Fine-scale acoustic telemetry reveals unexpected lake trout, *Salvelinus namaycush*, spawning habitats in northern Lake Huron, North America

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Abstract
Previous studies of lake trout, *Salvelinus namaycush*, spawning habitat in the Laurentian Great Lakes have used time- and labour-intensive survey methods and have focused on areas with historic observations of spawning aggregations and on habitats prejudged by researchers to be suitable for spawning. As an alternative, we used fine-scale acoustic telemetry to locate, describe and compare lake trout spawning habitats. Adult lake trout were implanted with acoustic transmitters and tracked during five consecutive spawning seasons in a 19–27 km² region of the Drummond Island Refuge, Lake Huron, using the VEMCO Positioning System. Acoustic telemetry revealed discrete areas of aggregation on at least five reefs in the study area, subsequently confirmed by divers to contain deposited eggs. Notably, several identified spawning sites would likely not have been discovered using traditional methods because either they were too small and obscure to stand out on a bathymetric map or because they did not conform to the conceptual model of spawning habitat held by many biologists. Our most unique observation was egg deposition in gravel and rubble substrates located at the base of and beneath overhanging edges of large boulders. Spawning sites typically comprised <10% of the reef area and were used consistently over the 5-year study. Evaluation of habitat selection from the perspective of fish behaviour through use of acoustic transmitters offers potential to expand current conceptual models of critical spawning habitat.

Keywords
Laurentian Great Lakes, positional acoustic telemetry, spawning habitat selection, spawning reefs, VEMCO positioning system

1 | INTRODUCTION

Restoring self-sustaining lake trout, *Salvelinus namaycush*, populations in the Laurentian Great Lakes has been a management goal since the late 1950s, after basin-wide collapse of most populations as a result of overfishing and predation by invasive sea lampreys, *Petromyzon marinus* (Hansen, 1999; Muir, Krueger, & Hansen, 2012). Despite annual stocking of hatchery-reared juvenile lake trout since the 1970s (Hansen, 1999) and a successful sea lamprey control programme that has reduced sea lamprey abundance in the upper Great Lakes by about
90% (Smith & Tibbles, 1980), maintenance of most populations outside of Lake Superior continues to depend on stocking. The specific reasons for the failure of lake trout to establish self-sustaining populations are not fully understood (Krueger & Ebener, 2004), but possibly involve several bottlenecks (Bronte et al., 2003), including excessive predation by exotic species (He et al., 2012; Krueger, Perkins, Mills, & Marsden, 1995), thiamine deficiency in eggs and fry (Riley, Rinchard, Honeyfield, Evans, & Begnoche, 2011) and impaired spawning behaviour and spawning site selection in hatchery-reared fish (Bronte et al., 2003).

The possibility that recruitment failure may occur between egg deposition and first year of life has prompted numerous studies to define lake trout spawning habitat in the Great Lakes (Fitzsimons, 1994; Marsden, Casselman, et al., 1995; Thibodeau & Kelso, 1990). Methods used to survey lake trout spawning habitat have included side-scan sonar (Edsall, Holey, Manny, & Kennedy, 1995; Edsall, Poe, Nester, & Brown, 1989), habitat surveys with divers (Claramunt, Jonas, Fitzsimons, & Marsden, 2005; Kelso, MacCallum, & Thibodeau, 1995; Marsden, 1994; Marsden, Ellrott, Claramunt, Jonas, & Fitzsimons, 2005; Marsden & Krueger, 1991), underwater photography/videography (Nester & Poe, 1987), remotely operated vehicles (Edsall et al., 1995; Janssen et al., 2006) and submarine (Edsall & Kennedy, 1995; Manny & Edsall, 1989). Most habitat studies in the Great Lakes have focused on sites historically reported by commercial fishermen to have supported high densities of adult lake trout during the autumn spawning season (Claramunt et al., 2005; Edsall & Kennedy, 1995; Marsden et al., 2005; Wagner, 1982). In addition, researchers in the Great Lakes have drawn inferences about what comprises suitable lake trout spawning habitat from studies in small inland lakes (Callaghan, Blanchfield, & Cott, 2016; Ellrott & Marsden, 2004; Gunn, Conlon, Kirk, & McAughey, 1996; Martin, 1957; McAughey & Gunn, 1995; Sly & Evans, 1996), where spawning occurs at shallow nearshore sites where it is easier to visually observe fish behaviour than spawning sites in the Great Lakes. However, what constitutes adequate habitat in small lakes may not be appropriate for the Great Lakes given their larger size, and the high energy wind and wave conditions associated with nearshore sites.

