Barbour, Boucek, & Adams, 2012). Finally, Fouchet, Santin Janin, Sauvage, Yoccoz, and Pontier (2016) proposed an approach for temporally continuous data that combines survival analysis with an inhomogenous Poisson process for modelling detection probability.

We fitted several Cormack–Jolly–Seber models using MARK (White & Burnham, 1999) and **RMark** (Laake, 2013) to test whether sex or length were associated with weekly bull trout survival, and whether the receiver array detection probability changed over time. We compared candidate models using corrected Akaike's information criterion (AICc), and found that the best model estimated intercepts only for both survival and the detection probability (Table 1). The apparent weekly survival probability was estimated at 0.91. In addition, the detection probability was estimated at 0.69, which suggests that a combination of receiver coverage/efficiency, environmental conditions, and fish behaviour limited the array's ability to detect bull trout.

TABLE 1 Model fits with corrected AIC (AICc) values from the mark recapture analysis of the illustrative bull trout dataset. Construction of the model is given by the Model Formula, where Φ(·) denotes the effects related to the apparent survival probability and p(·) denotes those related to the probability of detection. ~1 denotes an intercept only model. DeltaAICc is the difference in AICc from the best model

Model formula	No. parameters	AICc	ΔAICc
Φ(~1)p(~1)	2	258.0	0.00
Φ(~length)p(~1)	3	259.4	1.41
Φ(~sex)p(~1)	3	260.0	2.02
Φ(~sex × length) p(~1)	5	260.6	2.59
Φ(~sex + length) p(~1)	4	261.5	3.42
Φ(~1)p(~time)	4	261.5	3.50
Φ(~length)p(~time)	5	263.3	5.29
Φ(~sex)p(~time)	5	263.6	5.58
Φ(~sex × length) p(~time)	7	264.6	6.57
Φ(~sex + length) p(~time)	6	265.4	7.39

3.4 | Network analysis

Networks are mathematical objects consisting of nodes connected by edges (Dale & Fortin, 2010). They can be used to study animal movement by analysing the relationships between nodes, which can represent receivers or tagged animals separately (unipartite graphs; e.g. Jacoby, Brooks, Croft, & Sims, 2012) or simultaneously in the same graph (bipartite graphs; e.g. Finn et al., 2014). To study movement, nodes are often specified as the stationary receivers and edges represent either the directed or undirected movements of animals between receivers. Social aggregations can also be studied when the animals are treated as nodes, e.g. by testing whether there exist preferred associations among individuals (Stehfast et al., 2013).

A network's response variable is an adjacency matrix, which describes the connections between pairs of nodes (Farine & Whitehead, 2015). For example, the adjacency matrix

$$\begin{array}{c} R1 \\ R2 \\ R3 \\ \\ \end{array}\begin{array}{c}\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 3 \\ 0 & 0 & 4 \end{pmatrix} \\ R1\ R2\ R3 \end{array} \tag{8}$$

describes a system of three receivers (*R*1, *R*2, and *R*3), where three movements were recorded from *R*2 to *R*3 and four records indicate animals staying at *R*3. Adjacency matrices for null networks can also be of interest, e.g. to document potential direct routes among receivers. For the above example, the following null network

$$\begin{array}{c} R1 \\ R2 \\ R3 \\ \\ \end{array}\begin{array}{c}\begin{pmatrix} 1 & 1 & 0 \\ 1 & 1 & 1 \\ 0 & 1 & 1 \end{pmatrix} \\ R1\ R2\ R3 \end{array} \tag{9}$$

indicates that movements are possible between all pairs of receivers except from *R*1 to *R*3 in either direction. Once the adjacency matrix is defined, visuals and metrics can be calculated that describe the network connectivity (Dale & Fortin, 2010). For example, the node degree is the number of incoming and outgoing edges of a node, which describes the amount of traffic through a receiver and therefore may indicate areas of importance (Farine & Whitehead, 2015; Jacoby et al., 2012), whereas edge density is the fraction of observed edges to all theoretically possible edges, and can help indicate the amount of random/non-random movement (Jacoby et al., 2012).

