University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Papers in Natural Resources

Natural Resources, School of

1-18-2018

Evaluation of acoustic telemetry grids for determining aquatic animal movement and survival

Richard T. Kraus
U.S. Geological Survey, rkraus@usgs.gov

Christopher M. Holbrook
U.S. Geological Survey

Christopher S. Vandergoot
U.S. Geological Survey

Taylor R, Stewart
University of Vermont

Matthew D. Faust
Ohio Department of Natural Resources

See next page for additional authors

Follow this and additional works at: https://digitalcommons.unl.edu/natrespapers

Part of the Natural Resources and Conservation Commons, Natural Resources Management and Policy Commons, and the Other Environmental Sciences Commons

Authors

Richard T. Kraus; Christopher M. Holbrook; Christopher S. Vandergoot; Taylor R, Stewart; Matthew D. Faust; Douglas A. Watkinson; Colin Charles; Mark A. Pegg; Eva C. Enders; and Charles C. Krueger

RESEARCH ARTICLE

Methods in Ecology and Evolution | BRITISH ECOLOGICAL SOCIETY

Evaluation of acoustic telemetry grids for determining aquatic animal movement and survival

Richard T. Kraus[1] [iD] | Christopher M. Holbrook[2] [iD] | Christopher S. Vandergoot[1] [iD] | Taylor R. Stewart[3] | Matthew D. Faust[4] | Douglas A. Watkinson[5] | Colin Charles[5] | Mark Pegg[6] | Eva C. Enders[5] | Charles C. Krueger[7]

[1]Lake Erie Biological Station, Great Lakes Science Center, U.S. Geological Survey, Sandusky, OH, USA; [2]Hammond Bay Biological Station, Great Lakes Science Center, U.S. Geological Survey, Millersburg, MI, USA; [3]Rubenstein Ecosystem Science Laboratory, University of Vermont, Burlington, VT, USA; [4]Division of Wildlife, Sandusky Fisheries Research Station, Ohio Department of Natural Resources, Sandusky, OH, USA; [5]Fisheries and Oceans Canada, Central & Arctic Region, Freshwater Institute, Winnipeg, MB, Canada; [6]School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE, USA and [7]Department of Fisheries and Wildlife, Center for Systems Integration and Sustainability, Michigan State University, East Lansing, MI, USA

Correspondence
Richard T. Kraus
Email: rkraus@usgs.gov

Abstract

1. Acoustic telemetry studies have frequently prioritized linear configurations of hydrophone receivers, such as perpendicular from shorelines or across rivers, to detect the presence of tagged aquatic animals. This approach introduces unknown bias when receivers are stationed for convenience at geographic bottlenecks (e.g. at the mouth of an embayment or between islands) as opposed to deployments following a statistical sampling design.

2. We evaluated two-dimensional acoustic receiver arrays (grids: receivers spread uniformly across space) as an alternative approach to provide estimates of survival, movement and habitat use. Performance of variably spaced receiver grids (5–25 km spacing) was evaluated by simulating (1) animal tracks as correlated random walks (speed: 0.1–0.9 m/s; turning angle SD: 5–30°); (2) variable tag transmission intervals along each track (nominal delay: 15–300 s); and (3) probability of detection of each transmission based on logistic detection range curves (midpoint: 200–1,500 m). From simulations, we quantified (i) time between successive detections on any receiver (detection time), (ii) time between successive detections on different receivers (transit time), and (iii) distance between successive detections on different receivers (transit distance).

3. In the most restrictive detection range scenario (200 m), the 95th percentile of transit time was 3.2 days at 5 km, 5.7 days at 7 km and 15.2 days at 25 km grid spacing; for the 1,500 m detection range scenario, it was 0.1 days at 5 km, 0.5 days at 7 km and 10.8 days at 25 km. These values represented upper bounds on the expected maximum time that an animal could go undetected. Comparison of the simulations with pilot studies on three fishes (walleye *Sander vitreus*, common carp *Cyprinus carpio* and channel catfish *Ictalurus punctatus*) from two independent

large lake ecosystems (lakes Erie and Winnipeg) revealed shorter detection and transit times than what simulations predicted.

4. By spreading effort uniformly across space, grids can improve understanding of fish migration over the commonly employed receiver line approach, but at increased time cost for maintaining grids.

KEYWORDS

acoustic telemetry, fish movement, habitat use and survival, simulation

1 | INTRODUCTION

Acoustic telemetry has gained widespread popularity as a tool to understand migration, habitat use and survival of aquatic animals (Cooke et al., 2013; Hussey et al., 2015). Acoustic telemetry functions similar to radiotelemetry in terrestrial environments (White & Garrott, 2012); an animal-borne transmitter emits an acoustic signal detected by a receiver, which in this case is an underwater microphone, or hydrophone (hereafter, receiver). The signal can be continuous or intermittent, and it can be coded to identify individuals and transmit information from sensors in the tag (e.g. temperature). At the most basic level, acoustic telemetry provides a chronology of observations from active or passive monitoring of specified areas with receivers. Compared with marking large numbers of animals in hopes that a small fraction are observed at a later time, usually, only once (Pollock, 1991), acoustic telemetry provides abundant information about individuals without the need to recapture the animal (Heupel, Semmens, & Hobday 2006). Furthermore, fates of individuals with acoustic transmitters can be known with greater temporal and spatial resolution, dramatically reducing tagged sample size requirements and increasing the diversity of inferences on animal movements than possible with conventional tagging. Just how much novel information can be obtained in an acoustic telemetry study pivots on the spatial arrangement of receivers, which are commonly moored at fixed locations to passively monitor tagged individuals.

In ecological field studies, the researcher has no control over the movement and habitat use of aquatic animals bearing acoustic tags; therefore, how to spatially distribute receiver sampling effort is a fundamental question for acoustic telemetry studies. Most acoustic telemetry studies have aimed to determine broad-scale migration across a landscape of aquatic habitats, using a one-dimensional arrangement of receivers (i.e. receiver "lines" or "gates") to detect passage of individuals through a river or along a coastline (Jackson, 2011; Welch, Boehlert, & Ward, 2002). Few studies have used two-dimensional grid deployments, where receivers are spread systematically through the environment to infer animal movements throughout a region (Hedger et al., 2008; Simpfendorfer, Heupel, & Hueter, 2002). Less frequently, movement has been determined through triangulation of a signal on multiple receivers, but such studies have been limited to small areas because of the need for overlapping detection ranges (Binder et al., 2017; Dance & Rooker, 2015; Meckley, Holbrook, Wagner, & Binder, 2014; Romine et al., 2014). Strategic placement of receivers in bottleneck areas (e.g. narrow sections of a continental shelf, river channels or island passes) has been rationalized as a trade-off between a limited number of receivers and the need to time movements past landmarks (e.g. Wingate, Secor, & Kraus, 2011). Success of this approach is evidenced by an exponential growth of peer-reviewed literature in recent decades (Hussey et al., 2015), but the arrangement of receivers in many studies often is as much a matter of convenience as it is a demarcation of relevant zoogeographical areas. The receiver-line strategy emphasizes redundancy with overlapping detection radii to ensure that every occurrence of a tagged animal is recorded on multiple receivers (Kessel et al., 2014), and in specific cases, this design is duplicated to evaluate the directionality of movement across an imaginary boundary (e.g. Hayden et al., 2014). Thus, concentration of receivers into bottleneck areas markedly reduces the area effectively sampled, and substantially increases duplicate detections of transmitters on multiple receivers. Subjective selection of receiver locations based upon luck of geography also imposes unquantified biases on the spatial interpretation of telemetry data while leaving vast sections of the ecosystem unmonitored. Moreover, some aquatic ecosystems may not have obvious bottlenecks through which animals must travel to migrate between habitats.

Like any sampling tool, the number, timing of deployment and locations of telemetry receivers define the sampling design. Use of receivers only at strategic locations (e.g. lines) represents a distribution of sampling effort that is neither random nor uniform. Such narrowly focused receiver arrangements may represent the most effective designs for addressing a specific set of questions, but may preclude inferences about animal movement and habitat use beyond parochial information needs. If movement routes are known, then arrangement of receivers (i.e. lines) along those routes will provide efficient and unprecedented detail of the movement history of tagged animals, but initially, knowledge of an animal's migration is often characterized by little more than anecdotes between mark–recapture end points. When prior knowledge regarding movement is limited, how should receivers be distributed? We know from our own experiences and through conversations with colleagues that a common solution is to recast the research question to fit the bottleneck-receiver-arrangement strategy. Alternatively, some telemetry researchers have employed grids (two-dimensional receiver arrays) with non-overlapping detection radii to gain broader spatial coverage and elucidate heterogeneous use of habitats across an aquatic landscape (Heupel & Simpfendorfer, 2002). Although such an approach risks

monitoring unused habitats, importantly it provides the capability to distinguish non-use of a habitat from absence of data. Much attention has been paid to the performance of one-dimensional receiver lines (Steckenreuter et al., 2017), but rigorous evaluation of grids as a method for discerning details of acoustically tagged animal movements has been lacking. The two approaches achieve the same goal of defining when animals move between habitats; however, the grid design generates additional spatial information on the behaviour of the animal after it enters an adjacent habitat.

