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ARTICLE

Seasonal Movements and Spatial Overlap of Juvenile and Adult Lake Sturgeon in Lake Champlain

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Abstract
The lake sturgeon *Acipenser fulvescens* is a large, long-lived, potamodromous species that is widely distributed throughout freshwater systems in the central part of North America. In this study, we used acoustic telemetry to examine seasonal distribution and movement patterns of endangered Lake Sturgeon in Lake Champlain, Vermont. Acoustic tags were implanted in 29 juvenile Lake Sturgeon (453–874 mm TL) and 19 adults (1,215–1,615 mm TL) from the Winooski River and nearby areas of Lake Champlain between 2015 and 2019; tags were detected with 23 passive acoustic receivers deployed in the river and delta area and an additional 34 receivers deployed throughout Lake Champlain. Home range analysis using a lattice-based density estimator indicated that juvenile home range sizes were the same as adult home range sizes in spring and summer but were statistically larger than adult home ranges in winter. Cumulative home range analysis showed that juvenile and adult home ranges overlapped in shallow (<10-m) water in the summer and fall. In winter and spring, cumulative home ranges from juveniles included deepwater sites (>25 m), while adults remained in shallow water near the mouth of their spawning river. Seven juveniles made long-range movements (18–34 km) during the winter and spring months, and 13 juveniles moved back into the lower section of their natal river after overwintering in Lake Champlain. This study is the first to directly compare adult and juvenile Lake Sturgeon distribution, home range size, movements, and habitat use in a large lake system and provides a baseline for further research on the movement ecology of Lake Sturgeon in Lake Champlain.

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The Lake Sturgeon *Acipenser fulvescens* is a large, long-lived, potamodromous species that is native to the Great Lakes, Hudson Bay, and Mississippi River drainages in central North America (Peterson et al. 2007). Like other sturgeons, Lake Sturgeon have declined throughout their range due to overfishing and habitat destruction. These factors have caused Lake Sturgeon populations to be listed as extirpated, endangered, threatened, or of special concern in 18 U.S. states and 4 Canadian provinces (Bruch et al. 2016). One of the foci of recovery efforts is to gain more information on the ecology of various life stages. In particular, Lake Sturgeon movements and habitat selection have been noted to be highly plastic (Pollock et al. 2015; Bruch et al. 2016) and are often variable across the wide range of freshwater ecosystems inhabited by the species. Gaining an understanding of the spatial use of habitat by Lake Sturgeon throughout their life cycle in various systems can be vital to the protection of critical habitats and to population recovery.

Lake Sturgeon generally adhere to the triangle of migration, where adults spawn at times or locations that favor dispersal of larvae away from spawning habitats into suitable nursery habitats. The triangle implies that there is some separation of optimal juvenile ("nursery") habitats and adult habitats, with juveniles undergoing a migration out of these nursery habitats to join the adult population. Lastly, adults migrate between foraging areas, overwintering areas, and spawning sites that are favorable for egg survival, and the triangle begins again (Harden Jones 1968; Secor 2015). Lake Sturgeon adults enter or move upstream in rivers to spawn from mid-April to mid-June (Bruch and Binkowski 2002; Peterson et al. 2007) and then return to either lakes or the lower sections of large rivers to forage and overwinter (Rusak and Mosindy 1997; Ecclestone et al. 2020). Riverine nursery habitat is thought to be important for juvenile Lake Sturgeon, with age-0 individuals typically remaining in their natal rivers for at least the first few months of life before moving into lakes or larger rivers in the late summer or fall (Holtgren and Auer 2004; Benson et al. 2005).

As is characteristic of sturgeons, Lake Sturgeon are late to mature, with males typically reaching maturity at 12–15 years of age and females reaching maturity even later at 18–27 years (Peterson et al. 2007). The movement of juvenile Lake Sturgeon out of their natal rivers to productive lacustrine foraging areas allows them to grow rapidly during the protracted juvenile stage, attaining a large size (>1,000 mm TL) before their first spawn. In some systems, these "late-stage juveniles" (juveniles that have left the nursery habitat of their natal river) are found in the same habitats as adults, but there is also evidence of juveniles using habitats that are spatially distinct from those used by adults even after leaving their natal river. For example, juvenile Lake Sturgeon use the drowned river mouth that forms Muskegon Lake, Michigan, before moving into Lake Michigan (Altenritter et al. 2013). An understanding of why juvenile and adult Lake Sturgeon may be using distinct habitats in some systems and not in others is largely unknown, likely in part because the distribution, movement, and habitat selectivity of juvenile Lake Sturgeon have been noted as one of the primary data gaps in the current understanding of the species (Bruch et al. 2016).

Variability in Lake Sturgeon behavior across systems can make it challenging to effectively sample populations or identify areas of conservation concern. In many systems, information on juvenile Lake Sturgeon movements —as well as how those patterns relate to adults in the same system—is lacking. Electronic tagging technology has allowed researchers to investigate individual behavior and is increasingly being used to inform management of both freshwater and marine species (Hussey et al. 2015; Crossin et al. 2017). Acoustic telemetry is a valuable tool that can be used to collect an extensive amount of information from a small number of fish, especially when passive receiver arrays are included in the study design. Therefore, acoustic telemetry is useful for studying a depleted species that is difficult to capture in large numbers.

Previous research directly comparing the movements, distribution, and habitat use of juvenile and adult Lake Sturgeon has focused on riverine systems in which Lake Sturgeon are resident throughout their lives (Trested et al. 2011; Lacho 2013; Thayer et al. 2017). Limited information is available from large lake systems on these life stages and how they overlap. In this study, we used passive acoustic telemetry to study seasonal patterns of movement and habitat use of Lake Sturgeon in Lake Champlain (surface area = 1,269 km^2) and one of its tributaries: the Winooski River, Vermont. Lake Sturgeon were listed as endangered in Vermont in 1972. Recent efforts by the Vermont Fish and Wildlife Department (VFWD) have documented successful spawning in the Winooski River (MacKenzie 2016); however, no information exists on juvenile and adult Lake Sturgeon movements within the Lake Champlain system. Our objectives were to (1) describe seasonal patterns of movement and distribution of Lake Sturgeon in a large lake system, (2) compare size and spatial distribution of seasonal home ranges of adults and juveniles from the same population, and (3) describe areas and seasons of overlap between juvenile and adult Lake Sturgeon in Lake Champlain and the Winooski River, which could point to areas that are uniquely used by different life stages or that are critical to both.

METHODS

Study area.— Lake Champlain (Figure 1) is a long (193 km) and narrow (20 km at its widest point) lake that is bordered by New York, Vermont, and the province of Quebec, Canada. Historical records indicate that spawning occurred in four tributaries to Lake Champlain: the Missisquoi, Lamoille, and Winooski rivers and Otter Creek (Moreau and Parrish 1994). Following a sharp decline in harvest during the late 1940s and 1950s (Halnon 1963), the fishery was closed in 1967 and the species was listed as endangered in 1972 (MacKenzie 2016). Prior egg and larval sampling has indicated that Lake Sturgeon spawning still occurs in at least three of the four historic spawning tributaries (MacKenzie 2016), but overall information on the species in Lake Champlain is limited.

Lake Champlain reaches a maximum depth of 122 m and has a mean depth of 19.4 m (Myer and Gruendling 1979), but large areas of shallow-water habitat (<9.1 m) that can support an adequate benthic forage base for Lake Sturgeon are found throughout the system (Moreau and Parrish 1994). One of these areas is the delta of the Winooski River; the river is a historic spawning tributary and is considered important habitat for Lake Sturgeon (C. MacKenzie, VFWD, personal communication, June 2016). The large, shallow portion of the delta drops off rapidly from 10 to 60 m over 1 km. Less than 3 km south of the Winooski River delta is Burlington Bay, a basin that ranges from 10 to 60 m in depth. Preliminary results from a mobile telemetry study of adult Lake Sturgeon suggested that they are generally not found in Burlington Bay (MacKenzie, personal communication), but in 2016, a single juvenile Lake Sturgeon (683 mm TL) was incidentally caught during trawl sampling in the bay.

The lower 17 km of the Winooski River (Figure 1) are accessible to Lake Sturgeon. Adults use the Winooski River for spawning from April to June. The river also provides nursery habitat for juvenile Lake Sturgeon (MacKenzie 2016), although the timing and duration of juvenile use are unknown.

