

RESEARCH ARTICLE

A comparative analysis of common methods to identify waterbird hotspots

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Abstract

1. Hotspot analysis is a commonly used method in ecology and conservation to identify areas of high biodiversity or conservation concern. However, delineating and mapping hotspots is subjective and various approaches can lead to different conclusions with regard to the classification of particular areas as hotspots, complicating long-term conservation planning.
2. We present a comparative analysis of recent approaches for identifying waterbird hotspots, with the goal of developing insights about the appropriate use of these methods. We selected four commonly used measures to identify persistent areas of high use: kernel density estimation, Getis-Ord G_i^* , hotspot persistence and hotspots conditional on presence, which represent the range of quantitative hotspot estimation approaches used in waterbird analyses. We applied each of the methods to aerial survey waterbird count data collected in the Great Lakes from 2012–2014. For each approach, we identified areas of high use for seven species/species groups and then compared the results across all methods and to mean effort-corrected counts.
3. Our results indicate that formal hotspot analysis frameworks do not always lead to the same conclusions. The kernel density and Getis-Ord G_i^* methods yielded the most similar results across all species analysed and were generally correlated with mean effort-corrected count data. We found that these two models can differ substantially from the hotspot persistence and hotspots conditional on presence estimation approaches, which were not consistently similar to one another. The hotspot persistence approach differed most significantly from the other methods but is the only method to explicitly account for temporal variation.

4. We recommend considering the ecological question and scale of conservation or management activities prior to designing survey methodologies. Deciding the appropriate definition and scale for analysis is critical for interpretation of hotspot analysis results as is inclusion of important covariates. Combining hotspot analysis methods using an integrative approach, either within a single analysis or post hoc, could lead to greater consistency in the identification of waterbird hotspots.

KEYWORDS

gamma distribution, Getis-Ord G_i^* , Great Lakes, kernel density estimation, log-normal distribution, parametric and nonparametric models, persistence, spatial models, spatial statistics

1 | INTRODUCTION

Hotspots are defined as small geographic areas (within a predefined larger region) that exhibit persistent high concentrations of individuals or species (Harcourt, 2017; Possingham & Wilson, 1993). In the three decades since Myers (2008) first introduced the term, the definition of hotspots has expanded and adapted to reflect changes in conservation goals (Briscoe, Maxwell, Kudela, Crowder, & Croll, 2009). Animal hotspots are generally defined as areas with high levels of at least one of the following biological measures: species abundance, richness or endemism; rare, threatened or endangered species; and/or taxonomic distinctiveness (Briscoe et al., 2009; Prendergast, Quinn, et al., 1993). Hotspots are typically designated on a case-by-case basis because patterns vary by species and location; thus, the threshold to differentiate between hotspots and other locations naturally varies (Nelson & Boots, 2011). For example, common definitions of hotspots focus on determining areas with consistent high species abundance (Davoren, 1983; Piatt et al., 2005), richness or biological activity (Sydeman, Brodeur, Grimes, Bychkov, & McKinnell, 2006) or some combination of these (Nur et al., 2012). Hotspots have also been defined as locations where some metric exceeds a predefined threshold, such as the top five percent of the data (Harvey et al., 2013) or locations outside one (Santora & Veit, 2012; Suryan, Santora, & Veit, 2012) or three (Zipkin et al., 2015) standard deviations above the mean of a particular region or area sampled. Such definitions attempt to quantify hotspots (allowing for direct location comparison) as opposed to identifying hotspots using only qualitative criteria, which was common until recently (Mittermeier, Turner, Larsen, Brooks, & Gascon, 1988). The different approaches to identify hotspots have become increasingly complex and may lead to dissimilar or inconsistent results (Araujo, 2014; Daru, Bank, & Davies, 2015; Harvey et al., 2013; Hobday & Pecl, 2000; Orme et al., 2007; Prendergast, Quinn, et al., 1993; Prendergast, Quinn, Lawton, Eversham, & Gibbons, 1993). The consequence of applying different metrics to define hotspots is a lack of congruence across measures and, thus, hotspot locations, culminating in controversy and conflict over long-term conservation efforts (Marchese, 2011; Orme et al., 2007; Prendergast, Quinn, et al., 1993). Such controversies could

potentially be avoided through a transparent statement of objectives at the start of analysis accompanied by a thorough explanation for selecting a specific method or metric.

Waterbird species display extreme variability in habitat use over both space and time (Certain, Bellier, Planque, & Bretagnolle, 2007; Piatt, Sydeman, & Wiese, 2006; Votier et al., 2008). They often exhibit large, patchy aggregations offshore, making it difficult to measure their spatial distributions. As such, the foremost method to determine patterns of waterbird species is to identify locations of persistent aggregation or high use, such as hotspots. Hotspot identification is useful in studies of highly mobile organisms, such as waterbirds, because the likelihood that a survey event of any given location is representative of true abundance at that location is low due to the extreme variability of their distributions (Santora & Veit, 2012). There are many methods to examine the diversity and abundance patterns of open water populations, but locating persistent high-use areas is a frequent first step towards understanding the processes that generate spatial patterns of species distributions and informing effective conservation action (Nelson & Boots, 2011).

For waterbird abundance data, hotspot analyses are typically conducted using one of the following approaches: (1) qualitative analyses (e.g. through mapping abundance); (2) spatial statistics; or (3) classic statistical modelling (parametric or nonparametric) techniques (Tremblay et al., 2009). Historically, areas of high density or concentration were displayed and compared visually, and mapping relative species abundances remains a prevalent conservation tool (Harvey et al., 2013; Tremblay et al., 2009). Yet, qualitative approaches are limited because they often do not reflect temporal changes (i.e. they are simply a snapshot in time), cannot adequately account for aggregations and can be misleading based on how data are collected, classified and presented (Marchese, 2011). As a result, more rigorous quantitative approaches, typically in the form of spatial statistics or generalized linear models (GLMs), were developed. Spatial statistics use data collected in both focal and surrounding locations to identify areas of high use. As their name suggests, these techniques account for spatial patterns in the data (Harvey et al., 2013). In contrast, classic statistical modelling techniques, which use GLM-based frameworks, do not typically consider explicit spatial

correlation in hotspot identification and instead require the use of statistical distributions and a metric or threshold to account for variations in abundance patterns (Oppel et al., 2005; Santora & Veit, 2012; Zipkin et al., 2015). Waterbirds are highly mobile and tend to aggregate in large groups, resulting in highly skewed data with many absences in space and over time. As such, selecting an appropriately skewed statistical distribution to model waterbird data is fundamental to accurately identifying hotspots using statistical modelling approaches (Zipkin, Leirness, Kinlan, O'Connell, & Silverman, 2014).

