Animal Biotelemetry

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Random swims: an evaluation of acoustic telemetry thresholds for shark behavior and residency

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Abstract

Background Passive acoustic telemetry is a method used to quantify residency within an array of receivers, but this technology has limitations for capturing complex behaviors in sharks: pulse delays and detection range drop-offs in near-shore habitats. This study addressed residency calculation methodologies by examining visitation qualifier functions (thresholds) in commonly used R packages.

Methods Random walk models simulated the mismatch between detections on acoustic receivers and modeled shark movements, by testing 30-min, 1-h, 2-h and 24-h visit thresholds to compare gaps between shark detections at different transmitter settings (1- and 5-min delays). We also modeled tracks of transient sharks to show how these animals may interact with passive acoustic receivers differently than resident individuals.

Results Our results suggested that longer transmitter (tag) pulse delays (1–5-min standard for sharks and larger fish) required short (< 30 min) visit thresholds, as they reduced variability in residency times. Consequently, using thresholds of less than 2 h increased the number of counted visits that stemmed from the same events. Similarly, the 5-min delay also predicted greater elapsed residency times than did the real path. Our directional walks sent transient sharks through a receiver at 0–1 and 1–2 m/s; under these scenarios, transmitters were unlikely to ping twice (default minimum visit qualifier) if 5-min pulse delays were set on their transmitters (16.4%), whereas 1-min delays did frequently (84.2%). This indicated that a 5-min delay may misrepresent residency time for transient sharks.

Conclusions Thresholds and detection qualifiers manually set during passive acoustic surveys can bias residency and visitation results, and careful consideration should be applied on the basis of the life history (residential or transient) of the target species.

Keywords Acoustic telemetry, Sharks, VTrack, VEMCO, Shark tracking, Residency, Random walks

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Background

Sharks play pivotal ecological roles in marine ecosystems by maintaining the balance of prey fish communities and stabilizing the trophic structure of coral reefs [1]. The conservation of sharks promotes marine biodiversity, top-down regulation processes, and ecosystem health [17], and evaluating their movement and residency patterns helps us understand the functionality of reefs and connectivity between marine protected areas (MPAs) [1, 2, 26]. Acoustic telemetry (AT) enables scientists to observe these population dynamics across many different taxa [4] and is primarily used to understand migration patterns, home-range, seasonal residencies, and behavioral states that are difficult to study via other conventional methods like mark and recapture, or baited cameras [5]. Residency is a metric that quantifies site use as an individual's presence or absence [6] and is somewhat arbitrary based on what the researcher has defined as a particular site, jurisdiction, or region. However, AT tags (transmitters) have programmed delays when sending out signals to a receiver [7], and the effects of pulse delays on the precision of residency time estimates remain poorly described. Coded tags are commonly set for 1–5 min between pulses, a decision primarily meant to maximize battery life, as shorter delays reduce battery life longevity exponentially, and to avoid signal collisions, where multiple tags are deployed in the same study area [7].

In general, AT studies include a calculation of a residency index, calculated as the proportion of detection events relative to the total time an individual is available for detection (i.e., hourly, daily, weekly, and monthly) [1, 8]. Scientists record the number of visitations at a given site, defined as multiple detections (2 is standard) of an individual animal at the site within a specified time period [8]. The methods used for calculating these metrics vary depending on the study site, duration, scale, focus species, and overall research goals [3, 9, 10]. For long-term residency studies, the use of 'daily presence or absence' suffices to evaluate long-term space occupancies in sharks and thereby the simplest approach to determining overall site residency can be accomplished by dividing the number of days on which the individual was detected at a given site by the entire study period in days [1]. For finer-scale studies of residency or use of a particular site, data resolution from pulse delay and how residency is calculated, may have a significant impact. Accurately assessing shark residency at particular locations is challenging to perform on the basis of hourly, daily, weekly, or monthly movement patterns with a small number of deployed receivers [3].

Residency is punctuated by periods of absence, which are inferred by missed detections and data gaps. One of the most commonly used packages that evaluates animal movement and residency patterns, *VTrack* [9], filters out singular detections (false positives), and calculates residency by sorting the data into specific site visit events for scientists to extract individually. The number of visits and the duration per visit can then be analyzed for metrics of habitat utilization [9]. Especially for studies that use visits numerically as a measure of site preference, determining what qualifies as a new arrival versus a subsequent detection during the same event raises a caveat; sharks that move outside the receiver range show up as empty spaces in detection timelines. Depending on the thresholds set to determine new visits, these data gaps may be misinterpreted as missed detections, and transient sharks may be missed altogether. The *VTrack* package uses an {iResidenceThreshold}, which determines how many detections are considered a visit, and an {iTimeThreshold}, which determines how much time between these detections can pass before the event of a separate arrival to a site is considered [9]. These functions are used to optimize event recognition by determining how many minutes must pass between consecutive ping occurrences to constitute a new arrival. Therefore, it is assumed that gaps falling above these thresholds mean that a shark left the area. Their function also enhances site-specific residency data by subsetting individual residency scores for several visitation events (found in the *residenceslog* table output), which compiles the time from all events. Absence-time thresholds are set at default values of 2 detections per 24 h but are adjustable to whatever values the scientist considers are appropriate [9]. Receiver detection ranges and array design may influence these decisions, since the number of detections will likely increase with a larger detection range, and therefore, it is important that scientists standardize receiver ranges throughout an array as not to skew absence-time thresholds.