In terms of statistical analysis of telemetry data, systematic sampling represented by a grid is more defensible than the subjective monitoring of convenient landmarks (Krebs, 1989; Legendre et al., 2002). A stratified random sampling approach to arrange receivers may provide additional quantitative advantages, but we are not aware of any acoustic telemetry studies that have proposed this. In practice, evenly spaced sampling of a continuous environment has both statistical rigour (Stevens, 1997) and flexibility to support iterative modification through feedback from inferences on movement via adaptive sampling (Stein & Ettema, 2003; Thompson & Seber, 1996). Given the potential advantages of improved statistical inferences, and additional movement information, the one-dimensional receiver line approach surprisingly remains the favoured design over a grid or random sampling design. Two likely explanations are that: (1) field experiments to test performance of acoustic telemetry grids at realistic spatial scales could be prohibitively costly (but see, Heupel & Simpfendorfer, 2002), and (2) proposing a grid design without some proof-of-concept evidence risks fatal criticism from research sponsors.

In response, we simulated tagged animal movements in a realistic virtual arena populated with a variably spaced receiver grid. We asked basic, universally applicable, questions about the capabilities of a receiver grid: how frequently is an animal within the grid detected, and if it left one receiver, how much time would pass, and how far would it travel before we would expect to detect it on a different receiver? Answers to these questions are critical for understanding study design resolution for determining when an animal dies or leaves the ecosystem and whether it occurred in a particular habitat. Scenarios in our simulation represented a fully crossed view of biological characteristics of a correlated random walk (speed and turn angle) and physical characteristics of equipment (tag transmission delay interval) and environment (grid spacing and detection range). Researchers will note that many telemetry studies have been resource limited in terms of numbers of receivers and time to deploy and maintain receiver stations, and consequently, effective grid designs with limited resources appear impractical. As the questions for the grid simulation had no analogs for receiver lines (i.e. once the animal leaves the line, there is nothing to quantify), we compared the time cost to tend grids vs. lines with a thought experiment. In developing the grid simulation, we created useful tools in the open-source programming language, R (version 3.3.3, (C) 2017 The R Foundation for Statistical Computing), and these are freely available to be adapted for specific acoustic telemetry studies in any aquatic environment that can be represented in two-dimensions (Holbrook, Hayden, & Binder, 2017). Finally, we presented pilot field studies using three fish species that demonstrated the applicability and limitations of the simulation results.

2 | MATERIALS AND METHODS

2.1 | Background

Our interest in developing a simulation was inspired by current research in Lake Erie on the migration of walleye *Sander vitreus*, in which a double receiver-line was initially used with overlapping detection ranges and took advantage of geographic bottlenecks between islands that naturally partitioned spawning areas from seasonal feeding habitats (Raby et al., 2018). Securing funding for that study was in part conditioned on a convincing rationale for our ability to successfully time passage of fish around the islands. Later, in the study, opportunistic deployment of receivers to the east of the islands hinted at much more interesting and complex patterns of migration. Furthermore, most of our data from receiver lines were redundant, with detection of single coded transmissions on two to five receivers. We surmised that a different arrangement of receivers could both continue to provide timing information of fish movement past the islands and additional information on time spent in various spatial management units. Simply put, we had enough receivers ($n = 72$) to redistribute into a 15-km grid across the central basin of the lake, but we had scant information on whether this change would still achieve our objective of timing fish passage around the islands and reduce redundancy in our data. Thus, we evaluated this question through a simulation.

2.2 | Simulations

To accomplish our simulation, we generated: (1) virtual paths as correlated random walks within a shoreline boundary represented by Lake Erie (the arena was approximately 388 km long with an area of 25,700 km^2); (2) tag transmissions along each track; and (3) detection of each transmission based on logistic detection range curves and tag-receiver distances for each virtual receiver grid. No single virtual track was intended to represent any actual tagged fish, because movement characteristics (i.e. random walk parameters) of walleye in the wild were unknown. Rather, we evaluated a range of characteristics to encompass typical movements of a wide range of aquatic animal species. Each movement path, tag transmission and detection scenario were evaluated on one of 26 receiver grids. Within each grid, receiver spacing was uniform, and across grids spacing ranged from 5 km ($n = 1,028$ receivers) to 25 km ($n = 39$ receivers), in 1 km increments (Figure 1). Here, we measured spacing in the x and y directions, as opposed to the diagonal distance between receivers (which would simply be a constant 41.4% greater distance).

Virtual paths were generated by calculating points every 100 m along an azimuth drawn from a zero-mean normal distribution of turn angles. If the path crossed the shoreline boundary, the step was repeated until the path remained in the virtual lake. The starting location was randomly assigned to one of two locations where actual
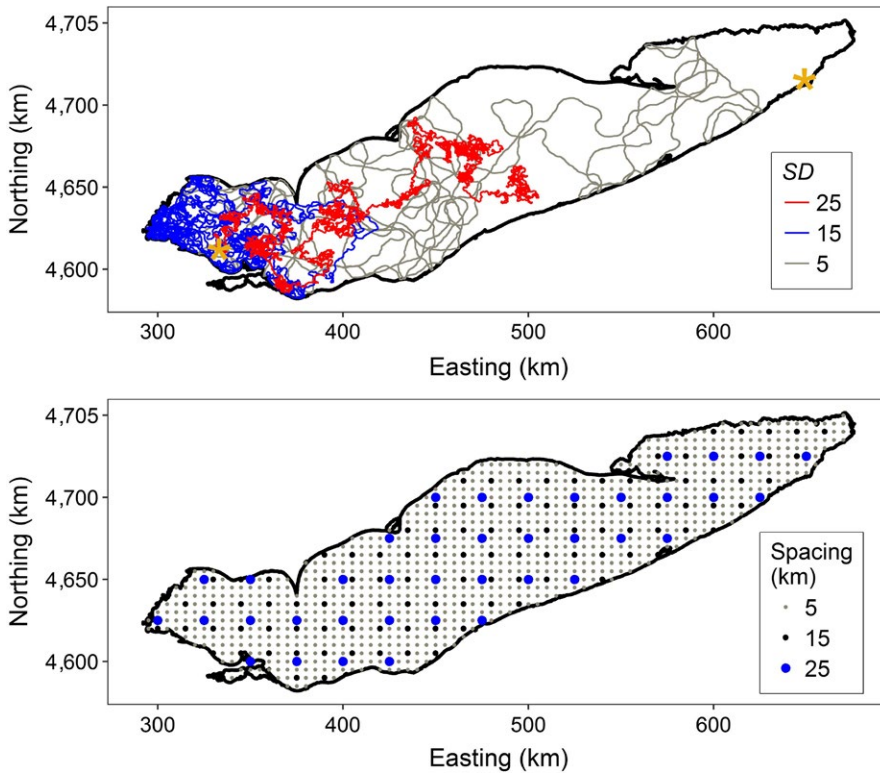
FIGURE 1 Examples of simulated fish tracks and receiver spacing scenarios in a closed two-dimensional arena, representing Lake Erie. In the upper panel, track starting locations (asterisks) are indicated for Toussaint Reef (to the west) and Van Buren Bay (to the east)

tagged walleye had been released in Lake Erie: Toussaint Reef in the western basin or Van Buren Bay in the eastern basin (Figure 1). The standard deviation (*SD*) of turn angles was fixed within each track but varied among tracks. We simulated six turn angle schemes, which ranged from *SD* 5 to 30° in 5° increments (Figure 1). A timestamp was assigned to each point based upon four swimming speeds, which ranged from 0.1 to 0.9 m/s in 0.2 m/s increments. Furthermore, we simulated three path durations: 30, 90 and 150 days.

For each path, a series of transmission timestamps was generated, and then the coordinates of each transmission were assigned using linear interpolation. We simulated four transmission delay schemes (nominal delays: 15, 30, 120 and 300 s) spanning the range of intervals commonly used in acoustic telemetry field studies (e.g. VEMCO PPM coding). Each interval between transmissions (Δt) was drawn from a uniform distribution, such that $\Delta t \sim uniform\ (0.5 \cdot d + b, 1.5 \cdot d + b)$ where d (nominal delay) was the average time between the end of one coded burst (signal) and the start of the next coded burst, and b represented the duration of each coded burst. Similar to field studies, b was fixed at 5.0 s for all transmission delay schemes.

Detection range was modelled as a nonlinear decay function typical of what has been observed in previous studies (Hayden et al., 2016; Huveneers et al., 2016). Stochastic detection (or non-detection) of each transmission based on a Bernoulli distribution with probability, p, determined by a logistic curve:

$$1 - \frac{1}{1 + 10^{-\beta_1 \times (D - \beta_2)}},$$

where D was the distance between each tag and receiver at time of transmission, β_1 determined the steepness of the curve and β_2 was

the mid-point of the curve (i.e. where $p = .5$). We simulated detections for three range curves (i.e. detection radii), representing poor ($\beta_1 = 0.006$; $\beta_2 = 200$ m), average ($\beta_1 = 0.0025$; $\beta_2 = 800$ m) and good ($\beta_1 = 0.015$; $\beta_2 = 1,500$ m) environmental conditions. These curves were based upon detection range data from VEMCO transmitters (model V16-6H, Amirix Systems Inc., Bedford, Nova Scotia) in lakes Erie, Huron (Hayden et al., 2016) and Winnipeg.

