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Spatial ecology of reintroduced walleye (*Sander vitreus*) in Hamilton Harbour of Lake Ontario

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ABSTRACT

Many coastal embayments in the Laurentian Great Lakes have been subjected to extensive human physical modification and pollution that has led to the loss of freshwater biodiversity. For example, Hamilton Harbour is a large coastal embayment situated at the western end of Lake Ontario, with a long history of industrial and urban development that has resulted in the loss and degradation of aquatic habitat and the extirpation of several fish species. To restore the fish community in Hamilton Harbour, several attempts have been made to increase apex predator biodiversity by reintroducing native walleye (*Sander vitreus*). To assess how reintroduced (i.e., stocked) walleye use Hamilton Harbour, we used acoustic telemetry to characterize the residency of individuals within the boundaries of the harbour as well as their seasonal space use, with a focused interest on the spring spawning period. During the 1 yr tracking period tagged walleye spent an average of 357 days (range 135–365 days) within the harbour. Most individuals (12/15) remained within the harbour during the entire spring spawning period, and over half of the tagged fish departed ($n = 7$) at the end of summer and beginning of fall. Core use areas appeared to gradually shift more easterly as the seasons progressed from winter to summer. Results from this study indicate that stocked fish are resident within Hamilton Harbour for most of the year, including the reproductive period, which suggests that stocking efforts to re-establish walleye populations may be an effective restoration strategy if recruitment is successful.

Introduction

Through regulation of food web dynamics, recycling of nutrients, and transportation of energy, fish play a major role in enhancing the biodiversity and integrity of aquatic ecosystems (Holmlund and Hammer, 1999; Lynch et al., 2016). Inland fishes and fisheries represent diverse economic, cultural, nutritional, and ecological values in North America (Malvestuto and Hudgins, 1996). However, the degradation of water quality and modifications of physical habitat by urbanization, industrialization and agriculture, combined with resource exploitation and invasive species have substantial negative effects on freshwater ecosystems (Richter et al., 1997; Strayer and Dudgeon, 2010). Fishery professionals have been successful in addressing many of these threats and challenges by imposing regulations that restrict exploitation, enhance the conservation and restoration of fish habitat, and assist control of invasive species (Arlinghaus et al., 2016). The Laurentian Great Lakes are an example of a large freshwater ecosystem heavily affected by multiple anthropogenic stressors. In this region, fisheries have undergone dramatic changes in the 20th Century (Christie, 1974; Hansen, 1999; Allan et al., 2005). Consequently, ongoing, evidence-based management efforts are therefore vital to safeguard long-term sustainability of Great Lakes fisheries (Landsman et al., 2011).

Walleye (*Sander vitreus*) is an ecologically and economically important piscivore, indigenous to all the Laurentian Great Lakes (Brownscombe et al., 2014). As such, their movement ecology has been studied using mark-recapture and biotelemetry throughout the Great Lakes in efforts to understand habitat use, reproductive biology (i.e. spawning sites, dispersal rates, homing tendencies), and stocking success (Crowe, 1962; Todd and Haas, 1993; Fielder and Thomas, 2006; Hayden et al., 2014). Walleye have been known to travel long distances to spawn in deep, gravel-bottomed, tributaries, lake shoreline and shoals, before returning to more suitable feeding areas post spawning (Fielder, 2002; Hayden et al., 2014). There is also evidence of high levels of spawning site fidelity (Bozek et al., 2011; Hayden et al., 2017). Seasonal migrations are common as walleye seek out desirable prey (Bowlby and Hoyle, 2011; Hoyle et al., 2017a, 2017b) and thermal conditions (Peat et al., 2015; Raby et al., 2018). Walleye in

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eastern Lake Ontario are known to travel into the Bay of Quinte to spawn in April, and then return to eastern Lake Ontario post-spawning. It is thought that adult walleye avoid warm temperatures in the upper Bay of Quinte, forage on abundant alewife (*Alosa pseudoharengus*) prey during the summer in the lower bay and eastern Lake Ontario, and then return up the Bay of Quinte during the fall to prey on young-of-the-year fishes (Bowlby and Hoyle, 2011). To date, research has focused on wild populations, particularly in Lakes Erie and Huron, but much less is known about movements of stocked walleye which have been introduced to some areas of the Great Lakes where wild populations were depressed or extirpated.

Hamilton Harbour, a 21 km^2 embayment at the western end of Lake Ontario (Fig. 1), was Canada's largest contaminated site in the Great Lakes and designated as an Area of Concern (AOC) in 1985 (Hamilton Harbour RAP, 2003). The harbour has been the focus of restoration efforts for over 30 years with the bulk of the physical habitat enhancements constructed by 1996. As of 2006, after 15 years of restoration activities and improved water quality management, the state of the fish community had improved (Hall et al., 2006); however, the fish community continues to reflect an impaired ecosystem (Brousseau and Randall, 2008; Boston et al., 2016). Walleye were purportedly extirpated from Hamilton harbour during the mid-20th century, and multiple efforts have been made to reintroduce this ecologically and economically valuable species into the harbour. In the 1990s, the Ontario Ministry of Natural Resources and Forestry (OMNRF) transferred adult fish from the Bay of Quinte, Lake Ontario and stocked small numbers of fingerlings originating from Bay of Quinte strain fish. The abundance of these stocked walleye declined in OMNRF's Nearshore Fish Community Index Trap Netting (NSCIN) surveys conducted between 2006 and 2012, suggesting stocking efforts were not successful at re-establishing a naturally reproducing population (Hoyle, 2015). Stocking efforts were resumed beginning in 2012, with further additions of fish in subsequent years (of the same genetic strain; Electronic Supplementary Material (ESM) Fig. S1). NSCIN efforts in 2014 observed walleye catch rates 20% higher than their target catches (Hoyle, 2015), and netting in subsequent years indicated that the walleye stocked in 2012 showed high survival and growth rates.