Capture and tagging.— Juvenile Lake Sturgeon were sampled between April and November in 2017, 2018, and 2019 using three methods: (1) small-mesh, monofilament gill nets; (2) baited trotlines; and (3) incidental capture in bottom trawls during the Lake Trout *Salvelinus namaycush* survey conducted by the University of Vermont. Gill nets were 90 m long and consisted of three 30-m panels of 7-, 10-, and 12-cm stretched mesh. Gill-net sampling took

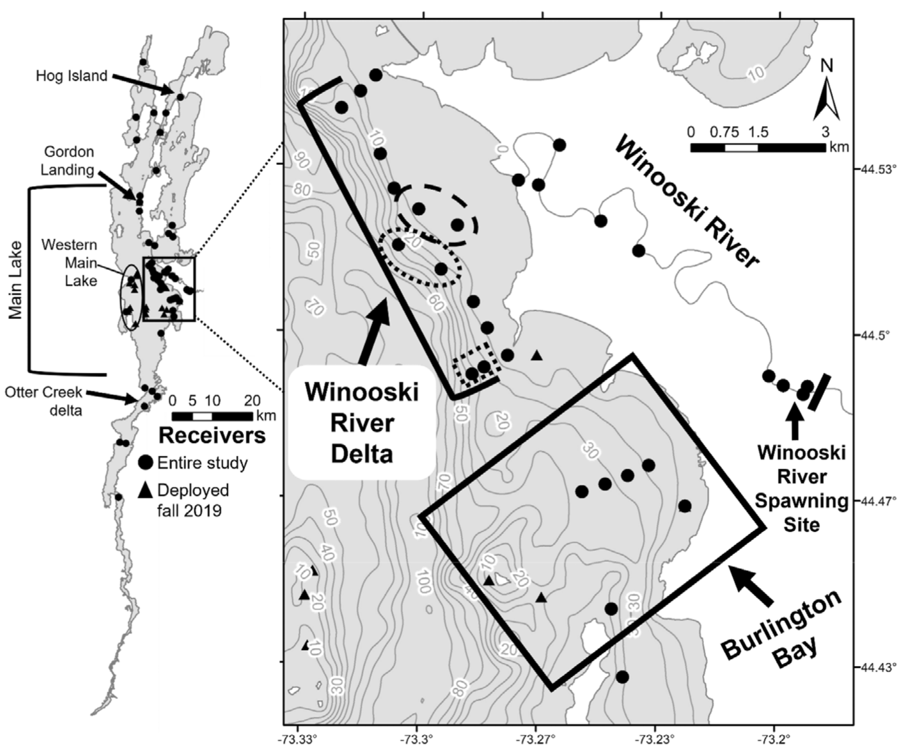

FIGURE 1. Map of acoustic receiver locations in Lake Champlain. Black circles show receivers deployed for the duration of the project (August 2017–July 2020); black triangles show receivers that were deployed in the fall of 2019 through the remainder of the project. Focal areas of the study in the Winooski array are labeled in the inset map (Winooski River, Winooski River delta, and Burlington Bay) with 10-m depth contours. The black line in the river denotes the Winooski One Dam, which is the upstream extent of Lake Sturgeon habitat in the system. The three primary overwinter sites are the Central Delta Shallow (dashed oval), Central Delta Deep (dotted oval), and South Delta Deep (dotted square) sites. Receivers outside of the Winooski array on which Lake Sturgeon were detected (mentioned in the text) are individually labeled.

place during dawn, dusk, and daylight hours, with sets lasting between 2.0 and 7.5 h. Trotlines used in the Winooski River consisted of 20 or 25 droplines with 1/0, 2/0, 3/0, and 4/0 circle hooks attached, while trotlines used in Lake Champlain consisted of 100 droplines with 2/0, 3/0, and 4/0 circle hooks attached. Hooks were baited with either nightcrawlers or pieces of frozen Rainbow Smelt *Osmerus mordax*, Sea Lamprey *Petromyzon marinus*, or Alewife *Alosa pseudoharengus*. Trotlines were set during both day and night, with daytime sets lasting between 2 and 8 h and overnight sets lasting between 8.7 and 20.5 h. The Lake Trout trawl was a three-in-one bottom trawl with an 8-m headrope, a 9.3-m footrope with chains attached, and a 1.25-mm stretch cod-end liner; 10-min tows were conducted during the day throughout the main lake from April to November.

Adult Lake Sturgeon were captured and tagged by VFWD between 2015 and 2018 using large-mesh, multifilament gill nets that were 36 or 46 m long and consisted of 20-, 25-, and 30-cm stretched-mesh panels. Gill nets were usually set in the morning and checked after 3–5 h. Occasionally, nets were set overnight, with sets lasting no more than 14 h.

Targeted sampling for both juvenile and adult Lake Sturgeon as part of this study was conducted either within the Winooski River or in shallow (<15-m) portions of the Winooski River delta (Figure 1). The Winooski River was chosen as the focal area because prior sampling by VFWD suggested that the Winooski River may be home to the most productive remaining spawning population in Lake Champlain, as it had the highest number of adult Lake Sturgeon captured before 2015 (MacKenzie 2016). Increasing reports of incidental capture of adult Lake Sturgeon by anglers and VFWD during the spawning period (MacKenzie, personal communication) suggested that areas in close proximity to the Winooski River would give us the highest chance of capturing juvenile Lake Sturgeon. Although we acknowledge that this sampling bias likely led to us capturing only individuals that were produced in or that spawn in the Winooski River, the depleted status of the other historic spawning runs made it infeasible to attempt to capture sufficient numbers of adults and juveniles from additional populations.

After capture, Lake Sturgeon were measured for TL and FL to the nearest millimeter, weighed to the nearest 0.01 kg, and tagged with a 12-mm PIT tag (Biomark, Boise, Idaho) that was inserted to the left of the first dorsal scute. For adult Lake Sturgeon captured during the spawning period, sex was determined when possible based on expression of gametes. Based on permit requirements, only Lake Sturgeon <900 mm TL could be tagged as part of the juvenile telemetry project. Pectoral fin ray samples were also taken from a subset of juvenile Lake Sturgeon for age analysis (see Izzo et al. 2021 for detailed methods).

For tagging of both juveniles and adults, Lake Sturgeon were placed in a sling with the head and gills immersed in ambient river or lake water. Fish were not chemically anesthetized prior to or during surgery and were instead flipped ventral side up, where they exhibited behaviors consistent with tonic immobility. Three sizes of Vemco (Halifax, Nova Scotia, Canada) 69-kHz tags were used in this study. For juveniles, either V9-2L (9×29 mm, 2.9 g in water, with a 60-s average delay and an estimated tag life of 476 d) or V13-1L (13×36 mm, 6 g in water, with a 120-s average delay and an estimated tag life of 4 years) tags were used depending on the weight of the fish and tag availability. For adults, V16-6L (16×95 mm, 14.9 g in water) tags were used, which had a 120-s average delay and an estimated tag life of 10 years. Tags were inserted into the body cavity through a small incision made anterior to the pelvic fins, offset from the midline. Incisions were closed with one to four absorbable sutures (depending on the incision size) in a simple interrupted suture pattern. After surgery, fish were checked to ensure normal upright orientation and swimming ability and then were released at or near the site of capture.

Stationary acoustic telemetry array.— Juvenile and adult Lake Sturgeon were tracked using an array of Vemco 69-kHz VR2W receivers (Figure 1) operated by the Vermont Cooperative Fish and Wildlife Research Unit, the University of Vermont's Champlain Acoustic Telemetry Observation System (CATOS), and VFWD. Receivers placed as part of the Winooski array focused on the Winooski River, the surrounding delta (including shallow, flat areas in 5–10 m of water as well as deeper, sloped areas with receivers located at depths >25 m), and Burlington Bay. Receivers in the Winooski array were deployed continuously from August 1, 2017, to July 15, 2020, so the following analyses focus on that time period only. Receivers deployed as part of the CATOS were focusing on movements of Lake Trout and Walleye *Sander vitreus* throughout Lake Champlain and either were deployed prior to the start of this study and remained in place for the duration of the study period or were deployed in fall 2019 for a new project and were in place through the remainder of the Lake Sturgeon study (Figure 1).

Range testing.— Range testing was only conducted for the smallest tags (V9-2L); detailed information on the test is reported in the Supplementary Material (available in the online version of this article). The V9-2L test tags were programmed with a 60-s fixed delay. Tags were moored <1 m from the bottom in 7.2–7.6 m of water among multiple receivers on the Winooski River delta (Supplementary Figure S1). Test tags were deployed on August 21, 2019, and retrieved on August 29, 2019. Data were processed using Vemco Range Test software, and range was determined as the distance at which the detection probability was greater than 70%. Range test results were only used for data interpretation and thus are only reported here and in the Supplementary Material. Using the above criteria, range testing for V9-2L tags in our study location indicated a range (detection probability >70%) of 250 m. Previous work in Lake Champlain determined that the range of V13-1L tags was 250 m (Pinheiro et al. 2017). We do not have range test information for V16-6L tags in Lake Champlain; however, work in Lake Ontario indicated that V16 tags can be detected over 1,000 m away (Klinard et al. 2019).

Analysis of telemetry data.— All receiver files were corrected for clock drift using Vemco VUE software, and data were then exported for further analysis in R version 4.0.2. Acoustic telemetry data were processed to identify potential false detections as recommended by Pincock (2012). If the time between two successive detections of a transmitter on a single receiver was more than 30 times the average tag delay, the detection was identified as a suspected false detection and was removed from further analysis. This filter resulted in the removal of 1.1% of juvenile Lake Sturgeon detections (of ~4.4 million detections total) and 1.4% of adult Lake Sturgeon detections (of ~6.9 million detections total).

Detections were divided into seasons as follows: spring (April 1–June 30; the spawning season for adult Lake Sturgeon), summer (July 1–August 31; Lake Champlain stratified with maximum epilimnetic temperatures), fall (September 1–October 31; Lake Champlain stratified but with temperatures declining), and winter (November 1–March 31; no stratification in Lake Champlain). Stratification and temperature data used to determine seasons were based on a series of HOBO MX TidbiT 400 (Onset, Cape Cod, Massachusetts) temperature loggers that were attached to stationary receivers in November 2018 and deployed until July 2020. Two loggers were placed on receivers on the Winooski River delta, with a logger on a receiver at 6–9 m deep and the other on a receiver at 24 m deep. Loggers recorded temperature at 1-h intervals. Potential differences in temperature during winter between shallow-water and deepwater locations were explored by calculating the accumulated degree-days for each winter on each receiver as the average of the maximum temperature and minimum temperature for each day summed over the duration of the season.