Three paths were simulated for each combination of variables (21 grids × 6 turn angles × 5 swimming speeds × 4 transmission delay schemes × 3 detection radii × 3 path durations) for a total of 68,040 paths, with up to 224,474 detections per path and a total of *c.* 299 million detection events. Equivalently, note that for each turn angle, a single arbitrarily long path could have been used for the same purpose (applying various grid, radius, speed and transmission delay characteristics), but this approach can become memory resource limited on a typical desktop workstation. Consequently, replicate paths ($n = 3$) and path durations (which had no discernable effects on the characteristics of the movement metrics) were pooled. Thus, sample sizes of detection events were unbalanced for analysis, varying between 20 and *c.* 1.1 million among all 7,560 scenarios (mean detections per scenario = 39,488).

2.3 | Simulation analyses

Three primary metrics were calculated to characterize each simulation: (1) detection time: elapsed time between successive detections; (2) transit time: elapsed time between successive detections on different receivers; and (3) transit distance: distance between successive detections on different receivers. The mean values of these metrics were less important to us than understanding the

upper end of the range; thus, we calculated the 95th percentiles. Due to a lack of data in some tracks (≤3 detections and no transit events), n = 2,399 (3.5%) of tracks were excluded from analyses of transit time and transit distance. Initially, we observed that grid spacing and detection radius accounted for the majority of variability; therefore, we graphed each variable as a function of grid spacing and radius while pooling across other variables (turn angle, speed and transmission delay). These graphs demonstrated an approximately log–loglinear relationship between response and grid spacing.

Transit times were of greater interest than detection times because in nature these values could represent a habitat change, behavioural change, initiation of migration or some other ecological process. Consequently, to understand the relative importance of each variable's effect on transit time, we developed GLMs for each detection radius using an ANCOVA approach (assuming a Gaussian distribution with identity link). Spacing (log-transformed) was the covariate and transit time (95th percentile) was the response. Because each varwiable was fully crossed with the others, we modelled all possible interactions and calculated marginal (least-squared) means, conditioned on an intermediate grid spacing (15 km). For that single grid spacing value, means were calculated for each level of a single variable while holding other variables constant at intermediate values (swimming speed = 0.5 m/s, turn angle SD = 20, delay = 120 s).

2.4 | Pilot studies

Simulations of animal movement may provide a powerful tool for selecting an appropriate field sampling design (Turchin, 1998), but they are no substitute for empirical validation. We were fortunate to have pilot data from three fish species with contrasting life histories for comparison with our simulation results: a pelagic freshwater piscivore, walleye in Lake Erie; a benthic freshwater piscivore, channel catfish Ictalurus punctatus in Lake Winnipeg; and a benthic freshwater omnivore, common carp Cyprinus carpio in Lake Winnipeg.

The study on walleye was initiated to understand survival and behaviour of fish captured, tagged and released from the summer recreational fishery in Lake Erie. Adult walleye were surgically implanted with model V13-1H tags (VEMCO) with a nominal transmission delay of 180 s, following protocols described in Hayden et al. (2014). During July to August 2015, walleye were released into a grid of 25 receivers with an average spacing of 7 km (Figure 2). The Lake Erie grid was deployed for 122 days to focus on near-term survival and behaviour. Although receivers deployed elsewhere in the lake also detected walleye, we limited our analysis to detections on the grid of 25 receivers. We also limited our analysis to fish that were known to be alive (n = 18 out of 30 total tagged individuals) for the duration of the pilot study.

The study on channel catfish and common carp was initiated to understand population connectivity and habitat use among riverine, lacustrine and marsh habitats in Lake Winnipeg. These species were surgically implanted with model V16-4H tags (VEMCO) with a nominal transmission delay of 120 s, following protocols described in Hayden et al. (2014) for the common carp. Channel catfish were anaesthetized using a 20 mg/L eugenol solution (Keene, Noakes, Moccia, & Soto, 1998) and surgical procedures followed Siegwarth and Pitlo (1999). During June to August 2016, channel catfish (n = 97) were tagged and released in the Red or Winnipeg rivers and common carp (n = 40) were tagged and released in the Netley/Libau
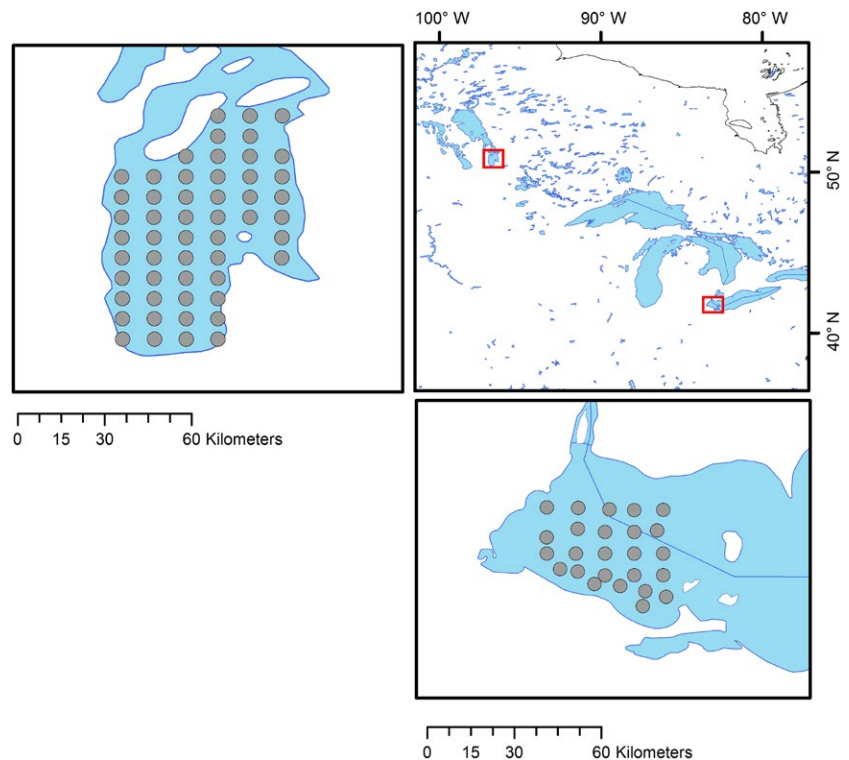
FIGURE 2 Gridded acoustic telemetry arrays (dots) used in large lake ecosystems (Lake Erie, bottom right panel; and Lake Winnipeg, left panel) for understanding migration, habitat use, and survival of three species of fish (walleye, channel catfish and common carp). The top right panel shows North America with inset rectangles delineating the extent of the other panels

marshes. Similar to Lake Erie, the Lake Winnipeg grid covered only a small portion of the system, and was comprised of 53 receivers with 7 km average spacing (Figure 2). The grid was fully deployed on 22 July 2016 and downloads began on 19 September 2016 allowing for 58 days of full deployment in 2016. All fish were released in tributaries outside the Lake Winnipeg grid. Data from receivers deployed in other areas such as tributaries were not considered. Only when fish entered the grid during the study period were they included for comparison.

For all species in the pilot studies, we calculated detection and transit time for graphical comparison with simulations, matching 7-km grid predictions for the 200, 800 and 1,500 m detection range scenarios.

2.5 | Time cost comparison

Financial costs of fieldwork can vary idiosyncratically given available tools, institutional facilities and ecosystem characteristics; therefore, we estimated time required to tend grids vs. comparable scenarios with receiver lines in a rectangular arena representing an estuary, coastal embayment or small lake with an area of 2,500 km². The long-side dimension of the rectangle was four times the short side (25 km). To calculate time, we assumed 12 knot average transit speed between stations and 0.5 hr to retrieve and re-deploy each receiver. We varied grid spacing from 7 to 16 km to match a relevant range of simulation scenarios, and used a fixed 1-km spacing in receiver lines—similar to other studies (e.g. Hayden et al., 2016; Knip, Heupel, & Simpfendorfer, 2012a; Raby et al., 2018; Steckenreuter et al., 2017). The time cost for receiver lines was fixed as the sum of the time to travel between sites and the time required to tend each receiver once. The total travel and tending time varied with grid scenario, and we assumed an orthogonal path weaving to and fro along the long axis. The calculations did not include time to travel between a port and the first station.

