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# Spatial and temporal variation in positioning probability of acoustic telemetry arrays: fine-scale variability and complex interactions

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## Abstract

**Background:** As popularity of positional acoustic telemetry systems increases, so does the need to better understand how they perform in real-world applications, where variation in performance can bias study conclusions. Studies assessing variability in positional telemetry system performance have focused primarily on position accuracy, or comparing performance inside and outside the array. Here, we explored spatial and temporal variation in positioning probability within a 140-receiver Vemco Positioning System (VPS) array used to monitor lake trout, *Salvelinus namaycush*, spawning behavior over 23 km$^2$ in Lake Huron, North America.

**Methods:** Variability in VPS positioning probability was assessed between August and November from 2012 to 2014 using 43 stationary transmitters distributed throughout the array. Various analyses were used to relate positioning probability to number of fish transmitters in the array, wave height, and thermal stratification. We also assessed the prevalence of 'close proximity detection interference' (CPDI) in our array by analyzing detection probability of 35 transmitters on collocated receivers.

**Results:** Positioning probability of the VPS array varied greatly over time and space. Number of fish transmitters present in the array was a significant driver of reduced positioning probability, especially during lake trout spawning period when the fish were aggregated. Relationships between positioning probability and environmental variables were complex and varied over small spatial and temporal scales. One possible confounding variable was the large range of water depth over which receivers were deployed. Another confounding factor was the high prevalence of CPDI, which decreased exponentially with water depth and was less evident when wave heights were higher than normal.

**Conclusions:** Some variables that negatively influenced positioning can be minimized through careful planning (e.g., number of tagged fish released, transmitter power level). However, results suggested that the acoustic environment was highly variable over small spatial and temporal scales in response to complex interactions between many variables. Therefore, models that predict positioning or detection efficiencies as a function of environmental variables may not be attainable in most systems. The best defense against biased study conclusions is incorporation of in situ measures of system performance that allow for retrospective analysis of array performance after a study is completed.

**Keywords:** Vemco Positioning System, Positional telemetry, Performance, Detection probability, Close proximity detection interference, Thermal stratification, Wave height, Signal code collision

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## Background

Recent advances in aquatic animal telemetry technologies now provide researchers with an unprecedented ability to track animal movements at fine spatial and temporal scales, and answer behavioral and ecological questions that were previously beyond reach. One such advancement that has become increasingly popular over the last decade is use of telemetry systems to estimate two-dimensional (2D) or even three-dimensional (3D) positions of transmitter-implanted animals using time difference of arrival (TDOA) of acoustic transmissions at three or more acoustic receivers [1–4]. 2D and 3D tracks from aquatic animals have been used to study behaviors ranging from broad spatial habitat use and home ranges [4–7] to swimming speed [2, 8] and fine-scale responses to environmental stimuli [9, 10]. A variety of positioning systems exist, each with its own set of strengths and weaknesses, but they can be generally reduced to two categories: (1) cabled systems that use a single receiver with multiple hydrophones tethered with cables and (2) non-cabled systems that use multiple independent receivers, each with a single independent hydrophone. Cabled systems tend to be limited in size and location of deployments due to need for long cables between each hydrophone and receiver [3]. Non-cabled systems offer more flexibility with respect to array size and are better suited for remote locations [1, 11]. However, position processing with non-cabled systems is more complicated than with cabled systems because of the need to account for differences between receiver clocks, which drift over time due to effects of temperature and subtle manufacturing differences. Nonetheless, non-cabled systems have become increasingly popular due to ease of deployment and flexibility to accommodate project designs and large study areas.

Similar to the presence/absence telemetry systems that provide coarse-scale behavioral data, positional telemetry systems are subject to performance variability [12], which can complicate interpretation of animal tracks and possibly bias study conclusions [8, 13]. Studies describing variation in detection probability of presence/absence telemetry systems are abundant (reviewed in [12, 14]), but perhaps due to the relative novelty of positional telemetry and also possibly a disconnect between the end user (researcher) and the position estimation process, few papers have assessed spatial and temporal performance variability of positional telemetry systems [11, 15–18]. The primary focus of most positional telemetry performance studies has been position accuracy. Position accuracy has been well established as largely a function of the geometry of receivers relative to transmitters [1, 11, 17, 19–21] and varies little in comparison with positioning probability (i.e., the probability that a position was estimated by the array for a given transmission, [16, 18]). Less is known about the effects of environmental variables (e.g., thermal stratification and waves) or more complex processes, such as destructive code collisions or the so-called close proximity detection interference (i.e., detection interference as a result of transmission echoes being heard by nearby receivers; hereafter, CPDI; [22]), on positioning probabilities. Nonetheless, because the absence of evidence (i.e., positions) in telemetry studies is not necessarily evidence of absence [13], understanding variation in positioning probability is critical to interpreting study results.

Transmitter detections are the basis of position estimation; therefore, positioning probability should be influenced by many of the same variables that drive variability in detection probability in presence/absence telemetry systems (e.g., environmental noise, aquatic vegetation, biofouling; [13, 23, 24]). However, the issue of positioning probability in telemetry systems is complicated by the fact that the contribution of a given receiver to position estimates depends not only on the performance of that receiver, but also on the performance of receivers around it. Moreover, because questions addressed with positional telemetry arrays are often limited to finer spatial and temporal scales than those addressed with the presence/absence systems, studies that use positioning systems may be more sensitive to biases resulting from variability in performance [8, 11], particularly if the measured response variable is based on the number of positions returned by the system.

In this study, we assessed spatial and temporal variability in positioning probability of a large acoustic telemetry positioning system (Vemco Positioning System; hereafter VPS, Vemco Inc., Halifax, NS Canada) over three consecutive seasonal deployments. At the time of writing, this positional telemetry array was the largest ever constructed, consisting of 140 autonomous receivers and 43 stationary transmitters with a spatial coverage of approximately 23 $\mathrm{km}^2$. Our specific objectives were: (1) to quantify the degree of spatial ($<0.5$ $\mathrm{km}^2$) and temporal (6 h) variation in positioning probability that occurred over three seasonal deployments between 2012 and 2014 and (2) to determine whether variation in positioning probability could be predicted by environmental variables (e.g., surface waves and water temperature) and other site-specific variables such as signal code collisions and CPDI.

## Methods

### Study site and the Vemco Positioning System

Spatial and temporal variation in performance of the VPS (Vemco Inc.; Halifax, NS Canada) was assessed in a large acoustic telemetry array designed to study spawning behaviors of lake trout (*Salvelinus namaycush*) in northern

Lake Huron, North America. The array, which consisted of 140 VR2W-69 kHz autonomous receivers (Vemco Inc.; Halifax, NS Canada) and 43 stationary V16-6H transmitters (Vemco Inc.; Halifax, NS Canada), covered an area of approximately 23 km$^2$ and was deployed for between 87 and 100 days each year from August to November, 2012–2014. Stationary transmitters (hereafter, 'sync tags') with known locations were deployed primarily to synchronize clocks among receivers and secondarily to evaluate array performance. Each sync tag transmitted a unique ID code every 500–700 s (nominal delay = 600 s), with each time between transmissions (delay) being drawn from a uniform distribution. The site encompassed several shoal and reef areas with complex bathymetric features (Fig. 1) and depths ranging from ~2 m to over 38 m. Vertical temperature profiles in the study site were monitored using two lines of four temperature loggers (HOBO Water Temp Pro v2; model U22-001; Onset Computer Corporation, Bourne MA) that measured temperature to a resolution of 0.02 °C, with an accuracy of ±0.21 °C. A weather buoy (Tidas 900 buoy; S2 Yachts, Holland MI) was also moored within the array. The buoy logged air temperature, surface water temperature, wind speed and direction, and wave height and direction every 5 min for the duration of the study.

At the end of each study season, receivers were retrieved and downloaded, and data files were sent to Vemco for processing using their proprietary hyperbolic positioning algorithms [25]. Position estimates of transmitters were based on TDOA of each transmission at a minimum of three and a maximum of six (limit set by manufacturer) receivers with synchronized clocks. When a transmission was detected on more than six receivers, positions were estimated using data from the first six receivers that detected a transmission based on linear time-corrected detections. Hypothetically, the first six receivers that detected a transmission should represent the six closest receivers to the transmitter, but in practice that may not be true because of nonlinear drift of receiver clocks. The VPS returned a weight-averaged position among all combinations of three receivers that detected each transmission, as well as position precision estimates (horizontal position error; abbreviated 'HPE') that described the relative error sensitivity of each calculated position [25].