Network metrics can be compared amongst groups, e.g. to determine sex-specific differences in movement (Jacoby et al., 2012) or preferred areas (Stehfast, Patterson, Barnett, & Semmens, 2015). When the groups are not necessarily known *a priori*, community detection algorithms can be used to identify groups of receivers or animals that are closely related, for example to identify home ranges (Finn et al., 2014). If an observed network can be classified as a theoretical network pattern, then known properties can be interpreted (e.g. Fox & Bellwood, 2014). Finally, disrupting the networks by removing nodes and studying the subsequent network fragmentation can help to assess the effects of habitat disruption (Jacoby et al., 2012) and the protective capabilities of potential marine reserves (Espinoza, Lédée, Simpfendorfer, Tobin, & Heupel, 2015).

Direct hypothesis testing on network measures is possible using GLMMs, but the assumption of independence may be violated (Farine & Whitehead, 2015). Permutation and randomization techniques provide non-parametric methods for hypothesis testing by comparing an observed statistic to those calculated from randomly generated networks (Dale & Fortin, 2010), and have been used to assess whether animals are moving randomly (Espinoza et al., 2015). In addition, networks can be compared to each other or other dyadic variables using a Mantel test which assesses the correlation between two matrices (Farine & Whitehead, 2015; Urban, Minor, Treml, & Schick, 2009), e.g. to test whether yellowfin tuna (*Thunnus albacares*) social associations are related to pre-defined cohorts (Stehfast et al., 2013). Relationships between networks and more than one covariate can be evaluated using the multiple regression quadratic assignment procedure (Farine & Whitehead, 2015), which has been used to assess the effect of environmental variables on small-spotted catshark (*Scyliorhinus canicula*) movements (Jacoby et al., 2012).

We applied network analysis to the bull trout dataset (Figure 2) after summarizing detection data into directed movements between pairs of receivers. Using the R package **igraph** (Csárdi & Nepusz, 2006) and treating the receivers as nodes, we plotted a network for each sex making the size of each node proportional to its degree and using weighted edges to represent the number of directed movements between nodes. These networks suggest that the main pool of the reservoir experiences more fish traffic compared to either of the reaches, and therefore likely contains important bull trout overwintering habitat. In addition, a Mantel test between the two networks suggested a weak but statistically significant ($r = 0.17$, $p < 0.05$) correlation in movement patterns between the males and females.

4 | FUTURE DIRECTIONS

4.1 | Gaussian random fields

Gaussian random fields (GRFs) are a promising approach for analyzing detection data within a spatial context. Specifically, GRFs estimate the residual spatial correlation remaining after accounting for measured explanatory variables (Thorson & Minto, 2015). In fisheries, they have been used to model the spatial dependence of population processes and to understand the relationship between fish distribution and habitat (Carson, Shackell, & Mills Flemming, 2017; Thorson & Minto, 2015; Thorson et al., 2015). With telemetry data, GRFs have been used to show how the number of at-sea seal encounters co-varied with bathymetry and distance to the seal haul-out site (Carson & Mills Flemming, 2014). In that study, the receiver locations changed through time; here, we demonstrate the potential of GRFs for detection data collected at fixed locations by investigating whether the presence of the dam affects bull trout distribution using the illustrative dataset. Because the GRF is a flexible hierarchical model, these data could have been modeled in several different ways. For example, we could have: modeled the duration or number of detections (e.g. Carson & Mills Flemming, 2014); accounted for false absences by using a zero-inflated distribution (e.g. Cosandey-Godin, Krainski, Worm, & Mills Flemming, 2015); or used a state-space model to account for technological error (e.g. Thorson et al., 2015).

We assumed that the number of individuals y_s detected at a given receiver location s (of which there are n) was Poisson distributed:

$$y_s \sim \text{Poisson}\left(\lambda_s\right). \tag{10}$$

We linked the mean of the distribution, λ_s, to the linear predictor, η_s, through a log-link function:

$$\log\left(\lambda_s\right) = \eta_s. \tag{11}$$

In turn, η_s was related to the distance between the receiver and the dam through the linear equation:

$$\eta_s = \beta_0 + \beta_1 x_s + \xi_s, \tag{12}$$

where β_0 represents the log of the number of detections expected when the distance to the dam (x_s) and the spatial random effect (ξ_s) both have no effect, and β_1 is the regression coefficient for x_s. The