3 | RESULTS

3.1 | Detection time

Based on simulations, grid spacing and detection radius had the most prominent effects on grid performance metrics (Figure 3). Under best conditions (detection radius = 1,500 m) in the grid with the fewest receivers (spacing = 25 km), for 95% of cases, the time between successive detections was ≤5.2 hr, compared with 9.9 days for the worst conditions (detection radius = 200 m; Figure 3, upper). These values (means of 95th percentiles averaged across tracks) can be interpreted as upper confidence limits. For example, with 95% confidence under intermediate conditions (detection radius = 800 m), the average maximum time an animal went undetected ranged from 1.7 hr to 1.1 days for the 5- and 25-km grids respectively (Figure 3, upper). Note that detection times were inclusive of transit times, which were special cases when successive detections occurred on different receivers.
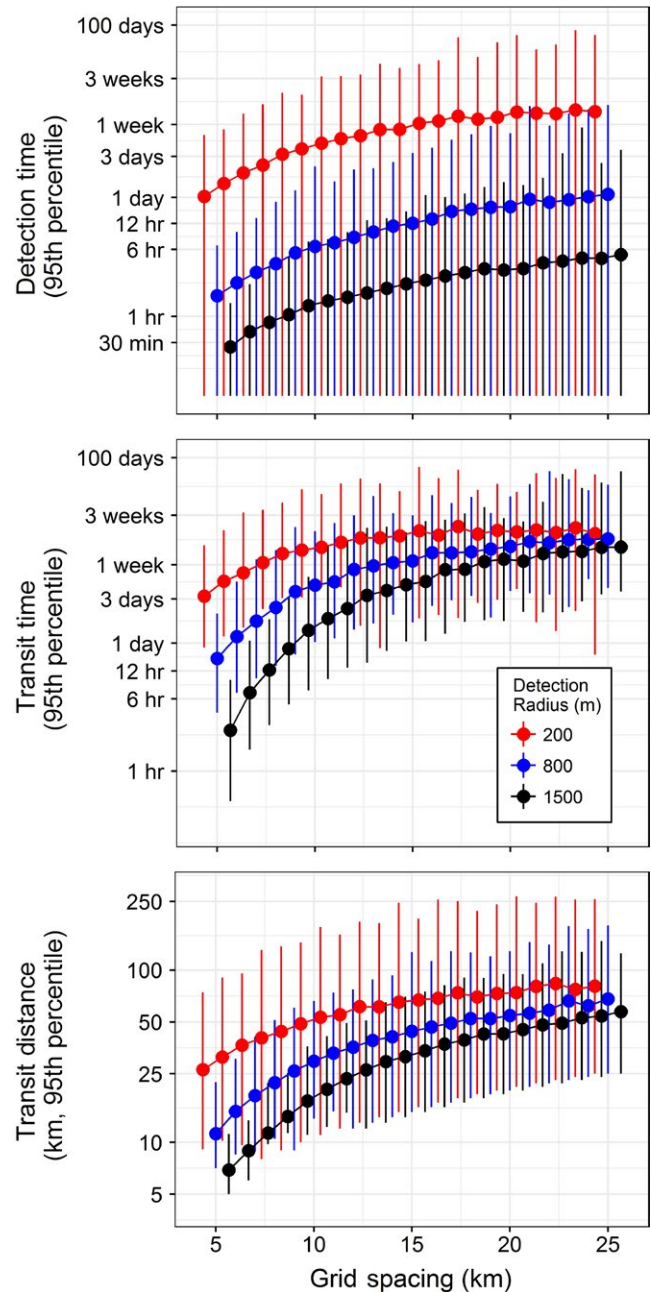

FIGURE 3 Detection time (upper), transit time (middle) and transit distance (lower) as function of telemetry receiver grid spacing for simulated fish tracks in Lake Erie. The 95th percentiles were averaged across tracks (dots), and plotted with range bars showing the minimum and maximum observed 95th percentile values. Data from all simulation scenarios (i.e. combinations of tag delay, swimming speed and turn angle *SD*) were pooled, and the minimum values in the time plots were truncated at 7 min. The key defines three scenarios of varying detection radii (note: the 200 m and 1,500 m scenarios are staggered left and right, respectively, to reduce symbol overlap). The vertical axis is plotted on a log-scale

3.2 | Transit time

Transit time increased more rapidly with grid spacing for the 1,500 m detection radius than for the 200 m detection radius; the 800 m

FIGURE 4 Marginal (i.e. least squared) mean transit time (95% percentile) estimated from log-loglinear models of grid spacing. Estimates were conditioned on 15 km grid spacing, and compared scenarios where swimming speed (m/s, left panel) transmission delay (seconds, middle panel), or turn angle (*SD* in degrees, right panel) varied while the other variables were held at an intermediate level (defined in each panel). Separate models were fitted for each detection radius (defined in the key). The vertical axis is plotted on a log-scale
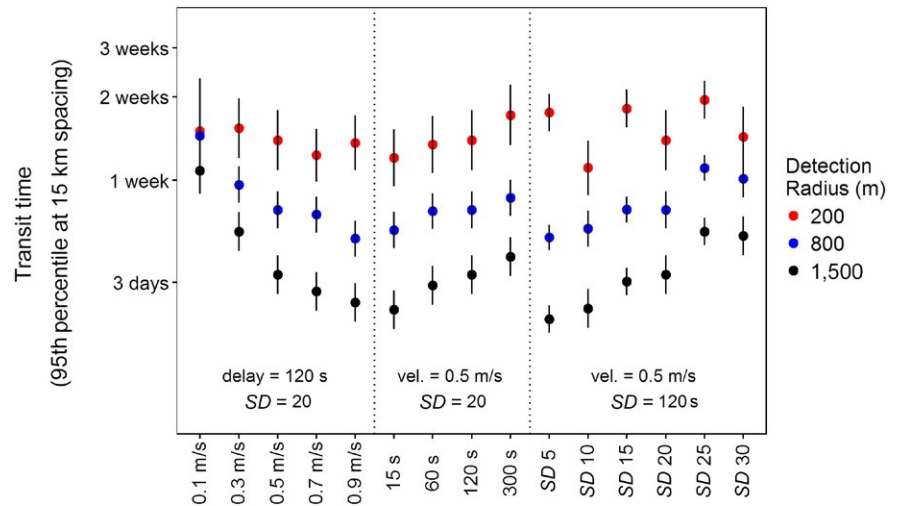
radius scenario was intermediate (Figure 3, middle). This simply reflected a more rapid decrease in the proportion of grid spacing represented by the detection radius. Intuitively, scenarios with a higher proportion of the simulation grid covered by the larger detection radius would lead to a greater probability of detection and lower transit time. Across the range of grid spacing, the 200 m detection radius changed from 4% to 0.8% of the spacing value, whereas the 1,500 m detection radius changed from 30% to 6%. Similarities in the proportion of grid spacing covered by the detection radius at the highest grid spacing value (25 km) resulted in relatively small variation across detection radius scenarios: mean 95th percentile of transit times ranged from 10.8 to 15.2 days, respectively, for the 1,500 m and 200 m detection radius scenarios—a 1.4-fold difference (Figure 3, middle). By comparison at 5 km grid spacing, with 95% confidence, the longest average duration an animal went undetected as it moved to a different receiver was 2.4, 16.4 and 76.8 hr, respectively, for the 1,500 m, 800 m and 200 m detection radii—a 32-fold change (Figure, middle). On average, the maximum duration that an animal went undetected between receivers for any scenario was 18.1, 13.3 and 10.8 days, respectively, for the 200 m, 800 m and 1,500 m detection radii.

3.3 | Transit distance

As the spatial complement to time, the pattern for transit distance was essentially the same as transit time, except that minimum values were constrained by grid spacing (Figure 3, lower). Transit distance was lowest and increased most rapidly with grid spacing for the longest detection radius (1,500 m; Figure 3, lower). Transit distance for the 1,500 m detection radius ranged from 6.9 to 57.4 km, which, respectively, corresponded to 1.3 to 2.3 times the grid spacing value (Figure 3, lower). By comparison for the 200 m detection radius, the transit-distance grid-spacing ratio ranged from 3.2 to 5.3. Thus, under the most favourable conditions (1,500 m detection radius) for a transit event, an animal would be detected on the next or second-to-next closest receiver. For poor conditions (200 m detection radius), this increased to the third to fifth closest receiver. The 800 m

detection radius was intermediate between the favourable and poor conditions (Figure 3, lower).

3.4 | Generalized linear models

Linear models of transit time emphasized that variation due to detection radius was greater than either biological variables (swimming speed and turn angle *SD*) or transmission delay (Figure 4). Overall, marginal mean transition time tended to be <2 weeks conditioned on a grid spacing of 15 km, and showed 6.2-fold variability across detection radius scenarios compared to 1.8- to 3.4-fold variability within a detection radius (Figure 4). With few exceptions, trends for each of the variables generally matched intuition: faster swimming speeds, shorter transmission delays or less tortuous paths (i.e. smaller *SD*) resulted in shorter transit times (Figure 4). One exception was the 200 m detection radius scenario, which showed no obvious trend for *SD*, and only non-significant trends for swimming speed and transmission delay (Figure 4). Other exceptions were for the 800 m and 1,500 m detection radius scenarios at higher *SD* scenarios (*SD* = 20, 25 and 30°; Figure 4), which showed more variable transit times. Although not presented here, similar plots were inspected for other grid spacing scenarios: for the 5-km grid, the pattern was similar but shifted to lower transit times, and for the 25-km grid, the detection radius scenarios were broadly overlapping with less evident trends in the other variables. In each of the models (one for each detection radius), residuals were approximately normally distributed with some evidence of minor heteroscedasticity (increasing variance at higher transition times), this contributed to the lack of pattern at the largest grid spacing.

