Journal of Great Lakes Research 47 (2021) 475–485

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/ijglr

Seasonal movements of muskellunge in the St. Clair – Detroit River System: Implications for multi-jurisdictional fisheries management

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ARTICLE INFO

Article history:
Received 25 June 2020
Accepted 21 December 2020
Available online 10 March 2021
Communicated by Tim B. Johnson

Keywords:
Muskellunge
Acoustic telemetry
Spatial ecology
Movement

ABSTRACT

The St. Clair-Detroit River System contains a world-class Great Lakes muskellunge (*Esox masquinongy*) fishery that has avoided the declines observed in many Great Lakes muskellunge populations. Muskellunge are an upper trophic level predator, and therefore a naturally low-density species. Limited fishery-independent data exist on which to base management decisions. To remedy this, we initiated an acoustic telemetry study in May of 2016, in collaboration with the Great Lakes Acoustic Telemetry Observation System. Our objective was to describe patterns of movement of muskellunge in this large and open system to better understand their spatial ecology. We acoustically tagged 133 muskellunge in the Detroit River and Lake St. Clair, and movements of 58 fish that passed our data quality control screens were analyzed. We utilized mixed modelling to assess the effects of sex, length, release location, and season on daily movement rates. We found that movement rates only differed among seasons, with highest movement rates occurring in the fall and lowest movement rates in the winter. Muskellunge tagged at different locations exhibited distinct residency patterns, and fish frequently crossed jurisdictional and waterbody boundaries. Ultimately our study highlights the scope and patterns of muskellunge movement in a large, unimpounded system and demonstrates that management of these fish would benefit from consideration of their full distribution covering multiple management jurisdictions.

Introduction

The muskellunge *Esox masquinongy* is a low-density, predatory fish that is among the most popular sportfishes in North America. Within the Laurentian Great Lakes, muskellunge were once widespread and commercially fished until the end of the 19th century (Schrouder, 1973). However, a combination of commercial overfishing and habitat degradation contributed to substantial declines in muskellunge abundance throughout the Great Lakes (e.g., Kapuscinski et al., 2007; Leblanc et al., 2014). In contrast to other populations in the Great Lakes watershed, muskellunge have remained numerous through time in Lake St. Clair (Fig. 1). For instance, muskellunge were still considered abundant in Lake St. Clair during the 1950s and supported an extensive recreational fishery in both American and Canadian waters of the system (Williams, 1961). Bryant and Smith (1988) noted that muskellunge of Lake St. Clair have not exhibited the same "level of stress and dependency on supplemental stocking that has occurred in other parts of its range" and have overcome new stressors such as outbreaks of viral hemorrhagic septicemia virus in recent years (Elsayed et al., 2006). The abundance of muskellunge in Lake St. Clair remains comparatively high as evidenced by strong charter catches (e.g., Hessenauer et al., 2020) and the system's reputation as a world-class muskellunge fishery. This reputation drives substantial economic activity in both the United States and Canada.

Despite the resilience of the muskellunge population in Lake St. Clair and its connecting waters, collectively referred to as the St. Clair-Detroit River System (comprised of the St. Clair River, Lake

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https://doi.org/10.1016/j.jglr.2020.12.006
0380-1330/

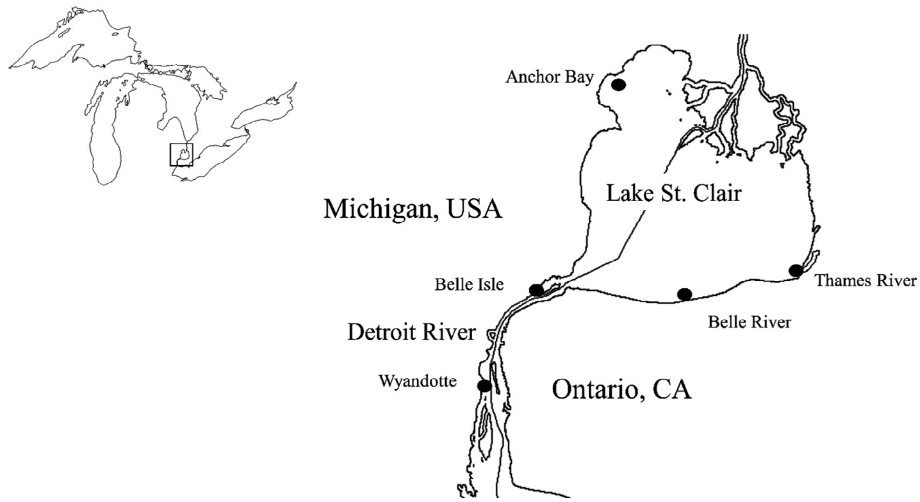

Fig. 1. Map of the study system. Release points are indicated by the labeled black dots. International boundary between United States and Canada represented by thin black line.

St. Clair, Detroit River, and Western Basin of Lake Erie; SCDRS), there is still substantial uncertainty regarding population characteristics of critical management importance. For example, due to low catchability in traditional fisheries assessment gears, few muskellunge are routinely captured during annual fishery independent netting surveys conducted by resource management agencies. Thus, managers have limited fishery-independent data to assess muskellunge population characteristics. Further, little information is available on the spatial and temporal extent of muskellunge movements in this open system. For example, is the fishery exploiting a single stock, or multiple stocks? If multiple stocks exist, what level of spatial overlap occurs and at what times of year? Muskellunge are known to exhibit spawning site fidelity (e.g., Jennings et al., 2011; Wilson et al., 2016; Weller et al., 2016) which could facilitate the development of discrete stocks within the system. Likewise, identification of specific spawning locations and management of subpopulations utilizing those areas is likely important for maintaining population abundance and genetic diversity (Kapuscinski et al., 2013).