In this study, we evaluate four quantitative methods to identify waterbird hotspots using data collected in the Great Lakes: kernel density estimation, Getis-Ord G_i^* , hotspot persistence and hotspots conditional on presence. We selected these four techniques because they are commonly used and represent the range of quantitative hotspot estimation approaches that have been employed in waterbird analyses, incorporating spatially explicit processes to varying degrees. Kernel density estimation is perhaps the most well-known and widely used spatial method for identifying hotspots. Kernel density estimation is an interpolation technique that is used to estimate the probability density function of a variable of interest (e.g. abundance) to identify areas of high density (O'Brien, Webb, Brewer, & Reid, 2012; Suryan et al., 2012; Wilson et al., 2009; Wong, Gjerdrum, Morgan, & Mallory, 2014). A less common spatial statistic for detecting hotspots is the Getis-Ord G_i^* statistic (G_i^*), which allows for cluster evaluation within a specified distance of a single point but does not smooth over grid cells (Getis & Ord, 2019; Kuletz, 2018; Santora, Reiss, Loeb, & Veit, 2013). G_i^* analysis is a spatial tool that identifies spatially explicit areas with values higher in magnitude than would be expected due to random chance, independent of the magnitude of abundance (Kuletz et al., 2018; Santora et al., 2013). For the other two models, we adapted GLM-based techniques which have been used to identify waterbird hotspot locations. Hotspot persistence defines hotspots for every unique sampling event and calculates persistence over time (Johnson, Zipkin, O'Connell, & Caldow, 2012; Santora & Veit, 2012; Suryan et al., 2012). Hotspots conditional on presence combines survey data from all sampling events and defines hotspots as locations with a long-term average abundance greater than three times the regional mean, conditional on species presence (Kinlan et al., 2015; Zipkin et al., 2015).

Our objective was to compare consistency across methodologically different, yet commonly used, hotspot analysis techniques for several waterbird species and species groups. Other methods for identifying hotspots exist and may be useful, but we restricted our analysis to techniques that have been used for waterbird analyses. We applied the four hotspot methods to the species data and then performed pairwise correlations with each method and to the mean effort-corrected count data to measure the strength and association between the different approaches. This allowed us to quantify the degree to which the various estimators aligned in their assessments of waterbird hotspots. The results of our analyses can provide insights for more objective and goal-driven hotspot delineation to inform species conservation and research priorities.

2 | MATERIALS AND METHODS

2.1 | Study area & data description

We conducted systematic aerial transect surveys of waterbirds in portions of Lakes Erie, Huron and Michigan, as well as Lake St. Clair during fall, winter and spring seasons from late September 2012 through early June 2014 (Figure 1a, Appendix S1). The data used in our analysis were collected as part of ongoing long-term survey efforts to monitor waterbirds in the Great Lakes. Although not collected for the explicit purpose of comparing hotspot identification techniques, these data provide an excellent case study because of the geographic scope and number of species observed. Transects ranged in length from 3 to 177 km covering approximately 8,000 km within the entire study area. Most of the transects (97%) were surveyed repeatedly with an average number of 10.68 (SD: 3.85) sampling events per transect with approximately 83,000 km flown over the duration of the survey period. We defined a sampling event as a unique year-month-day (survey date) combination within each region of the Great Lakes. Transects were spaced 3.2–5 km apart and flight altitude ranged from 61 to 100 m above the lake's surface. Two observers, one on either side of the plane, recorded every waterbird flock that was detected in the observable portion of the transect (the area not obscured by the plane); observers were not permitted to use binoculars, and thus all detections were made using the naked eye. For each sighting, we recorded the species, flock size (i.e. number of individuals seen), and latitude and longitude (using onboard GPS) on the transect line. For large flocks that covered many square kilometres (i.e. up to 30 km), the location recorded was an approximate to the centre of the flock. Birds were identified to the lowest taxonomic group possible when observers were unable to determine species.

We integrated the data into the open access Midwest Avian Data Center (MWADC), a regional node of the Avian Knowledge Network (AKN), hosted by Point Blue Conservation Science (<http://data.pointblue.org/partners/mwadc/>). In some cases, observational data (e.g. location, species and flock size) were collected separately from effort data (e.g. survey date, location, transect flown, etc.) such that waterbird observations did not include the corresponding transect attribution (23.4% of records). For these records, we used a 1-m buffer to identify the closest transect, matched by survey date, to each observation record. We used data collected on the location of the transect line when available (42.26% of transect lines) and GIS to reconstruct the transect lines from observations in instances when that information was not recorded. Inclement weather and extensive ice coverage necessitated some surveys to be halted prematurely or conducted over a short period of time. We, thus, assumed that instances in which an area was surveyed over multiple consecutive days were a single sampling event. During the survey period, 253 transects were surveyed resulting in 136 unique sampling events.

