Spawning season distribution in sub-populations of Muskellunge in Georgian Bay

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Abstract

Loss of spawning and nursery habitat has been implicated as a major factor in the widespread decline of Muskellunge *Esox masquinongy* populations in N. America. Although there is limited evidence of spawning-site fidelity in the Great Lakes populations of Muskellunge, such behaviour could result in recruitment failure if individuals return each year to spawning sites that have become degraded. In this study, we compare the spawning behaviours of individuals across three Muskellunge sub-populations in Georgian Bay, Lake Huron to address the hypothesis that the use of specific spawning sites and spawning-site fidelity is independent of the suitability of that habitat for successful recruitment. The study regions in Southeastern, Northeastern, and Northern Georgian Bay have experienced different impacts from human development and sustained low water levels. We used radio telemetry to tag 49 adult Muskellunge and tracked them for up to three years (between 2012 and 2015). Sufficient multi-year data were only acquired for 18 individuals in the Southeastern region, but of those, 17 showed fidelity to at least one activity center over two or more years. We found that male Muskellunge occupied significantly smaller activity centers and shallower depths than females during the spawning season. The locations of adult Muskellunge during this study were found in close proximity to current and historic nursery sites identified in each region by other studies, supporting the close spatial linkage between spawning and nursery habitats. This is the first study that confirms spawning-site fidelity in Georgian Bay Muskellunge and supports the spatial association between spawning and nursery habitat. The repeat 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 habitat.

Introduction

Georgian Bay, Lake Huron currently supports a self-sustaining Muskellunge 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 may be responsible for reproductive failure in the sub-population of Muskellunge in southeastern Georgian Bay, including alteration of nursery habitat in coastal wetlands by sustained low water levels and increased human modification of the shoreline.

The Georgian Bay Muskellunge population, as with most Muskellunge populations, is managed to support and sustain a recreational fishery. Common strategies to protect Muskellunge populations have included restrictions on harvest size and possession limits (Wingate 1986; Casselman et al. 1999), and a strict catch-and-release ethic of dedicated anglers (Kerr 2007). Despite these efforts, intended to protect reproductively valuable adults, many populations have declined due to loss or degradation of suitable spawning and nursery habitat (Dombeck et al. 1984; Dombeck 1986; Zorn et al. 1998; Rust et al. 2002; Farrell et al. 2007). Survival rates of Muskellunge from egg through the first year are naturally very low (Scott and Crossman 1998; Farrell 2001), so additional stresses during that vulnerable time period could affect recruitment success. The 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 aquatic plant and fish communities (Midwood and Chow-Fraser 2012). Either could adversely affect the quality of the coastal wetlands that Muskellunge use for spawning and nursery (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 some structural complexity, usually provided by aquatic vegetation (Craig and Black 1986; Farrell and Werner 1999; Murry and Farrell 2007; Kapuscinski and Farrell 2014), as well as 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 its 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 degradation of nursery habitat can be a serious problem if Muskellunge cannot seek out suitable habitat when spawning or nursery habitat 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 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 Georgian Bay Muskellunge, this could explain why the age-0 Muskellunge can no longer be found in the relatively disturbed wetlands in the Southeastern portion of Georgian Bay (Leblanc et al. 2014). Assuming spawning 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 radio telemetry 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 and provide 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 a relatively undisturbed area underlain by Precambrian Shield and consisting of a complex array of sheltered embayments and protected wetlands (DeCatanzaro and Chow-Fraser 2011). This study was conducted at three regions in 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). Severn Sound (Figure 1B) covers approximately 200 km^2 and is underlain by limestone to the south and Precambrian Shield to the north. The Northeastern segment of the shoreline, where our work was focused, is characterized by a 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 (pop. 12,000) and the town of Honey Harbour (pop. 2,500) are located along the northeast shoreline of Severn Sound where most homes and cottages have road access. The Northeastern region (Figure 1C) consists of primarily Sturgeon Bay and the Pointe au Baril Channel (10 km^2). The area is underlain by Precambrian Shield and has generally steep-sloping nearshore bathymetry. During the summer months the population in the area is 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 has undergone some level of human modification, including docks, boathouses and maintained lawns. The Northern site (Figure 1D) covers approximately 20 km^2, consisting 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 while Plant Lake is connected by the inland channel to Eager Bay in the east and Georgian Bay to the west. The area is characterized by steep-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 area is limited to less than 100 seasonal cottagers, fishermen, and recreational boaters.