Maintenance of trophy-sized muskellunge is a community objective of the Lake Erie Committee of the Great Lakes Fishery Commission (Francis et al., 2020), and there is still much to be learned about muskellunge behavior and ecology that is required to inform fisheries management strategies within the SCDRS. Muskellunge are assumed to be relatively sedentary ambush predators based on laboratory assessments of foraging behavior (e.g., Webb and Skadsen, 1980; New et al., 2001), and this has been validated in the field to some extent (Landsman et al., 2015). However, much of what is known about the spatial ecology of muskellunge has come from relatively small systems or study areas that may constrain the range of behaviors possible in other larger systems (but see Weeks and Hansen, 2009; Diana et al., 2015; Schaeffer, 2018). For example, if muskellunge in larger systems make larger-scale movements than previously thought, the fish periodically captured by commercial and recreational fishers in the western basin of Lake Erie could be migrants from the SCDRS and not remnants of Lake Erie's population(s). This differentiation of sources has significant implications for management of the fishery. In a migrant scenario, management actions would need to focus on managing the SCDRS fishery including the acknowledgement that exploitation within the SCDRS may have regional-scale effects; while in the remnant population scenario, management actions might include coastal wetland habitat restoration and protection along the shoreline of Lake Erie's western basin.

A combination of technological improvements and research collaborations now make it possible to examine the behavior of fishes at a variety of spatial and temporal scales. The Great Lakes Acoustic Telemetry Observation System (GLATOS; Krueger et al., 2018) is a large-scale research collaborative that uses acoustic telemetry to study the movement of fishes in the Great Lakes. Researchers associated with the GLATOS network have deployed an extensive network of acoustic receivers throughout the Great Lakes and share data on the detection of tagged fish, expanding the area in which an individual fish could be detected to a basin wide scale. Here, we capitalize on the existing infrastructure within the Great Lakes to describe the spatial and temporal scope and patterns of muskellunge movement in the SCDRS, and develop baseline data which can inform the development of hypotheses for future testing. Specifically, we examine factors related to movement rate such as fish size, sex, release location and season and examine the residency times of fish among waterbodies and management jurisdictions (Michigan, Ontario, Ohio) of the SCDRS.

Methods

Study site

Muskellunge were collected from various locations within the SCDRS (Fig. 1) and released at those same locations. Collectively, the SCDRS forms the international boundary between the United States of America and Canada and represents a diverse array of habitat including deep, swift rivers and straits, shallow lentic habitat, and Great Lakes wetlands. Importantly, the SCDRS has remained barrier free such that muskellunge can move freely through the system and into connecting waters (e.g., lakes Erie and Huron).

Capture methods

Capturing large numbers of a naturally low-density fish species like muskellunge is a challenge (e.g., Dembkowski et al., 2020), particularly in a system as large and heterogenous as the SCDRS; therefore, we opportunistically relied on multiple sampling methods as described briefly below.

Volunteer anglers

Most muskellunge tagged during this study (N = 91) were captured by volunteer anglers participating in fishing events organized by the co-authors because muskellunge captured by specialized anglers typically have high survival rates (e.g., Landsman et al., 2011). These events primarily occurred in Anchor Bay (May 2018, 2019) and Belle River (November 2017, October 2018, 2019) in Lake St. Clair (Fig. 1). During these events the co-authors liaised with muskellunge angling clubs, whose members possessed the appropriate gear for the safe landing, handling, and transport of muskellunge (e.g., large landing nets, livewells). Anglers were given instructions detailing the minimum size of fish that could be tagged (762 mm), locations to target, and what to do with fish that had been captured (i.e., bring fish to a tagging location or wait for the fish to be picked up by project personnel). After we took possession of fish from anglers, we noted any external injuries or other signs of stress that would prohibit tagging. In all cases, fish that were deemed unsuitable for tagging (generally due to external injuries associated with hooking or landing) were judged likely to survive the capture process and therefore released. Total handling time for fish from capture to tagging and release was generally less than two hours.

Electrofishing

Muskellunge were captured by boat electrofishing (N = 39) in the Detroit River (May 2016) and Thames River (October 2016, Fig. 1). Electrofishing settings were matched to ambient conductivity to ensure that fish were adequately stunned for capture but recovered quickly. All fish recovered in onboard livewells following capture and prior to tag implantation surgery. Fish captured in the Detroit River were collected in conjunction with the Michigan Department of Natural Resources (MDNR) egg take, such that fish were captured during night time shocking, and held in net pens (1.2 m $\times$ 1.8 m $\times$ 0.9 m) overnight prior to tag implantation the following day (but within 12 h of capture). Some of these fish were stripped of eggs or milt prior to tagging as part of egg take procedures. In the Thames River, fish were collected specifically for tag implantation and surgeries were conducted within 2 h of capture.

Trap netting

Three muskellunge were captured by trap netting in Anchor Bay (May 2018) of Lake St. Clair (Fig. 1) during the MDNR's annual spring trap net survey. The trap net survey occurred in April and May at fixed index sites in Anchor Bay, along the 3.1 m depth contour using nets with a pot depth of 1.8 m, pot mesh of 5.1 cm, 6.1 m wings and 91.4 m leads. Nets were checked every 48–72 h as allowed by weather conditions. Once removed from the trap net the fish was tagged and released within two hours.

Fish tagging and data collection

Fish tagging procedures were identical, regardless of the method of capture. Fish were electroanesthetized via a 4 s exposure to 100 Hz pulsed DC, 25% duty cycle, and 50 V. We define electroanesthesia as a reversable loss of sensory reception and equilibrium (Reid et al., 2019). These settings ensured immobilization of fish sufficient for surgical tag implantation, but also resulted in quick recoveries with fish generally regaining equilibrium within four to five minutes. Anesthetized fish were moved onto a padded v-board where a hose providing fresh water was inserted into the mouth to ensure that oxygenated water flowed over the gills for the entirety of the surgery. The surgeon then made a 2.5–3 cm incision in the ventral body wall and inserted a Vemco V16-4H (Vemco, Halifax, Nova Scotia) tag inside the body cavity. These tags emitted a tag specific code at 69 kHz randomly every 120–240 s and have an approximate battery life of 3400 days. While all tags used were V16-4H some of the tags used in the Detroit River in 2016 were previously recovered tags from other projects, meaning these tags were initially implanted in another fish and had since been recovered with remaining battery life. These tags were thoroughly cleaned and sterilized before reuse. The incision was then closed using 2 or 3 sutures, generally size 0 monofilament absorbable suture or similar. All surgical instruments were sterilized in a betadine solution and rinsed in deionized water prior to and after each surgery. All fish also received an external Floy loop tag (FT-4 lock on tags, Floy Tag, Seattle, Washington), which was inserted through the musculature of the dorsal fin and then cinched closed. These external tags provided a unique identification number that could be used to identify fish captured by anglers or other sampling gears.

