

Distinguishing residency behavior from random movements using passive acoustic telemetry

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ABSTRACT: Passive acoustic telemetry is a powerful tool for tracking aquatic animals, yet the data derived from acoustic tags have important limitations. For example, inferences about habitat associations rely on statistical correlations, where frequent observations within a given habitat are interpreted as habitat preference. However, tagging data are not measures of movement per se, or even behavior more generally; rather, tagging data are representations of locations in space and time and can reflect limitations in the sampling technology as much as animal behavior. This interaction between sampling technology and resulting data means it is necessary to have some null expectation in order to evaluate a hypothesis predicting a habitat association. Here, we developed a null model for animal movement based on random walk simulations and examined our ability to distinguish random from intentioned movements when using passive acoustics. By comparing simulations to telemetry observations, we provide guidance for both data interpretation and future study design. We found that (1) real-world telemetry observations cannot be distinguished from random walks during initial portions of sampling and (2) researchers must account for the interaction between study duration and the ratio of organismal step size relative to detection radius when calculating site fidelity. To assist in the interpretation of passive acoustic data, we provide an analytical solution to forecast when real-world observations are reliably distinguishable from simple random walks.

KEY WORDS: Passive acoustic telemetry · Habitat preference · Monitoring · Hypothesis testing

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1. INTRODUCTION

Specific and precise information on the location of animals is essential for answering ecological questions on habitat use. Inferences about habitat use typically rely on statistical correlations of animal observations located within specific habitats given that alternative habitats are available (Vaughan & Ormerod 2005, Nielson & Sawyer 2013). The affinity of an animal for a specific habitat is often characterized by a residency index (RI), i.e. the proportion of time or fraction of observations spent within a particular site, and large RI values are treated as evidence of preferential habitat use (Filous et al. 2017, Couturier et al. 2018, Gandra et al. 2018). Alternatively, preference for a habitat can be expressed as site fidelity or the number of times an animal is observed at a site after a period of absence (although the terms are sometimes used interchangeably) (Switzer 1993). High site fidelity is also viewed as evidence of preferential habitat use (Kneebone et al. 2012, Bass et al. 2017). In either case, inferences regarding behavioral choices rely on interpreting observational data and correctly appreciating the idiosyncratic nature of those data.

Importantly, animal observations are typically not continuous measures of actual behaviors, nor even movement. Rather, data are discrete representations of animal locations in space and time (DeCelles & Zemeckis 2014, Ogburn et al. 2017) obtained through a variety of monitoring techniques, such as wildlife cameras or GPS transmitters (Turchin 1998, Hulbert 2001, Beyer et al. 2010, O'Connell et al. 2011). Regardless of the method, the resulting data are typically represented with a common data structure: individual identifier, date, time, location (e.g. latitude, longitude), and perhaps covariates (e.g. temperature, altitude, depth). This similarity in data structure occurs despite the often considerable differences in the temporal and spatial resolution and extent of sampling technology. Correctly drawing ecological inferences, such as residency, from these discrete data requires an appreciation of how the diverse sampling technologies represent, or 'map', the movement information onto a common data structure.

In the aquatic environment, there has been a growing reliance on acoustic telemetry to obtain location observations over the last quarter century (O'Dor et al. 1998, Lindholm 2005, Hussey et al. 2015). Acoustic telemetry is well suited to answering questions regarding fish habitat utilization (Heupel et al. 2006, Lindholm et al. 2007) across many scales of space and time (Lowe & Bray 2006, Lindholm et al. 2010, Bryars et al. 2012, Donaldson et al. 2014). Acoustic telemetry uses receiver/data-loggers to detect ultrasonic transmitters (= acoustic tags) attached to individual animals (Simpfendorfer et al. 2008, Donaldson et al. 2014). Commonly, the tags report tag IDs and sometimes additional data, such as depth and temperature (Vemco 2015), but in each case the location is inferred from the location of the receiver. Receiver location varies among study designs. For example, receivers can be on mobile platforms such as boats or autonomous vehicles (Holland et al. 1985, Bellquist et al. 2008, Shinzaki et al. 2013, Ennasr et al. 2020) so as to log the specific locations of individual tags (i.e. 'active' or Lagrangian tracking). Alternatively, a receiver can be moored at a specific location to log the passing of any tag through its detection radius (i.e. passive telemetry; Heupel et al. 2005). Our study focuses on data issues related to the latter study design, i.e. passive telemetry.

Regardless of study design, logging fish movement with acoustic telemetry has a number of technical issues that affect ecological interpretations. Telemetryderived data are restricted to only those animals with tags, and this is usually a small fraction of the animals present. The detection radius of a receiver depends on tag power output, with larger species often getting larger transmitters, and consequently potentially being detected from farther away (Donaldson et al. 2014). The topography of the area adjacent to a receiver can also be very important. For example, high relief spur and groove topography on a Floridian (USA) coral reef significantly impeded the 'line of sight' between tagged demersal fishes and fixed acoustic receivers deployed on the seafloor (Lindholm et al. 2009), making predictions about detections based only on range estimates potentially problematic. Of particular interest here, moored receivers are limited to detecting only those tags that come within their detection radius. Recent advances in proprietary data-processing software have resulted in more precise triangulation of fish position from receivers configured in arrays (e.g. Campbell et al. 2012, Wolfe & Lowe 2015), effectively turning passive tracking receivers into an active tracking study design. While this is an attempt to reduce the uncertainty in location of the fish, deploying numerous receivers can be prohibitively expensive, and the location data they generate are referenced to the tag rather than the receiver and therefore become a different informatics problem than considered here.