Lake trout spawning has been observed on rocky substrates at depths ranging from about 0.3 to 20 m, depending largely on the surface area of a given lake (Fitzsimons, 1994), and historically may have occurred at depths of 80 m or more in the Great Lakes (Marsden, Casselman, et al., 1995). Spawning substrate has most commonly been described as layered, rounded or angular, rubble, cobble and boulders (~4 cm to >100 cm in diameter) with at least 30 cm of sediment-free interstitial space to protect eggs from predation and dislodgment (Fitzsimons, 1994; Marsden, Casselman, et al., 1995). Reported spawning sites have often been associated with steep slopes (5–45°), which may serve to accelerate currents, provide juveniles with access to deep-water habitat when they leave spawning reefs (Bronte, Selgeby, Saylor, Miller, & Foster, 1995) or act as an aggregating feature for spawning adults (Marsden, Casselman, et al., 1995). Surficial substrate characteristics appear to be similar between the Great Lakes and inland lakes, although studies in the Great Lakes have emphasised the importance of larger substrate sizes and deep interstitial spaces (Jude, Klinger, & Enk, 1981; Kelso et al., 1995; Marsden & Krueger, 1991; Marsden, Perkins, & Krueger, 1995; Marsden et al., 2005; Nester & Poe, 1987) compared to smaller lakes (Callaghan et al., 2016; Gunn et al., 1996; Royce, 1951; Sly & Evans, 1996).

Despite decades of research into Great Lakes lake trout spawning habitat, why some habitats are used for spawning while other seemingly suitable habitats are not is poorly understood. Little progress has been made towards developing a conceptual model of critical spawning habitat beyond the requirement for rocky substrates with deep, sediment-free interstitial spaces, located along a steep slope (Marsden, Casselman, et al., 1995). We posit four possible explanations for this lack of progress. First, most putative lake trout spawning sites in the Great Lakes have not been verified by direct observation of reproductive end products (i.e., eggs or fry) or spawning activity. Indeed, Thibodeau and Kelso (1990) compiled an extensive list of putative lake trout spawning sites in the Great Lakes, but noted that only 28 of 812 (3.4%) were associated with direct evidence of spawning. Second, lake trout spawning habitats in the Great Lakes have likely been studied at too coarse a spatial scale. Spawning reefs often contain large amounts of seemingly suitable spawning substrate, but studies have found that lake trout may select only a small portion of available substrate for spawning (Kelso, 1995; Marsden & Krueger, 1991). Third, research has tended to focus on habitats that are presumed by researchers to be high-quality sites based on preconceived ideas about what characteristics comprise suitable spawning habitat (Edsall et al., 1989; Ellrott & Marsden, 2004; Flavelle, Ridgway, Middel, & McKinley, 2002; Manny & Edsall, 1989; Marsden et al., 2005). This type of sampling bias may limit our understanding as to what habitat characteristics are attractive to spawning lake trout. Moreover, even presumed expert observers have difficulty accurately predicting spawning sites based on visual inspection of habitat characteristics (Gunn et al., 1996). Lastly, observations of spawning on habitats that do not conform to preconceived models of suitable habitat have largely been dismissed as unique or abnormal behaviour (Beauchamp, Allen, Richards, Wurtsbaugh, & Goldman, 1992) when in fact such behaviours may represent adaptive phenotypic plasticity.

Identifying locations of gamete deposition is a necessary first step in expanding conceptual models of lake trout spawning behaviour and habitat in the Great Lakes. Identifying lake trout spawning habitat in the Great Lakes has been difficult due in part to the large size of the lakes, the logistics of working in dangerous autumn lake conditions and time-consuming and labour-intensive survey techniques required. However, recent advances in wireless positional acoustic telemetry have provided researchers with novel opportunities to remotely study the fine-scale behaviour of fishes and other aquatic organisms over relatively large spatial areas. Here, we used a fine-scale acoustic telemetry array (i.e., 2D positions accurate to within 5–10 m) to determine precise locations of spawning activity in a 19–27 km² region of the Drummond Island Refuge, in northern Lake Huron. This site was selected because surrounding waters have experienced dramatic increases in wild reproduction since 2002. Parental stock, and relative abundance of wild juveniles, has increased significantly based on assessment monitoring...
(He et al., 2012; Riley, He, Johnson, O’Brien, & Schaeffer, 2007), and currently more than 50% of the adult spawning population are wild-bred fish (He et al., 2012).

Our objective was to use a fine-scale acoustic telemetry array to locate, describe, and compare key critical spawning habitats in the Drummond Island Refuge over a 5-year period. We hypothesised that discrete areas of reefs used for spawning (i.e., egg deposition) could be discerned based on the relative distribution and abundance of fish positions in the acoustic telemetry array.

2 | MATERIAL AND METHODS

2.1 | Study animals

Adult lake trout (N = 390; mean ± SE length = 689 ± 3 mm) were implanted with V16-6H transmitters (VEMCO; Halifax, NS, Canada) just prior to the autumn 2010 and 2011 spawning seasons (Binder, Riley, et al., 2016). The tagged trout were captured within 5 km of the study site, in nets tended by the Chippewa Ottawa Resource Authority (using gill nets) and a local commercial fisher (using trap nets). Tagging occurred in August–October 2010 and September–October 2011 (Binder, Riley, et al., 2016). Transmitters broadcasted a uniquely coded acoustic signal at random intervals between 50 and 130 s and had a battery life of about 5 years. Slightly more than half of the transmitters (N = 201) contained a pressure sensor, which reported swimming depth at time of detection. The transmitters were divided as equally as possible among hatchery-reared and wild males and females (Binder, Riley, et al., 2016).

