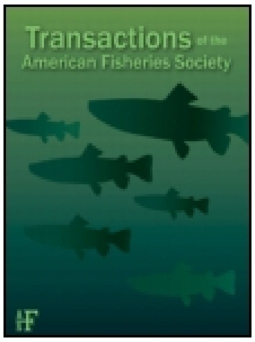

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ARTICLE

Spawning Season Distribution in Subpopulations of Muskellunge in Georgian Bay, Lake Huron

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Abstract
Loss of spawning and nursery habitats has been implicated as a major factor in the widespread decline of Muskellunge *Esox masquinongy* populations in North America. Although there is limited evidence of spawning site fidelity in Great Lakes populations of Muskellunge, such behavior could result in recruitment failure if individuals return each year to spawning sites that have become degraded. We compared the spawning behaviors of individual Muskellunge across three subpopulations in Georgian Bay, Lake Huron, to address the hypothesis that the use of specific spawning sites and spawning site fidelity are independent of the habitat's suitability for successful recruitment. The study regions (southeastern, northeastern, and northern Georgian Bay) have experienced different impacts from human development and sustained low water levels. We radio-tagged 49 adult Muskellunge and tracked them for up to 3 years (between 2012 and 2015). Sufficient multiyear data were only acquired for 18 individuals in the southeastern region; among those fish, 16 showed fidelity to at least one activity center over 2–3 years. Male Muskellunge occupied significantly smaller activity centers and shallower depths than females during the spawning season. The locations of adult Muskellunge were in close proximity to current and historic nursery sites that had been identified in each region by other studies, supporting the close spatial linkage between spawning habitat and nursery habitat. This study is the first to confirm spawning site fidelity in Georgian Bay Muskellunge, and our results support the spatial association between spawning and nursery habitats. The repeated use of degraded habitat by spawning adults, as appears to be the case in southeastern Georgian Bay, highlights the need to identify and protect spawning and nursery habitats.

Georgian Bay in Lake Huron currently supports a self-sustaining Muskellunge *Esox masquinongy* population. Despite the apparent health of the population as a whole, a recent study in southeastern Georgian Bay failed to find age-0 Muskellunge at historic and suspected nursery sites (Leblanc et al. 2014), even though reproductively mature adults were still being captured in the area. Leblanc et al. (2014) proposed multiple stressors that could be responsible for reproductive failure in the southeastern subpopulation of Georgian Bay Muskellunge, including alteration of nursery habitat in coastal wetlands by sustained low water levels and increased human modification of the shoreline.

As with most Muskellunge populations, the Georgian Bay population is managed to support and sustain a recreational

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fishery. Common strategies for protecting Muskellunge populations have included restrictions on harvest size and possession limits (Wingate 1986; Casselman et al. 1999) and encouraging a strict catch-and-release ethic among dedicated anglers (Kerr 2007). Despite efforts that are intended to protect reproductively valuable adults, many Muskellunge populations have declined due to the loss or degradation of suitable spawning and nursery habitats (Dombeck et al. 1984; Dombeck 1986; Zorn et al. 1998; Rust et al. 2002; Farrell et al. 2007). Survival rates of Muskellunge from the egg stage through the first year are naturally very low (Scott and Crossman 1998; Farrell 2001), so additional stressors during that vulnerable time period could affect recruitment success. The over 10 years of sustained low water levels in Georgian Bay (Sellinger et al. 2008) have been linked to a loss of wetland area (Fracz and Chow-Fraser 2013) and a homogenization of the aquatic plant and fish communities (Midwood and Chow-Fraser 2012). Either type of alteration could adversely affect the quality of the coastal wetlands that Muskellunge use as spawning and nursery areas (Scott and Crossman 1998). Similarly, increased shoreline modification has also been linked to the loss and degradation of wetland habitat (Radomski and Goeman 2001; Radomski et al. 2010) and Muskellunge habitat in particular (Dombeck 1986; Rust et al. 2002).

In general, suitable spawning habitat is described as exceeding some minimum level of substrate dissolved oxygen required for spawning (Dombeck et al. 1984) but can occur over various types of substrate (Strand 1986; Zorn et al. 1998; Farrell 2001; Rust et al. 2002; Crane et al. 2014; Nohner and Diana 2015). By comparison, age-0 Muskellunge require (1) some structural complexity, usually provided by aquatic vegetation (Craig and Black 1986; Farrell and Werner 1999; Murry and Farrell 2007; Kapuscinski and Farrell 2014); and (2) the presence of suitable prey (Wahl and Stein 1988; Kapuscinski et al. 2012). It has been hypothesized that there is a close spatial linkage between Muskellunge spawning sites and nursery sites (LaPan et al. 1996; Zorn et al. 1998; Farrell et al. 2007). The underlying assumption is that after hatching, the vulnerable age-0 Muskellunge will not stray far from the safety of their wetland habitat, which should provide both suitable forage and refuge from predators (Crowder and Cooper 1982; Eadie and Keast 1984; Diehl and Eklov 1995). If so, then the degradation of nursery habitat can be a serious problem if Muskellunge cannot seek out suitable habitat when spawning or nursery habitats become degraded.

Spawning site fidelity in Muskellunge has been documented over a range of habitat types, including large lake chains (Crossman 1990), inland lakes (Jennings et al. 2011), and large rivers (LaPan et al. 1996; Younk et al. 1996; Farrell et al. 2007), and such fidelity is consistent with the genetic evidence for distinct populations of Muskellunge throughout the Great Lakes (Kapuscinski et al. 2013). Even though spawning site fidelity has not been documented in the Georgian Bay population, this could explain why age-0 Muskellunge can no longer be found in the relatively disturbed wetlands of southeastern Georgian Bay (Leblanc et al. 2014). Assuming that spawning habitat and nursery habitat are closely linked, then if nursery habitat has become degraded and adults are spawning in the same areas year after year, we would expect limited recruitment success.

The goal of this study was to use radiotelemetry to identify the locations and distribution of adult Muskellunge in Georgian Bay during the spawning season. We investigated the specificity of spawning site use by individual fish and explored the hypothesis that Georgian Bay Muskellunge demonstrate spawning site fidelity. Our intent was to advance the understanding of Muskellunge spawning in Georgian Bay while providing a mechanism to explain the apparent absence of age-0 Muskellunge in southeastern Georgian Bay.

METHODS

Study area.—The eastern and northern shores of Georgian Bay (Figure 1A) are relatively undisturbed areas that are

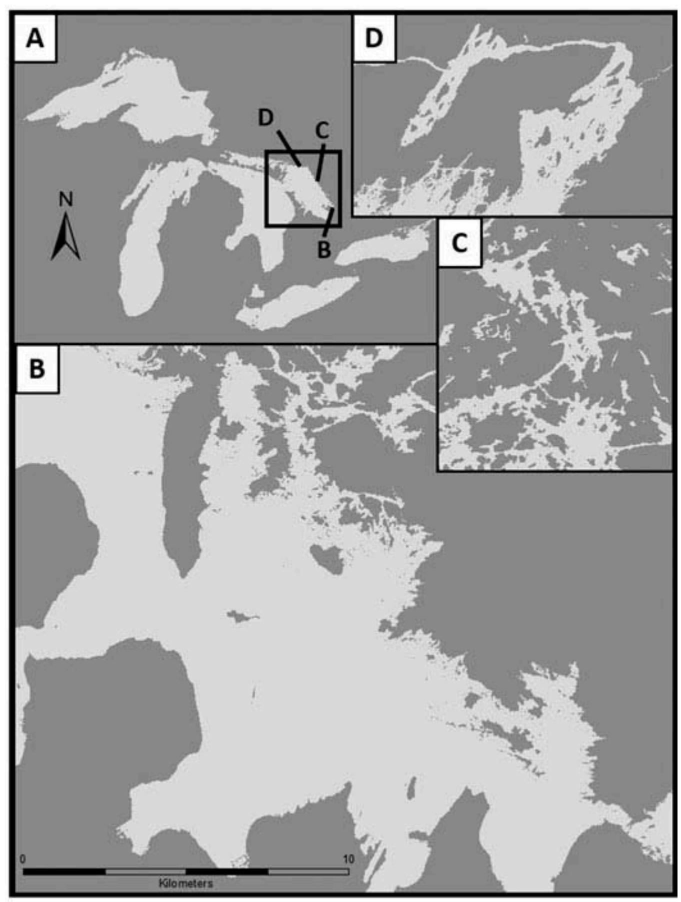

FIGURE 1. Maps of **(A)** Georgian Bay, Lake Huron, and our study areas in the **(B)** southeastern, **(C)** northeastern, and **(D)** northern regions of the bay. Panels B–D are all drawn to the same scale.