Understanding Hamilton Harbour reintroduced (i.e., stocked) walleye movement, migration, and space-use throughout the year will enable fisheries managers to determine what habitat features and environmental conditions stocked walleye select and provide guidance for future habitat restoration, such as physical habitat addition and addressing water quality issues. Movement and distribution patterns during walleye spawning season could focus efforts to locate spawning areas and guide subsequent egg and fry survival studies. The objectives of this study were to 1) determine the extent and seasonal patterns of harbour residency for walleye and 2) characterize seasonal patterns of space use within the harbour. We hypothesized that the walleye would follow a post-spawning outmigration pattern similar to Bay of Quinte/Eastern Lake Ontario and Lake Erie walleye.

Methods

Study location

This study was set in Hamilton Harbour, at the western end of Lake Ontario (43.30048 N, 79.80591 W; Fig. 1). The western, northern and north-eastern portions of the harbour are characterized by rocky shorelines, shallow vegetated areas, and man-made rock islands and shoals. The southern shoreline, however, is characterized by hardened

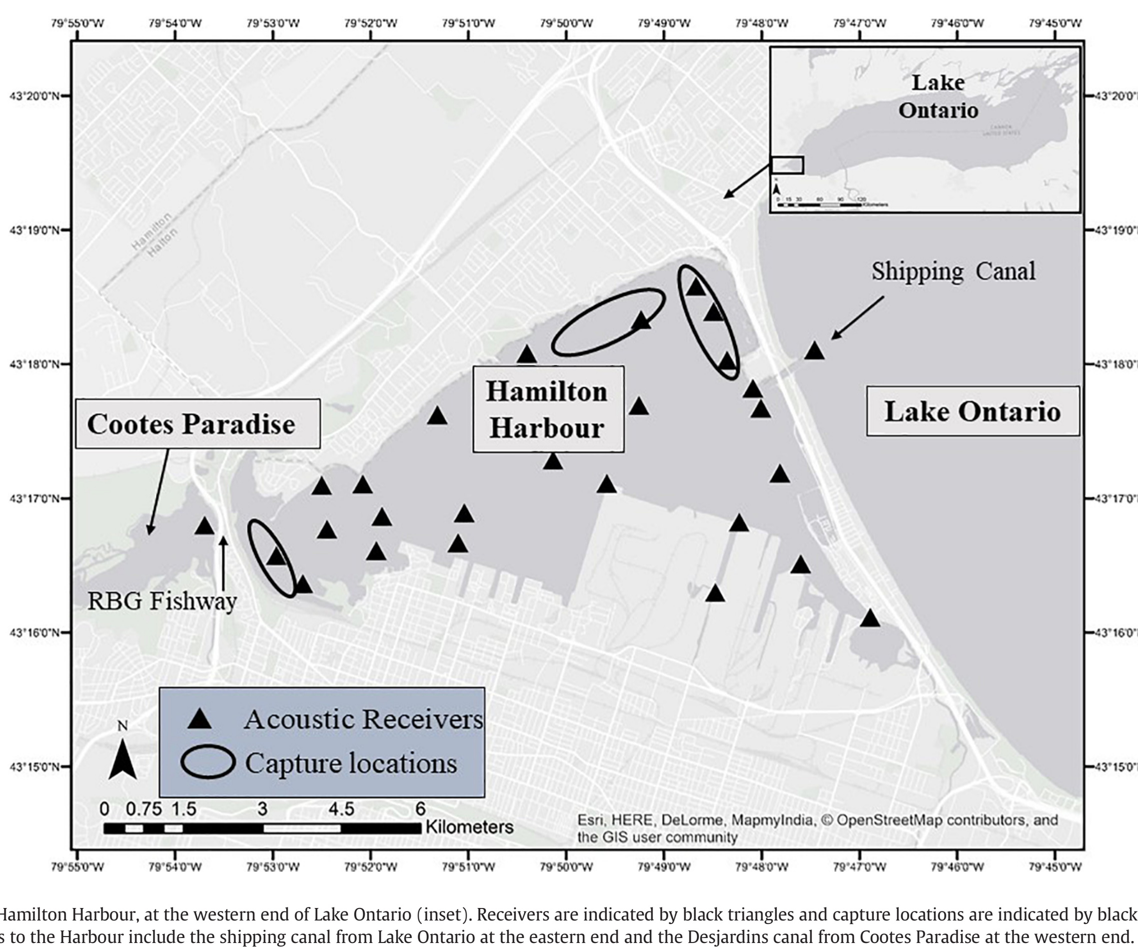

Fig. 1. Map of Hamilton Harbour, at the western end of Lake Ontario (inset). Receivers are indicated by black triangles and capture locations are indicated by black circles. Available entrance points to the Harbour include the shipping canal from Lake Ontario at the eastern end and the Desjardins canal from Cootes Paradise at the western end. Fish passage into Cootes Paradise is regulated and monitored via the Royal Botanical Gardens (RBG) fishway.

shorelines (steel and concrete walls), two steel plants, and several marinas. The maximum depth in the harbour is 24.9 m. The study area was divided into Cootes Paradise Marsh to the western end of the harbour the central main harbour, and Lake Ontario. The Royal Botanical Gardens Fishway connects the marsh to the harbour at the western end and the shipping canal at the eastern end connects the harbour to Lake Ontario (Fig. 1).