Passive telemetry using moored receivers is a common study design (e.g. Carrier et al. 2018, Klinard & Matley 2020, Williamson et al. 2021), but the data representation that results generates uncertainties that, to our knowledge, have not previously been addressed. For example, a tagged fish immediately moving beyond a detection radius without returning produces only a few observations at the start of sampling; this may be evidence that the habitat is not preferred or may be escape behavior in response to the trauma of the tagging event. Alternatively, a fish may move but not leave the detection area (e.g. Alós et al. 2012), producing continuous observations throughout sampling. In this case, a high RI might be evidence of preferred habitat, but would also be indistinguishable from the 'residency' of a dead fish (Klinard & Matley 2020). Given this, on what basis do we interpret our observations as residency? What expectation, or 'null model', can we use to test residency models when relying on categorical measures of location (i.e. within range of a sensor or not), such as that produced by passive telemetry?

Here, we present a null model for interpreting residency from passive acoustic telemetry data. Given that location is categorical, we cannot rely on observations of individuals to discriminate patterns of detection, for example from a dead fish. Rather, we must look at properties of the population of observations to develop expectations of how the habitat choices of fish are expressed within these data sets. To do this, we simulated populations of individual fish that each move in random walks starting at a simulated acoustic receiver. These random walks represent movements that are not associated with habitat as a null model against which we then compared observations of actual fish. We also developed an analytical expression that predicts the changing probability of random walkers remaining within the detection radius of an acoustic receiver over time, providing a guide to the ecological information value of tag detections. We then compared these estimates to published studies to evaluate how well this issue is addressed in practice and provide guidance on improving future studies.

2. METHODS

2.1. Random walk simulations

To examine how fish movement is represented by the data generated in passive acoustic telemetry, we used a 2-dimensional random walk simulation. Although acoustic telemetry occurs within a 3-dimensional marine environment, many telemetry studies are performed with tags that do not report depth, and in habitats that are relatively shallow compared to the typical detection area of acoustic receivers (400-800 m radius) (Loher et al. 2017), making a 2-dimensional simulation appropriate. There are multiple approaches to specifying a random walk; here, we modeled the random walk as a freely jointed chain (FJC). This is a common framework for evaluating the statistical thermodynamics of long-chain polymers, and many of the statistical properties of these random walks have been developed previously in that context (Kuhn 1934, 1936, Treloar 1975, Lezon 2018).

In an FJC random walk, each walker has an equal, or uniform, probability of moving in any direction at each step, but the step lengths are all the same. The location of a random walker at any given time (*t*) is thus determined by the number (n) of randomly directed steps of length (l) taken since the start of monitoring (t = 0) (see Table 1 and Fig. 1 for terms and definitions). Thus, an FJC random walk consists of *n* rigid lengths, which at each junction point can freely rotate in all dimensions. In the context of animal movement, step length is not necessarily related to anatomy, gait, or speed; step length represents the distance moved, where the directions at the beginning and ending of a movement are uncorrelated, and is sometimes referred to as the 'mean free path' (Bovet & Benhamou 1988, Beverton & Holt 1993). Across the ecological literature, there are conflicting definitions of mean free

Table 1. Definitions of terms for random walks. Some terms express movement in space (see Fig. 1), others relate to the distribution of locations over a given time

Term Definition

Movement-related

- t Time
- n Number of randomly directed steps
- *r* Distance of walker from the origin
- L Length of each step, step size in real space
- R_r Detection radius in real space
- *l* Scaled step size, relative to detection radius, $l = L/R_r$
- *R* Scaled detection radius (1 for our simulations)

Distribution-related

 $\sqrt{nl^2}$ Standard deviation of the distribution, σ

$$b_1$$
 1-dimensional Kuhn's length, $\frac{\sqrt{1}}{\sqrt{2nl^2}}$

 b_2 2-dimensional Kuhn's length, $\frac{\sqrt{2}}{\sqrt{2}}$

path depending on the research question and sampling approach. Here, we adopted the definition of step length based on mean free paths from Sims et al. (2008). They determined the frequency of step sizes for 1 min time intervals across a diversity of marine



Fig. 1. Parameterization of tagged fish movement along a modeled path (grey line) with reference to an acoustic receiver. Here, 5 timesteps have lapsed (t = 5). The circle represents the detection radius (R_r in real space or R when scaled). The distance moved between timesteps (step length, L) is uniform in the modeling framework and is the distance where the directions at the beginning and end are uncorrelated ('mean free path'). Typically, fish do not make straight line movements between abrupt direction changes, but given that the locations between time steps are undefined in the model, the paths are modeled here as freely jointed chains (see Section 2). The distance of the fish from

the origin (black dot) at any timestep is *r* (arrows)

species and predicted that average distance moved between time steps ranged from 0 to 3 body lengths (Sims et al. 2008). Simulations performed here adopted a minimum mean free path of 1 body length. Consistent with this parameterization, we used a time interval of 1 min for all simulations.