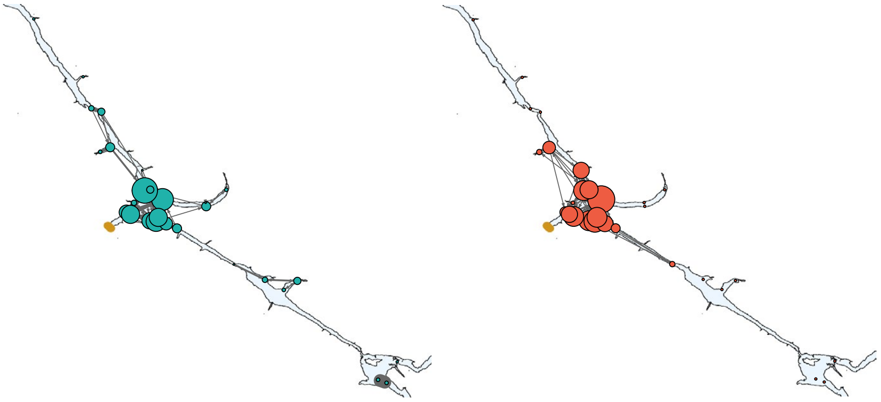


FIGURE 2 Sex-specific results from applying network analysis to the illustrative dataset. Yellow represents the position of the dam. Circles denote the receiver positions, and are weighted based on their node degree, i.e. the number of incoming and outgoing edges of a node. Edges are weighted based on the number of directed bull trout movements between receivers. Males are on the left (green), and females are on the right (orange)

random effect ξ_s accounts for the effect of unknown spatial factors influencing the response and we model it as a GRF, meaning that for any $\xi_s \in D \subset \mathbb{R}^2$, where D is the domain, we let $\xi = (\xi_1, \dots, \xi_n)^T$ be distributed as a multivariate normal:

$$\xi \sim \mathrm{MVN}\left(\mathbf{0}, \boldsymbol{\Sigma}\right). \tag{13}$$

Here, $\boldsymbol{\Sigma}$ is a $n \times n$ covariance matrix where the (i, j)th element of Σ is defined by the Matérn covariance structure, which for $i \neq j$ is defined as:

$$\mathrm{Cov}\left[\xi_i, \xi_j\right] = \frac{\sigma^2}{\Gamma(\nu)\, 2^{\nu-1}} \left(\kappa h_{i,j}\right)^{\nu} K_{\nu}\left(\kappa h_{i,j}\right), \tag{14}$$

where $h_{i,j}$ is the Euclidean distance between receiver locations s_i and s_j, the smoothness parameter ν is set equal to 1, and the spatial scale κ and marginal variance σ^2 are both estimated. As in Thorson et al. (2015), we used R-INLA (Illian, Sørbye, & Rue, 2012) to simplify model implementation with stochastic partial differential equations (SPDEs) and we used TMB (Kristensen, Nielsen, Berg, Skaug, & Bell, 2016) to estimate the model parameters.

Model fitting resulted in parameter estimates of β_0 = 2.42 (95% CI: 1.73–3.12) and β_1 = − 0.042 (95% CI: −0.063 to −0.022), indicating that as distance to the dam increased the number of individuals detected decreased. This may result in part because the distance from the dam increases proportional to the distance from the main lacustrine habitat for most locations within the reservoir. In addition, the spatial correlation of the GRF accounts for some of the bull trout distribution not explained by distance from the dam (Figure 3).