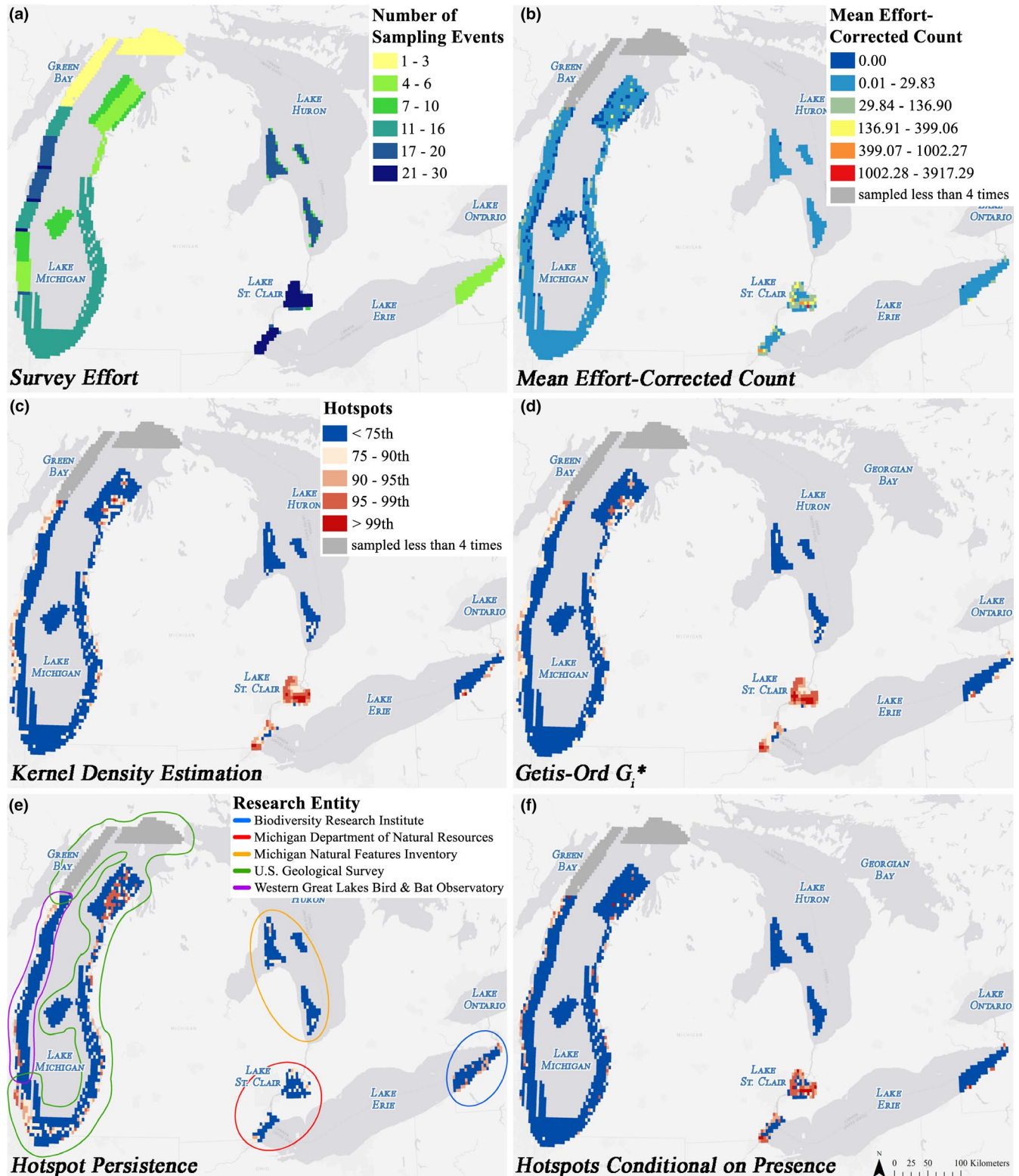


FIGURE 1 (a) Map of the study area showing the number of sampling events per 5×5 km grid cell during the entire survey period. (b) Mean effort-corrected count data for the all-species-combined species group (species list found in Table 1). Potential hotspots (values above the 75% percentile) across all sampled locations for the all-species-combined group as estimated with each of the four hotspot analysis approaches: (c) kernel density estimation, (d) Getis-Ord G_i^* , (e) hotspot persistence, and (f) hotspots conditional on presence. The “Hotspots” legend on panel (c) is used for all four hotspot analysis approach maps (c–f). Grid cells sampled less than four times were excluded from the analysis and are shaded in grey. Note the survey regions are delineated for the hotspot persistence approach (e) because hotspots in this method are calculated relative to other grid cells within these specific regions

TABLE 1 List of species and species groups used in the analysis, including the total number of encounters and total number observed

| Species/ Species Group | Number of Encounters | Number Observed | Species Included |
|------------------------------|-------------------------|-----------------|---|
| Diving/sea ducks | 19,183 | 1,700,311 | Bufflehead <i>Bucephala albeola</i> , canvasback <i>Aythya valisineria</i> , common eider <i>Somateria mollissima</i> , long-tailed duck <i>Clangula hyemalis</i> , redhead <i>Aythya americana</i> , ring-necked duck <i>Aythya collaris</i> , ruddy duck <i>Oxyura jamaicensis</i> , all eiders <i>Somateria</i> sp., all golden-eye <i>Bucephala</i> sp., all mergansers <i>Mergus</i> sp., all scaup <i>Aythya</i> sp., all scoters <i>Melanitta</i> sp., and all unidentified diving ducks <i>Aythya</i> sp. |
| Gulls | 12,233 | 81,399 | Bonaparte's gull <i>Chroicocephalus philadelphia</i> , glaucous gull <i>Larus hyperboreus</i> , great black-backed gull <i>Larus marinus</i> , herring gull <i>Larus smithsonianus</i> , Iceland gull <i>Larus glaucoides</i> , mew gull <i>Larus canus</i> , ring-billed gull <i>Larus delawarensis</i> and all unidentified gulls <i>Laridae</i> sp. |
| Long-tailed duck | 6,011 | 149,542 | Long-tailed duck <i>Clangula hyemalis</i> |
| Mergansers | 4,865 | 95,702 | Common merganser <i>Mergus merganser</i> , hooded merganser <i>Lophodytes cucullatus</i> , red-breasted merganser <i>Mergus serrator</i> , all unidentified mergansers <i>Mergus</i> sp and all unidentified merganser/goldeneye <i>Mergus/Bucephala</i> sp. |
| Scaup | 3,431 | 383,495 | Greater scaup <i>Aythya marila</i> , lesser scaup <i>Aythya affinis</i> and all unidentified scaup <i>Aythya</i> sp. |
| Loons | 2,111 | 4,364 | Common loon <i>Gavia immer</i> , red-throated loon <i>Gavia stellata</i> and all unidentified loons <i>Gavia</i> sp. |
| Common loon | 1,688 | 2,922 | Common loon <i>Gavia immer</i> |

2.2 | Species groups and composition

We recorded over two million individual birds representing 76 unique species in 41,803 observations. We focused our analysis on seven species/species groups: long-tailed duck *Clangula hyemalis*, common loon *Gavia immer*, gulls *Laridae* sp., mergansers *Mergus* and *Lophodytes* sp., scaup *Aythya affinis* and *A. marila*, loons *Gavia* sp., and diving/sea ducks *Aythya* sp., *Bucephala* sp., *C. hyemalis*, *Melanitta* sp., *Mergus* sp., *Oxyura jamaicensis* and *Somateria* sp. (Table 1). We chose these species and species groups (hereafter referred to as species groups) because they were fairly evenly distributed across the study area (i.e. occurred in most lakes with data), with observations in at least 200 grid cells (see Data Standardization in Methods), and were encountered at least 1,000 times during the survey period. The seven species groups used in our analysis comprised 33 species (Table 1) and nearly 90% of all observed birds, including some individuals that could not be identified to species (which were only used in multispecies group analyses). Canvasback was the most abundant bird species observed (i.e. most individuals), but long-tailed duck was encountered most often (Table 1).

We identified potential hotspots for the seven species groups, and then used the data from all species groups to analyse hotspots for an all-species-combined group. Some individual species appeared in multiple groups; for example, long-tailed duck was analysed individually and in the diving/sea duck group. In such instances, an individual species was used only once in the all-species-combined group (i.e. not double counted). Additionally, to maximize data availability, we included some species that did not

fall within an obvious or distinct species group. For example, ruddy duck is included in the diving/sea duck group (although it is not a diving or sea duck) because it is often found with other more typical open water species which dominate our surveys on the Great Lakes.

2.3 | Data standardization

We imposed a 5 × 5 km grid (consisting of 17,746 cells) over the entire Great Lakes region and assigned transects to grid cells based on their spatial locations. We chose this scale because the maximum distance between survey transects was 5 km. Thus, a smaller grid would create a very patchy system of survey effort with many empty cells, whereas a larger size would lump together more data, obscuring fine scale aggregations of species. We segmented all transects using the grid system so that grid cells contained only the portion of the transect that occurred within the cell, such that a cell could contain anywhere from zero to many transect segments. Then, we calculated the total length of the transect segments(s) within a grid cell to determine the number of kilometres flown for all sampling events within each cell. We included in our analysis only those cells which contained a transect of at least 1 km length. The sum of transect lengths within cells ranged from 1 to 16.02 km with an average of 4.69 km (*SD*: 2.16 km). A total of 1,699 of the 1,767 grid cells included in our analysis had bird observations on at least one sampling occasion.

We standardized the observation data within grid cells (Johnson et al., 2012) because the survey effort was unequal and highly

variable across cells within the study area (Figure 1a). We divided the number of observations of a species for the sampling event-grid cell combination by the summed transect length, resulting in a continuous effort-corrected count (Figure 1b). We used data from all sampling events in our hotspot analysis; however, we limited the method comparisons, correlations and hotspot maps to grid cells that contained at least four sampling events, for a total of 1,473 grid cells (83.4% of surveyed cells). Using grid cells with at least four sampling events allowed for analysis across the study region, while minimizing the chances of false hotspot identification due to insufficient data (Figure 1a; Kuletz et al., 2018; Zipkin et al., 2015). To calculate a mean effort-corrected count for each species group in surveyed grid cells, we divided the summed effort-corrected counts in a grid cell (across all sampling events) by the total number of sampling events for that grid cell.