underlain by the Precambrian Shield and consist of a complex array of sheltered embayments and protected wetlands (DeCatanzaro and Chow-Fraser 2011). This study was conducted in three regions of Georgian Bay (Figure 1A): southeastern (Severn Sound), northeastern (Pointe au Baril), and northern (Eager Bay and Plant Lake; lake names have been changed to satisfy local stakeholders). All three locations support recreational Muskellunge fisheries that produce adults in excess of the legal harvest size (137 cm TL). Severn Sound (Figure 1B) covers approximately 200 km^2 and is underlain by limestone to the south and the Precambrian Shield to the north. The northeast segment of the Severn Sound shoreline, where our work was focused, is characterized by shallow-sloping nearshore bathymetry, with complexes of small bays, wetlands, and islands. The majority of the Severn Sound shoreline has experienced some level of human development, mostly residential or recreational, and there is significant boat traffic during the summer months. The township of Severn (population = 12,000 people) and the town of Honey Harbour (population = 2,500) are located along the northeast shoreline of Severn Sound, where most homes and cottages have road access.

The northeastern region of Georgian Bay (Figure 1C) primarily consists of Sturgeon Bay and the Pointe au Baril Channel (10 km^2). The area is underlain by the Precambrian Shield and generally has steeply sloping nearshore bathymetry. During the summer, the human population in this area consists of approximately 8,000 local and seasonal residents, and the eastern and northern shorelines are accessible by road. Similar to the southeastern region, much of the shoreline in the northeastern region has undergone some level of human modification, including docks, boathouses, and maintained lawns.

The northern region of Georgian Bay (Figure 1D) covers approximately 20 km^2 and consists of Eager Bay (15 km^2) and Plant Lake (4 km^2), which are connected by a 3-km inland channel. The mouth of Eager Bay opens directly into Georgian Bay, whereas Plant Lake is connected via the inland channel to Eager Bay in the east and Georgian Bay to the west. The area is characterized by steeply sloping nearshore bathymetry and small wetland complexes. The town of Killarney is approximately 50 km away, and the area is only accessible by boat. Human influence in the northern region is limited to less than 100 seasonal cottagers, fishermen, and recreational boaters.

We conducted the present study across these three regions to (1) account for potential differences in terms of shoreline modification and nearshore bathymetry and (2) evaluate differences in spawning season behavior among geographically distinct populations of Muskellunge.

Tagging and tracking.—Muskellunge tagging and tracking occurred during the spawning season (~April–May) in the spring of each year and began approximately 1–2 weeks after ice-off. The exception to this was in 2012, which had a very warm winter, with open water occurring on some areas of Georgian Bay by late March. The tagging and tracking effort encompassed approximately 2–3 weeks, and we attempted to be on the water each day when boating conditions were safe. Due to the size of the Severn Sound area, we had to split our efforts between the northern and southern reaches of the Severn Sound shoreline. Tagging was carried out in Severn Sound during spring 2012 (May 1–2), 2013 (April 24–May 9), and 2014 (May 7–15) and in Pointe au Baril during spring 2015 (May 15–20) in conjunction with the Ontario Ministry of Natural Resources and Forestry's (OMNRF) Spring Muskellunge Index Netting Program (A. Liskauskas, unpublished data). In northern Georgian Bay, tagging was conducted during spring 2012 (May 25 and 27) and 2013 (May 4–18) by researchers and field technicians (without assistance from OMNRF biologists).

Adult Muskellunge were caught with trap nets (40-mm mesh; 1.83- × 1.83-m crib) and hoop nets (40-mm mesh; 91-mm-diameter hoops) that were deployed in coastal wetlands for 24 h. Muskellunge that were suitable for tagging (>1,000 g) were isolated and transferred to a floating pen (1.0 × 1.5 m; 1.0 m deep) attached to the boat. We did not tag any fish that exhibited signs of injury or stress while in the floating pen; those individuals were monitored in the pen and were released when they appeared to have recovered. Research-quality clove oil (Xenex Laboratories, Inc., Coquitlam, British Columbia, Canada) was used to anaesthetize the fish during surgery. A single dose (60 mg/L) was added to the anesthetic bath (60–100 L of water obtained from the capture site), and a maintenance dose of 30 mg/L was pumped across the gills during surgery. Clove oil was dissolved with ethanol in water temperatures below 15°C (Anderson et al. 1997). Each fish was placed individually into the anesthetic bath and was monitored for up to 10 min until equilibrium was lost and the opercular rate slowed. The fish was placed in a supine position on a foam surgery platform. The maintenance dose of clove oil was supplied through a plastic tube that was inserted into the mouth and positioned to permit the flow of anesthetic across the gills. Muskellunge were tagged with MCFT2-3A radio tags (Lotek, Newmarket, Ontario; 16-mm diameter, 46-mm length, and 16-g weight). Although a subset of tags transmitted pressure and temperature information, only locational data from the tags were examined for this study. A 2–3-cm incision was made midventral and anterior to the pelvic girdle, and the radio tag was inserted. The tag was anchored to the body cavity by feeding the trailing whip antenna through a hollow, 16-gauge needle that was inserted adjacent to the incision. The incision was closed with two or three interrupted sutures (3-0 monofilament). Total surgery time was 5–10 min, after which the Muskellunge was transferred to a cradle secured in the floating pen and was allowed to recover. Individuals took up to 1 h to regain equilibrium and become responsive to external stimuli, at which point they were released.

Fish were not actively tracked until 2 weeks after surgery. Tagged Muskellunge were tracked from an open boat with a Lotek SRX600 receiver and three-piece Yagi antenna. Where possible, the boat was positioned over the tracked fish, and geographic coordinates were acquired with a handheld GPS (3–5-m accuracy; Garmin, Olathe, Kansas).

When conditions precluded approaching the tagged fish (e.g., areas that were too shallow or with high wave action), we approximated the fish's location by taking the strongest signal bearing and estimating the distance from the boat based on the signal strength.

Since Severn Sound was the most intensively studied of our Georgian Bay regions (three consecutive years of tagging and tracking compared to 2 years in the northern region and 1 year in the northeastern region), our data analysis focused primarily on Severn Sound. We present our results separately for two distinct sections (south and north) of Severn Sound because (1) greater effort was expended in south Severn Sound in terms of capture and tracking, and (2) no tagged Muskellunge were found outside of the section in which they were originally tagged. Where possible, we used data from the northern and northeastern regions of Georgian Bay to compare against the results from Severn Sound, which allowed us to evaluate the transferability of results across different regions of the bay.