Receiver array

In the summer of 2015, 27 acoustic receivers (Vemco-Amirix, VR2W 69 kHz, Bedford, Nova Scotia) were deployed throughout Hamilton Harbour. Receivers were positioned to 1) maximize spatial coverage, 2) cover a variety of available types of habitat, and 3) determine whether tagged fish left the harbour (Fig. 1). Receivers close to shore were cabled to structures such as concrete walls or trees, and receivers at the offshore locations (further than 30 m from shore) were deployed with an anchor and a U-shaped mooring that could be retrieved with a grapple and winch. Receiver deployment occurred from August 6th to August 28th, 2015. They were downloaded and serviced in April (13th–22nd) 2016 and again in October (22nd–29th) 2016. As such, the 12-month passive monitoring period commenced from October 21st, 2015, to October 20th, 2016, inclusively, once all receivers were in position and transmitters deployed. Data collected prior to installing the full array or deployment of walleye transmitters were not used in the analyses to balance sampling effort throughout the study period.

Fish capture and transmitters

Most of the walleye ($n = 17$) used in this study were captured in August 2015, in trap nets set as part of the OMNRF's NSCIN survey (Lester et al., 1996). The remaining fish ($n = 8$) were captured in October 2015, with either trap nets or using an electrofishing boat (Smith-Root electrofishing boat model SR 18.EH; 250 V and 7 A for intervals of ~1000 s) (Table 1). Upon capture, walleye were placed in holding tanks filled with ambient lake water to await surgical procedures. During the capture period, no tagged walleye were recaptured while netting or electrofishing.

Fish were immobilized using either a Portable Electroanesthesia System (PES; Trushenski et al., 2012, Rous et al., 2015) or using the boat's e-fishing electrodes - methods that have previously been used to immobilize fish for surgeries (Jennings and Looney, 1998) including walleye (Vandergoot et al., 2011). Individuals were placed in a padded trough, oriented ventrally, and to maintain normal respiration during the surgeries, ambient lake water was poured into the trough to cover both the head and gills. Water was refreshed throughout each surgery. Transmitters fitted with pressure sensors to determine depth (Vemco V13P-1x-069k-1-0034m, 13 mm diameter, dry mass 11 g, battery life 1386 days) were inserted into the body cavity through a 2–3 cm midventral incision. The acoustic transmitters were manufactured with a random delay range of 130–270 s to reduce transmitter collisions from multiple fish. Incisions were closed with 2-3 interrupted sutures (3-0 polydioxanone-II violet monofilament, 24 mm; Ethicon, USA). All surgical equipment and tags were cleaned with 10% povidone-iodine solution before each surgery. An external anchor tag (Floy Manufacturing Inc., USA) printed with a unique identification number, and Carleton University's phone number was then inserted into the muscle by the dorsal fin. Total lengths were measured for each fish before they were placed into the recovery live well containing fresh, recirculating lake water. The average processing time was 3.5 min and the fish typically recovered within 10 min. To ensure full recovery of fish prior to release, fish were tested for sufficient equilibrium, body flex, tail clamp, and eye movement (Raby et al., 2012). Fish were released within 100 m of their capture location. Three fish died during the August surgeries, possibly because of warm water and the duration of their holding in the trap nets, and possible exposure to hypoxic waters. Fish handling and surgical procedures were approved and followed a Canadian Council on Animal Care protocol administered by Carleton University.

Table 1
Individual walleye identification number, tagging date, fish total length (TL), the percentage of study spent within the harbour, and the (unweighted) minimum and maximum seasonal 95 and 50 Percent Volume Contour area (km^2).

Walleye ID	Tagging date	TL (mm)	Residency in Harbour (%)	95PVC range (km^2)	50PVC range (km^2)
754	12-Aug-15	521	1	N/A	N/A
755	12-Aug-15	490	100	2.2–9.0	0.3–1.8
756	13-Aug-15	700	69	0.4–9.4	0.0–2.0
759	13-Aug-15	471	100	6.5–9.0	0.7–2.6
760	13-Aug-15	512	85	2.6–7.8	0.2–1.2
761	13-Aug-15	485	37	[a]7.8–9.0	[a]1.0–2.3
766	13-Aug-15	430	52	3.6–9.6	0.3–2.1
769	13-Aug-15	513	94	3.6–10.2	0.4–2.3
79	20-Oct-15	520	100	2.1–8.9	0.4–2.0
83	20-Oct-15	515	99	5.4–9.0	0.8–1.4
763	20-Oct-15	506	98	4.5–7.5	0.2–1.2
764	20-Oct-15	570	98	2.5–6.4	0.3–0.8
765	20-Oct-15	521	87	3.29–8.08	0.3–1.2
771	20-Oct-15	562	100	3.6–8.9	0.04–0.7
772	20-Oct-15	555	100	5.1–9.8	0.77–1.8
774	20-Oct-15	525	96	5.6–10.2	0.87–1.8

[a] ID761 was not present during the summer.

Data preparation

Exported detection data from receivers were sorted and plotted on a "per fish" basis to visually check for mortality or expelled tags. Any detections recorded continually at a similar depth and on the same receiver(s) throughout the study period were removed from the database. False-positive detections can occur when multiple transmissions collide when detected by a receiver, resulting in erroneous tag IDs being recorded (Skalski et al., 2002; Pincock, 2011). Single detections and random tag IDs were filtered and removed from the data using R Statistical Environment (R Core Team, 2018). Nine fish were removed from the analyses as they were potentially harvested, died at some point after tagging, or had expelled their transmitter. An additional fish was removed from analysis because it exited the harbour shortly after release and only returned for two days (ID = 754). Consequently, data from fifteen individuals were analyzed within the 12-month study period. Residency per individual across the 365 days of the study was plotted to visualize departures throughout the year.

Residency

Residency within three zones (Cootes Paradise, Hamilton Harbour, and Lake Ontario; Fig. 1) was determined using fish capture information obtained from the Royal Botanical Gardens fishway staff and the two receivers at both ends of the shipping canal into Lake Ontario. Fish that were detected at either of the canal receivers were isolated and the direction of travel was determined. There is no detection range overlap between the two receivers. Therefore, fish were deemed to have exited the harbour after a detection was recorded on the inside receiver followed by the outside receiver, and subsequently not heard on any receiver within the harbour. Residency within the harbour was calculated as a proportion of the total number of days in the study and season.