2.2 | Fine-scale acoustic telemetry

This study made use of the VEMCO Positioning System (VPS) to track fine-scale movements of acoustically-tagged adult lake trout in an area along the south shore of Drummond Island. The area was suspected, based on capture of mature adults during the spawning season, to contain one or more important spawning sites. The premise of the VPS is that simultaneous detection of a single acoustic transmission by three or more acoustic receivers allows the location (e.g., <10 m precision) of transmitters (at time of transmission) to be estimated using the principle of time difference of arrival (TDOA), in a process known as hyperbolic positioning (Smith, 2013).

A VPS receiver array was deployed at the study site each autumn (August through November) between 2010 and 2014 (Figure 1). At the time of writing, the VPS arrays used in this study were the largest fine-scale positional telemetry arrays ever deployed, ranging from 108 receivers in 2010 to 151 receivers in 2011 (VR2W receivers; VEMCO), and covering an area ranging from 19 to 27 km² (Table 1). The spatial coverage of the arrays changed between 2010 and 2012, but remained the same between 2012 and 2014. The 2011 array was the same as the 2012–2014 arrays, except that it also covered the same area to the east of a large reef (named “Big Shoal” on navigation charts) with emerging substrate that largely isolated the area acoustically from the main array. At the end of each spawning season (i.e., mid to late November), receivers were retrieved and detection data were downloaded and sent to VEMCO for processing.

Calculation of positions from raw detection files was done by VEMCO using proprietary software. Briefly, position estimates were based on TDOA of each transmission at a minimum of three and a maximum of 6 receivers with synchronised clocks (maximum was set by the manufacturer). Positions for transmissions detected on more than six receivers were estimated using data from the first six receivers (hypothetically the six closest receivers) that detected a transmission based on linear time-corrected detections. A weight-averaged position was then calculated based on all three-receiver combinations among the up to 6 selected receivers, and an estimate of the relative error sensitivity of each calculated position (horizontal position error; abbreviated “HPE”) was provided (Smith, 2013).

2.3 | Fine-scale acoustic telemetry analysis

Potentially important lake trout spawning sites in our VPS array were identified by mapping the relative distribution of fish positions across the VPS array. Mapping was accomplished using a custom R function (Data S1) that divided the study site into a grid of equally sized cells and then calculated: (i) number of unique fish IDs (i.e., unique
TABLE 1  Annual characteristics of the Drummond Island acoustic telemetry study, including number of lake trout tagged, number of receivers used and area of the deployed VEMCO Positioning System (VPS) acoustic telemetry array, estimated start of the spawning season, last day of operation, number of lake trout detected and total number of positions analysed

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<td>NA</td>
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<tr>
<td>No. of receivers in VPS array</td>
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<td>151</td>
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<td>140</td>
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<td>25</td>
<td>25</td>
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<td>02 Oct</td>
</tr>
<tr>
<td>Last day of array operation</td>
<td>08 Nov</td>
<td>15 Nov</td>
<td>13 Nov</td>
<td>19 Nov</td>
<td>17 Nov</td>
</tr>
<tr>
<td>No. of lake trout detected</td>
<td>112</td>
<td>182</td>
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<td>160,609</td>
<td>116,088</td>
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<td>322,333</td>
</tr>
</tbody>
</table>

*Estimated using change-point analysis on mean swimming depth of male lake trout (see Binder, Riley, et al., 2016).

transmitter identification number) positioned within each cell, (ii) total number of positions in each cell and (iii) sum of the number of unique fish positioned in each cell during user-defined time intervals (e.g., 1-hr time intervals) in the time series (i.e., repetitive positions for a given fish ID within the same grid cell and time interval were scored as a single position). The latter two calculations were intended to represent level of activity within a cell and were used as a surrogate for total relative time spent within a given cell summed across all fish. The unique fish by time interval calculation (calculation 3 above) is useful in replacing number of positions as a measure of time spent within a cell in cases where temporal or spatial heterogeneity in positioning probability is likely to significantly bias the spatial distribution of positions returned by the VPS (e.g., aggregation of tagged fish on spawning sites can cause a high rate of destructive code collision, resulting in lower probability of positioning an individual tag transmission at those locations, relative to other less-used areas of the array (Binder, Holbrook, Hayden, & Krueger, 2016). Outputs of the custom function included comma-separated values (.csv) text files containing the calculated values for each grid cell, heat map image files depicting the spatial variation in each measure and a keyhole markup language (.kml) file for viewing the heat maps as overlays in Google Earth.

