Received: 16 May 2019 | Accepted: 23 September 2019

DOI: 10.1111/2041-210X.13322

RESEARCH ARTICLE

Methods in Ecology and Evolution

A practical method to account for variation in detection range in acoustic telemetry arrays to accurately quantify the spatial ecology of aquatic animals

Jacob W. Brownscombe[1,2] | Lucas P. Griffin[3] | Jacqueline M. Chapman[1] | Danielle Morley[4] | Alejandro Acosta[4] | Glenn T. Crossin[2] | Sara J. Iverson[2] | Aaron J. Adams[5,6] | Steven J. Cooke[1] | Andy J. Danylchuk[3]

[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, ON, Canada; [2]Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada; [3]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA, USA; [4]Florida Fish and Wildlife Conservation Commission, Marathon, FL, USA; [5]Bonefish and Tarpon Trust, Coral Gables, FL, USA and [6]Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, FL, USA

Correspondence
Jacob W. Brownscombe
Email: jakebrownscombe@gmail.com

Funding information
Bonefish and Tarpon Trust (BTT); Natural Sciences and Engineering Research Council of Canada; Canada Research Chairs; National Institute of Food & Agriculture; U.S. Department of Agriculture; Massachusetts Agricultural Experiment Station; Massachusetts Department of Environmental Conservation

Handling Editor: Edward Codling

Abstract

1. Acoustic telemetry is a popular tool for long-term tracking of aquatic animals to describe and quantify patterns of movement, space use, and diverse ecological interactions. Acoustic receivers are imperfect sampling instruments, and their detection range (*DR*; the area surrounding the receiver in which tag transmissions can be detected) often varies dramatically over space and time due to dynamic environmental conditions. Therefore, it is prudent to quantify and account for variation in *DR* to prevent telemetry system performance from confounding the understanding of real patterns in animal space use. However, acoustic receiver *DR* consists of a complex, dynamic, three-dimensional area that is challenging to quantify.
2. Although quantifying the absolute *DR* of all receivers is infeasible in the context of most acoustic telemetry studies, we outline a practical approach to quantify relative variation among receiver *DR* over space and time. This approach involves selecting a set of sentinel receivers to monitor drivers of variation in detection range. Each sentinel receiver is subject to a range testing procedure to estimate detection efficiency (*DE*; the proportion of total transmissions detected by the receiver), at a range of distances from the receiver, to derive the maximum range (*MR*; distance from the receiver where *DE* is 5%) and *Midpoint* (distance from the receiver where *DE* is 50%). A reference transmitter is then placed at the *Midpoint*, providing a standardized measure of long-term variation in *DE*, with each station having similar freedom of variance. Variation in reference tag *DE* is then combined with *MR* to calculate a *DR* correction factor (*DRc*). A modelling approach is then used to estimate *DRc* for all receivers in the array at spatial and temporal scales of ecological interest, which can be used to correct animal detection data in various ways.

3. We demonstrate this method with a hypothetical dataset, as well as empirical data from an acoustic telemetry array to delineate spatio-temporal patterns of fish habitat use.
4. This is a flexible and practical approach to account for variation in acoustic receiver performance, allowing more accurate spatial and temporal patterns in aquatic animal spatial ecology to be revealed.

KEYWORDS

acoustic telemetry arrays, animal tracking, bioacoustics, biotelemetry, data analysis, detection range, machine learning, spatial ecology

1 | INTRODUCTION

Passive acoustic telemetry arrays have become one of the most popular approaches for quantifying the spatial, behavioural, and physiological ecology of aquatic animals (Cooke et al., 2016, 2004; Donaldson et al., 2014; Hussey et al., 2015). This tracking technique involves tagging animals with acoustic transmitters that periodically emit acoustic signals with unique identification codes (tag IDs), which are detected by acoustic receivers placed throughout the study area (or roving on autonomous vehicles or even other animals) to continuously monitor for tag transmissions. In studies to date, receivers are usually configured in one of two ways: at fixed locations within a study area where they function as non-overlapping nodes in a broad-scale telemetry array (Brownscombe, Lédée, et al., 2019; Heupel, Semmens, & Hobday, 2006), or in closer proximity with overlapping detection ranges to enable high-resolution estimates of animal positions (up to sub-meter accuracy in some cases; Cooke et al., 2005; Espinoza, Farrugia, Webber, Smith, & Lowe, 2011).

For acoustic telemetry systems to function effectively, the transmissions emitted from animal-borne tags must travel through the water uninterrupted so the unique tag ID can be fully decoded by one or more receivers. However, acoustic transmissions are routinely attenuated, refracted, or lost due to spreading in water (Singh et al., 2009), disrupted by physical barriers, and/or muted by environmental or biological noise prior to reaching receivers (Kessel et al., 2014). False detections (i.e. erroneous or incorrect tag IDs) can also occur when tag IDs become mutated by noise but are still decoded by the receiver, or by code collision when transmissions from multiple tags, operating on the same frequency, arrive simultaneously at a receiver (Simpfendorfer et al., 2015). For these reasons, passive acoustic telemetry arrays are imperfect sampling systems which, depending on the physical and environmental conditions in which they are placed, vary in their ability to accurately detect tagged animals in time and space (Kessel et al., 2014; Mathies, Ogburn, McFall, & Fangman, 2014). If not accounted for, variation in system performance has the potential to cause erroneous conclusions regarding animal distribution and behaviour. For example, Payne, Gillanders, Webber, and Semmens (2010) demonstrated how diel patterns in cuttlefish *Sepia apama* space use could have been grossly misinterpreted without correcting for diel variation in the performance of the tracking system. In that case, raw acoustic detections suggested cuttlefish utilized a nearshore area most often during daylight hours, but after correcting for acoustic receiver detection efficiency, the data suggested cuttlefish were present more often at night. This example demonstrates the saliency of correcting for acoustic receiver performance to reveal true patterns in animal spatial-temporal ecology.

Many studies have explored the factors that influence the ability of acoustic receivers to detect acoustic transmitters, with some interchangeable use of the terms 'detection range' (*DR*), 'detection efficiency' (*DE*), 'detection probability', and 'system performance' (see Gjelland & Hedger, 2013; Huveneers et al., 2016; Kessel et al., 2014; Mathies et al., 2014; Simpfendorfer, Heupel, & Collins, 2008). Kessel et al. (2014) define *DR* as 'the relationship between detection probability and the distance between the receiver and tag'. Alternatively, *DR* can be considered the three-dimensional area surrounding an acoustic receiver in which tag transmissions can be effectively detected by the receiver (see Table 1 for definition of terms). The size and shape of *DR* varies amongst receivers, as well as over time, due to dynamic environmental conditions that influence the efficacy of signal transmission (see Kessel et al., 2014; Loher, Webster, & Carlile, 2017; Selby et al., 2016 for examples). Quantifying absolute *DR* of all receivers in a telemetry system (i.e. system performance) would therefore require extensive reference tag deployments (i.e. stationary transmitters placed in proximity of receivers) at a range of distances in three dimensions around every receiver, which is infeasible for most telemetry studies. The time, financial commitment, and computational effort needed to quantify variation in and among *DR*s may be why the majority of telemetry studies to date have failed to account for it (Kessel et al., 2014). Fine-scale tracking systems typically require 'synchronization tags' to function, which also provide reference data that can be used to correct for system performance (e.g. Binder, Holbrook, Hayden, & Krueger, 2016; Brownscombe, Griffin, et al., 2019). Within broad-scale telemetry arrays, many studies have used reference tags at set distances from receivers to explore the environmental factors that influence *DR* (see Kessel et al., 2014 and references therein) with a particular focus on its relevance to array design (Reubens et al., 2018; Selby et al., 2016; Stocks, Gray, & Taylor, 2014). In one of the most extensive applications to date, Selby et al., (2016) used a combination of range testing procedures for a short time period to predict detection probability across an acoustic array. However, few studies to date

TABLE 1 Variables relevant to quantifying acoustic receiver performance and correcting animal detection data using passive acoustic telemetry systems

Variable	Acronym	Definition
Detection range	*DR*	Three-dimensional spatial region surrounding an acoustic receiver in which transmitters can be detected
Detection efficiency	*DE*	The number of acoustic transmitter detections effectively logged by an acoustic receiver in a given time period, expressed as a percentage (or proportion) of total potential detections based on transmission rate
Maximum detection range	*MR*	Maximum distance from an acoustic receiver in which transmitters can be detected (5% *DE*), estimated via range testing
Detection efficiency variance	*DEv*	Difference between detection efficiency in a given time period and the mean detection efficiency of a reference tag by an acoustic receiver; Equation 1
Corrected detection efficiency variance	*DEvc*	*DEv* standardized to ±50%; Equation 2
Midpoint	*Midpoint*	Estimated distance from an acoustic receiver where mean detection efficiency is 50%
Detection range correction factor	*DRc*	Detection range correction factor derived from *MR* and *DEv* or *DEvc*; Equation 3
Animal tag detections	*Det*	The number of detections from animal-borne acoustic transmitters
Corrected animal detections	*Detc*	The number of detections from animal-borne acoustic transmitters corrected using *DRc*; Equation 4

have quantified long-term variations in *DR* over the course of a study and applied these measures to separate system performance from patterns in animal spatial ecology.