There is a need to provide guidance on visit thresholds, how adjusting them may affect the validity of residency scores, and how this may alter how we interpret shark movement behaviors. To evaluate these uncertainties in visit qualification and overall telemetry accuracy, here we (1) quantify how pulse delay affects residency times and visit counts, (2) reveal the main drivers of inaccuracy between acoustic receiver data and actual shark behavior day-to-day, (3) generate new theories for interpreting abacus plot data (commonly used illustrations of detection timelines) for singular visits, and (4) provide decision-making guidelines for setting visit thresholds.

Methods

Through R-Studio's base package, we coded a two-dimensional constrained random walk model to simulate the movement of individual sharks in a semi enclosed environment. Varying shark swimming speeds and turn angles replicated sharks moving through or around habitat areas, and transmitter–receiver communications (tag signals) were collected by recording grid-positions throughout their paths. In addition to evaluating daily site visits and shark residency proportions for telemetry data sets, this adjustable model also offers a theoretical methodology design for testing AT technology.

Random walk model

Sharks were programmed to begin their paths at a random point between the outer boundaries of the receiver (between red and orange), which replicated a shark that had just entered the receiver. We elected this to maximize shark-receiver interactions, and to reduce the number of non-visit events. This model operates within a domain of 50 km^2 of available space for sharks to move in- and outside of the receiver. If the shark reached the study area boundary, it was redirected back toward the center by programming 180° direction changes for brief (1-min) stretches after contact with any boundary. Our model enforced a vertical boundary at $x=0$, where the shark's position was adjusted to remain at or above $x=0$, simulating land at negative x values. Each random walk simulation lasted 24 h to account for continuous movement during an entire day and night, and with each time step representing 1 s of real time, the shark moved in a random direction in the two-dimensional grid. Receiver depth was an unnecessary consideration, since we assumed that receivers placed by divers along coastlines are able to reach all available depths within their horizontal range [7, 25]. More complex scenarios representing different habitats were considered, but intentionally left out to keep the modeled scenarios simplistic. Following [25], depth likely has a factor in detection probabilities, but the relationship between the effect size on detection probabilities and depth class is inconclusive. The movement direction was randomly chosen between 0 and 2π radians at each step (providing 360° of direction change), and the velocity was also randomized and sampled from a uniform distribution between 0 and 1 m/s swimming speed [11, 12, 24]. The system included one receiver placed near a linear coastline, with a resulting semicircular detection range, defined by three concentric zones within the semicircle, that provided a probability of missed detections depending on the distance from the center. These probabilities are derived from the literature on detection probability drop-offs in VEMCO receivers [7, 13]: inner zone (pink): 125-m radius with 100% detection probability. Middle Zone (Orange): between 125- and 187.5-m radii with a 75% detection probability. Outer Zone (Red): between 187.5- and 250-m radius with 50% detection probability. We assumed that weather conditions did not alter drop-off probabilities throughout the simulation.

Residency data extraction

We performed 1,000 random walks under these conditions, counting the number of true and missed detections, the proportion of true detections overall (residency proportion), the visit count, and the amount of time for each visit. Following the generation of each walk, detection points were placed along the paths according to the delay and detection drop-offs. Gaps were classified as occurrences of a shark leaving the receiver range and re-entering OR missed detections along the abacus plot, and gap durations averaged the number of seconds for each gap (enabling a distinction between separate visits and an extended visit). Residency for 1-s, 1-min, and 5-min delays was calculated by dividing the total number of detections by the number of possible detections during each trial. We analyzed the "inaccuracy" of the receiver settings by comparing residency scores from the 1-min and 5-min delays to the score of the base scenario (real-time tracking). For example, if the proportion of residency for 1-min delay data was 0.30 and the 1-s delay was 0.50, the inaccuracy score would equal 0.2; thus, our inaccuracy scores assigned a value to the amount of error between AT data and actual shark detection proportions.

Visit thresholds and residency times

Visit thresholds were chosen to be 30 min, 1 h, 2 h, and 24 h to cover the most common settings from previous publications using *VTrack* [2, 3, 14]. We extracted the presence and absence data for each delay from our random walks. Depending on the experimental thresholds, a consecutive number of false detections constituted a separate visit, absence strings equal to or greater than each threshold of absence was required before counting a new visit. The residency time was marked as the duration of seconds from the first detection to the last detection of each visit string, and all visit durations were compiled to calculate the total residency time. This system allowed us to compare the visit counts and elapsed residency times between each delay, with the actual path in seconds. We set these functions to contain a minimum detection requirement which only counted events of 2 or more detections as separate arrivals and illustrated the differences in visit counts and residency times through modeled correlations and figures. We ran 2-way analysis of variance (ANOVA) for each iteration of the delay and threshold with residency times, Poisson regressions for visit counts (skewed distribution), Tukey's HSD test for pairwise comparisons of transient visits, and Levene's test for homogeneity of residency proportions. Levene's test was chosen to check the equality of variances across groups to ensure the assumptions of ANOVA could be met. All statistical tests were conducted with a significance threshold of 0.05.