Our analyses used a grid cell size of 20 × 20 m and a time interval of 1 hr. Both variables were selected based on our initial analysis of VPS positioning performance and were meant to be conservative. Grid cell size was selected based on the measured VPS horizontal position error (HPEm; i.e., linear distance between the VPS position and true GPS location) of between 29 and 46 (depending on year) stationary transmitters scattered throughout the VPS arrays for the duration of each deployment. Mean ± SE measured HPEm of the stationary transmitters was 5.81 ± 0.01 m, and 90% of HPEm values were <12.4 m. Positioning probability in our VPS arrays varied both spatially and temporally (Binder, Holbrook, et al., 2016). However, use of a 1-hr time interval allowed for much lower positioning probabilities than were typically observed during our study. For example, with an average of 40 transmissions per hour for each fish with a transmitter (mean transmission delay was 90 sec), positioning probability would have been <2.5% for a fish that was present in the grid not to have been positioned at least once during that 1-hr interval. In 2011 and 2012, some receivers located in heavily used areas of the array experienced memory saturation before they were retrieved (Binder, Holbrook, et al., 2016). This issue likely biased results in those years by underestimating the relative attractiveness of the most heavily used areas compared to other less-used areas of the array. However, given that memory saturation was confined to heavily used areas, it is unlikely that this bias severely affected our ability to estimate relative habitat use in those years.

VEMCO Positioning System data were collected for up to 3 months each year, but this analysis focused on position data that were collected during the spawning period. The start of the spawning period for each year was estimated statistically based on the changing behaviour of male lake trout using change-point analysis (Binder, Riley, et al., 2016), which moved from deep offshore water to shallow nearshore spawning reefs at the start of the spawning period (Table 1). The behaviour of males was used to estimate the start of the spawning season because male lake trout tend to arrive first on spawning reefs and are generally present in greater numbers than females (Bronte et al., 2007; Muir, Blackie, Marsden, & Krueger, 2012). Given the spatial resolution of our analysis (i.e., 20-m resolution), no attempt was made to filter the data to exclude positions with potentially high sensitivity to error (i.e., positions with high HPE). Ninety per cent of estimated positions with known location had <12.4 m of horizontal position error (95% had <21 m of error); therefore, we concluded that including positions with potentially high HPE would have negligible effect on our interpretation of spatial habitat use patterns.

2.4 Verification of spawning and habitat characteristics

Areas identified as potential spawning sites based on acoustic telemetry position data were verified to have been used for spawning via visual observation of deposited eggs by scuba divers. Divers searched for eggs by lifting rocks and fanning the interstices with a hand to suspend deposited eggs in the water column and took multiple scaled underwater photographs of spawning substrate at each site, which were later used to characterise substrate size and cleanliness. Substrate size was categorised based on a modified Wentworth scale recommended for use in lake trout spawning habitat studies (Marsden, Casselman, et al., 1995). Multiple measures of interstitial depth were also made at each site using a rigid ruler.

Spawning site depth and bathymetric slope were estimated from high-resolution multibeam surveys (Reson Seabat 7101; operating at 240 kHz with 511 beams) conducted in 2010 and 2011. Processed
multibeam data were used to produce a high-resolution bathymetric map with a vertical resolution of approximately 1.25 cm and a horizontal resolution of 1 m. Slopes were estimated for each 20 m grid by determining the angle in degrees between the high and low points in each grid cell.

2.5 | Statistical analyses

Total activity was compared among spawning reefs (delineated based on bathymetry) each spawning season using one-factor repeated-measures ANOVAs ("aov"; \( \alpha = .05 \); R Project Statistical Software, version 3.2.2). The response variable in the ANOVAs was number of 1-hr intervals each fish was detected on each reef (hereafter "fish-1-hr intervals"), which was first square-root-transformed (0.1 was added to each value to accommodate zeros in the data) to improve normality of residuals. Reef was the fixed factor in the ANOVAs, and fish ID was the repeated measure. Where repeated-measures ANOVAs indicated a significant difference, pairwise comparisons with paired t tests (\( \alpha = .05 \)) were performed to determine which reefs differed significantly from one another ("pairwise.t.test"; R Project Statistical Software, version 3.2.2). P-values were adjusted using the Bonferroni correction to compensate for the increased chance of type 1 errors when making multiple comparisons.

Among-season consistency in the spatial pattern of activity on each reef was compared using Pearson’s product moment correlation ("cor.test"; \( \alpha = .05 \); R Project Statistical Software, version 3.2.2). The variable compared was mean number of fish-1-hr intervals (all fish) in every grid cell of each reef; 2014 was used as the baseline against which other years were compared. 2010 was not included in the among-season consistency analysis because array coverage over the spawning reefs differed from that in 2011–2014.

3 | RESULTS

3.1 | Identification of putative lake trout spawning sites

Fine-scale acoustic telemetry revealed areas of lake trout aggregation (i.e., interpreted here as putative spawning sites) on at least five reefs in the VPS array (Figure 2a). The greatest number of fish were positioned on Horseshoe Reef (HR) and Boulder Alley (BA). Between 66% and 73% of all fish positioned in the VPS array during the spawning period each year were positioned on HR, the reef with the greatest number of fish positions. Slightly higher proportions of fish than on HR were positioned each year on BA (between 71% and 84% of all fish), and slightly fewer were positioned on Big Shoal (BS; between 51% and 68% of all fish) and Scammon Shoal (SS; between 43% and 64% of all fish; Figure 3). Of the five identified putative spawning reefs (Figure 2a), Deep Reef (DR) received the fewest number of positioned fish (Figure 3; between 25% and 40% of all fish). Other potential spawning locations were visible in the telemetry data (e.g., area SE of BA, N-S line of bathymetry ESE of HR; Figure 2a), but they were not investigated further because time available for survey was limited and the level of activity on these sites was low compared to the five spawning reefs described above.