Fish length and weight were measured to the nearest mm and 0.1 kg. In the spring it was sometimes possible to determine fish sex by visually examining extruded gametes. During other times of year, we examined the urogenital openings to assign sex (Lebeau and Pageau 1989). These methods were not employed on the Thames River during October 2016, and hence all fish tagged were recorded as unknown sex. Sex assignments were made conservatively and thus were biased towards larger fish which have higher assignment accuracy, due to our inability to sacrifice fish to definitively determine sex (Lebeau and Pageau, 1989). Immediately following surgery, we moved fish to a holding tank for a minimum of a half hour recovery period prior to release. Reflex action mortality predictors, e.g., ensuring fish regained equilibrium and exhibited escape response to tail grab (Raby et al., 2012), were monitored for all muskellunge to ensure that they were recovering properly and suitable for release. After this recovery period, fish were released back into the waters from which they originated; and a GPS release location was recorded.

Passive tracking of individuals

This study was associated with the GLATOS network of acoustic receivers (https://glatos.glos.us; Krueger et al., 2018), which is a network of researchers conducting fish acoustic telemetry studies in the Great Lakes using compatible equipment. Tag detections from the acoustic receivers of each individual project are uploaded to a centralized database against which tag queries can be made. This network allows for expanded spatial coverage compared to the spatial coverage of each individual project. Throughout the course of the current study the GLATOS receiver network changed (Fig. 2) as participating GLATOS projects began, expanded, or ended. Some receivers were permanently deployed at a given location, which meant receivers were kept in the same location year-round, year after year, while other receivers were seasonal deployments, which meant receivers were deployed for specific time periods often tied to project-specific objectives (e.g., describing spawning behavior; Bade et al., 2019). Because of the nature of the GLATOS network it is not possible to describe the individual maintenance schedules of all receivers on which muskellunge detections occurred. Nevertheless, a strong receiver presence existed throughout the SCDRS, particularly within Lake St. Clair, the Detroit River and the deltaic channels of the St. Clair River where it enters Lake St. Clair, through all periods of our study (Fig. 2). In contrast, the western basin of Lake Erie had relatively limited coverage by receivers initially, but greatly expanded beginning in 2017 (Fig. 2).

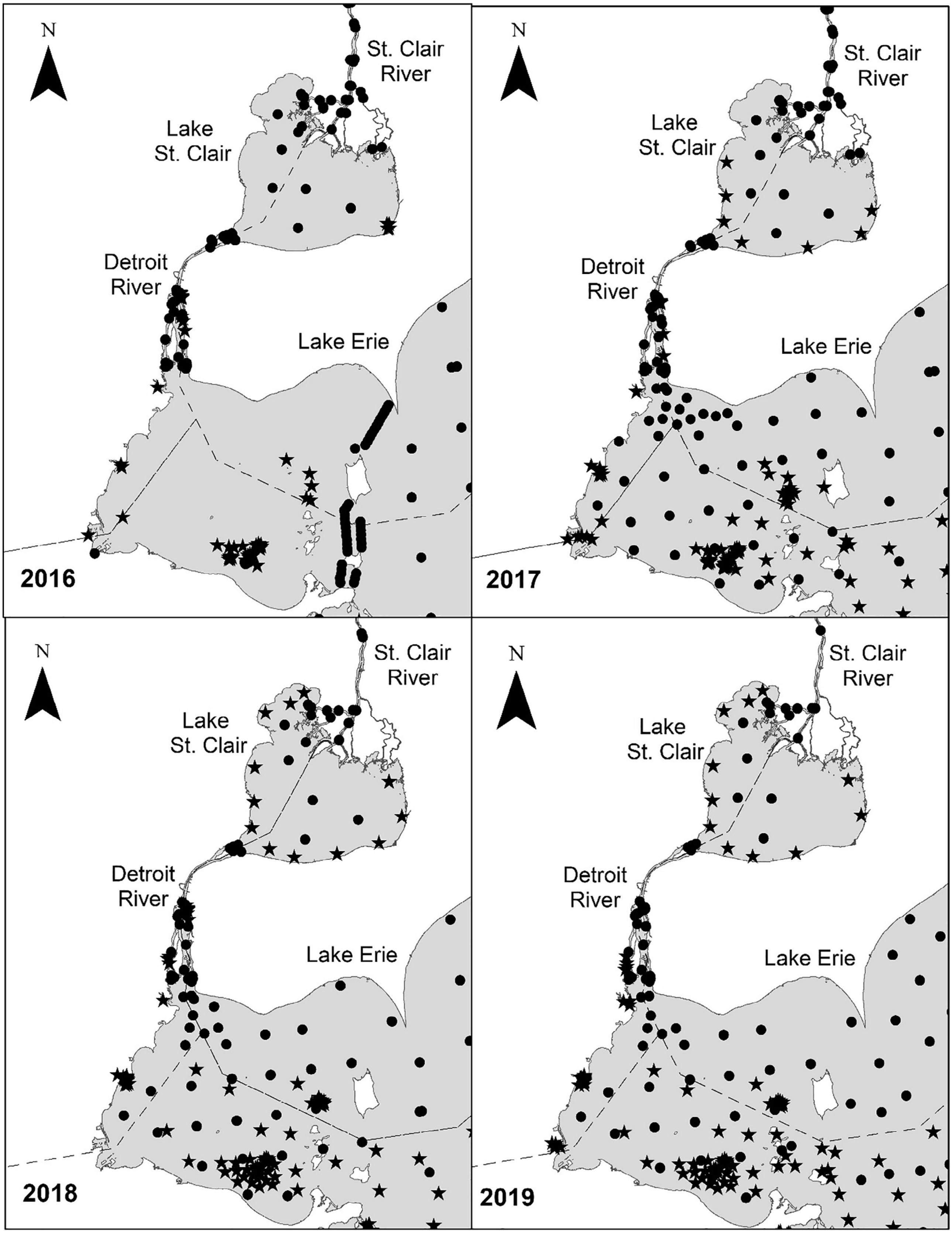

Fig. 2. Distribution of acoustic receivers within the St. Clair – Detroit River system 2016–2019. Permanent receivers (circles) and seasonal receivers (stars) shown. The dashed lines represent the jurisdictional boundaries between Michigan, Ontario and Ohio.