To investigate both individual- and population-level distribution patterns on a seasonal basis, detections on stationary receivers were used to calculate home ranges for each tagged fish during each season of each year. Because three different tag models were used and the larger tags that produced stronger signals often had detections on multiple receivers at the same time, hourly short-term centers of activity (COAs) were calculated for use in home range analysis. The COA method estimates the position of a tagged animal based on weighted means of the number of detections at each receiver during an hourly interval (Simpfendorfer et al. 2002). Hourly COAs were calculated using the R package VTrack (Campbell et al. 2012).

Using the hourly locations calculated from the COA method, we employed a lattice-based density estimator (LDE) as an alternative to the traditional kernel density estimator to calculate home ranges in terms of core use areas (50% LDE) and overall use areas (95% LDE) for tagged Lake Sturgeon. The LDE, which was implemented using the R package latticeDensity (Barry 2020), uses a random walk to account for study areas with irregular boundaries (Barry and McIntyre 2011). The lattice created for analysis included the Winooski River delta and Burlington Bay as well as the western portions of the central main lake. The Winooski River was not included in home range analysis. The lattice used had a node spacing of 250 m. The node spacing was chosen for two reasons: (1) the range of both the V9-2L (Supplementary Figure S2) and V13-1L (Pinheiro et al. 2017) tags was estimated to be 250 m; and (2) receivers on the Winooski River delta were spaced <1,000 m apart, so we assumed that fish with detections on only a single receiver during a 1-h period were likely close to the given receiver. Estimation of the optimal smoothing parameter (k) using unbiased cross validation was not possible because many positions of tagged fish were either in the same location or close to each other. Therefore, a k-value of 3 was chosen based on visual inspection of density estimates after varying k-values (Kneebone et al. 2012; Legare et al. 2018).

Home range matrices created in R were imported into ArcMap version 10.7 (ESRI, Redlands, California) and converted to raster files with a cell size of 250×250 m. Individual home range sizes were calculated from raster files. Home range sizes (50% LDE, core use area; 95% LDE, overall use area) of adults and juveniles in each season were compared using a Mann–Whitney U-test. Cumulative overall use and core use area maps were created for each season in each year by adding individual raster files together so that the value of each cell would correspond to the number of individuals having that cell as part of their 95% or 50% LDE home range. The area of overlap between the cumulative adult and juvenile home ranges for each season in each year was calculated in ArcMap. Finally, cumulative maps for the entire study period were created for each season by adding the raster files created for each year. The cumulative maps for each season are the result of individual home ranges collected over 3 years of study.

Three primary overwinter locations were identified from telemetry data: (1) Central Delta Shallow (6–9 m), (2) Central Delta Deep (>30 m), and (3) South Delta Deep (>20 m; Figure 1). Individuals were considered to have overwintered in each location if the majority of detections during the winter months were recorded on receivers in the center of each site: two receivers in 6–9 m in the center of the Winooski River delta, two receivers in 30–38 m on the slope of the Winooski River delta, and two receivers in 24–40 m at the south end of the Winooski River delta.

Residency within the Winooski array (Winooski River delta, Winooski River, and Burlington Bay) was represented by a residency index (RI). The RI was calculated by dividing the total number of days on which a given tag was detected in the array by the total number of days that each tag was active. Abacus plots were then created to identify when tagged Lake Sturgeon were present and absent from receivers in different areas of Lake Champlain.

RESULTS

We tagged 29 juvenile Lake Sturgeon ranging in size from 453 to 874 mm TL (Table 1). In April 2017, one juvenile (595 mm TL) was captured incidentally in the trawl in Burlington Bay at a depth of 43–46 m and two juveniles (770 and 808 mm TL) were captured incidentally in the trawl on the slope of the Winooski River delta at a depth of 17–29 m. In October 2018, three juveniles (453–475 mm TL) were captured on trotlines in the Winooski River, all on a slope of 5–10 m at the site of one of the deep holes in the river. The remaining 23 juveniles (555–874 mm TL; $n = 2$ in gill nets and $n = 21$ on trotlines) were captured on the Winooski River delta in 2017, 2018, and 2019, with capture depths ranging from 2.3 to 12.0 m. The majority of individuals captured on the Winooski River delta were captured from September through early November ($n = 22$), and one individual was captured in July.

Pectoral fin spine samples were taken from 10 juvenile Lake Sturgeon that were captured in October or November of 2018 and 2019, so they had experienced an additional summer of growth. These juveniles included one yearling (470 mm TL), three 2-year-old fish (560–638 mm TL), five 4-year-old fish (694–808 mm TL), and one 5-year-old fish (848 mm TL). The yearling was captured in the Winooski River, whereas the rest of the fish were captured on the Winooski River delta.

Adult Lake Sturgeon sampling conducted by VFWD resulted in 19 tagged adult Lake Sturgeon (1,215–1,615 mm TL; Table 1) that were captured in the Winooski River. All 19 individuals (18 males and 1 female) were caught at the Winooski River spawning site (Figure 1) during the spawning run in 2015 and 2016. After August 2017, the tag from the female was only detected a few days each year and at the same receiver on the Winooski River delta. All other tagged fish were detected consistently throughout the study period at multiple receivers on the Winooski River delta. We assumed from this change in behavior that the female either died or lost the tag; therefore, the data from the female were removed from the following analyses.

Home Ranges

Individual seasonal core use areas (50% LDE home ranges) ranged from 0.1 to 2.9 km^2 for both adults and juveniles (Figure 2a). Overall use areas (95% LDE home ranges) ranged from 0.6 to 15.4 km^2 for juveniles and from 0.3 to 13.4 km^2 for adults (Figure 2b). There was a significant difference between the home range sizes (both core use and overall use) of juveniles and adults in fall and winter (Mann–Whitney U-test: $P < 0.05$) but no difference during spring and summer. Juvenile home ranges were smaller overall than adult home ranges in the fall (median 95% LDE home range = 5.5 km^2 for juveniles, 7.0 km^2 for adults) but were larger than adult home ranges in the winter (median 95% LDE home range = 7.2 km^2 for juveniles, 4.6 km^2 for adults).

Cumulative home range analysis indicated that adult and juvenile home ranges had the highest overlap during spring in all 3 years of the study; overlap was also high during summer and fall (Figure 3). The amount of area that was unique to juvenile Lake Sturgeon was the highest in the winter and spring. The amount of area that was unique to adult Lake

TABLE 1. Summary of capture year, season, location, and TL of adult and juvenile Lake Sturgeon tagged for this study.

Year	Season	Capture location	Life stage	Number of Lake Sturgeon tagged	TL range (mm)
2015	Spring	Winooski River spawning site	Adult	10	1,234–1,390
2016	Spring	Winooski River spawning site	Adult	9	1,215–1,615
2017	Spring	Burlington Bay	Juvenile	1	595
2017	Spring	Winooski River delta (slope)	Juvenile	2	770–808
2017	Summer	Winooski River delta (flat)	Juvenile	1	582
2017	Fall	Winooski River delta (flat)	Juvenile	6	616–874
2018	Fall	Winooski River	Juvenile	3	453–475
2018	Fall	Winooski River delta (flat)	Juvenile	8	562–842
2019	Fall	Winooski River delta (flat)	Juvenile	8	555–860

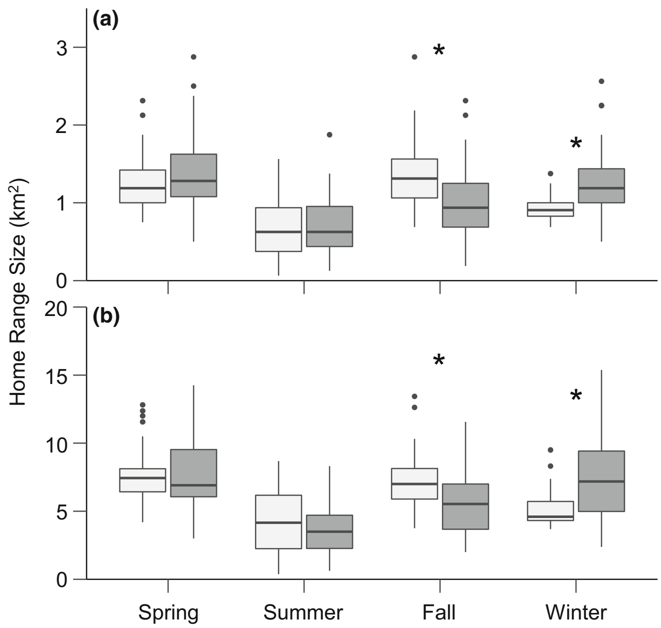

FIGURE 2. Box plots of seasonal **(a)** 50% lattice-based density estimator (LDE) home range size and **(b)** 95% LDE home range size for tagged adult (light gray) and juvenile (dark gray) Lake Sturgeon in Lake Champlain. The thick horizontal line in each box indicates the medians, with boxes showing the interquartile range and whiskers showing the extremes (1.5× the interquartile range). Outliers are included as black points. Home range sizes include individual home ranges across all years of the study (August 2017–July 2020). Seasons with significant differences (Mann Whitney *U*-test: $P < 0.05$) between adults and juveniles are denoted by an asterisk.