Directional nonrandom walks

We simulated two different types of transient shark encounters (15 min long each with 1,000 trials) and compared a highly transient individual with a slower swimming speed and greater turn angle. The fast shark swam at randomized speeds generated every 1 s between 1 and 2 m/s, with turn angles randomized every second between pi/144 (near straight line). The slower shark was set between 0 and 1 m/s with turn angles of pi/36 (directional but with wider turn radius) on the basis of [15, 24], for average shark cruising speeds driven by metabolism. These models operated under the same receiver ranges and boundaries as the prior residency models (Fig. 1).

Results

Compared with the base scenario, both the 1-min and 5-min delays produced different detection proportions. For the 5-min delay, the ANOVA results indicated a significant effect of residency (DFs = 338, F = 8.866, p = 0.0025) on inaccuracy. The average inaccuracy scores for the 1-min and 5-min delays were 0.20 (95% CI [0.1963, 0.2147] and 0.20 (95% CI [0.1970, 0.2155]), resulting in residency being underestimated by both delays by approximately 20% compared with the actual shark path when the number of detections over time was used as the calculation for residency. Correlations and fitted quadratic models to differentiate the inaccuracy scores of the 5-min delay settings (residual standard error: 0.06698 on 343 degrees of freedom; multiple R-squared: 0.3721; F-statistic: 101.6 on 2 and 343 DFs**,** p < 2.2e-16) revealed that nearly 37% of the variance in inaccuracy could be explained by the residency proportion alone. However, with residency as an indicator, inaccuracy increased with respect to margin of error toward higher residency proportions. The inaccuracy with highly residential sharks (50–99% residency) produced more variability than sharks with a residency between 0 and 50% (Levene's test p value = 2.2e-16), reducing the predictability of inaccuracy at higher residencies. For this modeling, Quadratic models showed the lowest AIC (− 4474.875), indicating the best fit to our data followed by the second-best model (Generalized Linear Models) with an AIC of − 3318.181.

Thresholds and visit counting

All 3 thresholds were set under 24 h, and the number of visits by a shark with 5-min transmitter pulse delays was overcalculated (p < 0.001 each; see Table 1). Between the 1-min and 5-min delays, visit counts differed for each threshold (p < 0.001 each), indicating that 5-min delays generated higher visit counts than 1-min delays across the board. Referring to Table 1: for the 30-min threshold, the mean visit counts are as follows: 1-s delay: 2.68 (SD = 1.39); 1-min delay: 2.76 (SD = 1.43); and 5-min delay: 3.25 (SD = 1.66). For the 1-h threshold, the mean visit counts are as follows: 1-s delay: 2.18 (SD = 0.98); 1-min delay: 2.23 (SD = 1.01); and 5-min delay: 2.34 (SD = 1.04). For the 2-h threshold, the mean visit counts are as follows: 1-s delay: 1.84 (SD = 0.73); 1-min delay: 1.87 (SD = 0.72); and 5-min delay: 1.92 (SD = 0.73).

Elapsed visit residency times

Residency times differed across different thresholds (half hour, 1 h, and 2 h; p < 0.0001) and delay types (p < 0.001). We discovered that visit time increased with longer set thresholds, particularly for 5-min delays. The 5-min delays produced longer visit times across each threshold, and the variability between all delays was the lowest under a 30-min threshold. We found a difference in visit time between the 5-min path and the actual path, which was highest under the 2-h threshold and lowest under the 30-min threshold (Levene's test: p = 0.001). Interquartile range (IQR) was used to measure statistical dispersion, along with means for averages. Based on Fig. 2, for the half-hour threshold, the mean visit times were as follows: actual: 988.04 min (IQR = 702.75); 1 min: 927.35 min (IQR = 707.00); and 5 min: 1,011.41 min (IQR = 760.00). At the 1-h threshold: actual: 988.44 min (IQR = 706.52); 1 min: 927.27 min (IQR = 701.50); and 5 min: 1,048.18 min (IQR = 735.00). For the 2-h threshold: actual: 1,046.73 min (IQR = 696.06); 1 min: 968.35 min (IQR = 703.50); and 5 min: 1,191.64 min (IQR = 635.00).

Directed random walks: transient sharks

In our directional models, migratory sharks presented shorter lengths of time inside a receiver than did resident sharks did, as predicted, and their abacus plots presented varied detection counts between 1- and 5-min delays. We modeled this behavior and found that the success rate of 2-detection minimums disproportionately affected the higher delays (5 min). Overall, slower sharks spent

(See figure on next page.)

Fig. 1 Random walk trial example simulating a shark swimming in a receiver. 1.1 shows the path illustrated in blue with a starting point (black point "A") and ending point (black point "**B**") throughout the 24-h trial. The semicircles represent each detection range for one acoustic receiver placed along a shoreline. The paths visualized an example route taken randomly from our simulated shark individual data sets. 1.2 shows detections and missed detections (missed = red, detected = green). The random walk parameters were as follows: semicircle diameter: 500 m; swimming speed: 0–1 m/s (changed every 1 s); trial duration: 86,400 s (1,440 min; 24 h); and steps: turn angle randomized every 1 s of swim time