Data processing

We used detection data for all tagged fish available within the GLATOS database through 12/10/2019. Detection data were analyzed in Program R (R core development team 2018) using the GLATOS Package (https://gitlab.oceantrack.org/GreatLakes/glatos). Detection data were screened for potential false detections (Simpfendorfer et al., 2015), by eliminating single detections more than 60 min apart from one another. We also eliminated fish that were detected for fewer than 90 days (i.e., must have a minimum of 90 days between the first and last detection in the database) to ensure adequate time at liberty for inference, and ensured detection data across at least two seasons. Positional estimates of tagged fish were interpolated using the interpolate_path function of the GLATOS package to fill in gaps between observed detections. These interpolations utilize the shortest straight-line distance between two detections unless such a movement would be impossible (e.g., over land), in which case the shortest non-linear path is calculated. Movement data were standardized to daily movement (m/day) by summing the movement distances occurring within a day for observed detections. For interpolated data, daily movement was calculated as the total interpolated distance estimated between detections divided by the number of days between detections. For all individuals we calculated the percent of days with interpolated data aggregated across the entire time period at large.

We estimated the residency time that individual fish spent in the various management jurisdictions and waterbodies. For detection data, detections on a unique receiver were assigned to a jurisdiction and waterbody (based on the location of that receiver) and summarized daily. For interpolated data, the interpolate_path function provides an estimated latitude and longitude for each day of interpolation, which was used for assignment. We then counted the number of daily occurrences for each jurisdiction and waterbody. In the event that an individual fish was detected in more than one waterbody or jurisdiction in a single day, we did not attempt to partition the time among jurisdictions or waterbodies (e.g., 0.6 days Michigan, 0.4 days Ohio), rather each occurrence was counted individually; and thus the percentages of time that each fish spent in a jurisdiction or waterbody that we calculated should be thought of as a relative estimate rather than absolute.

Data analyses

Descriptions of movement in passive telemetry studies such as this are biased toward underestimating movements because of the inability to account for movements that occur in the coverage gaps among network receivers (Crossin et al., 2017). This bias can be further exacerbated by shifts in the GLATOS receiver network as individual projects adjust their receiver arrays. We tested for bias by examining the relationship between average daily movement (sum of total distance moved divided by days at large) and the percent of data interpolated. We predicted a relationship between the percent of total days that used interpolated positions and daily movement with higher percentages of interpolated data related to decreased daily movement (α = 0.05). If such a relationship exists, the bias due to the detection range of receivers was partially accounted for by systematically removing fish with high rates of interpolated data until there was no longer a statistically significant relationship with daily movements.

We next tested for potential effects from tagging by examining rates of daily movement among 12 thirty-day periods following surgery (modeled after Hondorp et al., 2015). Daily average movement was calculated for all fish passing the initial data quality screens within these 30-day periods by summing the total movement and dividing by the number of days. Thirty-day periods were chosen primarily for two reasons. First, surgery incisions likely take at least 30 days to heal (e.g., Walton-Rabideau et al., 2019), but an examination of walleye (*Sander vitreus*) tagged in the same system and with similar methods revealed that incision wounds were generally completely closed within about 90 days (Schoonyan et al., 2017). Second, it was determined that 30 days was the minimum time period over which enough movement data could be collected to ensure robust analysis. We then used a mixed-model regression analysis to compare movement rates (log transformed) among these 30-day periods. Average daily movement (m/day) within each period was the response variable, 30-day movement period was entered as an ordinal predictor variable, along with season (Winter = December, January, February; Spring = March, April, May; Summer = June, July, August; Fall = September, October, November), and fish-ID as a random effect to account for the multiple observations per individual fish. Comparisons among 30-day periods were made using Tukey's Honest Significant Difference test. A pattern of increasing or decreasing movement rates among 30-day periods eventually leveling to a plateau might indicate recovery from tagging and provide insight into the length of time muskellunge require to recover from a tagging surgery. Finally, we compared the daily average movement of fish across the entirety of their first 360 days after surgery, with daily movement thereafter using a paired *t*-test, based on the assumption that the fish would be completely recovered from surgery after approximately one year and thus if movement in the first year after surgery did not differ from movement after completely recovery than it was unlikely that tagging adversely affected the fish.

We used linear mixed model regression to explore the relationships between fish length, fish sex, release location, and season on average daily movement (log transformed) calculated for each month the fish was at liberty. Variables were assessed individually with fish-ID as a random effect in each model to account for the multiple observations per individual. Year was also entered as a random effect in each model to account for yearly changes that occurred in the GLATOS receiver array. The percent of data interpolated for each month was also included as a predictor variable to further account for potential bias associated with movement rates and the receiver array. Finally, we constructed a null model that contained only a random fish-ID term to assess the magnitude of any effects that other covariates had.

Due to the opportunistic sampling strategy we employed, fish were tagged and released at different times of year and sampled with different gears, often with all fish from a particular site being sampled with a single gear at a single time of year. Therefore, we sought to estimate apparent mortality among the release locations. Apparent mortality could include mortality from tagging, tag loss or failure, natural or fishing mortality, or a fish leaving the GLATOS receiver array. To estimate apparent mortality we compared the number of fish detected with movement for at least 90 days post tagging compared to the number of fish tagged at each location (2019 data were excluded because these fish may have higher apparent mortality based on receiver recovery schedules among GLATOS projects).

Because of differences in the season when tagging events occurred, we focused on graphically comparing the residency of fish from each of the release locations by jurisdiction and waterbody. This analysis allows for the qualitative comparisons among release locations to provide the basis for future hypothesis testing. Due to their low sample size and similar movement patterns from pilot data, fish tagged at the two Detroit River sites were aggregated for this analysis. Likewise, we also investigated if fish returned to their tagging location in the same month as they were released in subsequent years, by examining their detection histories each year. Such analyses provide the opportunities for establishing patterns among groups against which the behavior of individuals can be compared in the future.