Spatial and statistical analysis.—All spatial analyses were completed in ArcMap version 10.2 (ESRI, Inc., Redlands, California); statistical analyses were performed with PASSaGE 2 software (Rosenberg and Anderson 2011) and JMP version 12.0.1 (SAS Institute, Inc., Cary, North Carolina). All geographic coordinates corresponding to sites where Muskellunge had been captured or tracked during this study were imported into the GIS environment. Capture locations were pooled with the tracking locations because the location of capture and the time of tagging were considered to constitute a spatially (±50 m) and temporally (within 24 h) accurate representation of a location that was used by the fish during the spawning season. Since the purpose of this study was to investigate the distribution of adult Muskellunge during the spawning season, we only included locations that were deemed representative of the spawning period. This included all locations that were recorded between late April and May, the typical spawning season for Georgian Bay Muskellunge, with the exception of locations acquired late in the season that were consistent with postspawning behavior. A Muskellunge was considered to have finished spawning if locations were obtained late in the expected spawning season (i.e., mid- to late May) and if the individual was detected as using offshore areas away from potential spawning locations (i.e., coastal wetlands). Hereafter, we use the term "locations" in reference to the observed locations of Muskellunge during this study, which include the capture locations and all tracked locations that were representative of spawning season behavior. When locations for an individual were collected across multiple years, all data were pooled. We follow Crossman's (1990) usage of "spawning sites" to represent specific areas where Muskellunge are thought to be spawning, and we consider the term "spawning grounds" to represent general habitat that is used during the spawning season. We limit our presentation and discussion of results to "spawning ground use" and "spawning ground fidelity" since we could not confirm that spawning had taken place (e.g., we did not conduct visual observations or collect eggs). We also imported the locations of historic (Craig and Black 1986) and current (J. P. Leblanc, unpublished data; J. D. Weller, unpublished data) Muskellunge nursery sites from each region to provide spatial context for the spawning season locations we acquired relative to known nursery habitats.

Distribution during the spawning season.—We limited our formal analysis of spawning season distribution to individuals with at least five locations. To characterize the distribution of a Muskellunge's locations during the spawning season, we calculated the average nearest-neighbor distance ($\bar{d}_{min}$) for each individual as a relative measure of clustering or dispersion in the observed locations (O'Sullivan and Unwin 2010). Ripley's *K*-function (Ripley 1976, cited by O'Sullivan and Unwin 2010) was used as a means to further group individuals based on the extent and type of clustering observed. Ripley's *K* compares the observed number of neighboring points to the number of neighbors that would be expected within a given radius around each point; this is repeated for multiple values of the radius to evaluate how the clustering or dispersion in the point pattern changes over a range of distances. We performed this analysis in ArcMap at 100 different distances in 40-m increments to a maximum distance of 4,000 m (the maximum distance moved by a Muskellunge over a 1-d period during the present study). The maximum boundary was set to encompass the areas to which an individual could have moved during our study. Confidence limits were established from 999 permutations. Individuals were classified based on the significance of clustering over the majority of the distances evaluated. Clustering was defined as tightly clustered (significant clustering over the majority of distance bands), loosely clustered (nonsignificant clustering over the majority of distance bands), or dispersed (dispersion of points over the majority of distance bands). No category was created for significantly dispersed points, as that would represent a uniform pattern, which would not be expected to occur naturally. This analysis was used only as a means to further classify the degree of clustering observed rather than to examine the spatial scale of clustering.

We also used activity centers to approximate areas in which an individual Muskellunge spent the majority of its time during the spawning period in each year. The kernel density function in ArcGIS was used to estimate a kernel utilization distribution (KUD)—a technique that is widely used in animal movement and home range analysis (e.g., Worton 1989; Laver and Kelly 2008). The KUD is a probability surface based on known locations (i.e., observed Muskellunge locations) and predicts the likelihood that an individual will be found at a particular location. High-use areas as determined by the investigator are bounded by isolines that contain a set percentage of the distribution. For example, 95% of the KUD is a typical boundary for home range analysis (Worton 1989). Since we were interested in "core" use areas, we bounded the Muskellunge activity centers with 10, 25, and 50% isolines (Afonso et al. 2008). A kernel density surface was determined for each individual in ArcMap (cell size = 10 m; bandwidth from Silverman's rule; Silverman 1986), and we used a custom-built tool in ArcMap to delineate the activity centers. The total area within each activity center (excluding land) was calculated, and areas for all activity centers were pooled under each KUD boundary condition. Spawning ground fidelity was assessed based on the repeated use of the same activity center over multiple years. Activity centers were also calculated for the subpopulation by pooling the locations from all individuals to identify any regionally important spawning grounds.

To assess differences in the size of activity centers and the depths of areas used by male and female Muskellunge, we used a partial Mantel test, which examines for correlations between two distance matrices while controlling for the effects of a third distance matrix (Legendre and Legendre 1998). We tested whether male and female Muskellunge were using different depths (sex = matrix 1; maximum depth at spawning season locations = matrix 2) or different-sized activity centers (sex = matrix 1; KUD area = matrix 2). Matrix 3 included the weight at capture, which was held constant to account for size differences between males and females. Available topographic and bathymetric data (OMNR 2006; NOAA 1996) were compiled to create a digital elevation model for estimating the maximum depth at each location. The depth comparison refers to the maximum water depth corresponding to the observed location rather than the depth at which the fish were found within the water column. Results were tested for significance by permutation (999 times at α = 0.05).

RESULTS

Tagging and Tracking

Overall, 49 Muskellunge were tagged and tracked from 2012 to 2015 across all three study regions of Georgian Bay (Figure 2). We tagged 24 adult Muskellunge in the southeastern region

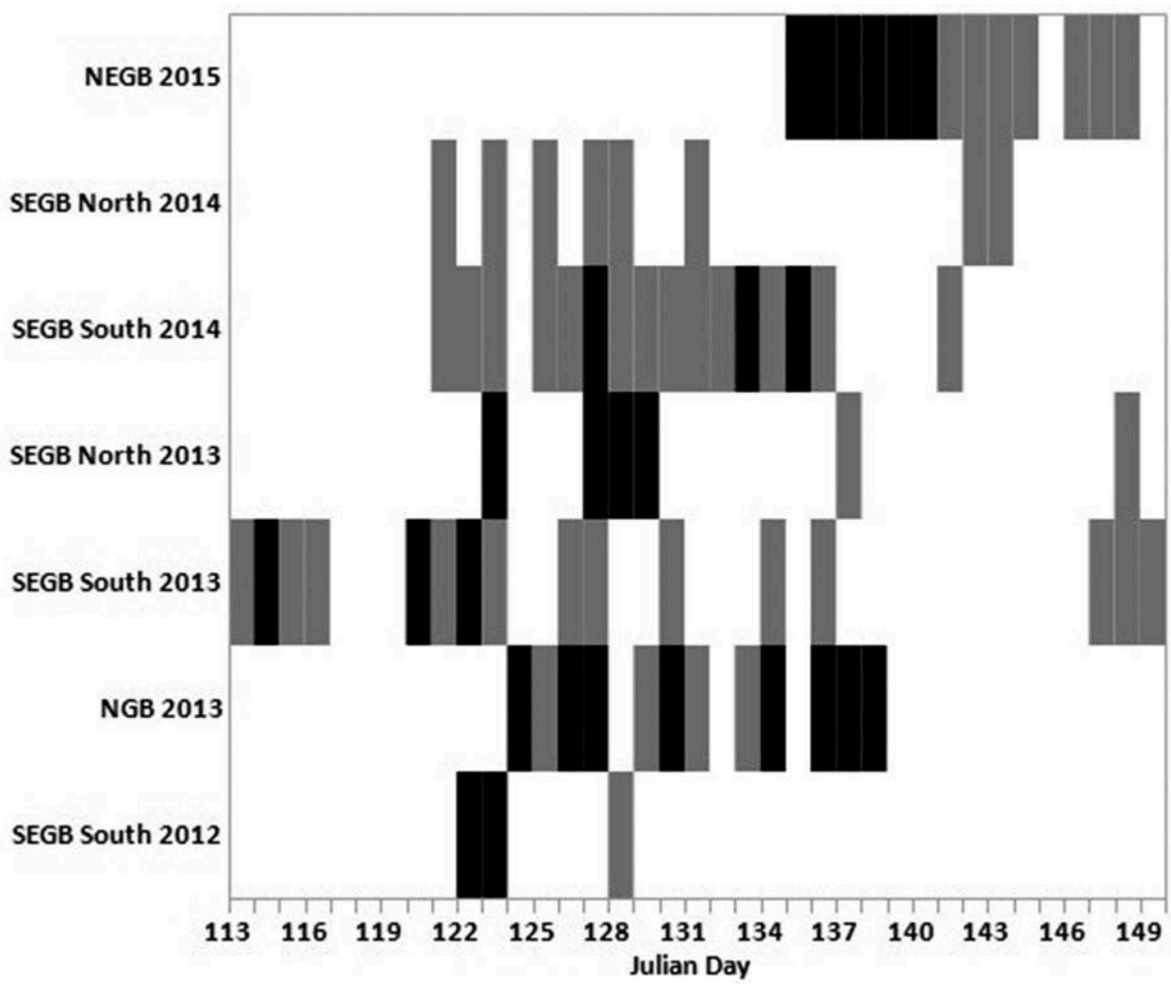

FIGURE 2. Tracking effort from each study region of Georgian Bay (SEGB = southeastern; NEGB = northeastern; NGB = northern) during each year. Each shaded box indicates that tracking occurred on that day; a black box indicates that a fish was also tagged. Tracking effort in NGB during 2012 was omitted because only two fish were tagged and no tracking occurred during the spawning season.