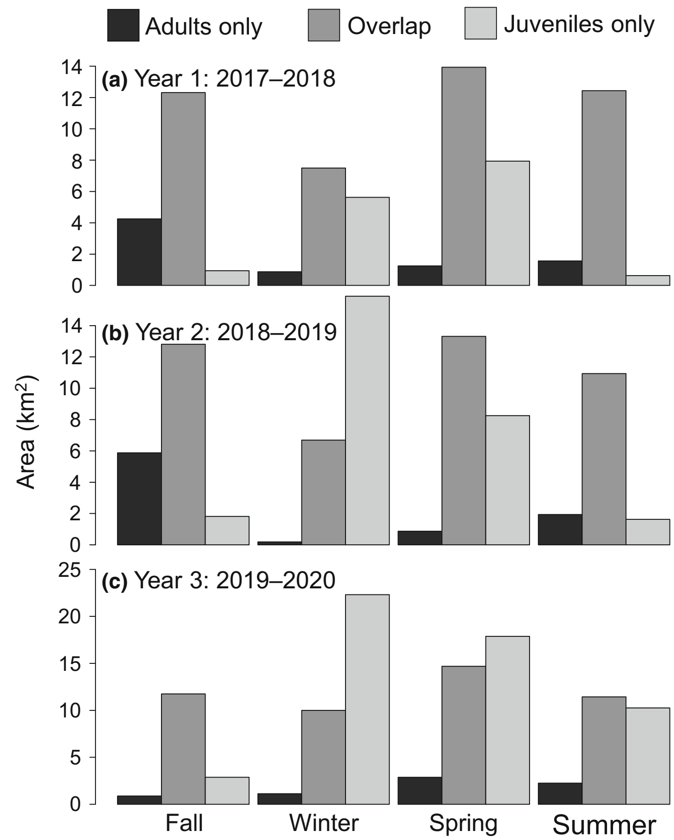

FIGURE 3. Area of the cumulative home range for adult Lake Sturgeon only (black), juveniles only (light gray), and the area of overlap between the two life stages (dark gray) for each season in **(a)** year 1, **(b)** year 2, and **(c)** year 3 of the study.

Sturgeon varied across seasons in the 3 years of the study but was always lowest in the winter of each year. These results correspond with the spatial trends observed in the seasonal cumulative home range maps (Supplementary Figures S3–S10). Juvenile and adult distributions overlapped in the summer (Figure 4), with the areas around the shallow-water receivers being included in the home ranges of a higher number of individuals. During winter, the distribution of adults contracted to the shallow area of the central portion of the Winooski River delta, near the mouth of the Winooski River (Figure 5, right panels). Tagged juveniles remained dispersed throughout the Winooski River delta in winter, with aggregation locations shifting to the deepwater receivers that were identified as overwinter locations (Figure 5, left panels). Juveniles used areas outside of the Winooski River delta, specifically the deep (>30-m) central portion of Burlington Bay, more frequently than adults, particularly during the winter (Figure 5).

Primary Overwinter Locations

Juvenile Lake Sturgeon were detected at the three identified overwintering locations in all years of the study (Figure 1; Table 2). While many individuals across all 3 years were detected primarily at a single overwintering location during a season, some individuals were detected equally at multiple overwintering locations (25–56% depending on the year, indicated as "Mixed" in Table 2). Of the individuals that were tracked over multiple winters during the study period ($n = 18$), only six of them used the same wintering site in consecutive years. Of those six, four were tracked during all three winters of the study and were detected at a different overwintering site in the third year. In the winter of 2018–2019, all adults overwintered at the Central Delta Shallow site. In the other two winters, a single adult was considered to reside at a "Mixed" overwintering site because it was detected equally at the Central Delta Shallow and Central Delta Deep sites. The remaining 17 adults overwintered at the Central Delta Shallow site in both winters.

Although temperatures were similar between the Central Delta Shallow and South Delta Deep overwinter sites, fluctuations in temperature were less pronounced at the South Delta Deep location (Supplementary Figure S11). The temperature variability was the lowest in the early spring of 2019, when Lake Champlain was fully ice-covered. The lake

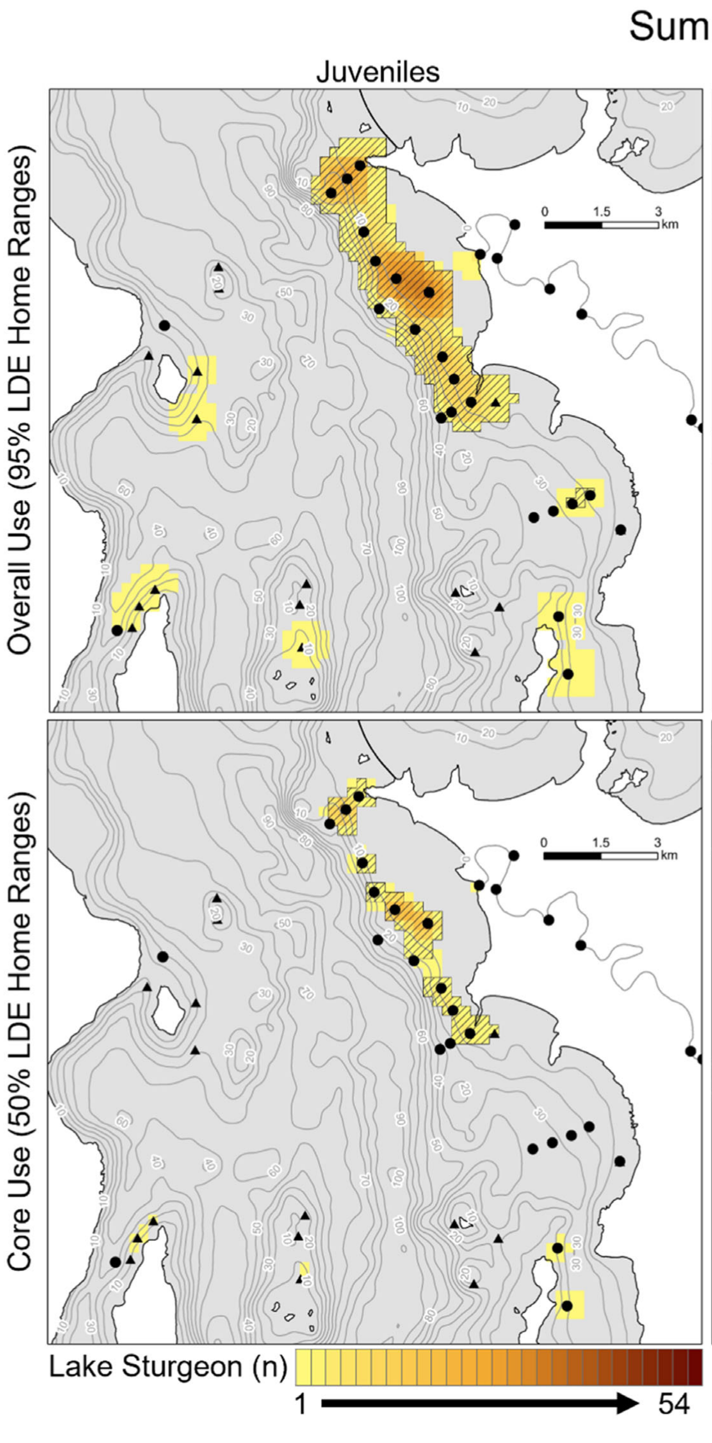

FIGURE 4. Cumulative overall use areas (95% lattice-based density estimator [LDE] home ranges; top panels) and core use areas (50% LDE home ranges; bottom panels) for tagged juvenile (left) and adult (right) Lake Sturgeon in the summer in Lake Champlain. Shading of each cell (250 × 250 m) is based on the number of Lake Sturgeon that had the given cell as part of their home range. The area of overlap between adults and juveniles is shown by the black hatch pattern. These maps are the result of combining home ranges for each season for each year of the study (August 2017–July 2020). Black circles denote receivers that were deployed for the duration of the study; black triangles denote receivers that were deployed in fall 2019. Depth contours (10 m) are included in each panel.