Currently, there is no standardized protocol to quantify and correct for the variation in acoustic telemetry system performance, despite the fact that it could severely bias study findings if not accounted for, especially in studies focused on spatio-temporal aspects of animal ecology. There has been a rapid increase in acoustic telemetry studies in recent years (Hussey et al., 2015), and this issue is relevant to many of these studies but is rarely addressed. Although quantifying absolute *DR* for all receivers within an acoustic telemetry system is ideal, it is impractical for most studies due to logistical constraints (i.e. time and money), which is likely why it is rarely accomplished. Instead, a relative measure of system performance could serve to correct animal detection data over ecological (spatial and temporal) scales of interest. Here, we present a practical approach to generate a relative measure of telemetry system performance and apply this measure as a correction factor to reveal more accurate patterns in animal ecology. The general approach we propose could be followed with a number of variations that we describe here, with more extensive sampling approaches being more ideal and less prone to error, balanced with the realities of conducting tracking studies. It is our hope that this approach will be accessible for researchers and become a routine method for system performance correction that will improve the reliability of findings from aquatic animal telemetry studies.

2 | MATERIALS AND METHODS

2.1 | An approach to quantify and correct for system performance

Our conceptual approach for quantifying and accounting for variation in acoustic receiver *DR* and correcting animal detection data is outlined in Figure 1; R code and sample data for implementing these analyses are included in Supporting Information I. Recognizing that it is impractical for most telemetry studies to quantify variation in the size and shape of the three-dimensional *DR* of every receiver within an acoustic array, our approach involves the analysis of a subset of 'sentinel receivers', at which variation in detection ranges are monitored. These receivers must capture the range of environmental and physical conditions present in the system (e.g. different water depths, substrate types, regions, and locales that may experience varied effects of temporal factors such as wind) because data from these sites will be used to predict *DR* correction factors (*DRc*; Table 1) at additional receiver sites in the array. If the sentinel receivers are not representative of the system, the predictions have the potential to be biased. At each sentinel receiver, *DRc* is estimated in a two-step process, involving (1) a range testing procedure to estimate maximum detection range (*MR*; i.e. the distance where *DE* is estimated at 5%; Table 1) and *Midpoint* (i.e. the distance where *DE* is 50%), and (2) placing a reference transmitter in proximity to sentinel receivers at the *Midpoint* to characterize variation in *DE* over

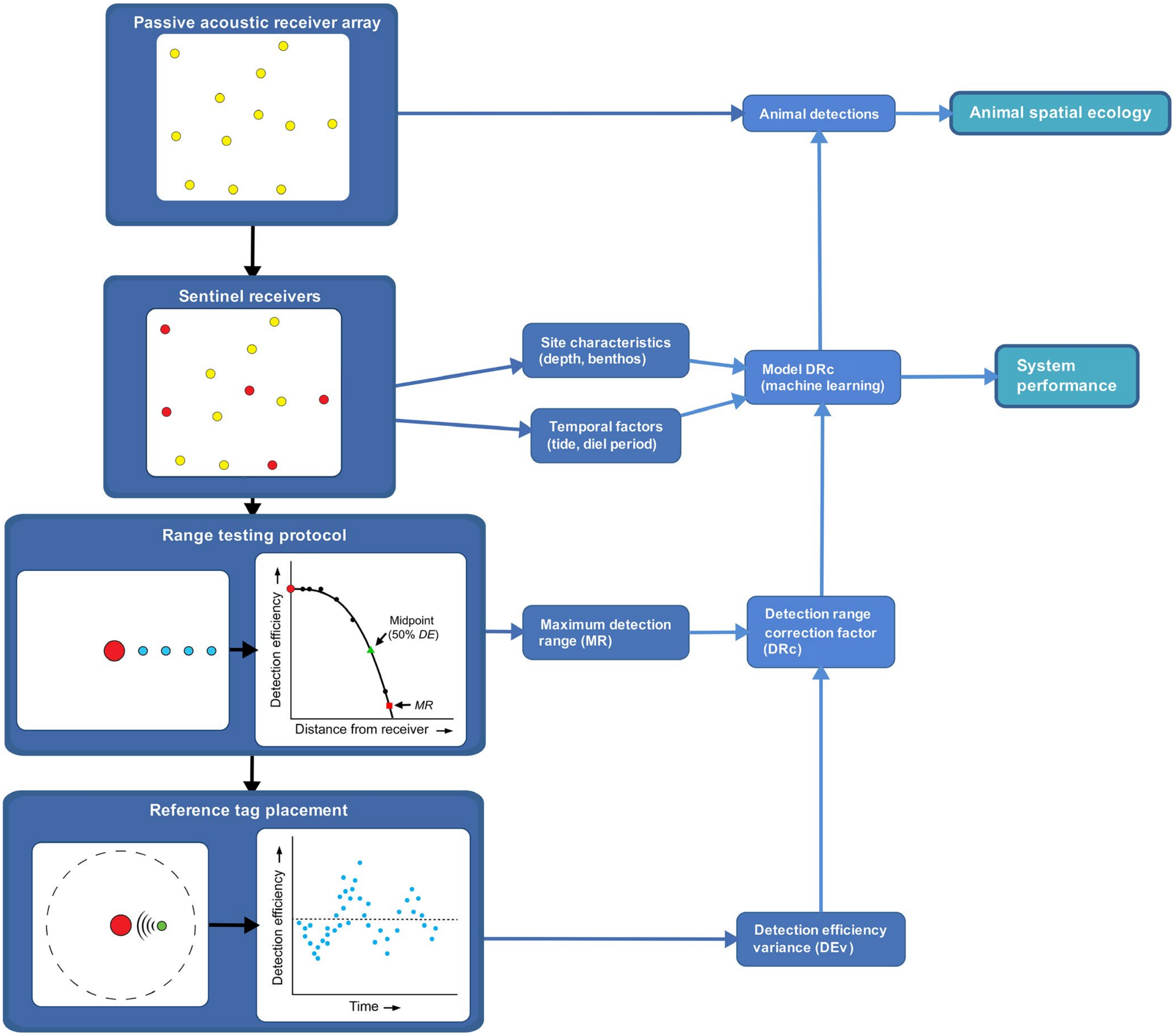

FIGURE 1 Conceptual diagram outlining an approach to quantify variation in acoustic receiver detection range (*DR*) to correct animal detections, separating the performance of the acoustic receiver system from patterns in animal spatial ecology. On the left, yellow circles illustrate acoustic receivers, red circles sentinel tag sites, blue circles range testing locations, and the green circle a reference tag. *DE* = detection efficiency; *MR* = maximum range; *DEv* = detection efficiency variance; *DRc* = detection range correction factor

the course of the entire study period. These two measures are then combined to derive *DRc* (Figure 1). Stage (1) can be accomplished either by placing a range testing transmitter (i.e. one emitting regular transmissions at relatively short intervals, often 10 s) at a range of distances from the receiver for short periods (i.e. minutes to hours) off the side of a boat, or by placing stationary (moored to the benthos) transmitters for longer periods (i.e. days to weeks; see Kessel et al., 2014 for review of approaches). Importantly, acoustic transmitters often have a burst period (the period of time that the tag is transmitting the acoustic signal; e.g. ~3 s with Vemco range testing tags), which must be accounted for when calculating the expected number of detections within a given period (e.g. below, range testing tags had a delay of 7 s, with a burst period of 3 s – transmissions are expected every 10 s). These data are then used to model the relationship between the distance from the receiver and *DE* to predict *MR and Midpoint*. Based on this information, in stage (2) a reference transmitter (i.e. one with a relatively long transmission delay, often 200–700 s) is stationed at the *Midpoint* for the entire study period. By placing the reference tag at the *Midpoint*, each reference tag has a similar freedom of variance (i.e. ±50%) from the mean *DE* at each sentinel receiver, which is important for further calculations used to correct animal detection data.