4.2 | Accounting for spatial correlation and measurement error

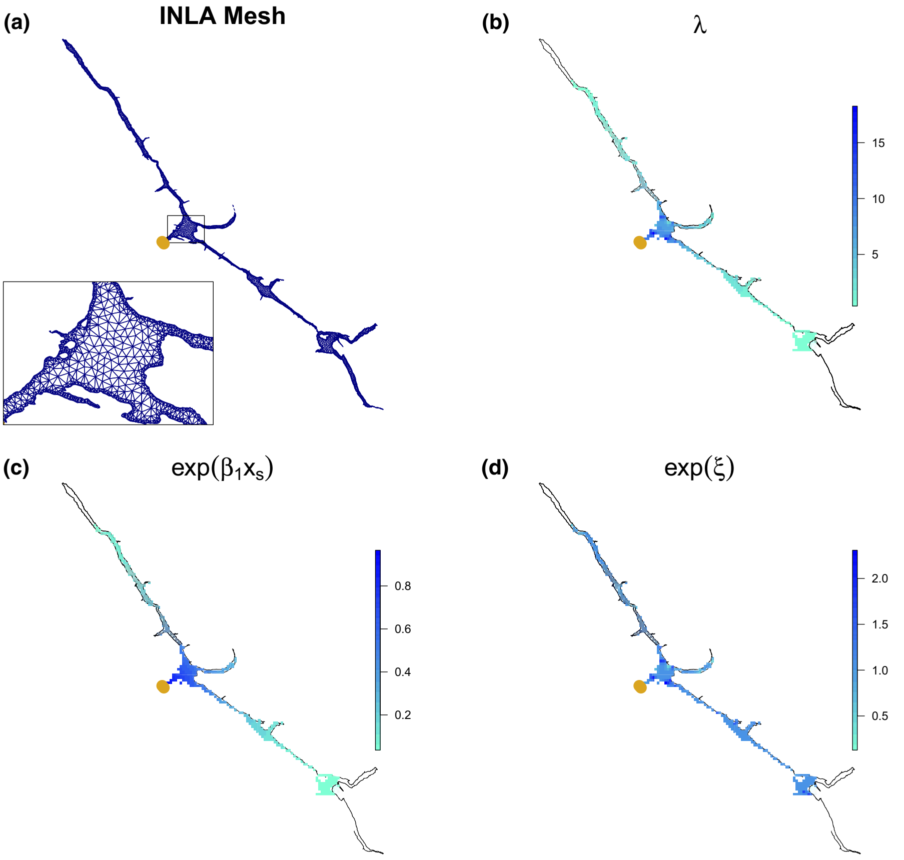
We expect that methods for estimating spatial correlation associated with animal movement will grow in popularity as receiver coverage and method documentation continue to expand. While we proposed the GRF as a flexible method for modelling animal movement data with a spatial component, other spatial methods exist that could be applied to detection data. For example, one terrestrial study used a spatial (and temporal) correlation structure within a GLMM to assess the factors affecting home range size of radio-tracked roe deer (*Capreolus capreolus*; although home range in this case was calculated from spatially continuous detection data, similar principles would apply to responses calculated from discrete detection data; Börger et al., 2006). Network autocorrelation models (Leenders, 2002) could be used to estimate the correlation between network attributes caused by receiver location. In addition, spatial capture–recapture models are a spatial extension of mark-recapture models, and are well established in terrestrial studies with encounter data like those generated by camera trapping (Royle, Chandler, Sollmann, & Gardner, 2014). These models involve hierarchical modelling of a spatial point process of unobserved animal activity centres and a detection probability function depending on distance from the activity centres (Efford & Fewster, 2013). Despite similarities with terrestrial encounter data, we have seen few studies that apply spatial capture–recapture methods to aquatic detection data, but see Raabe, Gardner, and Hightower (2014), who studied the survival and movement of PIT-tagged American shad (*Alosa sapidissima*) using these methods.

Many studies have investigated the measurement error of aquatic tracking technology by estimating the detection efficiency (the frequency with which a receiver will detect a fish within its given range; Simpfendorfer, Heupel, & Collins, 2008), detection range (the probability of detection given distance from a receiver; Kessel et al., 2014b), or the frequency of false detections (when a receiver logs a false ID or detects an absent animal; Heupel, Semmens, & Hobday, 2006). However, few studies incorporate this information into their biological inferences. Those that do may use it to pre-process their data (e.g. Hoenner et al., 2018; Kessel et al., 2014a), or directly incorporate measurement error into the statistical method (Pedersen & Weng, 2013; Simpfendorfer et al., 2008; Winton, Kneebone, Zemeckis, & Fay, 2018). Measurement error can additionally be used to help numerically optimize the spatiotemporal design of a receiver array before deployment, resulting in a study design with enhanced ability to acquire high-quality data (Pedersen, Burgess, & Weng, 2014).