We conducted this study across these three regions to account for potential differences in terms of shoreline modification, nearshore bathymetry, and to evaluate spawning-season behaviour between geographically distinct populations.

Tagging and Tracking

Muskellunge tagging and tracking occurred in the spring of each year during spawning season (approximately April – May) and started approximately one to two weeks after ice-off. The exception to this was 2012 which was a very warm winter with open water on some areas of

Georgian Bay by late March. The tagging and tracking effort consisted of approximately two to three weeks and we attempted to be on the water each day, assuming 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 shoreline. Tagging in Severn Sound was carried out during the spring of 2012 (May 1 and May 2), 2013 (April 24 – May 9) and 2014 (May 7 – May 15), and in Pointe au Baril during spring of 2015 (May 15 – May 20), in conjunction with the Ontario Ministry of Natural Resources and Forestry (OMNRF) Spring Muskellunge Index Netting (SMIN; A. Liskauskas, unpublished data). Tagging in northern Georgian Bay took place during the spring of 2012 (May 25 and May 27) and 2013 (May 4 - May 18) by researchers and field technicians without assistance from OMNRF biologists.

Adult Muskellunge were caught with trap-nets (40 mm mesh, 1.83 m x 1.83 m crib) and hoop-nets (40 mm mesh, 91 mm diameter hoops) that were deployed for 24 hours in coastal wetlands. Muskellunge suitable for tagging (greater than 1000 g) were isolated and transferred to a floating pen (1.0 m x 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; these individuals were monitored in the floating pen and released when they appeared to have recovered. Research quality clove oil (Xenex Laboratories Inc., Coquitlam, BC, Canada) was used to anaesthetize the fish during surgery. A single dose (60 ppm) was added to the anaesthetic bath (60-100 L water obtained from the capture site) and a maintenance dose of 30 ppm 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 anaesthetic bath and monitored for up to 10 minutes until equilibrium was lost and opercular rate slowed. Fish were placed supine on a foam surgery platform. A maintenance dose of clove oil was supplied through a plastic tube inserted into the mouth and positioned to flow across the gills. Muskellunge were tagged with MCFT2-3A radio tags (LOTEK, Newmarket, Canada; 16mm diameter, 46mm length, 16g weight). Although a subset of tags transmitted pressure and temperature information, only locational data from the tags were examined for this study. An incision (2-3 cm) was made mid-ventral and anterior to the pelvic girdle and the tag was inserted. Tags were anchored to the body cavity by feeding the trailing whip antennae through a hollow 16-gauge needle inserted adjacent to the incision. The incision was closed with two or three interrupted monofilament 3-0 sutures. Total surgery time lasted 5-10 minutes, after which Muskellunge were transferred to a cradle secured in the floating pen and the fish were allowed to recover. Individuals took up to an hour to regain equilibrium and become responsive to external stimuli, at which point they were released.

Fish were not actively tracked until two weeks after their surgery. Tagged Muskellunge were tracked from an open boat with an SRX800 receiver and three-piece Yagi antennae (LOTEK, Newmarket, Canada). Where possible, the boat was positioned overtop the tracked fish and geographic coordinates were acquired with a handheld GPS (Garmin Ltd., 3-5m accuracy). When conditions precluded approaching the tagged fish (e.g. too shallow, wavy conditions), we approximated its 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 two years in Northern Georgian Bay and one year in Northeastern Georgian Bay) the data analysis focuses primarily on Severn Sound. We will present our results separately for two distinct sections in Severn Sound (South Severn Sound and North Severn Sound) because a greater effort was expended in South Severn Sound in terms of capture and tracking, and secondly because 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 to compare against results from Severn Sound to evaluate the transferability of results across different regions in Georgian Bay.