(Severn Sound) during 2012–2014 (Table 1). Capture and tracking efforts in this region were focused primarily along the northeast segment of the Severn Sound shoreline. In total, 298 locations were acquired over the 3 years of tagging and tracking in Severn Sound (245 in south Severn Sound, 53 in north Severn Sound; Figure 3A, B). Of the 24 tagged adults, 22 were confirmed as being active at the end of May in 2014. The signal from tag identification number (ID) 15 was found in the same location for the duration of 2013 tracking and again in 2014, so we presumed that the fish died prior to the 2013 season. One individual, ID 32, had been tagged in 2013 but was not located again in 2014. In the northeastern region, we tagged and tracked 13 Muskellunge during the spawning season in 2015 and acquired a total of 86 locations for those fish (Figure 4A; Table 2). In the northern region, 12 Muskellunge were tagged and tracked, with a total of 30 locations (Figure 4B; Table 2). Due to the early spring in 2012, our capture and tracking effort in the northern region missed the majority of the spawning season, so no tracking data were acquired during that year.

Distribution during the Spawning Season

Among the 24 adult Muskellunge that were tagged in Severn Sound, 18 had at least five locations. Of those, 17 were tracked for more than one season; ID 48 had one season of locations available. Twelve of these Muskellunge were from south Severn Sound. The $\bar{d}_{min}$ for these individuals ranged from 53 ± 29 m (ID 19) to 600 ± 213 m (ID 28), with a median value of 162 m (Table 3). Of the nine females, seven had $\bar{d}_{min}$ values greater than the median; IDs 18 and 31 were the exceptions. The majority of males (7 of 9) had $\bar{d}_{min}$ values that were less than the median; the exceptions were IDs 35 and 40. The $\bar{d}_{min}$ values were consistent with the groupings based on Ripley's *K*-function (Table 3). Of the 18 individuals evaluated, 10 were classified as exhibiting tight clustering, 7

TABLE 1. Biological information and telemetry data from each Muskellunge that was captured and tracked in the southeastern region of Georgian Bay, Lake Huron (south and north shorelines of Severn Sound). Size measurements and fish sex were determined prior to radio tag implantation (Tag ID = tag identification number). The number of locations acquired in each year is presented relative to the number of days spent tracking the fish (in parentheses).

						Locations			
Origin	Tag ID	Sex	Weight (g)	TL (mm)	Date tagged	2012	2013	2014	Total
Muskellunge tagged in 2012									
South	19	M	4,500	935	May 1	1 (3)	12 (16)	15 (16)	28 (35)
South	20	M	8,000	1,050	May 1	2 (3)	13 (16)	16 (16)	31 (35)
South	11	M	6,500	1,005	May 2	2 (2)	11 (16)	15 (16)	28 (34)
South	15	M	8,000	1,060	May 2	2 (2)	0[a]		2 (2)
South	16	M	5,000	930	May 2	1 (2)	4 (16)	16 (16)	21 (34)
South	18	F	9,000	1,040	May 2	1 (2)	6 (16)	1 (16)	8 (34)
South	22	M	8,500	1,090	May 2	1 (2)	9 (16)	16 (16)	26 (34)
Muskellunge tagged in 2013									
South	39	F	12,750	1,190	Apr 24		6 (15)	16 (16)	22 (31)
South	28	F	7,500	954	Apr 30		5 (12)	12 (16)	17 (28)
South	30	F	12,000	1,178	Apr 30		4 (12)	9 (16)	13 (28)
South	29	F	13,000	1,115	May 2		4 (10)	13 (16)	17 (26)
South	31	F	16,500	1,275	May 2		2 (10)	14 (16)	16 (26)
North	32	F	15,000	1,233	May 3		1 (6)	0 (8)	1 (14)
North	33	M	5,500	968	May 7		1 (5)	6 (8)	7 (13)
North	34	M	12,000	1,185	May 8		4 (4)	6 (8)	10 (12)
North	35	M	10,000	1,100	May 8		4 (7)	5 (8)	9 (12)
North	36	F	20,500	1,410	May 8		1 (4)	2 (8)	3 (12)
North	37	F	8,750	1,030	May 8		2 (4)	3 (8)	5 (12)
North	38	F	18,000	1,300	May 8		1 (4)	3 (8)	4 (12)
North	40	M	6,250	940	May 9		2 (3)	7 (8)	9 (11)
North	41	F	12,750	1,270	May 9		1 (3)	4 (8)	5 (11)
Muskellunge tagged in 2014									
South	48	F	17,500	1,329	May 7			9 (11)	9 (11)
South	47	M	10,000	1,105	May 13			4 (5)	4 (5)
South	50	F	20,500	1,377	May 15			3 (3)	3 (3)

[a]Fish ID 15 was confirmed deceased during 2013.