State-space models are hierarchical models that can pair a measurement equation with a model for animal movement, and simultaneously estimate both processes (Auger-Méthé et al., 2017). Two notable examples with detection data include: (a) a non-parametric function for detection probability paired with an Ornstein–Uhlenbeck movement process to estimate the home range of a humphead wrasse (*Cheilinus undulatus*; Pedersen & Weng, 2013); and (b) a Gaussian decay measurement equation coupled with a binomial spatial point process to estimate centres of activity of a black sea bass (*Centropristis striata*; Winton et al., 2018). State-space models have gained popularity for analyzing spatially continuous animal movement data, likely because of their flexibility—multiple measurement error distributions can be included and matched specifically to the tracking technology (e.g. Winship et al., 2012), and the movement process can range from individual models of movement (e.g. Auger-Méthé et al., 2017) to GRFs (e.g. Thorson et al., 2015). We believe that state-space models could provide a framework that improves the reliability of statistical analyses of detection data.

4.3 | Broadening the scope of animal movement analyses

Telemetry technology will continue to improve technically in ways that will increase study longevity, target more species or life stages, and expand the scope of data collection (Lennox et al., 2017a). Study designs will also evolve, as auxiliary biological and environmental variables are collected during sampling or independently, and as telemetry networks facilitate the sharing of resources and multi-species data (Lennox et al., 2017a). As a result, telemetry studies will have the potential to generate massive, interdisciplinary datasets, and statistical methods for analysing such complex data will have to adapt appropriately. In the future, movement ecologists may look



INLA Mesh

λ

$\exp(\beta_1 x_s)$

$\exp(\xi)$

FIGURE 3 Results from the GRF analysis on the illustrative dataset. (a) shows the mesh calculated by the INLA SPDE; (b) represents the expected number of bull trout across the reservoir returned by the full model; (c) represents the expected number of fish as influenced by distance from the dam; and (d) represents the expected number of fish based on the effect of the GRF only. Yellow represents the position of the dam

to the burgeoning research field of human mobility, which has exploded since the advent of the smartphone with GPS tracking and geolocated social media postings (Thums et al., 2018). Because humans and non-human animals appear to conform to similar ecological principles, e.g. site fidelity, aggregation, and sociality (Meekan et al., 2017), movement ecologists will have the opportunity to readily appropriate big data approaches from human mobility studies (Thums et al., 2018).