Spatial and Statistical Analysis

All spatial analyses were completed in ArcMap 10.2 (ESRI Inc., Redlands CA, USA, 2014) while statistical analyses were performed with PASSaGE 2 software package (Rosenberg and Anderson 2011) and JMP Version 12.0.1 (SAS Institute Inc, Cary NC, USA 2015). We imported all geographic coordinates corresponding to sites where Muskellunge had been captured or tracked during this study into the GIS environment. Capture locations were pooled with the tracking locations because the location of the capture and time of tagging were considered a spatially (±50m) and temporally (within 24 hours) accurate representation of a location used by the fish during spawning season. Since the purpose of this study was to investigate the distribution of adult Muskellunge during the spawning season, we only included those locations deemed representative of that period. This included all locations collected 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 post-spawning behaviour. We considered a Muskellunge to have finished spawning if locations were acquired late in the expected spawning season (i.e. mid to late May) and the individual was found using offshore areas away from potential spawning locations (i.e. coastal wetlands). Hereafter, we use of the term "locations" in reference to the observed locations of Muskellunge during this study, which includes the capture locations and all tracked locations representative of spawning-season behaviour. When locations were collected for an individual 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 "spawning grounds" as general habitat that are 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. visual observation or egg collection). We also imported the locations of historic (Craig and Black 1986) and current (JP Leblanc, unpublished data; J.D. Weller, unpublished data) Muskellunge nursery sites from each region to provide spatial context for the spawning-season locations acquired during this study relative to known nursery habitats.

Distribution during spawning season

We limited our formal analysis of spawning-season distribution to individuals with ≥ five locations. To characterize the distribution of a Muskellunge's locations during spawning season we calculated the average nearest neighbour distance ($\bar{d}_{min}$) for each individual as a relative measure of clustering or dispersion in the observed locations (O'Sullivan and Unwin 2010). We used Ripley's K function (Ripley 1976, cited by O'Sullivan and Unwin 2010) as a means to further group individuals based on the extent and type of clustering observed. Ripley's K compares the observed number of neighbouring points to the number of neighbours 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, at 40m increments to a maximum distance of 4000m (the maximum distance a Muskellunge moved over a one day period during this study). The maximum boundary was set to encompass the areas an individual could have moved to during our study. Confidence limits were established by 999 permutations.

Individuals were classified based on the significance of clustering over the majority of the distances evaluated. Clustering was defined as tightly clustered (T: significant clustering over the majority of distance bands), loosely clustered (L: non-significant clustering over the majority of distance bands), or dispersed (D: dispersion of points over 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 and not for an examination of 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 each year. We used the kernel density function in ArcGIS to estimate a Kernel Utilization Distribution (KUD), a technique 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) that 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 are interested in "core" use areas in this study, we bounded our activity centers using 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 activity centers. We calculated the total area within each activity center, excluding land, and pooled areas for all activity centers under each KUD boundary condition. We assessed spawning-ground fidelity based on repeated use of the same activity center over multiple years. Activity centers were also calculated for the sub-population by pooling the locations from all individuals to identify any regionally-important spawning grounds.

To test differences in the size of activity centers and the depths of areas used by male and female Muskellunge we used a Partial Mantel Test. This tests for correlations between two distance matrices while controlling for the effects of a third (Legendre and Legendre 1998). We tested if male and female Muskellunge were using different depths (sex = Matrix 1, maximum depth at SSL = Matrix 2) or different sized activity centers (sex = Matrix 1, KUD area = Matrix 2). Matrix 3 included weight at capture which was held constant to account for differences in size between males and females. Available topographic and bathymetric data (National Oceanic and Atmospheric Administration, Ontario Ministry of Natural Resources and Forestry) were compiled to create a digital elevation model (DEM) to estimate the maximum depth at each location. The depth comparison refers to the maximum water depth corresponding to the observed location, not the depth at which the fish were found within the water column. Results were tested for significance by permutation (999 times at $\alpha = 0.05$).

Results

Tagging and Tracking

A total of 49 Muskellunge were tagged and tracked from 2012 to 2015 across all three of our study regions (Figure 2). We tagged 24 adult Muskellunge in Severn Sound during 2012-2014 (Table 1). Capture and tracking efforts in this region focused primarily along the Northeastern segment of the Severn Sound shoreline. A total of 298 locations were acquired over the three years of tagging and tracking in Severn Sound (245 in South Severn Sound, 53 in North Severn Sound; Figure 3A and Figure 3B respectively). Of the 24 tagged Muskellunge, 22 were confirmed active as of the end of May 2014. The signal from ID 15 was found in the same location for the duration of 2013 tracking and again in 2014 so we presume the fish died prior to the 2013 season. 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 for a total of 86 locations (Figure 4A; Table 2). In the Northern region, we tagged and tracked 12 Muskellunge for 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 was acquired that year.