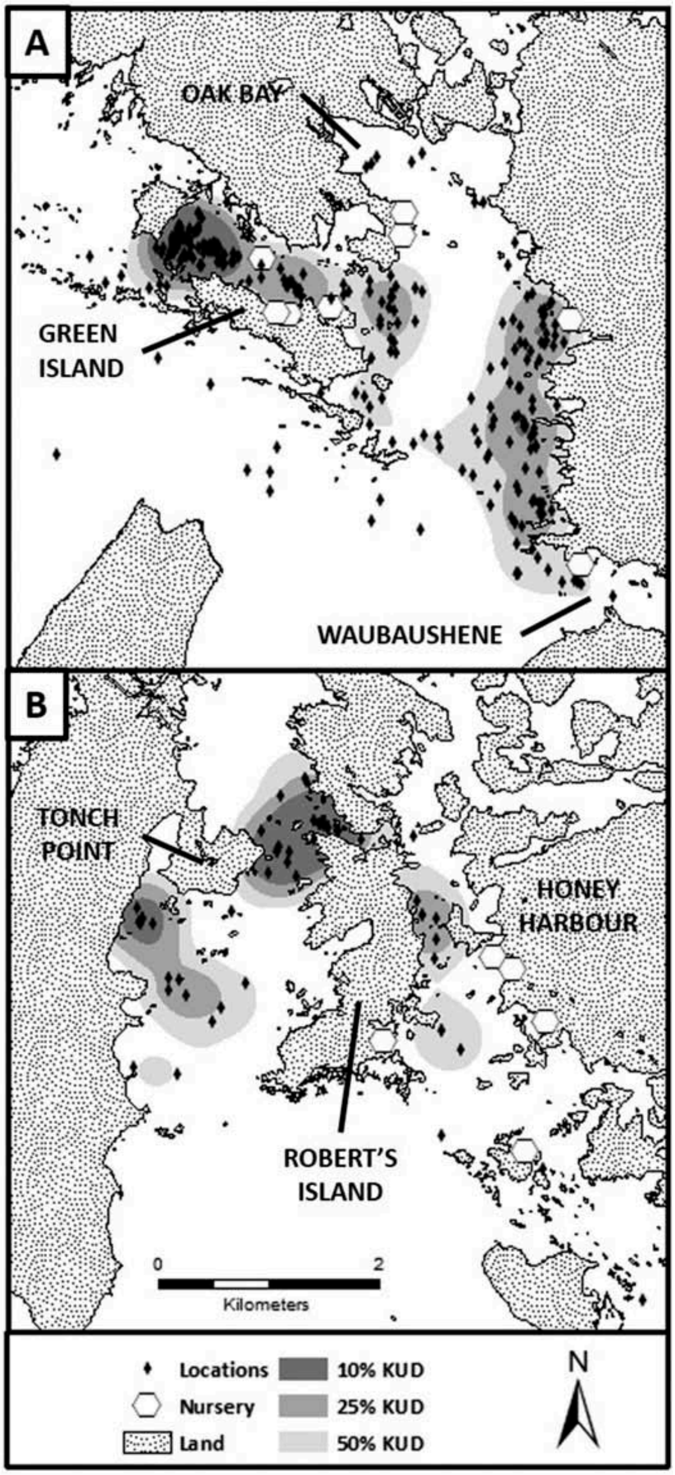

FIGURE 3. Locations of tracked Muskellunge from the southeastern region of Georgian Bay, partitioned into **(A)** south Severn Sound and **(B)** north Severn Sound. Activity centers for each group indicate major spawning grounds in the respective sections. Nursery sites were identified in 1981 (Craig and Black 1986).

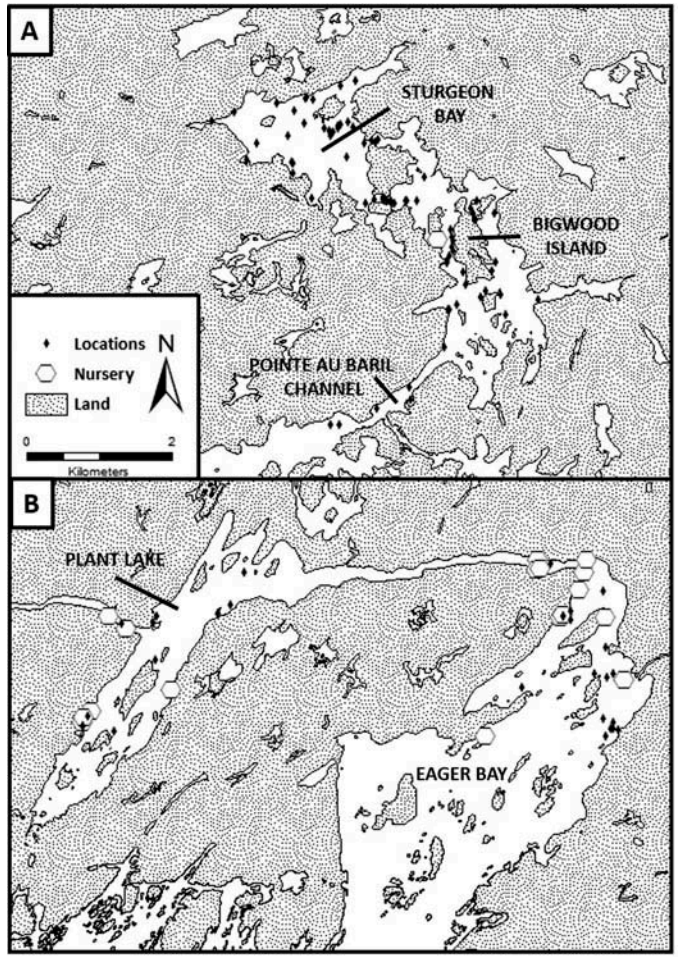

FIGURE 4. Locations of tracked Muskellunge from the **(A)** northeastern and **(B)** northern regions of Georgian Bay. Nursery sites were identified concurrently with this study.

were classified as having loose clustering, and 1 was classified as showing a dispersed pattern. The individuals with tight clustering were mostly males (8 of 10) except for IDs 18 and 31. The individuals with loose clustering were mostly females (6 of 7), with the exception of ID 40. The only individual that demonstrated dispersion was a female (ID 28).

The 18 fish were localized to between one and five activity centers, depending on the KUD boundary condition (Table 4). Due to the number and distribution of locations for some individuals, some of the delineated activity centers only contained one location, and those activity centers were eliminated from further consideration. There was a large range in the total area of activity centers for each Muskellunge both within and between KUD boundaries (e.g., 0.7–209.9 ha at 10% KUD; 2.0–866.2 ha at 50% KUD). The number of activity centers delineated was variable, but several patterns of use were

TABLE 2. Biological information and telemetry data from each Muskellunge that was captured and tracked in the northern region (2012 and 2013) and northeastern region (2015) of Georgian Bay. Size measurements and fish sex were determined prior to radio tag implantation (Tag ID = tag identification number). The number of locations acquired in each year is presented relative to the number of days spent tracking the fish (in parentheses).

						Spawning season locations			
Origin	Tag ID	Sex	Weight (g)	TL (mm)	Date tagged	2012	2013	2015	Total
Muskellunge tagged in the northern region, 2012									
Eager Bay	8	M	5,200	963	May 25	1 (1)	6 (12)		7 (13)
Plant Lake	4	F	12,600	1,180	May 27	1 (1)	3 (12)		4 (13)
Muskellunge tagged in the northern region, 2013									
Plant Lake	22	M	11,000	1,160	May 4		3 (12)		3 (12)
Plant Lake	19	M	6,800	1,030	May 6		2 (10)		2 (10)
Eager Bay	10	M	9,800	1,060	May 7		3 (9)		3 (9)
Eager Bay	6	F	12,800	1,080	May 10		4 (7)		4 (7)
Plant Lake	5	M	8,400	1,000	May 10		1 (7)		1 (7)
Plant Lake	20	M	7,000	1,000	May 14		1 (4)		1 (4)
Plant Lake	3	F	9,800	1,010	May 16		2 (3)		2 (3)
Plant Lake	11	M	6,800	975	May 16		2 (3)		2 (3)
Plant Lake	18	F	17,300	1,320	May 17		1 (2)		1 (2)
Plant Lake	2	F	17,300	1,320	May 18		1 (1)		1 (1)
Muskellunge tagged in the northeastern region, 2015									
Sturgeon Bay	52	F	17,300	1,338	May 15			11 (13)	11 (13)
Sturgeon Bay	58	M	15,300	1,205	May 16			11 (12)	11 (12)
Sturgeon Bay	46	F	14,800	1,249	May 17			5 (11)	5 (11)
Sturgeon Bay	44	M	11,300	1,105	May 17			7 (11)	7 (11)
Sturgeon Bay	45	M	10,800	1,155	May 17			8 (11)	8 (11)
Shawanaga[a]	59	F	7,300	984	May 17			2 (3)	2 (3)
Shawanaga[a]	49	M	8,800	1,090	May 17			1 (3)	1 (3)
Sturgeon Bay	60	F	14,800	1,215	May 18			9 (10)	9 (10)
Sturgeon Bay	53	F	15,300	1,235	May 18			8 (10)	8 (10)
Sturgeon Bay	42	F	15,800	1,148	May 18			7 (10)	7 (10)
Sturgeon Bay	54	F	16,500	1,296	May 19			9 (9)	9 (9)
Pointe au Baril	56	M	13,500	1,151	May 19			5 (9)	5 (9)
Pointe au Baril	43	F	14,500	1,262	May 20			3 (8)	3 (8)

[a]Fish was tagged at the mouth of the Shawanaga River, and only two attempts were made to track this fish.

evident. The most common example was the use of one main activity center. This included individuals that only had one identifiable activity center (e.g., IDs 18, 20, and 29; Figure 5) and individuals that had several activity centers but one obvious "primary" activity center, which accounted for the majority of the total activity center area (e.g., IDs 11, 16, and 39; Figure 5). The "secondary" activity centers were generally areas in which an individual was found only two or three times over the course of the study. The other major pattern of use was a relatively even split between two main activity centers. Locations for ID 19 were split between two activity centers at the western and central areas of the Green Island channel (Figure 6); locations for ID 22 were split between two activity centers north of Waubaushene (Figure 6). The only individual that was classified as dispersed, ID 28, was found across nearly all of south Severn Sound (Figure 5) during this study but was located on five occasions in or adjacent to Oak Bay, which is a large wetland area and possible spawning ground. When individuals had more than one activity center, they were never separated by a distance greater than 1 km (Table 4). Two individuals, IDs 37 and 19, had the most spatially distinct activity centers, as the centers were separated by 854 and 827 m, respectively (10% KUD boundary).