2.4 | Hotspot analysis

2.4.1 | Kernel density estimation

Kernel density estimation is a common method for estimating relative density in animal populations that aggregate and has been used repeatedly to identify waterbird hotspot locations and marine areas in need of protection (Wilson et al., 2009, O'Brien et al., 2012, Suryan et al., 2012, and Wong et al., 2014). This modelling approach converts point data (i.e. effort-corrected counts) into a continuous surface grid reflecting relative densities across all grid cells, where the resulting density of each grid cell is weighted according to the distance from the focal location/grid cell (Wong et al., 2014).

To implement the *kernel density* method, we calculated the midpoint of each grid cell and assigned all effort-corrected counts of the species group (across all sampling events) to the midpoint of the grid cell in which they occurred. We accounted for uneven sampling effort (grid cells were surveyed 1–30 times, Figure 1a) by dividing the summed counts in a grid cell by the total number of sampling events for that grid cell. We used the kernel density tool in the Spatial Analyst extension of ArcGIS 10.3.1 (ESRI, 1992) to estimate bird density, inputting values for both bandwidth and cell size. The bandwidth, or size of the neighbourhood over which the density is averaged, is the amount of smoothing applied to each kernel (Nelson & Boots, 2011). Smoothing allows for abundance prediction in non- (or low-) sampled areas by assuming that neighbours behave more similarly to one another than at locations that are further away. Small bandwidth values may result in fragmented small-scale kernels, leading to underestimation of hotspots, whereas large values result in oversmoothed general kernels, overestimating hotspots (Wong et al., 2014). We selected a 5-km bandwidth for kernel smoothing based on both the geographic extent of the data and the distance between survey transects (Suryan et al., 2012). Kernel density estimation results in a raster, which is a matrix of pixels where each pixel contains a value representing information (e.g. estimated bird abundance; ESRI, 1992). The cell size for the output raster can also affect the interpretation of the kernel estimate: large cell sizes may

result in a blocky raster that is a poor approximation of a continuous surface, and small cell sizes may result in a raster of many cells that is over-fit or takes an inordinate amount of time to calculate (Beyer, 2015). We selected a cell size of 1 × 1 km for the output raster. For each species group, we extracted the mean expected count from the resulting kernel density raster back to the 5-km² grid for comparison with the other methods. Each raster cell was assigned to a corresponding 5 km² grid cell based on its midpoint; we then averaged the density values from all raster cells for each grid cell, where the higher the value, the more likely it is to be a hotspot.

2.4.2 | Getis-Ord G_i^*

The Getis-Ord G_i^* (G_i^*) statistic detects hotspots while also indicating the statistical significance of those hotspots (Kuletz et al., 2018; Santora et al., 2013). The G_i^* technique identifies grid cells whose data points cluster spatially by examining each grid cell within the context of the neighbouring cells (Getis & Ord, 2019). G_i^* differs from kernel density estimation because it incorporates the value of each feature in the context of its neighbours, whereas *kernel density* estimates the neighbours based on the focal feature and then applies a smoothing over those neighbours.

To implement the G_i^* statistic, we again calculated the midpoint of each grid cell and assigned all effort-corrected counts of the species group across all sampling events to the midpoint of the cell into which they occurred. We accounted for uneven sampling effort by dividing the summed effort-corrected grid cell counts by the total number of sampling events for that cell. We built a neighbours list for all grid cells using Rook's case contiguity (i.e. grid cells that share a border), and then used the neighbours list to calculate a row-standardized spatial weights matrix (*spdep* package in R; Bivand, Hauke, & Kossowski, 2018, Bivand & Piras, 2008, R Core Team, 2010). The matrix informs every grid cell's relationship to all other cells in the neighbourhood (Kuletz et al., 2018). We used the effort-corrected counts and the spatial weights matrix to calculate the G_i^* for each grid cell (*spdep* package in R; Bivand et al., 2018, Bivand & Piras, 2008, R Core Team, 2010). G_i^* produces a z-score for each grid cell, where high positive values are statistically significant and indicate the possibility of a local cluster of high species abundance (i.e. a hotspot) that is unlikely due to random chance.

2.4.3 | Hotspot persistence

The hotspot persistence method quantifies the persistence of species counts within individual grid cells (Johnson et al., 2012; Santora & Veit, 2012; Suryan et al., 2012). To implement this method, we first fit a gamma distribution to the effort-corrected continuous species group count data, summed within grid cells, for each unique sampling event (*fitdistrplus* package in R; Delignette-Muller & Dutang, 2015, R Core Team, 2010). We selected the two-parameter gamma distribution (shape and scale) because it can fit a variety of continuous right-skewed data (Bolker, 2014; Dennis & Patil, 2010) and because it has been used before with

this hotspot analysis technique (Johnson et al., 2012). We then assigned a probability to each grid cell based on the fit of the data within the cumulative distribution curve for that sampling event. This allowed us to identify grid cells (for each unique sampling event) with high abundance of the target species group relative to other cells. Within a unique sampling event, we identified grid cells as hotspots if the value of the cumulative distribution for the cell, based on the fit of the gamma distribution, was above the 75th percentile for that sampling event. After identifying which grid cells were categorized as hotspots for every unique sampling event, we calculated the proportion of sampling events in which a grid cell was identified as a hotspot to examine persistence. The final output was the proportion of sampling events, ranging from zero to one, in which a grid cell was considered a hotspot for the target species group. Values of zero indicate the grid cell was never a hotspot. The higher the proportion, the more frequently the grid cell was considered a hotspot, with a value of one indicating the grid cell was a hotspot for all sampling events.

2.4.4 | Hotspots conditional on species presence

The hotspots conditional on presence method calculates the long-term probability that a grid cell is a hotspot for a particular species given observed abundances over time (Kinlan et al., 2015; Zipkin et al., 2015). To implement this method, we fit the effort-corrected count data using a log-normal distribution (*fitdistrplus* package in R; Delignette-Muller & Dutang, 2015, R Core Team, 2010). Because the log-normal distribution does not contain zero in its support, we used only the positive effort-corrected counts. The log-normal is a two parameter (mean and standard deviation), positive, continuous probability distribution characterized by a heavy tail and has been shown to fit waterbird data well because of its flexible shape and ability to fit heavily skewed data (Limpert, Stahel, & Abbt, 2015; Zipkin et al., 2014). We then estimated prevalence in the reference region as the proportion of cells with occurrences for the target species group (at least one individual observed within the cell over all sampling events) relative to the total number of cells surveyed (Kinlan et al., 2015). We defined the reference region as the entire area sampled across the Great Lakes. We then simulated data with a two-part Monte Carlo approach to calculate hotspot locations using the estimated mean and standard deviation from the log-normal distribution (the count component) and the prevalence estimate (the Bernoulli component; Kinlan et al., 2015, Zipkin et al., 2015). We defined a hotspot as a grid cell in which the long-term average effort-corrected count conditional on presence (with $\alpha = 0.05$ threshold) was at least three times the mean of the reference region, also conditional on presence (Kinlan et al., 2015). The resulting values, ranging from zero to one, represent the proportion of simulated sample means that are greater than three times the average count. Values close to zero indicate the grid cell is not a hotspot. Values close to one indicate a high probability that the long-term average abundance in the grid cell is greater than three times the mean of the reference region.