All simulated random walks began at the location of a simulated acoustic receiver. This reflects our experience with studies where fish are often collected, tagged, and released coincident with receiver deployment. Thus, simulated receiver detection areas were represented by a circle with the receiver at the origin of a coordinate system (0,0), and with a detection range of radius R. Simulated random walks of individuals, hereafter referred to as walkers, were detected by the receiver if their distance from the origin (r) was less than the detection radius (r < R). At a given time, any fish located at a distance greater than the detection radius (r < R) was scored as not detected by the simulated receiver. For these simulations, we scaled step size relative to the receiver detection radius, using a detection radius of R = 1 and a relative step size of $l = L/R_r$ —i.e. step size in real space (L) divided by the detection radius in real space (R_r) . Three sets of simulations were performed in R (R Core Team 2015) using relative step sizes of 0.01, 0.05, and 0.1. Each simulation modeled a population of 100 walkers with a duration of 10 000 time steps. In each simulation, we recorded the location of every step and whether or not it was detected by the acoustic receiver at that time.

Simulations were evaluated by plotting the resulting pattern of tag detections for each walker, along with intervening non-detections, in what is referred to as an 'at-liberty' plot (DeCelles & Zemeckis 2014). We also calculated the fraction of time that simulated fish were within range of the receiver to generate an RI for each walker, estimated by dividing the total number of time steps that the fish was detected by the total time steps (= 10 000). For the population of walkers in each simulation, the fraction of walkers within the detection radius was logged at each time step.

2.2. Distinguishing random from real movements

We examined how distinguishable real-world telemetry data are from non-preferential movement data in 2 ways. First, we compared simulated random walks to a real-world telemetry data set of Atlantic cod *Gadus morhua* to examine how frequently simulated results reflected real observations of individual fish. Second, we performed a systematic literature review to estimate the probability of detecting random walkers at the end of a study and determined if studies ran long enough for observations of tagged fish to be distinguishable from random movement.

Data on Atlantic cod were extracted from Lindholm et al. (2007), and their methods will be briefly summarized. Ten Atlantic cod (mean = 51.5 cm total length; SD = 6.24) were tagged between 20 May and 2 July 2002 with data collected from May to September 2002 (i.e. spring to fall). Each fish was tagged with a V8SC-1H-R256 coded transmitter (Vemco 2015) and monitored using an omni-directional, singlechannel (69 kHz) VR2 acoustic receiver (Vemco 2015). A single VR2 receiver was placed near the center of a deep boulder reef at 60–65 m water depth. The range of detection (R_r) for the acoustic tags was approximately 400 m, or a detection area of 0.5 km². Data were collected for 95 d.

Signal detections for each fish were assigned to 1 h time bins throughout the study period. Isolated detections which were not within 59 min of another observation were removed to reduce the likelihood of false positives in the data (Lindholm et al. 2007). The RI of a tagged fish was calculated as the total number of hourly time bins in which the fish was recorded, divided by the total number of 1 h bins possible (up to a maximum of 2280 h [= 95 d]). Benchmarks for what constitutes a low, medium, or high degree of residency were chosen to maintain consistency with literature values (Robichaud & Rose 2004). A 'high' RI was defined as those fish recorded at the receiver for \geq 80% of the potential 1 h time bins, while 'low' residency represented those fish recorded < 20% of the potential 1 h time bins (Lindholm et al. 2007), with intermediate values rated as 'medium.'

For comparison, we approximated these same conditions for simulated walkers. Using our time interval of 1 min, we ran 100 simulations for 136800 time steps of 1 min (i.e. 95 d). Each of these 100 simulations contained 10 walkers reflecting the body lengths of the individual tagged fish. We ran 3 versions of these simulations with varying step sizes to represent 3 different assumed movement patterns based on potential ecology of Atlantic cod, resulting in a total of 300 simulations. The smallest step size, 1 body length per time t, assumes sedentary behavior, while the larger 6 body length step size assumes cod are more mobile; the third step size of 3 body lengths represents an intermediate movement ecology. All step sizes were scaled to the 400 m receiver detection radius. To obtain comparable data, we grouped our simulated minute by minute data into hourly bins (60 steps per bin) and calculated the number of simulated walkers in each of the 3 residency bins used by Lindholm et al. (2007), i.e. high, medium, and low.

To assess the sensitivity of these simulations to step size, we calculated the number of simulated walkers within each residency bin while varying the step sizes. Sensitivity plots were generated for all 3 residency bins using a step size of 4 body lengths as the standard. Sensitivity simulations used 1000 walkers per step size, with step sizes ranging from 1 to 7 body lengths (i.e. ± 75 %).