Distribution during spawning season

There were 18 Muskellunge from Severn Sound with ≥ five locations. Of those, 17 were tracked for more than one season and only 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 m ± 29 (ID 19) to 600m ± 213 (ID 28) with a median value of 162 m (Table 3). Of the eight females, all had $\bar{d}_{min}$ greater than the median and with the exception of ID 18 and ID 31. The majority of males (7 of 10) had $\bar{d}_{min}$ values less than the median, with the exceptions of ID 35, ID 40, and ID 41. The $\bar{d}_{min}$ values were consistent with the groupings based on Ripley's K function (Table 3). Of the 18 individuals evaluated, we classified 10 as tightly clustered, seven as loosely clustered, and one as dispersed. The tightly clustered individuals were mostly males (8 of 10) except for ID 18 and ID 31. The loosely clustered individuals were mostly females (5 of 7) with the exceptions of ID 40 and ID 41. The only dispersed individual was a female, ID 28.

All 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 of some individuals, some delineated activity centers only contained one location and these were eliminated from further consideration. There was a large range in 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 ha-866.2 ha at 50% KUD). The number of activity centers delineated varied but several patterns of use were 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. ID 18, ID 29, ID 20; Figure 5) or those that had several but one “primary” activity center was obvious and accounted for the majority of the total activity center area (e.g. ID 11, ID 39, ID 16; Figure 5). The “secondary” activity centers were generally areas that an individual was only found 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), and ID 22 was split between two activity centers north of Waubaushene (Figure 6). ID 28, the only individual that was classified as dispersed, was found across nearly all of South Severn Sound (Figure 5) during this study but was found 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 more than one kilometer (Table 4). ID 37 and ID 19 had the most spatially distinct activity centers that were separated by 854m and 827 m, respectively (10% KUD boundary).

Some level of spawning-ground fidelity was observed in all but one fish tracked in Severn Sound for two or more years (17 individuals; Table 4). Since we measured fidelity as the use of the same activity center over multiple years, the 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 (ID 18, ID 40, ID 41). Multi-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 (Figure 6; ID 20, ID 16) or loosely clustered individual (Figure 6; ID 29, ID 39). Muskellunge were found using mainly these activity centers over multiple years, although multi-year use of other, smaller activity centers was also observed (ID 39 and ID 16). ID 19 and ID 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 favoured one activity center in each of those years.

The activity centers for the pooled locations from each South Severn Sound and North Severn Sound revealed several major spawning grounds. In South Severn Sound (Figure 3A), the channel on the north side of Green Island was a hotspot for spawning activity in the area, as well as 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 distribution. 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 for males was 9.5 ha (n = 10; SE = 2.9) compared to 77.4 ha (n = 8; SE = 25.1) for females (Partial Mantel Test, $P = 0.002$). The magnitude of the difference in activity center areas between males and females was consistent at the 25% KUD and

50% KUD boundary conditions. ID 18 and ID 31 were both females with total activity center areas, 1.9 ha and 14.9 ha, respectively (10% KUD), closer to the male average while the remaining females had activity center areas in excess of 20 ha. Similarly, two males (ID 40 and ID 41) had activity center areas (21.2 ha and 30.1 ha, respectively; 10% KUD) that were larger than those of other males (< 12ha; 10% KUD). Female Muskellunge were also found in significantly deeper areas than were males (females: 2.4m ± 0.1 males: 1.8m ± 0.1; Partial Mantel Test, $P = 0.023$; Table 5). In general, males occupied smaller areas and were found in shallower waters than were females.

Tracking data from the Northern and Northeastern regions appeared consistent with our observations from Severn Sound. Of the Northeastern Muskellunge 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 size of the areas the individuals were using appeared consistent with that of the tight clustering and loose clustering groups identified in the Severn Sound analysis (approximately 10ha for males). Tracking data from the Northern region were sparse during spawning season and was mostly from the 2013 season. ID 8, a male, appeared to be using a specific area towards the northeast shore of Eager Bay which was also where it was captured in 2012. Besides ID 8, there were insufficient multi-year data to provide further support for spawning-ground fidelity.