3.5 | Empirical examples

In the pilot studies, 95th percentiles of detection and transit time were typically shorter than simulated values, ranging from 28 to 56 min and from 37 min to 1.2 days respectively (Figure 5). One exception was common carp, which had slightly higher detection and transit times than the 1,500 m detection radius scenario. The
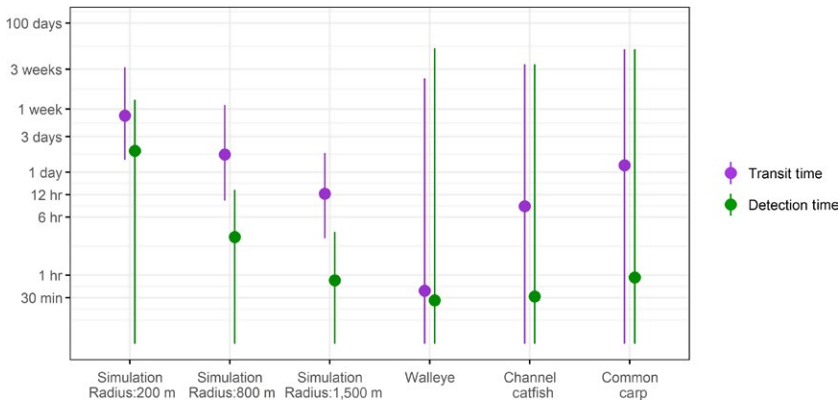
FIGURE 5 Detection and transit times (defined in text) for two simulation scenarios compared with pilot study results for walleye, channel catfish and common carp. The grid spacing for each case averaged 7 km. For the simulated scenarios, the plots are the same as in Figures 3 and 4. For the pilot study species, the dots are 95th percentiles and the range represents all of the data per species (pooled across individuals), thus the error bars cover a broader range of time. Note that the vertical axis is plotted on a log-scale

simulated scenarios with 7 km spacing predicted ranges of 0.8 hr to 1.9 days and 12 hr to 5.7 days, respectively, for detection and transit time (Figure 5). Mean detection and transit times for walleye were nearly identical, reflecting a tendency for successive detections to occur on different receivers. Channel catfish and common carp showed a tendency for successive detections to occur on the same receiver as evidenced by mean transit times that were approximately 5–24 hr higher than detection time for these species (Figure 5).

3.6 | Grid-line time cost comparison

Given 25 receivers per line deployed at 1-km intervals across the short dimension of the rectangular arena, the time costs for tending receiver lines were 14 and 27 hr for the single- and double-line scenarios, respectively (Figure 6). By comparison, as expected, time costs for tending grids increased monotonically and approximately linearly with number of receivers (Figure 6). For an equivalent number of receivers, the grid time cost was approximately 170%–300% greater than the line time cost for the single- and double-line scenarios respectively. In the pilot studies, time cost was qualitatively similar to the hypothetical scenario. Our calculations suggested an approximate time cost of 41 hr (about one work week) to tend 51 receivers with 7 km spacing (Figure 6). From recent experience in the Lake Erie pilot study, it took approximately 2 days to deploy and retrieve 25 receivers with 7 km average spacing (Figure 2) placed on the bottom with snag lines or acoustic releases. In Lake Winnipeg, it took approximately 7 days to tend 68 receivers using only snag lines (53 with 7 km spacing from the pilot study, plus 15 ancillary stations not included in our grid analysis; Figure 2).

4 | DISCUSSION

The simulation approach for evaluating two-dimensional acoustic telemetry grids represents a useful tool for researchers wishing to determine the fates of aquatic animals. Surprisingly, even under the least favourable conditions (200 m detection radius with a sparse 25-km receiver grid), the time step at which individual fates

could be inferred (<10 days) represents far greater resolution than existing stock assessment methods (yearly). Intuitively, grids provide coarser resolution for timing fish passage at specific locations (e.g. around islands) than the bottleneck-receiver-arrangement used in Lake Erie (Raby et al., 2018), but more importantly, simulation results can be used to optimize resource allocation (study design) when high-resolution timing is not required. Better grid performance observed in the pilot field studies (i.e. shorter time undetected) reinforced our results (Figure 5). This result provides a basis both for study design and the analysis and interpretation of acoustic telemetry data, which is critical for classifying telemetry data to understand animal movements and survival, but the overall pattern from the simulations was entirely expected. If an animal goes undetected for longer than predicted, the researcher may infer emigration from the receiver grid or mortality (excepting tag expulsion or tag failure events). The grid design for receivers is fundamentally different from other approaches in which the researcher can determine only whether an animal occurred in the vicinity of the receiver line or gate. On either side of this narrow strip, an animal may show unobservable complex behaviour or survive to leave the system permanently (the latter would be indistinguishable from mortality). Obviously, failing to observe an animal across a broad area is only important with respect to study objectives. We simply caution that the design of a receiver network follow from specific questions about animal movement rather than the other way around. The design of a network is a challenging task primarily because the deployment and maintenance of expansive acoustic receiver networks may be beyond the capabilities of most single organizations, and thus requires interagency coordination. Consortiums and organizations, such as the Great Lakes Acoustic Telemetry Observation System (GLATOS; http://glatos.glos.us/, Krueger et al., 2017), Integrated Marine Observing System (IMOS; http://imos.org.au/home/) and the Ocean Tracking Network (OTN; Cooke et al., 2011), are becoming increasingly important for the success of acoustic telemetry studies, but this enterprise requires compromise in the sampling design to manage financial resources and achieve a network that will function for multiple objectives and species. Studies initiated after a network is established will be forced to consider whether
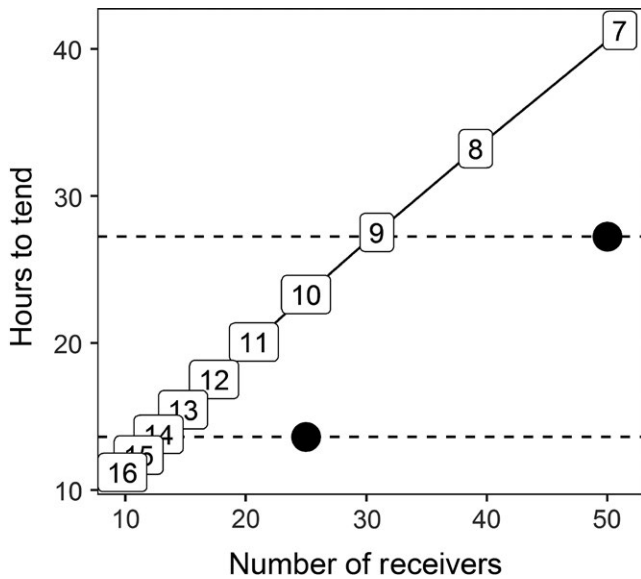
FIGURE 6 Estimated time cost of tending various grids (spacing in km shown as text on symbols) as a function of the number of receivers in a 2,500 km² rectangular arena in which the long side was four times the short side. For comparison, two receiver line scenarios with 1 km spacing (dashed lines with dots showing number of receivers tended) are plotted for single and double lines of receivers spanning the short side (79 km) of the rectangle. The plotted values assume vessel speed between receivers was 12 knots and that time on station to retrieve and re-deploy a receiver was 0.5 hr

the existing array addresses the objective(s) or whether augmentation of the network would be necessary. Fortunately, our simulation results bode well for optimizing a receiver network through simulations. The effects of movement speed and tortuosity (i.e. *SD* of turn angle) of simulated movement paths, which we selected to represent a range of possible species, were important but small relative to the effects of grid spacing and detection range (Figure 4). Thus, a researcher with knowledge of detection range but little or no knowledge of the movement characteristics of the study animal would be able to develop a receiver grid design using the simulations we presented.

4.1 │ Developing a receiver grid to understand habitat use

Analogous to plot-based census studies of plants or animals in terrestrial environments, the key for applying our results to telemetry studies is matching the grid with the desired scale of inference. For instance, consider a researcher who wishes to understand whether an animal makes diel movements between adjacent habitats in a system where the mean detection radius is 800 m. At a grid spacing of 15 km, 95% of simulated detection time intervals were <12 hr (Figure 3, upper); therefore, this maximum grid spacing would likely provide multiple detections within a 12-hr period to assess habitat occupancy. If the researcher also wished to understand whether movement between habitats was crepuscular (to within ±1 hr of

sunrise or sunset: a 2-hr period), then the maximum spacing should be no more than 5 km (Figure 3, upper). While one could conceivably achieve useful results for a system in which the habitat area approached the grid spacing (i.e. a minimum of one receiver per habitat), we advocate a complementary spatial benchmark for transit distance.