Results

We analyzed 1,119,990 detections from 133 muskellunge (mean length + SD: 1007 + 125 mm; range: 660–1330 mm). A total of 10,329 (0.92%) detections were identified as potentially false and removed from the dataset. Finally, we removed detections from 57 fish that were not at large for at least 90 days, most of which (n = 33) were tagged in October 2019 and had not had sufficient time at large, although others (n = 24) were presumed mortalities based on limited movements, resulting in a dataset comprised of 76 muskellunge that was further analyzed. The apparent mortality rate across all sites was 12% and ranged from 55% in the Detroit River, 30% in Anchor Bay, and 5% each in the Thames River and Belle River.

We identified a weak but statistically significant negative relationship between the percent of daily positions calculated by interpolation and the average daily movement of muskellunge ($F_{1,74}$ = 11.23, P = 0.001, R^2_{adj} = 0.12). In our dataset the relationship between percent interpolated data and average daily movement was no longer significant when individuals with greater than 85% interpolated data (meaning 85% of their daily positions were calculated from interpolation) were removed ($F_{1,56}$ = 3.58, P = 0.06, R^2_{adj} = 0.04). This process resulted in the removal of 18 additional fish from our dataset, such that the final dataset included detections from 58 muskellunge (Table 1).

The 58 fish which comprised the final dataset had an average daily movement rate of 881 + 622 m (mean + SD, calculated as total distance traveled divided by days at large), and were tracked for an average of 668 + 330 days (range 90–1271 days). The interquartile range of average daily movement was 410–1279 m/day, with maximum of 2757 and minimum of 42 m/day. The percent of interpolated data averaged 73 + 9%. One individual made round trips to the Eastern Basin of Lake Erie in 2016–2017 and again in 2018–2019, each round trip representing at least 1000 km.

Season was a significant predictor of daily average movement for muskellunge ($F_{3,1274}$ = 36.0, P < 0.001). Tukey Honest Significant Difference tests revealed that movement during the fall (least square mean + SE: 314 + 1.24 m) was greatest among all the seasons. Movements during spring (126 + 1.24) and summer (119 + 1.24 m) were not different from one another, while less movement occurred during the winter (40 + 1.25 m). No effect of any other predictor variable of interest was detected (Table 2), though the percent of days interpolated was significant in all models (Table 2) and negatively associated with average daily movement rates.

Our analysis of tagging effects revealed no clear pattern between average daily movement among 12 30-day periods following release. While both season ($F_{3,540}$ = 11.89, P < 0.001) and period ($F_{11,538}$ = 5.26, P < 0.001) were significantly related to the average daily movement of fish, no clear pattern (e.g., continuous increase or decline of average daily movement) occurred which might indicate a tagging effect (Fig. 3). Likewise, there was no significant difference (t = 1.38, d.f. = 44, P = 0.17) in mean daily movement among the first 360 days after tagging (mean + SD: 946.5 + 900 m) and daily movement thereafter (mean + SD: 1215.4 + 846 m).

Given their geographic similarity and relatively small sample sizes, fish tagged at Belle Isle and Wyandotte were aggregated into a single Detroit River group for comparison of the residency of fish in each jurisdiction and waterbody. Fish tagged in the Belle River and Thames River spent most of their time in Canadian waters (87% and 99%, respectively), primarily in Lake St. Clair (85% and 96%, respectively; Fig. 4), though Belle River muskellunge also spent time in the Michigan waters of the Detroit River and the Michigan and Ohio waters of Lake Erie. Fish tagged in the Detroit River spent roughly half of their time in Ontario waters, but their time was almost evenly divided among Lake St. Clair, the Detroit River and Lake Erie (Fig. 4), with a few detections in the St. Clair River (<1% of total time). Fish tagged in Anchor Bay spent just over half their time in Michigan waters, and nearly 70% of their time in Lake St. Clair (Fig. 4). Fish tagged in Anchor Bay were also rarely detected in the St. Clair River accounting for about 2% of their total time.

Fish frequently returned to their tagging location regardless of season in which tagging occurred. Five out of seven fish tagged during May of 2016 in the Detroit River returned to the Detroit River in May of subsequent years, with four of those five returning to the Detroit River near their release location in May of both 2017 and 2018 (the fifth returned in only 2017). Six of eight fish tagged in Anchor Bay of Lake St. Clair in May of 2018 were back in Anchor Bay in May of 2019. Similar patterns emerged among individuals tagged in the Thames River in October of 2016, where 14 of 17 fish tagged returned to the Thames River in October of subsequent years. Of these 14 returning fish, 11 returned in 2017, 2018, and again in 2019.

Discussion

We found substantial daily movements of muskellunge averaging nearly 900 m per day in the barrier-free St. Clair – Detroit River System. These movements were generally widespread among waterbodies that comprise the system (e.g., Lake St. Clair, Detroit River and Lake Erie); and substantial movement occurred among management jurisdictions within the system. Similar to previous work, we found that movement was greatest in the fall, and least in the winter, while spring and summer had intermediate and roughly equal movement rates (e.g., Dombeck, 1979; Weeks and Hansen, 2009; Pankhurst et al., 2016). Distinct movement patterns emerged among fish released at different locations. These findings have several important implications for understanding the ecology

Table 1
Waterbodies, primary capture methods, tagging month and year for fish tracked for at least 90 days by males (M), females (F) and unknown sex (U). Numbers in parentheses indicates the number of fish removed from the data due to high percentage of interpolated data. Length is average total length by sex with number in parentheses indicating the standard deviation, dashes indicate no data.

Release Location	Waterbody	Primary Cap. Method	Tagging Month/Year	N			Length (mm)		
				M	F	U	M	F	U
Belle Isle	Detroit River	Electrofishing	May-16	3 (2)	0	0	964 (37)	–	–
Wyandotte	Detroit River	Electrofishing	May-16	2	2	0	982 (84)	1207 (83)	–
Thames River	Lake St. Clair	Electrofishing	Oct-16	0	0	17 (1)	–	–	992 (54)
Belle River	Lake St. Clair	Angling	Nov-17, Oct-18	9 (9)	16 (3)	1	976 (96)	1072 (96)	890 (NA)
Anchor Bay	Lake St. Clair	Angling*	May-18	5 (2)	2 (1)	1	989 (92)	1104 (16)	719 (NA)

* One fish captured by trapnetting in Anchor Bay.