Spatial analysis

After data filtering, the telemetry data were used to determine an individuals' Center of Activity (COA; Simpfendorfer et al., 2002). The COA algorithm produced a weighted, arithmetic mean position for each hour the fish was detected within the acoustic array. After successive visual trials, an interval of 1 h was selected as walleye are a mobile fish species and two-hour intervals are more suitable for sedentary species (Simpfendorfer et al., 2002; Matley et al., 2016). However, the use of COA did mean that final fish positions were constrained to areas that fell within the receiver array and therefore were biased away from more coastal areas that generally fall outside of the array. Hourly COAs were imported into ArcMap (ESRI, 10.4.1) to calculate individual seasonal kernel-utilization distributions (KUD; Worton, 1989) from which 50 and 95 Percent Volume Contours (PVCs) were obtained to show activity space (95% of predicted space use) and core ranges (50% of predicted space use). A smoothing factor of 500 m and grid size of 5 m^2 were used in all KUD estimations, based on an Incremental Spatial Autocorrelation analysis in ArcGis (ESRI) and successive visual trials testing different values. Individual 95 and 50 PVC raster files were combined into a single layer to visualize the extent of overlap in activity space and core ranges amongst individuals (after Veilleux et al., 2018). The resulting raster file was re-classified to show the number of individuals using an area during each season (as described below).

Detection efficiency

Five sentinel transmitters (Vemco V13-1x-069k-3, 13 mm diameter, dry mass 11 g, battery life 1825 days) were deployed throughout the harbour to determine seasonal variability in array performance. Unfortunately, a full chain of two receivers and three sentinel transmitters were stolen just after the spring 2016 download and were no longer detected on any of the surrounding receivers or by the VR100 hydrophone during active tracking attempts. Data collected on these two receivers were not included in this study. Daily detection probabilities were calculated using Vemco's Range Test software (actual detections/expected detections) using the two remaining sentinel transmitters at the eastern end of the harbour. Transmitters were positioned at distances 161 m, 210 m, 273 m, and 347 m from receivers and data from all four distances were grouped together to determine seasonal trends.

Statistical modelling procedures

For both the residency and activity-space analyses, we examined the data at a seasonal level where seasons included fall (September–November), winter (December–February), spring (March–May), and summer (June–August). Seasons were classified to correspond with biologically meaningful thermal periods within the harbour. Hamilton Harbour experiences thermal stratification and the 'summer' months of June, July, and August were selected as they were fully within the stratified period (ESM Fig. S2). Spawning behaviour for walleye is known to occur after ice-off in March and April, and spawning activity was corroborated in mid-April with opportunistic electrofishing surveys by Fisheries and Oceans Canada (D. Reddick, pers. comm.). Spring and fall periods represented the transition period between the comparatively stable cool temperatures in the winter and stratification in the summer. This classification ensured that the study period contained four biologically relevant seasons.

Daily detection efficiencies were used to determine seasonal changes in the performance of the acoustic array. The median detection rates were calculated per season and used to weight each individual's seasonal 95% and 50% activity spaces. This was achieved by multiplying each activity space value by one minus the seasonal median detection efficiency.

Relative differences amongst seasons in the proportion of time spent within the harbour and size of both the weighted 95% and 50% activity-space sizes were analyzed using Generalized Linear Mixed effects Models (GLMM). All three models included fish identification number as a random effect, and season as a fixed effect. Data exploration was performed using standard tools including Cleveland dot plots (to identify outliers) and box and whisker plots (to identify relationships between continuous and categorical variables). Residency data were binomially distributed and fitted using the 'lme4' package (https://cran.r-project.org/web/packages/lme4/lme4.pdf). Activity space models were normally distributed and generated using the 'nlme' package (https://cran.r-project.org/web/packages/nlme/nlme.pdf). A variance structure was included to account for residual heterogeneity (constant variance structure), as opposed to transforming the response variable, which can possibly alter the relationship with the predictor variable (Zuur et al., 2009). If the model indicated a significant result for seasonal effect, a Tukey post-hoc test using the 'multcomp' package (Hothorn et al., 2008) was used to make pairwise comparisons. Residuals were plotted to assess parametric assumptions. Residual independence was determined by generating correlation lag plots, using the 'acf' function (Fox and Weisberg, 2011), which indicates autocorrelation in observations.

Results

Twenty-five walleye were tagged in August and October 2015, ranging from 430 to 570 mm in total length (mean of 517 mm) and with one larger individual (700 mm; Table 1). Acoustic data were collected from 21st October 2015 to 20th October 2016 and used to create 152,300 COA locations. Sixteen walleye were found to be alive throughout the entire study with one individual suspected to be a transient walleye as it only spent 2 days within the harbour during the study and was consequently dropped from further analysis. The COA locations for fifteen walleye were plotted per season prior to running the Kernel Density Estimates tool in ArcMap (ESRI, 2017).

Residency

No walleye were found to have passed through the RBG fishway during the study period therefore residency in Cootes Paradise was nil. Tagged walleye were present within the harbour for 135–365 days (median = 357; mean ± s.e. = 323 ± 19 days), including six walleye that never left the harbour (Fig. 2). The lowest residency occurred in fall with an average of 75% of the season spent within the harbour, followed by summer (89%), winter (91%), and spring (95%). Of the nine walleye that did leave the harbour, residency during fall was significantly lower than spring, winter, and summer ($p < 0.0001$), and these fish were more resident in spring than in both summer and winter ($p < 0.0001$) (Tables 2 and 3; Fig. 3). Twelve individuals remained within the harbour for the entire spring period. Several walleye ($n = 7$) departed prior to the fall turnover, which occurred between 13th–28th September (Fig. 2).