The most highly used reef in the array, in terms of activity level, was HR. Mean number of fish-1-hr intervals (a surrogate for relative time spent in each grid cell; Figure 2b) identified putative spawning sites with greater spatial precision than proportion of fish positioned (Figure 2a), particularly on HR where relatively high numbers of fish were positioned in most grid cells, but positions were heavily focused at the two northern tips. Mapping mean number of fish-1-hr intervals across the entire array identified three major “hotspots” of activity, two on the northern tips of HR and another in the northwest corner of SS; note that the activity hotspots on the west arm of HR and SS were quite small (Figure 2b), demonstrating the unique ability of positional acoustic telemetry to identify hotspots of behaviour. Nonetheless, high levels of activity on HR and SS tended to obscure activity levels on the other three putative spawning reefs when fish-1-hr intervals...
were mapped. Therefore, to identify the most likely spawning sites on each reef, it was necessary to map mean number of fish·1-hr intervals for each individual reef separately (Figure 4).

Use of HR among tagged fish was significantly greater than on all other reefs (Figure 3; Table 2), and use of SS and BA was significantly greater than BS and DR (Figure 3; Table 2). On HR, the mean number of fish-1-hr intervals was about four times greater than on any other reef, with 63 ± 9% of all spawning reef-related fish·1-hr intervals each year occurring on HR (Figure 3). Lake trout showed about 75% fewer fish·1-hr intervals on BA and SS (16 ± 3% and 14 ± 5% of spawning reef-associated activity) and the lowest number of fish-1-hr intervals on BS and DR (4 ± 2% and 2 ± 1% of spawning reef-associated fish-1-hr intervals). Interestingly, the 4 to 16 times fewer fish-1-hr intervals on BA and BS, as compared to HR, occurred despite nearly equal numbers of fish being detected on the three reefs each year (Figure 3). Number of fish-1-hr intervals differed significantly between BS and DR during the first three years of the study (Table 2), but this result may have been biased by differences in array coverage (i.e., less spatial coverage in 2010 and less temporal coverage in 2011 and 2012 due to receiver memory saturation).

Activity on all 5 putative spawning reefs was highly localised to relatively small, discrete patches of habitat. Between 48% and 84% (depending on year and reef) of all fish-1-hr intervals for each spawning reef occurred in the top 10% of ranked grid cells. These discrete hotspots of activity on each reef were consistent among years (Figure 4). Spatial distributions of fish-1-hr intervals during 2011, 2012 and 2013 were moderately to highly correlated with the spatial distribution of fish-1-hr intervals in 2014 on all reefs (showing consistency among years; Table 3). HR and BA showed the highest degree of spatial correlation among years, with a mean $r = .83$ and .87 respectively followed closely by SS with a mean $r = .73$. The lowest degree of spatial correlation among years occurred on the two least-used spawning reefs, DR and BS (mean $r = .57$ and .49 respectively; Table 3).

### 3.2 Verification of spawning and habitat characteristics

While not quantified, observations of large numbers (e.g., dozens to hundreds of eggs per m²) of deposited lake trout eggs in the substrate at each activity hotspot (two hotspots on HR) on the five putative lake trout spawning reefs (Figure 3) confirmed that spawning occurred at these sites. Egg surveys conducted annually by divers between 2011 and 2014 on HR and SS and between 2012 and 2014 at BA and DR verified that spawning occurred every year at these sites. Similarly, egg deposition was confirmed at the hotspot on BS in 2012 and 2013, but this site was not adequately surveyed in 2014 to assess whether spawning occurred there that year. Extensive egg surveys by divers on HR and SS suggested that egg deposition was limited to areas of the reefs with high levels of activity. A sixth reef (“Unused” on Figure 1) was surveyed by divers in 2012 because it had similar depth and bathymetric features to the primary spawning site on the east arm of HR. Divers found surficial substrate characteristics similar to that used by lake trout on HR, but saw no evidence that the site was used for spawning. Subsequent surveys of this site in 2013 and 2014 indicated that this site was not used by lake trout in those years either.

Physical habitat characteristics varied widely among the six confirmed spawning sites (Table 4). Surficial substrate at spawning sites on HR and SS consisted of a mixture of clean gravel and rubble. Gravel and rubble substrate was also used for spawning at BA, but the spawning substrate at this site was unique because it occurred in small patches (i.e., <2 m²) at the base of and beneath overhanging edges of large boulders ranging between 1.3 and 4.5 m in diameter. At DR and BS, surficial substrates were a mixture of rubble and cobble, but were densely covered with Cladophora sp. At DR, the substrate was heavily covered with live dreissenid mussels (Dreissena sp.) in addition to Cladophora sp.