Some level of spawning ground fidelity was observed in all but one fish that were tracked in Severn Sound for 2 or more years (17 individuals; Table 4). Since we measured fidelity as the use of the same activity center over multiple years, the

TABLE 3. Relative measure of clustering in Muskellunge that were tagged in the southeastern region of Georgian Bay and that had more than five locations (Tag ID = tag identification number). Average nearest-neighbor distances ($\bar{d}_{min}$ ± SE) and grouping category from Ripley's *K*-function analysis are also presented.

Tag ID	Total locations	$\bar{d}_{min}$ (m)	Grouping category
11	28	89 ± 14	Tightly clustered
16	21	110 ± 27	Tightly clustered
18	8	149 ± 45	Tightly clustered
19	28	53 ± 29	Tightly clustered
20	31	99 ± 41	Tightly clustered
22	26	63 ± 16	Tightly clustered
28	17	600 ± 213	Dispersed
29	17	245 ± 79	Loosely clustered
30	13	580 ± 150	Loosely clustered
31	16	92 ± 12	Tightly clustered
33	7	84 ± 19	Tightly clustered
34	10	125 ± 73	Tightly clustered
35	9	174 ± 51	Tightly clustered
37	5	589 ± 53	Loosely clustered
39	22	191 ± 25	Loosely clustered
40	9	511 ± 299	Loosely clustered
41	5	559 ± 222	Loosely clustered
48	9	292 ± 11	Loosely clustered

KUD boundary condition affected the degree of fidelity observed. Moving from the more conservative estimate of core use areas (10% KUD) to the more generous estimate (50% KUD), the activity centers expanded and encompassed more locations, which led to higher incidences of repeat use with the larger KUD boundaries. As such, under the 50% KUD boundaries, ID 41 was the only individual that did not show fidelity to at least one activity center between years. Under the 10% KUD, three individuals displayed no sign of fidelity (IDs 18, 40, and 41). Multiple-year use was observed in individuals from the tightly clustered, loosely clustered, and dispersed groups and in both sexes. The most common occurrence was fidelity to one primary activity center from a tightly clustered individual (Figure 6; IDs 16 and 20) or a loosely clustered individual (Figure 6; IDs 29 and 39). Muskellunge were found to use mainly these activity centers over multiple years, although multiyear use of other, smaller activity centers was also observed (IDs 16 and 39). Fish IDs 19 and 22 showed fidelity to each of their two main activity centers (Figure 6); however, ID 22 appeared to use both activity centers in both 2013 and 2014, whereas ID 19 heavily favored one activity center in each of those years.

The activity centers for pooled locations from the south and north areas of Severn Sound revealed several major spawning grounds. In south Severn Sound (Figure 3A), the channel on the north side of Green Island was a hot spot for spawning activity in the area, as was the eastern portion of the shoreline to the north of Waubaushene. Notable spawning grounds in north Severn Sound included the areas to the immediate east and south of Tonch Point and the eastern shore of Robert's Island (Figure 4B).

Male and female Muskellunge in Severn Sound exhibited different patterns in their spawning season distributions. Males had significantly smaller activity center areas than did females under each KUD boundary condition (Table 5). For example, under the 10% KUD condition, the average total activity center area was 7.2 ha (SE = 2.1; n = 9) for males compared with 67.1 ha (SE = 22.5; n = 9) for females (partial Mantel test: P = 0.001). The magnitude of the difference in activity center areas between males and females was consistent at the 25% KUD and 50% KUD boundary conditions. Fish IDs 18 and 31 were both females with total activity center areas of 1.9 and 14.9 ha, respectively (10% KUD), closer to the male average; in contrast, the remaining females had activity center areas in excess of 20 ha. Similarly, one male (ID 40) had an activity center area of 21.2 ha (10% KUD) that was larger than that of other males (<12 ha; 10% KUD). Females were also found in significantly deeper areas than were males (females: 2.6 ± 0.3 m; males: 1.9 ± 0.2 m; partial Mantel test: P = 0.042; Table 5). In general, males occupied smaller areas and were found in shallower waters than females.

Tracking data from the northern and northeastern regions appeared consistent with our observations from Severn Sound. Of the northeastern Muskellunge that were tagged and tracked in Sturgeon Bay and Pointe au Baril (11 individuals), six showed obvious clustering at specific sites and three showed possible evidence of clustering. The sizes of the areas used by these individuals appeared to be consistent with those of the tightly clustering and loosely clustering groups identified in the Severn Sound analysis (~10 ha for males). Tracking data from the northern region were sparse during the spawning season and were primarily obtained in 2013. One male, ID 8, appeared to use a specific area towards the northeast shore of Eager Bay, which was also where that individual was captured in 2012. Besides ID 8, there were insufficient multiyear data to provide further support for spawning ground fidelity in the northern region.

DISCUSSION

The apparent absence of age-0 Muskellunge in southeastern Georgian Bay (Leblanc et al. 2014) is puzzling. Even though the quality of some coastal wetlands in that region is lower than the quality of those in the rest of eastern and northern Georgian Bay, they are still in excellent condition relative to the remainder of the Great Lakes (Cvetkovic and Chow-Fraser 2011). The extent of shoreline modification within Muskellunge nursery sites in Severn Sound has increased in recent years (Leblanc et al. 2014) but is limited primarily to residential development (e.g., docks and boathouses), whereas strong populations of Muskellunge (adults and age 0) appear to be persisting in areas that have

TABLE 4. Activity center analysis for Muskellunge from the southeastern region of Georgian Bay (Tag ID = tag identification number); the number of locations for each individual (Total) is shown along with kernel utilization distributions (KUDs) indicating the number of activity centers delineated (No.), the total area of activity centers (Area; ha), the average nearest-neighbor distance between activity centers (Near; m), the number of locations within the activity centers (Core), and the percentage of activity centers that were used over multiple years (MYU).

Tag ID	Total	No.	Area	Near	Core	MYU
			10% KUD			
11	28	2	9.1	117	16	100
16	21	1	5.6		12	100
18	8	1	1.9		3	0
19	28	2	12.0	827	24	50
20	31	2	3.8	56	19	100
22	26	2	6.3	428	16	50
28	20	3	133.0	498	13	100
29	17	1	22.0		10	100
30	13	3	202.9	633	8	33
31	16	2	14.9	718	13	50
33	7	1	3.4		4	100
34	10	2	0.7	55	7	50
35	9	1	3.1		3	100
37	6	2	121.7	854	5	50
39	22	1	36.0		11	100
40	9	1	21.2		5	0
41	5	1	30.1		2	0
48	9	3	87.1	223	9	
			25% KUD			
11	28	1	17.4		19	100
16	21	2	10.2	591	15	100
18	8	1	3.5		4	0
19	28	2	20.9	730	27	100
20	31	1	6.9		26	100
22	26	2	11.2	332	19	50
28	20	1	249.2		13	100
29	17	1	41.1		13	100
30	13	2	443.5	647	9	50
31	16	2	26.1	638	15	50
33	7	1	5.8		5	100
34	10	2	1.3	37	8	50
35	9	1	8.7		6	100
37	6	2	187.1	669	5	50
39	22	3	81.6	499	19	100
40	9	2	53.1	299	7	50
41	5	1	49.3		3	0
48	9	2	142.1	351	9	
			50% KUD			
11	28	5	43.6	207	27	100
16	21	2	18.9	522	17	100
18	8	1	8.7		6	100
19	28	2	32.0	613	27	100
20	31	1	10.5		28	100
22	26	2	24.8	87	24	100
28	20	1	343.8		13	100
29	17	1	63.4		14	100

TABLE 4. Continued.