The simulation arena (Lake Erie) was relatively large compared with the range of grid spacing values, and for spatially explicit study design, the researcher would need to evaluate the density of receivers. Again, for the hypothetical diel movement scenario, consider that each habitat is approximately square with an area of 400 km² (20 km on each side). The detection time benchmark of 15 km spacing would yield, at most, two receivers in each habitat. Simulated transit distance for the 800 m detection radius scenario is roughly invariant of spacing and twice the spacing distance (Figure 3, lower); thus, the researcher would fail to detect most transit events within a habitat. To ensure that at least some within-habitat transit events would be detected, we recommend a maximum grid spacing that is scaled to the longest axis of the habitat: there should be a minimum spacing of $a \div (r + 1)$ where a is the length of the axis and r is the ratio of the transit distance 95th percentile to grid spacing. With a 20-km axis, the grid spacing should be no more than *c.* 7 km, requiring nine receivers in each habitat. To emphasize the efficiency of this scenario, the boundary between two habitats would require approximately the same total number of receivers ($n = 18$) to establish a single line with overlapping 800 m detection ranges, but line-based results would not provide information about which habitat the animal occupied.

Particular study objectives may require alternative benchmark development, but the above scenario illustrates how our simulations can aid the design of telemetry sampling. In reality, habitats are amorphous, and selection of appropriate grid spacing will require adaptation instead of strict application of the guidelines above. Furthermore, the researcher should account for temporal and spatial variations in detection efficiency to ensure observed patterns are reflective of actual movement instead of changes in grid performance. Diel changes in detection range performance have previously been interpreted as animal movement (Payne, Gillanders, Webber, & Semmens, 2010); thus, the researcher may be able to account for spatial heterogeneity of receiver performance with habitat-specific grid spacing. A number of dynamic variables, including weather, boat traffic, density gradients across an estuary or thermocline, and noise from other organisms (reviewed by Kessel et al., 2014), can introduce uncertainty in grid performance, but we did not evaluate these in our simulations. However, more important than these dynamic variables is the placement and orientation of receivers, which can have a substantial effect on detection range and is not generalizable between systems (Huveneers et al., 2016). For spatial heterogeneity in detection range, more closely spaced receivers in one habitat may be required to equal the detection efficiency in adjacent habitats. In habitats with high bathymetric relief where detection efficiency varies substantially, adaptive receiver placement is a paramount consideration (Binder, Holbrook, Hayden, & Krueger, 2016). For temporal heterogeneity, if the research question

requires confirmation of the presence of an animal on time-scales much longer than sporadic interference from dynamic variables, then it may not be necessary to quantify such effects. Otherwise, additional system-specific simulations with the tool developed here (Holbrook et al., 2017) may be needed.

4.2 | Autonomous receiver sampling for survival

Quantitative methods for determining the mortality rates of animals have relied on gridded telemetry sampling for system-wide spatial coverage to satisfy the assumption that all marked animals have the same probability of being observed (Hightower, Jackson, & Pollock, 2001; Pollock, Jiang, & Hightower, 2004). In previous studies where sampling occurred during discrete events from a boat (i.e. active tracking) that travelled to each grid intersection to listen for tag signals for a prescribed period, inverse correlation between animal and observer movement could obscure detection. If such a phenomenon occurs, the probability of observing a dead fish (or one not moving) would be greater than the probability of observing an animal that avoids the observer (e.g. one that moves away from boat noise). This situation would violate a key assumption and be difficult to diagnose without autonomous receiver sampling. Thus, many small-scale studies combine mobile tracking with limited autonomous receiver sampling to understand whether an animal may be present in the system yet go undetected by mobile tracking (e.g. Wingate et al., 2011). Alternatively, exclusive use of autonomous receiver arrays (passive) of the kind we simulated satisfies the assumption of equal detection probability, and has provided mortality estimates for highly mobile (e.g. elasmobranchs) as well as highly resident (e.g. reef teleosts) species in a variety of semi-enclosed and open coastal marine ecosystems (Heupel & Simpfendorfer, 2002, 2011; Knip, Heupel, & Simpfendorfer, 2012b; Topping & Szedlmayer, 2011, 2013).

One of the most difficult aspects of determining the fates of tagged animals is distinguishing mortality from non-detection, and here, our simulations also provided insight. Generally, the likelihood of mortality increases with time elapsed since the last detection. In a closed system, when this period exceeds the simulated 95th percentile of transit time (or other appropriate benchmark), and no evidence exists that the animal was removed by fishing or similar activities, our simulations support an inference of mortality or tag loss. One source of mortality that would complicate this interpretation is a predation event. As Romine et al. (2014) observed, for predators that consumed a tagged fish, ingesting the tag would appear as an unexpected change in the behaviour of the prey. Presumably, subsequent detections would be a relatively short-term change as the prey is digested and the tag is either regurgitated or excreted by the predator (Kerstetter, Polovina, & Graves, 2004; Wahlberg et al., 2014). In addition, a nontrivial 3.5% of simulated tracks represented animals that were rarely or never detected, and were removed from our analyses of transit time and distance. In nature, such cases would be indistinguishable from fish that died. Note that inclusion of these data would have lowered our 95th percentiles; therefore, censoring of these data resulted in more conservative (slightly longer) values of transit time. Although

data quantifying the probability that an animal survived undetected would be difficult to obtain, we view non-detection as an important consideration for mortality estimation from acoustic telemetry data. Observation of such events would be limited to high exploitation fisheries and situations with high numbers of tagged fish, in which tags with few or no detections were reported by the fishery.

In semi-enclosed or open systems, emigration may be confounded with mortality when an animal leaves the monitored portion of the system. Determining the fate of animals in this situation would necessarily rely on complementary information from other data sources, such as conventional tag reporting from fisheries (Pollock et al., 2004). For an embayment, estuary or other discrete zoogeographical area, a properly constructed receiver grid may provide information about timing of immigration/emigration as well as preferred habitats within the system (Heupel, Semmens, et al., 2006; Heupel & Simpfendorfer, 2002; Heupel, Simpfendorfer, Collins, & Tyminski, 2006; Knip et al., 2012a). As mentioned above, grid sampling designs would have several advantages over receiver lines that have been more commonly employed. To understand seasonality of habitat use for migratory fish of conservation concern, grid sampling may help maximize information gained about the animal (e.g. Papastamatiou et al., 2015). Furthermore, grid sampling provides a more rigorous foundation to evaluate the interconnectedness of receiver locations through application of network analysis (Jacoby, Brooks, Croft, & Sims, 2012). Prior to conducting work in the field, our simulation would help the researcher answer a key sampling design question: how long must an animal be present in the grid before it will be detected? Extrapolations to completely open systems may also be worthwhile, but depend importantly on characteristics and habits of the animal. For species with a high affinity for small physical features in the environment (e.g. patch reefs) that punctuate an expanse of non-preferred habitat, successful telemetry studies have been conducted in open systems by simply populating preferred habitats with autonomous receivers (Topping & Szedlmayer, 2011).

4.3 | Comparisons with real animals

Despite lack of a priori models of individual movement for species in the pilot studies, our generic correlated random walk simulations provided a reasonable match to the field results, and on average pilot studies performed better (i.e. lower detection and transit times) than simulations predicted. A likely explanation for the improved performance is that detection ranges in the field were often longer than simulated ranges. For example, stationary transmitters placed within a line of receivers in Lake Erie had occasional detections at distances of up to 5 km (M. Faust, unpublished data). Although the probability of detecting a transmission from 3.5 km (half of the pilot study grid spacing) was predicted to be negligible in the simulations, it was still greater than zero, and periodic quiescent field conditions may have increased detection range substantially beyond the average. Due to the need to minimize detection of a single transmission on multiple receivers (which is ideal for triangulation studies but potentially problematic for grid-based sampling designs of the type we simulated), in

ecosystems where long-range detection occurrences are non-trivial, a detection radius based on a lower predicted probability of detection (e.g. $p < .5$) might be advantageous for planning a grid-based sampling design. This could also be accomplished by benchmarking to a longer detection range from our simulations (i.e. 1,500 m). Alternatively, developing methods for analysis of the timing of signal arrival for short intervals would aid in the assignment of an animal to the nearest receiver (Hedger et al., 2008; Simpfendorfer et al., 2015).

Field data are also subject to false detections, which occur due to signal collision from multiple tags on the same receiver. Filtering out false detections can be accomplished by removing data with long intervals between successive detections (Pincock, 2012). The selection of a filtering rule is subjective and dependent upon the number of tags expected at a single receiver and the nominal transmission delay. The process can also eliminate some authentic detections, but in total removes only a small fraction of data. We did not apply false detection filtering to the pilot study data, but we note that it would tend to reduce the quantity of long detection and transit times in these data, resulting in lower 95th percentile values for the pilot studies. Thus, further improvement in the pilot study results could be achieved through analysis of false detections. Decisions about how to account for false detections should account for habitat and species characteristics from the individual ecosystems where these studies occurred, and were beyond the scope of this study.