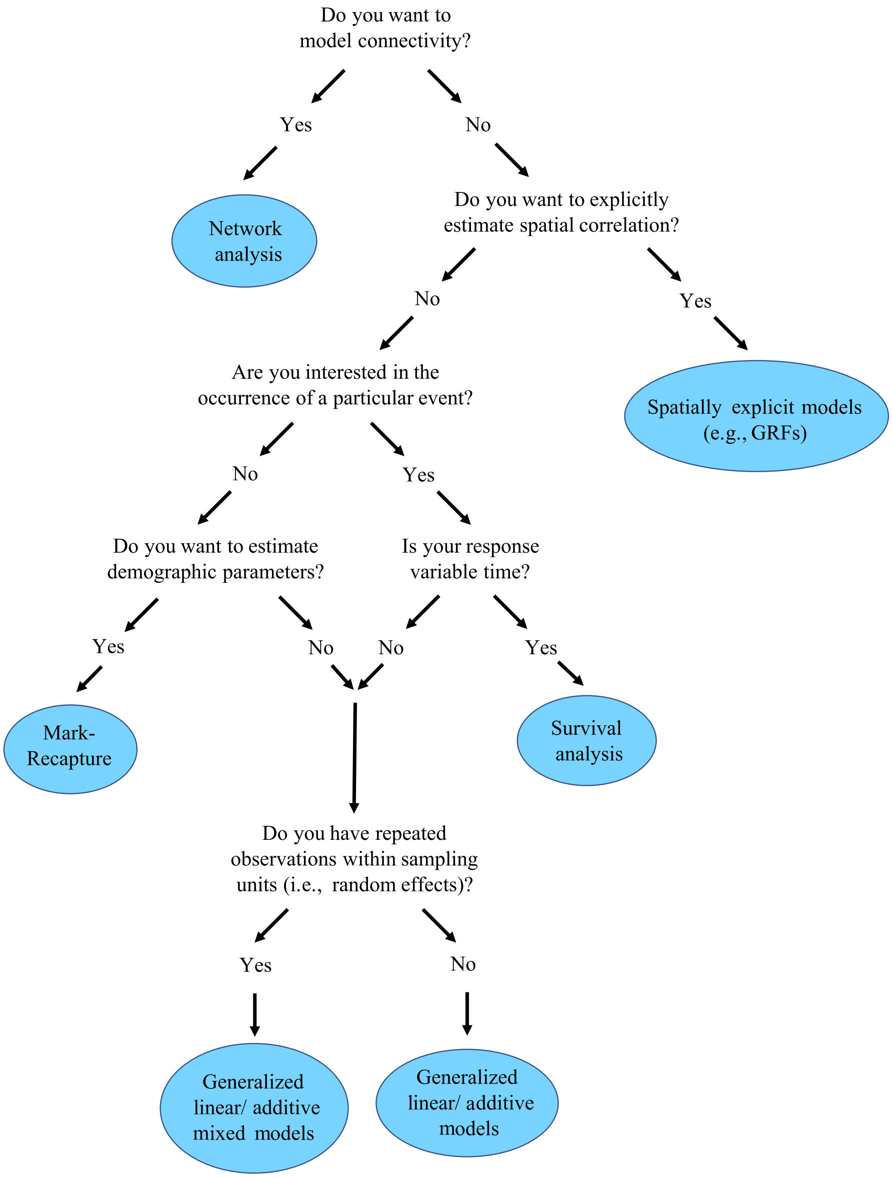
5 | DISCUSSION

To aid researchers in matching a statistical method to their data and study objective, we devised a decision tree which we present in Figure 4. We recognize that accounting for every possible study design would be unrealistic, therefore we suggest that researchers utilize our decision tree as a first general guide through some of the possible statistical methods, not an exhaustive instruction catalog. We hope that a tree will help researchers narrow their selection, but then we strongly suggest that this is followed by comprehensive study of the chosen method(s), and its(their) accompanying assumptions. To that end, we summarize our guide below.

We suggest using mark-recapture methods when studying population dynamics, especially when the detection ability of the array is suspect. However, note that the most commonly used mark-recapture method, the Cormack–Jolly–Seber model, is dependent upon the following assumptions: (a) tags are not lost and do not fail; (b) survival is not influenced by the tag or tagging procedure; and (c) survival and detection probability do not vary among tagged animals. Preliminary laboratory studies assessing tag attachment and retention can help to determine the risk of tag loss or failure (Holbrook, Perry, Brandes, & Adams, 2013). Holding studies can be used to assess whether tagging influences survival (Furey et al., 2016); however, tagging may negatively affect multiple traits in a cumulative way such that the full influence is not understood by assessing the effect on survival alone (Bodey et al., 2018). In fact, tagging can affect traits like growth, swimming performance, and social interactions (Jepsen, Thorstad, Havn, & Lucas, 2015), and these potential effects should be carefully considered in any analysis. Finally, some of the factors affecting individual variation in survival and detection (e.g. sex, age) can be incorporated into the Cormack–Jolly–Seber model through stratification or regression analysis (Williams et al., 2001).

To understand the occurrence of an event when temporal records for the event exist, consider using survival analysis. Survival analysis can be used to understand the survival of tagged animals; however, it is distinguishable from mark-recapture via their response variables. Survival analysis requires a temporal value for the response (e.g. y = 12 hr), whereas mark-recapture uses a discrete time series (e.g. 1001101), and time is often incorporated by allowing probabilities to be dynamic. Although a temporal response can also be modelled using GLMs/GLMMs/GAMs/GAMMs, survival

FIGURE 4 Decision tree for identifying appropriate statistical methodologies for analyzing detection data collected by acoustic, radio, or PIT telemetry



analysis can account for the fact that for some study animals it may not be possible to determine whether they experience the event (censoring). Censoring is appropriate as long as the probability of being censored is independent of the probability of the event (Harrell, 2015).

To describe the connectivity among receiver locations or tagged animals, we encourage the use of network analysis which provides easily interpretable visualizations of this connectivity. However, network analysis does assume that all the nodes of a system are represented in the graph (Dale & Fortin, 2010) and is therefore more useful for datasets collected by many receivers/individuals. Nodes and edges must be carefully defined in order to accurately represent the study system; any deviations from the true network, for example through data transformation, inclusion of false absences, or exclusion of individuals, can significantly impact network measures and the overall network structure (Farine & Whitehead, 2015).