Eggs were commonly found deposited in substrates with relatively little interstitial space (Table 4). Interstitial depths greater
than 30 cm were only observed at spawning sites on the two least popular spawning reefs (DR and BS). At the primary spawning site on the east arm of HR, interstitial depth ranged from 10 to 30 cm. In contrast, interstitial depths at spawning sites on the west arm of HR, SS and BA were often <10 cm. At BA, egg deposition occurred on gravel substrate with as little as 2 cm of interstitial depth, which appeared to be insufficient to retain the eggs. Nonetheless, lake trout fry have been captured in emergent fry traps at all confirmed spawning sites except BS (T. R. Binder & S. A. Farha, unpublished data). Confirmed spawning sites were only associated with steep bathymetric contours at HR and DR. At all other sites, bathymetric slope was <5° (Table 4).

4 | DISCUSSION

Fine-scale acoustic telemetry proved effective at identifying discrete patches of spawning habitat used by lake trout for egg deposition on five reefs in the Drummond Island Refuge. Notably, several of the spawning sites identified with acoustic telemetry likely would not have been discovered using traditional survey methods because the patches of spawning substrate were too small and obscure to be a focus of surveys, were not obvious on bathymetric maps (e.g., SS) or the site (e.g., BA) did not conform to the current conceptual model of suitable spawning habitat (Marsden, Casselman, et al., 1995). Ellrott and Marsden (2004) suggested that lake trout may have separate staging and spawning areas, but our results did not support this hypothesis. Rather, our discovery of deposited eggs at every major site of aggregation within the study area supported the assumption that lake trout aggregate on or nearby to spawning sites (Edsall & Kennedy, 1995). However, we also observed that lake trout were highly mobile during the spawning season and, therefore, high numbers of lake trout were detected for short periods on areas of spawning reefs not used for spawning (e.g., south side of HR; Figure 2a). This, in turn, suggests that surveying for ripe adults with passive netting may be an effective technique for identifying probable spawning reefs, but may not provide the fine-scale spatial resolution needed to identify actual spawning locations, which tended to be small relative to the total area of rocky substrates available.
The bulk of activity on each of the verified spawning reefs in our study area was confined to <10% of the total available habitat. This observation is consistent with previous findings in other lakes that lake trout spawning is patchy and limited to relatively small sections of available habitat (Gunn, 1995). For example, on Stoney Island Reef (Lake Ontario), the majority of lake trout spawning was found to occur along the northern half of the eastern slope of the reef, over an area comprising <5% of the total area of the reef (Marsden & Krueger, 1991). Similarly, Kelso (1995) surveyed 3,300 m² of apparently suitable habitat in Megisan Lake (Ontario, Canada) but found egg deposition over only about 25% of that habitat. It is not currently clear what characteristics are most important to lake trout in selecting specific spawning locations, nor why lake trout would choose one site over another site with seemingly similar habitat. Nonetheless, our observation of repeated use of localized areas of reefs over five consecutive seasons was consistent with findings of previous studies (Martin, 1960; McAughey & Gunn, 1995), and suggests that lake trout retain a "memory" of previously used spawning sites, or that lake trout use cues that are stable over time to assess the suitability of potential spawning habitat. Interestingly, among-year consistency in the spatial distribution of activity was greatest on the most highly used spawning reefs, which suggests that those reefs may possess cues for indicating...

### TABLE 2

Results of one-factor repeated-measures ANOVAs comparing the mean number of fish·1-hr intervals among spawning reefs each spawning season

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<th>Value</th>
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<td>49.001</td>
<td>50.272</td>
<td>50.794</td>
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<tr>
<td>df</td>
<td>4,396</td>
<td>4,656</td>
<td>4,540</td>
<td>4,420</td>
<td>4,340</td>
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<td>p-Value</td>
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<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Pairwise comparisons</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HR vs. SS</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>HR vs. BA</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>HR vs. DR</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>HR vs. BS</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>SS vs. BA</td>
<td>&lt;0.999</td>
<td>&gt;0.999</td>
<td>&gt;0.999</td>
<td>&gt;0.999</td>
<td>&gt;0.999</td>
</tr>
<tr>
<td>SS vs. DR</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>SS vs. BS</td>
<td>0.630</td>
<td>0.008</td>
<td>0.002</td>
<td>0.003</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>BA vs. DR</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>BA vs. BS</td>
<td>0.004</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>DR vs. BS</td>
<td>&lt;.001</td>
<td>0.003</td>
<td>&lt;0.001</td>
<td>&gt;0.999</td>
<td>&gt;0.999</td>
</tr>
</tbody>
</table>

Post hoc pairwise comparisons were made using paired t tests (adjusted using the Bonferroni correction) to determine which reefs differed significantly from one another. Reef abbreviations: HR, Horseshoe Reef; SS, Scammon Shoal; BA, Boulder Alley; DR, Deep Reef; BS, Big Shoal.