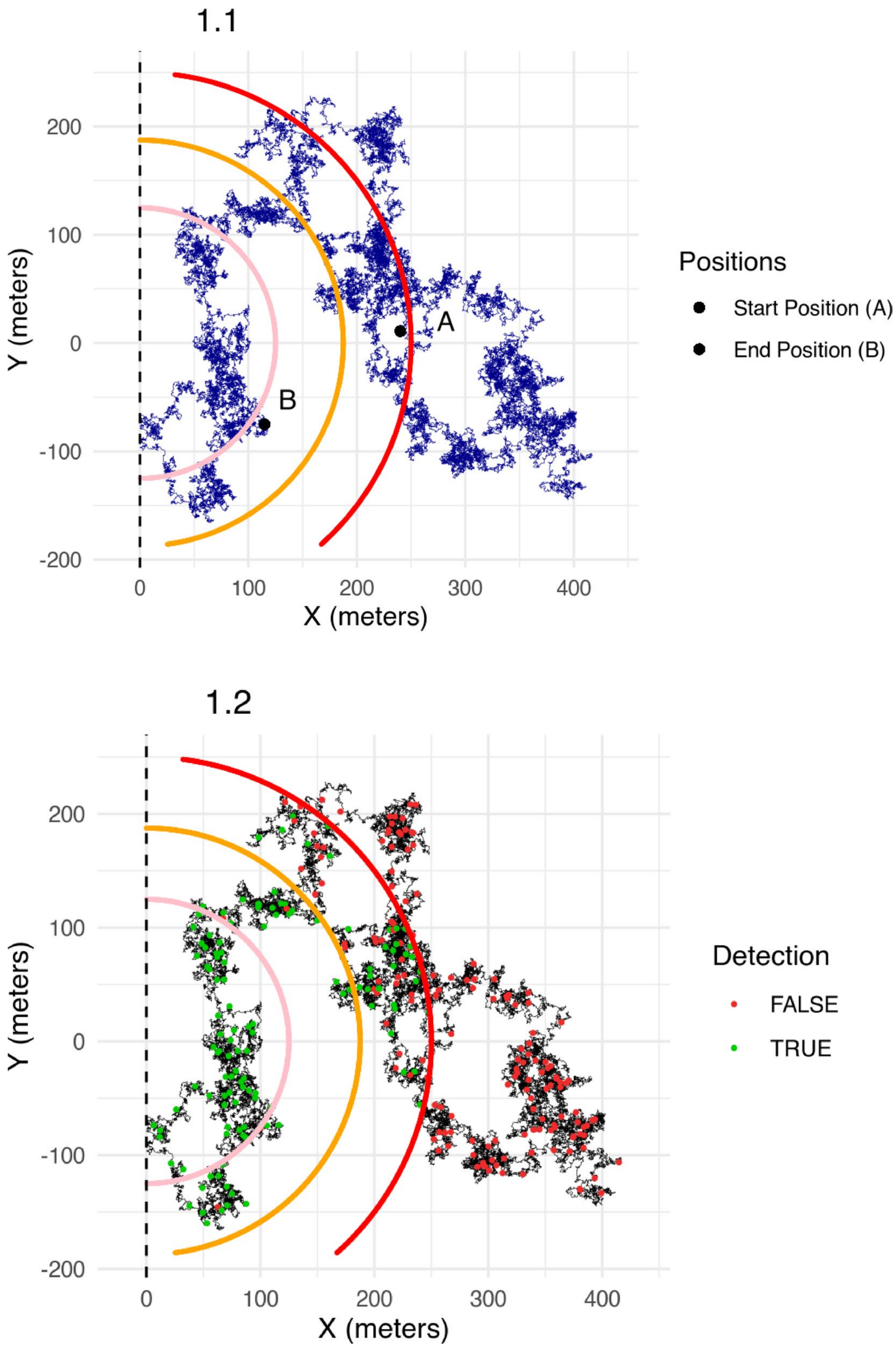

Fig. 1 (See legend on previous page.)

Table 1 Visit counts under different threshold (rows) and detection delays (columns)

Threshold	Actual	1 min	5 min
Half hour	2.68 ± 1.39	2.76 ± 1.43	3.25 ± 1.66
One hour	2.18 ± 0.98	2.23 ± 1.01	2.34 ± 1.04
Two hours	1.84 ± 0.73	1.87 ± 0.72	1.92 ± 0.73

Values are mean ± standard deviation. Standard deviation (SD) was a measure of dispersion for our set of values

an average of 6.1 min inside the receiver, whereas faster sharks spent 3.1 min ($p > 2.2e\text{-}16$).

Significant differences were identified in detection counts among the different shark movement behavior types and delays (ANOVA, $F(3, 3212) = 2780$, $p < 0.001$; Fig. 3). Pairwise comparisons via Tukey's HSD test revealed that fast swimming sharks with 5-min delays had significantly fewer detections than those with 1-min delays (mean difference = − 2.68 detections, 95% CI − 2.87– − 2.49, $p < 0.001$). Slower sharks with 1-min delays generated higher detection counts than faster sharks with 1-min delays (mean difference = 3.50 detections, 95% CI 3.31–3.69, $p < 0.001$). Slower sharks with 1-min tags also had significantly more detections than those with 5-min tags (mean difference = 5.38 detections, 95% CI 5.19–5.57, $p = 0.001$), suggesting that shorter delays increased the likelihood of a transient visit being counted.