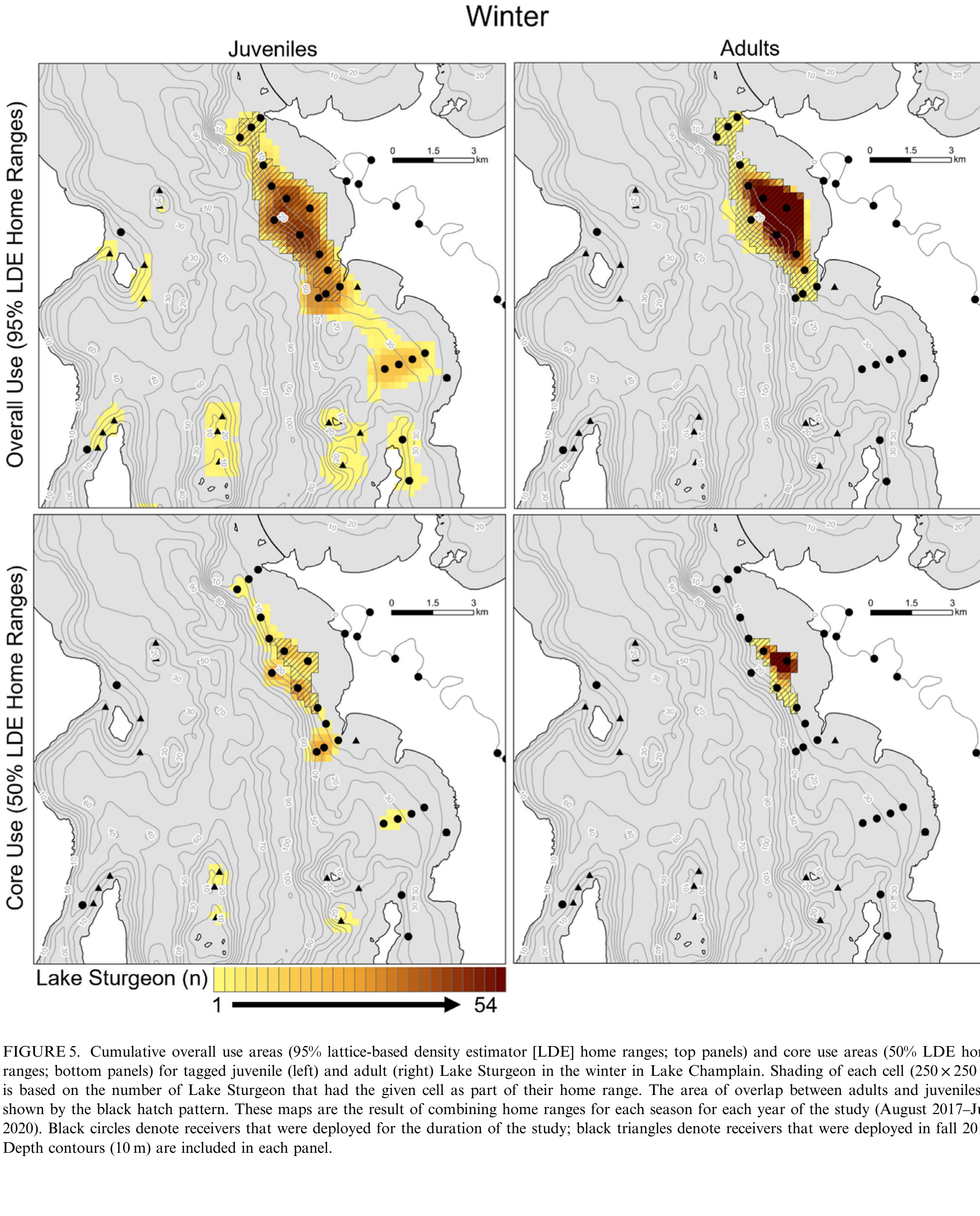

FIGURE 5. Cumulative overall use areas (95% lattice-based density estimator [LDE] home ranges; top panels) and core use areas (50% LDE home ranges; bottom panels) for tagged juvenile (left) and adult (right) Lake Sturgeon in the winter in Lake Champlain. Shading of each cell (250 × 250 m) is based on the number of Lake Sturgeon that had the given cell as part of their home range. The area of overlap between adults and juveniles is shown by the black hatch pattern. These maps are the result of combining home ranges for each season for each year of the study (August 2017–July 2020). Black circles denote receivers that were deployed for the duration of the study; black triangles denote receivers that were deployed in fall 2019. Depth contours (10 m) are included in each panel.

TABLE 2. Number of tagged Lake Sturgeon (juveniles; with number of adults in parentheses) overwintering in each location on the Winooski River delta in 2017–2018, 2018–2019, and 2019–2020. Primary overwinter locations were determined based on the set of receivers with the most detections during November–March of each year. Sites are described in the text.

Primary overwinter site	2017–2018 juveniles (adults)	2018–2019 juveniles (adults)	2019–2020 juveniles (adults)
Central Delta Shallow	2 (17)	1 (18)	2 (17)
Central Delta Deep	2 (0)	3 (0)	10 (0)
South Delta Deep	3 (0)	4 (0)	6 (0)
Mixed Central Delta	2 (1)	7 (0)	2 (1)
Mixed Delta Deep	1 (0)	1 (0)	2 (0)
Mixed all	0 (0)	2 (0)	2 (0)

was not fully ice-covered in the winter and spring of 2019–2020. The accumulated degree-days at the Central Delta Shallow site were lower than those at the South Delta Deep site during both years in which the temperature loggers were deployed (434 versus 475 degree-days in 2018–2019; 582 versus 615 degree-days in 2019–2020).

Movements into Burlington Bay

While most individuals (both adults and juveniles) were detected on the Winooski River delta throughout the study period (Figure 6a, 6d), both life stages made movements south into Burlington Bay. Throughout the duration of the study, more juveniles than adults were detected on the receivers located in deep water in Burlington Bay (Figure 6b, 6e). Adult Lake Sturgeon were primarily detected in the summer and fall, while juveniles were primarily detected during the winter and spring months. Most of the detections of juveniles on the Burlington Bay receivers lasted fewer than two consecutive days. There were a few notable exceptions; one juvenile was detected consistently in Burlington Bay from February through April in 2018, one was detected consistently for the month of June in 2019, and one was detected consistently from January to May in 2020.

Winooski River Movements

Of the three juvenile Lake Sturgeon captured in the Winooski River during October 2018, two remained at their capture site at river kilometer (rkm) 5.2 (rkm 0 = river mouth) for 2 weeks, while the third moved downstream 1 week after capture to rkm 3.1 (Figure 6c). All three individuals exited the Winooski River between November 3 and 4 and overwintered in Lake Champlain. The following spring, one of these individuals returned to the Winooski River on April 24, 2019, moving as far upstream as its previous capture site at rkm 5.2, and then exited the river on June 16.

In each year, a limited number of juveniles (1–8 individuals, depending on the month) were detected on receivers in the Winooski River during the spring and early summer (Figure 6c). The majority of tagged adults were also detected in the Winooski River during the same period (Figure 6f). Although the adults moved all the way upstream to the spawning site at rkm 17, none of the tagged juvenile Lake Sturgeon that entered the river were detected at the spawning site. Juveniles remained at the river mouth (rkm 0) or in the lower river (below rkm 8) during the spring and summer. Tagged juveniles that were detected in the Winooski River ranged in size from 470 to 874 mm TL, while individuals detected only in the river mouth ranged in size from 562 to 808 mm TL.

Movements Outside of Core Areas

The RIs for juvenile Lake Sturgeon in the Winooski River array were, on average, 0.75 (quantiles = 0.65, 0.80, 0.90). Although most tagged juveniles were detected the majority of the time in the Winooski array, seven juveniles notably were not detected on these receivers for 3–6 months at a time between December and June. Two of the fish missing from the Winooski array during the winter months made the longest movements undertaken by juveniles and were detected at a receiver on the Otter Creek delta, located approximately 34 km south of the Winooski River mouth (Figure 7a), in December and January. Three of the four tagged juveniles that were not detected on the Winooski array during the winter months of 2019–2020 were detected at multiple receivers on the western side of the central main lake portion of Lake Champlain (Figures 1 and 5). Additionally, seven juveniles were detected at Gordon Landing, approximately 18 km north of the Winooski River mouth, primarily in spring and summer (Figure 7a).

The RIs for adult Lake Sturgeon in the Winooski River array were, on average, 0.88 (quantiles = 0.79, 0.93, 0.95). When not within the Winooski array, the majority of adults ($n = 14$) were commonly detected at a receiver located 5 km north of the northern end of the Winooski River delta during the summer and early fall. Three adults were detected on the Gordon Landing receiver in April–October. The longest movements undertaken by an adult Lake Sturgeon were by a single fish that repeatedly left the Winooski River delta each summer and moved as far north as Hog Island, located 44 km north of the Winooski River mouth (Figure 7b).

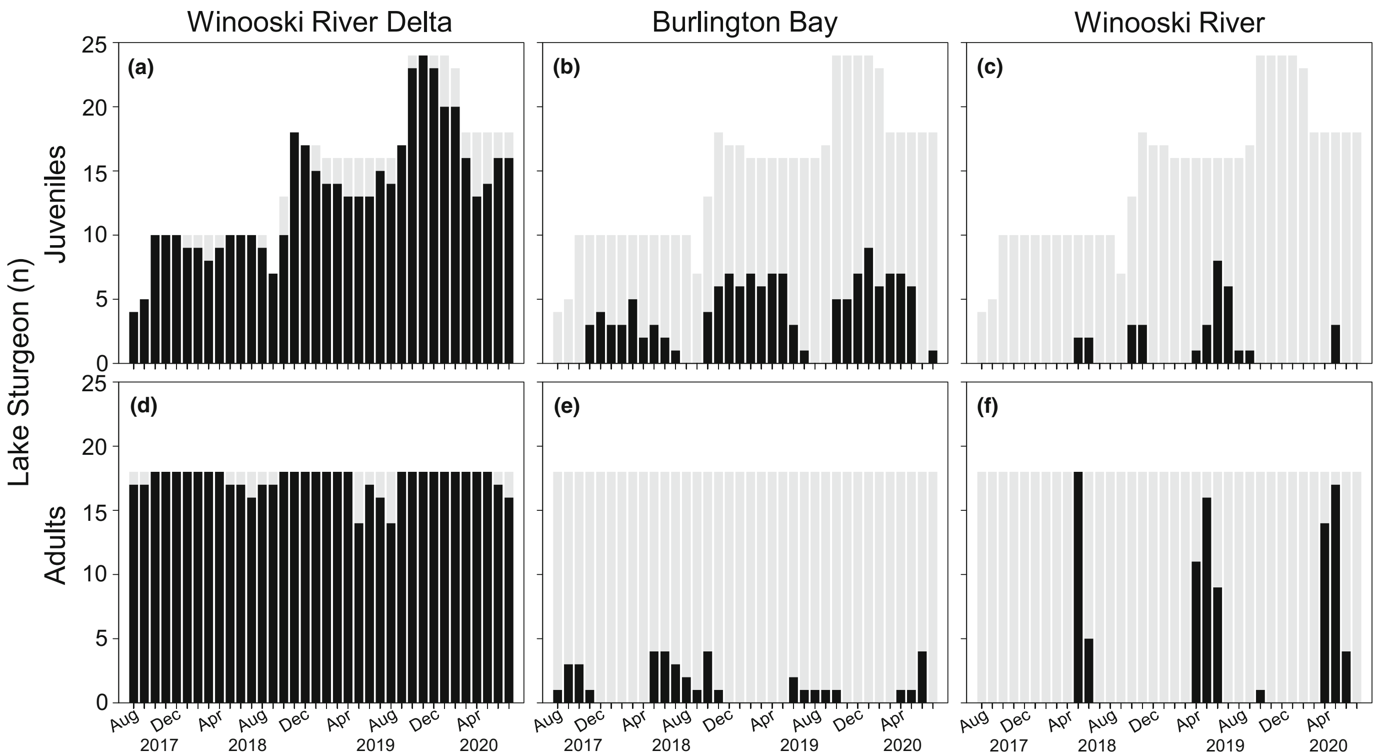

FIGURE 6. Number of tagged **(a–c)** juvenile and **(d–f)** adult Lake Sturgeon that were detected (black bars) on the Winooski River delta, in Burlington Bay, and in the Winooski River during each month of the study period. Gray bars indicate the number of fish with active tags during each month.