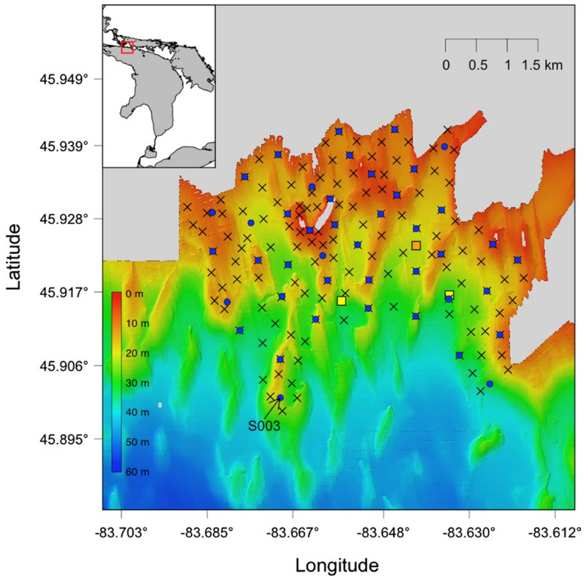

**Fig. 1** Bathymetric map (in m) of the Drummond Island acoustic telemetry study site. A 140-receiver Vemco Positioning System (VPS) was deployed at the site during late summer and autumn each year between 2012 and 2014. *Symbols*: *cross* = acoustic receiver (VR2W), *blue circle* = sync tag (V16-6H), *yellow square* = temperature line (containing 4 suspended HOBO temperature loggers), and *orange square* = Tidas 900 weather buoy. Site S003, representing a specific sync tag referred to in the text, was labeled and located in the southmost site in the array. *Inset* Location of the Drummond Island study site (*red square*) in Lake Huron, North America. *Square* indicates location only and is not to scale

### Spatial and temporal variability in positioning probability

Spatial and temporal variation in VPS array performance in each study year was assessed using positioning probability of 43 stationary sync tags distributed throughout the array (Fig. 1). Temporal variation in array performance was estimated by comparing performance metrics across 6-h time bins. Use of 6-h bins represented a compromise between having enough transmissions (36 on average) to accurately estimate a positioning probability and being a short enough time interval to reflect environmental variability at an ecologically relevant scale. Probability of positioning each transmitter during each 6-h bin was calculated based on the ratio of observed to expected positions (6 positions h$^{-1}$ × 6 h = 36 positions expected). Subsequently, for each 6-h time bin, we used 2D cubic spline interpolation (R package 'akima'; [26]) to estimate and visualize variation in positioning performance across the array. Mean array positioning probability during each 6-h bin was calculated from the 2D interpolations by taking the mean of all interpolated data points (spatial resolution of the interpolations was approximately 34 m$^2$). Mean positioning probability of the transmitters themselves was not used because transmitters were not equally spaced in the array, which meant some transmitters (particularly in the deep, less complex areas of the array) represented a greater area of the array than others. Due the random nature of sync tag transmissions (i.e., uniform distribution between 500 and 700 s), positioning probability estimates based on the mean of 36 transmissions per 6-h bin were subject to random error. Simulated transmission histories for 10,000 sync tags revealed a range of 34–37 transmissions during a single 6-h period, indicating a maximum of 6 % random error in our positioning probability estimates.

A generalized linear mixed-effect model with binomial error distribution (R Package 'lme4'; [27]) was used to model within- and between-sync tag variation in positioning probability against variables that could affect detection of acoustic transmitters. Fixed effects in the model included the number of unique fish transmitters within detection range of the closest receiver ('UniqueFish'), wave height measured at the within-array weather buoy ('WaveHt'), and degree of thermal stratification in the water column (i.e., difference between near-surface and near-substrate temperature in the array, as measured by HOBO temperature logger lines; 'DiffTemp'), as well as their interactions. Sync tag site ID was included as a random effect to account for inherent differences in positioning probability related to location of each transmitter in the array.

The mixed-effect model revealed complex interactions between variables, so rather than attempting to build a global model to describe variation in positioning probability of our sync tags, we fit separate logistic regression models (R Package 'stats'; [28]) for each transmitter site and examined spatial and temporal patterns in effect size (i.e., parameter estimates from logistic regressions) of three fixed-effect variables (i.e., UniqueFish, WaveHt, and DiffTemp). Preliminary inspection of the data suggested that the relative influence of the variable UniqueFish on variation in array performance changed markedly between the lake trout pre-spawning and spawning periods, and therefore, the two time periods were analyzed separately. Spawning period start dates were the same as were used previously at this site by Binder et al. [29], who used changepoint analysis to determine when male lake trout implanted with pressure-sensing transmitters moved from deep offshore water onto the shallow-water spawning shoals. During each time period, parameter estimates were inspected for obvious trends by mapping them on bathymetry. We then tested for significant relationships between parameter estimates and transmitter depth using linear regression (R Package 'stats'). Where scatter plots revealed a nonlinear relationship, segmented regression (i.e., broken-stick regression; R Package 'segmented'; [30]) was used in place of linear regression. Comparisons between pre-spawning and spawning period parameter estimates were made using paired t tests (R Package 'stats').

### Close proximity detection interference

CPDI is a phenomenon in acoustic telemetry whereby transmission sequences of a transmitter located in relative close proximity to a receiver are interrupted by strong echoes off reflective surfaces [22], in essence, causing the signal to collide with itself, and thus, not be properly decoded and logged on that receiver. We searched for evidence of CPDI in our array using data from 35 sync tags with collocated receivers (i.e., a receiver on the same mooring as the transmitter; Fig. 1). Prevalence of CPDI in our array was described by calculating the detection probability of each transmitter on collocated receivers during each 6-h bin. As with positioning probability, detection probability was calculated as the ratio of observed detections to expected detections (36 expected detections per 6-h time bin). Interpretation of inter-site variability in detection probability was complicated by spatial variation in detection probability related to varying local environmental conditions (e.g., number of fish transmitters within detection range of a receiver). To account for this variation, we standardized detection probabilities on collocated receivers to that on the non-collocated receiver with maximum detection probability for each transmitter. The new response variable, 'relative detection probability,' was the ratio of detection probability at the collocated receiver and detection probability for that transmitter at the non-collocated receiver (i.e., receiver not on the same mooring as the transmitter) with maximum detection probability. The relationship between relative detection probability of transmitters and water depth was modeled using nonlinear, least squares regression (R Package 'stats').

## Results

### Temporal and spatial variability in positioning probability

VPS array performance varied greatly within and among years. Mean, array-wide 6-h positioning probability ranged from 8 to 90 % in 2012, from 38 to 92 % in 2013, and from 59 to 95 % in 2014 (Fig. 2). The greater range in VPS positioning performance in 2012 compared with 2013 and 2014 was a result of extremely poor array performance during mid-to-late October and November in 2012 (Fig. 2). Upon investigation, poor performance during this period was caused primarily by widespread receiver memory saturation, which caused log files containing millisecond data required for positioning transmitters to be overwritten by detection data, which at the time was logged only to the nearest second (this issue was addressed in receiver firmware updates). The first instance of this issue occurred on 06 October, and by the end of the season, 81 of 140 (59 %) receivers reached memory capacity and stopped logging millisecond data. For this reason, 2012 VPS data collected on or after 06 October were excluded from subsequent statistical analyses.

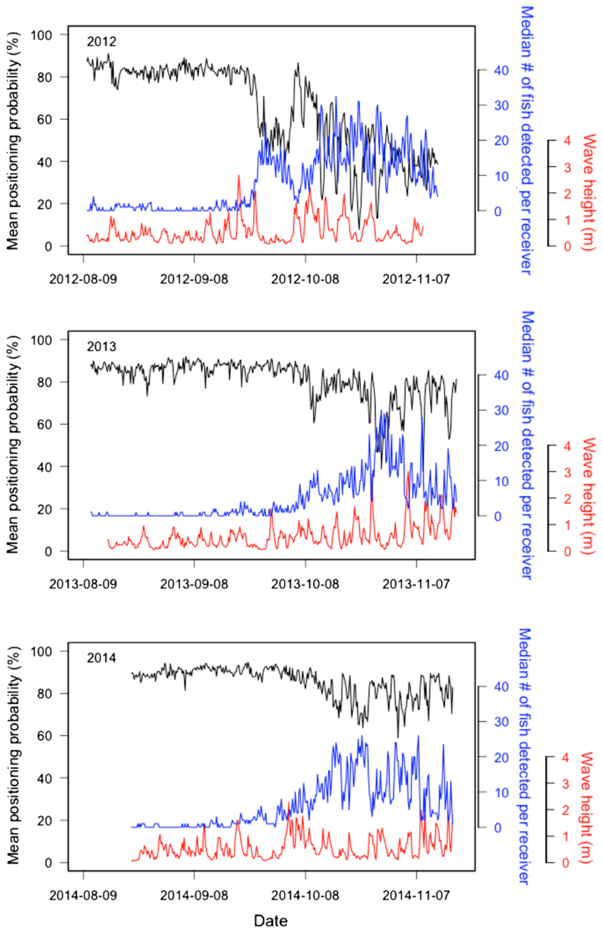

**Fig. 2** Mean estimated Vemco Positioning System (VPS) positioning probability (*black line*) in relation to wave height (*red line*) recorded by the on-site weather buoy and the median number of unique fish transmitters (*blue line*) detected per receiver during each year of the study. Mean positioning probability was calculated from 2D interpolations based on 43 sync tags distributed throughout the array (see Fig. 1). Each point on the graphs represents a 6-h time window