Tag ID	Total	No.	Area	Near	Core	MYU
30	13	2	866.2		12	50
31	16	2	42.9	415	16	100
33	7	2	14.6	373	7	50
34	10	2	2.0	19	8	50
35	9	1	15.8		7	100
37	6	2	267.5	523	5	50
39	22	3	145.5	314	20	100
40	9	1	93.3		7	100
41	5	1	104.1		4	0
48	9	2	206.0	90	9	

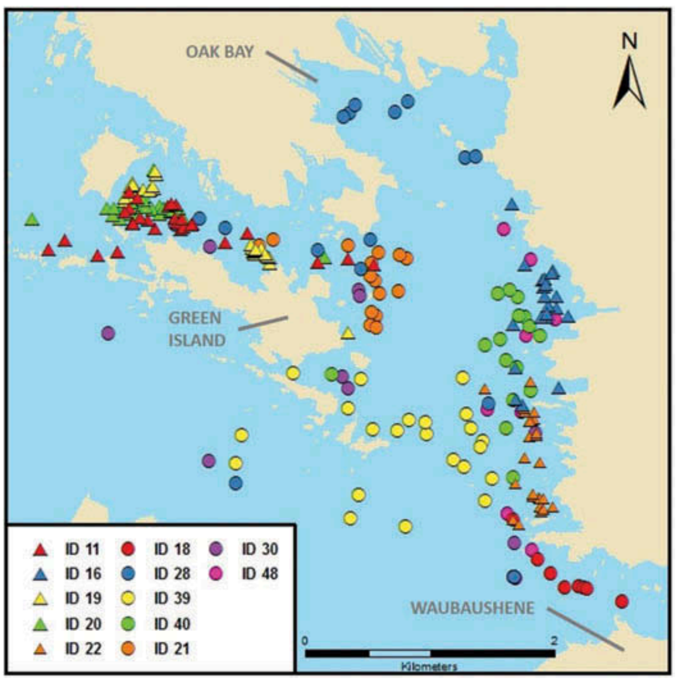

FIGURE 5. Locations of radio-tagged Muskellunge in south Severn Sound, Georgian Bay, with at least five locations acquired from 2012 to 2014 (ID = tag identification number). Differences in clustering and distribution between males (triangles) and females (circles) are depicted.

experienced much more significant modifications to the shoreline, such as the Niagara River (Kapuscinski et al. 2014) and the Fox River (Kapuscinski et al. 2007). Concurrent with our study, age-0 Muskellunge were observed in our northern and northeastern regions despite the fact that those regions have also experienced the same sustained low water levels as the southeastern region. It is therefore possible that other factors related to or independent of shoreline modifications or water levels (e.g., changes to fish community, habitat structure, or climate) could be affecting the recruitment success of age-0 Muskellunge in Severn Sound. Nevertheless, Muskellunge in Georgian Bay should theoretically be able to seek out other suitable breeding habitat since they are capable of moving great distances (e.g., Crossman 1977; LaPan et al. 1996), and the shorelines of eastern and northern Georgian Bay provide continuous access to thousands (Midwood et al. 2012) of high-quality coastal wetlands (Cvetkovic and Chow-Fraser 2011) that should be capable of supporting Muskellunge spawning and nursery activities. However, what is possible in theory has not proven to be the case in reality, and our findings support our main hypothesis of spawning site fidelity as a potential mechanism for the absence of age-0 Muskellunge in Severn Sound.

Movement to specific areas during the spawning season has been well documented in many Muskellunge populations (Miller and Menzel 1986; Strand 1986; Crossman 1990; LaPan et al. 1996; Younk et al. 1996; Farrell et al. 2007; Diana et al. 2015). Muskellunge in each of our study regions exhibited an affinity for particular areas during spawning, consistent with previous observations. Similarly, spawning site fidelity has also been documented in Muskellunge populations within multiple waterbodies throughout the species' range (Crossman 1990; LaPan et al. 1996; Younk et al. 1996; Farrell et al. 2007; Jennings et al. 2011), but this is the first study to document such behavior in Georgian Bay Muskellunge. Of the individuals that were successfully tracked for two or more years, only one (ID 41) did not use the same activity center across multiple years. The most conclusive evidence for spawning site fidelity came from the individuals that were tagged in south Severn Sound during 2012. Those fish were tagged relatively late in the spawning season but were tracked for the entirety of the subsequent two seasons. A full season of tracking was needed before preferential site use was obvious, and an additional season was required to confidently claim that the fish were displaying spawning site fidelity. Several multiyear telemetry studies (LaPan et al. 1996; Younk et al. 1996) have also observed strong spawning site fidelity in individual fish,