Variation in *DE* from reference tags (*DEv*) is calculated at any timescale of interest (e.g. hourly) by subtracting the *DE* for that time period (*t*) from the overall mean detection efficiency for each sentinel receiver (*r*) over the entire study period (μ_r) using Equation 1. In some cases, as below in our application, μ_r may deviate from 50% amongst receivers. In this case *DEvc* can be calculated using Equation 2 to scale the variability to ±50%. *DR* and *DEv* (or *DEvc*) are then used to calculate a detection range correction factor (*DRc*) using Equation 3. R code for these calculations is included in Supporting Information I.

$$DEv_{r,t} = DE_{r,t} - \mu_r \quad (1)$$

$$\begin{aligned} DE_{r,t} - \mu_r < 0 \Leftrightarrow DEvc_{r,t} &= \frac{DE_{r,t} - \mu_r}{\mu_r} \times 50 \\ DE_{r,t} - \mu_r \geq 0 \Leftrightarrow DEvc_{r,t} &= \frac{DE_{r,t} - \mu_r}{(100 - \mu_r)} \times 50 \end{aligned} \quad (2)$$

$$DRc_{r,t} = MR_r + MR_r \times \frac{DEv_{r,t}}{100} \quad (3)$$

DRc therefore integrates the initial estimate of *MR* with variations in *DE* over time to capture temporal variations in the performance of each sentinel receiver. Although *DRc* does not represent variability in absolute *DR* over time, it serves as a relative measure of performance amongst sentinel receivers. To generate an estimate of *DRc* for all receivers in a telemetry array, estimates of *DRc* from sentinel tag receivers must be used to predict *DRc* at all receivers in the array. This could be accomplished using various modelling approaches such as multivariate frequentist statistics, Bayesian inference, or, as used below, machine learning.

DRc can be applied to animal detections across an array of acoustic receivers in a variety of ways. Researchers are commonly interested in presence/absence of tagged animals, in which case *DRc* could be integrated into detection probability estimates with mark-recapture models (Amstrup, McDonald, & Manly, 2006; Whoriskey et al., 2019), occupancy models (MacKenzie et al., 2002; Tyre, Tenhumberg, Field, Niejalke, & Possingham, 2013), or integrated as fixed or random effects in Generalized Linear or Additive Mixed Effects models (Zuur, Ieno, Walker, Saveliev, Smith, & Ebooks Corporation, 2009) or Bayesian models (Zuur, Ieno, Anatoly, & Saveliev, 2017). *DRc* could also be used to generate more accurate estimates of animal spatial positions using state space models (Dorazio & Price, 2018; Pedersen & Weng, 2013). In simpler applications, researchers are interested in the number of animal detections over space and/or time. For example, Payne et al. (2010) used detection efficiency of reference tags to correct diel patterns in animal detection numbers. Here, we provide a simple example application of *DRc* to the number of animal detections (*Det*) amongst receivers (*r*) and time (*t*) with Equation 4 to derive the corrected number of animal detections (*Detc*), where μ is the overall mean *DRc* of the system.

$$Detc_{r,t} = \frac{Det_{r,t}}{DRc_{r,t}/\mu} \quad (4)$$

To illustrate how this approach performs, it is applied here to both a generated hypothetical dataset, as well as empirical telemetry data from a study of permit *Trachinotus falcatus* in the Florida Keys.

2.2 | Application to a hypothetical dataset

All analyses were conducted using R (R Core Team, 2018) via RStudio (RStudio Team, 2016). Our first analysis was applied to a hypothetical dataset generated with 1,000 data points, in which *MR* varied randomly between 50 to 500 m, *DEv* between −50 to +50%, and *Det* between 0 and 10. The relationship between *MR*, *DEv*, and *DRc* were plotted to illustrate how *DRc* is derived, and the relationship between *Det* and *Detc* were plotted to illustrate the level of variability that can occur between these metrics using this approach. This exercise did not address sentinel site selection, or *DRc* modelling and prediction to non-sentinel receivers, which is conducted below with a real-world telemetry dataset.

2.3 | Empirical telemetry data

An array of 60 acoustic receivers (Vemco VR2W and VR2Tx; Vemco Inc.) was established in nearshore shallow waters of the Florida Keys in August 2015, with additional receivers added over time for a total of 89 by May 2018. Acoustic receivers were moored to the substrate with 30 kg cement bases and suspended 1 m off the substrate via attachment to a rebar post. This array was established to track the movement patterns of permit, Atlantic tarpon *Megalops atlanticus* (see Griffin et al., 2018), and bonefish *Albula vulpes* in proximity to shallow water 'flats' habitats (i.e. <3 m water depth nearshore habitats). A total of 113 permits were surgically implanted with acoustic transmitters (Vemco V13, V13A, V16, 60–120 s transmission delay). Although not explored here, researchers should be aware that different tag types have varied transmission power outputs (e.g. Vemco V16 is higher than V13). If inter-individual variability in space use is of interest amongst individuals with different tag types, higher power tags are likely more detectable. To test the detection range correction method, a subset of receivers was selected from this array (see spatial configuration in Supporting Information II, Figure S1).

Physical and environmental attributes were measured at all acoustic receiver stations, including water depth, benthos type, benthic rugosity, and habitat type. Water depth was measured using a depth sounder (Garmin EchoMap Plus 44cv; Garmin). Benthos type was assessed visually within a 100 m^2 area around the receiver, including the biotic and abiotic conditions, and the predominant bottom cover type (i.e. seagrass, sand). Benthic rugosity was also visually estimated by a snorkeler while level with the benthos; it was scored from 1 to 3, with 1 representing little to no benthic structure (<50 cm variation in benthos height), 2 representing a moderate amount variation (50–100 cm), and 3 a large amount of variation (>100 cm). Variation was caused by the presence of coral heads, sponges, or seagrass beds. Habitat type was visually assessed using satellite imagery via Google Earth (https://www.google.com/earth/). Banks were considered to be on the outer edge of the flats, sloping off into either the Atlantic Ocean or Gulf of Mexico. Channels were narrow deeper-water cuts in the flats where tidal water flows more rapidly compared to surrounding areas. Basins were deeper-water

TABLE 2 Reference transmitter location characteristics at sentinel receiver sites in the Florida Keys acoustic telemetry array. *MR* = maximum detection range (5% detection efficiency) and *Midpoint* = location where detection efficiency is 50%, estimated with a range testing procedure

Station	*MR* (m)	*Midpoint* (m)	Depth (m)	Habitat type	Benthos	Rugosity score
BTT27	365	295	2.7	Bank	Sand	1
BTT17	349	282	3	Bank	Sand	1
BTT37	220	177	3	Bank	Seagrass	3
BTT7	144	116	1.6	Basin	Seagrass	2
BTT46	196	158	2	Basin	Seagrass	1
BTT13	180	145	2.8	Basin	Seagrass	3
BTT18	96	78	2.1	Channel	Sand	2
BTT49	95	77	3	Channel	Seagrass	3
BTT54	451	364	3.4	Channel	Sand	1

areas in the interior of the flats, separated by flats and/or mangrove keys from the ocean. All site characteristic estimates were conducted by the same researcher.

2.4 | Application to permit ecology in the Florida Keys

Within the Florida Keys acoustic receiver array, a subset (n = 9) of sentinel receiver sites was chosen to represent the range of conditions present. Receivers were stratified into bank, basin, and channel habitats (n = 3 in each) and sites were selected across a range of water depths and bottom types (Table 2). The two-stage approach described above was then applied. Firstly, from 2 to 3 August 2016, a range testing protocol was conducted at each sentinel receiver, in which an acoustic transmitter (Vemco V13, 7 s transmission delay plus 3 s burst period) was placed 1 m below the water surface from a stationary boat for 2 min at a range of distances from the receiver. Distance increments from the receivers were varied from 50 to 100 m depending on the projected range (i.e. low rugosity sand banks were correctly predicted to have greater ranges than rugose channels and basins), with a minimum of three sites at each station. These data were used to derive *DE* at each distance, as well as *MR* and *Midpoint* distance. Importantly, this short-term range testing procedure was conducted in near-optimal detection efficiency conditions, i.e. on calm days with minimal wind and at high tide, with minimal water flow. With more time and resources, researchers may consider placing range testing tags at set distances from each sentinel receiver for longer periods (i.e. days to weeks) at the outset of the study to acquire a more robust measure of *MR* and *Midpoint*. Secondly, range testing findings were used to guide the placement location of a single reference tag (Vemco V13; 270–330 s transmission delay) in proximity to each sentinel receiver at the *Midpoint*, which was unique for each receiver. Reference tag data reported here spanned from 13-June-2018 to 6-August-2018.