Clear seasonal trends were evident in all three years, with better performance in August and September than in October and November (Fig. 2). Within the array, a great deal of spatial variation occurred in positioning probability. Within some 6-h time periods, positioning probability of sync tags in some parts of the array was perfect (or near-perfect), while in other parts of the array, it was zero (Fig. 3). In general, positioning probability was poorer on the west side of the array (where the main lake trout spawning sites were located) than the east side of the array, particularly in the autumn during the lake trout spawning period. Nonetheless, all sync tags displayed perfect positioning probability during at least some periods, suggesting that spatial patterns were not a result of irregularities in array design (e.g., geometry, specific receiver locations).

Interestingly, positioning probability at some of the deeper receivers on the southwest side of the array (in particular S003; southernmost transmitter on the west side of array) consistently differed from other transmitter sites in the array. During the August dates, when mean whole-array positioning probability was relatively high, positioning probability at these sites was generally low (often less than 30 % of transmissions positioned; Fig. 3). Conversely, during the October and November dates when mean whole-array performance decreased, positioning probability at these sites tended to improve (see Additional file 1). Poor performance of these southwest receivers during summer months appeared to be related to thermal stratification in the water column, with positioning probability, particularly at site S003 (Fig. 1), improving during brief periods when little thermal stratification occurred in the array (Fig. 4). The negative relationship between positioning performance and thermal stratification was also evident in among-year comparisons, where performance at site S003 was greater in 2014, the year with the least thermal stratification, than in the previous 2 years (Fig. 4). Toward the end of each year when the thermal structure in the array became more homogenous, variation in positioning performance at this site was more closely related to the number of tagged fish within detection range of the site (Fig. 4).

Attempts to develop a meaningful global model relating sync tag positioning probability to local environmental variables such as number of tagged fish present (UniqueFish), wave height (WaveHt), and thermal stratification (TempDiff) revealed complex relationships and interactions that proved impossible to satisfactorily model using the predictor variables available. As expected, positioning performance was negatively correlated with the number of fish present within detection range across all receivers during both pre-spawning and spawning periods (Fig. 5a, d). However, relationships between positioning probability and both wave height and thermal stratification were site-specific. For example, at some sites positioning probability was negatively correlated with wave height, while at others a positive correlation occurred between positioning probability and wave height (Fig. 5b, e). Similar relationships were observed when comparing positioning probability against degree of thermal stratification (Fig. 5c, f). Moreover, at several sites, direction of observed relationships was reversed during the pre-spawning and spawning periods.

A portion of the inter-receiver variability in relationships between environmental conditions and positioning performance was related to the wide range of depths over which our array was deployed. However, relationships between parameter estimates (i.e., estimates of effect size) from transmitter-specific logistic regressions and

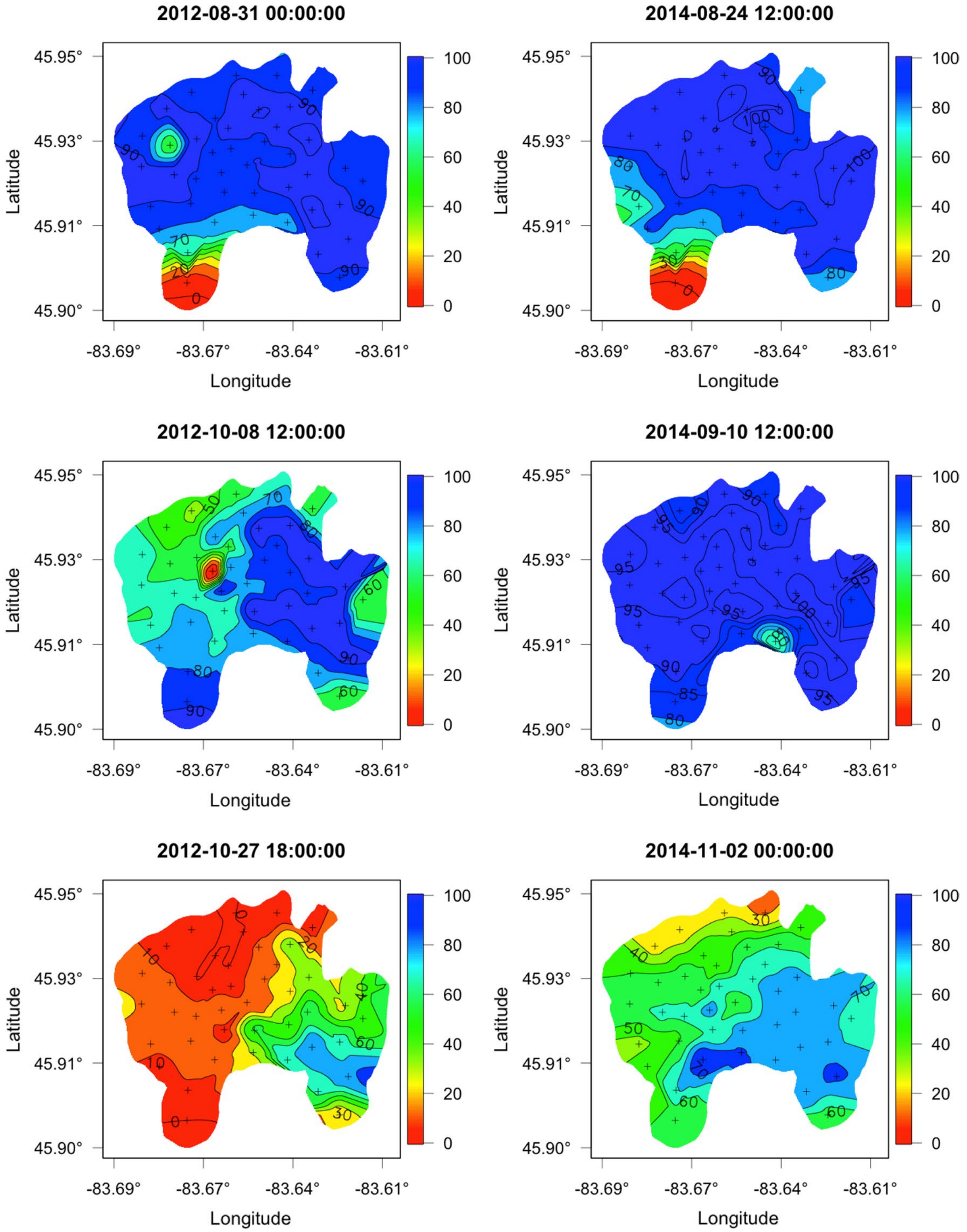

**Fig. 3** Estimated array-wide positioning probability (% positioning) of the Drummond Island Vemco Positioning System (VPS) during three arbitrary 6-h time periods in 2012 and 2014. Estimates of positioning probability were interpolated based on 43 sync tags distributed throughout the array (see Fig. 1). A high degree of spatial and temporal variability occurred in positioning probability of the Drummond Island VPS array. See Additional file 1 for complete records for all 3 years of the study