The probability of a 5-min delay transmitter being detected at least twice with highly transient (fast) individuals was 16.4%, whereas 1-min tags increased the probability to 85.2%. We confirmed that the delay with a shark moving at 2 m/s would fail a 2-detection minimum requirement 84% of the time, whereas the 1-min delay would fail for only 15% of visits under our simulated detection radius. We concluded that sharks may easily pass through a 500-m read range without being detected twice; therefore, the tag settings may control whether a visit is counted or not. Transient (faster) sharks spent an average of 2.9 min less inside the receiver than slower ones did and, as a result, would have captured fewer site visits with a 2-detection minimum (Fig. 3).

Discussion

Our results indicate that there is a nonnegligible error in AT data driven by high tag delay settings with low visit thresholds. Evaluations of diel behavior, habitat usage, and site fidelity for sharks or otherwise should consider species dispersal and mobility, appropriate technology

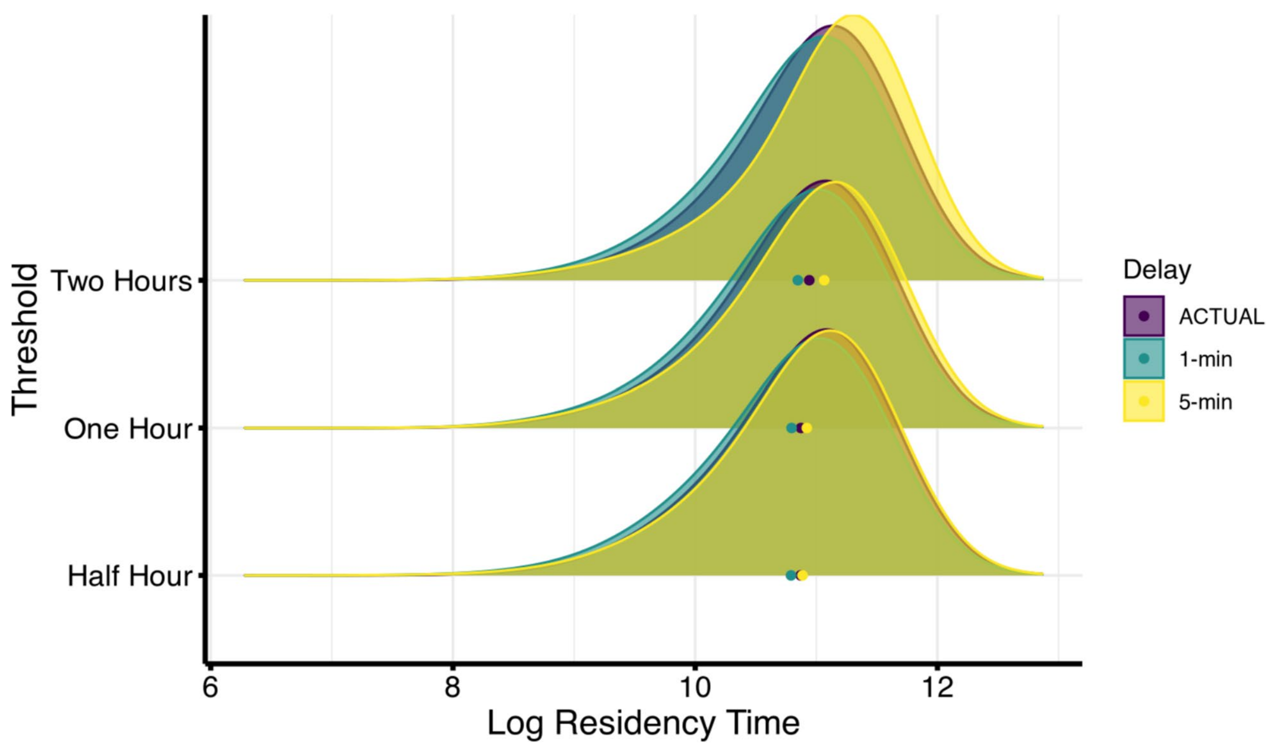

Fig. 2 Frequencies of visit times with their means (points) are presented across each time threshold and delay type (colors) in the ridgeline plot for 8991 observations. Mean points are placed along the x-axis lines for each y-axis group (thresholds), and the logarithm of residency times were measured in seconds