### TABLE 3

Results of Pearson's product moment correlation tests describing among-year repeatability of spatial activity patterns within an individual spawning reef

<table>
<thead>
<tr>
<th>Reef</th>
<th>Value</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horseshoe Reef (HR)</td>
<td>r (95% CI)</td>
<td>.78 (0.77–0.80)</td>
<td>.75 (0.72–0.77)</td>
<td>.95 (0.95–0.95)</td>
</tr>
<tr>
<td></td>
<td>t (df = 1,753)</td>
<td>52.84</td>
<td>46.86</td>
<td>127.82</td>
</tr>
<tr>
<td></td>
<td>p-Value</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Scammon Shoal (SS)</td>
<td>r (95% CI)</td>
<td>.78 (0.76–0.79)</td>
<td>.54 (0.52–0.57)</td>
<td>.97 (0.86–0.88)</td>
</tr>
<tr>
<td></td>
<td>t (df = 2,331)</td>
<td>59.96</td>
<td>31.35</td>
<td>85.35</td>
</tr>
<tr>
<td></td>
<td>p-Value</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Boulder Alley (BA)</td>
<td>r (95% CI)</td>
<td>.87 (0.86–0.88)</td>
<td>.85 (0.84–0.86)</td>
<td>.89 (0.88–0.90)</td>
</tr>
<tr>
<td></td>
<td>t (df = 2,688)</td>
<td>93.17</td>
<td>83.97</td>
<td>102.47</td>
</tr>
<tr>
<td></td>
<td>p-Value</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Deep Reef (DR)</td>
<td>r (95% CI)</td>
<td>.59 (0.55–0.63)</td>
<td>.50 (0.45–0.54)</td>
<td>.61 (0.57–0.64)</td>
</tr>
<tr>
<td></td>
<td>t (df = 1,040)</td>
<td>23.7</td>
<td>18.65</td>
<td>24.67</td>
</tr>
<tr>
<td></td>
<td>p-Value</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Big Shoal (BS)</td>
<td>r (95% CI)</td>
<td>.50 (0.47–0.53)</td>
<td>.44 (0.41–0.47)</td>
<td>.53 (0.50–0.55)</td>
</tr>
<tr>
<td></td>
<td>t (df = 2,744)</td>
<td>30.28</td>
<td>25.82</td>
<td>32.56</td>
</tr>
<tr>
<td></td>
<td>p-Value</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
<td>&lt;.001</td>
</tr>
</tbody>
</table>

The baseline for comparisons was the 2014 spawning season. 2010 was excluded from statistical comparisons because array coverage over the spawning reefs differed during that year.
suitable spawning habitat that was more obvious, or more consistent over time.

A past inability to distinguish between habitats not encountered by the fish and habitats encountered by the fish but not selected for spawning has likely hindered efforts to fully understand why some sites are selected by lake trout for spawning while other seemingly suitable sites are not. For example, in Thunder Bay, Lake Huron, lake trout took several years to use newly constructed lake trout spawning reefs that were purpose-built using best available knowledge of lake trout spawning habitat preferences (Marsden et al., 2016). Fine-scale acoustic telemetry at that location revealed that slow colonisation of the newly constructed habitat was likely the result of low initial encounter rates, as the number of fish detected on the artificial reefs was low to start and increased gradually over time (Marsden et al., 2016). In the present study, lake trout spawned on what appeared to be less suitable substrates on BA and BS, but did not spawn on a reef just north of BS that, visually, had similar physical characteristics (i.e., water depth, steep slope on north edge of the reef, gravel/rubble substrate, clean interstitial spaces) to the primary spawning site on HR. While the unused reef possibly lacked (or possessed) important characteristics that were not perceived by us, the telemetry data revealed that few tagged fish in our study swam near the unused reef (i.e., did not encounter it). The first evidence of natural reproduction in the Drummond Island Refuge did not occur until the early 2000s (Riley et al., 2007), and spawner densities on identified sites may not currently be high enough to incentivize fish to seek out new spawning habitats. Thus, low encounter rates may explain why the reef was not used for spawning. In contrast, BA and BS both had high encounter rates, possibly because they lie along likely shoreline migratory routes to and from HR and SS. Therefore, we posit that lake features (e.g., bathymetry or currents) that guide lake trout to potential spawning locations may be as important as the characteristics of the sites themselves in determining what habitats have thus far been colonised by recovering populations.