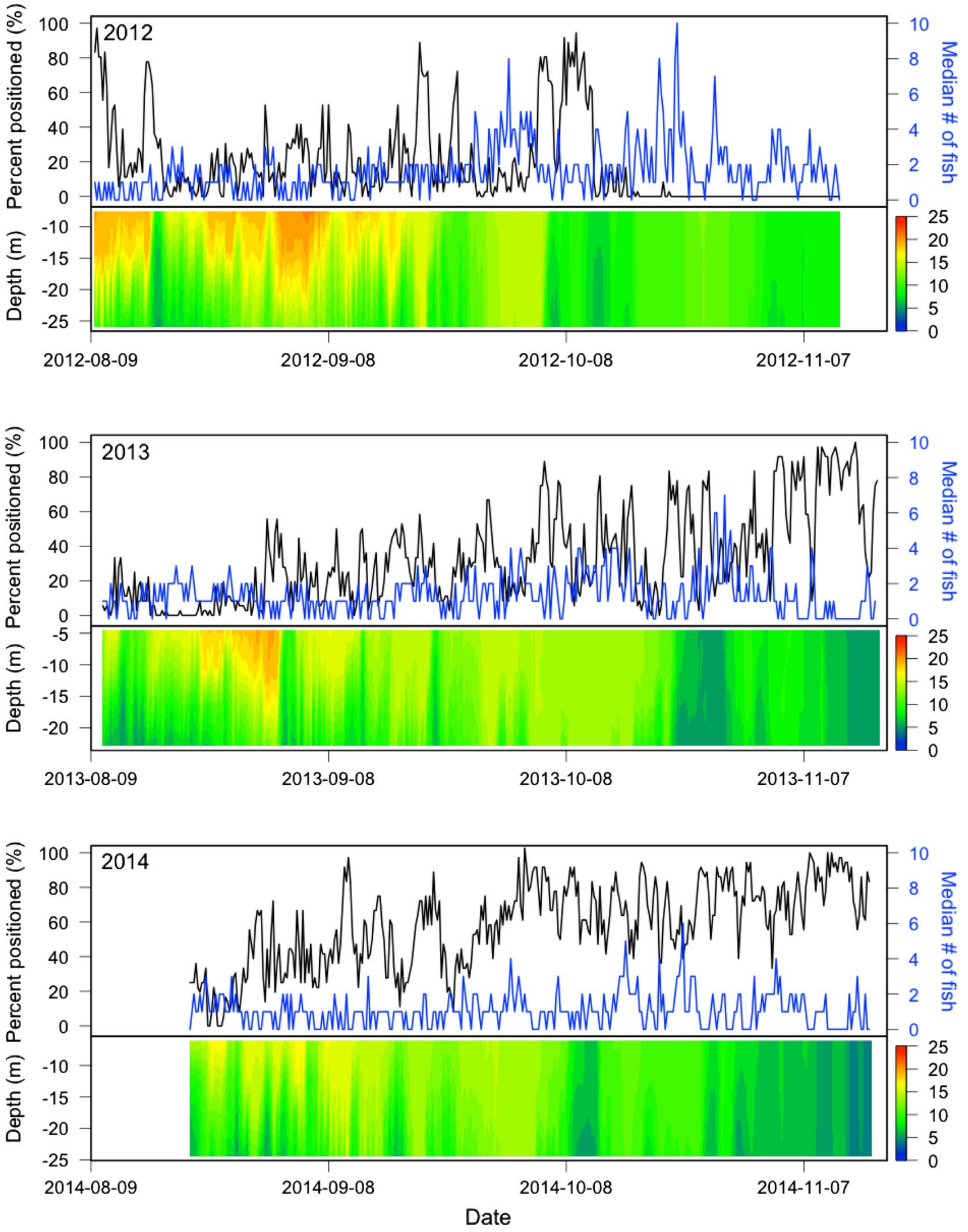

**Fig. 4** Positioning probability (*black line*) of sync tag S003, the southernmost transmitter in the Drummond Island Vemco Positioning System (VPS) array (see Fig. 1), relative to the median number of unique fish transmitters detected on receivers with line of sight and within 500 m of S003 and thermal stratification (*bottom graph in each panel*). Temperature profiles were interpolated from two separate temperature *lines* deployed in the array. Poor positioning probability at the end of the 2012 season was due to widespread receiver memory saturation, which began on 06 October. Each point on the *graphs* represents a 6-h time window. Temperatures are in °C

depth of the transmitter were not always linear and differed between pre-spawning and spawning periods. During the pre-spawning period, when few fish were present in the array (Fig. 2), WaveHt parameter estimates (i.e., relationship between WaveHt and positioning probability) were generally negative for shallow transmitters and positive for deep transmitters (Fig. 6a). A segmented regression indicated a positive relationship between

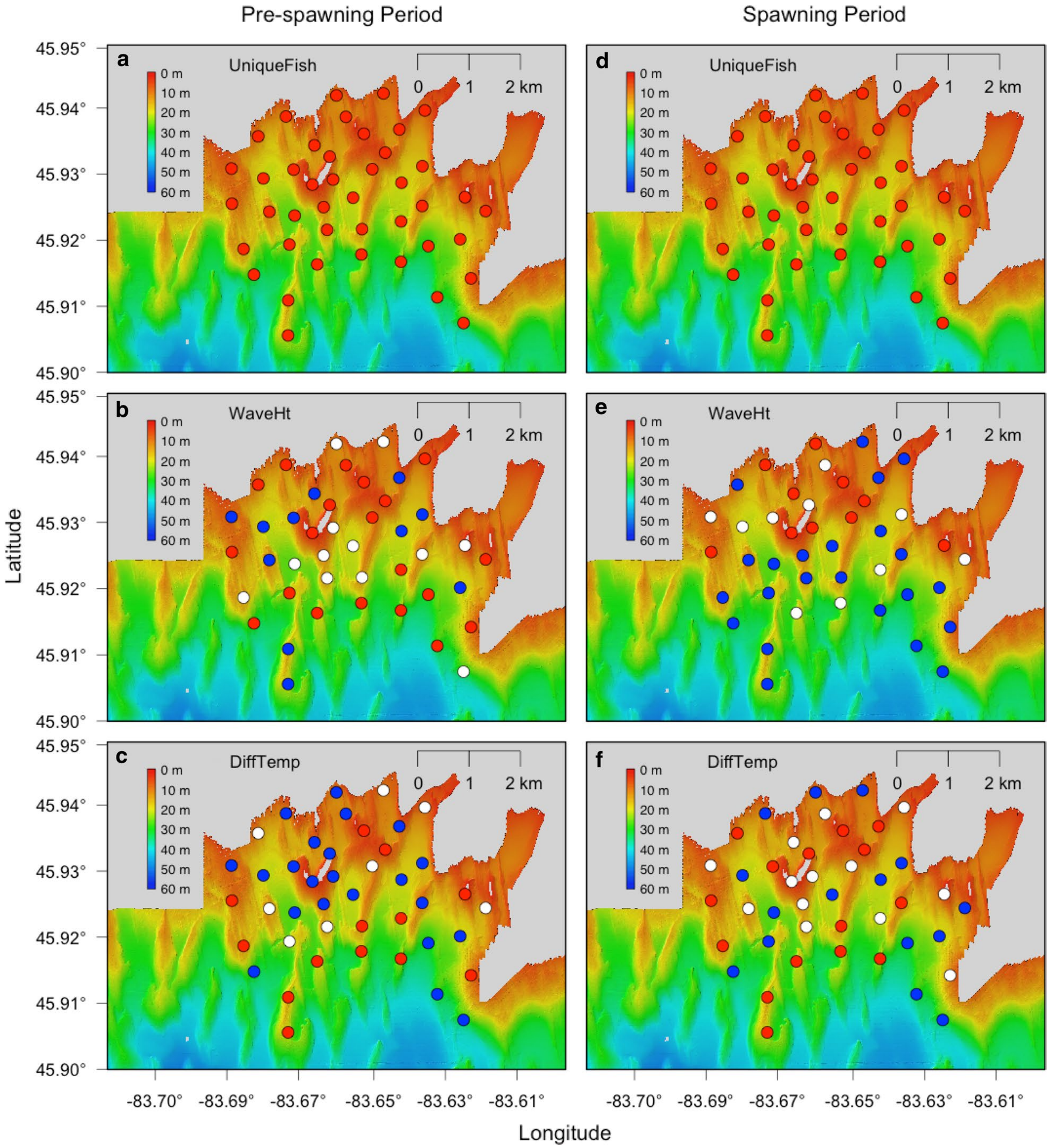

**Fig. 5** Results of logistic regression analysis relating positioning probability of each sync tag ($n = 43$) to the number of fish transmitters detected on the closest receiver ('UniqueFish'; **a**, **d**), wave height ('WaveHt'; **b**, **e**), and difference between near-surface and near-substrate temperature in the array ('DiffTemp'; **c**, **f**). Data from the lake trout spawning (*right column*) and pre-spawning (*left column*) periods are displayed separately. *Red symbols* indicate a significant negative relationship, *blue symbols* a significant positive relationship, and *white symbols* no significant relationship ($\alpha = 0.05$)