To evaluate if existing telemetry study designs have already addressed the technical limitations in detecting preferential movement outlined here, we performed a systematic review of the acoustic telemetry literature. Because the probability of detecting randomly moving fish changes throughout a study, we compared existing literature by calculating the probability of detecting fish at the end of each study duration, given the detection radius of the receivers and relative step size of the fish. To obtain telemetry literature, we queried the Web of Science literature database using the search terms 'passive acoustic telemetry' and 'residency,' 'site fidelity,' or 'at liberty.' The term 'passive' was included to focus on studies using the fixed receiver telemetry design; despite this, some active telemetry studies were returned and excluded. Studies were included only if they calculated an RI using location data from moored receivers. Included studies were surveyed for study duration (minutes), organism size (m), and reported receiver detection radius (m). Body size (fork length) and receiver detection radius reported in each study were used to estimate a relative step size per 1 min time step. At t = 0, all fish are presumed to be at the receiver, but after some period of time, an increasing fraction of fish will have left the detection area just from random movement. Thus, there is some 'burnin' time, after which more fish remaining within the detection area than predicted by random walks is evidence of habitat preference (since fewer fish left than chance predicts), and is also not purely a reflection of mortality since some fish do leave. For each study, the probability of observing a given fraction of a tagged, randomly moving population within the detection radius of a receiver at t = study duration was evaluated using the analytical relationship developed in Section 2.3.

2.3. Analytical development

It is desirable to have an expression to estimate the fraction of a population of random walkers remaining

within the detection area of an acoustic receiver at any time after being released. Here, we derived the probability distribution of distances of random walkers from the origin as a function of time. We assumed that all individuals are at the receiver (coordinate = (0,0) at t = 0. We then modeled the distance (r) between an individual's position as t increases determined by the number of steps taken in a 2-dimensional random walk (i.e. t = n), and the starting position at time t = 0, which is homologous to the distribution of chain end separations in a FJC polymer chain. The probability distribution of polymer chain end separation distances has been derived in the past (Kuhn 1934, 1936, Treloar 1975). Those authors derived the distribution of FJC for 3-dimensional polymers by building from the 1-dimensional case and generalizing to 3 dimensions. Consequently, the derivation of the 2-dimensional case is not at hand (Iliafar et al.; see preprint at https://arxiv.org/ftp/ arxiv/papers/1305/1305.5951.pdf). Kuhn (1934) did supply a 2-dimensional derivation of the probability distribution of chain end separations, but for reasons that were relevant to that context, did not collect terms in a manner that would allow us now to track the variance of the distribution. Therefore, we provide a brief, independent derivation of the 2-dimensional case here.

For a 1-dimensional FJC random walk of a large number of steps, the probability (P) that the end of a chain will exist anywhere along a coordinate axis, x, is approximated closely by the Gaussian distribution (Kuhn 1934, 1936, Treloar 1975):

$$P(x)dx = \frac{1}{\sqrt{2\pi}\sqrt{nl^2}} e^{-\frac{x^2}{2nl^2}} dx$$
(1)

where *n* and *l* are defined as in Section 2.1 for the random walk simulations, and $\sqrt{nl^2}$ here represents the standard deviation of the distribution, σ . By collecting terms, we can express this distribution in terms of a single parameter *b*, called Kuhn's length and defined for the 1-dimensional, or univariate, case as:

$$b_1 = \frac{\sqrt{1}}{\sqrt{2nl^2}} \tag{2}$$

After substitution, the probability distribution for the location of the ends of the chains in one dimension becomes:

$$P(x)dx = \frac{b_1}{\sqrt{\pi}} e^{-b_1^2 x^2} dx$$
(3)

In the 1-dimensional case, the variance is solely dependent on the number of steps, forward and backward, in the *x* direction. In 2 dimensions, the steps of the walk have an equal probability of moving in either the *x* or *y* direction. Thus, for a walk of *n* total steps, one expects *n*/2 steps to be taken in each direction. Alternatively, a single step of length *l* can be decomposed into its components such that $l^2 = x^2 + y^2$, and from isotropy it follows then that on average $I_x = I_y = 1/\sqrt{2}$. We can substitute $1/\sqrt{2}$ for *l* and gather the variables into a 2-dimensional Kuhn's length:

$$b_2 = \frac{\sqrt{2}}{\sqrt{2nl^2}} \tag{4}$$

Substitution of b_2 and $(x^2 + y^2)$ into the 1-dimensional probability distribution produces:

$$P(x, y)dxdy = \frac{b_2^2}{\pi} e^{-b_2^2(x^2 + y^2)}dxdy$$
(5)

This is the probability distribution of chain end locations in 2 dimensions. As in the 1-dimensional case, the highest probability value or the most likely location of the ends of the chain are at coordinates (0,0), or the origin.

To get from the probability of chain end locations to chain end separation (i.e. the distance the fish moves from the origin), we first need to resolve the distance moved in the x and y direction to any direction, as $(x^2 + y^2) = r^2$. Resolving the probability distribution in terms of distance from the origin, *r*, thus becomes:

$$P(r)dr = \frac{b_2^2}{\pi} e^{-b_2^2 r^2} \times 2\pi r \ dr \tag{6}$$

where we recognize that *r* can point in any direction; thus, we need to evaluate the probability that the end of the random walk is somewhere in a series of annular areas of radius *r* from the origin and d*r* thick.