DISCUSSION

To our knowledge, this is the first study to report free-ranging movements of both juvenile and adult Lake Sturgeon in a large lake system. We found that despite having access to a large area of diverse habitats in Lake Champlain, most juvenile and adult tagged Lake Sturgeon remained within the focal area of the Winooski River, the river delta, and Burlington Bay for the duration of the study period (August 2017–July 2020). Our results support what has been observed in other studies, where juvenile Lake Sturgeon have shown high site fidelity throughout the year (Holtgren and Auer 2004; Lord 2007; Altenritter et al. 2013; Trembath 2013; Boase et al. 2014). Similarly, although adults can move long distances, previous studies have indicated that they may return to core areas for foraging or overwintering (Knights et al. 2002; Gerig et al. 2011). We documented that both juvenile and adult Lake Sturgeon have high site fidelity to the Winooski River delta. Adults, in particular, rarely moved outside of the Winooski River delta, with the exception of movements into the Winooski River during the spawning period.

The high degree of residency on the Winooski River delta for both juveniles and adults suggests that this area is important for Lake Sturgeon throughout their life cycle in this system, likely due to the presence of adequate forage. Both juvenile and adult Lake Sturgeon have been noted to prefer shallow water (3–10 m) with fine substrates (sand and silt) that allow them to forage on benthic prey (Bruch et al. 2016). The home ranges of juvenile and adult Lake Sturgeon overlapped on the Winooski River delta, particularly during the spring, summer, and fall. The shallow, sand/silt area of the Winooski River delta likely provides substantial foraging opportunities for both juveniles and adults. Although we do not have data on the benthic invertebrate community of the delta, zebra mussels *Dreissena polymorpha* were often observed on the substrate during trotline surveys where Lake Sturgeon were captured. Small juvenile Lake Sturgeon (<200 mm) have difficulty foraging for infaunal prey in areas with heavy zebra mussel cover (McCabe et al. 2006). However, diet work in Oneida Lake and selectivity analysis in the North Channel Saint Clair River have suggested that zebra mussels may be an important food source for Lake Sturgeon larger than 700 mm (Jackson et al. 2002; Boase et al. 2014).

We observed juvenile Lake Sturgeon in parts of Lake Champlain that had limited or no adults present, particularly in the winter and early spring. Some juveniles moved south into deeper water in Burlington Bay during the colder months, when adults were not detected on the Burlington Bay receivers. Additionally, the juveniles that

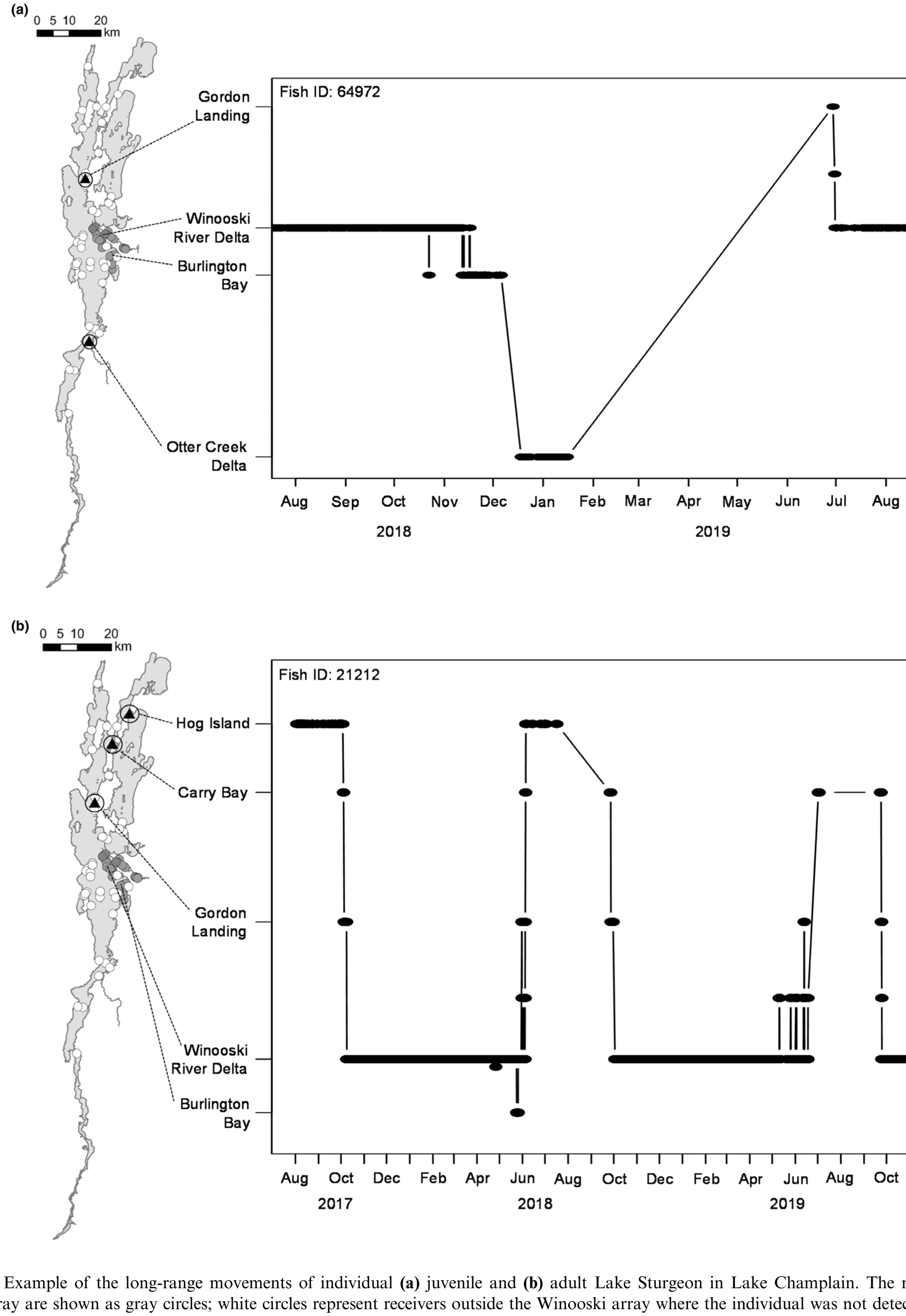

FIGURE 7. Example of the long-range movements of individual **(a)** juvenile and **(b)** adult Lake Sturgeon in Lake Champlain. The receivers in the Winooski array are shown as gray circles; white circles represent receivers outside the Winooski array where the individual was not detected, and black triangles represent receivers outside the Winooski array where the individual was detected. The *y*-axis of each plot is scaled to approximate the distance between receivers.

were captured incidentally by the bottom trawl were caught in over 40 m of water in Burlington Bay and greater than 15 m of water on the Winooski River delta in April, further supporting the results from our stationary acoustic receiver array. The differences between adults and juveniles were most evident in overwintering sites. During all 3 years, all of the tagged adult Lake Sturgeon moved to a shallow-water (6–9-m) overwintering site in the central part of the Winooski River delta, right outside the mouth of the river. While some juveniles in each year also overwintered in the same area as adults, more than half of the tagged juveniles in a given year overwintered in deep water (25–40 m) on the slope of the Winooski River delta. Lake Sturgeon are generally considered a shallow-water fish, with adults typically located in <11 m of water (Hay-Chmielewski 1987; Knights et al. 2002; Boase et al. 2011; Damstra and Galarowicz 2013). However, juvenile Lake Sturgeon have been found in deepwater areas when the habitat is available (>13 m: Smith and King 2005; >13 m: Barth et al. 2009; >15 m: Altenritter et al. 2013; >10 m: Trembath 2013; >16 m: Boase et al. 2014). Movement into deeper water may also have a seasonal component; a similar pattern of juveniles moving to deeper water in the winter was also observed in Muskegon Lake, Michigan, where tagged juvenile Lake Sturgeon moved from the shallow river mouth (6–8 m) in the summer to a deep hole (>15 m) for overwintering (Altenritter et al. 2013). Movement to deeper water during the winter could buffer against temperature fluctuations and provide more thermal stability for juvenile Lake Sturgeon. Although temperatures at the shallow and deep overwinter sites were similar in our study, there was less variability in temperature at the deepwater site and accumulated degree-days were higher than at the shallow site. Movement into deeper water in Lake Champlain may indicate that juveniles seek out warmer, more stable thermal conditions, as the Winooski River delta is one of the last areas of Lake Champlain to freeze each year.