2.5 | Comparative analysis of the methods

Our objective was to determine the degree of congruence among the four methods across species groups and for all-species-combined. We compared methods using only grid cells that were surveyed four or more times. To quantify the consistency among the four approaches in their ability to detect hotspots, we performed a Pearson's product-moment correlation to evaluate the pairwise associations of the four approaches with a Bonferroni adjustment and an alpha level of 0.05 (*Hmisc* package in R; R Core Team, 2010, Harrel, 2012). In addition to comparing the four hotspot analysis methods, we also compared the methods with the mean effort-corrected count using the same correlation test. We analysed the correlation coefficients (ranging from zero to one) to determine associations among the different approaches: the higher the value, the higher the correlation between two methods.

We produced maps for all species groups to visually compare the results of the four hotspot analysis approaches and mean effort-corrected counts (Appendices S2–S9). For the first set of maps, we plotted the values produced for each grid cell using each hotspot analysis technique. Direct visual comparison among the hotspot methods can be difficult because the scale of the results for each method varies (i.e. *kernel density* produces unbounded positive values, G_i^* produces both positive and negative values, and hotspot persistence and hotspots conditional on presence range between zero to one). To resolve this issue, we created a second set of maps for each species group in which we considered a hotspot as any grid cell with a value above the 75th percentile (of all values for that method) and plotted those according to their percentiles.

3 | RESULTS

The highest correlation between methods for all species groups occurred between *kernel density* and G_i^* estimation approaches with a correlation ≥ 0.80 for all species groups except mergansers (Table 2). For mergansers, the correlation between the two explicitly spatial methods was 0.67 and nearly identical to the correlation between G_i^* and the hotspots conditional on presence method. For the other species groups, including all-species-combined, there was much higher congruency between *kernel density* and G_i^* than any other combination of pairwise comparisons (excluding mean effort-corrected data, discussed below; Table 2; Appendices S2–S9). For example, for all-species-combined there was 94% overlap in identification of hot and non-hot grid cells between kernel density estimation and G_i^* (Figure 1c–d). In general, the two other methods were no more similar to one another than to either *kernel density* and G_i^* with correlations between the models that varied by species (Table 2). Kernel density estimation and hotspot persistence showed the lowest correlations (0.03–0.56) for the species groups that we examined. For the all-species-combined group, we found that the four methods identified the same 63% of grid cells as non-hot locations (below the 75th percentile), while approximately 8% of grid cells were identified

TABLE 2 Pearson correlation matrix of pairwise comparisons between the four hotspot analysis methods (kernel density estimation, Getis-Ord G_i^* , hotspot persistence, and hotspots conditional on presence) and mean effort-corrected counts, with a Bonferroni adjustment

| | Kernel density estimation | Getis-Ord G_i^* | Hotspot persistence | Hotspots conditional on presence | Mean effort-corrected count |
|----------------------------------|---------------------------|-------------------|---------------------|----------------------------------|-----------------------------|
| All species/groups | | | | | |
| Kernel density estimation | 1.000 | 0.870 | 0.121 | 0.441 | 0.928 |
| Getis-Ord G_i^* | 0.870 | 1.000 | 0.125 | 0.435 | 0.650 |
| Hotspot persistence | 0.121 | 0.125 | 1.000 | 0.332 | 0.093 |
| Hotspots conditional on presence | 0.441 | 0.435 | 0.332 | 1.000 | 0.375 |
| Mean effort-corrected Count | 0.928 | 0.650 | 0.093 | 0.375 | 1.000 |
| Diving/sea ducks | | | | | |
| Kernel density estimation | 1.000 | 0.874 | 0.160 | 0.467 | 0.929 |
| Getis-Ord G_i^* | 0.874 | 1.000 | 0.167 | 0.458 | 0.655 |
| Hotspot persistence | 0.160 | 0.167 | 1.000 | 0.364 | 0.123 |
| Hotspots conditional on presence | 0.467 | 0.458 | 0.364 | 1.000 | 0.395 |
| Mean effort-corrected Count | 0.929 | 0.655 | 0.123 | 0.395 | 1.000 |
| Gulls | | | | | |
| Kernel density estimation | 1.000 | 0.808 | 0.318 | 0.457 | 0.865 |
| Getis-Ord G_i^* | 0.808 | 1.000 | 0.325 | 0.459 | 0.715 |
| Hotspot persistence | 0.318 | 0.325 | 1.000 | 0.446 | 0.274 |
| Hotspots conditional on presence | 0.457 | 0.459 | 0.446 | 1.000 | 0.443 |
| Mean effort-corrected Count | 0.865 | 0.715 | 0.274 | 0.443 | 1.000 |
| Long-tailed duck (LTDU) | | | | | |
| Kernel density estimation | 1.000 | 0.804 | 0.407 | 0.475 | 0.725 |
| Getis-Ord G_i^* | 0.804 | 1.000 | 0.451 | 0.432 | 0.469 |
| Hotspot persistence | 0.407 | 0.451 | 1.000 | 0.583 | 0.350 |
| Hotspots conditional on presence | 0.475 | 0.432 | 0.583 | 1.000 | 0.495 |
| Mean effort-corrected Count | 0.725 | 0.469 | 0.350 | 0.495 | 1.000 |
| Mergansers | | | | | |
| Kernel density estimation | 1.000 | 0.672 | 0.433 | 0.600 | 0.739 |
| Getis-Ord G_i^* | 0.672 | 1.000 | 0.547 | 0.669 | 0.812 |
| Hotspot persistence | 0.433 | 0.547 | 1.000 | 0.575 | 0.539 |
| Hotspots conditional on presence | 0.600 | 0.669 | 0.575 | 1.000 | 0.778 |
| Mean effort-corrected Count | 0.739 | 0.812 | 0.539 | 0.778 | 1.000 |
| Scaup | | | | | |
| Kernel density estimation | 1.000 | 0.878 | 0.562 | 0.661 | 0.950 |
| Getis-Ord G_i^* | 0.878 | 1.000 | 0.586 | 0.623 | 0.707 |
| Hotspot persistence | 0.562 | 0.586 | 1.000 | 0.686 | 0.469 |
| Hotspots conditional on presence | 0.661 | 0.623 | 0.686 | 1.000 | 0.611 |
| Mean effort-corrected Count | 0.950 | 0.707 | 0.469 | 0.611 | 1.000 |
| Loons | | | | | |
| Kernel density estimation | 1.000 | 0.808 | 0.047** | 0.210 | 0.910 |
| Getis-Ord G_i^* | 0.808 | 1.000 | 0.063 | 0.258 | 0.517 |
| Hotspot persistence | 0.047** | 0.063 | 1.000 | 0.454 | 0.026** |
| Hotspots conditional on presence | 0.210 | 0.258 | 0.454 | 1.000 | 0.136 |
| Mean effort-corrected count | 0.910 | 0.517 | 0.026** | 0.136 | 1.000 |

(Continues)

TABLE 2 (Continued)

| | Kernel density estimation | Getis-Ord G_i^* | Hotspot persistence | Hotspots conditional on presence | Mean effort-corrected count |
|----------------------------------|---------------------------|-------------------|---------------------|----------------------------------|-----------------------------|
| Common loon (COLO) | | | | | |
| Kernel density estimation | 1.000 | 0.800 | 0.027** | 0.049** | 0.060 |
| Getis-Ord G_i^* | 0.800 | 1.000 | 0.032** | 0.075 | 0.087 |
| Hotspot persistence | 0.027** | 0.032** | 1.000 | 0.606 | 0.536 |
| Hotspots conditional on presence | 0.049** | 0.075 | 0.606 | 1.000 | 0.718 |
| Mean effort-corrected count | 0.060 | 0.087 | 0.536 | 0.718 | 1.000 |

Note: Correlations are significant unless otherwise denoted (**) at an alpha level of 0.05. Values above and below of the diagonals are mirror images (gray values are duplicates).

as hotspot locations under all four methods (above the 75th percentile). The remaining 29% of the cells were identified as hotspots by one, two or three of the methods. Loons and common loon were the only two species groups to have insignificant correlations ($\alpha = 0.05$, Table 2). The patterns observed with these two species groups may be due in part to insufficient data availability.