When we collect terms, this produces the probability distribution of chain end distances (probability distribution function, PDF), or in this present context, the distances of randomly moving fish from the acoustic receiver:

$$PDF(r) = 2rb_2^2 e^{-b_2^2 r^2} dr$$
(7)

As pointed out by Treloar (1975), the probability distribution of the locations of the chain ends (Eq. 5) can be thought of as describing the distribution of shots at a target. The holes in the target will be distributed around the bull's eye and the average location is expected to be at (0,0). However, the average distance of the holes in the target from (0,0) clearly will be greater than 0, as not only is *r* independent of direction, making all distances positive, but also holes that are far from the origin will necessarily contribute to the estimate of a non-0 average. At some distance *r* to infinity, the corresponding cumulative distribution function (CDF) of our PDF is:

$$CDF(r) = e^{-b_2^2 r^2}$$
 (8)

Rearranging the CDF and solving for the number of steps, n, within b, allows us to estimate the timepoint at which a given fraction of the random walkers (α) would be outside the detection area of radius r:

$$n = \frac{r^2}{l^2 \ln(\alpha)} \tag{9}$$

Simulations were validated by comparison of the fraction of random walkers outside the detection area with the forecast of the fraction of the CDF(r) that would have left the detection area as time passes (Fig. 2).

3. RESULTS

3.1. Data representation in passive acoustic telemetry

Simulations resulted in 100 paths of random walkers each for small, medium, and large step sizes (Fig. 3a–f). Random walkers left the origin and dis-



Fig. 2. Performance of analytical solution compared to simulated random walk results. For each sample of walkers, the fraction of the population outside of the detection radius at each time step was calculated (grey). The probability of walkers outside the radius at time t (red line) was calculated using the cumulative distribution function equation for a vector of distances at time t. Random walks and an analytical solution for freely jointed chains (see Section 2) are both based on a step size of 0.01. Simulations were run for 4000 time steps, in 20 batches of 100 individuals. The calculated fraction of walkers outside of the telemetry radius matches well with simulation results. The standard alpha probability (0.05) is represented by the horizontal blue line



Fig. 3. Data representation of acoustic telemetry across multiple scales. (a–c) Actual tracks from 100 random walks over 10 000 steps. (d–f) 2D histograms of the distance walkers are from the origin (*r*) over time. (g–i) The pattern of detection ('at-liberty plots') by the simulated Vemco radius (indicated by the circle in a–c) for the 100 random walkers. a, d, and g are for the small step size simulation (1% of the detection radius); b, e, and i are medium step sizes (5% of detection radius); and h, f, and i are large step sizes (10% of detection radius)

persed in all directions (x, y) randomly, with individual paths ranging from long ambits with few changes in direction (i.e. long chain end separation) to more clustered near the origin. At the end of 10000 time steps, all 3 simulations contained numerous walkers both inside and outside of the receiver detection zone (Fig. 3a-c). Walks of shorter steps took longer to leave the detection zone, and there were larger numbers of individuals within the range of the receiver at the end of the runs (66 walkers, shortest step length), whereas longer-step walks left sooner, and fewer walkers were within the detection zone at the end (6 walkers for medium steps, 1 walker for large steps). The maximum distance of any individual in the simulations varied by step size, with distances of 2.77, 14.32, and 26.89 normalized units from the receiver origin for small, medium, and large steps, respectively (Fig. 3d-f).

At-liberty plots of these simulations showed numerous detections for all walkers early in the time series regardless of step size (Fig. 3g,h). Departures from the receiver radius varied with step size, with the earliest departures at t = 20 for large steps, t = 76 for medium, and t = 2015 for small. In the small-step simulation, 59% of walkers remained within the detection radius for all 10 000 time steps. Across all step sizes, individual walkers left the detection radius and returned multiple times. The frequency of returns decreased over time; however, returns still occurred at the end of the 10 000 time steps in all simulations.

RIs across all simulations ranged from 0.002 to 1, with those that remained within the detection radius continuously representing 38% of all simulated walks. The majority of small-step walkers had 'high' residency, with 72 out of 100 having RIs above 0.8. No walkers in the medium and large-step simulations had high residency. The medium-step simulation RIs ranged from 0.009 to 0.703, while large-step RIs ranged from 0.002 to 0.22.

3.2. Distinguishing random from real movements

The population of tagged Atlantic cod had 2 individuals with high residency (RI > 0.8), 1 with medium residency (0.2 < RI < 0.8), and 7 with low residency (RI < 0.2) (Fig. 4a). Two fish were detected nearly continuously throughout the study, whereas 2 other fish were detected on the initial tagging date and then never seen again, resulting in low RIs. Other individuals had patterns of episodic detection (Fig. 4b).

Broadly, simulated random walkers taking longer steps move more, which is expected, but the specific relationship indicates departures from studies of living fish (Fig. 4a). Simulations with step sizes of 1 body length obtained high residency in nearly all cases, with 3 simulations resulting in a single walker in the middle residency bin with an RI < 0.8. The majority of 3 body length simulations had medium residency, with 54 % of all simulated walkers in the medium residency bin and 41% with high residency. The 3 body length simulations resulted in 35 of the 100 simulations having at least 1 walker with low residency. The maximum number of walkers with low residency in the 3 body length simulations was 3. Out of the 6 body length simulations (n = 100), 99 runs produced walkers of low residency. Most walkers in the 6 body length simulation had medium residency, with 62% of all walkers in the medium residency bin and 35% of all walkers with low residency. The 6 body length simulations had only 3% of walkers with high residency.