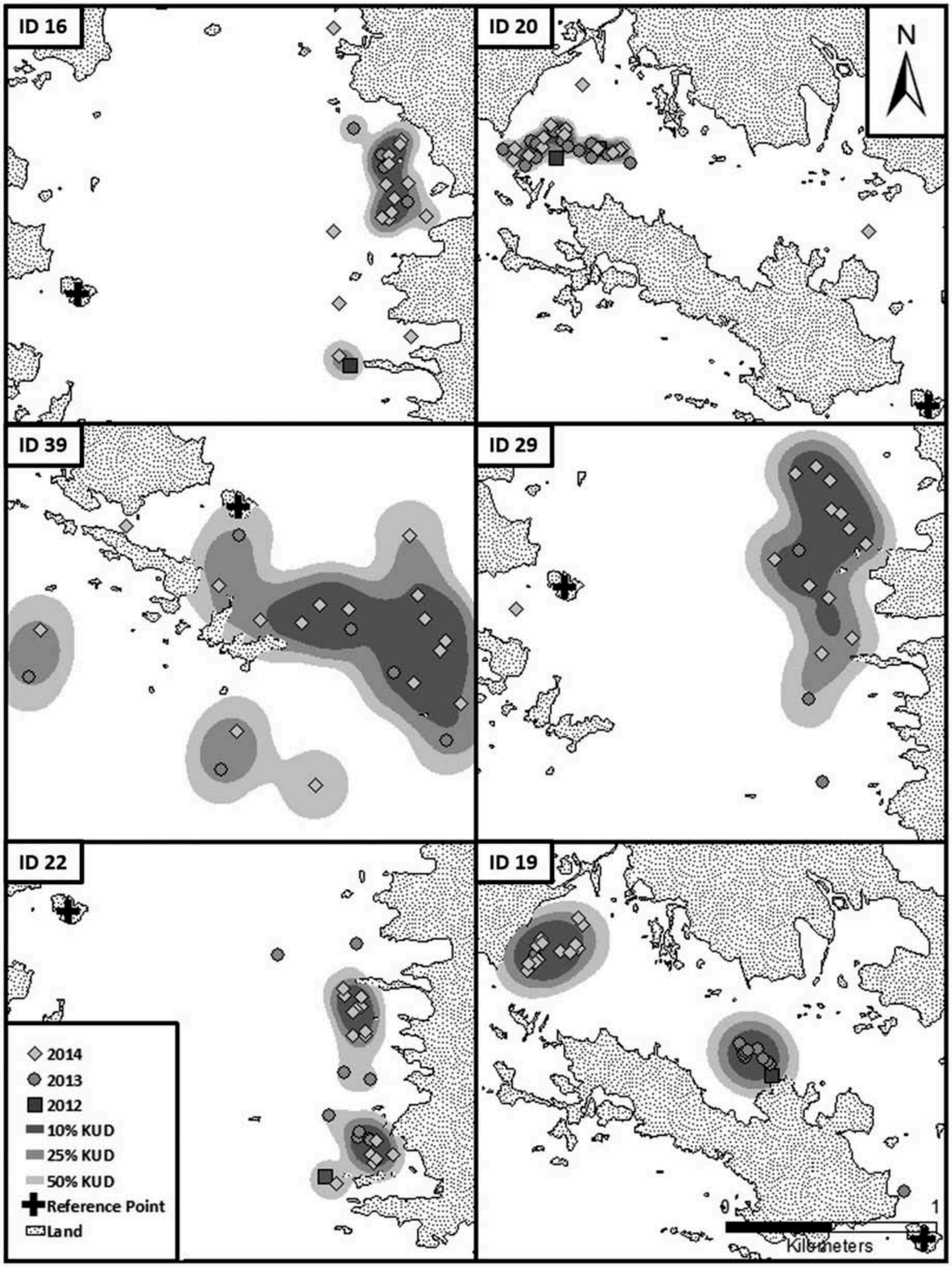

FIGURE 6. Yearly breakdown of locations from Muskellunge that were tracked in south Severn Sound, Georgian Bay, from 2012 to 2014 and their respective activity centers. Illustrative examples of clustering patterns are presented: tight clustering with one primary activity center (tag identification numbers [IDs] 16 and 20); loose clustering with one primary activity center (IDs 39 and 29); and tight clustering with split activity centers (IDs 22 and 19).

TABLE 5. Sex-based differences in spawning season habitat use by 18 radio-tagged Muskellunge in Severn Sound, Georgian Bay (partial Mantel test; significance set at $P < 0.05$ based on 999 permutations). Habitat use metrics (mean ± SE) are presented for each gender (KUD = kernel utilization distribution). Distance matrices for each habitat metric were respectively correlated with gender while weight at capture was held constant.

Habitat use metric	Males	Females	Mantel correlation	P
Maximum depth (m)	1.9 ± 0.2	2.6 ± 0.3	0.12787	0.042
10% KUD (ha)	7.2 ± 2.1	67.1 ± 22.5	0.18658	0.001
25% KUD (ha)	15.1 ± 5.1	127.7 ± 46.6	0.15920	0.001
50% KUD (ha)	28.4 ± 9.1	220.4 ± 89.4	0.13347	0.001

whereas studies using mark–recapture techniques have reported weaker fidelity (Crossman 1990; Jennings et al. 2011). This may be a result of behavioral differences between populations or, alternatively, a product of net avoidance. During the present study, we rarely recaptured tagged individuals despite the fact that they were frequently located in the immediate vicinity of deployed nets. Spawning site fidelity among Muskellunge also provides a mechanism for the genetically distinct populations (Koppelman and Philipp 1986; Kapuscinski et al. 2013) that are found throughout the Muskellunge's range. In Georgian Bay, Kapuscinski et al. (2013) identified three genetically unique populations along a 100-km reach of shoreline that extended from our southeastern region (Severn Sound) to our northeastern region (Pointe au Baril), where each population was separated by approximately 50 km. Bosworth and Farrell (2006) and Miller et al. (2001) documented similar genetic population structuring in the congeneric Northern Pike *Esox lucius*.

The literature indicates that male Muskellunge tend to arrive earlier to spawning grounds than females and then stay longer, whereas females are more often found staging offshore of the spawning grounds (Minnesota: Strand 1986; Mississippi River: Younk et al. 1996). Differences between sexes have been documented for Muskellunge during the spawning period. This is consistent with our observations of finding females in significantly deeper water, whereas males were usually found in shallower waters (<2 m), where spawning typically takes place (e.g., Farrell et al. 1996; Scott and Crossman 1998; Zorn et al. 1998). The fact that the smaller, shallower activity centers of male Muskellunge in Severn Sound were all in coastal wetland areas near probable spawning sites suggests that those males were staging at or near a spawning site. Female Muskellunge also showed spawning ground fidelity, but they staged in deeper waters over generally larger areas that were adjacent to multiple candidate spawning habitats. This appears to present the opportunity for females to spawn over a greater range of potential areas and to spawn multiple times during a given season (Lebeau 1991). Although we were unable to confirm that spawning had actually occurred, we did capture females that either (1) were full of eggs or (2) had no eggs but showed signs that they had recently spawned. Coupled with the observed degree of spawning ground fidelity, especially among males, we are confident that spawning did take place within the activity centers we determined for individuals and subpopulations. We propose that the site specificity and fidelity observed in male Muskellunge are driving the repeated use of potentially degraded breeding habitat, as females are spawning in locations near the staging males.

The results of this study were consistent with our hypothesis regarding spawning site fidelity as a mechanism for the absence of age-0 Muskellunge in Severn Sound; however, we did not directly address the presumed spatial association between spawning and nursery habitats. Since surveys of nursery habitat were conducted concurrently with this study, we are able to offer strong support for the spatial linkage of spawning and nursery habitats within each study region. Age-0 Muskellunge were found by seining in both northeastern Georgian Bay (during 2015; J. D. Weller, unpublished data; Figure 4A) and northern Georgian Bay (during 2012 and 2013; J. P. Leblanc, unpublished data; Figure 4B). One age-0 Muskellunge was found in the northeastern region west of Bigwood Island, within 300 m of a cluster comprising six locations that belonged mostly to one male (ID 58; Figure 4A). In the northern region, 17 nursery sites were identified. In particular, those towards the northwest end of Eager Bay and the western side of Plant Lake were in close proximity to the locations of adult Muskellunge during the spawning season (Figure 4B). Indeed, the nursery locations identified in 2012 were used to successfully guide the placement of nets during the 2013 tagging effort in the northern region. LaPan et al. (1996) similarly identified nursery sites in the St. Lawrence River that were in close proximity to capture sites or tracked locations of adults during spawning. Age-0 Muskellunge were not found in Severn Sound with this study (Leblanc et al. 2014), so we cannot evaluate the association between concurrent spawning season locations and nursery sites in the region. However, historic nursery sites (Craig and Black 1986) were close to the activity centers documented here (Figure 3). It is notable that the activity centers for south Severn Sound Muskellunge bordered six of the eight historic nursery sites in the region and were within 500 m of the remaining two nursery sites (Figure 3A). Furthermore, a previous Muskellunge telemetry study in Severn Sound (Black 1981, cited by Liskauskas 1996) found a Muskellunge using that same activity center. The continued use of this area by adult Muskellunge during the spawning season suggests that the multiple-year affinity we observed may in fact span decades.

Muskellunge in each of our Georgian Bay study regions showed an affinity for particular spawning grounds, and we have conclusive evidence of spawning ground fidelity in the southeastern region. Muskellunge may be unable to adapt to changing conditions if spawning habitat becomes degraded, as appeared to be the case in Severn Sound (Leblanc et al. 2014). Our findings highlight the importance of identifying and protecting Muskellunge habitat, which has long been a goal of managers (Craig and Black 1986; Farrell et al. 2007; Crane et al. 2015; Midwood et al. 2015). Shoreline modifications and anthropogenic impacts continue to be major stressors on spawning and nursery habitats (Dombeck 1986; Rust et al. 2002; Leblanc et al. 2014) and have been identified as critical issues for Lake Huron, including Georgian Bay (Liskauskas et al. 2007). Wetland mitigation strategies—notably habitat compensation or no-net-loss policies (e.g., Policy for the Management of Fish Habitats; DFO 1986)—are unlikely to be effective in offsetting lost or degraded Muskellunge habitat. The high affinity that adult Muskellunge display for specific spawning sites appears to be driven not by the suitability of that habitat but rather by the location of the habitat. Without a greater understanding of the mechanisms that drive spawning site fidelity (e.g., natal homing), the protection and restoration of identified breeding habitat should be of top priority if the overall management goal is to maintain a self-sustaining population of Muskellunge in Georgian Bay.

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