WaveHt parameter estimate and transmitter depth (segmented regression; $t = 3.351$, $df = 31$, $p = 0.002$) down to approximately 13.9 ± 2.4 m, after which WaveHt parameter estimates remained relatively consistent across depth (segmented regression; $t = -0.359$, $df = 31$, $p = 0.722$). TempDiff parameter estimates were also positively correlated with transmitter depth during the pre-spawning period (linear regression; $t = 3.723$, $df = 33$, $p < 0.001$),

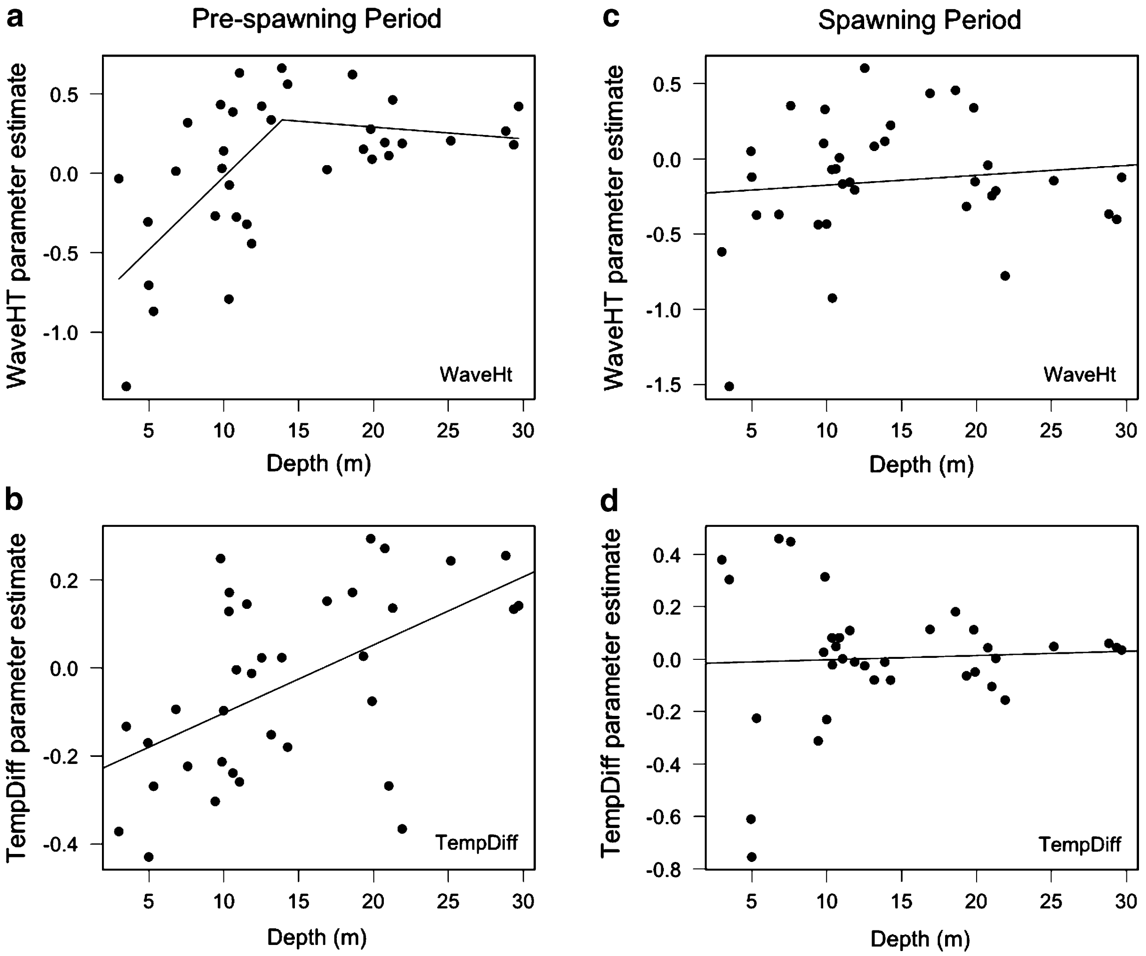

**Fig. 6** Relationship between logistic regression parameter estimates from positioning probability models ('WaveHt' = wave height, 'TempDiff' = difference between near-surface and near-substrate water temperature) and water depth at 43 sync tag sites. Data from the lake trout spawning (*right column*) and pre-spawning (*left column*) periods were analyzed separately. *Lines* in **b**, **c**, and **d** depict results of linear regression analysis, while *lines* in **a** depict results of segmented regression. Significant relationships occurred between parameter estimates and water depth during the pre-spawning period, but not during the spawning period ($a = 0.05$)

with negative parameter estimates predominant at shallow depths and positive parameter estimates predominant at deeper depths (Fig. 6b). In contrast, during the spawning period, neither WaveHt (linear regression; $t = 0.673$, $df = 33$, $p = 0.506$) nor TempDiff (linear regression; $t = 0.283$, $df = 33$, $p = 0.779$) parameter estimates were significantly correlated with transmitter depth (Fig. 6c, d).

Some of the discrepancy between the pre-spawning and spawning period is likely due to the fact that the presence of lake trout transmitters within the array ('UniqueFish') had a far greater influence on positioning probability during the spawning period (when far more fish were present in the array) than during the pre-spawning period. UniqueFish parameter estimates were negative during both pre-spawning and spawning period (i.e., relationship between UniqueFish and positioning probability was always negative) and did not vary with transmitter depth (linear regression; pre-spawning: $t = 1.471$, $df = 33$, $p = 0.151$; spawning: $t = -0.865$, $df = 33$, $p = 0.393$). Nonetheless, UniqueFish parameter estimates were on average 2.47 (±1.33) times greater during the spawning period than during the pre-spawning period (paired *t* test; $t = 7.344$, $df = 34$, $p < 0.001$), indicating a greater negative relationship with positioning probability during the spawning period than non-spawning period. In fact, number of fish present in the array appeared to be a predominant factor driving whole-array positioning probability during the spawning period (Fig. 2).

### Close proximity detection interference

One possible confounding factor in our analysis of positioning probability was CPDI [22]. Thirty-five of 43 sync tags in our array were collocated with an acoustic