To estimate *MR* and *Midpoint* for each sentinel receiver using range testing data, firstly, *DE* was calculated as the percentage of total potential detections (i.e. 12 in 2 min) recorded by the receiver at each location the range testing tag was placed, expressed as the distance of tag location from the receiver. Third-order polynomial regression models were used to describe the relationship between distance from the receiver and *DE* at each receiver separately (R code included in Supporting Information I). These models were used to predict *MR* (5% *DE*) and *Midpoint* (50% *DE*) for each sentinel receiver.

To assess variations in *DR* that occur over time due to variability in conditions that affect receiver detection performance, reference tag data were used to generate estimates of *DE* over time to serve as a proxy. For each study hour, *DEvc* was calculated for each sentinel receiver over the entire study period (13-June-2018 to 6-August-2018) using Equation 2. *MR* and *DEvc* were then used to calculate *DRc* using Equation 3. To estimate *DRc* at a subset of receivers (n = 20 for illustrative purposes), *DRc* from sentinel receiver data was fit with a random forests machine learning algorithm (Breiman, 2001) implemented with the randomForest r package (Liaw & Wiener, 2002). Random forests are a decision tree model, which uses predictor variables to create binary partitions in the data to optimize prediction of the response (Breiman, Friedman, Stone, & Olshen, 1984; De'Ath & Fabricius, 2000). These models are robust to many traditional statistical assumptions, integrate high-order interactions in the predictors, and are capable of making highly accurate predictions of the response variable. Random forests fit numerous (often 1,000+) decision trees with subsets of the data via bootstrapping with random feature selection, and aggregate the trees via bagging to reduce data overfitting and improve prediction accuracy (Breiman, 2001). Both random forests and a class of similar models, boosted regression trees, are growing in popularity in ecology research due to their ability to model diverse, complex data sets and make highly accurate predictions (Cutler et al., 2007; Elith, Leathwick, & Hastie, 2008).

Random forests was used to model *DRc* with predictors including site characteristics (water depth, benthos type, benthos rugosity, and habitat type) and temporal conditions (diel period, tide state, and tide height). Because the range testing and reference tag data were derived from an ongoing study, while transmitters were deployed in fish, the presence of other transmitters in the system may also impact receiver detection efficiency with Vemco acoustic receivers because they utilize a single detection frequency, blocking out detections during the reception period, and code collisions can also occur. Other transmitters,

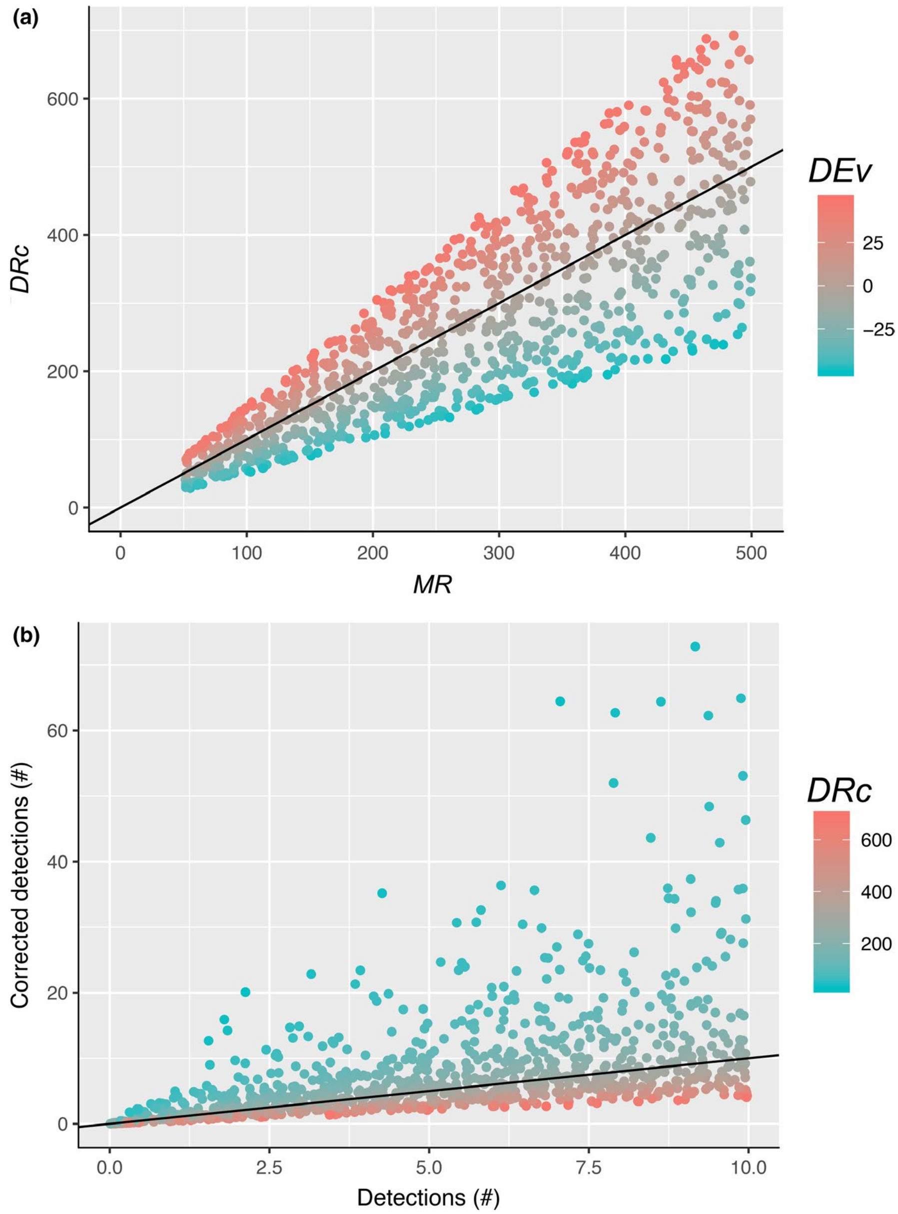

FIGURE 2 In a generated hypothetical dataset, (a) the relationship between maximum detection range (*MR*), detection range correction factor (*DRc*), and detection efficiency variance (*DEv*), and (b) the relationship between the number of raw animal detections and the corrected number of detections by *DRc*. The generated hypothetical acoustic telemetry data included 1,000 data points, with *DR* varying from 50 to 500 m, *DE* variation from −50 to 50%, and number of detections from 0 to 10. The black line indicates 1:1 ratio

presumably deployed on marine animals (including those tagged within our study and those tagged by other researchers that moved into our system) were not present at sentinel receivers during range testing but were present intermittently throughout the reference tag deployment period (see Supporting Information II; Figure S2). Animal detections were considered rare enough to have a minimal impact on detection efficiency of reference tags in this study, but should be considered in other systems, and could be accounted for by including other transmitter detections as a predictor of *DRc*. The random forests model was run with 1,000 iterations and an out-of-bag (non-training) sample of 30%. Variable importance was assessed using % mean-squared-error (%IncMSE; the amount of error incurred by removing the variable from the model) and model fit was assessed with the % variance explained in out-of-bag (non-training data) samples. The random forests model was used to predict *DRc* at a subset (n = 20) of receivers for every study hour of the study period. However, because this simple application corrects presence-only data and does not affect zeros, presence-only detections were corrected with *DRc* with Equation 3, generating *Detc*. To compare *Det* and *Detc* among environmental variables, a linear mixed effects model was fit to these values with data type (*Det*, *Detc*), diel period (day, night), and tide height (m), and two-way interactions between data type and diel period, and data type and tide height as predictors. Acoustic receiver was included as a random slope to account for repeated measures. Backward model selection was used to determine the final model structure using log-likelihood tests.