If spatial correlation is of interest then researchers should use spatially explicit methods like GRFs. It is possible to incorporate spatial information into some of the other statistical methods we have described. For example, with network analysis a receiver node can include a location, and with regression-type analyses (e.g. Cormack–Jolly–Seber models or GLMs) spatial references can be incorporated as covariates. However, spatial models are distinguishable from these methods because they estimate spatial correlation, which when ignored can invalidate analyses by violating the assumption of independence (Thorson & Minto, 2015). In addition, estimating spatial correlation can show how unobserved/unmeasured variables correlated in space affect the response variable (Carson & Mills Flemming, 2014; Thorson et al., 2015). Network autocorrelation models, spatial capture–recapture, or spatial generalized models (not reviewed here; see Zuur et al., 2009) can also be used to estimate spatial correlation.

Finally, for most other scenarios, we recommend using GLMs/GLMMs or GAMs/GAMMs. Generalized modelling is arguably the most accessible statistical method presented in this paper in terms of documentation and application. It is also flexible, as several different response variables can be used, both linear and nonlinear covariate relationships are possible, and random effects and correlative structures can be included (Zuur, Ieno, & Saveliev, 2017). However, these methods come with their own assumptions (e.g. distribution assumptions of the residuals) and complexities, therefore we would encourage readers to consult more specific guides (e.g. Bolker et al., 2009) before implementation.

6 | CONCLUSION

Telemetry is increasingly used to track aquatic animals. This has led to a massive expansion in the volume and detail of ensuing movement data, and significant growth in the availability of suitable statistical methods. It is often no longer sufficient to rely on relatively simple descriptive analytical techniques, yet choosing from among available methods can be daunting. We reviewed advanced statistical methods useful for detection data in order to introduce them to aquatic telemetry users and provide researchers with the tools necessary for more comprehensive detection data analysis. We focused specifically on detection data recorded in aquatic environments, which can differ in small but substantial ways from those collected in terrestrial studies. For example, the camera traps often used in terrestrial studies can detect previously unknown/unmarked individuals, whereas acoustic, radio, and PIT receivers can only identify tagged individuals, thus hindering our ability to estimate population size from these data using mark-recapture methods. However, some of the methods mentioned here (e.g. spatially explicit capture–recapture) have been established in terrestrial studies for 10+ years, and minor modifications could significantly enhance the analysis of aquatic detection data. Going forward, we recommend that aquatic ecologists look towards terrestrial studies and other fields like human mobility to help motivate the statistical advances that will be needed to analyse detection datasets that are rapidly growing in both size and complexity.

ACKNOWLEDGEMENTS

The authors are indebted to several funding agencies. This research was supported by the Ocean Tracking Network (OTN), a Canadian Statistical Sciences Institute (CANSSI) Collaborative Team Project, and grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) to M.A.-M., E.G.M., J.M.F., S.J.C. and M.P. K.W. was supported by an NSERC postgraduate scholarship and a Killam Predoctoral Scholarship, while M.A.-M. received an NSERC postdoctoral fellowship and E.G.M. was supported by a Liber Ero Postdoctoral Fellowship. S.J.C. acknowledges the Canada Research Chairs Program. The data used for the illustrative case study was collected as part of the NSERC HydroNet Strategic Network Grant Program with additional support from BC Hydro. This paper is a contribution of the ideasOTN committee of OTN. The authors sincerely thank Jonathon Pye and Fred Whoriskey for comments and support for the manuscript, as well as Luca Börger and two anonymous reviewers for their crucial input that significantly improved the paper.

AUTHORS' CONTRIBUTIONS

E.G.M. conceived the project idea. S.J.C. and M.P. provided the data. K.W. and M.A.-M. analysed the data with input from E.G.M. and L.F.G.G. K.W. led the writing of the manuscript, but all authors contributed significantly to all drafts and approved the manuscript for publication.

DATA ACCESSIBILITY

Supplementary code and data for the illustrative analyses are available via GitHub at https://doi.org/10.5281/zenodo.2628108. The data are also available publicly through OTN at https://doi.org/10.14286/2019-kinbasket-bulltrout.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Whoriskey K, Martins EG, Auger-Méthé M, et al. Current and emerging statistical techniques for aquatic telemetry data: A guide to analysing spatially discrete animal detections. *Methods Ecol Evol*. 2019;00:1–14. https://doi.org/10.1111/2041-210X.13188