Detection efficiency

The detection efficiency data showed some seasonal variation at the eastern end of the harbour, with median detection probabilities the highest for Winter (93%) and Spring (92%), then Fall (88%) and Summer (81%) (ESM Fig. S3).

Space use (extent)

Weighted activity space areas ranged from 0.4 km^2 to 11.4 km^2 (mean = 7.2 ± 0.5 km^2) and core use ranged from 0.02 km^2 to 2.9 km^2 (mean = 1.2 ± 0.1 km^2). Walleye had the largest activity space in the fall (mean = 8.7 ± 0.5 km^2), approximately double their activity space in the summer (4.5 ± 0.5 km^2). There were no apparent differences in size of activity space between fall and winter ($p = 0.17$), fall and spring ($p = 0.86$), and winter and spring ($p = 0.50$), whereas summer was characterized by the smallest activity space (in all cases, $p < 0.001$; Fig. 4; Tables 4 and 5 for 95PVC; Supplementary material Tables S1–S2 for 50PVC core-use). A repeat analysis of the original, unweighted areas showed the same overall trends amongst the seasonal activity space and core use (Supplementary material Table S3–S4) There was no significant difference between the area used by

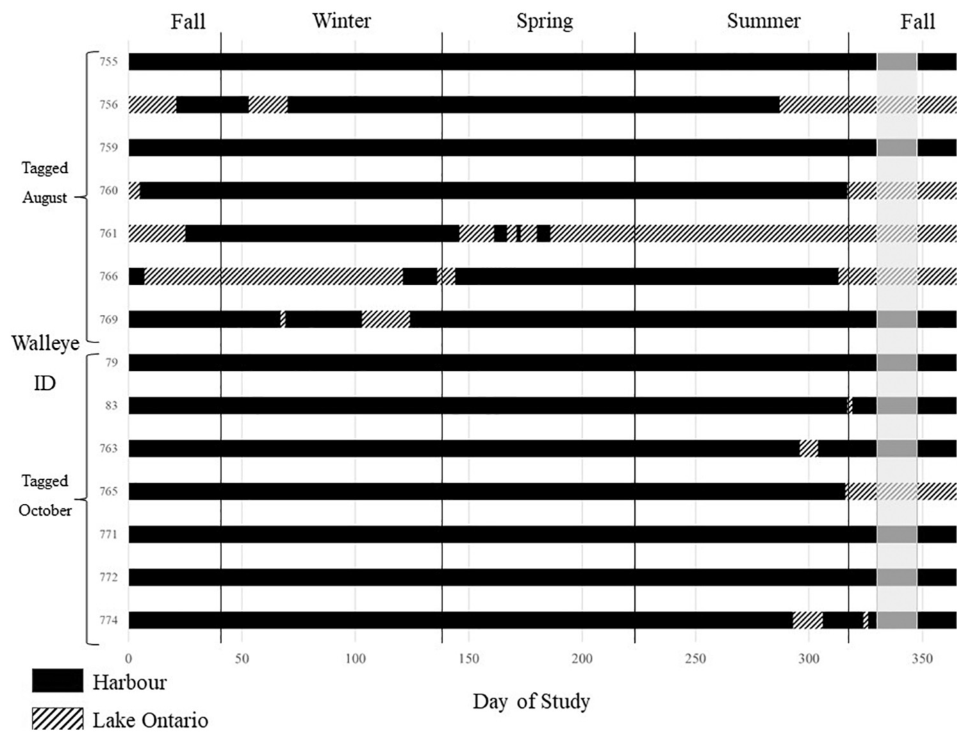

Fig. 2. *Sander vitreus* residency within Hamilton Harbour (solid bars) and Lake Ontario (hashed bars) of the two tagging batches (August and October) for 21st October 2015 to 10th October 2016.The light grey rectangle depicts the timing of the fall turnover.

walleye that were fully resident, and those that exited the Harbour ($p = 0.14$).

Space use (position).

Qualitatively, areas used in the spring and summer, both total activity space and core ranges were more dispersed than in fall and winter (95PVC activity space Fig. 5; 50PVC core space Supplementary Materials Fig. D). Walleye predominately used the western end of the Harbour during the fall, spring and summer and were more concentrated in the central, deeper basin of the Harbour during the winter. Core use areas appeared to gradually shift more easterly as the seasons progressed from summer towards winter. Areas used in the summer were coastal, i.e. most easterly and westerly shorelines with only one individual's core home range close to the central basin.

Discussion

Residency, space use, and areas used by walleye in Hamilton Harbour varied seasonally, presumably reflecting seasonal differences in environmental conditions (e.g., temperature, oxygen, food availability). Residency was highest during the spring period when walleye spawning would typically occur. Walleye mature at a total length larger than 300 mm (Colby et al., 1979), and approximately 3–4 years in the Laurentian Great Lakes (Scott and Crossman, 1973) and in Lake Ontario's largest walleye population specifically (i.e. Bay of Quinte/eastern Lake Ontario, Bowlby et al., 2010). Although there has not been genetic confirmation of the source of the captured walleye (hatchery or wild), most walleye tagged in this study were presumed to be from the 2012 fingerling stocking event (Bay of Quinte strain). In 2015 summer sampling, both male and female walleye gonad condition was judged to be maturing and capable of spawning the following spring (2016) at age 4 (Hoyle, pers. comms.). Indeed, spawning activity was confirmed by DFO's electro-fishing surveys in April 2016, with 49 ripe walleye (males = 47, females = 2) observed and caught in aggregations along the coastlines (Hoyle et al., 2017b). Results from the present study provide managers with general locations to survey for natural recruitment, including egg collection and egg and fry survival studies, such as along the northern shoreline, the shoals in the north-eastern corner and the rocky shorelines south of the canal entrance, but a more detailed assessment of telemetry-derived walleye positions, paired with field assessments during the spawning season, would help to more directly target and confirm spawning areas.