3 | RESULTS

3.1 | Application to a hypothetical dataset

In the generated hypothetical dataset, variability in *DRc* was driven mainly by *MR*, with additional variance occurring due to *DEv* (Figure 2a). Applying *DRc* to the hypothetical number of animal detections resulted, in some instances, in large differences between

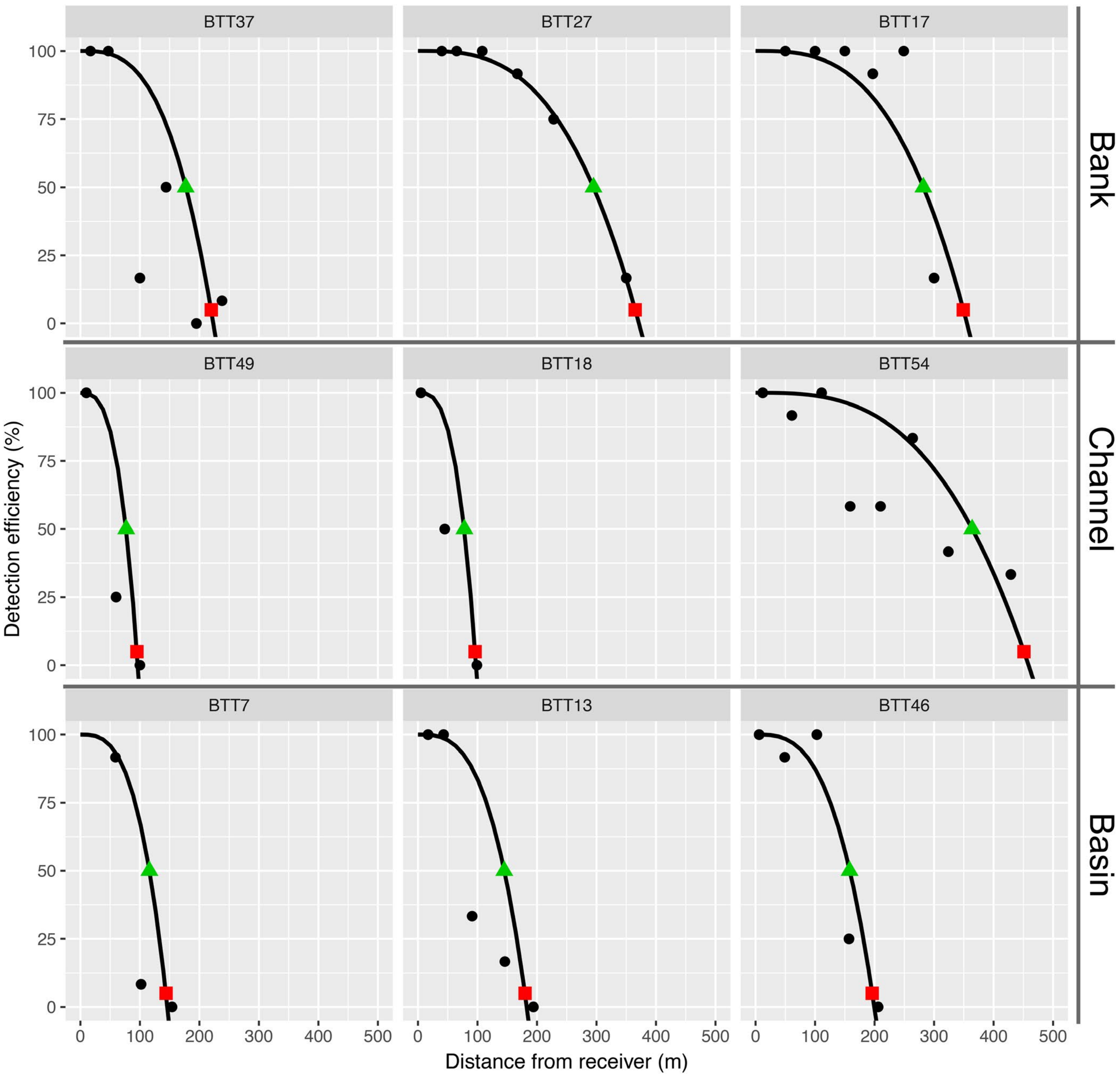

FIGURE 3 Detection efficiency of a range testing tag by distance from sentinel acoustic receivers from a range testing protocol used to determine maximum detection range (*MR*; red square) and the *Midpoint* (green triangle) locations for placement of reference tags. Data are fitted with a third-order polynomial regression model with a fixed *y*-intercept at 100

the raw detection values and the corrected number of detections due to variation in *MR* and *DEv* (Figure 2b). For example, two raw animal detections during a time period when detection range is low (relative to overall system performance) resulted in an underestimate of >1,000% in relative space use during that time period.

3.2 | Application to permit ecology in the Florida Keys

In the Florida Keys acoustic receiver array, *MR* varied widely amongst sentinel receivers from 95 to 451 m; it was generally higher in deeper-water and lower rugosity sites (Table 2; Figure 3). Receiver *DE* from reference tag detections also varied greatly over time and amongst sentinel sites (Figure 4). The random forest algorithm described 75.8% of variation in *DRc* in non-training data amongst receivers during the 2-month sampling period (Table 3). The algorithm identified site-specific characteristics as the most important predictors of *DRc*, with benthos type and water depth explaining the most variation. Using the random forests algorithm to predict *DRc* at a subset of receiver sites in the Florida Keys, large variation in *DRc* was observed amongst receiver stations due to their environmental characteristics (Figure 5). This resulted in varied interpretations of patterns of permit habitat use between raw (*Det*) and corrected (*Detc*) detection values (mean

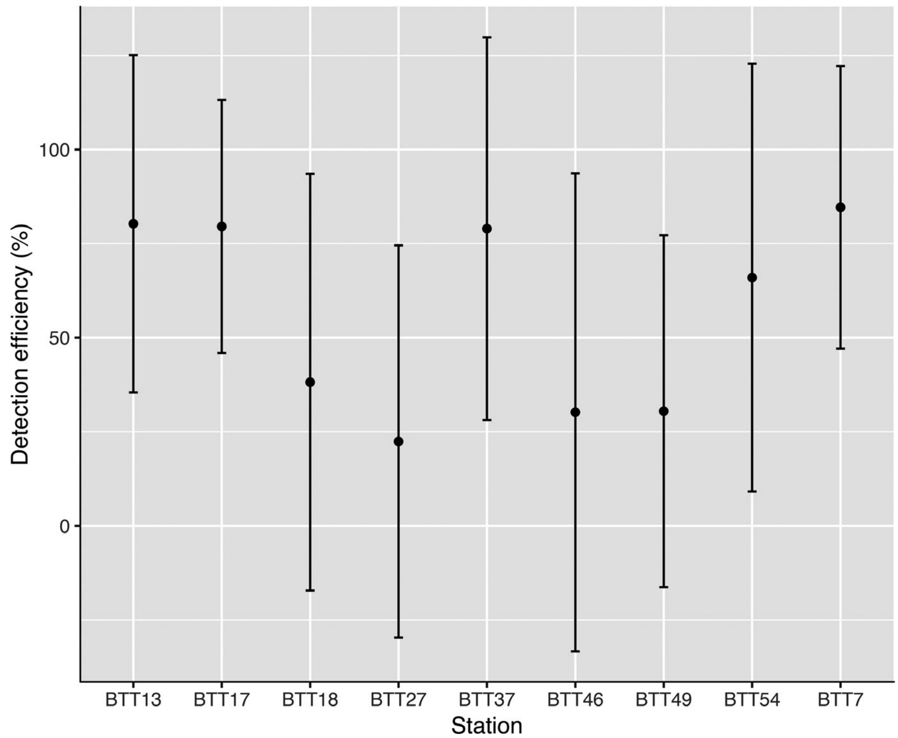

FIGURE 4 Mean detection efficiency (±95% confidence interval) of a reference tag at each sentinel receiver station over the course of the study in the Florida Keys

absolute difference = 20 ± 22% *SD*, 0.08%–127% range; Figure 6). There was no significant interaction between data type (*Det*, *Detc*) and diel period (LME; $F_{1,967} = -1.48$, $p = .14$) or data type and tide height (LME; $F_{1,967} = -0.32$, $p = .74$), but in the final model without interactions, there was a significant effect of data type (LME; $F_{1,970} = 2.45$, $p = .01$) as well as diel period (LME; $F_{1,970} = -3.76$, $p < .001$) on permit detections. Once system performance was accounted for, corrected values revealed higher use of channels and basins, and lower use of banks than raw values indicated, with the most prominent difference in channel habitats during the day (Figure 6).