Winter is typically a season of limited movement in fish populations, including sturgeons (Rusak and Mosindy 1997; Lachapelle 2013; Thayer et al. 2017); however, we observed that the tagged juvenile Lake Sturgeon in our study moved more than expected during the winter. Juveniles not only had larger home ranges than adults and moved into Burlington Bay (receivers >5 km south of the Winooski River delta), but also moved into the western part of the central main lake as well as outside of the main lake entirely (>30 km). Movements across the lake to the western side entailed passage through depths up to 100 m. To our knowledge, juvenile Lake Sturgeon have not been previously documented making long-range movements outside of their core areas during the winter. However, many studies do not have access to acoustic receivers outside of their focal study area. The development of large-scale telemetry networks makes it possible to examine large-scale fish movements even in large lake systems (Withers et al. 2021) and could lead to more observations of long-range movements by juvenile Lake Sturgeon. Although the reasons for the winter movements we observed are unknown, the juveniles may have been investigating alternative overwinter sites. All tagged juveniles that left the Winooski array eventually returned to the Winooski River delta in the spring or summer, suggesting that these movements may be indicative of juveniles leaving core areas to explore new habitats, but these fish continue to return to core areas at distinct times of the year.

As young of the year, Lake Sturgeon leave their natal river when temperatures drop in the fall and they overwinter in lakes (Holtgren and Auer 2004; Benson et al. 2005). Although we did not observe any age-0 Lake Sturgeon, we captured three juveniles in the Winooski River during October 2018. One of these juveniles was estimated to be age 1 based on examination of its pectoral fin spine, and we assume that the others were from the same cohort based on their similar length. All three fish exited the river in early November to overwinter in Lake Champlain, which suggests that Lake Sturgeon in the Winooski River may spend their entire first year in their natal river before exiting to the lake. However, one of these tagged juveniles did return to the river the following spring and summer after spending the winter in the lake. These results indicate that the capture of age-1 or age-2 juvenile Lake Sturgeon within a river may not necessarily mean that those individuals have been in the river since they hatched. Thus, it could be important to further investigate the duration of river residency for juvenile Lake Sturgeon in different systems.

Several juvenile Lake Sturgeon at a range of sizes (470–874 mm TL) moved back into the Winooski River during the spring and summer, even after overwintering in Lake Champlain. Juvenile Lake Sturgeon have been documented to move toward river mouths, likely for foraging (Altenritter et al. 2013), but movements of juveniles into the lower river after having left their natal system have not been reported. The tagged juveniles that were detected in the Winooski River can be divided into two groups: (1) individuals that moved into the Winooski River at the same time that adult Lake Sturgeon were moving into the river for spawning, and (2) individuals that moved into the Winooski River after spawning adults had left the river. Juvenile movements into the river during the spawning period may be related to the movements of adults. In some fishes, learning of migration circuits is thought to have a social component, with young individuals following experienced fish during migration (Secor 2015). Though examples of social migration are not evident for sturgeons, “prepubescent spawning runs” of larger juvenile Lake Sturgeon (>750 mm TL) have been observed in the Wolf

River, Wisconsin (Snobl et al. 2017). However, while the larger juveniles moved all the way to the adult spawning site in the Wolf River, juveniles in our study were generally smaller than 750 mm TL and did not travel all the way to the spawning site. The second pattern, in which juveniles moved into the river after adults had left, was only seen during 2019. These results suggest that conditions in the Winooski River may be suitable for juvenile Lake Sturgeon in some years, potentially for foraging, but unsuitable environmental factors (e.g., temperature, dissolved oxygen) may restrict juveniles from moving into the river during other years. Further research could identify the conditions that cue juveniles, both small and large, to move back into or avoid the Winooski River.

In this study, we tagged Lake Sturgeon from sampling locations in and around the Winooski River. While this sampling allowed us to capture both juveniles and adults, we acknowledge that the focus on the chosen sampling locations likely led to us tagging only Lake Sturgeon from the population that spawns in the Winooski River. There are three other historic spawning tributaries to Lake Champlain, with the furthest (the Missisquoi River) located approximately 50 km north of the Winooski River mouth. The scope of this study did not allow for additional tagging of Lake Sturgeon from other populations, so we do not know whether the patterns observed here are consistent with other populations in Lake Champlain or whether individuals from other spawning populations mix on the Winooski River delta at any time during the year. Previous studies on Lake Sturgeon in various systems have noted that fish occupying the same area at certain times of year can fall into multiple groups with distinct migration patterns (Rusak and Mosindy 1997; Kessel et al. 2018; Colborne et al. 2019). Ongoing research by VFWD in Lake Champlain is focused on tagging adult Lake Sturgeon from other spawning tributaries to gain insights into their movement patterns in comparison with fish from the Winooski River (M. Murphy and L. Simard, VFWD, personal communication, November 2021).

Another potential source of bias present in our study was that the tagged adult Lake Sturgeon consisted mostly of males, with no females used in analyses. Adults were tagged during the spawning period, when males are more likely to spend more time at the spawning site than females (Bruch and Binkowski 2002). However, studies outside of the spawning season have observed no differences in movement rates (Rusak and Mosindy 1997), distance traveled (Shaw et al. 2013), or movement patterns (Boase et al. 2011; Colborne et al. 2019) between male and female Lake Sturgeon. Therefore, we expect that our results describing the movements of adult male Lake Sturgeon could likely be extended to females as well, especially since our characterizations of behavior focused on movements outside of spawning locations.

Importantly, as with other acoustic telemetry studies, our analyses describing the distribution and movements of Lake Sturgeon in Lake Champlain and the Winooski River are limited by the locations of the stationary receivers. Because of shallow water depth and boat traffic, we could not deploy stationary receivers in the shallowest portion of the Winooski River delta (<4 m), near the shoreline. The extent to which juvenile or adult Lake Sturgeon use this shallower water is unknown, although both life stages were captured on trotlines occasionally in <4 m of water during fall sampling. However, the fact that tagged fish were detected in the study area during the majority of days in the study period suggests that we likely captured the main areas of use of the tagged individuals. It is also important to note that while tagged Lake Sturgeon, both adults and juveniles, were detected on a few receivers in other areas of Lake Champlain, overall there were many receivers throughout the lake that did not detect any Lake Sturgeon. The absence of tagged fish from this study on the other receivers suggests that Lake Sturgeon may not be using many areas of the lake despite their capacity for long-distance movements (Auer 1996; Rusak and Mosindy 1997; Knights et al. 2002).

Plasticity in movements and habitat use has allowed Lake Sturgeon to persist in a variety of freshwater habitats throughout the central part of North America, but this plasticity has made it challenging to transfer results from one system to another. Due to the Lake Sturgeon's long life span, an understanding of the spatial use of various life stages can be vital to identifying and protecting critical habitats. In this study, we described and compared the free-ranging movements of juvenile and adult Lake Sturgeon in a large lake system. Our results indicate that the distributions of juvenile and adult Lake Sturgeon in Lake Champlain overlap, particularly on the Winooski River delta. This area likely serves as important foraging habitat as well as overwintering habitat for multiple life stages of Lake Sturgeon from the Winooski River. Adults and juveniles in this system differ in their overwinter locations on the delta, with juveniles moving to deep (>25-m) sites in the winter while adults remain in shallow (6–9-m) water. Juveniles had larger home ranges and had a broader distribution during the winter months than adults, suggesting that in some Lake Sturgeon populations winter may be a time of more activity than previously thought. Future research into these behaviors and the existence of similar patterns in adult and juvenile Lake Sturgeon in other systems could be beneficial to understanding movement and habitat use variability in this species.

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REFERENCES

Altenritter, M. E. L., A. C. Wieten, C. R. Ruetz, and K. M. Smith. 2013. Seasonal spatial distribution of juvenile Lake Sturgeon in Muskegon Lake, Michigan, USA. Ecology of Freshwater Fish 22:467–478.

Auer, N. A. 1996. Importance of habitat and migration to sturgeons with emphasis on Lake Sturgeon. Canadian Journal of Fisheries and Aquatic Sciences 53:152–160.

Barry, R. P. 2020. latticeDensity: density estimation and nonparametric regression on irregular regions. R package version 1.1.6. Available: https://CRAN.R-project.org/package=latticeDensity. (December 2020).

Barry, R. P., and J. McIntyre. 2011. Estimating animal densities and home range in regions with irregular boundaries and holes: a lattice-based alternative to the kernel density estimator. Ecological Modelling 222:1666–1672.

Barth, C. C., S. J. Peake, P. J. Allen, and W. G. Anderson. 2009. Habitat utilization of juvenile Lake Sturgeon, *Acipenser fulvescens*, in a large Canadian river. Journal of Applied Ichthyology 25(Supplement 2):18–26.

Benson, A. C., T. M. Sutton, R. F. Elliott, and T. G. Meronek. 2005. Seasonal movement patterns and habitat preferences of age-0 Lake Sturgeon in the lower Peshtigo River, Wisconsin. Transactions of the American Fisheries Society 134:1400–1409.

Boase, J. C., J. S. Diana, M. V. Thomas, and J. A. Chiotti. 2011. Movements and distribution of adult Lake Sturgeon from their spawning site in the St. Clair River, Michigan. Journal of Applied Ichthyology 27:58–65.

Boase, J. C., B. A. Manny, K. A. L. Donald, G. W. Kennedy, J. S. Diana, M. V. Thomas, and J. A. Chiotti. 2014. Habitat used by juvenile Lake Sturgeon (*Acipenser fulvescens*) in the north channel of the St. Clair River (Michigan, USA). Journal of Great Lakes Research 40:81–88.