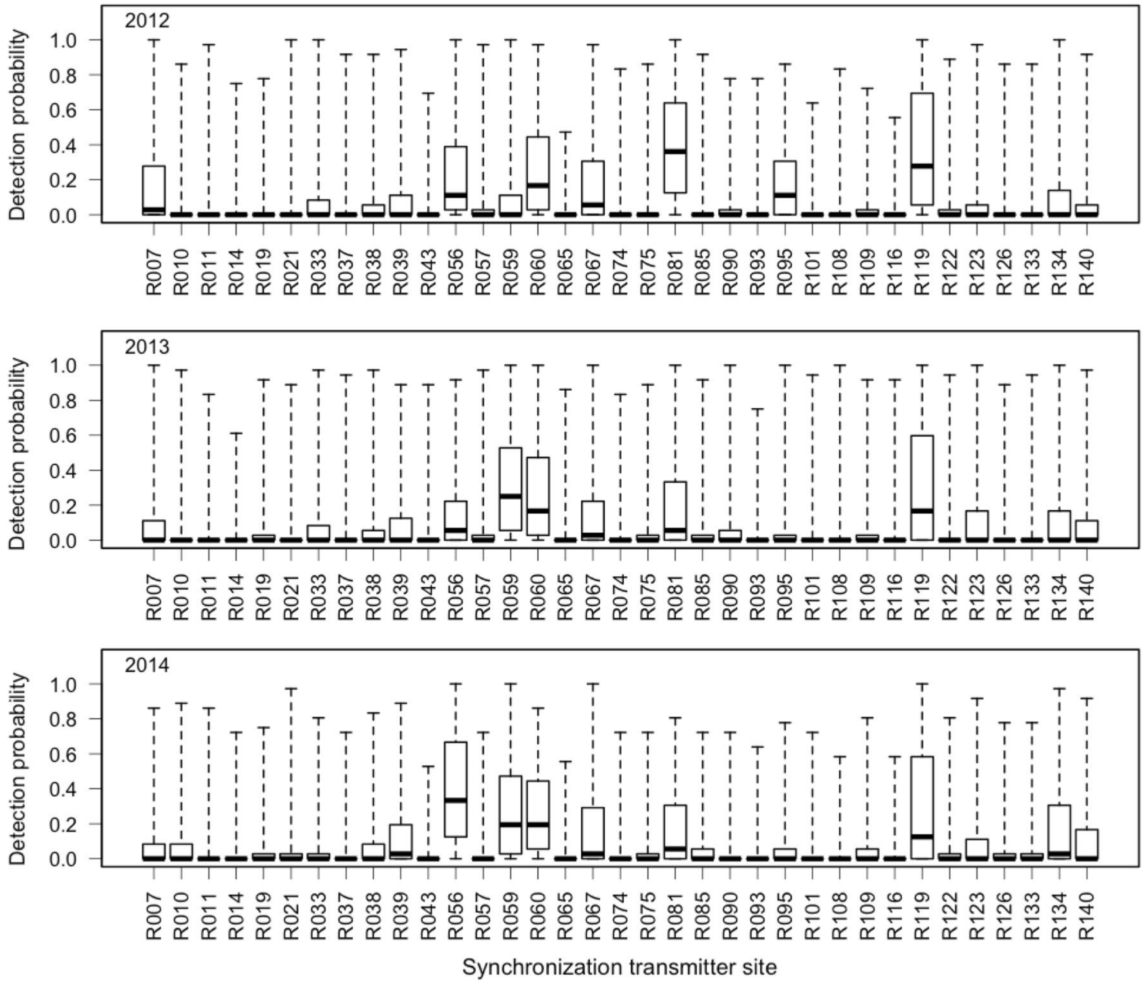

**Fig. 7** Boxplots displaying median (*center line*), 25th and 75th quartiles (*bounding box*), and range (*dashed line*) of detection probabilities on collocated receivers for 35 transmitters. *Each panel* shows results for a different year of the study (2012–2014). Individual detection probabilities were calculated based on 6-h time windows

receiver. Examination of detection probability of sync tags on collocated receivers revealed that this phenomenon was widespread in our array (Fig. 7). Collocated receivers never detected sync tags as well as other nearby surrounding receivers with line of sight to the transmitter (i.e., maximum detection probability for a given transmitter always occurred on a non-collocated receiver). Mean maximum detection probability for each transmitter on nearby non-collocated receivers ranged from 0.67 to 0.91. In contrast, mean detection probability on collocated receivers averaged only 12 % of maximum detection probability, ranging from 0.01 to 0.37 over the 3 years of study.

A high degree of intra-annual variability occurred in detection probability of transmitters on collocated receivers, both within and between sites (Fig. 7). However, mean relative detection probability of individual collocated transmitters was strongly correlated across all three years (Pearson's $r = 0.78$, 0.75, and 0.85 for 2012 vs. 2013, 2012 vs. 2014, and 2013 vs. 2014, respectively, $p < 0.001$ for all comparisons), which suggests that CPDI was location-specific and probably related to physical characteristics of the immediate environment that changed little over time (i.e., lake bottom composition and topography). Inter-site variation in mean relative detection probability was related negatively to water depth at the site and was best approximated with a decreasing exponential curve (relative detection probability $= 1.098 \times \text{depth}^{-0.892}$, $p < 0.001$ for both parameters; Fig. 8a), indicating that CPDI increased exponentially with increased water depth.

Within-site variability in relative detection probability of transmitters on collocated receivers was related to wave height (linear mixed-effect model, $t = 144.432$,

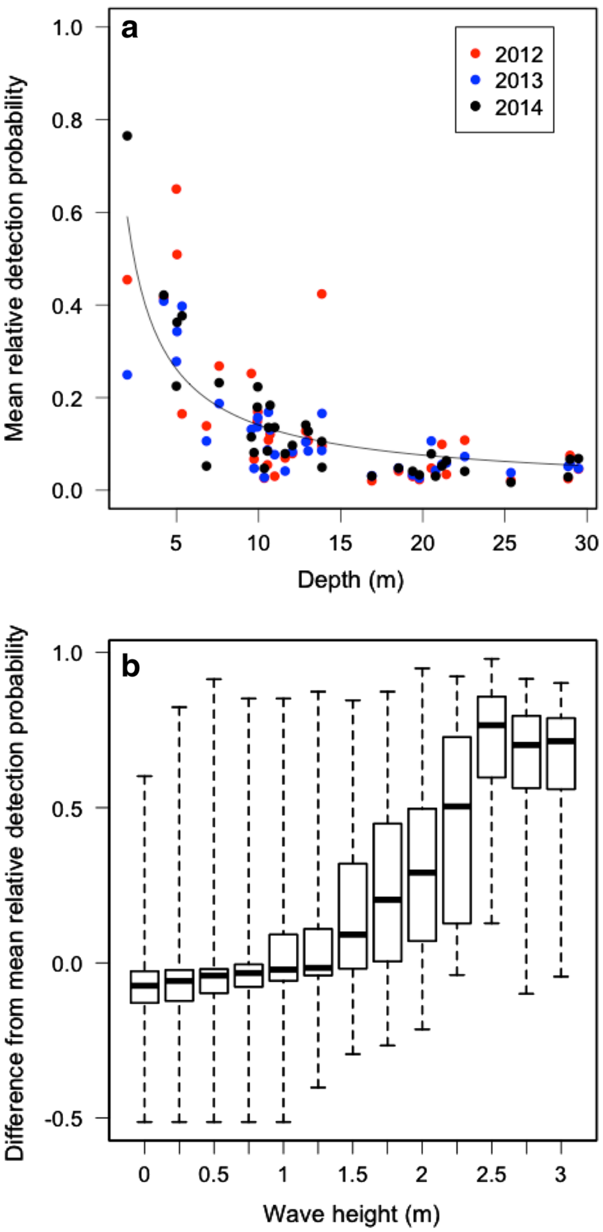

**Fig. 8** **a** Relationship between mean relative detection probability of sync tags on collocated receivers and water depth at each location. Data were normalized to the receiver with maximum detection probability for each transmitter. Individual points were color-coded by year. Data were best approximated with a declining exponential curve (relative detection probability $= 1.098 \times \text{Depth}^{-0.892}$). **b** Difference from mean relative detection probability of sync tags on collocated receivers across wave heights. *Boxplots* display median (*center line*), 25th and 75th quartiles (*bounding box*), and range (*dashed line*) of differences across 35 collocated sync tags during the three study years. Detection probability on collocated receivers was generally lower than average when wave height was less than approximately 1.25 m and greater than average when wave height was greater than 1.25 m

$df = 36{,}010$, $p < 0.001$; Fig. 8b). In general, mean relative detection probability of collocated transmitters was lower than average when wave height was less than approximately 1.25 m and greater than average when wave height was greater than 1.25 m (Fig. 8b). No significant relationship existed between maximum detection probability and wave height (linear mixed-effect model, $t = -1.021$, $df = 36{,}010$, $p = 0.307$), so the above relationship was not an artifact of decreased maximum detection probability at higher wave heights; mean maximum detection probability of sync tags was greater than or equal to 0.77 (range 0.77–0.89) at all wave heights.

## Discussion

Substantial spatial and temporal variability occurred in positioning probability of sync tags in our positional telemetry array. While spatial variation in positioning probability has been noted in other studies [15, 16], most studies have focused on receiver geometry and ignored temporal variability [16–18]. This trend may be due to the fact that most assessment studies were short in duration [1, 15, 17], or used positional arrays with relatively small spatial coverage [1, 11, 15, 18]. The long duration, high environmental complexity, and large spatial extent of our VPS deployment provided a unique opportunity to explore and quantify within-array variability in positioning probability. Some of the variability we observed could be explained by variables we measured in the field, but much of it could not, which highlights the complex nature of acoustics in natural systems. Some of the negative relationships we observed could be controlled (e.g., number of tagged fish in the array; transmitter power level), or at the least minimized by careful planning and study design.

Signal code collisions resulting from large numbers of fish transmitters in the array at the same time were a significant cause of decreased positioning probability in our system, particularly during the spawning period when they were the main driver of variation in array performance. A signal code collision occurs when transmissions from two or more transmitters are detected simultaneously on the same receiver [31], preventing the receiver from properly decoding either signal. Probability of code collisions is a function of the number of transmitters within range of a receiver, the duration of the code signal, and the period between transmissions [23]. The duration of a transmission, and thus the degree of susceptibility of a positioning system to signal code collisions, is dependent on the coding scheme used, which varies by manufacturer. With Vemco's current coding scheme, the transmission duration is relatively long (up to ~5 s; [32]); therefore, depending on the nominal delay of the transmitters (i.e., period between successive transmissions), the probability of collisions can be quite high at relatively low transmitter densities (see Fig. 9).