The hotspot persistence approach differed most significantly from the other three methods and had the lowest correlations overall with other methods (Table 2; Figures 1 and 2). Unlike the other methods, the hotspot persistence approach calculates hotspots relative to the survey region, rather than the entire study area (i.e. Figure 1a and e), and also explicitly incorporates temporal variability. For example, in the analysis of the scaup species group, we found that many grid cells in Lake St. Clair were identified as hotspots by all methods except for hotspot persistence (Figure 2; Appendix S7). The counts for scaup were generally quite high in Lake St. Clair relative to other surveyed locations. However, the hotspot persistence method revealed that individual grid cells within Lake St. Clair did not often have high counts on repeated occasions (as evidenced with zeros and other low values in grid cells; Figure 2e). The all-species-combined analysis produced similar results, with 9% of grid cells identified as hotspots by the persistence approach but not by the other three methods (Figure 1b–f; Appendix S2).

Kernel density and G_i^* , which consider space in an explicit manner, are inherently different from hotspot persistence and hotspots conditional on presence, which rely on parametric distributions, as is evident in both the correlations and maps (Table 2; Appendices S2–S9). Hotspot persistence and hotspots conditional on presence tended to select single grid cells as hotspots, whereas kernel density and G_i^* selected small clusters of grid cells as hotspots (Figure 3). In many cases, grid cells that were highly ranked with the hotspots conditional on presence approach, were also highly ranked with kernel density and G_i^* . However, the surrounding grid cells tended to also be highly ranked with kernel density and G_i^* (Figure 3).

Species-specific hotspots for common loon and long-tailed duck occurred in areas identified as hotspots for the corresponding species group (loons and diving/sea ducks, respectively). Common loon observations comprised 67% of the loon group observations (Table 1). A reanalysis of the loon group without common loons did not substantially alter correlations between the different methods

(Appendix S10). Yet, when long-tailed duck data were removed from the diving/sea duck group (9% of the data), G_i^* showed a higher correlation than kernel density estimation with hotspots conditional on presence (although kernel density and G_i^* were still highly correlated with one another; Appendix S10), suggesting that long-tailed ducks may be disproportionately influencing the results of the hotspot analysis for the diving/sea duck group.

Correlations between the mean effort-corrected counts and each of the four methods were highly consistent among the species groups (Table 2). For most species groups, kernel density estimation had the highest correlation with mean effort-corrected counts, followed by G_i^* and hotspots conditional on presence, with hotspot persistence being least similar. Correlations between mean effort-corrected counts and kernel density estimation tended to be fairly high; though this was not true for the mergansers group, which had the highest correlation between mean effort-corrected counts and G_i^* . The only species group to demonstrate its highest correlation between mean effort-corrected count and a GLM-based technique (hotspots conditional on presence) was the common loon. For seven of the eight species groups, mean effort-corrected count had the lowest correlation with the hotspot persistence approach (Table 2).

4 | DISCUSSION

Despite the frequent use of hotspot analyses in management and conservation, we found that the various hotspot analysis approaches resulted in inconsistent identification of hotspots within the Great Lakes waterbird dataset, and that the degree of this inconsistency varied by species group. If conservation and management decisions are based on hotspot analyses, it is important to understand the advantages, limitations, and potential biases in the various approaches to facilitate selection of the most appropriate method to answer the question(s) of interest. Our analysis revealed that methods to estimate hotspots using explicitly spatial approaches, specifically kernel density and G_i^* , produce highly correlated results and can likely be used as surrogates for one another. Not surprisingly, these spatial smoothing methods were often also highly correlated with mean effort-corrected counts. These approaches are likely to be most appropriate when the objective is to identify hotspot locations within

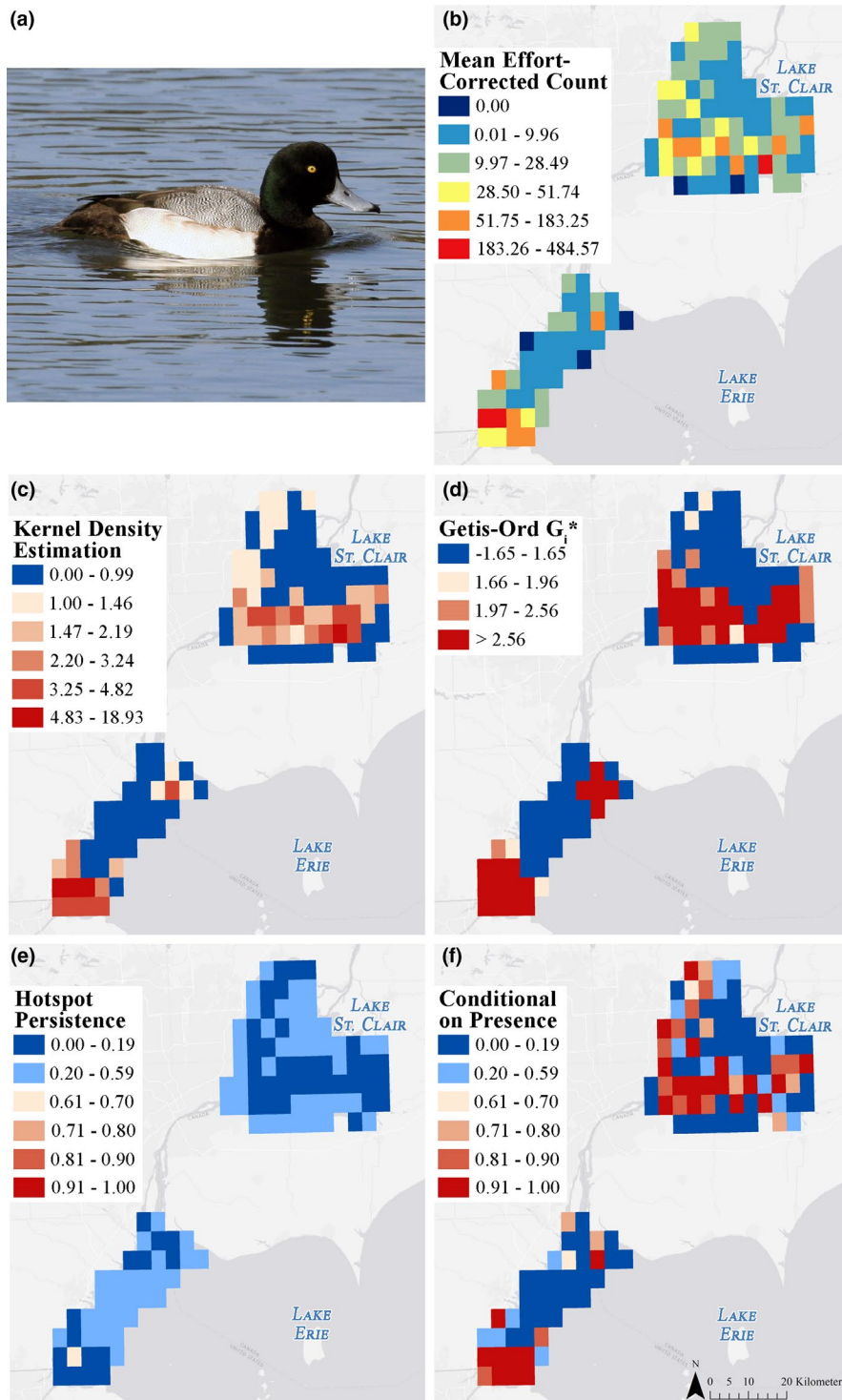
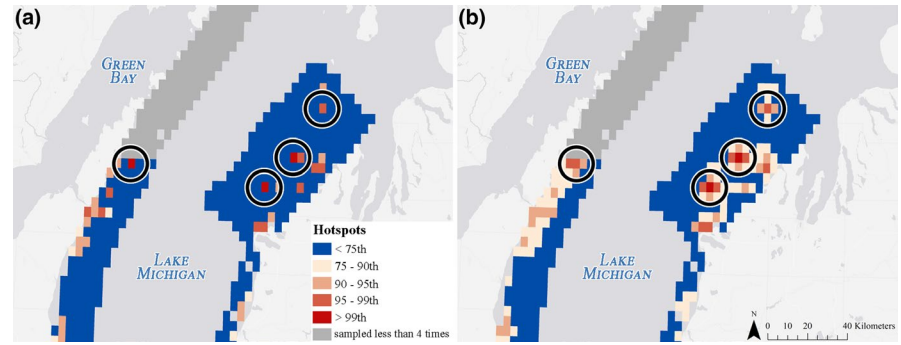