Table 2
Summary of mixed model results including amount of variance explained ($R^{2,}$ adjusted value shown), the F-statistic, the degrees of freedom (d.f.., numerator/denominator) and the P-value comparing average daily movement by month for each covariate. The 'None (Indiv. Only)' model only contains the animal ID as a random effect.

Model	R^2	Parameter	F-statistic	d.f.	P-Value
None (Indiv. Only)	0.19	NA	NA	NA	NA
Season	0.33	Season	36.5	3/1275	<0.001
		%Interpolated	55.0	1/1299	<0.001
Sex	0.28	Sex	0.99	1/53	0.38
		%Interpolated	131.8	1/1299	<0.001
Release Location	0.28	Release Location	1.34	4/49	0.27
		%Interpolated	131.2	1/1295	<0.001
Fish Length	0.27	Fish Length	0.13	1/57	0.72
		%Interpolated	136.0	1/1298	<0.001

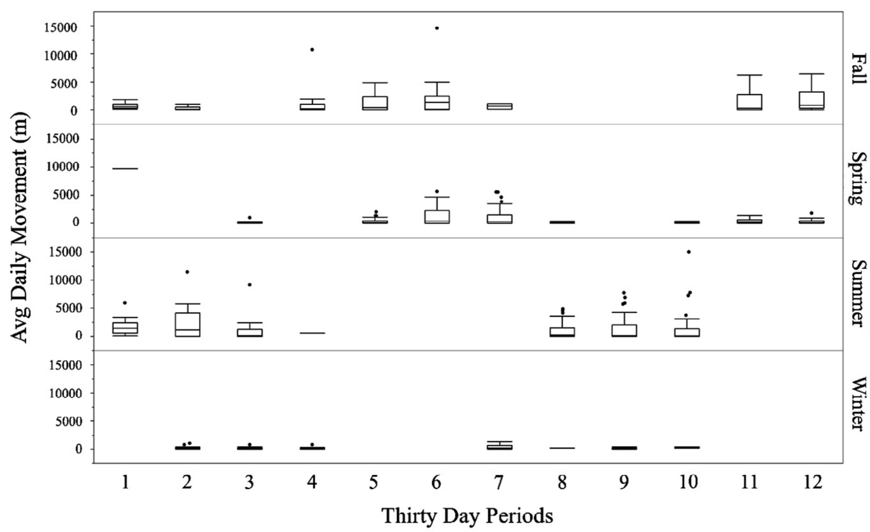

Fig. 3. Average muskellunge daily movement by 30-day period after tagging and broken out by season in which the period occurred. The top and bottom of each box represent the 1st and 3rd quartiles, with the line inside the box representing the median. The top and bottom whiskers represent the 2.5 and 97.5 percentiles. We hypothesized that tagging effects, if present, would manifest as a changing trend in movement rate among periods, which was not present.

of and managing muskellunge within the SCDRS. The most significant of these implications is that these large predatory fish are migrating long distances at relatively high swim speeds and are showing seasonality and repeatability in their movement patterns.

Several fish made large scale movements, often returning to locations near their initial tagging. For example, one fish nicknamed "James" due to his tag number of 007, moved from his tagging location near Belle Isle in the Detroit River to Buffalo Harbor of the East Basin of Lake Erie between May and August 2016. By January 2017, this fish was back in the Michigan waters of Lake Erie, and by May of 2017 he was within a few hundred meters of his release location, a round trip of at least 1000 km. Remarkably this behavior was repeated in 2018–2019. Other telemetry studies of muskellunge have reported long distance movements up to and exceeding 100 km one way (e.g., LaPan et al., 1996; Kerr and Jones, 2017; Schaeffer, 2018), but the travel conducted by James stands out and is the largest documented movement of a muskellunge to our knowledge. Although such large-scale movements were rare in this study, 16 tagged fish (28%) utilized Lake Erie, including individuals from three of the four tagging locations (the Thames River being the exception), indicating substantial movements from Lake St. Clair or Detroit River tagging locations. Five individuals representing 9% of the sample had daily movement rates exceeding 2000 m per day, indicating that "James" was not an outlier in terms of daily movement.

Our results of fish returning to proximity of tagging locations at similar times of year to when they were tagged appears to demonstrate seasonality of migrations. Previous tagging studies in many other systems suggests that muskellunge often return to the same areas in the spring to spawn over multiple years (e.g., Crossman, 1990; Weeks and Hansen, 2009; Jennings et al., 2011; Diana et al., 2015; Weller et al., 2016; Wilson et al., 2016). Indeed, five out of seven fish tagged at known spawning areas during known spawning times (i.e. April- June) in the Detroit River sites returned to proximity of these locations in the spring in at least one subsequent year. Likewise, six of eight fish tagged in Anchor Bay of Lake St. Clair in May of 2018 were back in Anchor Bay in May of 2019. Interestingly, we also observed similar patterns among fish that were tagged in the fall, when spawning behavior is likely not driving site fidelity. For example, 14 of the 17 fish tagged in the Thames River during the fall of 2016 returned to that immediate vicinity of the Thames River in subsequent years and 11 of these fish returned in all three possible years. Fall tagged Belle River fish also appeared to exhibit similar behavior, however the numbers returning were not as easy to estimate give the configuration of the receiver array and lack of clear geographic reference in this area. We hypothesize that these fish are returning to the Thames River, and perhaps the Belle River as well, to exploit foraging opportunities. The Thames River, for example, receives large runs of gizzard shad *Dorsoma cepedianum* each fall. Further work exploring this topic would be