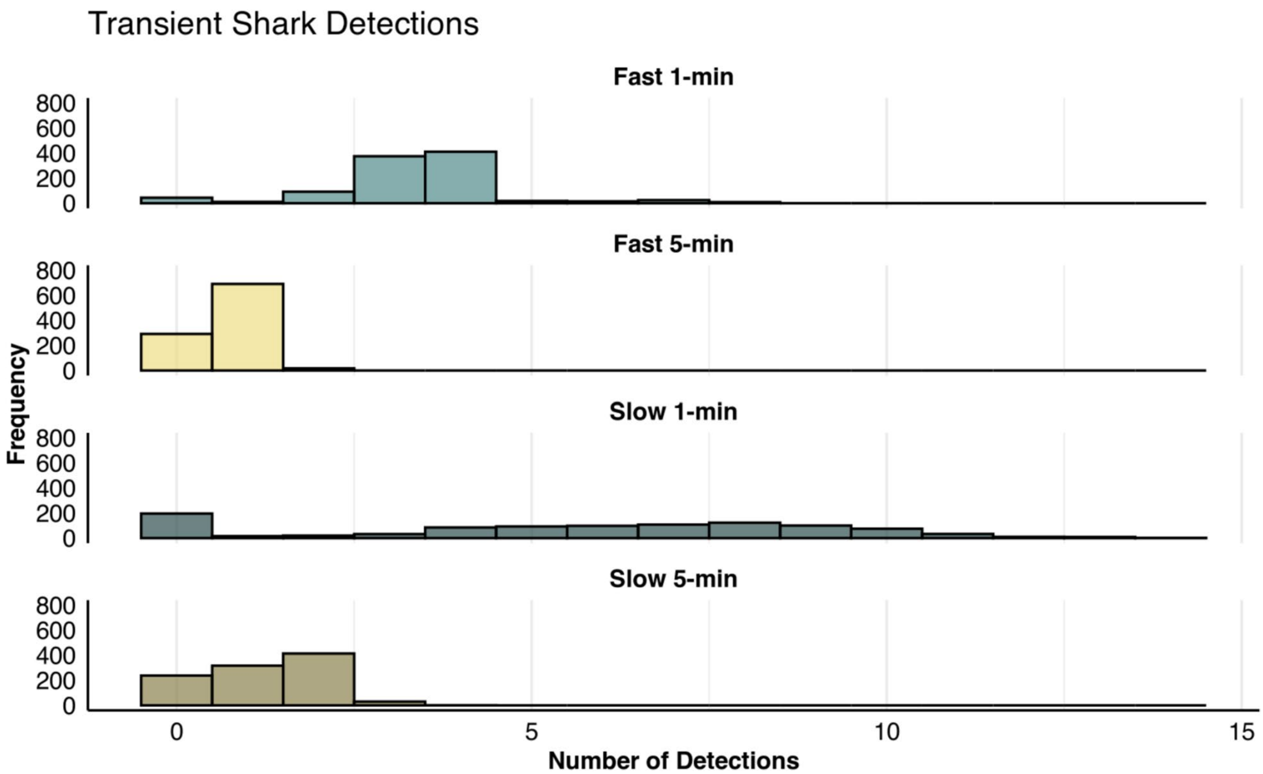

Fig. 3 Histogram plots of detection count with 1-min and 5-min delays for slow (highly mobile) sharks and fast (transient) sharks. Five-min delays peaked at 1 detection for fast sharks, with peaks at 1 and 2 detections for slow sharks. One-min delays peaked at 3 and 4 detections for fast sharks and between 2 and 11 detections for slow sharks

settings, and the potential for errors in analysis and interpretation. We encourage scientists to consider swim speeds, space use, and receiver ranges before concluding interspecies site usage. Some characteristics of sound propagation through water and their relation to environmental factors (i.e., meteorological, oceanographic and topographic) are reported to have a substantial effect on detection probability in AT [22]. Meanwhile, a review of more than three hundred acoustic tracking studies revealed that only 48.6% of the studies included results from equipment ranging experiments [7, 16]. Receiver performance (i.e., range drop-offs) can fluctuate with water conditions to cause missed detections, while weather, tides, and other abiotic factors also ultimately impact detections and our analysis of them [7]. This study revealed that a single missed detection for a shark could disqualify an entire visit count from the data set or divide a visit into multiple visits by extending gaps in detections, leading to an underestimation of residency time of 20% and different/missed transient visit counts. These results were also influenced by user-defined ping delays, showing that long delays for the conservation of battery life may disproportionately affect the accuracy of residency calculations. Scientists would ideally increase the quantity of receivers improving area coverage and reducing the impact that long tag delays have on residency calculations; however, adding additional receivers may be expensive and difficult to install. While most scientists design arrays consisting of several receivers, the distance between each site and potential overlap between coverage ranges, can play a major role in overall residency times. Tag battery-life should also be considered. Opting for shorter delays (1 min) will limit the duration of a study [7] but improve data resolution and residency accuracy.

Sharks spending longer periods of time around the perimeter of the receiver may produce weaker resolution in their tracks because of range drop-offs. With this in mind, scientists using the "number of detections over time" as a metric of site fidelity should treat their results as underestimations if some (or all) of their sharks exhibit faster than average swimming speeds, or wider space use which could imply a shark spending considerable time in the outer receiver ranges. Differences in speed, direction changes, and pulse delays can inflate or deflate the residency characteristics observed in sharks. Longer thresholds > 2 h are estimated to produce less frequent but more accurate visit counts to the real shark path, as shown in our results. In contrast, we found that 30-min thresholds among different tag delays tend to create greater similarity in residency time calculations. Therefore, threshold adjustments specific to delay and swim behaviors may prevent residential and transient visit mismatches, exaggerated visit counts, and skewed residency times. Studies of diel behavior using hourly detection data and "number of hours spent at a site" variables [17–19] are directly affected by these findings. Both the tag delay and visit threshold may have inflated the visit counts, potentially skewing the hours spent at sites. When analyzing hourly residency patterns, these sources of potential error can result in misinterpretations due to these fine-scale miscounts (one extra visit counted earlier than expected could change the entire narrative of a study; see [20] for more on the limitations of diel pattern analysis in AT).