FIGURE 2 Hotspot maps for the scaup species group (greater scaup *Aythya marila* pictured in top left, panel a) in western Lake Erie, including (b) mean effort-corrected counts. The hotspot values are shown on the raw scales for each of the four methods: (c) kernel density estimation, (d) Getis-Ord G_i^* , (e) hotspot persistence, and (f) hotspots conditional on presence

specific temporal constraints (e.g. within a single season). Spatial hotspot techniques might also be useful in the creation and delineation of open water sanctuaries or marine preserves, as these areas often encompass large geographic ranges such that the information of spatial neighbours can be helpful. The other two modelling techniques that we examined produce less consistent results with each other, the spatial methods and mean effort-corrected counts, the degree to which varied by species. The hotspot persistence approach differed the most from the other methods. Hotspot persistence estimates

hotspots based on unique sampling events within survey regions and then identifies whether those areas persist as hotspots over time, while the other three approaches (and mean effort-corrected count data) focus on average abundance over the entire survey period. The hotspot persistence approach (perhaps more so than the other approaches) may thus perform best with a high number of sampling events rather than our minimum of four surveys (Kinlan et al., 2015). Studies constrained to a small geographic range would benefit from the hotspot persistence approach because smaller areas are more

FIGURE 3 Potential hotspots (values above the 75% percentile) in a portion of Lake Michigan for the diving/sea duck species group, highlighting (a) single-cell selection in hotspots conditional on presence method (a GLM-based technique) and (b) clustered cell selection in kernel density estimation (a spatial statistic approach)



likely to be surveyed more often resulting in a high sampling frequency. For example, we found that the Lake St. Clair location was a hotspot under most techniques for many species groups, but the hotspot persistence approach revealed that no grid cell within Lake St. Clair was more important than any other (Figure 1e). The hotspot persistence approach could thus be useful in the assessment of development activities such as offshore wind energy. Analysing data over time would allow regulators and energy developers to determine whether there are specific locations within a predefined spatial area with repeatedly and consistently high abundance, which can be used to minimize risk to wildlife populations.

Our analysis cannot determine which hotspot identification method is most appropriate generally. The best method for any given analysis will depend on the question and study region. *Kernel density* and G_i^* are useful in assessing large areas where waterbirds have been present (with high densities) on at least one occasion. Yet *kernel density* and G_i^* can have difficulty identifying individual grid cells as hotspots, especially at small spatial scales and with heavily skewed data (Harris, 2017; Songchitruska & Zeng, 2010). Both kernel density estimation and G_i^* demonstrated high similarity to the mean effort-corrected count data for almost all species groups. This suggests that effort-corrected count data may be a sufficient surrogate for hotspot techniques in some situations, such as coarse summaries, particularly if one does not plan on including covariate data. The other two methods, hotspot persistence and hotspots conditional on presence, provide fundamentally different hotspot information than a simple summary of mean counts. These techniques are likely to be relatively more conservative in identifying hotspots (e.g. Figure 3), which may be desirable depending on conservation and management priorities.

There is subjectivity in all methods to identify hotspots because arbitrary thresholds are selected to delineate hotspot locations (Harvey et al., 2013). Thus, there is a natural trade-off in the rate of Type I and Type II errors in selecting a threshold level (Kinlan et al., 2015). A high threshold will constrain the number of hotspots and the likelihood that an area is falsely categorized as a hotspot is comparatively low. A low threshold will increase the number of hotspots, possibly including locations that should not be considered hotspots. All four methods we selected incorporate at least one user-determined decision or metric, which can be changed to suit the user (Canadas, Bellier, Planque, & Bretagnolle, 2007; Marchese, 2011) or

may be different across various software implementations (Bivand & Wong, 2016). The bandwidth and cell size must be specified in kernel density estimation and the neighbourhood must be defined in the G_i^* method. For the other two models, the user must decide the level that constitutes a hotspot (i.e. top 25% of cells in the hotspot persistence approach; three times the mean in the hotspots conditional on presence method; Canadas et al., 2007; Zipkin et al., 2015). The production of hotspot maps is also subjective (Carolan, 2015). We chose to classify and colour hotspots as the top 25% of grid cell values for the four methods (Figure 1c-f). However, a different threshold could produce maps that appear more or less similar (particularly when evaluating methods on their original scales; e.g. Figure 2) and possibly lead to different conclusions on the congruency of the four approaches, illustrating the importance of examining quantitative correlations between the methods.

A combination of methods using an integrative approach that synthesizes results, either within a single analysis or post hoc, could lead to greater consistency (Marchese, 2011) and reduce the impacts of survey bias. Nur et al. (2012) found that the use of multiple criteria (when defining a hotspot within a single method) prevents misidentifying areas that may be overlooked when using only a single criterion. An integrated model combining a spatial method with a GLM-based technique could provide a desirable balance between the potential for overestimation from spatial approaches and the more conservative non-spatial models. As waterbird data are often sparse or limited, an integrated approach will also help to identify hotspots in locations with possible data gaps and could be implemented by averaging standardized values from each model (e.g. Figure 4). Such an integrated model would be beneficial in scenarios where both spatial coverage and temporal consistency are important.