TABLE 3 Variable importance scores for predictors of a detection range correction factor (*DRc*) from a random forest model based on reference tag detections in the Florida Keys acoustic telemetry array. %IncMSE refers to the percent increase in mean squared error and IncNodePurity refers to mean increase in Gini score. Out of bag error refers to % prediction error in non-training data. Model: *DRc* ~ Habitat + Benthos + Rugosity + Water depth + Diel period + Tide state + Tide height

	%IncMSE	IncNodePurity
Benthos	14,417.7	45,401,253.3
Depth	10,454.8	35,827,973.3
Habitat	8,627.7	27,559,240.8
Rugosity	7,109.8	19,735,087.4
Tide height	913.5	3,529,671.7
Tide state	732.6	2,100,992.3
Diel period	230.0	456,008.5
Out of bag error:	24.2	
Mean of squared residuals:	5,951.9	

4 | DISCUSSION

Acoustic telemetry using fixed receiver stations is the most popular approach to quantify the long-term space use and ecological interactions of aquatic animals in the wild (Donaldson et al., 2014; Hussey et al., 2015), but for study findings to be accurate and thus meaningful it is essential to account for sampling efficiency (acoustic receiver performance in detecting tagged animals; Payne et al., 2010). Yet, studies rarely account for variation in receiver *DR* (Kessel et al., 2014), likely due to the challenges associated with quantifying and accounting for complex variations in *DR* over space and time. We present a relatively simple and practical approach to accomplish this. From our analysis of a generated hypothetical dataset, large differences between raw animal detection values and our corrected values (e.g. >1,000%) were observed, illustrating the major differences that could theoretically occur between raw and corrected animal detection values. In the real-world telemetry dataset, differences between raw and corrected detection values were smaller than the hypothetical dataset (max 127%), but these differences would influence interpretation of the spatial and temporal habitat use of permit in nearshore habitats of the Florida Keys. The greatest variation in permit space use patterns between raw and corrected data was observed between habitats and diel periods, with limited differences amongst tide heights, which is consistent with the variation observed in receiver *DR* based on range testing and reference tag data used to derive *DRc*. This approach could be applied at various scales of ecological interest and in diverse aquatic ecosystems with distinct causes of variations in system performance. For example, in other types of aquatic systems, major sources of *DR* variance could be seasonal macrophyte growth or ice cover.

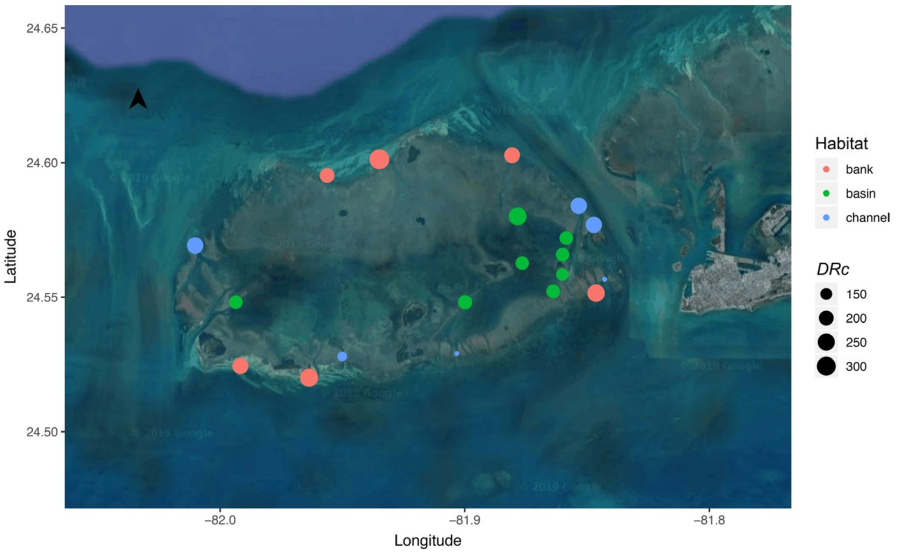

FIGURE 5 Map of detection range correction factor (*DRc*) values estimated using a random forest model at a subsample of receiver locations with habitat types marked in unique colours

The approach described here (outlined in Figure 1) could be adopted with many variations (outlined in Section 2.1 and further discussed below), with more extensive assessments being more ideal and less prone to potential errors. Here we used a minimalist approach (i.e. a relatively small number of sentinel receiver sites, and short-term range testing under near-ideal conditions to estimate *MR* and *Midpoint*). This approach requires relatively few resources, which may enable more widespread applications, even in studies with major logistical constraints. There is greater potential for error with a minimalist approach, although likely much less error than not correcting animal detection data for system performance at all. We encourage researchers to conduct the most extensive assessments of system performance that time and money allow, as well as conducting further research focused on identifying optimal methods to balance effort with accuracy.

Overall, our conceptual approach involves three critical components: (a) selection of sentinel receiver sites, (b) quantifying *MR* at the onset of the study, and (c) quantifying relative changes in *DR* (via reference tag *DE*) over time at sentinel sites throughout the study. All of these components require careful consideration to effectively quantify and account for system performance. Firstly, selecting sentinel sites that capture the range of environmental conditions (both site landscape characteristics and temporally varying conditions) that exist across the entire receiver array landscape is essential in order to utilize modeling techniques to accurately predict *DRc* at all receiver sites based on sentinel site data. Here, a random forests machine learning algorithm was used to accomplish this; these algorithms are highly effective at making data predictions, integrating numerous predictors of varied data classes, and integrating complex hierarchical relationships between these variables (Breiman, 2001; Liaw & Wiener, 2002). Intuitively, predictors used to model training data should match the range of variables that are explored in the animal detection dataset. With this approach, any temporal site-specific anomalies in reference tag *DE* data (e.g. low numbers of detections in a certain study hour at a sentinel receiver due to a site-specific effect such as boat motor noise) have a lesser impact on overall *DRc* predictions than if hourly site-specific reference tag data were used directly to make corrections.

Secondly, because it is well-established from empirical research that *DR* is the major driver of receiver performance (Kessel et al., 2014), *MR* estimation via a range testing protocols is a major component of the *DRc* used here to correct animal detection values (Figure 2a), and also serves to determine the location of the *Midpoint* for placement of a reference tag to monitor variations in *DE* over time. There are multiple potential range testing approaches. Here we used a simple approach in which a range testing tag was positioned for short periods of time at a range of distances from sentinel receivers. A more thorough approach would involve conducting this range testing procedure at all receivers in the array to provide more accurate estimates of *MR* at all receivers rather than assuming they have similar values to sentinel sites. Another more comprehensive approach to range testing would be to station reference tags (which generally have longer transmission delays than range testing tags) at a similar range of distances from the receivers over longer periods (i.e. days to weeks) prior to the initiation of the study, which would provide a more comprehensive estimate of *MR* that incorporates a broader range of conditions over time. Further, conducting range testing in multiple directions from the receivers would provide a more comprehensive measure, as was accomplished by Selby et al. (2016). Importantly, this practice alone would not account for long-term variation in system performance.

Thirdly, to quantify variation in *DR* over the full duration of a study, *MR* is combined with *DEv* derived from reference tag data. A key assumption with this step is that *DE* of the reference tag serves as an effective relative measure of receiver performance (i.e. *DR*). This assumption could be violated if variation in local conditions around the reference tag causes variation in *DE* to fail to represent absolute *DR*. This could occur, for example, if the reference tag is transmitting from a region within a receiver's *DR* that is relatively calm or stable (e.g. in deep water less affected by tidal changes) – but if an animal-borne tag transmits from another part of the *DR* where conditions are less stable/more complex (e.g. shallower areas prone