Notable increases in residency time were observed in delays from the 30-min threshold to the 2-h threshold. This pattern is likely attributed to the extended duration of the 2-h threshold, whereby two detections within the large time window are less likely to constitute a new visit (i.e., fewer visits = greater residency time, as we revealed). However, with a 5-min delay, the chance of these short detection strings occurring at the necessary delays to sustain a visit decreases, along with the missed detection probability. As a result, it is likely that shark movements and visits counted with 1-min delay data would be missed with a 5-min delay, leading to a decrease in residency time and visit count for that data set. While certain studies analyze visit count and duration synonymously [1], others contrast them to measure activity and time spent at each site [3]. This study revealed that visit counts are negatively correlated with total visit time and that higher thresholds increase this effect. To combat this in future studies, where visit count is the main response variable, scientists may wish to use higher thresholds (> 2 h) to mitigate variability with respect to their tag delays and focus species. Given that our models revealed that lower thresholds (30 min) reduced variability in elapsed visit duration, a lower threshold (< 30 min) would ultimately improve the comparability of visit durations between tag delays in studies focusing on elapsed visit time [10, 21].

Transient sharks of two different turn angles and swim speed criteria revealed significant probabilities of failing the two-detection minimum qualifier when passing through the receiver. The faster shark (1–2 m s^{-1} + low turn radius) failed the 2-detection minimum requirement in 84% of the trials for 5-min delays, whereas the 1-min delay resulted in only 15% of visits failing the qualifier for the same shark. This finding suggests that longer tag delays increase the likelihood of skewing visit counts and residency times for transient sharks. Previous studies have shown that swimming speeds of sharks vary depending on species and water conditions [11]. Since visit counts were higher (3.31 ± 3.69) with slower moving sharks than with faster swimming sharks in our models, we would expect to see a difference in transient versus residential visit proportions between sharks with different cruising speeds.

Marine protected areas (MPAs), regions that are reserved and regulated by law to protect natural and cultural resources, effectively reduce human impacts on marine life and conserve biodiversity [26]. The effectiveness of introducing MPAs for protecting shark populations is not fully understood; however, studies have shown that MPAs protect the marine environment especially in complex habitats like coral reefs [17, 23]. The consequences of inaccurate analysis in the field of AT include inconclusive site preference and diel activity findings, as well as false conclusions for MPA coverage. For example, when designing or extending MPA boundaries, precise knowledge about ecological hotspots and high productivity zones is crucial to document prior given that the degree of MPA effectiveness is reliant on how much overlap exists between species movements and the area of spatial protection [17, 23]. Our findings suggest that small differences in how researchers handle their detection data—such as filtering criteria (transient versus residential sharks), temporal binning, or gap handling, could lead to substantial variations in calculated residency patterns. This variability may confound the ecological patterns researchers aim to investigate with study-specific methodologies. This raises important questions about the comparability of acoustic telemetry studies and their ecological impacts. Any mismatch between studies with deflated or inflated residency times will affect result interpretation, and lead scientists to draw false conclusions about shark behavior.

The accuracy of detection counts can vary on the basis of delay settings. While higher thresholds may be necessary for calculating residential visits and times, transient events must be accounted for under different criteria. We recommend adjusting the minimum detection qualifier on the basis of the tag delay and a species' average swimming speed to improve the integrity of visit counts. Some R packages like *VTrack* sort transient visits into their own category [9]; however, "transient" may have different definitions based on species swimming behavior, which may result in different transient visit counts from each tag setting. Ultimately, a higher detection minimum when dealing with transient and faster swimming sharks may improve the comparability of cross-study analysis, where different tag settings (from 1 to 5 min) are used and where species of varying swim patterns are under scrutiny.

Conclusions

Small differences in how researchers handle their detection data—such as filtering criteria (transient versus residential sharks), temporal binning, or gap handling, could lead to substantial variations in calculated residency patterns, leading to a misinterpretation of ecological hotspots around an MPA. An analysis of visitation qualifiers and threshold settings revealed the following takeaways: (1) different tag delay settings (1 or 5 min) produce different visit counts for the same shark path and threshold. (2) Longer pulse delays generally inflate the number of visits and their duration; however, at times, this results in fewer visits, as 2 consecutive missed detections cause a missed visit that would have been picked up by the other delay settings. (3) Half-hour thresholds result in more visit counts but lower visit durations along the same path than longer thresholds do (1 h, 2 h), since individuals with more visits swam in and out of the receiver range for short bursts of time rather than long periods. (4) The longest thresholds (1–2 h) showed the lowest deviance between the number of site visits of 5-min and 1-min delays; however, the total duration of visits was more comparable between delays using 30-min thresholds. Therefore, electing a higher visit threshold may improve the uniformity of the number of visits among different delay tags, while lower thresholds may create greater residency time evenness between different tag delays.

Abbreviations

AT	Passive acoustic telemetry
MPAs	Marine protected areas
ANOVA	Analysis of variance

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Author contributions
GF: Directed the study, programmed model codes, wrote the main manuscript text, and prepared all figures. MW: Revised and coded models in R, guided statistical testing, and reviewed and revised manuscripts. AH: Masters advisor for GF, generated initial ideas for the project, and reviewed and revised final manuscripts.