The comparison of three species with contrasting life histories from two large lake ecosystems reinforced the applicability of the simulations to other species. Walleye are pelagic piscivores and seasonally migratory across Lake Erie (Knight, Margraf, & Carline, 1984; Raby et al., 2018; Vandergoot & Brenden, 2014; Wang et al., 2007). In Lake Winnipeg, common carp are primarily benthic herbivores or omnivores and channel catfish are benthic predators on both invertebrates and fishes (Stewart & Watkinson, 2004). The two species from Lake Winnipeg also migrate into tributaries or marshes during seasonal spawning periods. Higher transit times for channel catfish and common carp may indicate slower or more tortuous paths than for walleye or selection of habitats nearshore in shallower water at the periphery of the grid array where detection would be less likely. The Lake Erie walleye were tagged with V13-1H tags that transmit at 153 dB and the Lake Winnipeg channel catfish and common carp were tagged with V16-4H tags that transmit at 158 dB. This difference in transmission strength alone would result in a difference in detection radius opposite to the observed results if both lakes had similar acoustics; however, the detection radius in Lake Winnipeg may be smaller based on environmental conditions that influence detection radius (Kessel et al., 2014). Additional analyses beyond the scope of this study would be needed to further explore these inferences. For these species, the pilot studies were executed during summer and fall non-reproductive feeding periods; therefore, we would expect different results (e.g. smaller transit times due to a reduction in path tortuosity) during reproductive periods when these species show more directed movements to and from spawning sites.

4.4 | Time cost comparison

Because so many variables are potentially involved and financial considerations vary uniquely by project, detailed evaluation of the financial practicality of grid designs relative to receiver lines would be difficult. Time is a useful surrogate here because it can be converted to financial terms based upon a researcher's specific circumstances. Our approach to quantify the time cost of tending lines vs. grids confirmed that receiver lines can be maintained with less time—a useful quantification but nevertheless an expected outcome. Receiver lines can be less costly to maintain than grids because the receivers are concentrated in a small geographical area relative to grids. The actual scaling of time costs for grid designs across various spacing intervals (and also for lines) depends mainly on assumptions of speed of travel and time on station, but these factors will only slightly adjust the intercept and slope of the relationship. Furthermore, projects with only a small number of receivers may initially find grid-based designs of little value, and the efficacious solution to maximize information from few receivers is clearly what we have termed: bottleneck-receiver-arrangement strategy. For the resource-limited situation, the lesson from our grid simulations may be that while closely spacing few receivers with overlapping detection ranges can ensure high resolution of timing of occurrence at a bottleneck, an alternative scenario with staggered non-overlapping detection ranges (i.e. grid-like) may provide less redundant data with additional information on directionality. On the other hand, studies using acoustic telemetry have increased dramatically in the past few decades, and this will likely continue. This trend has helped encourage accumulation of telemetry equipment as well as collaboration and pooling of resources to develop large networks of receivers. Thus, we have emphasized situations where deployment of large numbers of receivers is possible, with insights and tools aimed at groups or research consortiums attempting to maintain telemetry infrastructure to support multiple projects.

5 | CONCLUSIONS

A quantitative description of individual aquatic animal movements has long been an active area of research, and random walk models have frequently provided either useful descriptions or valuable null models (Gurarie et al., 2016; Turchin, 1998). Here, we demonstrated how random walks simulating aquatic animal movements in an acoustic telemetry receiver grid compared with three fish species from two different large lake systems. The results have prompted spatially extensive application of two-dimensional telemetry grid sampling in Lake Erie (http://glatos.glos.us/map) and bolster outcomes of previous smaller scale studies (Collins, Heupel, & Motta, 2007; Dance & Rooker, 2015; Heupel, Semmens, et al., 2006; Heupel, Simpfendorfer, et al., 2006; Knip et al., 2012a, 2012b). We are hopeful that other researchers will see utility in our simulations, and respond with a more rigorous quantitative approach to autonomous receiver sampling. Finally, although we did not explicitly consider

rivers, which can usually be monitored efficiently with lines of receivers, our results would also apply to river systems large enough to deploy a two-dimensional receiver array with non-overlapping detection ranges.

Secor (2015) criticized telemetry work as suffering an embarrassment of riches from descriptive studies with too much data on too few animals. While recent advances in the field are making it possible to scale up to population-level inferences (Hussey et al., 2015), what we have characterized as the bottleneck-receiver-arrangement strategy (i.e. receiver lines with overlapping detection ranges concentrated in geographical areas of convenience) is more prone to an embarrassment of data redundancy. Additionally, employing a gridded receiver design combined with releasing organisms with animal-borne logging devices (e.g. thermal or depth sensors; Hussey et al., 2015) can further improve population-level inferences with acoustic telemetry studies. Thus, our simulations support a growing cadre of new telemetry studies that are being developed via experimental design. Coordinated inter-agency efforts with infrastructure for multiple projects (e.g. GLATOS, IMOS and OTN) will be essential for realizing the insights that acoustic telemetry technologies promise.

AUTHORS' CONTRIBUTIONS

R.T.K., C.M.H., C.S.V., T.R.S. and C.C.K. conceived the ideas, designed simulation methodology and led the data analyses; C.S.V., M.D.F., D.A.W., C.C., M.P. and E.C.E. designed and conducted the pilot studies and contributed to the analyses; R.T.K. and C.M.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.hm60m7n (Kraus et al., 2018).

ORCID

Richard T. Kraus http://orcid.org/0000-0003-4494-1841

Christopher M. Holbrook http://orcid.org/0000-0001-8203-6856

Christopher S. Vandergoot http://orcid.org/0000-0003-4128-3329

REFERENCES

Binder, T. R., Farha, S. A., Thompson, H. T., Holbrook, C. M., Bergstedt, R. A., Riley, S. C., … Krueger, C. C. (2017). Fine-scale acoustic telemetry reveals unexpected lake trout, Salvelinus namaycush, spawning habitats in northern Lake Huron, North America. *Ecology of Freshwater Fish*, *27*, 594–605. https://doi.org/10.1111/eff.12373

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*, 4. https://doi.org/10.1186/s40317-016-0097-4

Collins, A. B., Heupel, M. R., & Motta, P. J. (2007). Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a southwest Florida estuary. *Journal of Fish Biology*, *71*, 1159–1178. https://doi.org/10.1111/j.1095-8649.2007.01590.x

Cooke, S. J., Iverson, S. J., Stokesbury, M. J., Hinch, S. G., Fisk, A. T., VanderZwaag, D. L., … Whoriskey, F. (2011). Ocean Tracking Network Canada: A network approach to addressing critical issues in fisheries and resource management with implications for ocean governance. *Fisheries*, *36*, 583–592. https://doi.org/10.1080/03632415.2011.633464

Cooke, S. J., Midwood, J. D., Thiem, J. D., Klimley, P., Lucas, M. C., Thorstad, E. B., … Ebner, B. C. (2013). Tracking animals in freshwater with electronic tags: Past, present and future. *Animal Biotelemetry*, *1*, 5. https://doi.org/10.1186/2050-3385-1-5

Dance, M. A., & Rooker, J. R. (2015). Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery. *Estuarine, Coastal and Shelf Science*, *167*, 447–457. https://doi.org/10.1016/j.ecss.2015.10.025

Gurarie, E., Bracis, C., Delgado, M., Meckley, T. D., Kojola, I., & Wagner, C. M. (2016). What is the animal doing? Tools for exploring behavioural structure in animal movements. *Journal of Animal Ecology*, *85*, 69–84. https://doi.org/10.1111/1365-2656.12379

Hayden, T. A., Holbrook, C. M., Binder, T. R., Dettmers, J. M., Cooke, S. J., Vandergoot, C. S., & Krueger, C. C. (2016). Probability of acoustic transmitter detections by receiver lines in Lake Huron: Results of multi-year field tests and simulations. *Animal Biotelemetry*, *4*, 19. https://doi.org/10.1186/s40317-016-0112-9

Hayden, T. A., Holbrook, C. M., Fielder, D. G., Vandergoot, C. S., Bergstedt, R. A., Dettmers, J. M., … Cooke, S. J. (2014). Acoustic telemetry reveals large-scale migration patterns of walleye in Lake Huron. *PLoS One*, *9*, e114833. https://doi.org/10.1371/journal.pone.0114833

Hedger, R. D., Martin, F., Dodson, J. J., Hatin, D., Caron, F., & Whoriskey, F. G. (2008). The optimized interpolation of fish positions and speeds in an array of fixed acoustic receivers. *ICES Journal of Marine Science*, *65*, 1248–1259. https://doi.org/10.1093/icesjms/fsn109

Heupel, M., Semmens, J. M., & Hobday, A. (2006). Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, *57*, 1–13. https://doi.org/10.1071/MF05091

Heupel, M. R., & Simpfendorfer, C. A. (2002). Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 624–632. https://doi.org/10.1139/f02-036

Heupel, M. R., & Simpfendorfer, C. A. (2011). Estuarine nursery areas provide a low-mortality environment for young bull sharks *Carcharhinus*

leucas. *Marine Ecology Progress Series*, 433, 237–244. https://doi.org/10.3354/meps09191

Heupel, M. R., Simpfendorfer, C. A., Collins, A. B., & Tyminski, J. P. (2006). Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. *Environmental Biology of Fishes*, 76, 47–67. https://doi.org/10.1007/s10641-006-9007-6

Hightower, J. E., Jackson, J. R., & Pollock, K. H. (2001). Use of telemetry methods to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society*, 130, 557–567. https://doi.org/10.1577/1548-8659(2001)130<0557:UOTMTE>2.0.CO;2

Holbrook, C., Hayden, T., & Binder, T. (2017). glatos: A package for the Great Lakes acoustic telemetry observation system. https://gitlab.oceantrack.org/GreatLakes/glatos.git.