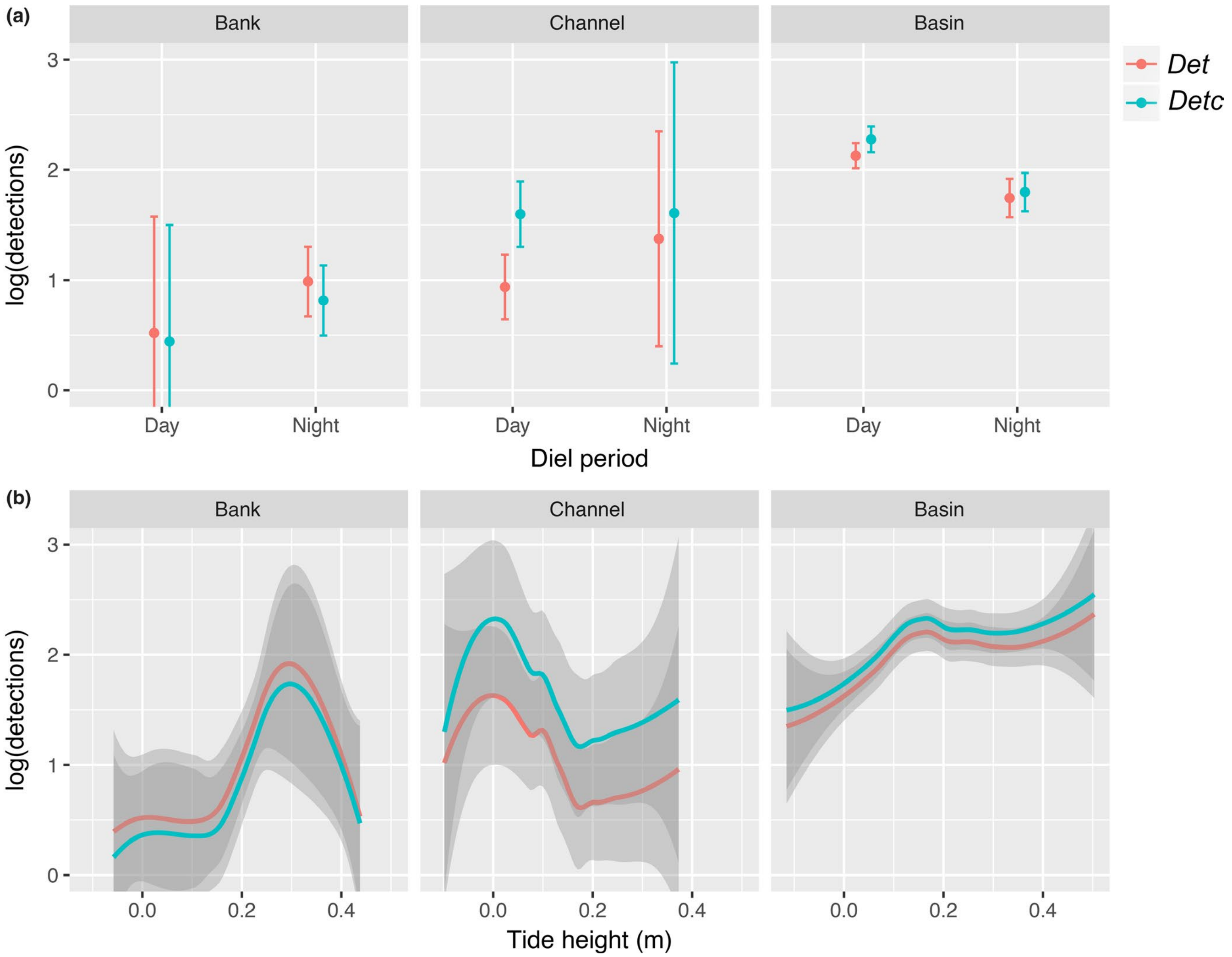

FIGURE 6 Raw (pink; *Det*) and corrected (blue; *Detc*) presence-only permit detections/h (±*SE*) at the receivers shown in the figure by habitat type and (a) diel period and (b) tide state

to tidal noise), then reference *DE* may not accurately reflect the true *DR* of the receiver. Reference tag *DE* may also fail to capture variability in receiver *DR* if it is placed too far from the *Midpoint*. Careful consideration of the reference tag location is necessary with this approach; the location should represent the average (e.g. mean water depth) of available conditions around the receiver within the region encompassed by the *MR*. Consideration of the ecology of the species (e.g. benthic vs. pelagic) could be warranted as well. A potential alternative to this approach would be to place multiple reference tags (i.e. 3 or more) at each sentinel receiver site to estimate variability in *DR* using the same approach described above to estimate *MR* and *Midpoint*. This approach would require more resources and computational effort. For example, using three reference tags per site in the Florida Keys telemetry array would require at least 27 reference tags and moorings, as opposed to the nine used here. This approach, like using a single reference tag, could also be vulnerable to localized effects of conditions on reference tag *DE*, especially with lower numbers of reference tags, with three being the bare minimum to establish a model (e.g. regression) to predict *DR*. Careful consideration of the location of reference tags would also be required, which could be informed by an initial *MR* range testing procedure.

In summary, we have developed and applied a relatively simple approach to characterize the complex variations in acoustic receiver performance over space and time to improve estimates of animal detection data to derive more accurate ecological findings and conclusions. Overall, the approach applied to the Florida Keys acoustic telemetry array was minimalist (i.e. required relatively little financial investment or time/effort) in terms of the spatial and temporal extent of the range testing procedure and deployment of reference tags. This minimalist approach could facilitate greater uptake and application of detection range corrections in fixed station acoustic telemetry studies, and the framework proposed here could also be adopted with more extensive applications of short and/or long-term range testing over greater spatial and temporal extents when resources (time and money) are available. With the increasing application of acoustic telemetry via passive receiver arrays to quantify long-term aquatic animal space use and movement patterns (Crossin et al., 2017; Hussey et al., 2015), it is essential to develop robust, comprehensive, and standardized telemetry practices that ensure the generated data are accurate and inform conservation actions effectively (Brownscombe, Lédée, et al., 2019). This is particularly salient because historically there has been a disconnect between telemetry-derived knowledge and resource management actions, due in part to distrust of telemetry findings (Nguyen, Young, & Cooke, 2018; Young, Gingras, Nguyen, Cooke, & Hinch, 2013). Social science surveys of researchers who routinely use telemetry revealed that issues related to detection efficiency and system performance had the potential to introduce biases that would reduce uptake of findings by knowledge users (Nguyen et al., 2018). Indeed, despite the fact that it is recognized that acoustic telemetry receivers are imperfect sampling instruments and their performance can seriously impact study findings, the majority of telemetry studies to date have failed to account for system performance (Kessel et al., 2014). It is our hope that researchers find our approach tractable and continue to develop and test these methods for further applications to increase the robustness and reliability of acoustic telemetry studies.

ACKNOWLEDGEMENTS

This research was supported by a variety of sources. Bonefish and Tarpon Trust (BTT) provided funding with support from Costa Del Mar, the March Merkin Fishing Tournament, Hell's Bay Boatworks, Maverick Boat Company, and numerous private donors. The Florida Fish and Wildlife Conservation Commission supported the field aspects of the permit empirical data. Fish tagging would not have been possible without the generous support of numerous fishing guides and anglers, providing their time and knowledge of the fishery to capture and tag permit. Funding for the conceptual aspects of the project was provided by the Ocean Tracking Network Canada. Brownscombe is supported by a Banting Postdoctoral Fellowship (Canada) and BTT. Cooke, Crossin, and Iverson are supported by the Natural Sciences and Engineering Research Council of Canada. Cooke is a BTT Research Fellow and further supported by the Canada Research Chairs Program. Danylchuk is a BTT Research Fellow, and also supported by the National Institute of Food & Agriculture, U.S. Department of Agriculture, the Massachusetts Agricultural Experiment Station and Department of Environmental Conservation.

CONFLICTS OF INTEREST

All authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

J.W.B. conceived, designed, and conducted this study, analyzed the data and wrote the manuscript. L.P.G., J.M.C., D.M. and A.A. contributed to study design, data collection, and manuscript preparation. G.T.C., S.J.I., A.J.A., S.J.C. and A.J.D. contributed to study design and manuscript preparation. All authors contributed substantially to this work and approved the final version.

DATA AVAILABILITY STATEMENT

All data and associated R code for analyses are included in Supporting Information I and publicly available on GitHub: http://github.com/jakebrownscombe/Acoustic-telemetry-detection-range-method (Brownscombe, 2019).

ORCID

Jacob W. Brownscombe https://orcid.org/0000-0003-2496-8764

REFERENCES

Amstrup, S. C., McDonald, T. L., & Manly, B. F. (2006). *Handbook of capture-recapture analysis*. Princeton, NJ: Princeton University Press. https://doi.org/10.1111/j.1442-9993.2006.01673.x

Binder, T. R., Holbrook, C. M., Hayden, T. A., & Krueger, C. C. (2016). Spatial and temporal variation in positioning probability of acoustic telemetry arrays: Fine-scale variability and complex interactions. *Animal Biotelemetry*, *4*(1), 4. https://doi.org/10.1186/s40317-016-0097-4

Breiman, L. (2001). Random forests. *Machine Learning*, *45*(1), 5–32. https://doi.org/10.1023/A:1010933404324

Breiman, L., Friedman, J., Stone, C., & Olshen, R. A. (1984). Classification algorithms and regression trees. *Classification and regression trees* (pp. 246–280). Retrieved from https://rafalab.github.io/pages/649/section-11.pdf.