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Availability of data and materials
Data tables derived from our random walk models in R, and an R Markdown file with codes used for random walks, can be found publicly on GitHub through this link: https://github.com/GarrisonFishes/Random-Walks-GF_MW.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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References
1. Hearn A, Ketchum J, Klimley AP, Espinoza E, Peñaherrera C. Hotspots within hotspots? Hammerhead shark movements around Wolf Island Galapagos Marine Reserve. Mar Biol. 2010;157(9):1899–915.
2. Baremore IE, Graham RT, Burgess GH, Castellanos DW. Movements and residency of Caribbean reef sharks at a remote atoll in Belize, Central America. R Soc Open Sci. 2021;8(8):201036.
3. Nalesso E, Hearn A, Sosa-Nishizaki O, Steiner T, Antoniou A, Reid A, et al. Movements of scalloped hammerhead sharks (Sphyrna lewini) at Cocos Island, costa Rica and between oceanic islands in the Eastern Tropical Pacific. PLoS ONE. 2019;14(3): e0213741.
4. Crossin GT, Heupel MR, Holbrook CM, Hussey NE, Lowerre-Barbieri SK, Nguyen VM, et al. Acoustic telemetry and fisheries management. Ecol Appl. 2017;27(4):1031–49.
5. Brooks E, Sloman K, Sims D, Danylchuk A. Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. Endanger Species Res. 2011;13(3):231–43.
6. Kraft S, Gandra M, Lennox RJ, Mourier J, Winkler AC, Abecasis D. Residency and space use estimation methods based on passive acoustic telemetry data. Mov Ecol. 2023;11(1):12.
7. Scherrer SR, Rideout BP, Giorli G, Nosal EM, Weng KC. Depth- and range-dependent variation in the performance of aquatic telemetry systems: understanding and predicting the susceptibility of acoustic tag–receiver pairs to close proximity detection interference. PeerJ. 2018;12(6): e4249.
8. Cramer A, Katz S, Kogan C, Lindholm J. Distinguishing residency behavior from random movements using passive acoustic telemetry. Mar Ecol Prog Ser. 2021;19(672):73–87.
9. Campbell HA, Watts ME, Dwyer RG, Franklin CE. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Mar Freshw Res. 2012;63(9):815.
10. Bessudo S, Soler GA, Klimley AP, Ketchum JT, Hearn A, Arauz R. Residency of the scalloped hammerhead shark (Sphyrna lewini) at Malpelo Island and evidence of migration to other islands in the Eastern Tropical Pacific. Environ Biol Fishes. 2011;91(2):165–76.
11. Webb PW, Keyes RS. Swimming kinematics of sharks. 1982. https://api.semanticscholar.org/CorpusID:86193750. Accessed 22 April 2024.
12. Watanabe YY, Lydersen C, Fisk AT, Kovacs KM. The slowest fish: swim speed and tail-beat frequency of Greenland sharks. J Exp Mar Biol Ecol. 2012;426–427:5–11.
13. Loher T, Webster RA, Carlile D. A test of the detection range of acoustic transmitters and receivers deployed in deep waters of Southeast Alaska, USA. Anim Biotelemetry. 2017;5(1):27.

14. Schlaff AM, Heupel MR, Udyawer V, Simpfendorfer CA. Sex-based differences in movement and space use of the blacktip reef shark, Carcharhinus melanopterus. PLoS ONE. 2020;15(4): e0231142.
15. Jacoby DMP, Siriwat P, Freeman R, Carbone C. Is the scaling of swim speed in sharks driven by metabolism? Biol Lett. 2015;11(12):20150781.
16. Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, et al. A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish. 2014;24(1):199–218.
17. Barnett A, Abrantes KG, Seymour J, Fitzpatrick R. Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. PLoS ONE. 2012;7(5): e36574.
18. Legare B, Skomal G, DeAngelis B. Diel movements of the blacktip shark (Carcharhinus limbatus) in a Caribbean nursery. Environ Biol Fishes. 2018;101(6):1011–23.
19. Hammerschlag N, Gutowsky LFG, Gallagher AJ, Matich P, Cooke SJ. Diel habitat use patterns of a marine apex predator (tiger shark, Galeocerdo cuvier) at a high use area exposed to dive tourism. J Exp Mar Biol Ecol. 2017;495:24–34.
20. Payne N, Gillanders B, Webber D, Semmens J. Interpreting diel activity patterns from acoustic telemetry: the need for controls. Mar Ecol Prog Ser. 2010;30(419):295–301.
21. Andrews KS, Williams GD, Farrer D, Tolimieri N, Harvey CJ, Bargmann G, et al. Diel activity patterns of sixgill sharks, Hexanchus griseus: the ups and downs of an apex predator. Anim Behav. 2009;78(2):525–36.
22. Reubens J, Verhelst P, Van Der Knaap I, Deneudt K, Moens T, Hernandez F. Environmental factors influence the detection probability in acoustic telemetry in a marine environment: results from a new setup. Hydrobiologia. 2019;845(1):81–94.
23. Knip DM, Heupel MR, Simpfendorfer CA. Evaluating marine protected areas for the conservation of tropical coastal sharks. Biol Cons. 2012;148(1):200–9.
24. Papastamatiou YP, Iosilevskii G, Leos-Barajas V, Brooks EJ, Howey LA, Chapman DD, et al. Optimal swimming strategies and behavioral plasticity of oceanic whitetip sharks. Sci Rep. 2018;8(1):551.
25. Selby TH, Hart KM, Fujisaki I, Smith BJ, Pollock CJ, Hillis-Starr Z, et al. Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. Ecol Evol. 2016;6(14):4823–35.
26. Maestro M, Pérez-Cayeiro ML, Chica-Ruiz JA, Reyes H. Marine protected areas in the 21st century: current situation and trends. Ocean Coast Manag. 2019;171:28–36.

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