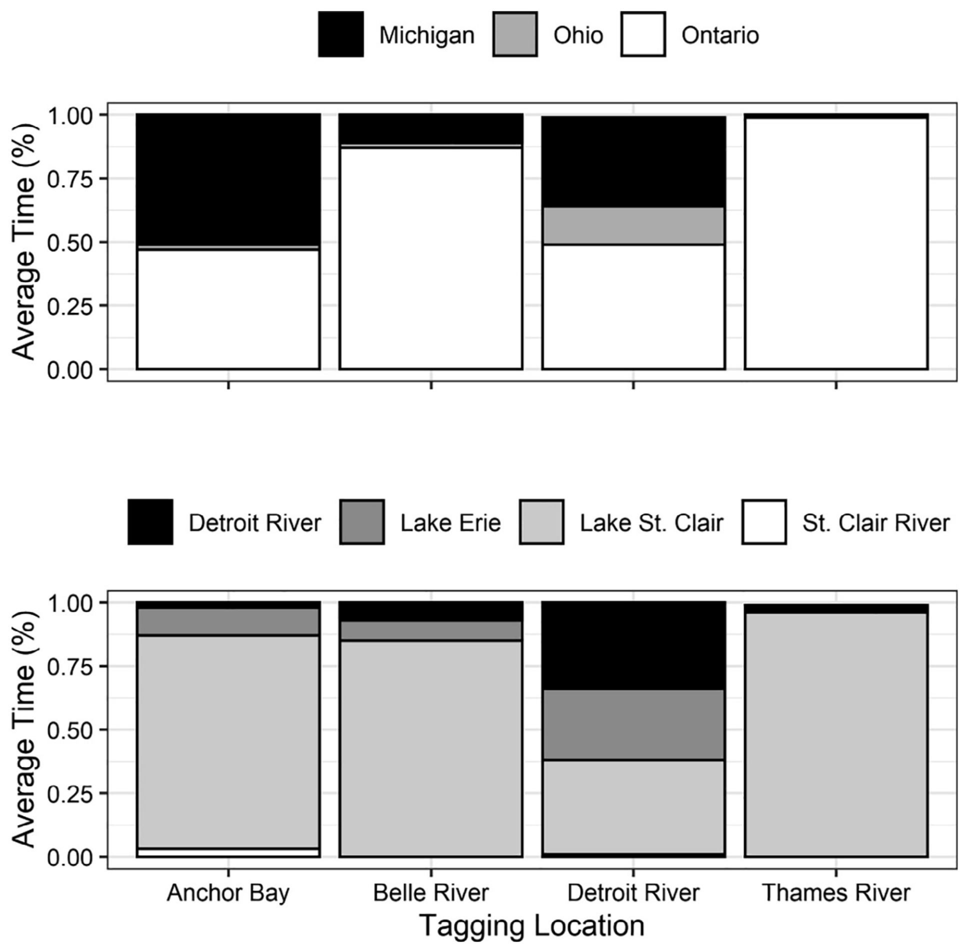

Fig. 4. Average percent of time spent by muskellunge in the jurisdictional waters of Michigan, Ohio and Ontario (A), and average percent of time spent by muskellunge in the waterbodies of the St. Clair-Detroit River System (B). Note, muskellunge tagged in the Detroit River also spent less than 1% of total relative time combined in the jurisdictional waters of Pennsylvania and New York.

of great interest to fisheries managers, anglers and scientists. If this pattern continues in future years of our muskellunge study, it will be the first documentation of large-scale seasonal migration routes in muskellunge not associated with spawning behavior. Furthermore, additional work during the remaining life span of the acoustic tags will be required to confirm the consistency of this pattern, but such a finding would have significance to fisheries managers because of the potential of disproportionate exploitation of components of the fishery by anglers that target aggregating fish. For fisheries scientists this could form some of the first evidence of large-scale seasonal migration routes in fish that comprised more than simple dispersal and return to spawning areas. If in fact fish are migrating to and from valuable foraging grounds and spawning locations, this would raise questions about evolutionary and behavioral processes from which such behavior could develop and the physiological ability to orientate and navigate through a system as complex and dynamic as the SCDRS.

While direct comparison of movements among release locations should only be made cautiously given the differences in season when releases occurred, we nevertheless find these data intriguing and worthy of additional study. For example, differences in waterbody and jurisdictional use by fish tagged and released near the Belle River and Thames River are interesting given the close geographic location of these systems (Figs. 1, 4), with Belle River fish being more likely detected outside Lake St. Clair when compared to Thames River fish. Likewise, it was interesting that fish tagged in Anchor Bay on Lake St. Clair appear to spend more time in Lake Erie than fish that were released in the Canadian waters of Lake St. Clair. Using conventional external tags and angler reporting, Haas (1978) reported that muskellunge from Anchor Bay made migrations to the southern part of Lake St. Clair, while muskellunge tagged in the southeastern portion of Lake St. Clair tended to stay there, consistent with the general trends observed in our data.

The general absence of muskellunge detections in the St. Clair River was unexpected. The St. Clair River harbors a robust population of muskellunge, where in 2019, catch rates of muskellunge reported by charter operators in the St. Clair River were higher (0.12 fish per hour) than those reported for Lake St. Clair (0.08 fish per hour; J.-M. Hessenauer MDNR unpublished data), though substantially less effort was expended in the St. Clair River (6490 h in Lake St. Clair, 104 h in St. Clair River). The lack of detections of fish in the St. Clair River that were tagged in Lake St. Clair or the Detroit River, despite the strong presence of permanent receivers in the St. Clair River (Fig. 2), is surprising. This suggests the presence of spatial structure of muskellunge populations which may inform future management. Telemetry studies of other species in the SCDRS have yielded similar results. For example, both Kessel et al. (2018) and Colborne et al. (2019) noted that lake sturgeon (*Acipenser fulvescens*) associated with the Detroit River were rarely found in the St. Clair River and vice versa, though both studies found that fish associated with Lake St. Clair frequently spend time in at least one of the adjoining rivers. Therefore, tagging muskellunge from the St. Clair River is a high future priority to resolve the potential for spatial structure in the SCDRS muskellunge populations. Identifying patterns similar to lake sturgeon may suggest some intriguing aspects of the history and biology of species within the SCDRS.