Brownscombe, J. (2019). jakebrownscombe/Acoustic-telemetry-detection-range-method v1.0 (Version v1.0). Zenodo. https://doi.org/10.5281/zenodo.3515997

Brownscombe, J., Griffin, L., Gagne, T., Haak, C., Cooke, S., Finn, J., & Danylchuk, A. (2019). Environmental drivers of habitat use by a marine fish on a heterogeneous and dynamic reef flat. *Marine Biology*, *166*(2), 18. https://doi.org/10.1007/s00227-018-3464-2

Brownscombe, J. W., Lédée, E. J. I., Raby, G. D., Struthers, D. P., Gutowsky, L. F. G., Nguyen, V. M., … Cooke, S. J. (2019). Conducting and interpreting fish telemetry studies: Considerations for researchers and resource managers. *Reviews in Fish Biology and Fisheries*, *29*(2), 369–400. https://doi.org/10.1007/s11160-019-09560-4

Cooke, S. J., Brownscombe, J. W., Raby, G. D., Broell, F., Hinch, S. G., Clark, T. D., & Semmens, J. M. (2016). Remote bioenergetics measurements in wild fish: Opportunities and challenges. *Comparative Biochemistry and Physiology – Part A: Molecular and Integrative Physiology*, *202*, 23–37. https://doi.org/10.1016/j.cbpa.2016.03.022

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G., & Butler, P. J. (2004). Biotelemetry: A mechanistic approach to ecology. *Trends in Ecology and Evolution*, *19*(6), 334–343. https://doi.org/10.1016/j.tree.2004.04.003

Cooke, S. J., Niezgoda, G. H., Hanson, K. C., Suski, C. D., Phelan, F. J. S., Tinline, R., & Philipp, D. P. (2005). Use of CDMA acoustic telemetry to document 3-D positions of fish: Relevance to the design and monitoring of aquatic protected areas. *Marine Technology Society Journal*, *39*(1), 31–41. https://doi.org/10.4031/002533205787521659

Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., … Cooke, S. J. (2017). Acoustic telemetry and fisheries management. *Ecological Applications*, *27*(4), 1031–1049. https://doi.org/10.1002/eap.1533

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random forests for classification in ecology. *Ecology*, *88*(11), 2783–2792. https://doi.org/10.1890/07-0539.1

De'Ath, G., & Fabricius, K. E. (2000). Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, *81*(11), 3178–3192. https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2

Donaldson, M. R., Hinch, S. G., Suski, C. D., Fisk, A. T., Heupel, M. R., & Cooke, S. J. (2014). Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Frontiers in Ecology and the Environment*, *12*(10), 565–573. https://doi.org/10.1890/130283

Dorazio, R. M., & Price, M. (2018). State-space models to infer movements and behavior of fish detected in a spatial array of acoustic receivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(4), 543–550. https://doi.org/10.1139/cjfas-2018-0067

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*(4), 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Espinoza, M., Farrugia, T. J., Webber, D. M., Smith, F., & Lowe, C. G. (2011). Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fisheries Research*, *108*(2–3), 364–371. https://doi.org/10.1016/j.fishres.2011.01.011

Gjelland, K. O., & Hedger, R. D. (2013). Environmental influence on transmitter detection probability in biotelemetry: Developing a general model of acoustic transmission. *Methods in Ecology and Evolution*, *4*(7), 665–674. https://doi.org/10.1111/2041-210X.12057

Griffin, L. P., Brownscombe, J. W., Adams, A. J., Boucek, R. E., Finn, J. T., Heithaus, M. R., … Danylchuk, A. J. (2018). Keeping up with the Silver King: Using cooperative acoustic telemetry networks to quantify the movements of Atlantic tarpon (*Megalops atlanticus*) in the coastal waters of the southeastern United States. *Fisheries Research*, *205*, 65–76. https://doi.org/10.1016/j.fishres.2018.04.008

Heupel, M. R., Semmens, J. M., & Hobday, A. J. (2006). Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, *57*(1), 1. https://doi.org/10.1071/MF05091

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., … Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science (New York, N.Y.)*, *348*(6240), 1255642. https://doi.org/10.1126/science.1255642

Huveneers, C., Simpfendorfer, C. A., Kim, S., Semmens, J. M., Hobday, A. J., Pederson, H., … Harcourt, R. G. (2016). The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods in Ecology and Evolution*, *7*(7), 825–835. https://doi.org/10.1111/2041-210X.12520

Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., & Fisk, A. T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, *24*(1), 199–218. https://doi.org/10.1007/s11160-013-9328-4

Liaw, A., & Wiener, M. (2002). Classification and Regression by RANDOMFOREST. *R News*, *2*(December), 18–22. https://doi.org/10.1177/154405910408300516

Loher, T., Webster, R. A., & Carlile, D. (2017). A test of the detection range of acoustic transmitters and receivers deployed in deep waters of Southeast Alaska, USA. *Animal Biotelemetry*, *5*(1), 1–22. https://doi.org/10.1186/s40317-017-0142-y

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248. https://doi.org/10.2307/3072056

Mathies, N. H., Ogburn, M. B., McFall, G., & Fangman, S. (2014). Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. *Marine Ecology Progress Series*, *495*, 27–38. https://doi.org/10.3354/meps10582

Nguyen, V. M., Young, N., & Cooke, S. (2018). Applying a knowledge-action framework for navigating barriers to incorporating telemetry science into fisheries management and conservation: A qualitative study. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(10), 1733–1743. https://doi.org/10.1139/cjfas-2017-0303

Payne, N. L., Gillanders, B. M., Webber, D. M., & Semmens, J. M. (2010). Interpreting diel activity patterns from acoustic telemetry: The need for controls. *Marine Ecology Progress Series*, *419*, 295–301. https://doi.org/10.3354/meps08864

Pedersen, M. W., & Weng, K. C. (2013). Estimating individual animal movement from observation networks. *Methods in Ecology and Evolution*, *4*(10), 920–929. https://doi.org/10.1111/2041-210X.12086

R Core Team. (2018). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reubens, J., Verhelst, P., van der Knaap, I., Deneudt, K., Moens, T., & Hernandez, F. (2018). Environmental factors influence the detection probability in acoustic telemetry in a marine environment: Results from a new setup. *Hydrobiologia*, 1–14, https://doi.org/10.1007/s10750-017-3478-7

RStudio Team. (2016). *RStudio: Integrated Development for R*. Boston, MA: RStudio Inc.

Selby, T. H., Hart, K. M., Fujisaki, I., Smith, B. J., Pollock, C. J., Hillis-Starr, Z., … Oli, M. K. (2016). Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. *Ecology and Evolution*, *6*(14), 4823–4835. https://doi.org/10.1002/ece3.2228

Simpfendorfer, C. A., Heupel, M. R., & Collins, A. B. (2008). Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. *Canadian Journal of Fisheries and Aquatic Science*, *65*, 482–492. https://doi.org/10.1139/F07-180

Simpfendorfer, C. A., Huveneers, C., Steckenreuter, A., Tattersall, K., Hoenner, X., Harcourt, R., & Heupel, M. R. (2015). Ghosts in the data: False detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Animal Biotelemetry*, *3*(1), 55. https://doi.org/10.1186/s40317-015-0094-z

Singh, L., Downey, N. J., Roberts, M. J., Webber, D. M., Smale, M. J., van den Berg, M. A., … Blows, B. M. (2009). Design and calibration of an acoustic telemetry system subject to upwelling events. *African Journal of Marine Science*, *31*, 355–364. https://doi.org/10.2989/AJMS.2009.31.3.8.996

Stocks, J. R., Gray, C. A., & Taylor, M. D. (2014). Testing the effects of near-shore environmental variables on acoustic detections: Implications on telemetry array design and data interpretation. *Marine Technology Society Journal*, *48*(1), 28–35. https://doi.org/10.4031/mtsj.48.1.8

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., & Possingham, H. P. (2013). Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. *Ecological Aplication*, *13*(6), 1790–1801.

Whoriskey, K., Martins, E. G., Auger-Methe, M., Gutowsky, L. F. G., Lennox, R. J., Cooke, S. J., … Mills Flemming, J. (2019). A guide to current and emerging statistical methods for analyzing aquatic telemetry data. *Methods in Ecology and Evolution*, *10*, 935–948. https://doi.org/10.1111/2041-210X.13188

Young, N., Gingras, I., Nguyen, V. M., Cooke, S. J., & Hinch, S. G. (2013). Mobilizing new science into management practice: The challenge of biotelemetry for fisheries management, a case study of Canada's Fraser River. *Journal of International Wildlife Law and Policy*, *16*(4), 331–351. https://doi.org/10.1080/13880292.2013.805074

Zuur, A. F., Ieno, E. N., Anatoly, A., & Saveliev, A. A. (2017). *Beginner's guide to spatial, temporal, and spatial-temporal ecological data analysis with R-INLA*. Newburgh, Scotland: Highland Statistics Ltd.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., Smith, G. M., & Ebooks Corporation. (2009). Mixed effects models and extensions in ecology with R. *Statistics for Biology and Health*, (i), (p. 579). New York, NY: Springer-Verla. https://doi.org/10.1007/978-0-387-87458-6

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Brownscombe JW, Griffin LP, Chapman JM, et al. A practical method to account for variation in detection range in acoustic telemetry arrays to accurately quantify the spatial ecology of aquatic animals. *Methods Ecol Evol*. 2019;00:1–13. https://doi.org/10.1111/2041-210X.13322