Regardless of assumed behavior, all cod simulations resulted in the same or higher proportion of high-residency individuals as the tagged cod (2 individuals) multiple times. The majority of the smallerstep-size simulations resulted in an equal or greater number of high-residency fish, with 99 of the 3 body length simulations, and all 100 of the 1 body length simulations, having at least 2 high-residency individuals. Of the 6 body length simulations (n = 100), 3 resulted in multiple high-residency fish, while an additional 25 simulations had a single high-residency fish. In contrast, tagged cod exhibited low residency more frequently than the simulations, with 7 lowresidency fish. Only 5 simulations, from the 6 body length case, resulted in 7 or more low-residency fish. Simulations also differed from observed data in intermediate residency values; only 1 cod was ever observed in the middle 0.2-0.8 RI bin. In the simulated fish, the middle RI bin contained more than 1 walker 100% of the time in both the 3 and 6 body length simulations.

Simulations assessing the sensitivity of estimated residency to step size showed a strong impact of step size on the high-residency bin (Fig. 5). As step size decreased by 50%, the fraction of the population with high residency changed from 18.3 to 76.9%, a 3.2-fold increase. A 50% increase in step size resulted in a 150% increase in the members of the population in lower residency bins, going from 13.8 to 34.6%. Smaller step sizes decreased the fraction of the population within both the medium- and low-res-



Fig. 4. Cod residency and atliberty detection pattern vs. simulations. (a) Number of fish in each residency bin (low, medium, high) for the cod telemetry study, and comparable simulations conducted with different step sizes. Box plots show the median and the upper and lower quartiles, with the box representing the inter quartile range (IQR). The whiskers show the highest or lowest values excluding outliers, calculated as Q(1,3)-1.5× IQR. The dots represent the outliers within the data. (b) Atliberty plot showing the pattern of detection of individual tagged cod over time. (c) Atliberty plot for 6 body length step size simulation over time. Both real and simulated cod were detected throughout the study period. Real cod exhibited immediate departures from the detection array, which simulated cod did not

idency bins, with the medium-residency bin the least sensitive to changes in step sizes. Once the step size is sufficiently large (approximately 3 body lengths), the fraction of the population in the medium-residency bin remained relatively consistent over the body sizes used for our sensitivity analysis, with 5 of the 7 sizes assessed having over 50% of the population within the medium-residency bin (ranging from 0 to 67.9). In contrast, the fraction of the population within the low-residency bin increased steadily as step size increased, moving progressively from 0 to 44.1% with over 20% increases between subsequent body sizes.

Our literature review identified 56 papers, with data for 65 species, ranging from turtles to sharks to parrotfish. Of these, 21 papers did not report RIs, while an additional 5 did not report the body size of the fish necessary to determine step size. From the remaining studies, 5 did not report the detection radius of their receivers to allow for a relative step size calculation. A total of 29 studies from this sample met the criteria for inclusion in this review of study duration (Table S1 in the Supplement at www.int-res. com/articles/suppl/m672p073_supp.pdf).

The studies used for analysis represented 26 species of fish ranging from 14.1 to 430 cm. Most of the



Fig. 5. Sensitivity of cod simulations to changes in relative step size. Step size is standardized to 100% at 4 body lengths, and 1000 random walk simulations were run for each body size. Sensitivity plotted for 3 residency calculations (high, medium, low) where high residency represents walkers remaining within the detection zone 80% of the time, low represents walkers remaining only 20% of the time, and medium represents intermediate residency values

qualifying studies focused on benthic or demersal species. The smallest fish species was the annular seabream *Diplodus annularis*, while the largest was the tiger shark *Galeocerdo cuvier*. Receiver detection radius ranged from 50 to 650 m. Using a step size of 1 body length and scaling to the size of the receiver radius, the relative step size within these studies ranged from 0.0005 to 0.025, with the smallest step representing white seabream *D. sargus*, and the largest representing the bull shark *Carcharhinus leucas*.

On average, there was a 47% probability that random walkers would be indistinguishable from resident fish monitored with an acoustic receiver for the study durations reported in the literature. Two studies, of painted comber Serranus scriba and annular seabream, had a 100% chance of random walkers remaining in the detection radius at the end of study duration. If these studies are treated as outliers and excluded, the mean probability of detecting random walkers was 42% at the end of the published study duration across these cases (min = 0.002, max = 0.98) (Fig. 6). Across all studies, only 6 (20%) had less than a 5% probability of detecting random walkers at the end of the study duration (i.e. $\sim 5\%$ of the starting population of randomly moving fish would remain within the detection radius).

4. DISCUSSION

Our simulations demonstrate some of the challenges that must be considered when interpreting passive acoustic telemetry data as evidence of animalhabitat association. In particular, randomly moving walkers take time to leave the detection radius, so at the beginning of studies there is a 'burn-in' time period where data reflect more frequent detections (Fig. 3). Even if individuals move directly from the center of the detection radius toward the edge in a straight line, there is still a minimum number of possible detections (nl = R) that would be inevitable. When moving randomly in 2 dimensions, the resulting unintentional, diffusive process away from the center of the detection zone can be very slow. Without addressing this directly, the rate of this diffusive process can suggest high residency and high site fidelity in studies of short duration relative to the ambits of the tagged individuals.