Importantly, we did not find evidence of significant tagging effects on the behavior of muskellunge. Apparent survival was sometimes low (see below) suggesting that some fish died as a result of handling and surgery. However, patterns of daily movement for fish that survived were lacking among twelve 30-day periods after tagging (Fig. 3), and no significant difference existed in daily movement in the first 360 days after tagging when compared to daily movements that occurred greater than 360 days after tagging. Together, we interpret these results as evidence that acoustic telemetry provides valid inferences on the behaviors of muskellunge in the SCDRS, and this is similar to findings examining post-tagging behavior of lake sturgeon within the same system (Hondorp et al., 2015). Additionally, while acoustic telemetry studies are known to underestimate movements of fish due to variance in the detectability of fish on individual receivers as well as the ultimate configuration of the receiver array (e.g., Crossin et al., 2017), we sought to correct for this bias by comparing calculated average daily movement with the percentage of the data that was interpolated. Interpolation of data is common with acoustic telemetry studies (e.g., Meckley et al., 2017; Harris et al., 2020) and is logically related to lower detectability as might occur when fish move between receiver arrays. Therefore, we feel that the relationship between the percentage of interpolated data and average movement can be used to reduce underestimation of movement rates by passive telemetry studies. In the present study, even after removing individuals with the highest rates of interpolation, interpolation rate was still negatively related to average daily movement, and accounting for interpolation likely improved estimates of movement rates. Future research evaluating the effects of interpolation on studies such of ours is warranted.

Overall, apparent mortality was 12% (ranging from 5 to 55%), similar to other acoustic telemetry studies conducted on other species (e.g., Faust et al., 2019; Slagle et al., 2020), though the current study considered a much longer mortality period (90 days compared to one or two days). The high apparent mortality rates of fish tagged in the Detroit River is likely the result of more extensive handling due to their participation in MDNR egg take activities (e.g., held overnight, stripped of eggs and milt). Additionally, about half of the fish were tagged with recycled tags (tags that had been initially used for other projects but had been recovered from harvested fish), which should have had at least 1000 days of battery life remaining based on their initial programming and time at large from initial tagging events; but, their actual performance or remaining battery life is unknown, thus Detroit River fish may have had higher rates of tag failure. Finally, given the amount of time that Detroit River fish spend in Lake Erie (Fig. 4) and the scarcity of Lake Erie acoustic receivers in 2016 (Fig. 2), it is possible that we lost contact with some Detroit River fish, and thus they appear as mortalities. The two spring tagging events (Detroit River 55% and Anchor Bay 30%) appeared to have higher apparent mortality than the fall events (Thames River 5%, and Belle River 5%). Increased mortality in these spring tagging events may be, in part, associated with spawning stress. However, this is difficult to parse out given the dissimilarity in fish handling that occurred in the Detroit River (as described above) compared to Anchor Bay fish. Interestingly, it seems that both electrofishing and the collection of fish by specialized angling can be done with low and potentially similar mortality rates. Thames River fish were collected via electrofishing in fall 2016 and Belle River fish by standardized angling in Fall of 2017 and 2018 and had apparent mortality rates of 5% (aggregated for the Belle River events). These findings support the conclusions of Landsman et al. (2011) that catch-and-release mortality for muskellunge is low when conducted by specialized anglers taking care to handle fish properly.

Management implications

Ultimately this study demonstrates the utility of acoustic telemetry for studying the spatial ecology of muskellunge within the St. Clair – Detroit River System with findings having important management implications. Individual fish regularly crossed jurisdictional boundaries within the system, while returning to similar geographical areas during known spawning seasons, and at other times of year. Given the changing nature of the receiver array and unknown detectability of fish among years these results are likely conservative, such that more frequent crossings of jurisdictional and waterbody boundaries likely occurred, particularly in areas with relatively poor receiver coverage (e.g., the Ontario/ Michigan boundary in Lake St. Clair; Fig. 2). These results demonstrate that to achieve management goals, local management actions such as protection of spawning individuals and protection or restoration of spawning habitats should be considered in relation to the full distribution of these fish which covers multiple management jurisdictions. In the system, such collaborative fisheries management is facilitated though the Lake Erie Committee of the Great Lakes Fishery Commission and "maintaining a high-quality trophy-sized Muskellunge fishery in the SCDR" is identified as one of the committee's fish community objectives (Francis et al., 2020). While our results also demonstrate a potential for spatial structure and multiple populations, previous work has demonstrated that the fish in the system form a single genetic cluster (Turnquist et al., 2017). It therefore remains unclear if managers should consider the SCDRS muskellunge as a single population unit or as a fishery made up of multiple smaller populations units. In other regions of the Great Lakes such as Lake Huron's Georgian Bay, muskellunge exhibited strong patterns of spatial structure within limited spatial extents (Wilson et al, 2016). Future work could use the movement patterns described in this study to help refine sampling and interpretation of genetic structure analyses. Furthermore, the ongoing telemetry data being collected for this project can be examined using clustering functions such as sequence analysis (Colborne et al., 2019; Lowe et al., 2020) to assign fish to groups based on their movement patterns. Such future analyses could identify spatial boundaries among populations and time of the year when they cohabitate specific areas of SCDRS. Identifying these groups could help inform estimates of population size and provide information about angling exploitation rates, beneficial to the management of muskellunge within the system.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We dedicate this manuscript to the memory of Jim Herod. Through his involvement with Muskies Canada, Mr. Herod was a champion of muskellunge conservation and research. His dedication to this project has been instrumental in securing funding and equipment and that has enabled the success of this project to date. Funding for this project was provided by Muskies Canada, the Michigan Muskie Alliance, Muskies Inc Lake St. Clair Chapter, two grants from the Hugh C. Becker Foundation, the Michigan

Department of Natural Resources, and the Ontario Ministry of Natural Resources and Forestry. This work was funded by the Great Lakes Fishery Commission (Grant ID #2013_BIN_44024) by way of Great Lakes Restoration Initiative appropriations (Grant ID #GL-00E23010). This paper is contribution 89 of the Great Lakes Acoustic Telemetry Observation System (GLATOS). We would like to acknowledge the crew of the R/V *Channel Cat* as well as members of the Ontario Ministry of Natural Resources, and the Michigan Department of Natural Resources for assistance in the field. This projected benefited greatly from the mobilization of voluntary recreational anglers, coordinated through strong partnerships with The Belle River Chapter of Muskies Canada, the Michigan Muskie Alliance, and Muskies Inc Lake St. Clair Chapter. Any use of trade, firm or product names are for descriptive purposes only and do not imply endorsement by the U.S. Government. All sampling and handling of fish during research carried out by all authors and affiliated agencies was done in accordance with guidelines for the care and use of fishes by the American Fisheries Society (http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf).

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