Signal code collisions have a high potential for creating spatial and temporal bias in telemetry studies because the presence of the study animals themselves alters the performance of the telemetry system. Therefore, investigators should assess the potential for, and implications of, signal code collisions (particularly if they are expected to be heterogeneously distributed) both during the study design stage and while interpreting results. In our case, the high prevalence of signal collisions in our system during the spawning period was due to several factors, including: (1) underestimation of lake trout annual mortality rate and spawning site fidelity [29], which caused high numbers of transmitters to return to the system during each year of the study (390 tagged trout released between 2010 and 2011), (2) high levels of aggregation at relatively few spawning site locations [33], and (3) use of high-powered tags (V16-6H, 158 dB, 90 s nominal delay), which at times had detection ranges of several kilometers. Based on our experience, we recommend adopting a conservative approach in study designs when determining how many transmitters to release in a study, particularly if researchers are new to a study site, or the behavioral ecology of the animal is not well understood.

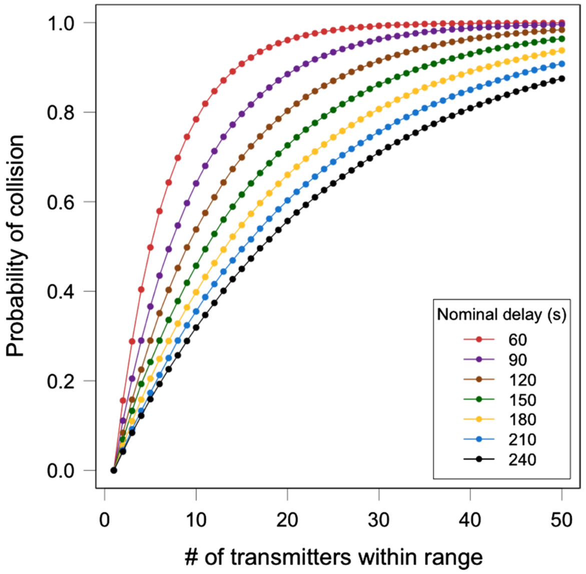

**Fig. 9** Estimated probability of a signal code collision (using Vemco's global coding scheme) based on the number of transmitters within detection range of a receiver. Collision probabilities were calculated by simulating transmission histories ($n = 10{,}000$ transmissions) for between 1 and 50 transmitters assuming transmission duration of 5.12 s. Transmitters were programmed to transmit at random intervals between ±50 % of nominal delay. R code for the simulation is provided as Additional file 2

As has been observed in other positional telemetry studies [16, 18], positioning probability of sync tags at our site was influenced by environmental variability. However, relationships between environmental variables and positioning probability in our array were location- and time-specific. Steel et al. [18] reported variation in the relative influence of environmental parameters on positioning probability across three study systems (coastal, estuarine, and riverine), but our results indicated that this variation can occur over relatively small spatial scales. Our observations have important implications for acoustic telemetry studies in general. First, fine-scale variation in response to environmental variables indicated that the nature of these relationships was complex. Therefore, while general rules of thumb regarding the effect of certain environmental variables on telemetry system performance may be evident, development of a universally applicable predictive model [34] using easy-to-measure variables is likely beyond reach prior to conducting a study. Second, because acoustic properties can vary over small distances, true optimization of an acoustic telemetry system at some sites may require fine-scale range testing and development of spatially heterogeneous array designs (e.g., differential receiver spacing across an array).

Water depth played an important role in the performance of our VPS array, particularly with respect to how the system responded to changes in wave height and thermal stratification. In general, shallow transmitters tended to be negatively affected by increased wave height and thermal stratification, while deeper transmitters often saw a boost in positioning probability under the same conditions. As far as we are aware, ours is the first study to report a positive relationship between positioning probability and wave height or thermal stratification; however, we are doubtful that the increase in positioning probability is directly related to these variables. Rather, because both of these variables tend to reduce the distance over which an acoustic transmitter is detected [23, 35], we hypothesize that the positive relationships are due to reduced transmission echoes and a consequent reduction in CPDI [22], which was most pronounced in deep water. This interpretation was supported by the observation that detection probability of transmitters on collocated receivers increased as wave heights increased. Interestingly, depth effects were only observed during the pre-spawning period. We attribute this to a masking effect by signal code collisions, which were more prevalent during the spawning period than during the pre-spawning period.

The high incidence of CPDI in our VPS array was likely due to the combined effect of our use of high-powered transmitters and a highly reflective acoustic environment [22] in which substrate was dominated by the hard surfaces of cobble, boulders, and bedrock. Although evidence of CPDI occurred for all collocated receiver/transmitter pairs, the prevalence of CPDI increased exponentially with receiver depth, a characteristic we attributed to an exponential decline in ambient noise from surface sources (e.g., wind and waves). Prevalence of CPDI is dependent on the coding scheme [21, 22, 32] and, therefore, is likely to vary among telemetry systems. Thus, researchers should assess the potential for this phenomenon when designing their study and choose transmitter specifications and receiver placements that minimize the effect with the equipment they plan to use. Without sufficient receiver overlap (i.e., redundancy), CPDI can create areas of low detection/position probability in receiver arrays and curtains [22]. Moreover, CPDI also has the potential to reduce accuracy of positions returned from VPS arrays. The reason for this inaccuracy is that position estimation will depend on detections at receivers that are further away from the transmitter, which could result in poor receiver geometry, imprecise signal arrival time estimates, and consequently higher horizontal position error [1, 18].

Receiver memory saturation (which caused raw log files to be overwritten by detection data) late in 2012 caused a drastic decrease in whole-array positioning probability. At the time, no mechanism was in place to flag this issue during either receiver download or position processing, and because it occurred during the peak of lake trout spawning, poor array performance was assumed to be due to signal code collisions. Indeed, it was not until we started work on this manuscript that the memory issue was identified, which highlights the need for researchers to take responsibility for quality checking results returned to them from positioning software. At a minimum, we recommend researchers create visual displays (e.g., graphs or maps, e.g., Fig. 4) for assessing positioning performance over space and time. Unexplained changes in performance should be investigated thoroughly to rule out equipment failure or processing errors. Early assessment of positioning performance, especially if assessed from a pilot study, may also provide an opportunity to correct deficiencies in array design. For example, poor positioning probability on the southwest side of our array during summer (top panels in Fig. 3) was likely due to the fact that transmissions on top of the reef had to transmit through the thermocline to reach surrounding receivers. Had we identified this issue in 2012, changes could have been made to the array (e.g., addition of more receivers or placing current receivers higher in the water column) to improve performance in subsequent years.

## Conclusions

The acoustic telemetry community is constantly expanding as new researchers adopt these technologies in their studies. Therefore, identification and discussion of issues related to study design and data interpretation is valuable to the community because it helps to improve the overall quality of data coming out of acoustic telemetry studies, as well as their interpretation. Positional acoustic telemetry, and more specifically VPS, is a relatively new technique for tracking movements of aquatic animals; thus, a need exists to better understand how these systems perform in real-world applications. Only a few published papers are available describing spatial or temporal variation in VPS performance, fewer still while the VPS system was used to track animals, and none that have spanned the spatial scale and range of environmental conditions that occurred in our study. Some of the variables we identified as negatively influencing positioning probability (e.g., signal code collisions) can be minimized through careful planning, but our results also suggest that the acoustic environment can be highly variable over relatively small spatial and temporal scales, which if unaccounted for, have the potential to bias study conclusions.

At complex study sites (e.g., sites with highly variable depth, substrate types, or water chemistry), fine-scale range testing may allow researchers to optimize receiver array design; however, we acknowledge that such intense pre-study testing is rarely practical. In most cases, the best defense against making biased study conclusions due to spatial and temporal changes in system performance will be to incorporate methods for measuring that variability into the study design. For most, that will involve deploying stationary transmitters throughout the study site for the duration of the study, with the number and location of these transmitters depending on the questions being addressed and the complexity of the study site. At a minimum, this approach will allow researchers to interpret results in the context of array performance. In some cases, results may be standardized by incorporating measures of system performance variability into analyses, either through use of correction factors [36], or through development of sophisticated statistical analyses that explicitly correct parameter estimates based on imperfect detection and positioning probabilities [37, 38].

## Availability of supporting data

The data supporting the results of this article are stored in the Great Lakes Acoustic Telemetry Observation System (GLATOS) database (http://data.glos.us/glatos).

Data availability is subject to data sharing policies currently under development by GLATOS, the Great Lakes Fishery Commission, and the United States Geological Survey.

## Additional files

**Additional file 1.** Video showing spatial and temporal variation in positioning performance of a 140-receiver Vemco Positioning System (VPS) array over three lake trout spawning seasons. Estimates of positioning probability were interpolated based on performance of 43 stationary tags (indicated by + symbol) scattered throughout the array.

**Additional file 2.** R script for estimating, based on simulation, the probability of a signal code collision based on the nominal delay, transmission duration, and number of tags within detection range of a receiver.