The patterns of detection in our simulations revealed a strong dependence on the relative step size of the walker in determining the burn-in period. Not surprisingly, walkers with large steps left the receiver radius faster than those with small steps (Fig. 3). As RIs are calculated from the pattern of



Fig. 6. Probability of detecting randomly moving individuals at the end of a study. Random movements are scaled by species and by study, with 'relative step size' representing 1 body length as a proportion of the study's telemetry detection radius (1 body length [m] / acoustic receiver radius [m]). Each dot represents a unique species–study pair. Some studies focused on the same species, while others studied more than one species. For further details, see Table S1. Probabilities of detection through time were estimated with Eq. (8). As the step size relative to the array increases, the probability of detecting randomly moving individuals decreases. Two studies (blue dots) had a 100% chance of detecting randomly moving fish at the end of the study duration

detection for given the study duration, at short durations, even larger steppers can exhibit high residency. This makes it particularly important to (1) characterize this sensitivity in detail and (2) understand how the simulated step size is parameterized in the behavior of actual fish.

4.1. Implications for passive acoustic telemetry studies

During the initial study period, only absence observations are distinguishable from random walks. Clearly, no fish can leave the study area prior to satisfying nl > R steps (Fig. 3), but the effect extends beyond this time interval. Although random walkers have a small, non-zero chance of moving directly away from the detection zone (i.e. approaching nl = R), this is a low-probability outcome, and was not

observed in any of our simulations. However, some monitored fish did leave the detection area immediately and did not return throughout the study period, suggesting that the initial locations were not preferred. Therefore, absence data have a different inferential value than presence data early in the study. For walkers that remain within the detection radius past the burn-in period, the inferential value of their presence observations increases as the likelihood of them remaining within R from random movement decreases over time (Fig. 2).

As time passes, the distribution of random walkers spreads out. One expects that at some point the distribution of random walkers will be sufficiently even in space that the number of walkers entering the receiver array will approximate the number leaving the array. Simulations of random walks with medium and long step sizes do approximate this pattern of both a high frequency of detection and a high frequency of returns (Fig. 3h,i). In the latter half of the time series, the random walkers are leaving and returning to the telemetry array with patterns that appear on inspection similar to intentional returns (Fig. 3b). These are patterns in at-liberty plots that have been used to describe habitat preference (Holland et al. 1993, Lowe et al. 2003, Starr et al. 2004, Beatty et al. 2017). At this point in the study duration, the observations of fish leaving and entering the telemetry array will carry similar inferential value.

Finding the time when presence observations have the same inferential value as absence observations depends on a continuous gradient of probability and does not provide a clear threshold. The specific values of the curve in Fig. 2 depend on the *b* parameter in our analytical solution, also known as Kuhn's length, and the choice of alpha, i.e. the fraction of the diffusing population remaining within the detection area. The *b* parameter dramatically alters the probability of a random walker being at a given distance *r*. The *b* parameter is a result of relative step size, *l*, and study duration, n. With these parameters, one can estimate the time when detections are unlikely for a random process. Within the telemetry literature examined in this study, only 20% of studies had a random detection probability <0.05 by the end of study duration (Fig. 6). At the end of their reported durations, the majority of studies still had a high probability of detecting individuals on a receiver if they were just moving randomly, compromising their ability to draw inferences from observations of organism presence. The shortest studies in the literature review, 36 and 31 d, had a 0% probability of rejecting randomly moving walkers based on this analysis.

It should be noted that the studies reviewed here calculated residency using the RI approach, but several have also assessed habitat use through different methods, such as path analysis or the calculation of kernel utilization distributions. In all but 2 cases, residency was calculated based on detections across an array of receivers, rather than with a single, fixed receiver (although 10 of these studies calculated single receiver residency as well). Our comparison represents a conservative estimate of residency based on the pattern of detection at particular locations. For large receiver arrays, the question and the uncertainties produced by the data representation change. In such cases, there is still the uncertainty presented by a single fish that never leaves the unique detection radius of a single receiver, and there is the trivial case of a fish that straight-line exits the entire array; there is also the intermediate case of fish that move from one receiver to the next without leaving the

array. Such movements may be directed or not, but the distances would be larger, suggesting that random null models would need to run longer. Returns to previously exited detection areas carry additional inferential value that could shorten study times. Extending these specific findings to arrays of receivers is the subject of future work.

Here, we used an alpha of 0.05 and observed few studies that were of sufficient duration to discriminate random from directed movement. Our suggestion is that studies could, if this issue is a concern, be run for longer durations. However, an alpha of 0.05 may be overly conservative in this context. Given the shape of the curve in Fig. 2, a significant reduction in burn-in time could be obtained with a relaxation of alpha to 0.1 or 0.2. Given that this condition is not a hypothesis test per se, but rather a criterion for evaluating study design, deciding on a critical value for broad application will likely require a consensus emerging from an evaluation of more detailed studies that combine fine animal movements with simulation.