Lake trout in our study spawned at sites with a wide variety of physical habitat characteristics. The two HR spawning sites conformed best to the accepted lake trout spawning habitat model, being located adjacent to a steep bathymetric slope and containing clean gravel and rubble substrates with clean interstitial spaces (Fitzsimons, 1994; Marsden, Casselman, et al., 1995). However, each of the remaining confirmed spawning sites had one or more characteristics that deviated from the accepted habitat conceptual model. For example, the surficial substrate at DR and BS was densely covered with *Cladophora* sp. (DR also was covered with dreissenid mussels), while slope angles at SS, BA, and BS were <5°. Interestingly, lake trout in our study also used small substrates (i.e., <15 cm in diameter), some with relatively little interstitial depth. Among confirmed spawning locations in our study, surficial substrates at HR, SS and BA (the three most popular reefs) were smaller in diameter than at BS and DR. Moreover, on the eastern HR site, egg deposition occurred over a range of substrate sizes, but the highest density of telemetry positions (and presumably egg deposition) occurred over substrates with the smallest diameter. A preference for small substrate has been noted previously in small inland lakes (Callaghan et al., 2016; Gunn, 1995), but not in the Great Lakes, where cobble substrates are thought to predominate (Marsden, Casselman, et al., 1995). Sly and Evans (1996) suggested that substrate particles between 5 and 10 cm in diameter may be optimal for spawning based on the fact that they create a sufficient void space for lake trout eggs while simultaneously excluding large-bodied egg predators. Our results lend support to this view; however, use of small substrates is likely limited to areas that are relatively protected from disturbance by wind-driven waves where they are more likely not to be displaced (Gunn, 1995). Thus, we predict that use of small substrates may be limited to lakes with small fetch, sites deeper than the maximum depth of wave action (maximum wave height measured at our study was 4 m), or, as was the case at HR and SS, shallow sites on the protected side of high-relief structures that dissipate wave energy.

We note that our research did not take lake currents into account, although it is probable that spawning habitat quality is dependent on the penetration of lake currents into the substrate, similar to salmonid spawning habitats in rivers (Geist & Dauble, 1998). We suggest that differences in habitat quality at our study site may vary over small spatial scales and may depend on currents. The lakebed south of Drummond Island is a drumlin field that may support high-quality spawning habitat due to relief created by glacially derived bedforms that provide surfaces where currents may penetrate the substrates

---

<table>
<thead>
<tr>
<th>Reef</th>
<th>Water depth (m)</th>
<th>Surficial substrate</th>
<th>Interstitial depth (cm)</th>
<th>Slope &gt;5°</th>
<th>Cleaned of algae</th>
</tr>
</thead>
<tbody>
<tr>
<td>HR—east</td>
<td>6.5</td>
<td>Gravel/rubble</td>
<td>10–30</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>HR—west</td>
<td>6.0</td>
<td>Gravel/rubble</td>
<td>6–12</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>SS</td>
<td>5.5</td>
<td>Gravel/rubble</td>
<td>4–6</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>BA</td>
<td>9.0</td>
<td>Gravel/rubble</td>
<td>2–21</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>DR</td>
<td>15.0</td>
<td>Rubble/cobble</td>
<td>&gt;30</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>BS</td>
<td>6.5</td>
<td>Rubble/cobble</td>
<td>&gt;30</td>
<td>No</td>
<td>No</td>
</tr>
</tbody>
</table>

Reef abbreviations: HR, Horseshoe Reef; SS, Scammon Shoal; BA, Boulder Alley; DR, Deep Reef; BS, Big Shoal.

Substrate definitions: gravel = 2–64 mm; rubble = 65–256 mm; cobble = 257–999 mm (based on modified Wentworth scale; [Marsden, Casselman, et al., 1995]).

Spawning substrate occurred at the base of large boulders with diameter ranging from 1.3 to 4.5 m.

Site also densely covered with live dreissenid mussels.
sites selected for spawning from sites that were potentially suitable but likely not encountered. A notable limitation of the telemetry-based approach is that the high cost of transmitters and receivers, relative to other tagging methods, means that often only a small portion of the population can be tracked. Researchers should, therefore, work to ensure that the sample of fish selected for tagging is an accurate representation of the entire spawning population.

In conclusion, fine-scale acoustic telemetry was found to be an effective tool for identifying lake trout spawning sites in northern Lake Huron. In our opinion, techniques like acoustic telemetry that allow evaluation of habitat selection from the perspective of fish behaviour hold the greatest potential for refining conceptual behavioural models for fish species. For example, one could use positional acoustic telemetry to contrast habitat characteristics at sites selected for spawning from other nearby sites that were confirmed to be encountered but not selected for spawning. Habitat differences among closely located sites with and without spawning are likely to yield the greatest information about spawning habitat preferences because habitat selection likely occurs at relatively small spatial scales. Therefore, sites selected for spawning are probably of higher quality than nearby sites not selected, but may not be the best available sites in the lake.

A better understanding of lake trout spawning behaviour and key spawning habitat characteristics could benefit lake trout restoration efforts in the Great Lakes in at least two ways. First, knowledge of what spawning habitat characteristics are most important to lake trout when selecting spawning sites would aid in design and construction of artificial reefs that increase the amount of high-quality spawning habitat available to recovering populations (Marsden et al., 2016). Second, targeted stocking of fertilised eggs or yearlings, as has been performed in lakes Superior (Bronte, Schram, Selgeby, & Swanson, 2002) and Michigan (Bronte et al., 2007), can be expanded to further encourage imprinting and colonisation of presumed high-quality habitats on reefs that are currently not used for spawning.

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