### Authors' contributions

TRB led all aspects of study design, executed the field portion of the study, and drafted the manuscript. TAH, CMH, and CCK participated in the design of the study, provided consultation on statistical analyses, and helped to draft the manuscript. All authors read and approved the final manuscript.

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### Competing interests

The authors declare that they have no competing interests.

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### References

1. Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res. 2011;108:364–71.
2. Rillahan C, Chambers M, Howell WH, Watson WH III. A self-contained system for observing and quantifying the behavior of Atlantic cod, *Gadus morhua*, in an offshore aquaculture cage. Aquaculture. 2009;293:49–56.
3. Cooke SJ, Niezgoda GH, Hanson KC, Suski CD, Phelan FJS, Tinline R, Philipp DP. Use of CDMA acoustic telemetry to document 3-D positions of fish: relevance to the design and monitoring of aquatic protected areas. Mar Technol Soc J. 2005;39:17–27.
4. Andrews KS, Tolimieri N, Williams GD, Samhouri JF, Harvey CJ, Levin PS. Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. Mar Biol. 2011;158:2377–87.
5. Coates JH, Hovel KA, Butler JL, Klimley AP, Morgan SG. Movement and home range of pink abalone *Haliotis corrugate*: implications for restoration and population recovery. Mar Ecol Prog Ser. 2013;486:189–201.
6. Espinoza M, Farrugia TJ, Lowe CG. Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. J Exp Mar Biol Ecol. 2011;401:63–74.
7. Reubens JT, Pasotti F, Degraer S, Vincx M. Residency, site fidelity and habitat use of Atlantic cod (*Gadus morhua*) at an offshore wind farm using acoustic telemetry. Mar Environ Res. 2013;90:128–35.
8. Løkkeborg S, Fernö A, Jørgensen T. Effect of position-fixing interval on estimated swimming speed and movement pattern of fish tracked with a stationary positioning system. Hydrobiologia. 2002;483:259–64.
9. McMahan MD, Brady DC, Cowan DF, Grabowski JH, Sherwood GD. Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*). Can J Fish Aquat Sci. 2013;70:1625–34.
10. Lynch BR, Rochette R. Circatidal rhythm of free-roaming sub-tidal green crabs, *Carcinus maenas*, revealed by radio-acoustic positional telemetry. Crustaceana. 2007;80:345–55.
11. Biesinger Z, Bolker BM, Marcinek D, Grothues TM, Dobarro JA, Lindberg WJ. Testing an autonomous acoustic telemetry positioning system for fine-scale space use in marine animals. J Exp Mar Biol Ecol. 2013;448:46–56.
12. Melnychuk MC: Detection efficiency in telemetry studies: definitions and evaluation methods. In: Adams NS, Beeman JW, Eiler JH, editors. Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland; 2012. p. 339–57.
13. Payne N, Gillanders B, Webber D, Semmens J. Interpreting diel activity patterns from acoustic telemetry: the need for controls. Mar Ecol Prog Ser. 2010;419:295–301.
14. Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT. A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish. 2014;24:199–218.
15. Baktoft H, Zajicek P, Klefoth T, Svendsen JC, Jacobsen L, Pedersen MW, March Morla D, Skov C, Nakayama S, Arlinghaus R. Performance assessment of two whole-lake acoustic positional telemetry systems—Is reality mining of free-ranging aquatic animals technologically possible? PLoS ONE. 2015;10:e0126534.
16. Bergé J, Capra H, Pella H, Steig T, Ovidio M, Bultel E, Lamouroux N. Probability of detection and positioning error of a hydro acoustic telemetry system in a fast-flowing river: intrinsic and environmental determinants. Fish Res. 2012;125–126:1–13.
17. Roy R, Beguin J, Argillier C, Tissot L, Smith F, Smedbol S, De-Oliveira E. Testing the VEMCO Positioning System: spatial distribution of the probability of location and the positioning error in a reservoir. Anim Biotelemetry. 2014;2:1.
18. Steel AE, Coates JH, Hearn AR, Klimley AP. Performance of an ultrasonic telemetry positioning system under varied environmental conditions. Anim Biotelemetry. 2014;2:15.
19. O'Dor RK, Andrade Y, Webber DM, Sauer WHH, Roberts MJ, Smale MJ, Voegeli FM: Applications and performance of radio-acoustic positioning and telemetry (RAPT) systems. In Lagardère J-P, Anras M-LB, Claireaux G, editors. Advances in invertebrates and fish telemetry. Berlin: Springer; 1998. p. 1–8. (Developments in Hydrobiology, vol. 130).
20. Ehrenberg JE, Steig TW. A method for estimating the "position accuracy" of acoustic fish tags. ICES J Mar Sci J Cons. 2002;59:140–9.
21. Yoshida N, Mlitamura H, Aria N, Yamane H, Mitsunaga Y, Viputhanumas T, Ratanachamnong D: Detection range and horizontal accuracy of a fine-scale positioning telemetry system at Kaeng Krachan Reservoir, Thailand. In: Proceedings of the design symposium on conservation of ecosystem (The 13th SEASTAR2000 workshop), vol. 2; 2014. p. 9–14.
22. Kessel ST, Hussey NE, Webber DM, Gruber SH, Young JM, Smale MJ, Fisk AT. Close proximity detection interference with acoustic telemetry: the importance of considering tag power output in low ambient noise environments. Anim Biotelemetry. 2015;3:5.

23. Simpfendorfer CA, Heupel MR, Collins AB. Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. Can J Fish Aquat Sci. 2008;65:482–92.
24. Heupel MR, Reiss KL, Yeiser BG, Simpfendorfer CA. Effects of biofouling on performance of moored data logging acoustic receivers. Limnol Oceanogr Methods. 2008;6:327–35.
25. Smith F. Understanding HPE in the Vemco Positioning System (VPS). Halifax, NS: Vemco Inc.; 2013.
26. Akima H, Gebhardt A: Interpolation of irregularly and regularly spaced data. 2015. R package version 0.5-12. http://CRAN.R-project.org/package=akima.
27. Bates D, Maechler M, Bolker BM, Walker S: lme4: Linear mixed-effects model using "Eigen" and S4. 2015. R package version 1.1-8. http://CRAN.R-project.org/package=lme4.
28. R Core Team: R: A language and environment for statistical computing. 2015. https://www.R-project.org/.
29. Binder TR, Riley SC, Holbrook CM, Hansen MJ, Bergstedt RA, Bronte CR, He J, Krueger CC. Spawning site fidelity of wild and hatchery lake trout (*Salvelinus namaycush*) in northern Lake Huron. Can J Fish Aquat Sci. 2016;73:18–34.
30. Muggeo V: Segmented: an R package to fit regression models with broken-line relationships. 2008. https://cran.r-project.org/web/packages/segmented/index.html.
31. Voegeli FA, Lacroix GL, Anderson JM. Development of miniature pingers for tracking Atlantic salmon smolts at sea. Hydrobiologia. 1998;371:35–46.
32. Pincock DG. Understanding the performance of VEMCO 69 kHz single frequency acoustic telemetry. Halifax NS: Vemco Inc; 2008.
33. Riley SC, Binder TR, Wattrus NJ, Faust MD, Janssen J, Menzies J, Marsden JE, Ebener MP, Bronte CR, He JX, Tucker TR, Hansen MJ, Thompson HT, Muir AM, Krueger CC. Lake trout in northern Lake Huron spawn on submerged drumlins. J Great Lakes Res. 2014;40:415–20.
34. Gjelland KØ, Hedger RD. Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. Methods Ecol Evol. 2013;4:665–74.
35. Singh L, Downey NJ, Roberts MJ, Webber DM, Smale MJ, Van Den Berg MA, Harding RT, Engelbrecht DC, Blows BM. Design and calibration of an acoustic telemetry system subject to upwelling events. Afr J Mar Sci. 2009;31:355–64.
36. Johnson BK, Ager AA, Findholt SL, Wisdom MJ, Marx DB, Kern JW, Bryant LD: Mitigating spatial differences in observation rate of automated telemetry systems. J Wildl Manag 1998;62:958–67.
37. Martins EG, Gutowsky LF, Harrison PM, Patterson DA, Power M, Zhu DZ, Leake A, Cooke SJ. Forebay use and entrainment rates of resident adult fish in a large hydropower reservoir. Aquat Biol. 2013;19:253–63.
38. Perry RW, Skalski JR, Brandes PL, Sandstrom PT, Klimley AP, Ammann A, MacFarlane B. Estimating survival and migration route probabilities of juvenile Chinook salmon in the Sacramento-San Joaquin River Delta. North Am J Fish Manag. 2010;30:142–56.