Walleye were largely resident to the harbour during the summer and, unlike their Bay of Quinte relatives, did not appear to migrate into Lake Ontario post-spawning, however the area used was significantly smaller during this season. Previous walleye telemetry studies have focused on spawning locations, habitats, and migration distances travelled (Crowe, 1962; Bunt et al., 2000; Fielder, 2002; Hayden et al., 2014; Hayden et al., 2017) such that there has been little research conducted on summertime space use of walleye, however, walleye from western Lake Erie, and eastern Lake Ontario have shown migration away from spawning areas within weeks of spawning (Wang et al.,

Table 2
Generalized linear mixed effects model estimates for seasonal residency (i.e. proportion of detections recorded in the Harbour) data for *Sander vitreus*. The table shows the model coefficient estimates, standard error (SE), degrees of freedom (df), *t*-test statistic (t) and *p*-value (p).

Model term	Value	SE	*Z* value	*P* value
Intercept	0.9235	0.73	1.26	0.207
Spr	3.1123	0.19	16.79	<0.0001
Sum	2.0331	0.16	12.86	<0.0001
Win	2.3384	0.17	14.17	<0.0001

Table 3
Post-hoc Tukey Pairwise comparison for the fitted model of seasonal residency.

Season pair	Estimate	SE	*Z* value	*P* value
Spr–Fall	3.1123	0.19	16.79	<0.0001
Sum–Fall	2.0331	0.19	12.86	<0.0001
Win–Fall	2.3384	0.17	14.17	<0.0001
Sum–Spr	−1.0791	0.18	−6.07	<0.0001
Win–Spr	−0.7739	0.18	−4.28	<0.0001
Win–Sum	0.3053	0.16	1.89	0.2295

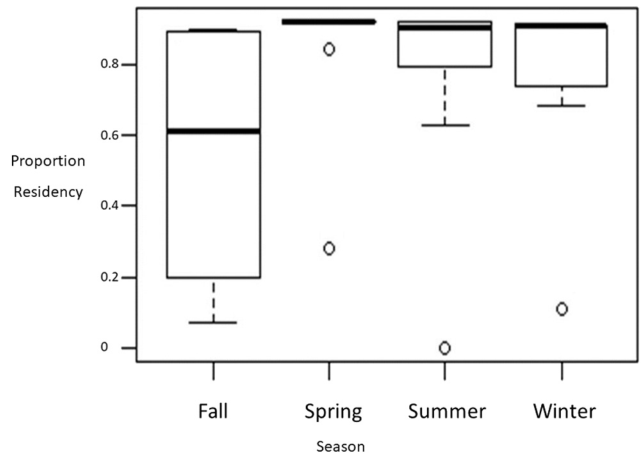

Fig. 3. Boxplot showing the residency proportions of all fifteen *Sander vitreus* by season in Hamilton Harbour for study period (21st October 2015- 20th October 2016). Box plot shows the median values (line), 25 and 75% quantiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).

Table 4
Generalized linear mixed effects regression model estimates for weighted seasonal activity space range (95 Percent Volume Contour) data for *Sander vitreus*. The table shows the model coefficient estimates, standard error (SE), degrees of freedom (df), t-test statistic (t) and p-value (p).

Parameter	Model term	Value	SE	df	*t*	P value
95% Volume contour	Intercept	8,769,484	560,990.7	41	15.63	<0.0001
	Spr	−378,826	671,811.9	41	−0.56	0.4292
	Sum	−4,290,684	684,143.2	41	−0.27	<0.0001
	Win	−552,504	779,504.0	41	−0.71	0.0459

2007; Hoyle et al., 2017a, 2017b; Raby et al., 2018). Our hypothesis that walleye would exhibit similar migration patterns to other walleye tracked in the Great Lakes was not supported.

Walleye activity space and core ranges were significantly smaller, and appeared to be more isolated, coastal, and shallow throughout the summer and spring when compared to fall and winter where there was an apparent preference for offshore, more thermally-stable areas. In Lake Erie, walleye distributions have been linked to the availability of both thermal (optimal temperatures for walleye growth 18–22 °C; Christie and Regier, 1988; Raby et al., 2018) and optical habitats, both of which seem ideal in the metalimnion or hypolimnion (Jones et al., 2006). Adults have been known to avoid temperatures exceeding 24 °C, if possible (Fitz and Holbrook II, 1978) with upper lethal temperatures reported at 29–32 °C (Hokanson, 1977) and 34–35° (Wrenn and Forsythe, 1978). However, in Toronto Harbour (situated approximately 50 km north-east of Hamilton Harbour on Lake Ontario), preliminary analyses of walleye seasonal detections between 2012 and 2015 have shown a preference for shallow (mean depth 0.5–2.5 m) and warm waters (mean 20–22 °C, range 16–27 °C) (Midwood, unpublished data). Consequently, the presence of walleye in comparatively shallow and warm habitats in Toronto Harbour may suggest they are using these areas for foraging and this could also be occurring in Hamilton Harbour, thus reducing the size of their ranges.

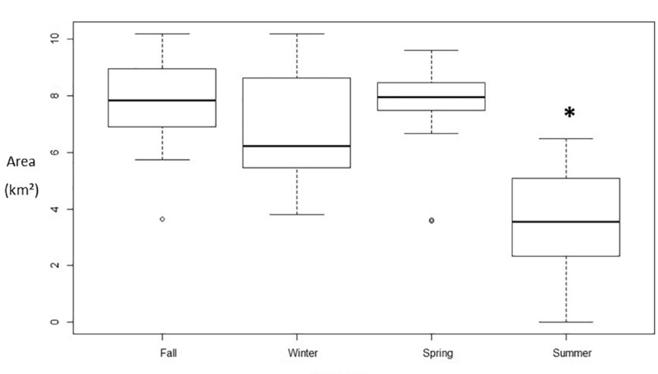

Fig. 4. Weighted activity space (95 Percent Volume Contour) of *Sander vitreus* (n = 15) per season in Hamilton Harbour for study period (21st October 2015–20th October 2016). Summer area use was significantly different to fall, winter and spring ($p < 0.001$). Box plot shows the median values (line), 25 and 75% quantiles (box), values < 1.5 times the interquartile range (whiskers), and outliers (circles).