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 are lower compared to the rest of eastern and northern Georgian Bay, they are still in excellent condition relative to the rest 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 development 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 experiencing much more significant modifications to the shoreline, such as the Niagara River (Kapuscinski et al. 2014) and the Fox River (Kapuscinski et al. 2007). Age-0 Muskellunge were found in both our Northern and Northeastern region concurrent with our study, despite also having experienced the same sustained low water levels as in 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, climate) could be affecting the recruitment success of age-0 in Severn Sound. Regardless, Muskellunge in Georgian Bay should theoretically be able to seek out other suitable breeding habitat since they are capable of moving large 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. Yet, 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.

The movement of Muskellunge 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) and we observed an affinity for particular areas during spawning in each of our study regions, consistent with previous observations. Similarly, spawning-site fidelity has also been documented in Muskellunge populations in multiple waterbodies throughout its 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 this behaviour in Georgian Bay Muskellunge. Of the individuals 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 tagged in South Severn Sound during 2012. These fish were tagged relatively late in the spawning season but were tracked for the entirety of the following two seasons. A full season of tracking was needed before preferential site use was obvious and an additional season to confidently claim these individuals were displaying spawning-site fidelity. Other multi-year telemetry studies (LaPan et al. 1996; Younk et al. 1996) have also observed strong spawning-site fidelity for individual fish, but when using mark-recapture techniques, others have reported weaker fidelity (Crossman 1990; Jennings et al. 2011). This may be a result of behavioural differences between populations, or alternatively a product of net avoidance. During the course of this study we rarely recaptured tagged individuals, despite their being frequently found in the immediate vicinity of deployed nets. Spawning-site fidelity among Muskellunge also provides a mechanism for the genetically distinct populations (Koppleman and Philipp 1986; Kapuscinski et al. 2013) of Muskellunge found throughout their range. In Georgian Bay, Kapuskinski et al. (2013) identified three genetically unique populations along a 100km reach of shoreline that extended from our Southeastern (Severn Sound) to Northeastern regions (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 shows that male Muskellunge tend to arrive earlier to spawning grounds than females and then stay longer, whereas females were more often found staging offshore of the spawning grounds (Strand 1986, Minnesota; Younk et al. 1996; Mississippi River). 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 (< 2m), where spawning usually takes place (e.g. Farrell and Werner 1996; Scott and Crossman 1998; Zorn et al. 1998). That the smaller, shallower activity centers of male Muskellunge in Severn Sound were all in coastal wetland areas near probable spawning sites suggest that they are staging at or near a spawning site. While female Muskellunge also showed spawning-ground fidelity, 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 potentially multiple times during the season (Lebeau 1991). Although we were unable to confirm that spawning had actually occurred, we did capture females that were either full of eggs, or had no eggs and showed signs that they had recently spawned. Coupled with the degree of spawning-ground fidelity observed, especially among males, we are confident that spawning did take place within activity centers determined for individuals and sub-populations. We propose that the site-specificity and fidelity observed in males is driving the repeat use of potentially degraded breeding habitat, in that female Muskellunge are spawning in locations near the staged 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, but did not directly address the presumed spatial association between spawning and nursery. 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 (2015; J.D. Weller unpublished data; Figure 4A) and Northern Georgian Bay (2012 and 2013; JP Leblanc unpublished data; Figure 4B). One age-0 Muskellunge was found in the Northeastern region within 300 m of a cluster of six locations west of Bigwood Island 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 locations of adult Muskellunge during spawning season (Figure 4B). Indeed, the nursery locations identified in 2012 were used to successfully guide placement of nets during the 2013 tagging effort in that region. Lapan et al. (1996) similarly found nursery sites in the St. Lawrence in close proximity to capture sites or tracked locations of adults during spawning. No age-0 Muskellunge were 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 in close proximity to the activity centers documented in this study (Figure 3). It is notable that the activity centers for the South Severn Sound Muskellunge bordered six of the eight historic sites in the region and were within 500m of the remaining two 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 spawning season suggests that the multi-year affinity that we observed in this study 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. It is possible that 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 et al. 1986; Leblanc et al. 2014; Rust et al. 2002) and have been identified as critical issues on 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 effectively offset lost or degraded Muskellunge habitat. The high affinity that adult Muskellunge display for specific spawning sites does not appear to be driven by the suitability of that habitat, but rather the location of that habitat. Without further understanding the mechanisms driving spawning-site site fidelity (e.g. natal homing), protection and restoration of identified breeding habitat should be top priority if the overall management goal is to maintain a self-sustaining population of Muskellunge in Georgian Bay.

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