Bruch, R. M., and F. P. Binkowski. 2002. Spawning behavior of Lake Sturgeon (*Acipenser fulvescens*). Journal of Applied Ichthyology 18:570–579.

Bruch, R. M., T. J. Haxton, R. Koenigs, A. Welsh, and S. J. Kerr. 2016. Status of Lake Sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. Journal of Applied Ichthyology 32:162–190.

Campbell, H. A., M. E. Watts, R. G. Dwyer, and C. E. Franklin. 2012. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Marine and Freshwater Research 63:815–820.

Colborne, S., D. W. Hondorp, C. M. Holbrook, M. R. Lowe, J. C. Boase, J. A. Chiotti, T. C. Wills, E. F. Roseman, and C. C. Krueger. 2019. Sequence analysis and acoustic tracking of individual Lake Sturgeon identify multiple patterns of river–lake habitat use. Ecosphere 10(12):e02983.

Crossin, G. T., M. R. Heupel, C. M. Holbrook, N. E. Hussey, S. K. Lowerre-Barbieri, V. M. Nguyen, G. D. Raby, and S. J. Cooke. 2017. Acoustic telemetry and fisheries management. Ecological Applications 27:1031–1049.

Damstra, R. A., and T. L. Galarowicz. 2013. Summer habitat use by Lake Sturgeon in Manistee Lake, Michigan. Transactions of the American Fisheries Society 142:931–941.

Ecclestone, A., T. J. Haxton, T. C. Pratt, C. C. Wilson, and T. Whillans. 2020. Seasonal use of two unregulated Lake Superior tributaries by Lake Sturgeon. Journal of Great Lakes Research 46:1369–1381.

Gerig, B., A. Moerke, R. Greil, and S. Koproski. 2011. Movement patterns and habitat characteristics of Lake Sturgeon (*Acipenser fulvescens*) in the St. Marys River, Michigan, 2007–2008. Journal of Great Lakes Research 37:54–60.

Halnon, L. C. 1963. Historical survey of Lake Champlain's fishery. Vermont Fish and Game Service, Federal Aid in Fish and Wildlife Restoration, Project F-1-R-10, Job 6, Essex Junction.

Harden Jones, F. R. 1968. Fish migration. Edward Arnold, London.

Hay-Chmielewski, E. M. 1987. Habitat preferences and movement patterns of the Lake Sturgeon (*Acipenser fulvescens*) in Black Lake, Michigan. Master's thesis. University of Michigan, Ann Arbor.

Holtgren, J. M., and N. A. Auer. 2004. Movement and habitat of juvenile Lake Sturgeon (*Acipenser fulvescens*) in the Sturgeon River/Portage Lake system, Michigan. Journal of Freshwater Ecology 19:419–432.

Hussey, N. E., S. T. Kessel, K. Aarestrup, S. J. Cooke, P. D. Cowley, A. T. Fisk, R. G. Harcourt, K. N. Holland, S. J. Iverson, J. F. Kocik, J. E. Mills Flemming, and F. G. Whoriskey. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science 348:1255642.

Izzo, L. K., D. L. Parrish, G. B. Zydlewski, and R. Koenigs. 2021. Second fin ray shows promise for estimating ages of juvenile but not adult Lake Sturgeon. North American Journal of Fisheries Management 41:217–228.

Jackson, J. R., A. J. VanDeValk, T. E. Brooking, O. A. VanKeeken, and L. G. Rudstam. 2002. Growth and feeding dynamics of Lake Sturgeon, *Acipenser fulvescens*, in Oneida Lake, New York: results from the first five years of a restoration program. Journal of Applied Ichthyology 18:439–443.

Kessel, S. T., D. W. Hondorp, C. M. Holbrook, J. C. Boase, J. A. Chiotti, M. V. Thomas, T. C. Wills, E. F. Roseman, R. Drouin, and C. C. Krueger. 2018. Divergent migration within Lake Sturgeon (*Acipenser fulvescens*) populations: multiple distinct patterns exist across an unrestricted migration corridor. Journal of Animal Ecology 87:259–273.

Klinard, N. V., E. A. Halfyard, J. K. Matley, A. T. Fisk, and T. B. Johnson. 2019. The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. Animal Biotelemetry 7:article 17.

Kneebone, J., J. Chisholm, and G. B. Skomal. 2012. Seasonal residency, habitat use, and site fidelity of juvenile Sand Tiger Sharks *Carcharias taurus* in a Massachusetts estuary. Marine Ecology Progress Series 471:165–181.

Knights, B. C., J. M. Vallazza, S. J. Zigler, and M. R. Dewey. 2002. Habitat and movement of Lake Sturgeon in the upper Mississippi River system, USA. Transactions of the American Fisheries Society 131:507–522.

Lachapelle, K. A. 2013. Wintering Shortnose Sturgeon (*Acipenser brevirostrum*) and their habitat in the Penobscot River, Maine. Master's thesis. University of Maine, Orono.

Lacho, C. D. 2013. Movement and habitat use of Lake Sturgeon (*Acipenser fulvescens*) in the South Saskatchewan River system. Master's thesis. University of Lethbridge, Lethbridge, Alberta.

Legare, B., G. Skomal, and B. DeAngelis. 2018. Diel movements of the Blacktip Shark (*Carcharhinus limbatus*) in a Caribbean nursery. Environmental Biology of Fishes 101:1011–1023.

Lord, K. 2007. Movements and habitat use of juvenile Lake Sturgeon in the north channel of the St. Clair River. Master's thesis. University of Michigan, Ann Arbor.

MacKenzie, C. 2016. Lake Champlain Lake Sturgeon recovery plan. Vermont Fish and Wildlife Department, Rutland.

McCabe, D. J., M. A. Beekey, A. Mazloff, and J. E. Marsden. 2006. Negative effect of zebra mussels on foraging and habitat use by Lake Sturgeon (*Acipenser fulvescens*). Aquatic Conservation: Marine and Freshwater Ecosystems 16:493–500.

Moreau, D. A., and D. L. Parrish. 1994. A study of the feasibility of restoring Lake Sturgeon to Lake Champlain. Lake Champlain Basin Program, Technical Report 9, Grand Isle, Vermont.

Myer, G. E., and G. K. Gruendling. 1979. Limnology of Lake Champlain. New England River Basins Commission, Lake Champlain Basin Study Technical Report 30, Burlington, Vermont.

Peterson, D. L., P. Vecsei, and C. A. Jennings. 2007. Ecology and biology of the Lake Sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Reviews in Fish Biology and Fisheries 17:59–76.

Pincock, D. G. 2012. False detections: what they are and how to remove them from detection data. Vemco, Application Note 902, Halifax, Nova Scotia.

Pinheiro, V. M., J. D. Stockwell, and J. E. Marsden. 2017. Lake Trout (*Salvelinus namaycush*) spawning site use in Lake Champlain. Journal of Great Lakes Research 43:345–351.

Pollock, M. S., M. Carr, N. M. Kreitals, and I. D. Phillips. 2015. Review of a species in peril: what we do not know about Lake Sturgeon may kill them. Environmental Reviews 23:30–43.

Rusak, J. A., and T. Mosindy. 1997. Seasonal movements of Lake Sturgeon in Lake of the Woods and the Rainy River, Ontario. Canadian Journal of Zoology 74:383–395.

Secor, D. H. 2015. The hidden lives of marine fish. Pages 1–22 *in* D. H. Secor, editor. Migration ecology of marine fishes. Johns Hopkins University Press, Baltimore, Maryland.

Shaw, S. L., S. R. Chipps, S. K. Windels, M. A. H. Webb, and D. T. McLeod. 2013. Influence of sex and reproductive status on seasonal movements of Lake Sturgeon in Namakan Reservoir, Minnesota–Ontario. Transactions of the American Fisheries Society 142:10–20.

Simpfendorfer, C. A., M. R. Heupel, and R. E. Hueter. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Canadian Journal of Fisheries and Aquatic Sciences 59:23–32.

Smith, K. M., and D. K. King. 2005. Movement and habitat use of yearling and juvenile Lake Sturgeon in Black Lake, Michigan. Transactions of the American Fisheries Society 134:1159–1172.

Snobl, Z. R., D. A. Isermann, R. P. Koenigs, and J. K. Raabe. 2017. Relative sampling efficiency and movements of subadult Lake Sturgeon in the lower Wolf River, Wisconsin. Transactions of the American Fisheries Society 146:1070–1080.

Thayer, D., J. L. W. Ruppert, D. Watkinson, T. Clayton, and M. S. Poesch. 2017. Identifying temporal bottlenecks for the conservation of large-bodied fishes: Lake Sturgeon (*Acipenser fulvescens*) show highly restricted movement and habitat use over-winter. Global Ecology and Conservation 10:194–205.

Trembath, C. A. 2013. As assessment of juvenile Lake Sturgeon movement and habitat use in the Namakan River of northwestern Ontario. Master's thesis. Lakehead University, Thunder Bay, Ontario.

Trested, D. G., M. D. Chan, W. C. Bridges, and J. J. Isely. 2011. Seasonal movement and mesohabitat usage of adult and juvenile Lake Sturgeon in the Grasse River, New York. Transactions of the American Fisheries Society 140:1006–1014.

Withers, J. L., H. Takade-Heumacher, L. Davis, R. Neuenhoff, S. E. Albeke, and J. A. Sweka. 2021. Large- and small-scale movement and distribution of acoustically tagged Lake Sturgeon (*Acipenser fulvescens*) in eastern Lake Erie. Animal Biotelemetry 9:article 40.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.