Hypoxia (depletion of dissolved oxygen in water) occurs frequently in Hamilton Harbour, particularly during summer stratification (Gertzen et al., 2014). Hypoxia can have adverse effects on the diversity of life and the availability of suitable habitats for aquatic organisms. Suitable habitat may be restricted, and overcrowding can ensue in oxygen-rich refugia (Coutant, 1987). Previous studies exploring the effects of hypoxia on the quality of walleye habitat in Lake Erie have shown a slight decline in the amount of high-quality habitat, however an enhancement of habitat quality may occur as prey are concentrated in favourable conditions (Rahel and Nutzman, 1994; Costantini et al., 2008; Brandt et al., 2011). Walleye in Hamilton Harbour may be either physiologically restricted from areas with low dissolved oxygen, or are foraging in oxygen-rich refuge areas; and therefore, not needing to use large areas of the harbour during the summer. Walleye were least resident within the harbour during the fall with seven walleye exiting the harbour either at the end of the summer or beginning of fall just prior to the turnover/mixing period. Walleye migrations in Bay of Quinte have been linked to the availability of prey sources such as alewife in the summer and young-of-the-year fish such as gizzard shad (*Dorosorma cepedianium*) in the fall (Hoyle et al., 2017a, 2017b). Walleye migrations out of Hamilton Harbour at the end of summer may be driven by prey fish distributions, temperature and/or dissolved oxygen. Further study on thermal and dissolved oxygen preferences, fine-scale movements, depth use, and prey availability is required to determine the mechanistic basis for their restricted space-use during the summer period.

Residency and survival appear to differ between walleye caught during the two sampling periods, with fish tagged in the fall remaining within the harbour throughout the entire fall, indicating potential evidence of divergent migration within the population. Divergent migration is the coexistence of distinct migration behaviours within a population (Bowler and Benton, 2005). The most frequently observed form of divergent migration is partial migration (Chapman et al., 2012) where individuals are either residents (like those tagged in the fall), or migrants (like some tagged in August). Further investigation into individual variation with regards to migration using longer-term and larger sample sizes is required to determine the levels of partial migration within the walleye population in Hamilton Harbour, and to

Table 5
Post-hoc Tukey Pairwise comparison (weighted 95 Percent Volume Contour) for the fitted model of seasonal activity space range.

Parameter	Season pair	Value	SE	Z value	P value
95% Volume contour	Spr–Fall	−527,994	661,256	−0.798	0.855
	Sum–Fall	−4,175,688	686,653	−6.081	<0.001
	Win–Fall	−1,476,969	717,297	−2.059	0.166
	Sum–Spr	−3,647,694	634,405	−5.750	<0.001
	Win–Spr	−948,974	634,405	−1.422	0.485
	Win–Sum	2,698,720	692,622	3.896	<0.001
50% Volume contour	Spr–Fall	82,847	203,771	0.407	0.9760
	Sum–Fall	−723,456	151,706	−4.769	<0.001
	Win–Fall	570,298	242,615	2.351	0.0817
	Sum–Spr	−806,302	165,420	−4.874	<0.001
	Win–Spr	487,452	251,418	1.939	0.2020
	Win–Sum	1,293,754	211,431	6.119	<0.001