Inconsistency in sampling required us to exclude data from areas that were sampled less than four times, although it is possible that even areas included in our analysis were not sampled enough for accurate hotspot detection (Hazen, 2009; Zipkin et al., 2015). Excluding grid cells with few visits may remove a substantial portion of available data, which is undesirable in any analysis. However, inclusion of low sampled grid cells could lead to false positives in the identification of hotspots, given the highly mobile and aggregated nature of waterbirds (Kuletz et al., 2018). For example, a specific grid cell that was surveyed only one time in our study had an effort-corrected count of almost 900 individuals (all-species-combined).

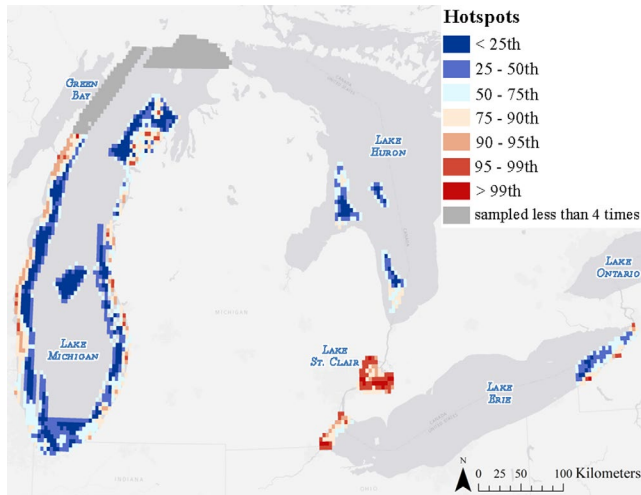


FIGURE 4 Potential hotspots from an integrated hotspot modelling approach across all sampled locations for the all-species-combined species group (species list found in Table 1). We combined two hotspot analysis techniques, one spatial statistic approach (Getis-Ord G_i^*) and one GLM-based technique (hotspots conditional on presence). The results shown in this map were produced by calculating the average percentile of the two selected methods for all grid cells, resulting in a value from zero to one where high values closer to one are more likely to be hotspots than low values closer to zero. Grid cells sampled less than four times were excluded from the analysis and are shaded in grey. We binned the percentiles for mapping purposes and consider a species hotspot as any grid cell with an average value above the 75th percentile

Had we included cells that were surveyed less than four times, this cell would have been designated as a hotspot by all four methods. Yet, it is difficult to assess the validity of this designation without repeated sampling. For some rare species, though, it may be necessary to reduce the threshold of required survey events to maximize data use.

Variation in hotspot identification across the methods may be due in part to scale. Scale is important to several aspects of hotspot identification: (1) the scale at which the data are collected, (2) the spatial scale at which the data are analysed, and (3) the scale at which management decisions will be made. It is important to account for potential discrepancies in the geographic scale of population-level processes and the resolution of different datasets when deciding the spatial scale for analysis. The 5-km² grid we used is a fine-scale resolution to identify and map hotspots and may result in less consistency across methods than a larger, coarser grid (Daru et al., 2015). The distance between and design of transect surveys can directly affect the outcome of hotspot analyses, and we, therefore, recommend simultaneous and thorough consideration of survey design and analysis prior to data collection. Survey bias, the presence of spatial patterns in survey effort, is a ubiquitous concern when delineating hotspots (Prendergast, Wood, Lawton, & Eversham, 2015), and its effects may lead to different results depending on the analytical methods used.

The four approaches used in this study were selected because they have been previously used to identify areas of high-use for waterbird species in other studies. However, variations of these models (e.g. selecting a different threshold cut-off or using a metric other than the mean, such as standard deviation) as well as other potential hotspot methods could be used to model abundance data. For example, cluster analysis models that have been developed for monitoring crime rates or traffic accidents and patterns, which have not yet been applied to wildlife data, may provide more nuanced approaches to hotspot analyses (Hengl, 2014; Tango, 1995). We used R and ArcGIS to run our analysis; however, other software packages may also be useful for hotspot modelling. For instance, SaTScan is free software developed to detect disease clusters by analysing spatial, temporal and/or space-time data (Kulldorf, 2006). The platform can run different types of models (such as normal, ordinal and exponential models, as well as those we implement in this paper) and adjust for underlying spatial inhomogeneity as part of the default software features. We expect that continued software and model development will allow for advances in hotspot analysis methods.

Hotspot analysis is a first step in understanding species distribution patterns, but it is often equally or more important to determine why certain areas contain persistent aggregations of waterbirds. The use of mechanistic or associative models with covariates that help explain and elucidate hotspots should be considered in those cases where knowledge of the system and adequate covariate data exist (e.g. Nur et al., 2012). We did not include environmental variables (e.g. bathymetry, surface temperature, ice coverage, etc.) or seasonality in our hotspot analysis, although they most certainly play an important role in explaining the distribution and abundance patterns of waterbirds (Nur et al., 2012; Suryan et al., 2012). Although excluding covariates does not affect our model comparison results, it precludes understanding why certain locations are identified as hotspots. Some environmental variables, such as habitat suitability and food availability, are critical to discerning species behaviours and patterns and are occasionally used as proxies for hotspots when data are limited (Shirkey, 2002; Briscoe et al., 2009; Folmer, Olff, & Piersma, 1999; Hyrenbach et al., 2015). However, challenges arise with incorporating environmental variables that are dynamic (e.g. ice cover or temperature), making identification of static hotspot locations relative to environmental variables difficult (Briscoe et al., 2009; Marchese, 2011) and perhaps less useful for certain management-related questions. Waterbird hotspots may not be fixed locations, and may vary by season, annually, or on even longer time frames. Seasonal variability in waterbird species is an important factor that we did not consider in our analysis; abundances can fluctuate during migration or at overwintering locations and shifts in distributions may occur even within seasons (Suryan et al., 2016).

Survey methods and modelling techniques have improved over time, but waterbird species are highly mobile, making the identification of priority areas difficult (Arcos, Hauke, & Kossowski, 2013; Harvey et al., 2013; Marchese, 2011). Through our study, we demonstrate that delineating hotspots is often subjective, as different

analysis techniques and thresholds can produce varying results. Regardless of their drawbacks, hotspot analyses are likely to remain an important tool for conservation because of their relative ease to implement. Thus, the inconsistencies we found in our comparisons necessitates attention by conservation practitioners. Researchers should clearly identify conservation and management goals to select the most appropriate analysis method(s). This, along with incorporation of covariates, will allow hotspot analyses to be both useful and meaningful. Conservation and management decisions on hotspots are often long-lasting and should be done carefully and with full understanding of model limitations.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.rs776p3>) and the Midwest Avian Data Center, a regional node of the Avian Knowledge Network, hosted by Point Blue Conservation Science (<http://data.pointblue.org/partners/mwadc/>). The data and code to run analyses are also available on GitHub (<https://zipkinlab.github.io/>).

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AUTHORS' CONTRIBUTIONS

A.L.S. and E.F.Z. conceived the ideas, analysed the data and led the writing of the manuscript; B.G. and E.M.A. contributed to the development of the methodology; K.P.K., D.R.L., M.J.M., W.P.M., and K.A.W. designed the surveys and collected the data; L.S. combined datasets and provided data management & G.I.S. support; M.L.L.

provided project oversight and management. All authors contributed to the drafts and gave final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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