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*, 348, 1255642. https://doi.org/10.1126/science.1255642

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

Jackson, G. D. (2011). The development of the Pacific Ocean Shelf Tracking project within the decade long Census of Marine Life. *PLoS One*, 6, e18999. https://doi.org/10.1371/journal.pone.0018999

Jacoby, D. M. P., Brooks, E. J., Croft, D. P., & Sims, D. W. (2012). Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods in Ecology and Evolution*, 3, 574–583. https://doi.org/10.1111/j.2041-210X.2012.00187.x

Keene, J., Noakes, D., Moccia, R., & Soto, C. (1998). The efficacy of clove oil as an anaesthetic for rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Aquaculture Research*, 29, 89–101. https://doi.org/10.1111/j.1365-2109.1998.tb01113.x

Kerstetter, D. W., Polovina, J., & Graves, J. E. (2004). Evidence of shark predation and scavenging on fishes equipped with pop-up satellite archival tags. *Fishery Bulletin*, 102, 750.

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

Knight, R. L., Margraf, F. J., & Carline, R. F. (1984). Piscivory by walleyes and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society*, 113, 677–693. https://doi.org/10.1577/1548-8659(1984)113<677:PBWAYP>2.0.CO;2

Knip, D. M., Heupel, M. R., & Simpfendorfer, C. A. (2012a). Evaluating marine protected areas for the conservation of tropical coastal sharks. *Biological Conservation*, 148, 200–209. https://doi.org/10.1016/j.biocon.2012.01.008

Knip, D. M., Heupel, M. R., & Simpfendorfer, C. A. (2012b). Mortality rates for two shark species occupying a shared coastal environment. *Fisheries Research*, 125–126, 184–189. https://doi.org/10.1016/j.fishres.2012.02.023

Kraus, R. T., Holbrook, C. M., Vandergoot, C. S., Stewart, T. R., Faust, M. D., Watkinson, D. A., ... Krueger, C. C. (2018). Data from: Evaluation of acoustic telemetry grids for determining aquatic animal movement and survival. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.hm60m7n

Krebs, C. J. (1989) *Ecological methodology*. New York, NY: Harper & Row.

Krueger, C. C., Holbrook, C. M., Binder, T. R., Vandergoot, C. S., Hayden, T. A., Hondorp, D. W., ... Cooke, S. J. (2017). Acoustic telemetry observation systems: Challenges encountered and overcome in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, https://doi.org/10.1139/cjfas-2017-0406.

Legendre, P., Dale, M. R. T., Fortin, M.-J., Gurevitch, J., Hohn, M., & Myers, D. (2002). The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, 25, 601–615. https://doi.org/10.1034/j.1600-0587.2002.250508.x

Meckley, T. D., Holbrook, C. M., Wagner, C. M., & Binder, T. R. (2014). An approach for filtering hyperbolically positioned underwater acoustic telemetry data with position precision estimates. *Animal Biotelemetry*, 2, 7. https://doi.org/10.1186/2050-3385-2-7

Papastamatiou, Y. P., Dean Grubbs, R., Imhoff, J. L., Gulak, S. J. B., Carlson, J. K., & Burgess, G. H. (2015). A subtropical embayment serves as essential habitat for sub-adults and adults of the critically endangered smalltooth sawfish. *Global Ecology and Conservation*, 3, 764–775. https://doi.org/10.1016/j.gecco.2015.03.003

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

Pincock, D. G. (2012). False detections: What they are and how to remove them from detection data. VEMCO Technical Document DOC-004691, version 03. 11 pp. Rterieved from https://www.vemco.com/pdf/false_detections.pdf .

Pollock, K. H. (1991). Review papers: Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: Past, present, and future. *Journal of the American Statistical Association*, 86, 225–238.

Pollock, K. H., Jiang, H., & Hightower, J. E. (2004). Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Transactions of the American Fisheries Society*, 133, 639–648. https://doi.org/10.1577/T03-029.1

Raby, G. D., Vandergoot, C. S., Hayden, T. A., Faust, M. D., Kraus, R. T., Dettmers, J. M., ... Krueger, C. C. (2018). Does behavioural thermoregulation underlie seasonal movements in Lake Erie walleye? *Canadian Journal of Fisheries and Aquatic Sciences*, 75, 488–496. https://doi.org/10.1139/cjfas-2017-0145

Romine, J. G., Perry, R. W., Johnston, S. V., Fitzer, C. W., Pagliughi, S. W., & Blake, A. R. (2014). Identifying when tagged fishes have been consumed by piscivorous predators: Application of multivariate mixture models to movement parameters of telemetered fishes. *Animal Biotelemetry*, 2, 1–13.

Secor, D. H. (2015). *Migration ecology of marine fishes*. Baltimore, MD: JHU Press.

Siegwarth, G. L., & Pitlo Jr, J. M. (1999). A modified procedure for surgically implanting radio transmitters in channel catfish. Catfish 2000: Proceedings of the international ictalurid symposium (pp. 287–292). American Fisheries Society, Symposium.

Simpfendorfer, C. A., Heupel, M. R., & Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 23–32. https://doi.org/10.1139/f01-191

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, 55. https://doi.org/10.1186/s40317-015-0094-z

Steckenreuter, A., Hoenner, X., Huveneers, C., Simpfendorfer, C., Buscot, M.J., Tattersall, K., ... McDowall, P. (2017). Optimising the design of large-scale acoustic telemetry curtains. *Marine and Freshwater Research*, 68, 1403–1413. https://doi.org/10.1071/MF16126

Stein, A., & Ettema, C. (2003). An overview of spatial sampling procedures and experimental design of spatial studies for ecosystem comparisons. *Agriculture, Ecosystems & Environment*, 94, 31–47. https://doi.org/10.1016/S0167-8809(02)00013-0

Stevens, D. L. (1997). Variable density grid-based sampling designs for continuous spatial populations. *Environmetrics*, *8*, 167–195. https://doi.org/10.1002/(ISSN)1099-095X

Stewart, K. W., & Watkinson, D. A. (2004). *The freshwater fishes of Manitoba*. Winnipeg, MB, Canada: University of Manitoba Press.

Thompson, S., & Seber, G. (1996). *Adaptive sampling. Wiley Series in probability and mathematical statistics: Applied probability and statistics*. New York, NY: John Wiley & Sons.

Topping, D. T., & Szedlmayer, S. T. (2011). Site fidelity, residence time and movements of red snapper *Lutjanus campechanus* estimated with long-term acoustic monitoring. *Marine Ecology Progress Series*, *437*, 183–200. https://doi.org/10.3354/meps09293

Topping, D. T., & Szedlmayer, S. T. (2013). Use of ultrasonic telemetry to estimate natural and fishing mortality of red snapper. *Transactions of the American Fisheries Society*, *142*, 1090–1100. https://doi.org/10.1080/00028487.2013.790844

Turchin, P. (1998). *Quantitative analysis of movement: Measuring and modeling population redistribution in animals and plants*. Sunderland, MA: Sinauer.

Vandergoot, C. S., & Brenden, T. O. (2014). Spatially varying population demographics and fishery characteristics of Lake Erie walleyes inferred from a long-term tag recovery study. *Transactions of the American Fisheries Society*, *143*, 188–204. https://doi.org/10.1080/00028487.2013.837095

Wahlberg, M., Westerberg, H., Aarestrup, K., Feunteun, E., Gargan, P., & Righton, D. (2014). Evidence of marine mammal predation of the European eel (*Anguilla anguilla* L.) on its marine migration. *Deep Sea Research Part I: Oceanographic Research Papers*, *86*, 32–38. https://doi.org/10.1016/j.dsr.2014.01.003

Wang, H.-Y., Rutherford, E. S., Cook, H. A., Einhouse, D. W., Haas, R. C., Johnson, T. B., … Turner, M. W. (2007). Movement of walleyes in Lakes Erie and St. Clair inferred from tag return and fisheries data. *Transactions of the American Fisheries Society*, *136*, 539–551. https://doi.org/10.1577/T06-012.1

Welch, D. W., Boehlert, G. W., & Ward, B. R. (2002). POST–the Pacific Ocean salmon tracking project. *Oceanologica Acta*, *25*, 243–253. https://doi.org/10.1016/S0399-1784(02)01206-9

White, G. C., & Garrott, R. A. (2012). *Analysis of wildlife radio-tracking data*. Amsterdam, The Netherlands: Elsevier.

Wingate, R. L., Secor, D. H., & Kraus, R. T. (2011). Seasonal patterns of movement and residency by striped bass within a subestuary of the Chesapeake Bay. *Transactions of the American Fisheries Society*, *140*, 1441–1450. https://doi.org/10.1080/00028487.2011.630279