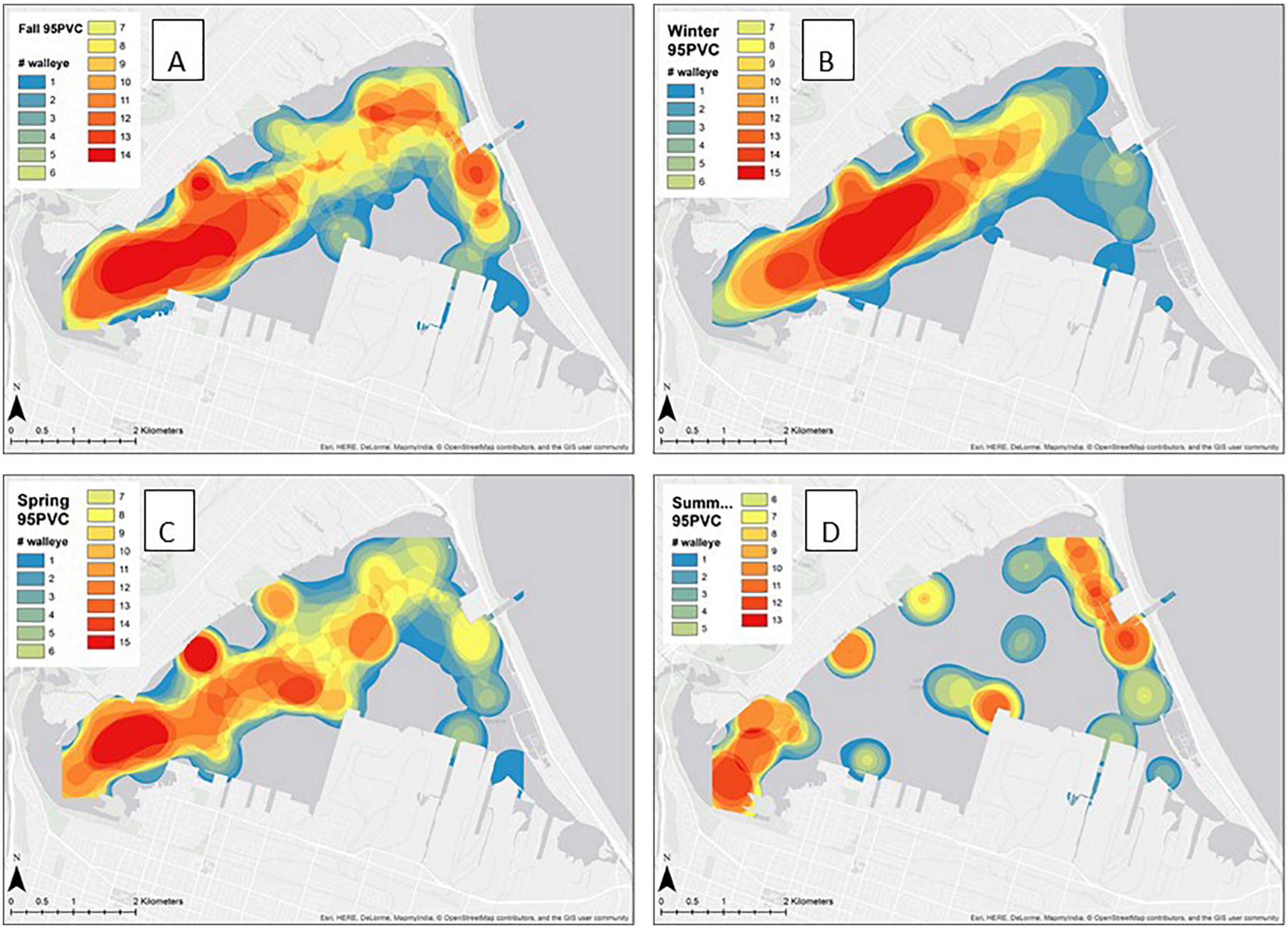

Fig. 5. Estimated seasonal activity space (unweighted 95 Percent Volume Contour) plots for fall (A), winter (B), spring (C) and summer (D) of *Sander vitreus* ($n = 15$) per season in Hamilton Harbour for study period (21st October 2015–20th October 2016). Red/darker shades indicate areas of high use by individuals.

further understand the ecological impacts of divergent migration on walleye populations.

Study limitations

There were some limitations to this study which are germane to most field telemetry studies. The detection range for any acoustic receiving equipment is influenced by the surrounding environmental conditions (wind, wave, turbidity, sounds, depth, vegetation etc.; Kessel et al., 2014). An increase in submerged aquatic vegetation throughout the summer could possibly lead to a reduction in the acoustic performance of the receivers and could explain the overall reduction in detections in summer. Three sentinel tags were placed along the receiver mooring line in front of the Grindstone Marsh/Cootes Paradise fishway area and two were positioned around the canal exit at the eastern end of the harbour. The eastern tags were too deep (~10 m) to assess the influence of vegetation during the summer. Preliminary analyses of detections have shown a decrease in array performance during the summer season; however, this only captures one habitat type. Further investigation of how environmental factors may influence the efficacy of the acoustic telemetry equipment in various other habitat types is required.

Like all forms of aquatic biotelemetry equipment, the telemetry infrastructure we used also had some inherent limitations. Fish detected on a receiver could be anywhere within the 360° dome of detection range and therefore, directionality cannot be determined by a single receiver. To address this limitation, gates such as the canal array allowed directionality to be determined and the COA (Simpfendorfer et al., 2002) provided interpolated potential locations for each fish that both reduced the volume of data that had to be processed (by aggregating numerous detections into a single position) and provided more detailed spatial information than just a detection of a fish on a single receiver.

This study suffered from a high mortality rate during the August trap netting efforts. Three fish died during the surgeries, and nine of the tagged and released fish either expelled their tag or died post-release. Previous studies on walleye using the same surgical techniques and involving some of our team members have yielded high levels of post-surgery survival such that this observation was anomalous. Trap nets were set overnight, therefore there is potential for walleye to be held in nets for up to 20 h. If these nets are positioned in or near areas with fluctuating dissolved oxygen levels, this could further add to the stress of the capture and tagging procedures. Post-release mortality from electrofishing in the October tagging period by the same surgeon was low. We would suggest focusing future fishing efforts during the cooler spring and fall periods.

Management relevance

Understanding the spatial ecology of fish is important for effective management of fisheries (Cooke et al., 2016). Our data has shown that, even in a relatively small study system, walleye change how they use the area on a seasonal basis; and, although only preliminary, our data has indicated the potential occurrence of partial migration. Population estimates obtained from sampling in the fall would differ greatly to those in the summer and provide biased results, potentially reducing the effectiveness of future management efforts. This study highlights the importance of tracking individuals across all seasons to understand the spatial ecology of a population and to appreciate where and when potential sampling biases during traditional fishery sampling methods may occur.

The reintroduction of walleye into the Hamilton Harbour has been attempted on several occasions over the previous thirty years and has shown little success until 2012. A common goal of species reintroduction programs is for natural recruitment to occur, enabling a self-sustaining population without the requirement of further stocking. The OMNRF's summer trap netting surveys have provided an indication that the stocked population of walleye are surviving and growing at comparable rates to natural populations and have reached sexual maturity. Telemetry data from this study suggested that many of the walleye remain within the harbour for most of the year including, and more importantly, during the springtime spawning period. Although residency and spawning behaviour does not indicate spawning or natural recruitment success, it provides managers with answers to the first step in this process. Core use area data can also inform sampling efforts for egg and fry surveys and help target future habitat enhancements efforts in areas where recruitment may be restricted. Future monitoring is needed to determine whether observed patterns are consistent across multiple years. Additionally, an expansion of the current array into Lake Ontario will help to evaluate the migration behaviour of walleye after leaving Hamilton Harbour to determine the connectivity of nearshore habitats in Lake Ontario, and compare broad-scale movements to recent walleye tracking studies in eastern Lake Ontario.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2018.11.011.

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