4.2. Random vs. real movements

Movement of real animals is presumably driven by behavioral processes rather than random draws, but real animal movements can be successfully modeled as random walks when sampled at specific scales and time intervals (Beverton & Holt 1993, Turchin 1998). This scaling is reflected in the step size (or mean free path) and can be impacted by environmental factors such as resource density or the presence of conspecifics (Beverton & Holt 1993, Bartumeus et al. 2005, Powell & Mitchell 2012, Gautestad 2015). In our simulations, the step size represents a priori the scale where movements (= steps) are uncorrelated, rather than directed movements towards a resource or goal. At smaller scales (i.e. shorter time periods), it is quite likely that sequences of steps have some degree of autocorrelation, and these correlated random walks have been fruitful models in other contexts to explore specific behaviors, particularly in insects (e.g. Kareiva & Shigesada 1983, McCulloch & Cain 1989, Turchin 1998). Lacking a specific behavioral hypothesis that would apply generally to fish, the appropriate null model formulation of the FJC is the limit as the autocorrelation on step direction goes to zero, producing a first-order Markov process and a uniform 2-dimensional random walk (Kareiva & Shigesada 1983). Were specific ecological hypotheses in hand, such as predatory searching behaviors or the presence of directional gradients, homing behaviors, or currents,

then null model modifications, such as autocorrelated step directions or the addition of convective terms (i.e. biased random walks; Blackwell 1997, Codling et al. 2008), would be reasonable extensions to explore.

In the case where the observed movement is indistinguishable from random, it is not proof that the movement of a single fish is non-directed. Indeed, there are a number of animal-animal and animalenvironment interactions that can explain observations of sedentary behavior (Tolimieri et al. 2009, Andrews et al. 2011, Harasti et al. 2014, Gristina et al. 2017). In the Atlantic cod data set used here, 2 of the 10 tagged fish remained within the receiver detection radius for the entire duration of the study (Fig. 4b). This degree of residency was observed in nearly 100% of the short and medium step length simulations. Only the longest step length simulation, assuming a highly mobile movement ecology, was distinguishable from the real cod data in this regard. There is a similar lack of explanatory ecological process behind the 5 Atlantic cod which left the receiver array soon after tagging. Given the lack of specific ecological information that might otherwise distinguish a random walk from behavioral choice in a single observation, the evidence provided by telemetered observations of single fish is limited to presence or absence in the data set. It is largely for this reason that inferences of habitat associations demonstrated with acoustic telemetry must rely on the properties of the population of observations, and likewise the utility of the simulations and analytical results is at the level of the sampled population rather than the individual (Gerber et al. 2017).

Many of the species of interest in telemetry studies inhabit relatively deep water in remote locations. Deploying research projects in these cases is logistically challenging and often expensive. Not surprisingly, therefore, telemetry studies often have small sample sizes and are rarely represented by a large sample population (Aarts et al. 2008). Thus, there are questions about extending inferences to a larger population from data that can reveal a range of behavioral patterns but may not be characteristic of population-level responses (i.e. means) (Gaillard et al. 2010, Violle et al. 2012). Methods of quantifying habitat associations in relation to environmental variables, such as species distribution modeling, assume data are representative of a population and hinge on estimating the population mean (Skov et al. 2008, Johnson et al. 2013). The simulation approach developed here provides a bridge between individual behaviors and a mean expectation for a populationlevel response. For example, the population of Atlantic Cod observations re-examined above deviated from a population of random walkers, which may add inferential strength to the observations of those individuals that demonstrate low site fidelity. Viewing the cod data in this context allows us to make specific predictions for cod movement patterns at a broader scale (Johnson et al. 1992).

4.3. Improving data interpretation

The broader application of this study may lie less in the specific design of new field data collection efforts than in the qualified interpretation of the resultant data. These findings indicate that evaluating habitat association requires nuance when using passive acoustic tracking. Because patterns in these data do not record actual behavior, but rather location in an idiosyncratic manner, a conservative approach to data interpretation is warranted. For example, when interpreting RIs, the early period of the study may be indistinguishable from diffusive dispersal. Absent other observations (i.e. visual observations) to contextualize early movement, detections from later portions of the study period hold higher inferential value.

While acoustic telemetry technology continues to evolve, the considerable environmental challenges inherent in field studies will no doubt continue to confound researchers. When investigating marine animal behavior, it is therefore critical to carefully design new data collection efforts and develop a priori reasonable expectations for evaluating data based both on the ecology of the animals and on the limitations of acoustic telemetry. This study clearly demonstrates that the pattern of detection in random walkers is sensitive to the estimate of step size; observations of high residency in particular are dramatically impacted by the step size of the organism relative to the detection zone (Fig. 3). To improve data interpretation, researchers can develop null expectations for telemetry data given the step size of their study organism (see Eq. 9). As this step size, or 'mean free path', may not be approximated on the level of minutes (as we have done here), researchers should take the behavioral ecology of the target species into account when developing step size estimates. Transmitter battery size and ping rate will also influence both the strength of a signal and the duration for which a fish will be recorded. Attending to the interaction of ecology and technology via conservative step sizes will yield higher confidence in the results of telemetry studies, and ultimately in the application of those results to management.

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